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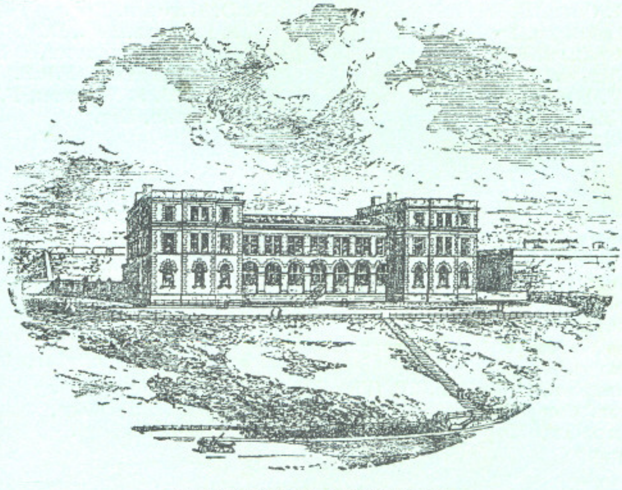

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A Short Investigation into the Habits, Abundance, and Species of Seals on the North Cornwall Coast.

By

G. A. Steven, B.Sc., F.R.S.E.,
Assistant Naturalist at the Plymouth Laboratory.

(Report to the Ministry of Agriculture and Fisheries—30th December, 1932.)

With Charts I–III.

I. Introductory.

During recent years Cornish fishermen have been complaining bitterly of the damage wrought by seals amongst their several fisheries. The fishing communities in the Lizard and Land's End areas claim that these animals rob their trammel nets and also that they not infrequently disperse shoals of mullet, a single haul of which in favourable circumstances will often yield a large sum of money—enough to ensure for the inhabitants of an entire fishing village a good winter's livelihood.

The most serious charges against the seals have been received, however, from the North Cornwall coast. The fishing communities situated along that shore complain that the seals frequent the herring fishing grounds and remove from the drift nets many of the herrings which have become enmeshed therein. The loss of fish thus entailed does not seriously embarrass these men in a good fishing season. But when fish are scarce and the catches small it is claimed that the activities of the seals constitute a grave menace to their already precarious livelihood.

According to reports sent in by the fishermen, the Grey Seal is the chief offender in this respect.

At the request of the Ministry of Agriculture and Fisheries, the Director of the Plymouth Laboratory of the Marine Biological Association instructed the writer to visit some of the Cornish fishing ports during the present herring season and find out by direct observation* with the

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* It must here be pointed out that herring drifting takes place mainly during the hours of darkness. The fishing vessels leave harbour in time to reach the fishing grounds at or just before sundown. Opportunity for the clear observation of seals and their activities amongst the boats and by the fishing nets is restricted therefore to the hours of failing daylight when the boats are proceeding to the grounds or while they are returning to harbour after daybreak—if they remain out until that time. After darkness falls, unless in very bright moonlight, a seal can be seen only if it should come within the circle of light cast upon the water by the boat's fishing lamps.

fishing fleets to what extent these complaints are justified, and at the same time to determine—if possible—whether Grey Seals are numerous in the area.

The observations made and the results obtained form the substance of this report.

II. Places Selected.

It was ascertained from the Cornwall Sea Fisheries Committee that serious complaints concerning the depredations of seals are most frequently received from the fishermen of St. Ives, Port Isaac, and Padstow. Arrangements were accordingly made to go to sea with one of the herring drifters operating from each of those places. Owing to the success which attended the work at the two first-named ports, Padstow was not visited. At the special request of the Chairman of the Cornwall Sea Fisheries Committee, however, a visit was paid to Sennen Cove, near Land's End.

It was found that the Sennen fishermen, having heard that an investigation was in progress, wished merely to make verbal testimony to the damage wrought by seals amongst their several fisheries. It is from this village, for example, that the complaints regarding trammel nets and mullet shoals mainly have emanated. As no trammels were in use at the time of the visit and no mullet shoals in the vicinity, more direct evidence* of the activities of the seals in that locality could not be obtained. Two attempts were made, however, to visit the Longships Rocks where, the fishermen stated, seals may frequently be seen in considerable numbers. Although the sea was calm in Sennen Bay it was found to be too rough outside to approach the Longships on both the occasions on which an attempt was made.

III. The Seal Menace.

As will be seen from the Appendix (p. 496) subjoined to this report, three trips were made to the herring grounds in the vicinity of St. Ives in a herring drifter normally employed in fishing. While thus accompanying the herring fleet, five seals were sighted.

None were observed during the first night at sea in the vicinity of Cligga Head and Perran Beach (see Chart II, p. 499). On the second evening three seals were passed on the way to the fishing grounds off Zennor Head, only about 5 miles distant from the harbour (see Chart I, p. 497). Another seal was later observed about 150 yards away from the boat while the nets were being "shot." On the following morning in the vicinity of Pen Enys Point, a very large seal was seen within the circle of light cast by the boat's fishing lamps. It appeared to have come from the direction of the land, but just as it was sighted it turned towards the near

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* Which was the object of this investigation.

net along the side of which, swimming rapidly, it disappeared outwards in the darkness.

During the single night spent at sea in Port Isaac Bay eight seals were sighted (see Appendix, p. 500). Before reaching the fishing ground only 2 miles distant from the harbour, three seals were passed. One of these appeared and disappeared several times by the side of another boat's train of nets. A fourth seal subsequently appeared close by the cork-rope supporting our own near net and a fifth about half-way along it. The latter disappeared in the gathering darkness following the line of the cork-rope. A sixth seal made its appearance a short distance to seaward of the boat. While the nets were being hauled, one seal remained for a considerable time close behind the vessel's stern, apparently following in her wake as she moved slowly along. Still another made its appearance near the outer edge of the illuminated area around the boat hard by the side of the net which was then being hauled in. Several times this seal disappeared only to reappear in the same relative position.

These are all the observations which were made actually with the fishing fleets at sea. More time spent with them would have produced only a needless repetition of the same kind of data without adding in any way to the value of those already obtained*—which show very clearly that seals are numerous on the North Cornwall inshore herring fishing grounds and that *they do haunt the nets of the herring drifters.*

IV. Abundance of Seals.

In addition to keeping a look-out for seals on the fishing grounds, two special exploratory cruises were made in search of them. From St. Ives, on Monday, 21st November, a cruise was made along the shore, eastward from the harbour, as far as Basset Island, where seals are reported to be very numerous (see Appendix and Chart III, p. 500). Only four seals were sighted during the entire trip which extended to about 18 miles† and occupied approximately three hours. This may have been due to the fact that a heavy ground swell was running, and it is much more difficult to catch sight of a dark object in the water when its surface is very broken and uneven than when it is calm and smooth. It is of particular interest to note, therefore, that on Monday, 5th December, over 100 seals of all sizes were reported to have been seen lying on a sand beach at the foot of a cliff on the mainland immediately opposite Basset Island. This beach is inaccessible except by sea, and then only in calm weather.

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* See also p. 494 of this report.

† On the return journey a "wide circle" was made to seaward as it was thought that the stormy sea might have caused the seals to forsake the immediate vicinity of the rocks.

On Wednesday, 7th December, a visit was paid to some caves—locally known as " seal holes "—about two miles west from Boscastle, in which seals were said by the Port Isaac fishermen to make their homes and to breed. All but one of these caves are inaccessible except by sea, and it was just about high water when they were reached by boat from Port Isaac. The caves are four in number,* situated close together some hundreds of yards north of the Gull Rock (also known as Beeny Island). All have relatively very small openings in the face of high rocks. One of the openings was too small for a boat to enter it, but the cave could be seen to " open out " inside to unascertainable dimensions. A second cave had its opening completely submerged so that it became visible only when the water subsided between successive waves. The two others it was found possible—though difficult because of the swell—to enter.

The northernmost cave was penetrated for a distance of about 100 yards. Here further progress was checked by the complete darkness ahead. Even at this distance from its mouth the water in the cave was over 8 feet deep and it was sufficiently disturbed to make an unseen rock a dangerous obstacle in the way of the heaving dinghy. It was possible to make out, however, that at this point the tunnel-like neck of the cave expanded into a vast cavern in which the troubled waters made loud and fearsome noises. No seals could, of course, be discerned in the darkness, and, unfortunately, no lantern was available.

On arrival at these caves not a single seal was to be seen. On emerging again from the first one entered, and in which a commotion had been made by beating empty petrol cans and buckets, a large number of seals were found to have made their appearance. They were in a state of much activity and excitement, diving and reappearing with great frequency, but always remaining close to the base of the cliffs.

The second accessible cave was then entered but its roof was so low that the rise and fall of the surging sea made it dangerous to venture far for fear that the dinghy might be crushed against the rocks above and swamped. On coming out, still more seals were in evidence. Loud noises were made at the mouths of the other two caves, which could not be entered because of the conditions prevailing, in order to cause the seals to come out if any were inside.

Because of the rough sea a more thorough exploration of the caves was impossible. There can be but little doubt, however, that the seals which made their appearance in the sea at their mouths had emerged from them. Having been disturbed, they came out—as was to be expected—under the water, which was then sufficiently deep in all the caves for them to emerge unseen. One large seal was observed, however, swimming rapidly out of one of the caves on the surface of the sea, and two

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* There are other " seal holes " in this vicinity which were not visited.

others on being approached disappeared into the submerged opening already mentioned.

At the end of 1½ hours in the vicinity a great many seals had appeared. Their number could not be ascertained with any degree of accuracy as they were in a state of too much activity. Nevertheless, six or seven heads were generally to be seen on the surface at one time, and in one instance no less than nine different seals were in view near the mouth of one cave at the same moment.

It can safely be stated, therefore, that *in addition to the numerous seals scattered over the various herring grounds at this time, there is at least one seal colony of considerable size in the vicinity of Boscastle,* on the North Cornwall coast. It is probable that there are other such colonies in the same locality and at other places along that county's northern shore. Little evidence has as yet been collected which will either support or contradict the view that these seal resorts may also be breeding places. It may be significant, however, that among the seals which were seen near Boscastle there were several very young individuals* present among others which were obviously old adults.

V. Species of Seals.

It is very difficult, while actually at sea, to distinguish *with certainty* the Brown Seal (*Phoca vitulina*) from the Grey Seal (*Halichœrus grypus*) unless a clear view of the animal can be obtained at very close range. When, in the course of this investigation, a seal was sighted, but in such conditions that identification was impossible, the animal was recorded simply as "SEAL." When a better view was obtained and the species could be determined with reasonable certainty, this additional information is added to the log (see Appendix to this report). It is clearly to be understood, however, that these tentative identifications of live animals must be considered fallible and by no means final.

It will be seen in the Appendix that for only five animals are such identifications given. Of these, one is recorded as a Brown Seal and four as Grey Seals. In addition, *all those seen near Boscastle appeared to be Grey Seals.* If these identifications are correct, *it would appear that the Grey Seal (Halichœrus grypus) is much the more common of these two species along the shores of Cornwall.* This conclusion is supported by the fact that the seal which was washed up dead on the beach at Porthminster, near St. Ives, was found on examination to be *Halichœrus grypus.* Two other dead seals were later washed ashore near St. Ives both of which were also *Halichœrus grypus.*

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* See also p. 494.

VI. Discussion of Results.

Although there can be no doubt that seals do haunt the nets of the herring fishermen along the North Cornwall coast, definite proof that they actually rob the nets could not be obtained. Nor will this information readily be secured simply by making observation from a herring drifter normally employed. For complete elucidation of this problem a separately-conducted investigation would be required and special methods adopted or devised. If fish are removed from the nets by seals, this is done under water where—except in exceptional circumstances—their actions cannot be observed. An investigator might, therefore, spend a whole season, or even many seasons, in an ordinary fishing boat without adding materially to the information contained in this report. He might not for a long time be fortunate enough even to catch sight of a seal rising to the surface with a fish in its mouth*—an observation which the Cornish fishermen claim occasionally to make and to which they attach very great significance. For the purpose of their argument in favour of the destructive activities of seals they ignore the fact that some herrings are always lost from herring nets before they can be hauled inboard. In the absence of definite proof one way or the other two possibilities must, therefore, be kept in mind: (1) that the seals are attracted to the nets by these "dropped" herrings (which sink to the sea bottom where, in shallow water, they form an easily available food supply); and (2) that the seals definitely rob the nets.

One thing, however, is certain. Very seldom indeed does a seal become entangled in a drift net or is it responsible for causing damage to it in any other manner whatsoever. This statement can be made with complete confidence. It is backed by the present observer's knowledge of seals in other localities and the Cornish fishermen acknowledge that it holds good also in their waters.

As regards the species of seal at present found on the Cornish fishing grounds, it is interesting to note that the Grey Seal (*Halichœrus grypus*) was recorded from the North Cornwall coast as long ago as 1883. In that year Sir E. Ray Lankester found a newly born Grey Seal on the shore at Pentargon Cove, near Boscastle, and had it conveyed to the Zoological Gardens, Regent's Park, but it soon died in captivity. Lankester believed, however, that the Grey Seal was extremely rare in Cornwall and that the Brown Seal was the more abundant species (*Diversions of a Naturalist*, 1915; p. 32 *et seq.*). The very opposite appears to be true at the present time. This fact is of particular importance in view of the statement made by Hjort and Knipowitsch (*Rapports et Procès-Verbaux*, Vol. VIII,

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* On one occasion, many years ago, the writer himself caught sight of a seal rising to the surface of the water with a fish (not a herring) in its mouth.

1907 ; p. 114) concerning the Grey Seal. According to these authors " fish form its main food and it is in the Baltic, probably, the most harmful of the three species occurring there." The stomachs of three individuals of this species from the vicinity of St. Ives have been examined with the following results.

Date Examined.	Locality where found.	Stomach Contents.
21/11/32	Porthminster (St. Ives).	Herring Bones and traces of Herring Spawn.
28/11/32	St. Ives.	Beak of Cuttlefish (Sepia sp.).
13/12/32	St. Ives.	Clupeoid remains.

These data from Cornwall are too scanty as yet to justify any definite conclusion being drawn from them other than that *fish* (*herrings*) *do to some extent enter into the diet of the Grey Seal in those waters.*

Little is known, and the present writer has been able to find out nothing, concerning the breeding places (if any) of seals in Cornwall. Lankester (*op. cit.*, p. 33) was of opinion that whilst " the Brown Seal produces its young most usually in caves or rock-shelters, the Great Grey Seal chooses a remote sand island or deserted piece of open shore for its nursery." Sufficient evidence is not available to settle the question of whether or not this statement is justified—at any rate as far as the Cornish coast is concerned. Unless the present writer be in error concerning the seal colony at Boscastle, *Halichœrus grypus* is an inhabitant of caves in that locality. It probably also breeds there. (See also p. 492 of this report.)

The presence or absence of a cave-dwelling habit will have a marked effect upon the results which will attend any effort to reduce the numbers of seals. If a reward be offered for every head produced few seals will meet death by shooting, as only a small percentage of the animals so killed are recoverable. Two other methods will probably be extensively employed : (1) that of entering the caves in which seals are known to congregate and killing as many as possible with heavy cudgels ; and (2) that of driving them out of such caves to be entangled in strong nets previously fixed across the cave openings. Both these methods of hunting were formerly practised in Cornwall when the killing of seals was a profitable pursuit because of the good prices which could be obtained for their skins and oil. *It is possible that the netting method, if intensively employed, will reduce cave-frequenting species to the point of extinction in a very short time —say, in a single year.* If, therefore, rewards are to be offered for the destruction of seals in Cornwall it is, in the writer's opinion, highly desirable that a detailed survey of their ordinary haunts and breeding places be undertaken in order to assess as accurately as possible the relative abundance of the Grey and Brown species and to obtain reliable knowledge of their separate habits. If it is the Grey Seal which is abundant on the Cornish coast, the complete extermination of this attractive and interesting member of the British Marine Mammalian Fauna from a locality which, apparently, it finds congenial, seems scarcely to be desirable. Should such a survey as that suggested above be carried out, periodic return visits to the Grey Seals' ordinary haunts and breeding places (say, once a year during the breeding season) would serve to reveal the extent of the depletion which was being brought about in their numbers.

VII. SUMMARY.

1. In the course of three trips to the herring grounds in the vicinity of St. Ives five seals were sighted. Seven others were also seen at various other times and places in the course of five days spent in that locality.

2. During a single night at sea in Port Isaac Bay eight seals were sighted.

3. It was obvious from the movements of certain of the seals observed on the fishing grounds that they were attracted to the herring nets.

4. Direct evidence that the seals actually remove fish from the nets was not obtained.

5. Damage done to drift nets by seals is negligible.

6. Grey Seals (*Halichœrus grypus*) are present in considerable numbers, and are probably the commonest seals in Cornish waters.

7. Brown Seals (*Phoca vitulina*) appear to be few—they may even be rare—around Cornwall.

8. There is at least one seal colony of considerable size in certain caves near Boscastle. This appears to consist of Grey Seals. Probably other such colonies exist on the Cornish coast.

9. Clupeoid remains have been found in two out of the three Grey Seal stomachs which have been examined.

10. Further and more exact knowledge of the habits and relative abundance of Grey and Brown Seals around the Cornish coast is desirable.

VIII. APPENDIX.

DETAILED LOG OF OBSERVATIONS AND EVENTS.

Thursday, 17/11/32.

2.30 p.m. Arrived St. Ives.

3.45 p.m. Went on board M.B. *Grateful* (J. Boase, Master) which put to sea immediately for the fishing grounds.

6.05 p.m. Commenced " shooting " nets (14 in number) off Cligga Head (see Chart II). Wind NNE. Innermost (off-end) net about ½ mile from the shore.

No seals were sighted along the whole route to this fishing ground, nor did any appear within range of the lights while fishing was in progress during the night. There was thus absolutely no evidence of the presence of seals obtained during this trip.

Friday, 18/11/32. (St. Ives.)

(See Chart I.)

3.50 p.m.	Proceeded to sea in *Grateful*.
3.55 p.m.	1 seal (large brown)—sighted some distance to seaward of St. Ives Head, just outside St. Ives harbour.
4.10 p.m.	1 seal—swimming close to the rocks at Clodgy Point.
4.16 p.m.	1 seal—in small bay between Hor Point and Pen Enys Point.
4.54 p.m.	Commenced "shooting" nets off Zennor Head. Wind NNE. Innermost (near) net about ¼ mile from the shore.
5.15 p.m.	Nets all out. 1 seal—sighted about half-way between boat and shore. (Made several appearances more or less in the same place after first seen.)
7.30 p.m.	"Looked at" nets. No herrings and "nets all on fire." Successful fishing, therefore, considered impossible. Commenced hauling.
9.15 p.m.	Boat returned to harbour.

Four seals were sighted on this trip. They are obviously fairly common around the rocks westward from St. Ives. But no seal approached the nets

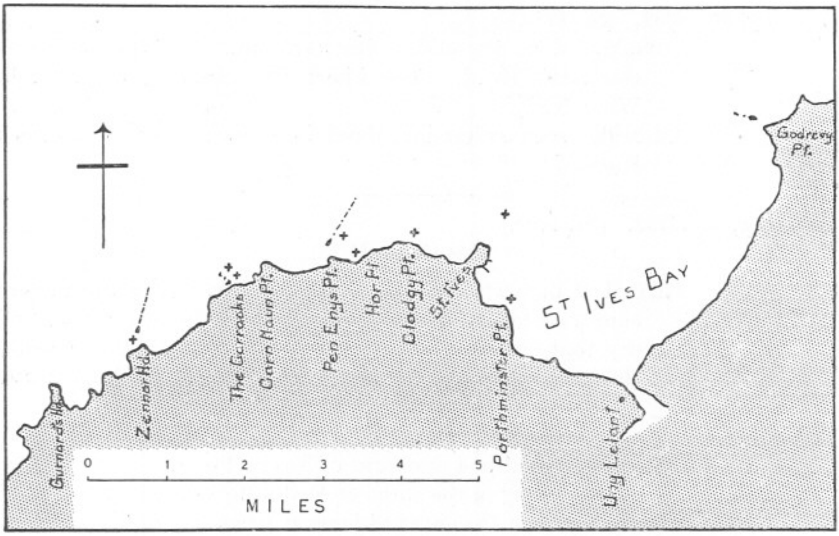

Chart I.—North Cornwall Coast—Gurnard's Head to Godrevy Point.
+ = Seals seen on 18th, 19th, and 20th November.
—.—.—.—. = Position where m.b. *Grateful* shot her net on 18th (evening) and 19th (morning).

while it was still light enough to see; and when hauled up they showed no signs of having been visited in the darkness.

Saturday, 19/11/32. (St. Ives.)

3.50 a.m. Left again for fishing ground.

4.55 a.m. Commenced " shooting " off Pen Enys Point (Chart I). Innermost (near) net about 300 yards from the shore.

5.15 a.m. Nets all out.

1 seal—appeared within circle of light cast by boat's lamps; swimming from direction of the shore; remained visible for short time and then disappeared in the darkness along the side of the near net.

8.35 a.m. Returned to harbour with about 700 herrings.

The single seal observed on this short trip was very definitely " making for " the nets.

2.30–6.15 p.m. Walked along the shore—eastward from St. Ives as far as Uny Lelant. Wind NNE. Heavy ground swell beginning to come in.

1 seal* (small grey)—observed at Porthminster Point, a few yards out from the rocks. No more were seen, though several reported to be in the vicinity by some boys playing on the beach.

Sunday, 20/11/32. (St. Ives.)

Walked along the cliffs—westward from St. Ives—as far as Gurnard's Head. (See Chart I.) Heavy ground swell. Wind NNE.

2 seals—seen swimming about in the sea near the Carrack Rocks.

Monday, 21/11/32. (St. Ives.)

(See Chart II.)

Hired M.B. *Grateful* for exploratory cruise along the eastern shores as far as Basset Island. The fishermen of St. Ives say that seals are usually more numerous in that locality than anywhere else in their area.† Wind N. Very heavy ground swell.

9.15 a.m. Left St. Ives harbour.

10.13 a.m. 1 seal—sighted just eastward of Navax Point.

10.35 a.m. 1 seal—playing in the surge at Hell's Mouth.

No more seals were seen on the outward journey or at Basset Island.

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* On Thursday, 17th, *a small seal*, swimming around the same rocks, was sighted from the train just before it entered St. Ives station. This may have been the same animal.

† See also p. 491 of this report.

Steered in a " wide circle " to seaward on the return journey.

11.42 a.m. 1 seal—in centre of St. Ives Bay.

12.03 p.m. 1 seal (very large grey)—playing in the breakers at Porthminster Point, just outside St. Ives harbour and to the westward of it.

Four seals (one grey) were sighted on this trip. The rough sea made it very difficult to observe dark objects amongst the waves.

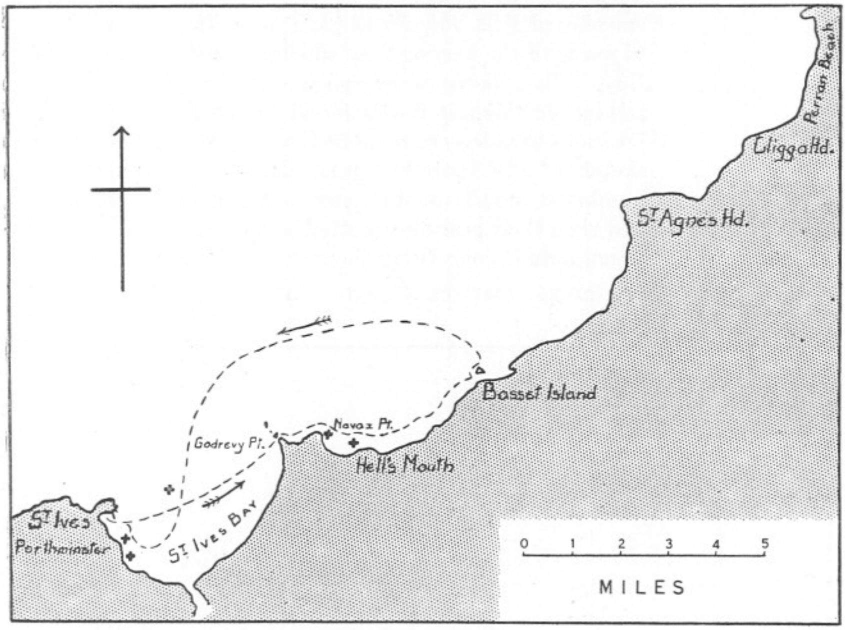

CHART II.—North Cornwall Coast—St. Ives Head to Perran Beach.
\+ = Seals seen on 21st November.
— — — — = Route of exploratory voyage undertaken on that day.

3.20 p.m. Examined a large seal which had been washed up dead on Porthminster Beach. This proved to be a large female Grey Seal (*Halichœrus grypus*). The head was removed and forwarded to the British Museum where this identification was confirmed.

Stomach contents : Herring bones and some remains of herring spawn.

7.00 p.m. Left for Plymouth.

Wednesday, 23/11/32.

Proceeded to Port Isaac. Found the sea too rough there to allow the boats to go out on that evening. Remained overnight.

Thursday, 24/11/32. (Port Isaac.)

Weather still bad. Made arrangements to be recalled immediately the weather moderated sufficiently to allow fishing to be resumed, and returned to Plymouth.

Tuesday, 6/12/32.

(See Chart III.)

Returned to Port Isaac.

Went aboard M.B. *Boy Fletch* (A. Provis, Master) and put out to sea with the herring fleet which was fishing in Port Isaac Bay. (In making notes concerning the seals which were sighted on this trip it was found impossible to record their positions by reference to named points on the land. A rough sketch of the shore-line was, therefore, made, the seals numbered serially in the order in which they were sighted, and then their positions plotted as on Chart III. The additional details concerning them are given below.)

3.49 p.m. 1 seal (grey)—seaward of boat. (1)

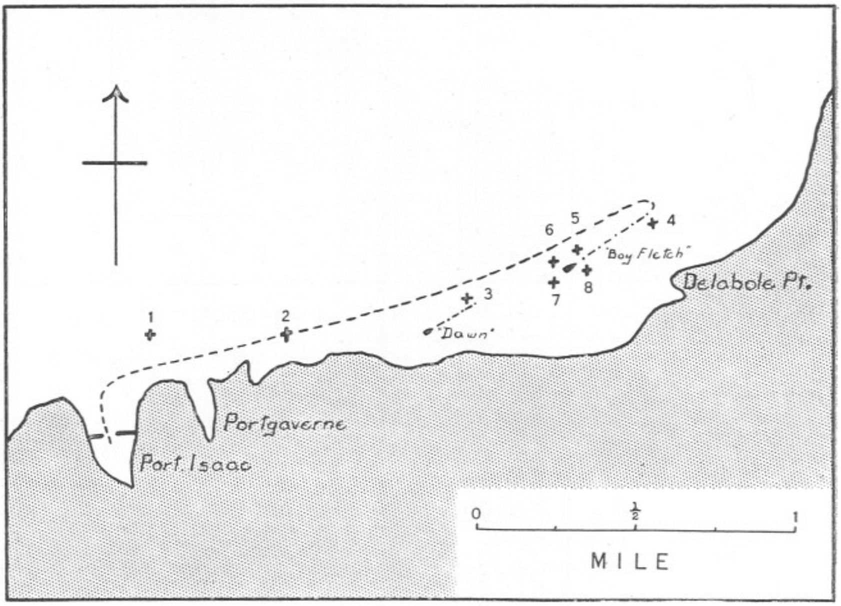

CHART III.—North Cornwall Coast—Port Isaac Harbour to Delabole Point.

\+ = Seals* seen on 6th December.

—.—.—.—. = Positions of nets of *Dawn* and *Boy Fletch* on shooting.

— — — — — = Course of *Boy Fletch* to fishing ground.

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* In plotting positions of the Seals the small changes in position occupied by the nets owing to drift have been ignored.

4.03 p.m. 1 seal (small grey)—rose to the surface about 20 yards ahead, right in the boat's track ; dived immediately (but reappeared astern several times in the next 5 minutes). (2)

4.17 p.m. 1 seal—hard by the cork-rope of the outermost (off-end) net of another fishing boat, the *Dawn*, which was then shooting the last of her nets. (3)

4.33 p.m. Commenced shooting nets (13 in all) off Delabole Point.

4.36 p.m. 1 seal (small)—bobbed up beside the cork-rope of our first net but promptly disappeared again. (4)

4.49 p.m. 1 seal—sighted close alongside near net, about half-way along it ; disappeared in the gathering dusk following the direction of the cork-rope. (5)

5.36 p.m. 1 seal (small)—close by and to seaward of boat. Possibly same as No. 4 above. (6)

7.00 p.m. Commenced hauling.

7.23 p.m. 1 seal (large)—about 6 yards behind the stern of the boat ; appeared to be following her as she moved along. (7)

1 seal—also sighted at the same time by the side of the net which was then being hauled inboard, near the outermost edge of the circle of light. (Disappeared and reappeared several times.) (8)

Eight seals were sighted on this trip, six of them in the immediate vicinity of herring nets or of a fishing boat while her nets were out. There can be no doubt that seals were numerous at this time in Port Isaac Bay, and that they were attracted to the herring nets.

Wednesday, 7/12/32. (Port Isaac.)

Visited seal caves at Boscastle (see p. 492 of this report).

Friday, 9/12/32, and *Saturday*, 10/12/32.

At Sennen Cove (see p. 490 of this report).

Tunny Investigations made in the North Sea on Col. E. T. Peel's Yacht, "St. George," Summer, 1933. Part I. Biometric Data.

By

F. S. Russell,

Naturalist at the Plymouth Laboratory.

With 8 Figures in the Text.

The occurrence of the Tunny, *Thunnus thynnus* L., in the waters of the North Sea during the summer months has in recent years aroused considerable interest owing to the possibilities of sport afforded by this fish to big-game anglers. It would seem also that the majority of commercial fishermen have only recently become aware that the tunny is a regular visitor to northern waters. Our knowledge of the northern migrations of the tunny has been summarised in two publications by Le Gall (**5** and **6**), and it is evident that a careful study of the fish occurring in northern waters might do much to help in elucidating the general problem of its life-story.

In the summer of 1933, at the kind invitation of Col. E. T. Peel, D.S.O., M.C., I had the opportunity of making a preliminary survey into the occurrence of this interesting fish in the North Sea. At the same time, largely due to the reports by Mr. W. J. Clarke, F.Z.S., on the occurrence of tunny in North Sea waters, and to the successful attempts of Mr. L. Mitchell-Henry and Col. R. Stapleton-Cotton to capture them on a rod and line, there came into existence an angling club known as the "British Tunny Club." The formation of the club has attracted a number of big-game anglers to the North Sea and has given rise to further opportunities for the study of this fish, especially by the use of marked hooks.

It is a pleasure for me here to record my grateful thanks to Col. Peel for the facilities for research he afforded me and for his most generous hospitality during nearly two months' cruising on his yacht, *St. George* : I should like also to thank Col. R. Stapleton-Cotton for his great assistance in many ways and for his advice on a subject that he had already studied for several years in co-operation with well-known European biologists. To the Captain and crew of *St. George* I owe a debt of gratitude for much help willingly rendered. My thanks are also due to all members of the

British Tunny Club who have helped by marking their hooks and allowing me to have access to their fish, and especially to the Honorary Secretary, Mr. H. J. Hardy, for his help and advice. I have received also much courteous treatment from those engaged in the fishing industry and would express my feelings of gratitude to the captains and crews of the many Danish, Dutch, and British fishing vessels we boarded, and also to Mr. Bamford, Mr. Catchpole, and the Pure Ice Company at Scarborough, and Mr. Spinks and Mr. D. Buchan at Peterhead. Lastly I am deeply indebted to Mr. W. J. Clarke for much useful information he has passed on to me as a result of his many years' study of the natural history of the fishes of Scarborough. Acknowledgements are due to Mr. Victor Hey, press photographer of 1 York Place, Scarborough, for his kind permission to reproduce Figure 8.

The programme of research was divided into two main fields of enquiry :

1. A study of the fish themselves, (*a*) by marking of living fish so that if caught at a later date they might be identifiable ; and (*b*) by detailed measurements and examination of the fish caught.
2. A study of the distribution of the tunny in the North Sea in relation to hydrographical conditions.

The present report deals only with the first of these two aspects.

(*a*) *The Marking of Fish.*

It has been shown by Sella that the migrations of the tunny may be traced to some extent by a study of the occurrence of hooks in fish that have broken away from fishing-lines. On the formation of the British Tunny Club it was felt that an opportunity was afforded to help in this study by using marked hooks which could be identified again ; in this way hooks which the angler lost in fish through broken tackle might nevertheless incidentally prove of value to science if at some later date the fish in which they were fixed should be captured. Accordingly members of the club were asked to mark their hooks with three saw cuts or punch marks. This simple method was adopted as a preliminary trial to a more detailed system of marking that might be used in future years should the method prove successful.

During the fishing season of 1933 in August and September a large number of hooks have been lost in fish in the North Sea between the Dogger Bank and the Yorkshire coast. The actual number is not known but it must be at least a hundred. Many of these hooks were marked with the three saw cuts, and all are probably distinguishable by their shape and make.

I give below a list of the types of hooks that have been used and in

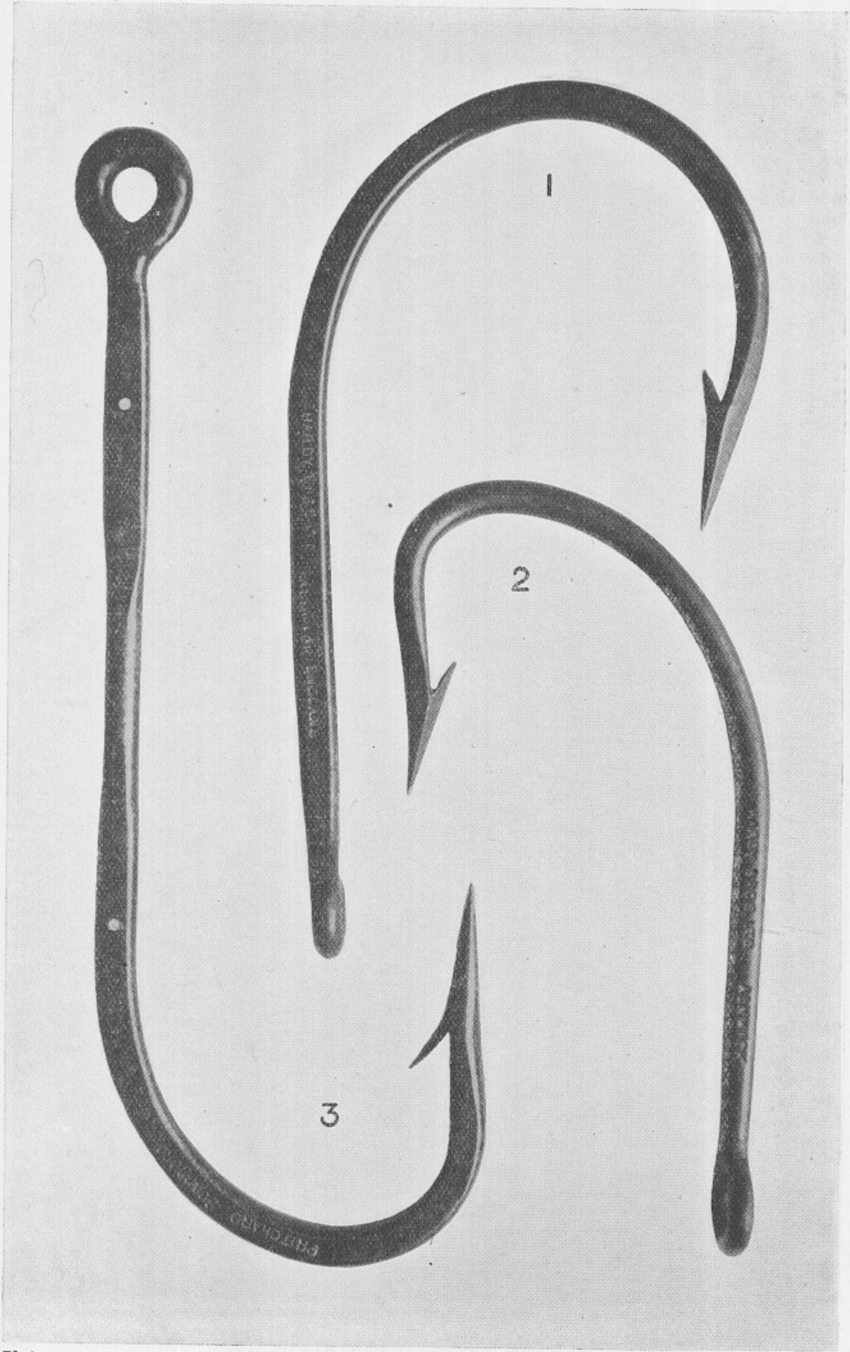


Photo. *F. S. R.*

FIG. 1.—Hooks used by anglers in the North Sea (natural size). 1. Hardy Zane-Grey; 2. Hardy Limerick; 3. Pritchard.

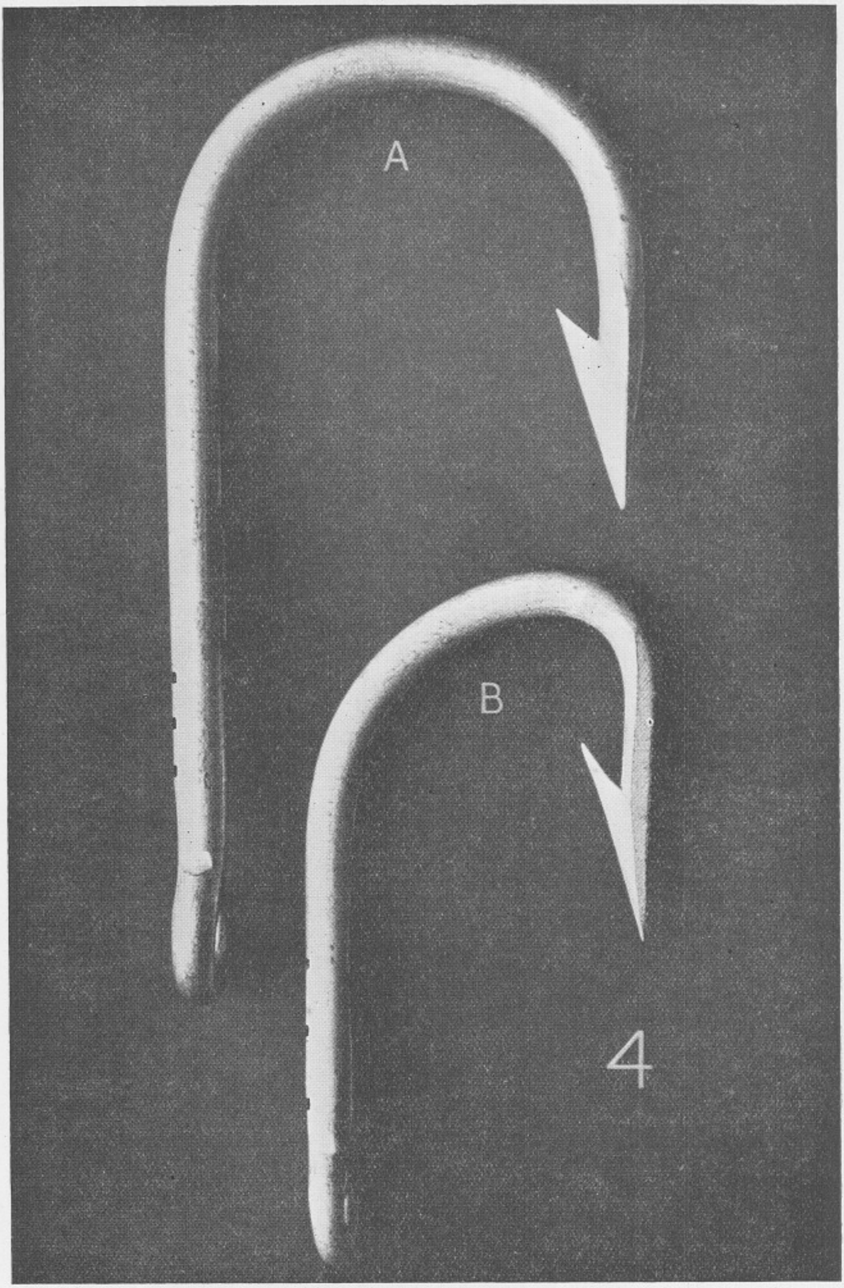


Photo. *F. S. R.*

FIG. 2.—Hooks used by anglers in the North Sea. 4. Norwegian Mustad: A, round bend; B, Limerick.

Figures 1 and 2 are given photographs of these hooks. Five kinds of hooks have been used and lost for certain.

1. Hardy Zane-Grey Hooks—Pfleuger type.
   Black hooks 4½ inches long, stamped " The Zane-Grey " on one side, and " Hardy Bros. Ltd., Alnwick, England " on the other side.
2. Hardy Limerick Hooks.
   Black hooks 4 inches long, stamped " Hardy Bros. Ltd. Alnwick " on one side, and " England " on the other side.
3. Pritchard's Hooks.
   Bronzed and steel hooks 6 inches long, with flattened sides and the name " Pritchard Scarboro " stamped on the bend on one side: there are two small holes through the shank about 1½ inches and 4¼ inches from the eye end respectively.
4. Norwegian Mustad Hooks: galvanized iron.
   A. Round Bend, 5 inches long.
   B. Limerick, 3½ inches long.

(*b*) *Measurements of the Fish.*

At a joint meeting of the International Council for the Exploration of the Sea and the International Commission for the Exploration of the Mediterranean in 1932 to discuss investigations into the biology of the tunny, a number of biometric measurements were agreed upon in the hope of obtaining information on the possibility of the occurrence of racial variations in the tunny. Some measurements of this nature had already been made by Heldt (**4**) on fish from Tunis and by Frade (**2**) on fish from Algarve on the south coast of Portugal. Frade's results showed that the fish he measured apparently differed significantly from those measured by Heldt, but the observations were insufficient to be conclusive. Both workers studied fish which were preparing to spawn.

This cruise afforded a good opportunity to make similar measurements on the migrating fish occurring in the North Sea, and great attention was paid to this side of the work to see whether either or both of the types of fish described by the above workers occurred. At the outset difficulty was experienced in deciding from the International Council Report which were the exact points of reference for some of the measurements, a matter of considerable importance in such large fish if a high degree of accuracy was to be obtained. Accordingly I give below a very detailed statement of the measurements I have made so that other workers may know to what extent their results are comparable. Measurements were made, as suggested by Frade (**2**, p. 93), with a ribbon tape that could be fixed by an awl or skewer into the centre point of the snout as a point of origin for the length measurements. The tape was graduated to half-centimetres.

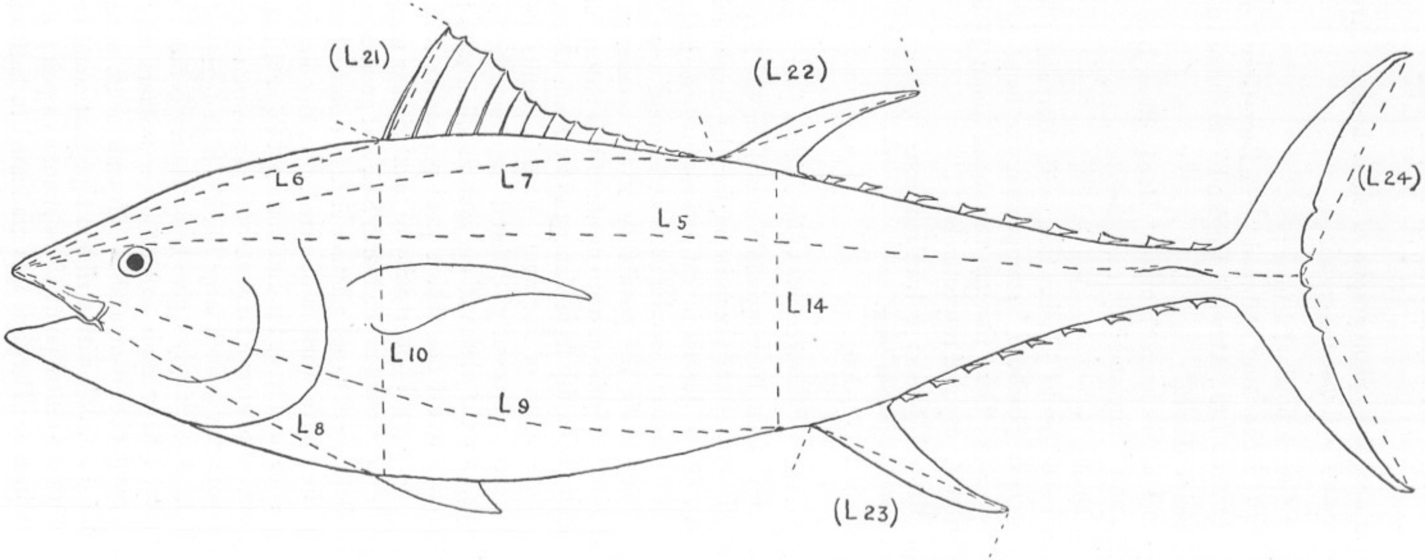


FIG. 3.—Diagram showing body measurements made on tunny.

The notations used below for the different measurements were those given in the International Council Reports (**1**). See Figures 3, 4, 5, 6 and 7.

In fixing the point of origin in the centre of the snout the skewer was inserted on the most anterior point of the nose immediately above the median groove which occurs in the front end of the roof of the mouth: this ensured that it was central.

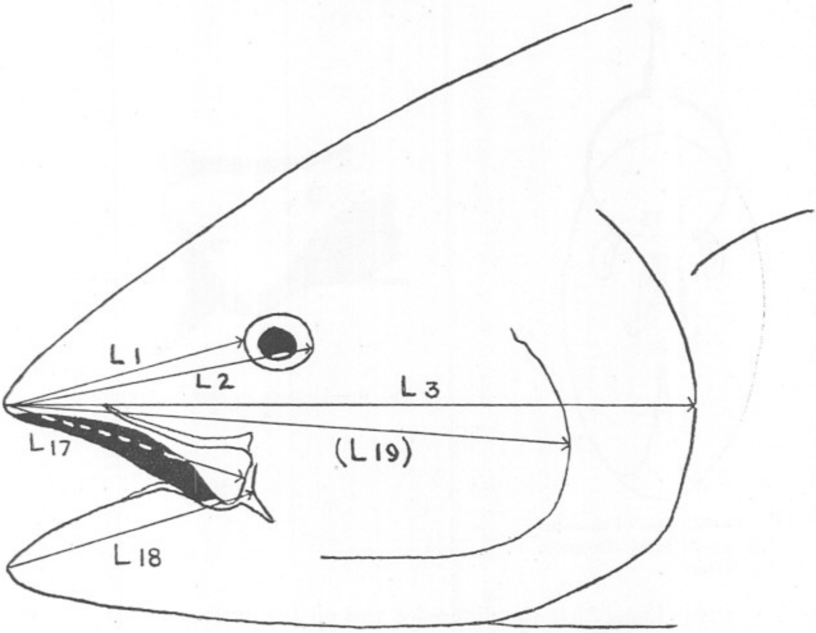


Fig. 4.—Diagram showing measurements on head.

L_1. From the origin to the anterior edge of the eye (preorbital distance).

L_2. From the origin to the posterior edge of the eye.

In the above two measurements the "eye" was taken to mean the actual eye-opening in the skin of the fish: if the eye be pushed inwards the hard edge of the skin can be clearly seen. Measurements were taken to the most anterior and most posterior points of this skin opening.

L_3. From the origin to the most distant point of the free edge of the operculum (length of the head).

In taking this measurement the soft flap of skin which extends beyond the edge of the bony operculum along its hinder margin was included; it is usually about one centimetre in width. The hindermost point of the operculum generally lay below the middle line of the body.

L_4. From the origin to the upper point of the origin of the pectoral.

Difficulty was experienced in deciding which this latter point should be. When the fin is lying flat along the side of the fish it appears to start from the point indicated A in Figure 7; if however the fin be fully extended at right angles to the body, the point of articulation is found to be behind A, namely, at B, Figure 7. In the measurements of the earlier fish the point B was taken as being the origin of the pectoral since A is merely the front point of a flap of skin in continuation of the flattened groove into which the fin fits. But it appeared that this point of reference might easily be confused by other workers and therefore in later fish measurements were made both to A and to B: it was found that the difference was on the average about 1·5 centimetres.

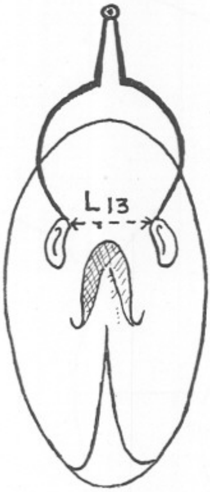


FIG. 5.—Method of measuring interorbital distance, L_{13} (after **1**).

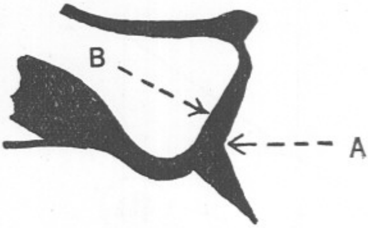


FIG. 6.—Details for jaw measurements, see Text.

L_5. From the origin to the centre of the caudal furca (length of the body).

This measurement was made by laying the tape along the body of the fish just above the eye and the pectoral fin and allowing it to lie along the body-surface and along the tail region above the lateral keel.

L_6. From the origin to the base of the first ray of the first dorsal fin.

This measurement was taken down the centre of the back to the front edge of the first spine of the first dorsal fin when fully erected, this being the shortest distance.

L_7. From the origin to the base of the first ray of the second dorsal fin.

L_8. From the origin to the base of the first ray of the ventral fin.

This measurement was made with the fin fully extended.

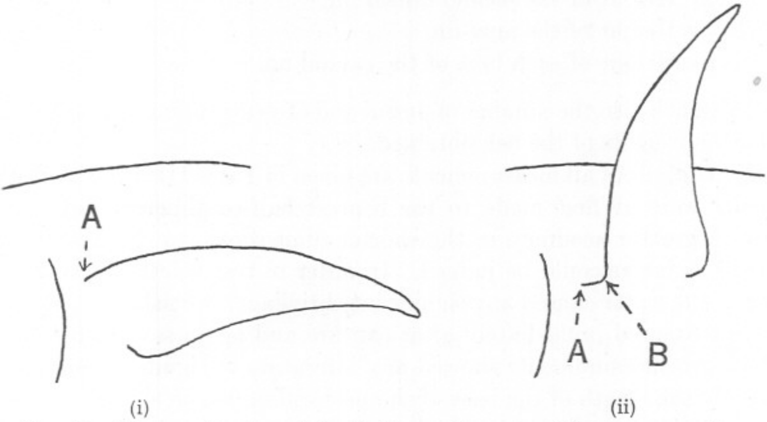
L_9. From the origin to the posterior edge of the anus.

L_{10}. Height of the body at the level of the first ray of the first dorsal.

Taken between upright boards.

L_{12}. Length of the pectoral fin.

This measurement presented the same difficulty as did L_4. It was decided that the fin proper started at the point B (Fig. 7); however, later a few measurements were also made from the point A with the fin pressed flat against the side of the body. The difference observed between the two measurements from A and from B was considerable, being about 5 to 5½ cm.



(i) (ii)

FIG. 7.—Diagram showing points of reference for pectoral fin measurements (i) with fin flat along body of fish; (ii) with fin extended.

L_{13}. Interorbital diameter (taken with calipers) (Fig. 5).
L_{14}. Height of body at level of anus (taken with calipers).
L_{15}. Interaxillary diameter.

Only a few measurements were made of this dimension owing to the difficulty of moving such heavy fish into the correct position.

L_{16}. Width of base of pectoral.

It was found that this dimension was rather unreliable as there was considerable shrinkage after a few hours due to drying.

L_{17}. Distance from the intermaxillary symphysis to the extremity of the upper jaw.

It was found that this measurement (taking the point A in Figure 6 as given in the International Commission Report Figure on p. 60) varied by as much as a centimetre between when the mouth was open and when it was shut. It seemed that the more constant point would be B, the centre point of the hind edge of the maxilla. Measurements were made in many fish both to the points A and B.

L_{18}. Distance from the mandibular symphysis to the buccal commissure.

In this measurement the point A in Figure 6 was taken as the point of reference for the buccal commissure.

(L_{19}.) From the origin to the most distant point of the edge of the preoperculum.
(L_{20}.) Length of the greatest transverse section of the lateral keels.
(L_{21}.) Height of the first dorsal fin (1st and 2nd rays).
(L_{22}.) Height of the second dorsal fin.
(L_{23}.) Height of the anal fin.
(L_{24}.) Height of each lobe of the caudal fin.

In all fish also the number of dorsal and of ventral pinnules was counted and the weights of the fish obtained.

Full details of all measurements are given in Table III, p. 521. Measurements were at first made to the nearest half-centimetre, and later, to ensure greater accuracy in the shorter dimensions, to the nearest millimetre as far as could be judged. In order to test whether a long period out of the water caused any significant shrinkage, two fish, Nos. 31 and 32, were measured immediately after capture and again several hours later. Only two measurements showed any alteration of significant magnitude, namely the length of the base of the pectoral fin which shrank by 2·5 and 1·5 cm. respectively, and the width of the lateral keels which shrank by 1·25 and 0·5 cm.: both were rather large shrinkages for such short measurements.

Biological Indices.

From the measurements obtained the following biological indices recommended in the International Reports were calculated :—

$$\mathrm{Oi}_1=\frac{2\mathrm{L}_3}{\mathrm{L}_1+\mathrm{L}_2} \qquad \mathrm{Oi}_2=\frac{\mathrm{L}_3}{\mathrm{L}_2-\mathrm{L}_1} \qquad (\mathrm{Oi}_3)=\frac{\mathrm{L}_3}{(\mathrm{L}_{13})}$$

$$\mathrm{Ti}=\frac{\mathrm{L}_5}{\mathrm{L}_3} \qquad (\mathrm{Hi})=\frac{\mathrm{L}_5}{(\mathrm{L}_{10})} \qquad \mathrm{Pi}=\frac{\mathrm{L}_5}{\mathrm{L}_{12}}$$

$$\frac{\mathrm{Pi}}{\mathrm{Ti}}=\frac{\mathrm{L}_3}{\mathrm{L}_{12}} \qquad \mathrm{Di}=\frac{\mathrm{L}_5}{\mathrm{L}_6} \qquad \mathrm{D^1i}=\frac{\mathrm{L}_5}{\mathrm{L}_7}$$

$$\mathrm{Vi}=\frac{\mathrm{L}_5}{\mathrm{L}_8} \qquad \mathrm{Ai}=\frac{\mathrm{L}_5}{\mathrm{L}_9} \qquad \mathrm{H^1i}=\frac{\mathrm{L}_{10}}{\mathrm{L}_{14}}$$

$$\mathrm{Ei}=\frac{\mathrm{L}_{10}}{\mathrm{L}_{15}} \qquad \mathrm{P^1i}=\frac{\mathrm{L}_{12}}{\mathrm{L}_{16}} \qquad \mathrm{M^1i}=\frac{\mathrm{L}_{17}}{\mathrm{L}_{18}}$$

COMPARISON OF NORTH SEA TUNNY WITH THOSE MEASURED BY HELDT AT TUNIS AND FRADE AT ALGARVE.

In order that a strict comparison may be made between my results and those of Frade and Heldt the same statistical data have been calculated, viz.: average deviation, $\frac{\Sigma d}{n}$; probable error, $h=\pm 0{\cdot}6745\times\pm\sqrt{\frac{\Sigma d^2}{n}}$;

Probable error of the mean, $\frac{h}{\sqrt{n}}$; the practical error, $\frac{5h}{\sqrt{n}}$ and the probable and certain limits.

The full details are given in Table I, in which the data obtained by Frade and Heldt, on fish in the G_4 group (viz. 200 to 260 cm., **4**, p. 14), are also given for comparison. It will be convenient to compare each biological index in turn. All the 32 fish that I have measured were large fish between 223 and 271 cm. in length.

Oi_1: for the North Sea fish this index lies midway between those for Tunis and Algarve and the certain limits almost exactly extend over the whole range for these limits in both Tunis and Algarve fish.

Oi_2: for the North Sea fish this index is higher than in either the other two types but lies nearer that of those from Tunis and is very near that given by Heldt (**4**, p. 14) for fish 235 cm. in length.

Oi_3: North Sea fish have a lower index than the Algarve but no comparable data are available for the Tunis fish.

Ti: for the North Sea fish this index lies between that of those from Algarve and from Tunis, but is considerably nearer that for those from Algarve.

Hi: for North Sea fish lies below that for Algarve; no comparable data are available from Tunis.

Di: for the North Sea fish lies above both Algarve and Tunis fish, being nearer the Algarve type.

D^1i: lies above that for both Algarve and Tunis fish.

Vi: lies below that for both Algarve and Tunis fish, but approximates very closely to those from Algarve.

Ai: approximates very closely to that for Algarve and Tunis fish, but is very slightly lower.

The fish examined in the North Sea would thus appear to differ in body proportions both from those between 200 and 260 cm. in length measured by Frade at Algarve and by Heldt in the Mediterranean at Tunis. The first and second dorsal fins are set slightly further forward in the North Sea fish than in the Algarve and Tunis fish: the ventral fin and anus are approximately in the same position as in the Algarve fish: in the North Sea fish the head is smaller than those measured by Frade; the eye is also considerably smaller and is slightly further forward on the head resembling the Tunis fish in these respects; the interorbital width is greater.

In no respect, except in the index Oi_1, was the spread of the variations in the biological indices sufficient to cover both Algarve and Tunis fish, but it was always of the same order of those given by Frade and by Heldt.

It is useless to discuss the significance of the difference between my results and those of Frade and Heldt until far more measurements have been made of large tunny from different regions and at different times of the year. It should however be stressed that all the fish I measured lay in the upper half of Heldt's G_4 group, taken as being 200 to 260 cm.; it is possible that this may account for some of the differences observed. It is likely also that there will be slight differences in body proportions before and after spawning.

Many fish showed a tendency towards the concavity of the snout mentioned by Heldt (in **1**, p. 215): this consequent shortening of the preorbital distance is clearly shown in Figure 8 in the fish nearest the camera.

TABLE I.

COMPARISON OF BIOLOGICAL INDICES OF NORTH SEA TUNNY (223 to 271 CM. IN LENGTH) WITH THOSE OF FISH FROM ALGARVE (ATLANTIC) AND TUNIS (MEDITERRANEAN) BETWEEN 200 AND 260 CM. IN LENGTH.

		North Sea.	Algarve. (Frade.)	Tunis. (Heldt.)
Oi$_1$				
Mean (M)	=M.	2·42	2·406	2·443
Average deviation	$\left(\frac{\Sigma d}{n}\right)$=A.D.	0·044	0·053	0·049
Probable error	(h)=P.E.	±0·040	±0·049	±0·0452
Probable error of the mean	$\left(\frac{h}{\sqrt{n}}\right)$=P.E.M.	±0·007	±0·0049	±0·0045
Practical error	$\left(\frac{5h}{\sqrt{n}}\right)$=Pr.E.	±0·035	±0·024	±0·023
Probable limits	=P.L.	2·413–2·427	2·401–2·411	2·429–2·437
Certain limits	=C.L.	2·385–2·455	2·381–2·430	2·410–2·456
Oi$_2$	M.	11·42	9·726	10·98
	A.D.	0·470	0·623	0·73
	P.E.	±0·386	±0·553	±0·63
	P.E.M.	±0·068	—	—
	Pr.E.	±0·341	—	—
	P.L.	11·352–11·488	9·627– 9·825	10·87–11·09
	C.L.	11·079–11·762	9·231–10·221	10·42–11·54
(Oi$_3$)	M.	2·51	2·70	—
	A.D.	0·086	0·076	—
	P.E.	±0·073	±0·069	—
	P.E.M.	±0·013	—	—
	Pr.E.	±0·065	—	—
	P.L.	2·497–2·523	2·693–2·707	—
	C.L.	2·446–2·575	2·665–2·735	—
Ti	M.	3·74	3·713	3·87
	A.D.	0·068	0·070	0·088
	P.E.	±0·066	±0·061	±0·066
	P.E.M.	±0·012	—	—
	Pr.E.	±0·059	—	—
	P.L.	3·728–3·752	3·702–3·724	3·86–3·88
	C.L.	3·681–3·799	3·658–3·768	3·81–3·93

		NORTH SEA.	ALGARVE. (Frade.)	TUNIS. (Heldt.)
(Hi)	M.	4·21	4·410	—
	A.D.	0·138	0·095	—
	P.E.	±0·118	±0·086	—
	P.E.M.	±0·022	—	—
	Pr.E.	±0·120	—	—
	P.L.	4·188–4·233	4·395–4·425	—
	C.L.	4·090–4·330	4·335–4·485	—
Di	M.	3·62	3·555	3·518
	A.D.	0·085	0·063	0·077
	P.E.	±0·070	±0·048	±0·066
	P.E.M.	±0·012	—	—
	Pr.E.	±0·062	—	—
	P.L.	3·608–3·632	3·546–3·564	3·506–3·530
	C.L.	3·558–3·682	3·510–3·600	3·458–3·578
D^1i	M.	1·93	1·886	1·887
	A.D.	0·026	0·029	—
	P.E.	±0·023	±0·029	—
	P.E.M.	±0·004	—	—
	Pr.E.	±0·021	—	—
	P.L.	1·926–1·934	1·883–1·889	1·881–1·893
	C.L.	1·909–1·951	1·871–1·901	1·858–1·916
Vi	M.	3·17	3·197	3·397
	A.D.	0·098	0·081	0·087
	P.E.	±0·084	±0·072	0·074
	P.E.M.	±0·015	—	—
	Pr.E.	±0·074	—	—
	P.L.	3·155–3·185	3·185–3·209	3·383–3·411
	C.L.	3·096–3·244	3·137–3·257	3·329–3·465
Ai	M.	1·64	1·660	1·657*
	A.D.	0·022	0·027	—
	P.E.	±0·019	±0·024	—
	P.E.M.	±0·004	—	—
	Pr.E.	±0·018	—	—
	P.L.	1·646–1·654	1·658–1·662	1·652–1·662*
	C.L.	1·632–1·668	1·648–1·672	1·634–1·680*

The biological index Pi has not been considered here owing to the doubt about the correct points of reference to take in measuring the pectoral fin. It was found that when measuring from the point B in Figure 7 the mean for Pi was 6·30, and the average of the four measurements made from the point A was 5·57.

THE LENGTH OF THE FINS.

In Table II are given the lengths of the 2nd dorsal, 1st dorsal, and anal fins, and upper caudal lobe, expressed as percentages of the total length of the fish (L_5). In this table the lengths of the second dorsal are arranged serially in order of size and there is a very distinct tendency for the fish with short second dorsals to have short first dorsal and anal fins and to a less extent narrower tails, and for fish with long second dorsals to have the

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* For (G_3+G_4) fish, i.e. 160 to 260 cm.

other two fins long also and the tail wider. There is considerable variation in fin-length, the range covered by the different fins being :—

2nd Dorsal . . .	12·4–17·0% of total length, L_5
1st Dorsal . . .	8·5–11·4% ,, ,, ,,
Anal	12·5–17·2% ,, ,, ,,
Upper Caudal Lobe . .	15·3–18·7% ,, ,, ,,

No correlation is shown between the length of the above fins and that of the pectoral fin which varies between 14·4 and 17·4% of the total length of the fish (L_5).

It is of interest also to note that the lengths of the 2nd dorsal fin show distinct bimodality, the two modes falling in the 13-cm. and the 15 to 16-cm. groups respectively. No such bimodality is however shown by other fins.

No correlation could be found between fin-length and other body proportions of the fish.

TABLE II.

LENGTHS OF SECOND DORSAL, FIRST DORSAL, ANAL AND CAUDAL FINS EXPRESSED AS PERCENTAGES OF BODY LENGTHS. (CAUDAL FIN BASED ON UPPER LOBE.)

Fish No.	2ND D.	1ST D.	A.	C.
24	12·4	8·9	13·0	16·3
31	12·9	9·8	12·5	16·3
3	13·0	9·5	13·4	17·3
4	13·0	9·4	13·5	16·4
28	13·4	10·7	14·4	18·0
29	13·4	10·5	14·9	17·9
7	13·5	8·6	14·8	17·6
22	13·6	9·0	13·2	16·8
19	13·8	9·8	13·6	16·6
21	13·8	9·7	13·1	16·4
2	13·8	9·1	14·6	17·8
10	13·9	10·5	13·1	15·3
11	14·1	10·7	13·7	16·7
12	14·6	11·4	13·0	17·5
5	15·0	10·0	14·6	17·9
13	15·0	10·0	13·7	17·2
16	15·0	11·1	15·8	17·4
23	15·3	9·2	13·4	17·1
8	15·6	11·2	16·4	18·0
14	15·8	10·0	14·1	18·7
15	15·9	11·3	14·9	16·9
27	15·9	11·1	14·9	18·1
1	16·0	10·4	16·8	17·6
26	16·0	10·6	14·8	17·0
18	16·2	10·0	15·5	17·0
6	16·3	8·5	15·4	16·7
9	16·3	10·0	15·5	17·5
17	16·3	10·7	17·2	17·0
31	16·5	10·4	14·0	18·7
32	16·5	11·2	15·3	17·8
20	16·7	9·7	15·7	17·5
25	17·0	10·0	15·3	18·5

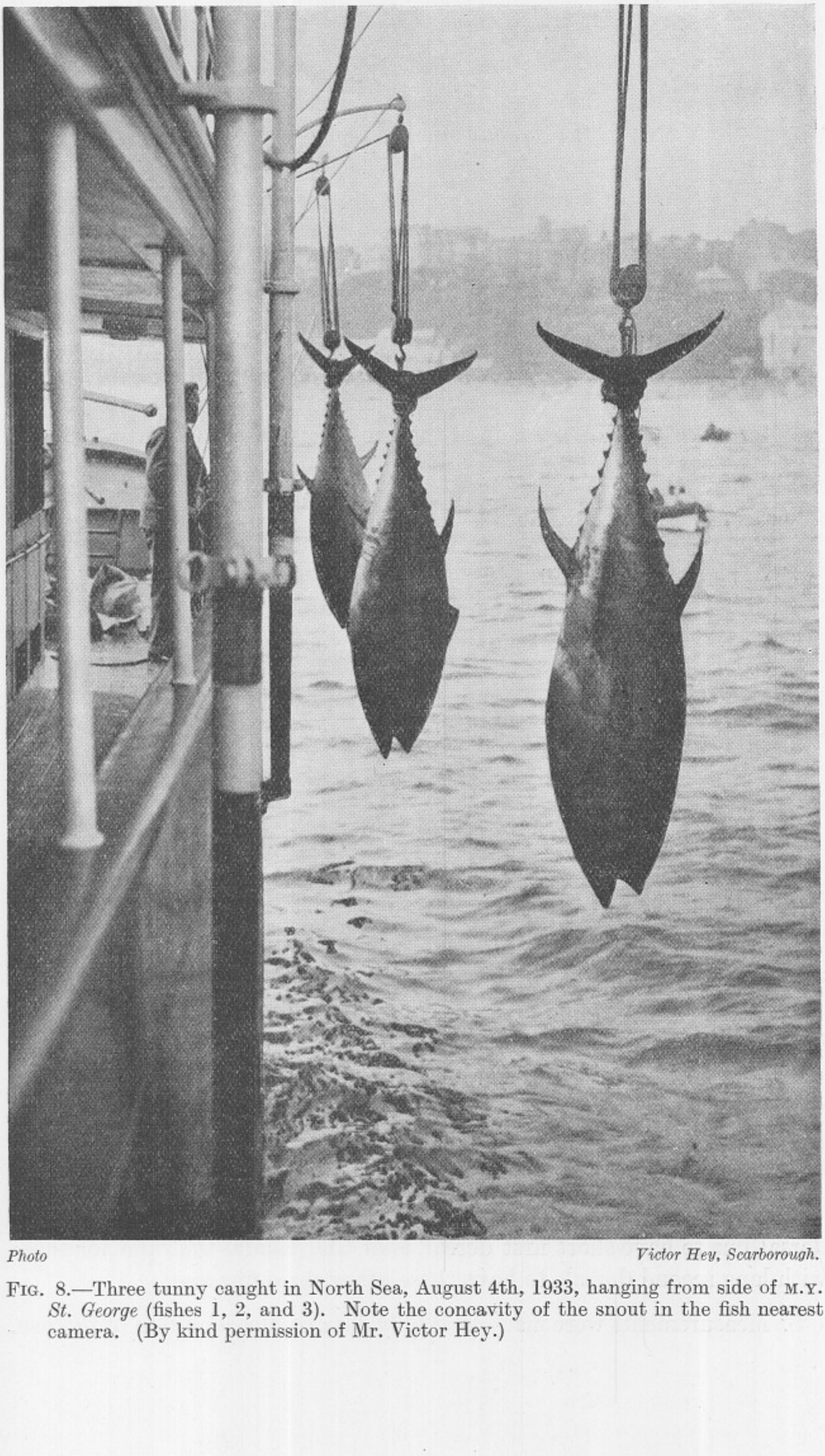

Photo *Victor Hey, Scarborough.*

FIG. 8.—Three tunny caught in North Sea, August 4th, 1933, hanging from side of M.Y. *St. George* (fishes 1, 2, and 3). Note the concavity of the snout in the fish nearest camera. (By kind permission of Mr. Victor Hey.)

DATA ON CONDITION OF FISH.

An additional series of measurements was made on the last twelve fish to give some idea of their condition. It is not easy to make an accurate measurement of the girth of such heavy fish when lying on the deck of a ship: therefore it was decided to adopt a measurement equal to half the girth taken round one side of the fish from mid-dorsal to mid-ventral lines. Owing to the obvious variation in the shape of the fish a number of these semigirth measurements were made at different points: the points of reference chosen were as follows:—

1. In the region of the front end of the first dorsal fin by slipping the tape under the pectoral fin as far forward as it would go when this fin was flat along the side of the fish: this ensured a very constant position.
2. At the anterior insertion of the second dorsal fin.
3. At the anterior insertion of the anal fin.
4. At the eighth ventral pinnule counted from the caudal end.
5. At the sixth ventral pinnule from the caudal end.
6. At the fourth ventral pinnule from the caudal end.

I am indebted to Mr. F. Hannam for suggesting the latter of these measurements. These measurements are given in Table IV, p. 522.

SUMMARY.

1. Details are given of the types of hooks lost in tunny in the North Sea in the summer of 1933.

2. Data are given on the measurements made on thirty-two large migrating fish caught in the North Sea in August and September, 1933.

3. In certain body proportions the tunny measured differ from those in the G_4 Group (200 to 260 cm. in length) given by Heldt for fish from Tunis and by Frade for fish from Algarve on the south coast of Portugal, while in some characters they resemble the Tunis fish and in others the Algarve fish, but all the North Sea fish were between 232 and 271 cm. in length.

4. It was found that there was a tendency for fish with short second dorsal fins to have short first dorsal, anal, and caudal fins, and for those with long second dorsals to have these other three fins long.

5. Measurements were made to supply data on the condition of the fish.

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DATE AND PLACE OF CAPTURE, ETC., OF THE THIRTY-TWO TUNNY FROM THE NORTH SEA MEASURED SUMMER, 1933.

All fish were caught on a rod and line except when otherwise stated.

FISH No.	CAUGHT BY.	DATE OF CAPTURE.	POSITION.		DATE AND PLACE OF MEASURING.	
1	Col. Cotton	4.viii.33	55°34′N.	3°26′E.	5.viii.33	on board.
2	On pellet (*St. George*)	,,	,,	,,	,,	,,
3	Col. Peel	,,	,,	,,	,,	,,
4	On pellet (*St. George*)	7.viii.33	55°18′N.	2°49′E.	8.viii.33	,,
5	Col. Cotton	,,	,,	,,		
6	Lady Broughton Lord Moyne	4.viii.33	55°19′N.	2°28′E.	9.viii.33	in Pure Ice Co. Factory.
7	F. Hannam, Esq.	26.viii.33	54°51′N.	0°19′E.	26.viii.33	on board.
8	L. Mitchell Henry, Esq.	,,	,,	,,	,,	,,
9	,, ,, ,,	,,	,,	,,	,,	,,
10	Col. Cotton	,,	,,	,,	,,	,,
11	Col. Peel	,,	,,	,,	,,	,,
12	On pellet (*St. George*)	,,	,,	,,	,,	,,
13	Col. Cotton	,,	,,	,,	,,	,,
14	Mrs. T. O. M. Sopwith	,,	55°05′N.	1°30′E.	28.viii.33	in fish market.
15	T. O. M. Sopwith, Esq.	,,	55°10′N.	1°00′E.	,,	,,
16	Miss G. Yule	,,		—	,,	in Pure Ice Co. Factory.
17	S. V. Hine, Esq.	,,	54°51′N.	0°19′E.	,,	in Mr. Bamford's cellar.
18	David Leigh, Esq.	,,	,,	,,	,,	in exhibition room.
19	E. Leigh, Esq.	,,	,,	,,	,,	,, ,,
20	Col. Cotton	29.viii.33	54°57′N.	0°50′E.	29.viii.33	on board.
21	,, ,,	,,	,,	,,	,,	,,
22	,, ,,	,,	,,	,,	,,	,,
23	On pellet (*St. George*)	,,	,,	,,	,,	,,
24	Col. Cotton	,,	,,	,,	,,	,,
25	,, ,,	30.viii.33	54°55′N.	0°25′E.	30.viii.33	,,
26	Col. Peel	,,	54°55′N.	,,	,,	,,
27	,, ,,	,,	,,	,,	,,	,,
28	On pellet (Col. Peel)	,,	,,	,,	,,	,,
29	Col. Peel	2.ix.33	54°48′N.	0°28′E.	2.ix.33	,,
30	,, ,,	,,	,,	,,	,,	,,
31	,, ,,	,,	,,	,,	,,	,,
32	Col. Cotton	,,	,,	,,	,,	,,

TABLE III.

MEASUREMENTS OF TUNNY FROM THE NORTH SEA: ALL MEASUREMENTS ARE IN CENTIMETRES.

NO. OF FISH.	1	2	3		5	6	7	8	9	10	11	12	13	14	15	16
L_1	25	27	22	21½	23½	25	27	24	24	22½	23	25	24	25	25	25
L_2	31	33	28	27	29	31	33	29½	29½	28	28½	31	30	31	30½	31
L_3	68	71	62·5	60	65	62	70½	66	65	62	63	67	68	69	67	68
L_4	69	73	64	62	66	70	75	67½	66½	65	65½	69	69	69½	69	71
L_5	250	253	231	223	240	246	266½	250	245	248	233½	246	256	241	252	253
L_6	67	73	65	61½	63½	71	72	66½	66½	63½	62	69	70	69	70	73
L_7	129	133	121	117	121	131	136	128	126	121	120	130	137	126	130	131½
L_8	82	81	73	69	79	81	90½	79	76	73½	76½	75½	76	81	79	81
L_9	154	151	139	135	144	152	166	154	147	143½	143	151	156	147	149½	154
L_{10}	59	64	56	48	56	62	68	63	58	57	56	54	60	60	61	60
L_{12}	40	42	38	36½	41	40	42	39	38½	40	34	41	40	40	38½	44
L_{13}	27	29	23	23½	25½	27	30	26	26½	24	24	26	26	25	25	28
L_{14}	45	46	45	41	45½	47	50½	50	45½	46	45½	43	50½	46½	51½	46½
L_{15}	40	42	39	40	40	41	–	43½	–	–	–	–	–	–	–	–
L_{16}	14	16	15	12½	13	13	15	14	14	13	12	14	13½	14	13½	13
L_{17}	26	27·5	23	23	26	27	27	25	24½	24	25	26	27	27	26	25
L_{18}	26	27	23	22	26	25	29	26	24½	23	24½	25	26	26	25	24½
(L_{19})	54·5	57	50	48	52½	55	58	54	51½	50	50	53½	56	54½	54½	55
(L_{20})	18	18	17	17½	18	17	20	**	17½	19	19	20	19	17½†	18½	18½
(L_{21})	26	23	22	21	24	21	23	28	24½	26	25	28	25½	24	28½	28
(L_{22})	40	35	30	29	36	40	36	39	40	34½	33	36	38½	38	40	38
(L_{23})	42	37	31	30	35	38	39½	41	38	32½	32	32	35	34	37½	40
(L_{24}) Upper	44	45	40	36½	43	41	47	45	43	38	39	43	44	45	42½	44
(L_{24}) Lower	44	45	40	36½	43	41	46	45	43½	38	39	43	42	45	42½	44
Fin formula																
Pinnules D.	10	10	10	10	10	10	10	–	–	10	11	5+3	10	10	10	10
Pinnules V.	9	9	9	9	9	9	9			10	10	9	9	9	9	9
Weight (lbs.)	524	542	459	–	461	532	705	532	514	511	476	434	616	505	575	561

NO. OF FISH.	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
L_1	22	27½	23	26·4	26·9	24·3	26	24	27·5	24·5	24·75	25	26·5	25·2	26	24·8
L_2	28	33½	29	32·2	32·8	30·2	32·4	30	33·7	30·2	30·25	31	32·8	31	32	30·2
L_3	62	73½	63	71·7	71	66	69	64·7	73·2	67·5	66	68·8	71·5	69·5	68·5	64
L_4	63½	76	65	71·9* 73	72* 73	68* 69·5	70* 71·5	– 67	73·4* 75	68·5* 70	66* 67·5	69* 70·5	71·5* 73·2	69·5* 71	68·7* 70	64·5* 66
L_5	233	271	235	260·5	268	250·5	251	242	270·5	264	248	261	268	264*p*	257	236
L_6	66	73½	66½	74	73·25	71·5	70	68	75	72·3	70·25	72·5	75	71	71	66
L_7	123	140	123	134·5	139·5	128	132·5	125·5	141	135	129	137·5	139	134	133	124
L_8	71½	96	74	81·5	81	81	78	76·5	85·5	79	76·5	79	83·5	80	78·5	76
L_9	140	170	142	157	163	150	151	145	164	157·5	151	159	163	155	155	148
L_{10}	55	–	–	63	65	59	57	55	68	65			62	62	60	55
L_{12}	39	40	39	41·5	41·5	36	38·5	37·5	42·5	40·5	40	40	45·5* 40	46·5* 41	47* 41·5	45* 40
L_{13}	24½	29	25	29	29·5	26	28	27	31·2	26	26	28	27	27·5	28	27
L_{14}	44½	53	44½	48·5	49	45	41·5	46	54	52	47	52	51·5	51·5	51·5	49
L_{15}	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
L_{16}	12	15	13	14·75	14	14	12·5	13	15·3	14·5	14	15	16	15	15·5	13
L_{17}	24½	30½	25	27*o* 26*s*	28*o* 27*s*	27*o* 26*n*	26·5*s*	25·5*o* 25*n*	28*o* 27·5*n*	26*o* 25·5*n*	25·5*o* 25*n*	25*s* 25*n*	27·5*o* 27*n*	26·5*o* 26*n*	26·5*o* 26*n*	25·5*o* 24·5*n*
L_{18}	23½	29	24	26*o* 25·5*s*	26	26*o*	25	24	26·5	25	24·5	25	26	25·5	25	24
(L_{19})	49½	60½	52½	58	58	52·75	56	52·3	60	54·5	53	56	57	56	55·5	53
(L_{20})	17	½ missing	16	19	20	18	20·5	17·5	21·8	20·2	20	20	21·75	21·5	20	17
(L_{21})	25	27	23	25	26	22·5	23	21·5	27	28	27·5	28	28	26	26·75	26·5
(L_{22})	38	44	32½	43·5	37	34	38·5	30	46	42·3	39·4	35	36	34	42·5	39
(L_{23})	40	42	32	41	35	33	33·5	31·5	42	39	37	37·5	40	33	36	36
(L_{24}) Upper	39½	46	39	45·5	44	42	43	39·5	50	45	45	47	48	43	48	42
(L_{24}) Lower	40	46	39	45	44	42	44	39·5	50·5	45	45	47·5	48	43	48	42
Fin formula																
Pinnules D.	10	10	11	10	10	11	10	10	4+5	10	10	11	10	11?	10	10
Pinnules V.	9	9	9	9	9	9	9	9	9	9	9	10	9	9?	9	9
Weight (lbs.)	428	763	456	643	735	492	546	469	714	664	549	695	709	659	687	554

** One side missing. † damaged.

* With pectoral fin flat by side (to point A, Fig. 7); other measurements to point B (Fig. 7).

L_{17}, L_{18}: *o*: mouth open, *s*: mouth shut } to point A, Fig. 6.; *n*: to point B, Fig. 6.

TABLE IV.

Body Measurements to Study Condition of Fish.

Fish No.	7	8	9	10	11	12	13	14	15	16	17	18	19
6th Pinnule	40	34½	38	35	36	32½	39	34	38	37	36	41	32½
4th Pinnule	27½	24	26	25	25½	25	27½	24	26	26	27	29	22½

Fish No.	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1st Dorsal	–	–	–	91	95	83	87	84	90	89	87	90·5	91·5	90·5	91	86
2nd ,,	–	–	–	77	87	69	73	70	80	79	72	79	80	78	83	75
Anal	–	–	–	67	72	59	62	62	69	71	62	69	70	70	72	64
8th Pinnule	–	–	–	55	62	44	50	50	51	52	48	56	58	54·5	55	50
6th ,,	36	41	32½	40	45	36	39	34	39·5	39	35	44	43½	40	41	39
4th ,,	27	29	22½	28	29	26	29	24	29	28	26	29	30	28·5	29·5	28

Rissoid Larvæ as Food of the Young Herring. The Eggs and Larvæ of the Plymouth Rissoidæ.

By

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With Plates I–IV.

The free-swimming young of the Rissoidæ are particularly important in the plankton for there is always one or more species present in any month and they usually occur in great abundance. The various species live between tide-marks, in the laminarian and coralline zones and in deeper water in several fathoms depth ; wherever tow-nettings are taken they usually contain some species of this family. The inshore waters, however, are the richest in rissoids. Even in winter certain species are common round the Plymouth coasts. Some years ago it was found that very young herring just before losing the yolk-sac and about a fortnight old had been eating small rissoids, evidently almost newly hatched (Plate I, Fig. 1). The herring up to a length of about 12 mm. and just after the yolk-sac had disappeared altogether continued to eat them but usually after this size they ate only small crustacea. From 1917 to 1921 it was found that out of 140 young herring examined, 91 had fed on these small gastropods. In later years they were also found feeding on them (Lebour, 1921, 1924). Other minute planktonic organisms were eaten, including algæ, tintinnids, copepod and cirripede nauplii and very small adult copepods ; also a minute bivalve larva but no other gastropod, although other veligers were present in the plankton, *Patella* being specially common. The young herrings hatch out from December to February, therefore these little gastropods must also hatch at this time and this proves to be the case for in the plankton there are large numbers of these very young veligers (Plate I, Figs. 7–8). Later on, in spring, older stages of the same mollusc abound and are quite the commonest veligers in the plankton near the coast (Plate I, Figs. 17–19). In the summer they have almost entirely disappeared.

In order to find out the species it was necessary to make a research on the eggs and larvæ of all the Rissoidæ available. It is now proved that the larva which the herrings eat is *Rissoa sarsii* Lovén. I have to thank

Mr. R. Winckworth for confirming this identification. *Rissoa sarsii* is not known from Plymouth in the adult state, although repeatedly sought, but later larvæ in plunger-jars grew up into this species. Its habitat should be just below low-water mark (Forbes and Hanley, 1853, Vol. III ; Jeffreys, 1867, Vol. IV) and it is probably in a region difficult of access, being just too far out for hand collecting and too far in for dredging. The species, it is now discovered from the Plymouth larvæ, has a characteristic sculpture on the embryonic whorls and it is easy to differentiate it from other near relatives. It is also found, however, that *Alvania punctura*, living further out, has similar sculpture on the extreme apex although it is easily separated from *R. sarsii* by its other embryonic whorls and it breeds in quite a different season (Plate IV, Figs. 1–7). The sculpture on the apex, not noted by previous workers, points to a very close relationship.

The following is a list of the known Plymouth Rissoidæ, new records being marked with a cross. Some early records are of dead shells only which have not been recorded again. The names are according to Winckworth's recent list of British Marine Mollusca (1932) ; when these differ from those in the Plymouth Fauna List (Mar. Biol. Assoc., 1931) the latter are added in brackets.

RISSOIDÆ. Genus **Cingula.** Sub-genus PARVISETIA, *Cingula fulgida* (J. Adams) ; × *C. alderi* (Jeffreys). Sub-genus HYALA, *Cingula vitrea* (Montagu) (=*Onoba vitrea*), dead shells only ; *C. proxima* (Forbes and Hanley) (=*Onoba proxima*), dead shells only. Sub-genus ONOBA, *Cingula semicostata* (Montagu) (=*Onoba candida*). Sub-genus CINGULA, *Cingula semistriata* (Montagu) ; *C. cingillus* (Montagu).

Genus **Alvania.** Sub-genus MANZONIA, *Alvania crassa* (Kanmacher). Sub-genus ALVANIA, *Alvania cimicoides* (Forbes), dead shells only ; *A. cancellata* da Costa, dead shells only ; *A. zetlandica* (Montagu), dead shells only (=*Manzonia zetlandica*). Sub-genus GALEODINA. *Alvania carinata* (da Costa), dead shells only. Sub-genus ACTONIA. *Alvania punctura* (Montagu) (=*Arsenia punctura*).

Genus **Rissoa.** Sub-genus TURBOELLA. × *Rissoa sarsii* Lovén ; × R. *inconspicua* Alder ; *R. parva* (da Costa) ; *R. guerini* Récluz. Sub-genus RISSOA, *Rissoa membranacea* (J. Adams).

Genus **Barleeia.** *Barleeia unifasciata* (Montagu) (=*Barleeia rubra*).

Of these the eggs have been obtained from *Cingula semicostata*, *C. semistriata*, *Alvania punctura*, *Rissoa inconspicua*, *R. parva*, *R. guerini*, *R. membranacea* and *Barleeia unifasciata* and the planktonic egg-capsules of *Rissoa sarsii* have been identified. The larvæ of all these have been distinguished. The veliger stage of *Cingula semicostata* and *Barleeia unifasciata* is passed within the egg and the young emerges crawling. *Rissoa sarsii* is the only species so far known with planktonic egg-capsules.

The remainder all lay lens-shaped egg-capsules deposited on some substratum which may be regarded as typical of the family.

Jeffreys (1867) states that in Rissoa " the spawn cases are solitary and hemispherical," including in the genus all those now placed in the family Rissoidæ by Winckworth. Jeffreys describes the egg-capsules of *Rissoa albella* thus : " the spawn cases are generally solitary, semiglobular and light yellowish brown ; the fry emerge from a large round hole at the top which appears when they are developed." In his account of the spawn of prosobranchs Lamy (1928) only mentions that of *Rissoa membranacea* described by Fischer (1892) and of *Rissoa parva* described by Jeffreys (1867), Caullery and Pelseneer (1910) and Pelseneer (1911). This appears to be all that is known of the spawn of any of the Rissoidæ and these three species *R. membranacea*, *R. parva* and *R. albella* have the typical capsules. The larvæ on hatching have a simple shell consisting of rather more than one whorl, and a well-developed bilobed velum. Until now few observations have been made on the older larvæ.

In the Laboratory *Rissoa membranacea* laid eggs on *Zostera*, so also did *R. parva*, *R. guerini* and *Cingula semistriata* as well as on other weeds and on the sides of a glass bowl, *R. inconspicua* on weeds and on one another, *Alvania punctura* on one another. *Cingula semicostata* laid them singly attached to bits of sand or debris in a glass jar and *Barleeia rubra* laid single eggs in tough capsules on weed in a bowl. If we examine the mode of life of these species we find that the six species with typical egg-capsules all live on weed with the possible exception of *Alvania punctura*. It is difficult to be certain of the true habitat of the last species as it is usually found in dredgings where it falls into the fine mud or sand at the bottom. *Rissoa membranacea* appears always to live on Zostera and since the disease of this plant during the last few years it has disappeared from the Plymouth coast. *R. parva* lives on many weeds, especially the large fronds of Laminaria, *R. guerini* also lives on various weeds, especially *Rhodomela subfusca** and Codium, *Cingula semistriata* on various weeds and stones below low-water mark. *R. inconspicua* is usually to be found among weeds and on shell gravel below low-water mark, *Cingula semicostata* on muddy sand and under stones between tide-marks and below low-water mark, *Barleeia unifasciata* at extreme low tide, especially on Fucus and *Calliblepharis jubata*, often with *Rissoa parva*.

The existing classification of the Rissoidæ is very unsatisfactory. Even Thiele (1929) does not notice the embryonic sculpture of our British forms (except *Alvania cimicoides* which he places in the section *Alcinulus* in the sub-genus *Alvania*), although there are certain rissoids described from Australia which have spirally ribbed apices (Thiele, Powell (1930) and

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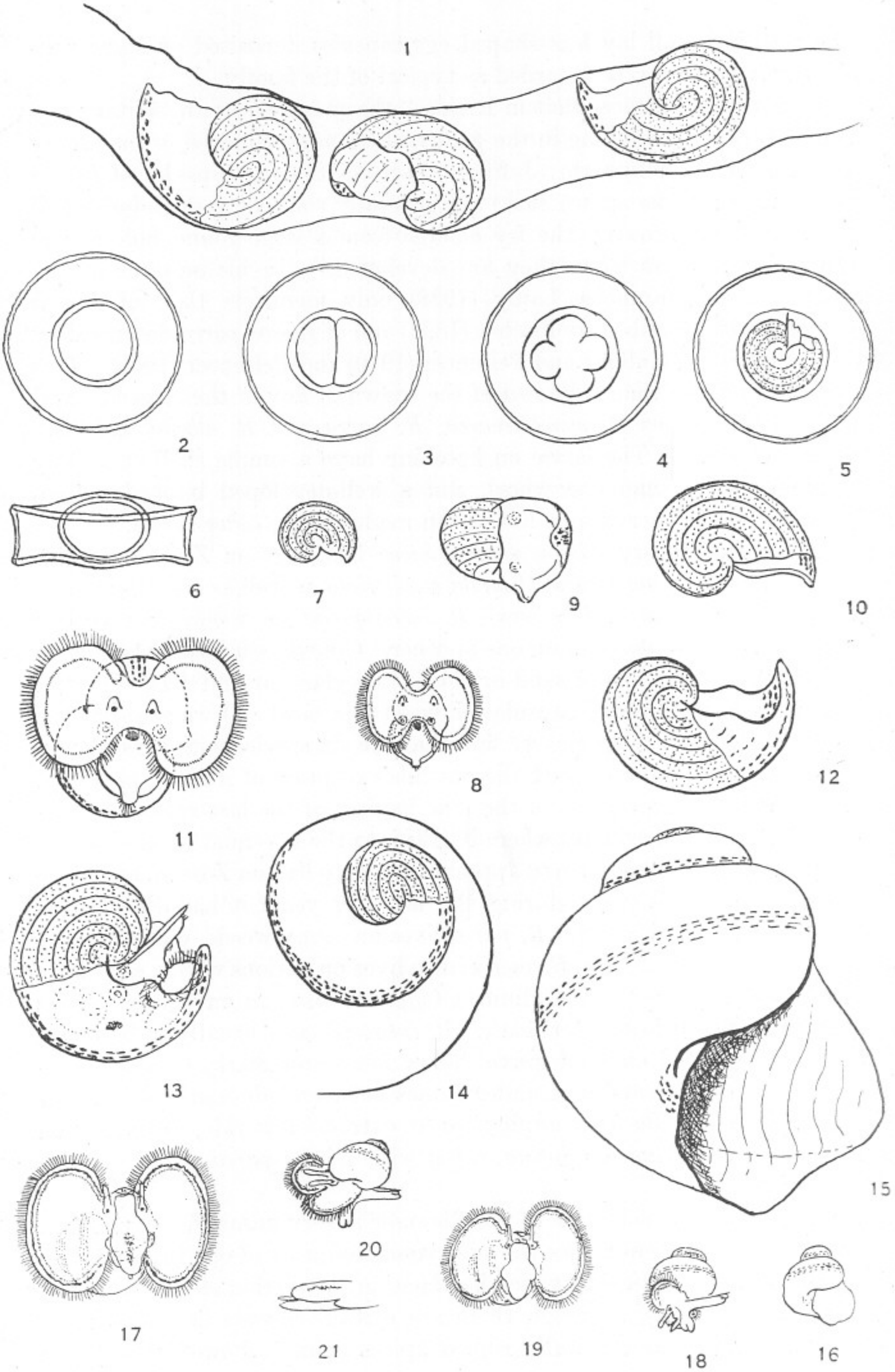
* I am indebted to Mrs. D. P. Wilson for the names of the seaweeds.

PLATE I.



others). A smooth apex is the commonest, such as *Rissoa membranacea*, *R. parva*, *R. guerini*, *R. inconspicua*, *Cingula semistriata* and *Barleeia unifasciata*. *Cingula semicostata* has a finely spirally sculptured apex, whilst *Rissoa sarsii* and *Alvania punctura* have spirally sculptured apices with dots in between which are so alike that except for size one could scarcely tell the newly hatched veligers apart should they occur together, which they do not. Surely this must mean a closer relationship than is generally supposed. It would be consistent to place *Rissoa sarsii* and *Alvania punctura* at least in the same genus and to remove *Cingula semicostata* from the genus *Cingula* for not only is *Cingula semistriata* very different in the apex, it also, as is well known, possesses three posterior tentacles instead of one. A detailed revision of the genus, both anatomical and conchological, is evidently highly desirable, and one which is helped enormously by the study of the larval stages. Jeffreys (1867) remarks that the embryonic whorls are important and frequently describes them. His only references to sculptured apices in the Rissoidæ are, however, in *R. Jeffreysii*, "the top whorls may be seen to have a few spiral rows of salient and re-entering angles, which last prefigure the cancellated structure of the adult shell," and further on, "the apex is marked with a Vandyke pattern instead of having rows of punctures" (as in *Rissoa punctura*), and in *Rissoa punctura* "the uppermost whorls exhibit under the microscope a few rows of punctures." *Rissoa cimicoides*, *R. Jeffreysia* and *R. punctura* are all now placed in the genus *Alvania*.

The form of the larval shell of the Rissoidæ is very like that of Lacuna, but the later stages can be distinguished by the shape of the end of the foot, in rissoids pointed, in Lacuna with two lobes. The rissoids have

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EXPLANATION OF PLATES.

(The figures are drawn to three scales, B six times A, C twice A)

PLATE I.

Rissoa sarsii.

(Figs. 1–15 scale B, 17 scale C, 16, 18–20 scale A.)

FIG. 1.—Very young larvæ in the intestine of a young herring before completely losing the yolk sac.

FIGS. 2–6.—Pelagic egg-capsules, 0·18 mm. across, (2, 6) newly laid; (3,4) dividing; (5) with larva ready to hatch. Larval shell 0·08 mm. across.

FIGS. 7–8.—Newly hatched larva, shell 0·08 mm. across.

FIG. 9.—Shell of slightly older larva, 0·15 mm. across.

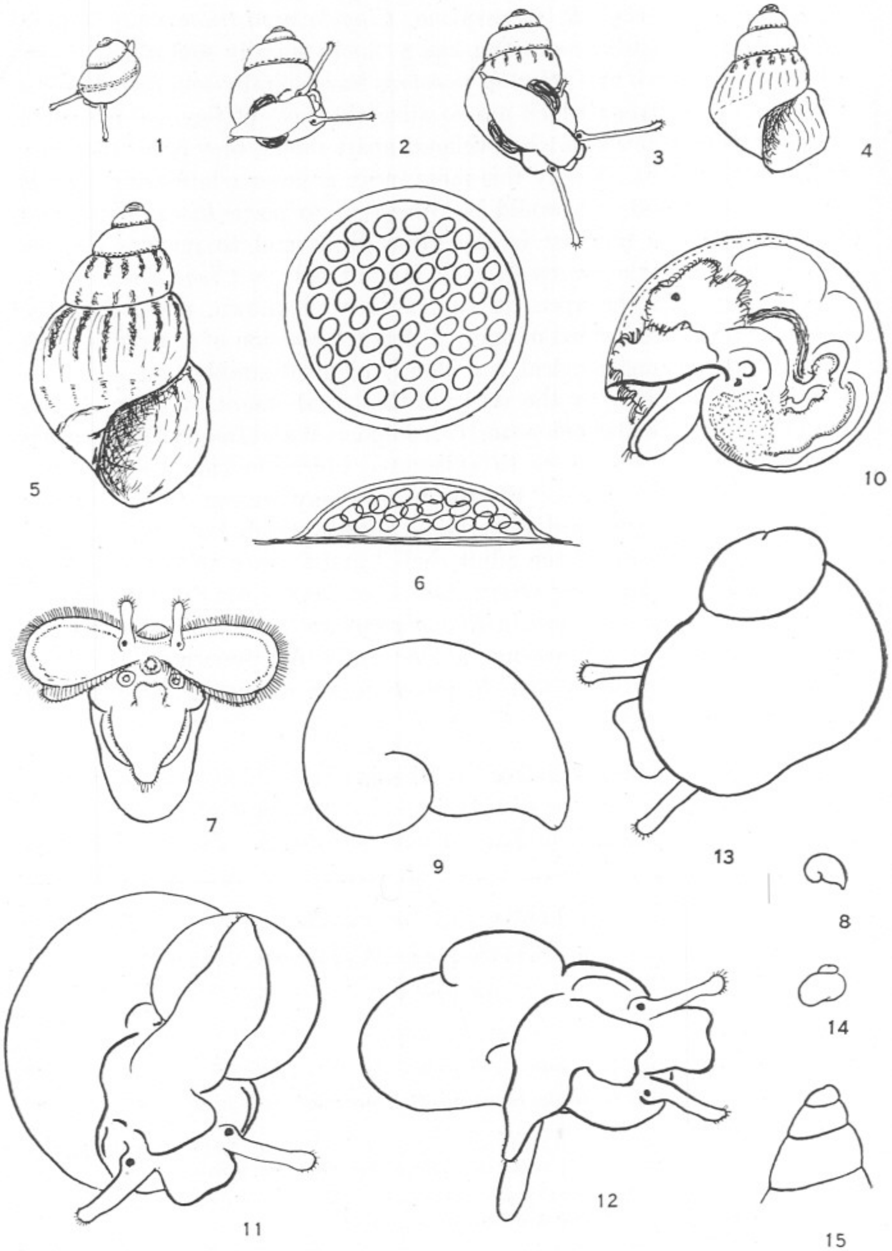
FIGS. 10–13.—Older larvæ.

FIGS. 14–15.—Shells of older larvæ.

FIGS. 16–20.—Late veligers, shell 0·48 mm. high.

FIG. 21.—Foot showing posterior process.

PLATE II.



a posterior tentacle, sometimes three, behind the operculum and above the foot, and a pendent tentacle at the upper junction of the inner and outer lip. This last is rarely absent, and in these cases probably has either escaped notice or the species should be placed elsewhere. The various larvæ can be distinguished by the size, absence or presence of sculpture on the embryonic whorls, absence or presence of colour on the velum, length of life in the plankton and general appearanc. Those which remain for some time in the plankton usually have 3 to 3½ whorls before losing the velum, the posterior and mantle tentacles then being formed and the foot assuming the adult shape.

The following shows the seasonal breeding actually observed at Plymouth :—

January : *Rissoa membranacea*, *R. parva*, *R. sarsii*, *Cingula semicostata.* February : *Rissoa membranacea*, *R. parva*, *R. guerini*, *R. sarsii*, *Cingula semicostata.* March : *Rissoa membranacea*, *R. parva*, *R. guerini*, *R. sarsii*, *Cingula semicostata.* April : *Rissoa parva*, *R. guerini*, *R. sarsii*, *Cingula semicostata*, *C. semistriata*, *Barleeia unifasciata.* May : *Rissoa parva*, *R. guerini*, *R. sarsii*, *Cingula semistriata*, *Barleeia unifasciata.* June : *Rissoa parva*, *Cingula semistriata*, *C. semicostata.* July : *Rissoa guerini*, *Cingula semistriata.* August : *Rissoa guerini*, *Alvania punctura*, unknown rissoid. September : *Rissoa parva*, *R. guerini*, *Alvania punctura*, unknown rissoid. October : *Rissoa parva*, *R. guerini*, *R. inconspicua*, *Alvania punctura.* November : *Rissoa parva*, *R. guerini*, *R. inconspicua*, *Alvania punctura*, unknown rissoid. December : *Rissoa parva*, *R. guerini*, *R. sarsii*, *R. membranacea*, *Cingula semicostata.*

RISSOA MEMBRANACEA (J ADAMS).

(Plate II, Figs. 6–15).

The largest of the Plymouth rissoids, usually occurring abundantly on *Zostera marina* on the Zostera beds. Egg-capsules of typical lens-like form, flat on the attached surface, rounded above. Actually seen from

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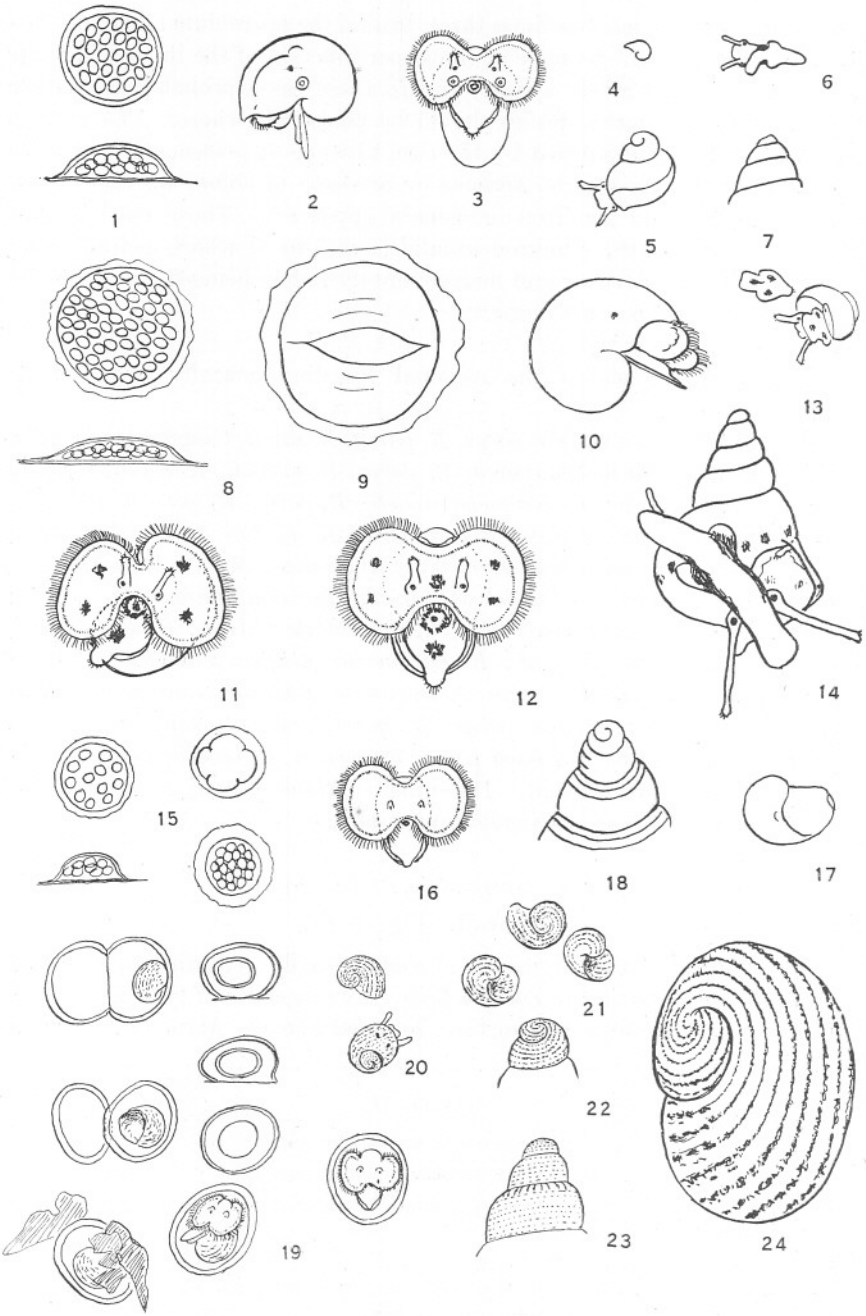
PLATE II.

Rissoa sarsii, *Rissoa membranacea.*

(Figs. 1–6, 8–15 scale A ; 7–13 scale B.)

FIGS. 1–5.—*Rissoa sarsii* reared from planktonic larvæ, shell 0·48 mm. to 2 mm. high.
FIGS. 6–15.—*Rissoa membranacea.*
FIG. 6.—Egg capsule, 1·5 mm. across.
FIGS. 7–8.—Newly hatched larva, shell 0·32 mm. across, from egg.
FIGS. 9–10.—Larvæ a few days old, reared in bowl.
FIGS. 11–14.—Young crawling, reared in bowl, shell 0·37 mm. across.
FIG. 15.—Apex of adult shell.

PLATE III.



December to March but breeding probably goes on through spring and summer as it does on the French coast. Some eggs were laid on Zostera in bowls during December and January. Fischer (1892) figures the spawn from Arcachon and describes it as watch-glass shaped, about 1·5 mm. across, with about 100 eggs, which, when ready to hatch, escape from a hole at the top formed when the larvæ are developed sufficiently to swim away. The Plymouth specimens agree in size, capsules 1·4 to 1·6 mm. across, 0·32 mm. high (Plate II, Fig. 6), but do not contain so many eggs. From 40 to 60, about 0·13 mm. across, is the usual number, and these did not all develop, several being apparently devoured by their neighbours. This may or may not be a case of true " nurse " eggs, for possibly the eggs in captivity were abnormal. In about 10 to 12 days the eggs hatched as free-swimming veligers, 0·32 mm. across the round, transparent and colourless shell of about 1½ whorls without sculpture (Plate II, Fig. 7). Animal, including velum, colourless, velum 0·32 mm. across, foot short, not reaching behind to end of shell, front part with process but not reaching mouth. Tentacles, eyes, otocysts and mouth well developed. The larvæ in a bowl with Nitzschia grew very quickly, front of foot soon covering mouth and in about 3 weeks or less were crawling, having lost velum. Larvæ hatched December 12th were crawling January 5th, shell about 0·37 mm. across and still without sculpture. The species can be recognised easily at this stage. Although when newly hatched it is larger than any of the rissoids known, it loses the velum at a smaller size and with fewer whorls than most of the others, having hardly 2½ whorls at metamorphosis (Plate II, Figs. 11–14). Capsules and larvæ were found in their natural surroundings on and near Zostera in spring.

PLATE III.

Rissoa parva, Rissoa guerini, Cingula semistriata, Cingula semicostata.

(Figs. 1, 4–9, 13–15, 18–23 scale A ; 10–12, 16, 17, 24 scale B.)

FIGS. 1–7.—*Rissoa parva.*

(1) egg-capsules laid in bowl, 0·64 mm. across ; (2–4) newly hatched larvæ from eggs, shell 0·13 mm. across ; (5) young just crawling, having lost velum, shell 0·48 mm. high ; (6) foot of same ; (7) apex of adult shell.

FIGS. 8–14.—*Rissoa guerini.*

(8–9) egg-capsule laid in bowl, (8) newly laid with eggs, capsule 0·96 mm. across ; (9) empty capsule showing hole from which the larvæ have emerged, capsule 0·14 mm. across ; (10) newly hatched larva from egg, shell 0·16 mm. across ; (11–12) slightly older veligers, reared from egg ; (13) young shell from red weed, crawling ; (14) half-grown shell.

FIGS. 15–18.—*Cingula semistriata.*

(15) egg-capsules laid in bowl, 0·64 mm. across ; (16–17) newly hatched larva from egg, shell 0·10 mm. across ; (18) apex of adult shell.

FIGS. 19–24.—*Cingula semicostata.*

(19) egg-capsules laid in glass jar, 0·48 mm. across ; (20) young newly hatched, shells 0·30 mm. across ; (21) slightly older shells ; (22) apex af half-grown shell ; (23) apex of adult shell ; (24) young shell much enlarged.

RISSOA PARVA (DA COSTA).

(Plate III, Figs. 1–7).

The commonest of all the rissoids, occurring abundantly between tidemarks and below on all parts of the coast, laying eggs on seaweeds where it lives. Pelseneer (1911) states that its spawn is abundant in spring and summer on red algæ (*Callithamnium*, *Griffithsia*, etc.) on the Brittany coast, capsules about 1 mm. in diameter, transparent and colourless, and contain from 6 to 35 eggs. Near Plymouth it lays eggs on both brown and green weeds, especially in the rock pools exposed at spring tides, where it is present in huge numbers, both the type and the var. *interrupta*. It appears to breed most of the year but chiefly in spring and summer, Veliger is usually to be found in the plankton, attaining 3 to 3½ whorls before losing velum. Specimens in bowls laid eggs on Zostera, December 4th. Capsules similar to those of *R. membranacea* but much smaller and higher in proportion to the width. Diameter 0·64 mm., height 0·30 mm., containing from 20 to 50 eggs, about 0·09 mm. across (Plate III, Fig. 1). All the eggs hatched out in about 10 days. Larva very like *R. membranacea* but smaller, 0·13 mm. across shell when newly hatched (Plate III, Figs. 2–3) with 1½ whorls, colourless, transparent, without sculpture. Velum colourless, about 0·13 mm. across. Eyes, otocysts, mouth and foot well developed but no front process to foot at first. Veliger alters little but grows quickly, foot becoming brownish and later having the dark purplish brown markings at junction with body on each side, velum remaining colourless but growing large, more than twice width of shell; body whorl (third) of late larva with fine line round periphery. Shell now 0·48 mm. long. Animal can now swim or crawl (Plate III, Figs. 5–6). Velum disappears and little Rissoa is like adult except for colouring which begins to be a pale horn-colour and even on third whorl at top of outer aperture on outside is a faint indication of the brown falciform mark separating this species from all others.

RISSOA GUERINI RÉCLUZ.

(Plate III, Figs. 8–14).

Fairly common round Plymouth coast among weeds at extreme low water and below, chiefly off Drake's Island in Sound. One specimen in bowl laid 2 egg-capsules on February 16th on Zostera. Later on the same animal laid several more capsules on the sides of the bowl, through February, March and April. First capsule 0·96 mm. across, 0·16 mm. high (Plate III, Fig. 8), thin-walled, colourless and transparent, containing about 80 eggs, 0·09 mm. across. Some of the later capsules are larger, 1·1 mm. across, with a broad margin making the whole 1·4 mm. (Plate III,

Fig. 9). The larvæ escaped in 10 days leaving a large hole at the top of the capsule and swam away as veligers. Larval shell 0·16 mm. across when newly hatched with about 1½ whorls, colourless, transparent, without sculpture; animal and velum also colourless at first, velum 1·2 mm. across (Plate III, Fig. 10). Shell rather more compact than *R. membranacea* and *R. parva*, slightly smaller. In a few days velum becomes characteristically spotted with dark brown (Plate III, Figs. 11, 12), spots also on body, 2 on each of velar lobes, one in centre between eyes, one in centre at base of foot and brown pigment round mouth. Veligers in this stage occur in plankton and also later stages in which colour has increased; foot yellowish brown with dark spots, velum bordered with brown spots more or less irregular. As soon as pigment appears, larva easy to distinguish. Metamorphosis when there are about 3 to 3½ whorls; no pattern on shell until about 5th whorl which suddenly enlarges and has brown spots round periphery (Plate III, Fig. 14).

RISSOA INCONSPICUA ALDER.

(Plate IV, Figs. 13–15.)

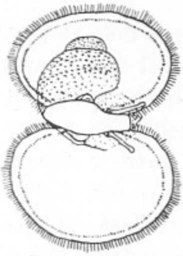
Fairly common on sandy gravel in parts of Sound, and among weeds, close to coast or beyond. Jeffreys (1867) has recorded it as common in trawl refuse at Plymouth but in those days this was brought close inshore, a practice now discontinued. It is still to be found sometimes in trawl waste and later stages just metamorphosed are sometimes in tow-nets from both inside and outside Sound. Most frequent off White Patch, on east of Sound, close to shore, beyond low-water mark. Adults from here laid eggs in bowls on Zostera and also on one another and on pieces of debris. Egg-capsules small, 0·48 mm. to 0·64 mm. across, sometimes smaller, about 0·12 mm. high, clear and colourless, containing about 6–9 eggs, 0·08 mm. across when newly laid. Young hatch as veligers in 10 days; shell smooth, unsculptured, about 0·10 mm. across; velum colourless at first, about 0·10 mm. across; foot, eyes, otocysts and tentacles all present. Velum later bordered with brown; older larvæ with two faint spiral lines round body whorl. These are common in early autumn. Newly metamorphosed shells have the purple apex characteristic of the adult, but there is no sculpture on the first 3 whorls except a slight spiral broken line just above periphery of third whorl.

RISSOA SARSII ALDER.

(Plate I, Figs. 1–16; Plate II, Figs. 1–5.)

Eaten when very small by young herrings (see page 523). Larvæ recognised in egg-capsules from which veligers were hatched. Later

PLATE IV.



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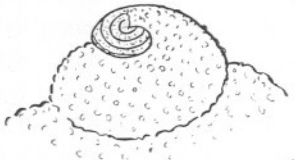

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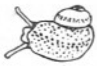

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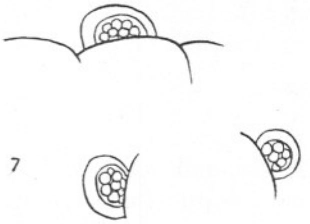

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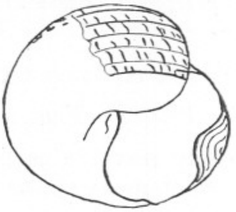

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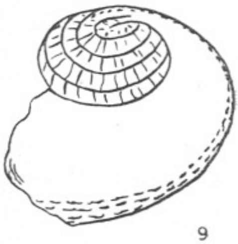

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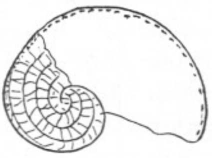

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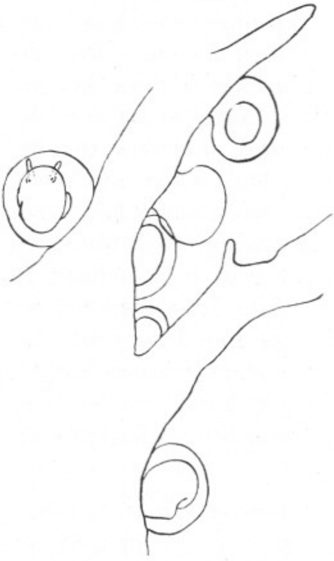

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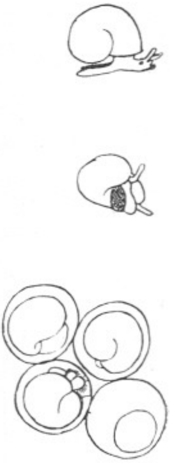

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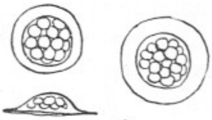

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larvæ from plankton reared in plunger-jars until species was distinguishable. One grew to adult size, several were three-parts grown. Egg-capsule planktonic, not unlike that of *Littorina littorea* but differs in shape, and size. Colourless, transparent and somewhat disc-shaped, it is rather more convex on one surface than on the other, and slightly indented near the margin, 0·18 mm. across, 0·08 mm. high ; contains only one egg, about 0·08 mm. across, situated in the centre of capsule with large space as broad as itself surrounding it (Plate I, Figs. 2–6). Before larva is hatched it shows characteristic sculpture of the shell consisting of longitudinal striations with small dots in between. When hatched shell measures 0·08 mm. across, growing quickly to 0·16 mm. with one and a half whorls after which the spiral sculpture ceases and just above and below periphery a series of dots forms an irregular spiral band leaving upper and under surface smooth except round the incipient umbilicus where are a few dotted striæ (Plate I, Figs. 7–15). Whilst the larva is still very small with hardly more than the whorls having dotted striæ it is eaten by the young herring (Plate I, Fig. 1). Shell colourless and transparent, soon assuming a pale horn-colour, aperture dark brown. Animal and velum typically rissoid in shape. Velum gradually becoming bordered with a fine brown band just inside the outer row of cilia, sometimes absent on one side. Characteristic sculpture easily seen when shell has about 3 or 3½ whorls, measuring 0·48 mm. high. Animal yellowish with a dark mass at origin of foot, purple streak on foot which is bluntly pointed and with a very flexible fore part. Tentacles long and contractile, mantle tentacle and hind tentacle above foot present, the latter very long. Larva is now ready to metamorphose and can both swim and crawl and soon loses velum (Plate I, Figs. 16–21 ; Plate II, Fig. 1). Just before it loses velum it is extremely common in the Plymouth plankton, both inside and outside Sound, especially inside, from early to late spring, hardly any being left in summer. Floating egg-capsules chiefly in late autumn and winter ;

PLATE IV.

Alvania punctura, *Rissoa inconspicua*, unknown rissoid, *Barleeia unifasciata*.

(Figs. 1, 4 scale C ; 2, 3, 6,7, 11–13, 15 scale A ; 5, 8–10 scale B.)

FIGS. 1–7.—*Alvania punctura*.

(1, 2, 4) late veligers, shell 0·50 to 0·64 mm. high ; (5) apex of same enlarged ; (3) larva crawling, having lost velum ; (6) apex of adult shell ; (7) egg-capsules laid on shells of neighbours in bowl, capsules 0·32–0·48 mm. across.

FIGS. 8–10.—Shells of unknown rissoid larvæ, 0·20 to 0·25 mm. across.

FIGS. 11–12.—Egg-capsules and larvæ of *Barleeia unifasciata*, laid in bowl on weed, capsules 0·56 mm. across.

FIGS. 13–15.—*Rissoa inconspicua*.

(13) egg capsules laid in bowl, 0·48 to 0·64 mm. across ; (14) Newly hatched larva from egg, shell 0·10 mm. across ; (15) Apex of adult.

young larvæ very abundant in plankton from December to February and March. Late larvæ (Plate II, Figs. 2–5) attained 6 whorls in 4 months, the adult having 7 whorls. Probably they become mature within a year. Older shells usually with brown streaks on fourth whorl running from suture, generally broken at periphery, often a brown line below last whorl, beginning at the sixth, shell sometimes clear brown without streaks. Animal with deep brown opercular lobes, very long light tentacles and processes.

Rissoa sarsii is not very well known. It was described by Lovén in 1864 from specimens found by Sars at Bergen. It is the *Rissoa inconspicua* var. *tenuis* of Forbes and Hanley (Plate LXXXII, Figs. 7–8) and the *Rissoa albella* var. *sarsii* of Jeffreys (1867). Alder found it at Rothesay a little below low-water mark and describes the animal but makes no reference to the long tentacles and posterior process (Forbes and Hanley, 1853). The only specimen reaching the adult stage at Plymouth was a brown variety having streaks only on upper whorls, last whorl with 2 dark bands above and one below periphery. Seven whorls; animal yellowish white, slightly spotted on head with brown; opercular lobes dark brown, tentacles and posterior processes light and very long. Outer lip of this specimen abnormally produced in an outstanding rib. Length 3 mm.

CINGULA SEMISTRIATA (MONTAGU).

(Plate III, Figs. 15–18.)

A very common rissoid, occurring between tide marks and below, on weeds, hydroids, bryozoa and stones. Laid eggs in bowl on Zostera in June. Similar capsules on weeds through summer. The fixed capsules of typical form but smaller and higher in proportion to diameter than *Rissoa membranacea*, *R. parva* and *R. guerini*, 0·56 mm. to 0·64 mm. across, 0·24 mm. high, colourless and transparent (Plate III, Fig. 15). Eggs usually from 12 to 22, about 0·08 mm. across. Newly hatched larva 0·10 mm. across shell (Plate III, Figs. 16–17) with rather more than one whorl, no sculpture, animal and velum colourless (Plate III, Fig. 16). Later stages only recognised in plankton when nearly ready to metamorphose when there are 2 conspicuous lines below suture as in adult (Plate III, Fig. 18); velum always colourless; 3 processes behind operculum.

CINGULA SEMICOSTATA (MONTAGU).

(Plate III, Figs. 19–24.)

Very common at Plymouth under stones between tide marks and in muddy gravel among stones further out. Eggs laid singly in jars standing in running water with gravel and small stones, in single capsules, sometimes one or two together adhering to small particles, March to May.

Unlike the usual rissoid capsules this is oval, very tough and thick-walled, 0·48 to 0·64 mm. by 0·32 to 0·48 mm., usually fixed by the centre of one side (Plate III, Fig. 19). Egg enclosed in membrane, 0·24 mm. across when newly laid; velum formed within capsule and reaching a width of 0·48 mm.; shell 0·32 mm. across; eyes and short tentacles present and a lobe in front of eyes; foot bluntly pointed; shell faintly but quite perceptibly striated longitudinally, the striæ formed by minute dots, sometimes irregular and rough, velum gradually disappears and before hatching is lost, the animal breaking out of the capsule in the crawling stage (Plate III, Figs. 20, 21). It can easily be recognised by its likeness to the adult and is present with these at various times of year. Both shell and animal creamy white.

ALVANIA PUNCTURA (MONTAGU).

(Plate IV, Figs. 1–7.)

Very common on the outside dredging and trawling grounds, rarely nearer the coast. Obtained alive from trawl and dredging refuse. Larvæ abundant in summer and early autumn in tow-nettings usually from outside. Egg-capsules laid in bowl on the shells of one another, small and thick-walled, 0·32 to 0·48 m.m. across, rather higher than most rissoid capsules but some are typically lens-shaped. Each contains about 12–14 eggs, 0·06 mm. across (Plate IV, Fig. 7). Young from these eggs did not hatch out but minute larvæ, evidently newly hatched, are very common in summer plankton which obviously belong to this species. It is easy to recognise them for they have at first the same sculpture on the apex as *Rissoa sarsii*, but the part striated with spots is smaller than in that species, 0·05 mm. across, and after this there are small raised spots on the whorls giving the shell a peculiar papillate appearance. As the larva grows the velum enlarges but is always colourless, animal yellowish white with a little brown, shell becoming a dark horn-colour. Breadth of velum in last stages more than twice length of shell (Plate IV, Fig. 1). Apical whorls of adult which constitute the larval shell are clearly seen (about $3\frac{1}{2}$) after which the adult sculpture begins (Plate IV, Fig. 6). Larval shell about to metamorphose 0·64 mm. long. Those kept in plunger-jars grew into adults.

BARLEEIA UNIFASCIATA (MONTAGU).

(Plate IV, Figs. 11, 12.)

Exceedingly common on weeds at extreme low tide in rock pools, Wembury, living on Fucus or *Calliplepharis jubata*, often with *Rissoa parva*. Unlike *R. parva* the eggs are laid singly in round capsules on the weed, adhering by only a small portion, and the velum is lost before hatching. Laid egg-capsules in the Laboratory on *Calliplepharis*, May 29th (Plate IV, Fig. 11), 0·56 mm. across, more or less round, egg 0·32 mm. across, develops into pale brown shell turning to dark brown, with small velum which soon disappears and red operculum. Shell 0·42 to 0·48 mm. across with 1½ whorls, smooth and without sculpture, apex very blunt, much blunter than any rissoid known. At this size the animal hatches without a velum and crawls about. Many are to be seen on the weed with adults and young of all sizes. No posterior and no mantle tentacle. Barleeia seems to be further removed from a true Rissoa than any of the other genera now placed in the family.

Several other larvæ which resemble rissoids in shape, and almost certainly belong to this family, are to be seen in the Plymouth plankton but have not yet been identified. Among these is one with a sculptured apex with spiral striæ divided up by lines (Plate IV, Figs. 8–10). After 1½ whorls the sculpture is irregular dot-like markings in a few lines round periphery, animal pale yellowish with large colourless velum. This is so much like *Rissoa sarsii* and *Alvania punctura* that there is probably some relationship. It occurs with the latter usually outside the Sound in summer.

The following species occurring alive near Plymouth have not yet had their eggs and larvæ identified : *Cingula fulgida*, *C. alderi*, *C. cingillus* and *Alvania crassa*, although the adults of all but *C. alderi* are common round our coasts.

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The Eggs and Larvæ of some British Turridæ.

By

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With Plates I–IV.

In a previous paper (Lebour, 1933) the eggs and larvæ of *Philbertia* (*Comarmondia*) *gracilis* were described, showing lens-shaped sessile egg-capsules and a planktonic larva with elaborately sculptured shell and large brightly spotted velum, which remained as a veliger until it had attained several whorls and was of a large size before metamorphosis. Lens-shaped capsules are apparently typical of the group (Jeffreys, 1867, and observations at Plymouth) and finely sculptured embryonic shells with several whorls are already known in many species (Jeffreys, 1867; Cossmann, 1895; Thiele, 1929). Researches in the Plymouth plankton show that members of this family are common and are some of the largest and most conspicuous gastropod larvæ. They are therefore of considerable economic importance in the sea.

Winckworth (1932) in his recent list of British Marine Mollusca recognises six genera in the Turridæ. Of these four occur at Plymouth: *Hædropleura*, *Lora*, *Mangelia* and *Philbertia*. Lora (*L. rufa*) has only been seen at Plymouth as a dead shell; Hædropleura (*H. septangularis*) has only been obtained once alive at Plymouth, but three species of Mangelia (*M. attenuata*, *M. nebula* and *M. coarctata*) and six species (all the British species known) of Philbertia occur, some of which are common. Winckworth recognises the sub-genus *Bela* in Mangelia to which both the common species of Mangelia belong (*M. nebula* and *M. coarctata*) and three sub-genera of Philbertia: *Comarmondia*, *Philbertia* and *Teres*. *Philbertia gracilis* belongs to the sub-genus Comarmondia and is fairly common, usually on the outside dredging grounds, alive; *Philbertia teres* is the only species belonging to the sub-genus Teres and has not yet been obtained alive at Plymouth, dead shells occasionally occurring in the shell gravel of the Eddystone Grounds; the sub-genus Philbertia contains *Philbertia leufroyi*, *P. purpurea*, *P. asperrima* and *P. linearis*. *Philbertia purpurea* has occasionally been found alive from low water to 5 fathoms (Mar. Biol. Assoc., 1931); *P. asperrima* is dredged sometimes in the Sound; *P. leufroyi* is fairly common in the outside waters and *P. linearis* is the commonest of all, occurring both in the Sound and outside but most commonly near the coast.

The turrids may be divided into two groups by the embryonic shell and these coincide with Hædropleura, Lora and Mangelia on the one hand, which have a smooth apex, and Philbertia on the other, the species of which have a sculptured apex. Hædropleura and Lora are operculated whilst Mangelia and Philbertia have no operculum in the adult, the larva shedding this on metamorphosis.

Sculptured apices in the species of Philbertia are already known as mentioned above, but the existing descriptions are not always altogether accurate, the fossil species frequently being described with the top whorls smooth when in the living form of the same species they are seen to be reticulated. This is not to be wondered at when one realises that the sculpture may wear away very soon. Tiele (1929) describes the top whorls of Philbertia as spirally sculptured when really it is usually reticulated but in a different way from the following embryonic whorls: Comarmondia, however, has minute flecks instead of reticulations on the top whorl. Mr. Dennis Curry has kindly sent me some specimens of turrids from the Barton Beds whose apices are very similar to the recent species *Philbertia linearis*, *P. leufroyi*, *P. purpurea*, *P. asperrima* and *P. teres*, and one which somewhat resembles that of *Mangelia coarctata*. In his book on shells of Port Alfred, South Africa, Colonel Turton (1933) figures and describes as a new species of Trophon (*T. ornatus*, Plate XVIII, Fig. 544) a shell which is almost certainly the young of a turrid of the Philbertia type with a similar sculpture. It is evident that the sculpture of the embryonic whorls of the Philbertias is an ancient character and one which is world-wide in distribution and we have in it a clear guide to the affinities of those shells which possess such markings.

The embryonic whorls of all the turrids show plainly on the adult shells and those of the Philbertias (excluding *P. gracilis*) are so much alike that it is difficult to see any differences at all. On very close examination, however, although the markings are all of the same type, it is seen that the number of embryonic whorls varies slightly with the species, the whorls may be different in breadth, the colour may be different and the quality of the markings may be more or less distinct. Larval shells of this Philbertia type are common in the plankton in spring and summer; only very occasionally in autumn and winter. They occur both in the inshore and outside plankton. Most of them belong to *Philbertia linearis*, but those of *P. leufroyi* can be recognised, and, probably, those belonging to *P. asperrima*. *P. purpurea* and *P. teres* have not been seen as larval forms. In all the Philbertias the embryonic shell is brown or more or less a dark horn-colour. The following is the sculpture in all the typical Philbertias, e.g. *P. linearis*, *P. leufroyi*, *P. asperrima* and *P. purpurea*;

also of *P. teres* : the first whorl or whorl and a half is reticulated (Plate III, Fig. 2), the reticulations being formed by raised spiral striæ and straight striae crossing them at right angles, the points where the striæ meet appearing as slight prominences ; the reticulations are thus straight up and down. Suddenly at about the second half of the second whorl the sculpture changes, a series of raised lines running out from the suture and from there oblique reticulations originate ; as Jeffreys puts it, " like the meshes of a fire-guard " (Plate III, Fig. 3). Here again, where the meshes cross there are raised points. The reticulations are now oblique instead of straight, and they run nearly to the base of the shell where spiral striæ are seen. The third and fourth whorls are carinated and the fifth also in those species which possess more than four embryonic whorls. Below the periphery the reticulations are not so regular, but spiral lines with flecks and smaller reticulations take their place (Plate III, Figs. 6–7 ; Plate IV, Fig. 1). On the last embryonic whorl, third, fourth or fifth, as the case may be, there are three spiral ridges forming the carinations which end in a broad rounded process curving inwards on the outside of the shell aperture and supporting the velum (Plate IV, Figs. 2–3). *Philbertia teres* has the longest embryonic shell (Plate IV, Fig. 11), consisting of 5 to 5½ whorls ; *P. linearis* and *P. asperrima* coming next (Plate IV, Figs. 7, 9) with 4 to 4½ whorls ; *P. leufroyi* (Plate IV, Fig. 8) with 3½ ; *P. purpurea* (Plate IV, Fig. 10) with 3. The embryonic sculpture ends with the loss of the velum, the shell afterwards taking on the adult pattern and losing the operculum (Plate IV, Figs. 4, 5). The animal in all the larvæ known is almost or completely colourless, very rarely with grey or pinkish in parts. The velum is spotted with orange in *Mangelia nebula* and *Philbertia gracilis*, but in all the true Philbertias known it is colourless. At first bilobed, the velum may grow to a large size and in the older larvæ has four lobes, in *Mangelia nebula* being capable of covering both shell and animal like a true veil ; in *Philbertia gracilis* the lobes are very long and narrow, and in the Philbertias proper they are large and broad. Two more larvæ have been seen in the Plymouth plankton which have not yet been attributed to any species. It is very probable that they belong to the smooth-topped turrids. Both have a large and conspicuous velum, with brown or orange colouring.

Description of the Eggs and Larvæ of the Plymouth Planktonic Forms.

Family **TURRIDÆ.**

The eggs and larvæ have been seen at Plymouth in *Mangelia nebula*, *Philbertia gracilis* and *Philbertia linearis ;* the larvæ hatched out from the egg in the first and second and the later larvæ from the plankton

PLATE I.

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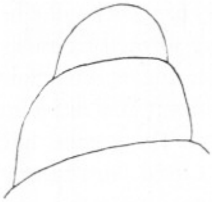

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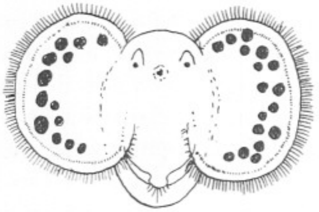

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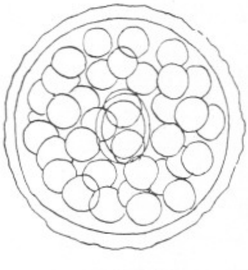

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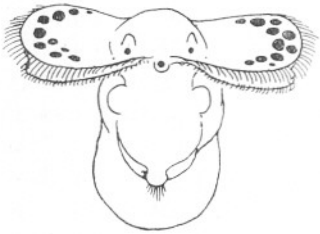

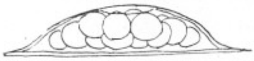

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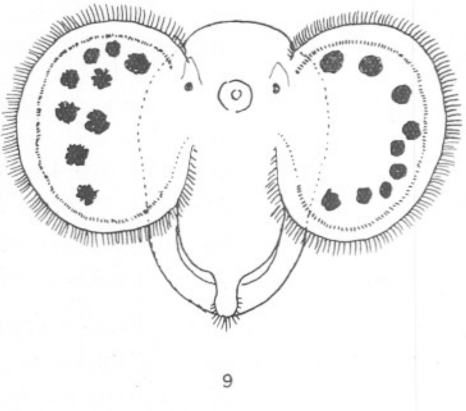

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in all three were reared until metamorphosis. The life-history of *Philbertia gracilis* has already been described (Lebour, 1933), those of *Mangelia nebula* and *Philbertia linearis* are described here for the first time. The eggs of the other species are not known, but the larvæ of *Philbertia leufroyi* and *P. asperrima* have been recognised in the plankton. The two last are so like those of *P. linearis* that a separate description is unnecessary.

In order to obtain the eggs the adults were kept in plunger-jars. It was difficult at first to keep them alive for long because the natural food was not known. The radula which consists of few long pointed teeth suggests carnivores of a predatory type. Most of the species naturally live on shelly or sandy gravel where numerous worms or foraminifera abound. Apparently they do not eat the latter which lived and multiplied quite happily in the same aquarium as the turrids, but it seems very likely that they eat small worms, for the one specimen of *Hædropleura septangularis* and several *Philbertia linearis* have lived for some months in a plunger-jar with brown deposits of some alga which harbours small worms and infusoria in abundance.

Genus HÆDROPLEURA.

Hædropleura septangularis (Montagu), (Plate I, Fig. 1). Only one specimen has been seen alive from Plymouth, dredged in the Sound. Apex smooth for 2½ whorls, the third whorl with fairly close ribs. Eggs and larvæ not known.

Genus LORA.

Lora rufa v. *ulideana* (Thompson), (Plate I, Fig. 2), dead shell only, found in outside dredgings, Eddystone Grounds. Smooth rounded apex,

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EXPLANATION OF PLATES.

(Scale B is 3 times the scale of A.)

PLATE I.

(Figs. 1–7 scale A, 8–9 scale B.)

FIG. 1.—Apex of adult *Hædropleura septangularis*

FIG. 2.—Apex of adult *Lora rufa*.

FIG. 3.—Apex of adult *Mangelia nebula*.

FIG. 4.—Apex of half-grown *Mangelia nebula*.

FIG. 5.—Apex of adult *Mangelia coarctata*.

FIG. 6.—Egg-capsules of *Mangelia nebula* laid in plunger-jar, 1·6 mm. across.

FIG. 7.—Egg-capsules of *Mangelia nebula* laid on siphon of Lutraria, 1·76 mm. across.

FIG. 8.—Newly hatched larvæ of *Mangelia nebula* from eggs in plunger-jar, shell 0·23 mm. across.

FIG. 9.—Newly hatched larva of *Mangelia nebula* from egg-capsule on *Lutraria* siphon, shell 0·30 mm. across.

PLATE II.


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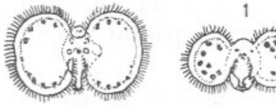
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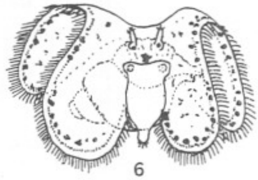
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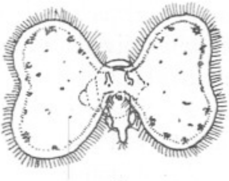
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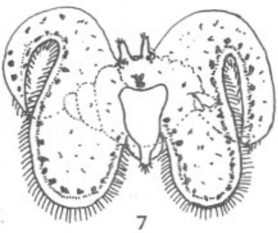
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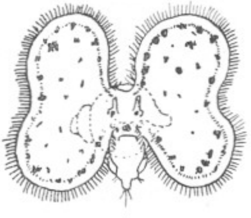
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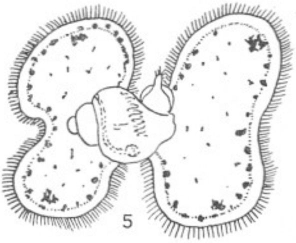
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very broad, of about 2 whorls, the extreme top hidden. Eggs and larvæ not known.

Genus MANGELIA.

Mangelia attenuata (Montagu). Although this species is recorded from Plymouth in the Fauna List it has not been seen recently.

Sub-genus **BELA**.

Mangelia coarctata (Forbes). (Plate I, Fig. 5).

This species occurs in the Sound, off Drake's Island, dredged in sandy gravel and is not uncommon. The first 2½ whorls are smooth, the third with close ribs with striæ in between. Eggs and larvæ not known.

Mangelia nebula (Montagu), (Plate I, Figs. 3, 4, 6–9; Plate II, Figs. 1–11).

This species is recorded only from one locality in the Plymouth Fauna list but it is in reality very common and frequently dredged in the Sound, especially in Cawsand Bay and off the White Patch, on the east side of the Sound. More rarely it is found further out. The adult which is a reddish brown colour has a smooth apex, at about the third whorl tending to be tuberculated (Plate I, Figs. 3–4), after which the adult sculpture begins. An adult kept in a plunger-jar laid one egg-capsule, the only one after repeated attempts at keeping the animals which lived for some time in various plunger-jars but never laid any more eggs. Mr. G. A. Steven, however, found some eggs on the dredged severed siphon of a lamellibranch, probably Lutraria, which agreed with those obtained from the mollusc itself in the plunger-jar, and the young which were hatched out were similar. The only difference was in the size, the capsules on Lutraria being larger and the newly hatched larvæ also larger. The larvæ are so peculiar and characteristic that there can be no doubt that they both belong to *Mangelia nebula*. Later larvæ in the plankton were identified as the same mollusc and by keeping these until metamorphosis it was proved that they were *Mangelia nebula*.

PLATE II.

(Scale A) *Mangelia nebula*.

FIG. 1.—Newly hatched larvæ from *Lutraria* siphon.

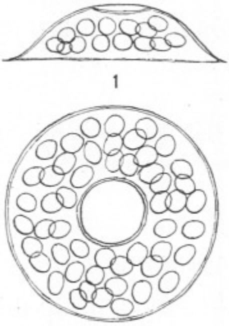
FIG. 2.—The same, 2 days old.

FIGS. 3–9.—Larvæ from plankton.
(3) shell 0·46 mm. long; (4) shell 0·76 mm. long; (5) shell 0·80 mm. long; (6) shell 0·90 mm. long; (7) shell 0·96 mm. long; (8) shell 0·90 mm. long; beginning to lose velum; (9) empty shell.

FIG. 10.—Metamorphosed larva, shell 1·12 mm. long.

FIG. 11.—Front of same.

PLATE III.



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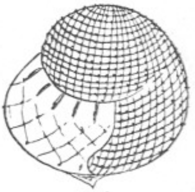

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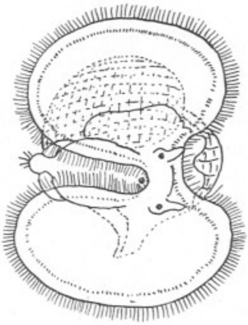

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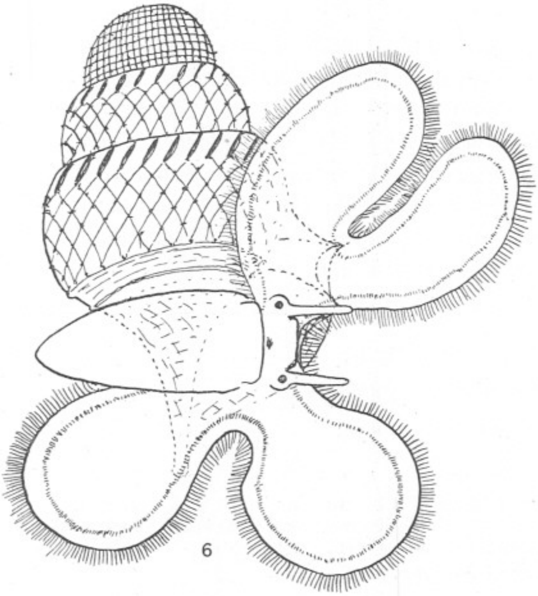

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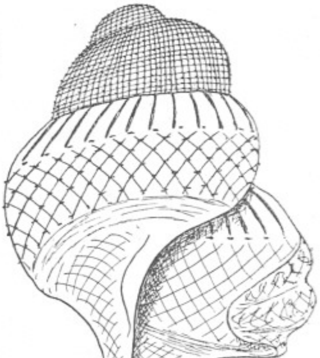

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The egg-capsules (Plate I, Fig. 6) are smooth and transparent, lens-shaped and attached by the under flat surface, the upper surface rounded with a thin part in the centre where a hole is formed when the larvæ are ready to emerge. Diameter of capsule laid in plunger-jar, 30.1.33, 1·6 mm., height 0·32 mm.; diameter of capsules laid on Lutraria siphon, 18.5.31, 1·76 mm. The eggs when newly laid measured about 0·16 mm. across. There were about 60 opaque eggs in the capsule laid in the plunger-jar; fewer in those from the siphon which were further advanced (Plate I, Fig. 7). Later on (14.2.33) the larvæ nearly ready to hatch were dying in the capsule and were removed to a fresh plunger-jar in which several veligers hatched out but did not grow and soon died. The newly hatched larva (Plate I, Figs. 8–9; Plate II, Fig. 1) is very peculiar. The shell measures about 0·23 mm. across in those from the eggs laid in the plunger-jar; the foot is short with a rounded ciliated lobe behind; in front of the eyes is a rounded prominence; the tentacles short. The velum is bilobed, having large rounded lobes with the usual cilia and measuring 0·4 mm. across or more, ornamented on each side with several large and conspicuous brilliant orange spots. The spots may vary in number and arrangement, about 9 to 12 being usual. Those hatched from the siphon of Lutraria were larger, the shell about 0·3 mm. across and the velum about 0·64 mm. across, but the larvæ were in other respects exactly alike. Those from the siphon lived for a few days and grew, showing a posterior siphon on the shell and the posterior knob of the foot long (Plate II, Fig. 2). Young larvæ were found in the plankton slightly older than this and through the spring and summer later larvæ were common in the tow-nettings both in the Sound and outside, but especially rather close to the coast. The largest numbers occurred from May to September, but specimens were seen also in early autumn. Very young metamorphosed forms were dredged in October and November. As the larva grows the spots on the velum increase and tend to form a border, but they are also irregularly scattered on the surface and sometimes the pigment congregates as a mass at the outer corner of each lobe. The shell is clear, transparent and colourless for about three whorls when it measures about 0·70 mm. in length, the apex slightly oblique, the posterior canal conspicuous; eyes and tentacles well developed; foot with three ciliated

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PLATE III.

(Fig. 1 scale A, Figs. 2–7 scale B.)

FIG. 1.—Eggs of *Philbertia linearis* laid in plunger-jar, 1·5 mm. across.

FIGS. 2.—Very young larval shell of *Philbertia linearis* from plankton, 0·19 mm. across.

FIG. 3.—Shell of *Philbertia linearis* slightly older, from plankton.

FIGS. 4–6.—Later veligers of *Philbertia linearis* from plankton.

FIG. 7.—Shell of *Philbertia leufroyi*, late larva, from plankton.

lobes posteriorly, the median lobe long and projecting beyond the foot. As the animal grows the front of the foot grows beyond the mouth. The velum tends to be four-lobed and grows very large, the breadth being more than three times the length of the shell and in the later stages being held over the shell and animal so that they are completely covered. Thus it swims covered over with a true veil. The shell 0·96 to 1 mm. long, has now $3\frac{1}{2}$ to 4 whorls and the animal is nearly ready to metamorphose. The shell and animal siphon are conspicuous, the eyes on short tentacles showing the adult form, the foot with the lobes dwindling and finally absent. The fourth whorl is now showing a tuberculated appearance, or even the third whorl may show this (Plate II, Figs. 7–9). Near the aperture there may be spiral striæ. The velum then dwindles, the operculum is shed and the animal crawls (Plate I, Fig. 10), becoming like a miniature adult. The front of the foot is almost square, the base a light grey, otherwise the animal is colourless. It is quite easy to recognise all these stages including the young crawling mollusc.

Genus PHILBERTIA.

Sub-genus **COMARMONDIA**.

Philbertia gracilis (Montagu). (Plate IV, Fig. 6).

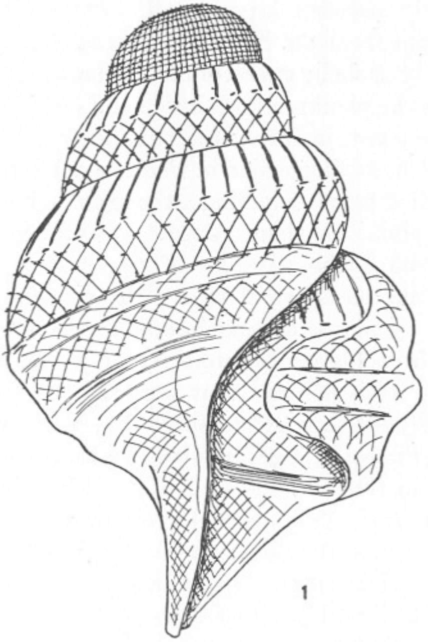
The egg-capsule and larvæ of this species have already been described. Egg-capsules lens-shaped with reticulations on the upper surface. In 1933 a further supply of egg-capsules was obtained in a plunger-jar, April–March, and the larvæ hatched out more successfully. These showed that all the larvæ developed and hatched in a very late stage of development with a long shell siphon and deeply coloured velum. It is thus abnormal for any to be eaten by the others and it is not a case of "nurse" eggs as was at first thought. The top whorls are flecked but not spirally striated and the later whorls conspicuously keeled and marked with oblique striæ. The larva grows to a large size in the plankton, the later stages having four very long velar lobes with orange spots. Both shell sculpture and velum are quite unlike the true Philbertias. The sub-genus should probably be raised to a genus.

Sub-genus **PHILBERTIA**.

Philbertia linearis (Montagu), (Plate III, Figs. 1–6; Plate IV, Figs. 3, 5, 7).

Jeffreys has described the egg-capsules and newly hatched larvæ of this species (as *Defrancia*), but the measurement of the capsule and number of eggs do not agree with the Plymouth specimen. He has also noticed the sculpture on the newly hatched larval shell. *Philbertia linearis* is fairly common in dredgings from the Sound and occasionally occurs on the outside grounds on sandy or shelly gravel or in hard-branched Bryozoa. The larvæ are common in the plankton both inside and outside the Sound, but particularly near the coast, in spring and summer, rarely in autumn. Egg-capsules were laid in a plunger-jar in February, 1932, and through March, but the larvæ died before hatching although moving about and possessing a shell and velum. A single capsule was laid by another individual in January, 1933. The capsules of the first lot measured 1·5 mm. across, the second measured 2 mm. The capsules described by Jeffreys measured $\frac{1}{5}$ inch across and contained 200 to 300 eggs whilst the eggs in the first lot from Plymouth numbered only about 60 and in the second lot about 80. It is possible that there was some mistake in Jeffreys' species. The Plymouth eggs measured 0·14 mm. to 0·15 mm. across The egg-capsule (Plate III, Fig. 1) is lens-shaped, like that of *Mangelia nebula*, and has no reticulations similar to *Philbertia gracilis*. It is colourless and transparent. Very young larvæ were found in the plankton and also all stages up to the latest larvæ which metamorphosed into *Philbertia linearis*. The earliest free-swimming larvæ (Plate III, Fig. 2) were seen in February and various stages were found throughout the spring and summer, dwindling in early autumn and absent in December and January. All the larvæ, even those quite newly hatched, have a dark brown shell with conspicuous straight reticulations, as described above. The velum is colourless, at first bilobed, then larger and slightly indented at the sides to form four blunt lobes. It has the usual cilia round the edge. Eyes and tentacles conspicuous. The rest of the animal is colourless, the foot at first short with a small knob posteriorly; round thin operculum; mouth showing in front; later the foot is pointed behind and the front part covers the mouth. The youngest larva seen measures about 0·19 mm. across the shell and has one whorl and a half; the outer lip produced for support of the velum. Very soon the oblique striations begin and the shell canal is formed (Plate III, Fig. 3). Later, the shell being about 0·44 mm. long with a conspicuous canal, there are $2\frac{1}{2}$ whorls and the velum is beginning to be four-lobed (Plate III, Fig. 5). The foot at this stage is bluntly pointed and the tentacles well developed. When the shell is about 0·52 to 0·80 mm. long there are $3\frac{1}{2}$ to 4 whorls, the velum is much larger and may project some way beyond the shell, the siphon projects from the shell siphon and the foot is like the adult. It is now nearly ready to metamorphose and when the shell has $4\frac{1}{2}$ whorls and measures about 0·96 mm. the animal can crawl as well as swim and very soon loses the velum and operculum, and the adult sculpture begins. This species must remain a long time as a veliger and is one of the common forms in the Plymouth plankton.

PLATE IV.



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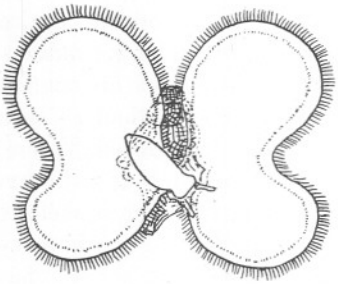

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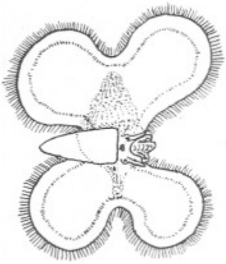

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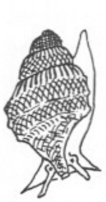

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Philbertia leufroyi (Smith), (Plate III, Fig. 7, Plate IV, Figs. 2, 4, 8).

Although the species is not recorded in the Plymouth Fauna list it is not uncommon in the outside dredging grounds and has probably been confused with *P. linearis* which it closely resembles. It is, however, broader and larger and more speckled with brown instead of having brown lines. The apex is very like that of *P. linearis* but with fewer whorls (Plate IV, Fig. 8) and broader, therefore by measurement the larval shells may be distinguished and as the veliger has fewer whorls for its size than *P. linearis* it may be distinguished in the later stages. The velum in the late stage is larger than in *P. linearis*, but the animals are very similar. There are 3½ whorls in the embryonic shell of *P. leufroyi* and they may be of a pinkish brown to deeper brown. Jeffreys has noticed the reticulations on the whorls. No egg-capsules were seen, but the breeding season appears to be in spring and summer and the larvæ are seen together with those of *P. linearis* or separate.

Philbertia asperrima (Brown), (Plate IV, Fig. 9).

Jeffreys noticed the sculpture on the embryonic whorls of this species. It is occasionally dredged in the Sound and outside but is not common. The larvæ are very like those of *P. linearis* and *P. leufroyi*, the animal being slightly grey on the body and foot. There are 4½ whorls as in *P. linearis* but the spire is rather longer and the markings are much more irregular, the colour being lighter. These larvæ are not at all common and are very difficult to distinguish from *P. linearis*. They occur in summer. No egg-capsules have been found.

PLATE IV.

(Fig. 1 scale B, Figs. 2–11 scale A.)

FIG. 1.—Late larval shell of *Philbertia leufroyi*, nearly ready to metamorphose, from plankton.

FIG. 2.—Late veliger of *Philbertia leufroyi*, just before metamorphosis, from plankton.

FIG. 3.—Late veliger ef *Philbertia linearis* not quite ready to metamorphose, from plankton.

FIG. 4.—*Philbertia leufroyi*, metamorphosed in plunger-jar.

FIG. 5.—*Philbertia linearis* metamorphosed in plunger-jar.

FIG. 6.—Apex of adult *Philbertia gracilis*.

FIG. 7.—Apex of adult *Philbertia linearis*.

FIG. 8.—Apex of adult *Philbertia leufroyi*.

FIG. 9.—Apex of adult *Philbertia asperrima*.

FIG. 10.—Apex of adult *Philbertia purpurea*.

FIG. 11.—Apex of adult *Philbertia teres*.

Philbertia purpurea (Montagu), (Plate IV, Fig. 10).

Jeffreys noticed the sculpture on the embryonic whorls. It is recorded from several localities in the Plymouth Fauna list but is seldom found, and only one dead specimen from the Eddystone sandy gravel has been seen in recent years. The embryonic shell has only 3 whorls, the smallest number of all the Plymouth species, but the same sculpture as the other Philbertias is present. The eggs and larvæ have not been seen.

Sub-genus **Teres.**

Philbertia teres (Reeve), (Plate IV, Fig. 11).

Jeffreys noticed the sculpture of the embryonic whorls of this species. It has not before been recorded from Plymouth and has only been seen as dead specimen from the Eddystone shell gravel. It has the typical Philbertia sculpture but the adult shell has spiral ribs on the adult whorls. This species has the largest number of embryonic whorls of any of the Plymouth Philbertias and is already know to have such a long apex, consisting of 4 or 5 whorls, 5 in the Plymouth specimen, 4 according to Thiele (1929). The eggs and larvæ are not known.

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On the Occurrence of the Siphonophores *Muggiæa atlantica* Cunningham and *Muggiæa kochi* (Will) in the English Channel.

By

F. S. Russell,

Naturalist at the Plymouth Laboratory.

In 1892 Cunningham described a new species of Siphonophore, *Muggiæa atlantica*, which was first noticed by him in the waters of the English Channel off Plymouth in the autumn of 1891. Since then there have been records from time to time of the occurrence of this species at Plymouth (see Plymouth Marine Fauna, 1931, p. 84), and its distribution in the English Channel and Irish Sea in 1904 was worked out by Gough (1905).

While examining a number of Muggiæa caught off Plymouth in the autumn of 1933 I noticed that the species differed slightly from Cunningham's description. On closer examination it was found that the species was *Muggiæa kochi* (Will) which although superficially resembling *M. atlantica* differs mainly in that the hydrœcium is shorter and the somatocyst only extends to between a third and a half the height of the nectosac. On examining large numbers of specimens it was found that in 1933 no *M. atlantica* occurred in the catches of plankton but all were *M. kochi*. It was of interest therefore to know whether *M. kochi* had appeared in the waters of the English Channel in previous years with *M. atlantica*. Opportunity for such an examination was afforded by the storage in the Plymouth laboratory of all the fortnightly catches taken from the Seven Stones Light-vessel since the year 1913. This collecting was stopped at the end of 1928, but in later years the data have been supplemented by the examination of weekly hauls taken with a 2-metre stramin ring-trawl 2 miles east of the Eddystone. Examination of all these collections has given the following interesting information (see page 556) on the occurrence of the two species.

From the data supplied it seems that *Muggiæa atlantica* occurred for an unbroken series of years from 1913 to 1924 (excepting 1915, when none were seen in the collections), but that in 1925 *M. kochi* first made its appearance and that since that time *M. atlantica* has disappeared from the area.

	M. atlantica.	*M. kochi.*
	Seven Stones.	
Aug. 5th, 1913	+	—
Nov. 1st ,,	+	—
Dec. 14th ,,	+	—
Jan. 28th, 1914	+	—
June 25th ,,	many	—
Aug. 24th ,,	+	—
July 2nd, 1916	many	—
Sept. 30th ,,	many	—
Aug. 5th, 1917	+	—
May 11th, 1918	+	—
Sept. 11th, 1919	+	—
Oct. 16th ,,	many	—
Oct. 28th ,,	+	—
Aug. 2nd, 1920	+	—
Oct. 27th ,,	+	—
Nov. 8th ,,	+	—
July 11th, 1921	+(1)	—
July 22nd ,,	+	—
Aug. 7th ,,	many	—
Sept. 6th ,,	many	—
Sept. 20th ,,	+	—
Oct. 26th ,,	many	—
Nov. 7th ,,	many	—
Dec. 1st, 1921	many	—
Dec. 14th ,,	+	—
Aug. 6th, 1922	many	—
Aug. 31st, 1923	+	—
Nov. 1st ,,	+	—
Nov. 12th ,,	+	—
Dec. 2nd, 1924	+	—
Oct. 4th, 1925	—	+(1)
Oct. 17th ,,	—	+(1)
Oct. 22nd, 1926	—	+
Jan. 4th, 1927	—	+(1)
Sept. 15th, 1928	—	+(1)
Sept. 30th ,,	—	+
	Plymouth.	
Oct., 1928	—	+
Aug.–Dec., 1930	—	+
Jan.–April, 1931	—	+
Aug. 28th ,,	—	+(1)
Oct.–Dec. ,,	—	+
Aug.–Dec., 1933	—	+
Jan.–Feb., 1934	—	+

+ = present.
— = absent.
(1) = only one individual in the catch.

There are no records for 1929. In 1932, although collections were examexamined weekly, no Muggiæa were found. Unfortunately I discovered the disappearance of *M. atlantica* after I published my report (1933) on the seasonal distribution of the ring-trawl plankton and in Table I in that publication the Muggiæa occurring in 1930–1931 are given as *M. atlantica*. These specimens have been re-examined and found to be *M. kochi*.

Both species are warm water forms and it is remarkable that they have not appeared together in some years or even alternated from year to year. One would like to have information from other regions to see if *M. kochi* now predominates in its area of distribution. The two species were at any rate present together in 1931, for I understand from Mr. A. K. Totton of the British Museum that he took both *M. atlantica* and *M. kochi* in the Bay of Algeciras. The actual geographical distribution of both species appears to be little known and they seem to have been rarely met with in the collections of oceanographical expeditions. Moser (1925, p. 107) remarks that *M. atlantica* has not been taken in the Atlantic outside British waters, but has been found twice in the Pacific, by Doflein in Sagami Bay on the Japanese coast and by Bigelow in the eastern tropical Pacific. More recently it has been recorded by Bigelow and Leslie (1930) as frequent in the plankton of Monterey Bay on the Californian coast of America. It is remarkable, however, that Bigelow (1911) did not find this species in the Biscayan plankton collected by Fowler on the *Research*, nor was the species recorded in the collections of the Plankton Expedition (Chun, 1897). That it probably does occur in the Atlantic outside British waters is, however, suggested by the statement of Totton quoted above.

Moser states on the other hand that *M. kochi* is very frequent not only in the Mediterranean but also in the whole central Atlantic, being recorded by Chun near the Canaries, Fewkes on the coast of N. Carolina and by herself in material collected by Hartmeyer from the Tortugas. Until now, Bigelow's record (1911) from the Bay of Biscay was the most northerly record for its occurrence.

It seems possible that both species are essentially inhabitants of less contaminated coastal waters, which would account for their absence in the collections of oceanographical expeditions. When occurring in our waters they generally first appear towards the end of the summer and often continue on through the autumn to the January or February in the following year.

A number of *M. kochi* were measured from the catches on October 25th and November 15th, 1933. These specimens had been preserved in formalin.

Overall measurements from the mouth of the nectosac to the exterior apex varied between 2·3 mm. and 4·9 mm., the majority lying between about 2·7 and 4·0 mm. Measurements of the distances between the mouth of the nectosac and the summits of the somatocyst and of the hydrœcium showed that on the average the somatocyst extended 51–52% of the height of the nectosac from its mouth, and the hydrœcium 15–16%, the range for the former being 41–59% (1 extreme measurement gave 68%) and for the latter 13–19%.

I am very grateful to Mr. A. K. Totton for kindly confirming the identification of many specimens of the two species.

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Variations in the Amount of Macroplankton by Day and Night.

By

A. C. Gardiner, M.A.

With 3 Figures in the Text.

THE investigations of the International Passamaquoddy Fisheries Commission were concerned, *inter alia*, with the principal food fishes of the region, one of which was the Herring. Demarcation of the spawning areas necessitated a study of the geographical distribution of the larvæ, for which purpose a modified Petersen's Young Fish Trawl was employed. My thanks are due to Mr. Michael Graham, to whom I am greatly indebted for the opportunity of examining the interesting collections of macroplankton on which this account is based.

My thanks are also due to Doctor C. J. Fish for his assistance, to Professor W. M. Tattersall for his help in the identification of the Euphausiids and to Professor Alexander Meek for confirmation of the Sagitta present in the material.

The collections covered a period of 48 consecutive hours, during the course of which 20 oblique hauls, from bottom to surface, were made with a stramin ring-trawl 5 feet in diameter. The net was fitted with two bridles only, a sinker being attached to the lower edge of the ring by means of a strop 6 feet long. The method of fishing was the same as that employed in an earlier experiment (Gardiner and Graham, 1925, p. 3), but with the additional precaution that the angle of the towing warp was kept at 35° to 45°. As before, each haul was of 30 minutes duration.

The times at which the hauls were made are given in Table I, and the approximate course of the boat, drifting under the influence of wind and tide, is shown in Figure 1. The twenty Stations were centred on the position 43° 50′ N. by 64° 30′ W., roughly 17 miles off Liverpool, Nova Scotia. Observations were continued from 8.42 p.m. on May 9th to 6 p.m. on May 11th, 1932. The wind was variable and light, and the sea, save at the first Station, comparatively smooth (0–3 Beaufort). With one exception, Station N. 234, when there was a haze, the sky was clear. Surface temperature ranged from 4·4° to 6·8° C.

The common species in the collections were :—

Thysanoëssa raschii M. Sars.
,, *inermis* Kröyer.
,, *longicaudata* Kröyer.
Sagitta elegans Verrill.
Calanus finmarchicus (Gunnerus).
Calanus hyperboreus Kröyer.

Specimens of *Themisto compressa* Goës, f. *compressa* Goës (Stephensen), *Metridia longa* (Lubbock) and *Pareuchæta norvegica* (Boëck) occurred in many of the collections in addition to occasional small hauls of Decapod larvæ and Cœlenterates. In the first haul, N. 217, the net touched bottom and this collection contained some 250 specimens of *Erythrops erythrophthalma* (Goës).

The numbers of the more abundant species taken in each of the 20 oblique hauls are given in Table I.

TABLE I.

NUMBERS OF SELECTED ORGANISMS IN EACH OF THE TWENTY COLLECTIONS, MAY 9–11TH, 1932.

Station.	Soundings in Fathoms	Time (A.S.T.).	*Th. raschii.*	*Th. inermis.*	*Th. longicaudata.*	*S. elegans.*	*C. finmarchicus.*	*C. hyperboreus.*	Herring Larvæ.	Fish Ova.
N. 217	56	2024	3,018	49	0	5,750	3,250	1,550	22	147
218	50	2206	3,210	350	0	6,100	1,100	275	29	260
219	51	0004	5,232	80	0	12,880	3,120	1,200	25	432
220	55	0151	2,886	240	0	10,800	4,800	1,440	12	438
221	65	0347	1,281	427	28	4,500	6,450	2,950	0	130
222	72	0628	59	59	2	2,475	6,050	1,400	1	244
223	56	0916	3	0	0	1,020	3,480	760	0	297
224	42	1214	0	0	0	1,180	1,380	520	1	305
225	45	1531	1	0	0	1,550	4,000	1,750	2	190
226	50	1819	6	0	0	2,375	3,750	1,250	5	365
227	50	2010	1,276	36	17	2,750	3,575	850	2	201
228	56	2214	2,427	218	0	3,300	10,200	3,400	0	137
229	65	0008	3,310	814	55	3,720	13,200	1,680	3	180
230	65	0144	3,147	725	0	7,350	11,600	5,500	2	164
231	64	0342	2,278	362	0	9,675	5,650	6,450	1	176
232	58	0623	33	12	1	2,550	6,300	5,800	0	64
233	58	0855	27	2	0	2,975	4,200	1,100	8	85
234	55	1148	7	13	0	1,175	3,250	1,450	5	121
235	60	1529	5	0	0	3,550	4,600	1,750	0	397
236	48	1809	10	2	0	2,925	2,525	675	2	445

The data are expressed graphically in Figures 2 and 3. The curve for Euphausiids is based on the totals of the three species.

As far as the Euphausiids are concerned, virtually none was taken in the daytime, and no statistical treatment need be invoked to demonstrate a significant difference. Sagitta, too, showed a marked discrepancy between day and night hauls, the latter comprising 75% of the total catch. In the cases of *Calanus finmarchicus* and *C. hyperboreus* 61% of the total numbers of each of these species were taken in the night collections. These differences can be shown to be significant, and are not to be ascribed to the operation of chance in irregularly distributed populations.

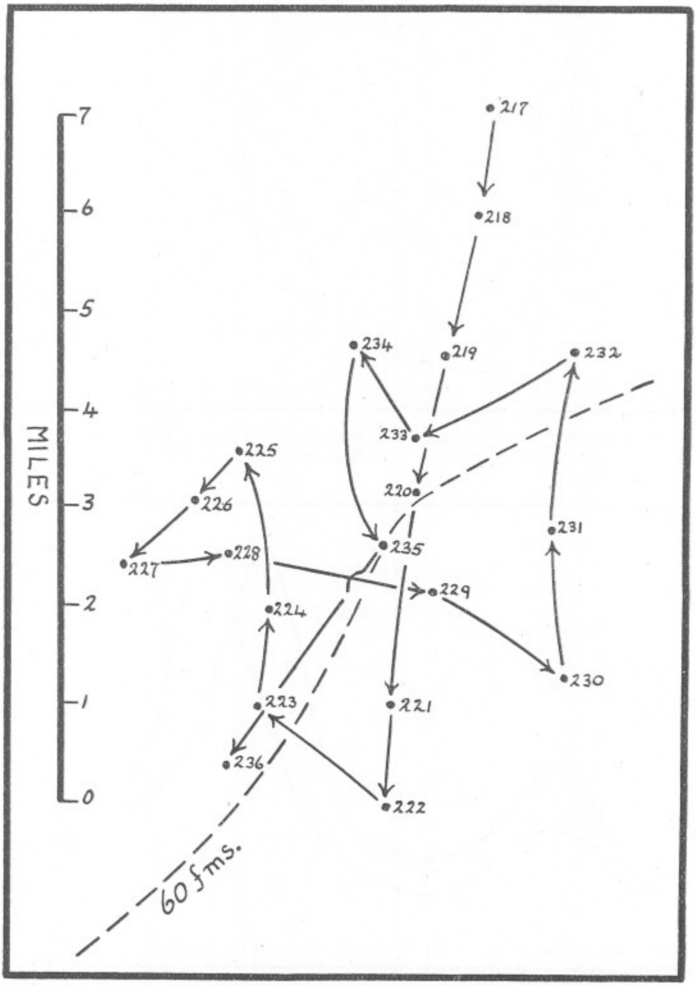

Fig. 1.—Approximate positions of Stations, and course of vessel drifting under influence of wind and tide.

No such difference exists in the case of the Fish Ova. The catches of Herring larvæ on the first night (Stations N. 217 to N. 220) were undoubtedly in excess of those made during the ensuing daylight period. At first sight this would seem to be in accordance with Russell's findings for Clupeid larvæ (Russell, 1930, p. 649), but the results of the second night's observations coupled with a study of the positions at which the bigger catches occur would suggest that the larvæ were restricted to a definite area (see Fig. 1, p. 561).

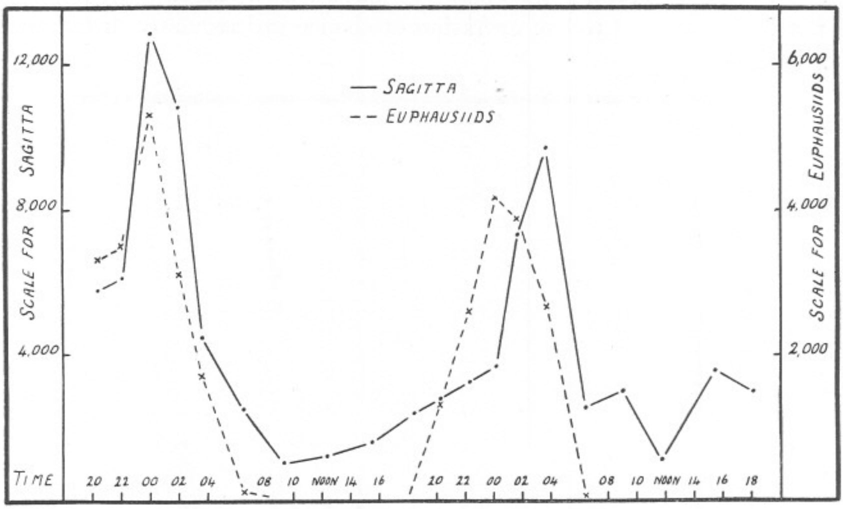

Fig. 2.—Actual numbers of Euphausiids and of Sagitta occurring in each of the twenty collections.

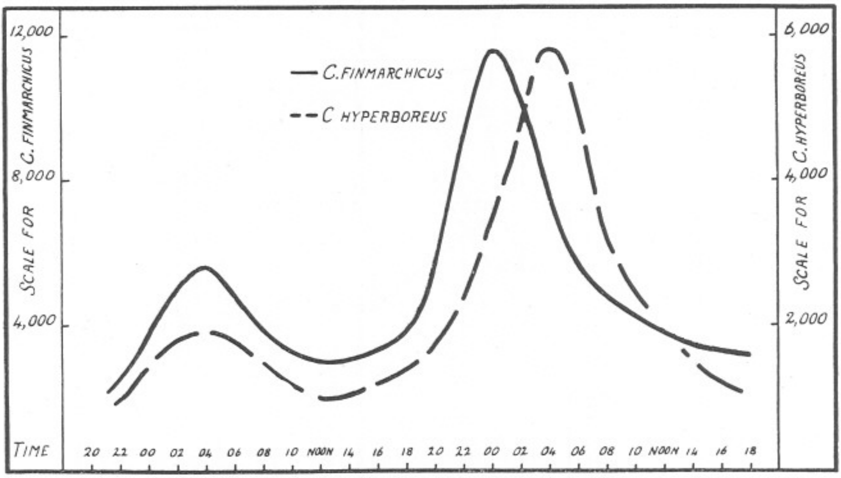

Fig. 3.—Abundance of *Calanus finmarchicus* and of *C. hyperboreus* throughout the period of 48 hours covered by the observations.

It has been shown in an earlier paper (Gardiner and Graham, 1925, p. 6) that consecutive hauls of a Petersen's Young Fish Trawl will not catch each time the same number of organisms, and it appeared that fluctuations in the region of ±40% were to be expected. The conclusion arrived at was that the greater part of such differences was due to irregularity in the horizontal distribution of the organisms themselves, a view which has been confirmed by more recent work (see Gardiner, 1931, p. 453). In these circumstances, then, one is clearly entitled to smooth the curves, especially since the purpose of the diagrams is to represent differences which, as already stated, are significant. Smoothing has been carried out in the cases of *C. finmarchicus* and *C. hyperboreus* only, the greater degree of uniformity in horizontal distribution rendering this unnecessary for the Euphausiids and for Sagitta.

Larger catches by night than in the adjacent hours of daylight have been recorded by a number of workers for many planktonic animals ; the reverse has also been observed. So far as can be ascertained it is usually held that in the former case such differences result from a proportion of the animals moving to depths greater than have been (or can be) fished by the net. In the case of some species, especially larger and more active ones, it has also been suggested that discrepancies may result from the animals' ability to dodge the net. In the present instance we have three classes of animals, differing in size and swimming power, all of which have been caught in greater numbers in the darkness, thus enabling these two suggested explanations to be examined.

EUPHAUSIIDS

There is abundant evidence from the literature that Thysanoëssa and allied forms live close to the bottom by day (Otterström, 1910, p. 10 ; Lebour, 1924, p. 404 ; Hickling, 1925, p. 741 ; Russell, 1927, p. 588 ; Southern and Gardiner, 1932, p. 155 and Macdonald, 1927, p. 756).

On the other hand, there is also no lack of evidence that Euphausiids may occasionally be found right at the surface in broad daylight (Hickling, *loc. cit.*, p. 742 ; Bigelow, 1926, p. 145 ; Macdonald, *loc. cit.*, p. 776).

In the present experiment a note was made in the Log : " At 12.30 p.m. *Shrimp* were visible in the water." On this occasion (Station N. 234, 11.5.32) Euphausiids were seen in fair abundance, and a single specimen taken in a bucket of surface water was found to be *Th. inermis*. Herring larvæ and Eel (Anguilla) were present, but in smaller numbers. By 4 p.m. (Station N. 235) the Log records that the plankton was no longer to be seen. In the tow-netting made when *Shrimp* were known to be in the surface water only 20 specimens occurred, 13 *Th. raschii* and 7 *Th. inermis*.

The possibility that Euphausiids may avoid a net has been recognised by most observers (e.g. Holt and Tattersall, 1905, p. 137 ; Ruud, 1932, p. 14 ; Frost, 1932, p. 203, etc.), and although I would hold this responsible for a small part of the paucity of Euphausiids at Station N. 234, to ascribe to this cause the whole of the enormous discrepancies between day and night collections would surely be to endow these animals with powers of swimming altogether too great. Moreover, such an hypothesis would entail the bulk of the population remaining by day in the upper illuminated levels, where, in point of fact, Hickling (*loc. cit.*, p. 739) shows that they are almost certainly not to be found.

SAGITTA.

Whatever explanation we may accept for this phenomenon with regard to the Euphausiids, it is impossible to believe that in the case of Sagitta it is due to the animals avoiding the net. They are by no means active creatures and, moreover, are known on occasions to migrate downwards by day (Russell, 1931 and 1933). It is thus tolerably certain that the discrepancies between day and night catches are due to a proportion of the population moving downwards to levels below those fished by the net.

It is well established that Sagittas of different size do not respond in the same way to changes in light intensity, and the present material was examined to see whether there was any indication that one size group more than another had sunk to those levels which the net could not sample. In all, over two thousand specimens of *S. elegans* were measured and the mean length in each of the twenty collections determined. This was found to vary between 22 and 25 mm., but no correlation with the hour at which the sample was taken could be detected.

CALANUS FINMARCHICUS AND *CALANUS HYPERBOREUS*.

The differences between the daylight and dark collections, whilst significant, were not so marked in the case of these two species as in those considered above.

The large mesh employed with the ring-trawl retains no more than a small proportion of *C. finmarchicus* in Stage IV and on this account only specimens in Stages V and VI were enumerated. In the case of the larger *C. hyperboreus*, individuals in Stage IV were more abundant and were included in the counts.

It is known that the older and larger individuals tend to live below the younger (see Gardiner, 1933, p. 464 ; Marshall, 1933, p. 128) and thus might be expected to disappear from the daylight catches to a greater extent than the younger stages. In order to test this, the percentage of adult specimens (♂ and ♀) of *C. finmarchicus* occurring in the 20 collections, together with the mean figure for each of the periods of daylight and darkness was determined. These are set out in Table II. It will be seen that during the daylight, adults disappear from the population to a small, but definite extent. According to the test provided by Fisher (1930, p. 114) the difference between the mean percentages in darkness and daylight is a significant one.

TABLE II.

PERCENTAGE OF ADULT SPECIMENS OF C. FINMARCHICUS OCCURRING IN EACH OF THE TWENTY COLLECTIONS.

	Station.	Time.	Percentage of Adults (Stage VI).		Station.	Time.	Percentage of Adults (Stage VI).
DARKNESS.	N. 217	2024	62%	DARKNESS.	N. 227	2010	54%
	218	2206	77		228	2214	65
	219	0004	77		229	0008	64
	220	0151	57		230	0144	48
	221	0347	59		231	0342	43
			Mean 66%				Mean 55%
DAYLIGHT.	222	0628	51%	DAYLIGHT.	232	0623	35%
	223	0916	54		233	0855	57
	224	1214	54		234	1148	54
	225	1531	46		235	1529	38
	226	1819	37		236	1809	49
			Mean 48%				Mean 47%

SUMMARY AND CONCLUSIONS.

1. Twenty oblique hauls of a stramin ring-trawl, diameter of mouth 5 feet, were made during a period of 48 hours off Liverpool, Nova Scotia, in May, 1932.

2. The common species were *Thysanoēssa raschii*, *Th. inermis*, *Sagitta elegans*, *Calanus finmarchicus* and *C. hyperboreus*.

3. All of the above occurred in the collections made during the night in larger numbers than in those in the daytime. No such discrepancy appeared in the case of the Fish Ova.

4. The discrepancy is held to be due in each case to a proportion of the population sinking to depths greater than could be sampled by the net.

5. Adult *Calanus finmarchicus* tended to disappear to a relatively

greater extent than individuals in Stage V. No such phenomenon could be detected in the larger specimens of *Sagitta elegans*.

6. Discrepancies of this kind would have to be taken into account when lines of Stations are worked by day and night. The probability of error will be greatest where the mesh employed is large, and particularly so in those cases where the lowest levels are left unsampled.

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The Vertical Distribution of Marine Macroplankton. XII. Some Observations on the Vertical Distribution of *Calanus finmarchicus* in Relation to Light Intensity.

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With 3 Figures in the Text.

In my previous reports on the vertical distribution of plankton animals off Plymouth the apparent importance of light-intensity as a major factor in determining the behaviour of some species has been repeatedly stressed. The results appeared to show that individuals of a species, when in a state in which they react towards light, will congregate in those water layers in which certain optimum light conditions are to be found. There seems now to be no doubt that at certain times in the life-history of a plankton animal the strength of light has a predominating influence so that in a study of the habits of plankton animals the light conditions must be measured as being a factor of the environment of equal importance to such factors as temperature and salinity. Now that the observation of the light conditions has been made possible through the researches of Poole and Atkins we are in a position to study this factor in research on the ecology of plankton animals.

The first contribution to this line of research has been made by Clarke (2) on the basis of observations made in the Gulf of Maine in July and August, 1931. During the same period in that year in collaboration with Dr. Atkins I made a number of observations on the vertical distribution of plankton animals off Plymouth with simultaneous measurements of light intensity beneath the sea surface. It is with some of the results of this work that the present report is concerned.

As a working hypothesis it had been assumed that for some species there is an absolute light intensity optimum, but that while this optimum may remain constant for short periods of time it changes from time to time in accordance with the various changes in development during the life-history of the animal and may be different for different broods.

For a preliminary test of this theory it was felt that it was better to make a number of observations on different days than to follow an actual migration through 24 hours. If in the middle of the day on different days the animals were found to be living at depths at which they experienced similar light intensities, better proof of the theory would be obtained than by attempting to correlate the light intensity with the distribution of the animal during active migration, when such factors as the swimming speed of the animal and its speed of reaction might tend to prevent it from keeping accurately within the zone of optimum light conditions. During full daylight the animals would have had more time to congregate around the region of their true optimum.

Ideally the observations should be made either on cloudless days or on days of uniform dullness ; under such conditions the animals would show best the light conditions they prefer. On days of constantly changing illumination it is doubtful whether at any one time the animals will be found accurately concentrated round the actual optimum light conditions. Unfortunately some of the days on which my observations were made were anything but ideal in this respect.

Seven series of observations were made on five days, July 21st, 22nd, and 29th, and August 5th and 12th, 1931, two observations being made on the first and last of these days respectively. The collections were made with usually six nets fished simultaneously in a horizontal direction for half an hour. Light measurements were made by Dr. Atkins at different depths immediately before or after the collecting period, and the air illuminations were observed during the time the nets were fishing. Most of the collections were made at a position 2 miles east of the Eddystone Lighthouse, the depth being about 50 metres.

Collecting Methods.

In my previous researches I had fished only with one net, a series of catches being made consecutively at different depths. Under such conditions the period of time between the first and last hauls of a series of six collections must necessarily be considerable. If accurate comparison was to be made with light conditions it was therefore essential that the six nets should be fished simultaneously. It was necessary that the depth at which each net was fishing should be known, and as closing mechanisms were not used it was essential that the nets could be attached to and detached from the towing wire as quickly as possible.

The nets used were coarse silk nets of the international pattern (silk No. 3 ; 58 strands to the inch ; diameter of opening 50 cm.). The silk was however attached directly by a calico band to the ring without the half-inch meshing used in the international design (**8**, p. 7) : the ring was made of brass $\frac{3}{8}$-inch diameter (weight *ca.* 2 lb. $1\frac{1}{2}$ oz.).

If six nets be attached at intervals to a wire with a single weight at its end the wire will be considerably curved when the nets are fishing somewhat after the style of A in Figure 1, and it would be difficult to estimate the depth of any one net. For any fishing method it would certainly be extremely complicated, if indeed possible, to predict by calculation the actual depths at which the nets would fish. A practical attempt was made to overcome this difficulty by using the Admiralty depth-recorder as the end weight and by attaching a metre below each net a lead weight whose weight in water was the same as that of the depth-recorder in water (Fig. 1, B).

The accuracy of this method was tested by taking a successive series of hauls and interchanging the depth-recorder with each of the lead weights in turn. It was found that on this occasion the average depths of each of five nets were as follows :—

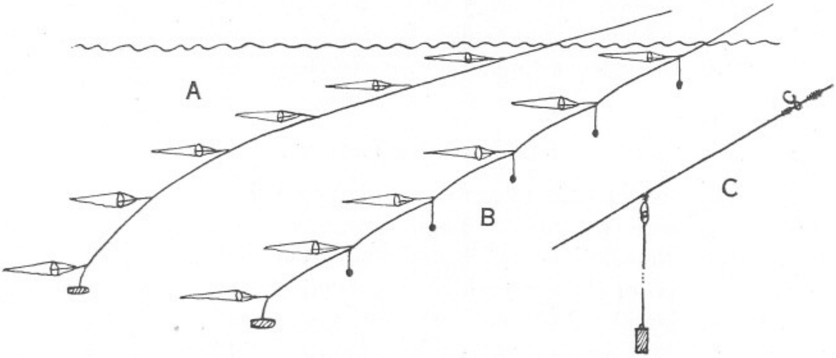

FIG. 1.—Fishing methods. A, with single weight at end of towing-wire ; B, with weights by each net on towing-wire ; C, method of attachment for nets and weights.

Surface, 7 m., 14·4 m., 22·6 m., and 29·5 m. : the depth intervals between each net were thus 7, 7·4, 8·2, and 6·9 m. These results were sufficiently close to enable one to assume that the nets in the other series of observations fished at approximately equal intervals of depth. In order to ensure that each series was hauled in exactly the same way and at the same speed a declinometer was hung on the wire as described in **8**, page 9. The angle aimed at was 30°, and by varying the speed of the ship's engine the pendulum was kept oscillating slowly about this angle. By observation of objects drifting past the ship's side it was found that with an average angle of 28·6° the speed averaged 1·2 knots : at an average angle of 31·2° it was 1·03 knots, and at 25·4° it was 1·42 knots : the extreme variation was thus probably between 1 and 1·5 knots.

In order to ensure rapidity of work the gear was attached in the following manner. The nets were fixed to the wire ($\frac{3}{4}$-inch circumference flexible steel) by signal halyard swivel clips: one half of each swivel was attached to a rope from the tow-net bridles; and the other halves were threaded on to the towing wire and fixed at intervals of 15 metres by stoppings of twine rove through the wire (Fig. 1, C). One metre below each swivel a small bight was made in the wire for the attachment of the lead weights. Each lead weight (*ca.* $9\frac{1}{4}$ lb. in air) had a length of rope with a slip-hook at its end. When shooting, a net was held by one man and a lead by another; as each bight and swivel attachment passed over the ship's side the net and weight were quickly hitched on without stopping the wire from coming off the winch; similarly each net and lead could be quickly detached as the wire came in. The errors due to the nets fishing in layers above their correct depths were thus reduced to a minimum. Each net was numbered serially to avoid confusion on deck; when all the nets were on board after fishing the washing down of the silk and preservation of the catches could thus be proceeded with carefully and at leisure.

THE LIGHT CONDITIONS.

The details of the light measurements have already been published by Atkins and Poole (**1**, p. 141). Measurements were obtained with a gas-filled potassium cell under a diffusing filter. This cell was sensitive only to the blue end of the spectrum with a maximum sensitivity probably near a wave-length of 440 mμ. Observations were made immediately before or after the net collections so that figures could be obtained for the coefficients of absorption of the water at different depths. During the hauls a photometer was used on the roof of the ship's deck-house to measure the air illumination; a number of measurements were made while the nets were fishing and a mean value was taken. From these mean values and the knowledge of the coefficients of absorption of the water the submarine illumination was calculated for the depths at which the nets were fishing. The details of these illuminations are given in Table I.

On July 21st, 1931, immediately after the first series of collections, further measurements were made on the penetration of other wave-lengths of light, using a thin film caesium on silver vacuum cell, with red, yellow, green, and blue filters under opal. On August 12th measurements were also made of the penetration of the near ultra-violet light with a Burt sodium vacuum cell and a 10 mm. Corex red-purple filter.

Full details of the general weather and lighting conditions on the days on which collections were made are given in the log at the end of this report. At the same time records were obtained of the illumination for some hours prior to the times of collecting by the photo-electric continuous light recorder on the roof of the Plymouth Laboratory. Although these results will not be a faithful reproduction of the light conditions ten miles out to sea where the collections were made, they nevertheless serve as a good guide to the average illuminations obtaining when our observations were made. The results are reproduced in Figure 2. It can be seen that on no day were the light conditions ideally constant ; on the other hand at the times that collections were made the light was evidently not varying as badly as it might have done. Examination of Figure 2 shows that on July 21st at the times when Series I and II were made the light conditions had become tolerably constant which is in agreement with the observations made on the ship and given in the log. On July 22nd the conditions had been fairly constant, increasing steadily until a short time before the period of collecting when they became more varied. On July 29th for an hour before the collections were made the illumination had been increasing and decreasing on a very smooth curve, but became more varied at the time of collecting. On August 5th both prior to and during the time of collecting there were a few short periods of increased intensity but on the whole the light had been varying constantly within small limits. On August 12th conditions had been varying to about the same extent as on August 5th but had been consistently low.

Of the five days July 21st was the only bright day ; the other four days, and particularly the last three were dull and overcast.

Examination of Figure 2, page 145 in the paper by Atkins and Poole (**1**) shows that for the five days (Series 55, 60, 61, 67 and 75 *loc. cit.*) the transparency of the water had been much the same, and that the transparency varied very little at different depths except on August 12th (Series 75) when the water became appreciably clearer in the deeper layers. Also " in Series 61 (July 29th) the zone of less transparent water, $\mu = 0{\cdot}173$ is found at 5–10 m., instead of 0–5 m." (**1**, p. 148). From these results I have calculated the depths at which the following intensities would, at the time of collecting, have been found on each day, viz. 80, 60, 40, 20, 10, 5, 4, 3, 2, 1, and 0·5 thousands of metre-candles. These have been plotted on Figure 3, drawing the curves of equal illuminations for the seven series of observations.

As a result of further photo-electric measurements on July 21st and August 12th we can get an approximate picture also of the penetration of light of different wave-lengths beneath the sea surface. Examination of Figure 5, p. 153 in **1**, shows that for the wave-lengths 580 mμ to 440 mμ, yellow→green→blue, there is comparatively little difference in the amount of absorption at any rate down to 30 metres. But light at the red end of the spectrum 660 mμ to 760 mμ is much more rapidly absorbed and has become reduced to 1 per cent of the illumination immediately below the surface before a depth of 10 metres has been reached. The violet and near ultra-violet rays, to 360 mμ, however, penetrate slightly further than

TABLE I.

VERTICAL ILLUMINATIONS, V, IN THOUSANDS OF METRE CANDLES, AT THE DEPTHS (*d*), IN METRES, AT WHICH THE SIX NETS WERE FISHING.

The depth of the water was about 50 m., and position 2 miles East of Eddystone Lighthouse. *r*=illumination on deckhouse roof.

Date 1931, July G.M.T.	21st. 2.24–2.54 p.m.		21st. 5.54–6.24 p.m.		22nd. 11.11–11.41 a.m.		29th. 11.39 a.m.–12.9 p.m.		Aug. 5th. 11.19–11.39 a.m.		12th. 10.55–11.25 a.m.		12th. 3.7–3.32 p.m.	
Series	I		II*		III		IV		V		VI		VII*	
	d	V	*d*	V	*d*	V	*d*	V	*d*	V	*d*	V	*d*	V
In air	*r*	88·6	*r*	27·1	*r*	91·5	*r*	50·0	*r*	26·9	*r*	35·4	*r*	45·8
1.	0·5	80·8	0·5	24·7	0·5	72·8	0·5	45·4	0·5	22·0	0·5	24·4	0·5	31·6
2.	7·2	34·4	7·9	9·36	8·1	19·7	7·1	16·4	7·2	7·05	7·5	11·5	7·0	15·7
3.	14·3	13·2	15·7	3·32	16·1	6·63	14·4	6·55	14·3	2·42	14·9	4·34	13·8	6·65
4.	21·4	5·18	23·5	1·24	24·1	2·78	21·7	2·22	21·4	0·88	22·3	2·07	20·6	3·11
5.	28·5	2·39	31·3	0·54	32·1	1·39	29·0	1·29	28·5	0·47	29·7	1·08	27·4	1·66
6.	35·6	1·03	39·1	0·16	40·1	0·43	36·3	0·53	–	–	37·1	0·58	34·2	0·91

* Had drifted a little further in.

do the red rays and are not reduced to 1 per cent until after 15 metres have been reached.

It is interesting that as regards the shorter anti-rachitic ultra-violet rays Atkins and Poole write, " Hulbert's coefficients have been used to show that even in the clearest ocean waters the anti-rachitic portion of the spectrum is reduced to 1 per cent of its subsurface value at 1·1 to 2·2 m., according to wave-length, and to 0·001 per cent at from 2·9 to

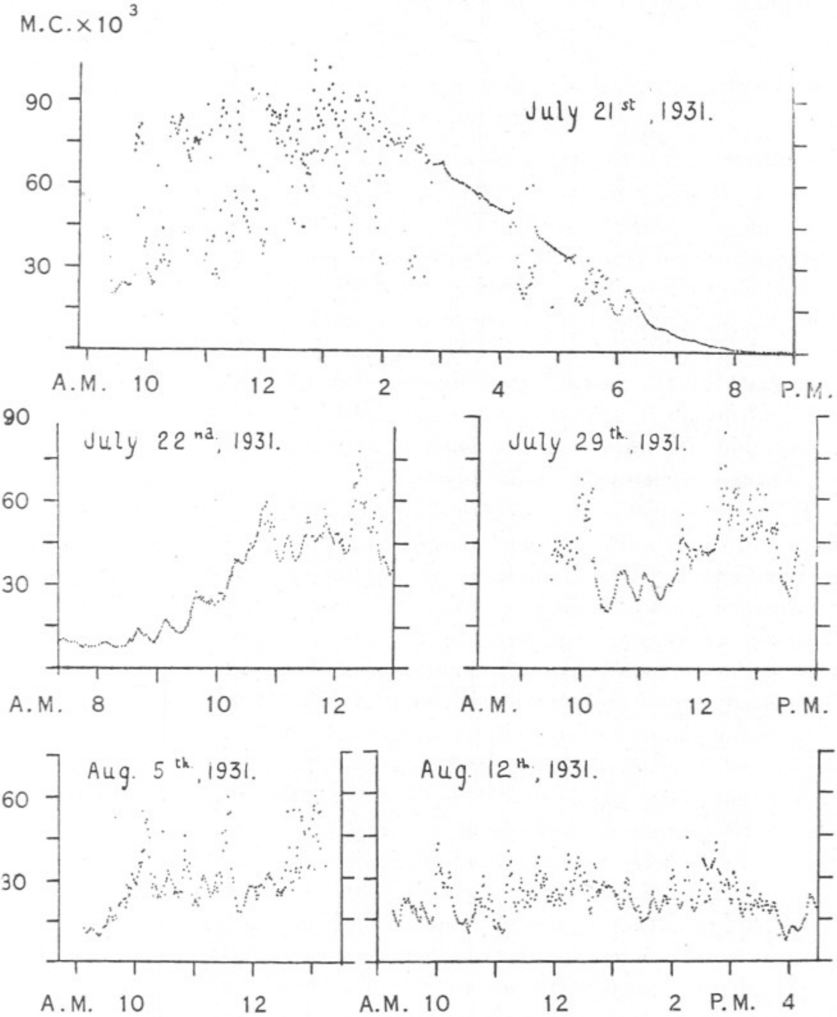

FIG. 2.—Records of light intensity obtained on roof of Plymouth Laboratory with vacuum photo-electric cell and thread-recorder, on July 21st, 22nd, and 29th, and August 5th and 12th, 1931. (By courtesy of Dr. W. R. G. Atkins.)

5·5 m." They suggest, however, that " it also seems possible that, though anti-rachitic action is but feeble at wave-lengths longer than 313 mμ, yet owing to their better penetration those somewhat longer than the limit given may be more effective in sea-water."

THE VERTICAL DISTRIBUTION OF *Calanus finmarchicus* IN RELATION TO LIGHT CONDITIONS.

In working up the material of the collections all the species were counted. It has, however, been shown previously that in order to elucidate the principles underlying the behaviour of the animals it is useless to work on a mixed population ; the population of any one species needs to be further analysed into the sexes and stages of development occurring therein. This further analysis has only been done for the copepod, *Calanus finmarchicus*, and in this paper I deal only with adult males and females. Owing also to the possibility of differences in behaviour shown between different broods it is necessary to make a further analysis of the Calanus by making size measurements as these may indicate differences in the populations occurring from day to day.

The general results of these observations on adult Calanus are given in Figure 3, which shows the percentage vertical distribution of the females and males on the days in question. The actual numbers of Calanus in the catches are given in Table II on page 583 ; it can be seen that the numbers are fully large enough to be significant. On the diagram in Figure 3 are also given the lines of equal illumination in thousands of metre-candles calculated as explained previously (see page 573). Underneath the depth distribution diagrams for each sex are given the median lengths (Q_2) and upper and lower quartiles (Q_3 and Q_1) being the lengths between which 50 per cent of the population lay on each day. The length measurements are the total length of the body to the end of the caudal furca but excluding the furcal setæ. A number of both sexes were measured from every catch (Tables III and IV, pp. 583 and 584). In estimating the median length the numbers measured at each depth in a series were added together. Gardiner has shown that there may be a slight difference in the depth distribution between individuals of different sizes in Stage V, the larger individuals in a population being deeper (**3**, p. 590) ; see also Marshall (**4**, p. 123). Insufficient numbers were measured on this occasion to show significant differences in size-composition of the catches from different depths, but it was evident that such difference if it occurred would not have been of the order of the differences that will be referred to later between one whole population and another in July and August.

An examination of Figure 3 shows that during the four observations in July (Series I–IV) the majority of the female Calanus were near the surface and living in the very high light intensities of 20,000 metre-candles and more: below 10,000 metre-candles the remaining Calanus appear to be evenly distributed. In August (Series V to VII) there is a definite change in the vertical distribution, the female Calanus now avoiding light intensities of 20,000 metre-candles and over. This change is very noticeable and at first sight would have been regarded as a change in the behaviour of the animal. A study of the length measurements shows, however, that instead of there being a change in behaviour there has been a change in population. We are quite definitely dealing with a different population in August from that we had in July. In July the median lengths of the female Calanus in the Series I to IV were 3·186, 3·169, 3·170, and 3·141 mm. respectively, while in August for Series V to VII these lengths were 3·068, 3·000, and 3·013 mm. The change in population receives further confirmation from the appearance in August catches of numbers of early stages of Calanus, whereas in July the catches consisted almost purely of adults. In August we have possibly therefore a new brood of adults which have just grown up, or one consisting perhaps of the smaller individuals that may be produced towards the end of a breeding period (Marshall, **4**, p. 122).* This difference in behaviour between different populations is in keeping with previous observations (**7**, p. 438) which led to the suggestion that the different broods were physiologically distinct and showed differences in their behaviour towards light intensity. It emphasises at once the danger of attempting to make conclusions on the effects of the environment on an animal without a certain knowledge of the population under examination. Analysis of the vertical distribution results of the female Calanus on July 29th and August 5th, 1931, would certainly have led to wrong conclusions if length measurements had not been made at the same time. If we turn now to the results for the male Calanus we notice a similar change in depth distribution coincident with a change of population. The male Calanus were living deeper in the water than the females and tended very definitely to avoid those high light intensities in which the females were living. In July (Series I to IV) the male Calanus definitely avoided intensities of 40,000 metre-candles and over, but below about 20,000 metre-candles they were rather evenly distributed in the water though there are indications in Series II and IV that they tried to keep above intensities of 500 metre-candles and less. In August (Series V to VII) the majority of the males were deeper in the water than in July and were now avoiding intensities as low as 10,000 metre-candles. Here again we find length differences between individuals

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* A number of female Calanus were stained and examined for state of maturity. In the limited number examined no significant difference could be found in the proportions of the different degrees of maturity occurring in the July and August populations. I am very grateful to Miss S. M. Marshall and Dr. A. G. Nicholls for examining these specimens for me.

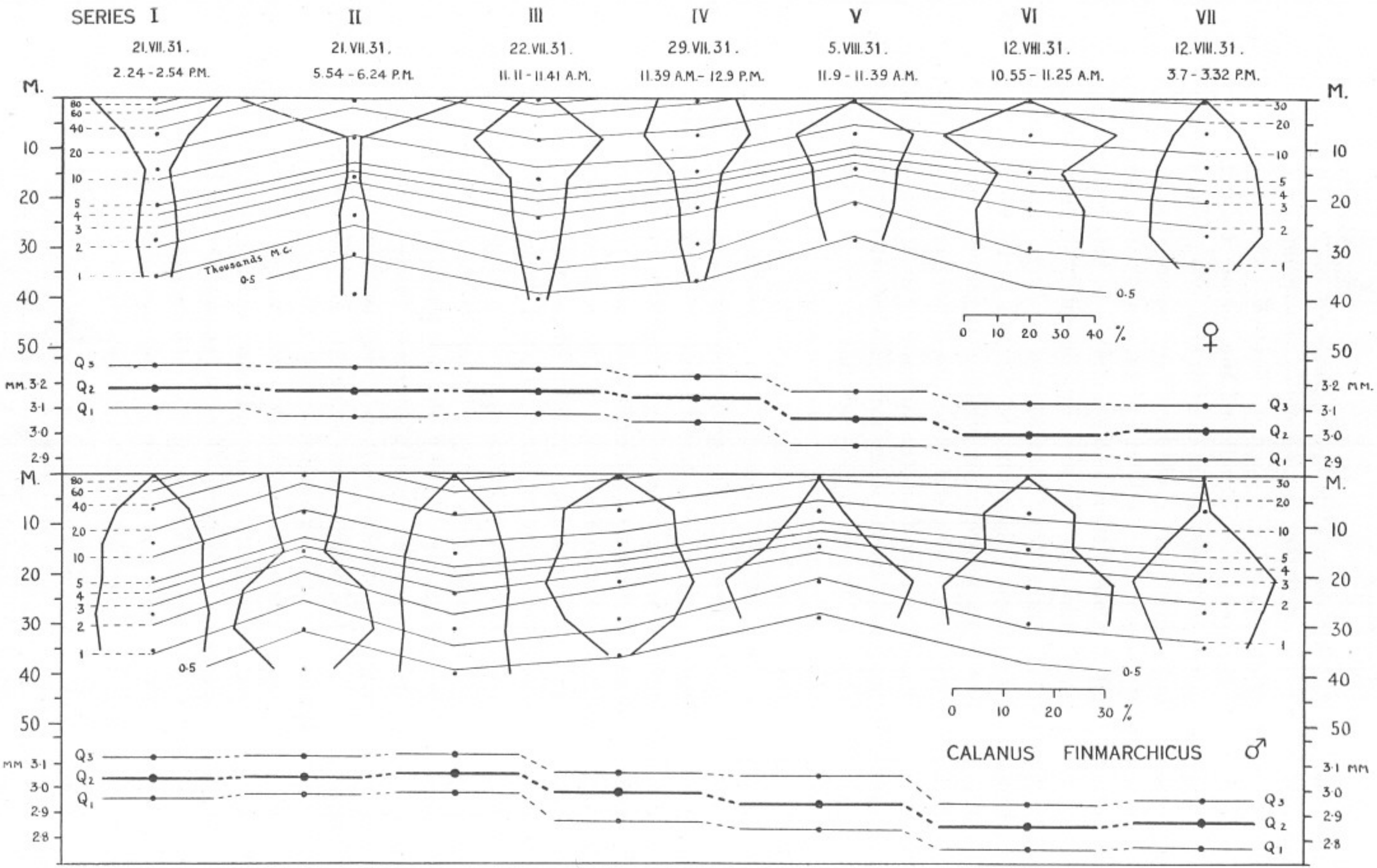

FIG. 3.—Percentage vertical distribution of adult *Calanus finmarchicus ;* females above, males below. The black spots indicate the depths at which the nets were fishing. For each day are plotted the light intensities beneath the surface and these points are joined to form the isointensity lines of 80, 60, 40, 20, 10, 5, 4, 3, 2, 1, and 0·5 thousands of metre-candles. Below each diagram is given the medium length (Q_2) and upper and lower quartiles (Q_3 and Q_1) of the Calanus. (The diagrams for the males Series II, III, and IV are slightly to the left of those for the females.)

of the July and August populations. While in Series I to III in July the median lengths were 3·034, 3·043, and 3·060 mm., in August, Series VI and VII, they were 2·837 and 2·873 mm. In Series IV and V, however, at the end of July and beginning of August they occupied an intermediate position of 2·987 and 2·943 mm. respectively, which may have indicated a mixing of the two populations.

This tendency for the males to avoid the bright intensities that the females can endure is in keeping with previous results for this region (**7**, p. 442). The very even distribution assumed below the upper limit at times appears also to be somewhat characteristic of the males and seems to imply a less sharply graded sensitivity to light intensities between the upper and lower limits than is shown by the females. This type of distribution for the males has recently been shown also by Nicholls (**5**, p. 146) to occur in the Clyde Sea area, where at different times during the day this difference in behaviour between male and female is clearly indicated. It is interesting that in the observations made by Nicholls the upper limit of intensity avoided by the male Calanus would appear to be as high as that avoided by females on the same day.

On the whole the present results appear to support the light optimum theory referred to above (p. 569). The preference of the July individuals for higher intensities than the August individuals is consistent. Very close agreement is shown between the distribution of the females and the light conditions in the two Series of observations made on July 21st (Series I and II). Between 2.24 and 2.54 p.m. the threshold intensity for stimulation of upward movement seems to have been somewhere between 20,000 and 10,000 m.c. By 5.54 to 6.24 p.m. the female Calanus have crowded very much more towards the surface and the threshold illumination still appears to lie at about 20,000 m.c. The males also show agreement in that while at 2.24 to 2.54 p.m. the upper limiting intensity was about 60,000 m.c., at 5.54 to 6.24 p.m., when intensities of 40,000 m.c. and over could no longer be experienced, the male Calanus had extended their distribution to the surface.

It is difficult, however, from these observations to decide on the optimum conditions except within very wide limits. The female Calanus, for instance, in Series III and IV would appear to have a slightly lower optimum than those in Series I and II. It is interesting, however, that if these four observations be arranged in the order of the time of day at which they were taken the Calanus are found to have slightly increasing optima, which might point to increasing adaptation on the part of the Calanus throughout the day. No such increase is, however, shown in the two series taken on August 12th (Series VI and VII). We must wait for further observations to be made before we can decide the cause of these discrepancies or whether indeed they may not be false impressions brought about by the inability of the animals to keep accurately to their optima during rapid fluctuations in light intensity.

These collections were made at a time of year when Calanus is living nearer the surface than earlier in the year. The present observations confirm the results of two previous years (**6** and **7**), although the August population was living deeper than might have been expected. It is possible, however, that they are more recently moulted from Stage V than those occurring in the July collections and have not yet developed to the age at which they desire bright light. It should also be mentioned that the upper water layers were considerably warmer on August 12th than on July 22nd, the temperatures at 15 m. being 15·0°C. and 12·4°C., respectively (see Log, p. 582).

It is a great pleasure for me to thank Dr. W. R. G. Atkins for his willing co-operation and assistance in this work, and for his kind permission to reproduce the light measurements in Figure 2. My thanks are also due to Captain Lord and the Crew of s.s. *Salpa* for their great help while the collections were being made, and to my wife for the assistance she gave me in helping to sort and count the collections.

SUMMARY.

1. Observations are given on the vertical distribution of adult *Calanus finmarchicus* in the daytime off Plymouth in July and August, 1931, as a result of collections made simultaneously with the photo-electric measurement of submarine illumination.

2. A series of nets, usually six, was towed simultaneously in such a manner that the depth of each net was known approximately.

3. The female Calanus in July preferred higher intensities of light than did the females in August; this change was coincident with a change in the Calanus population as shown by size measurements. A similar change in distribution and in population was shown by the males.

4. The females in July were living in intensities of 20,000 m.c. and more; but those in August were avoiding such high intensities. The males in July avoided intensities of 40,000 m.c. and over, while in August their upper limit was about 10,000 m.c.

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LOG.

July 21*st*, 1931.

From 12.15 p.m. until 1.25 p.m. there had been high clouds and blue sky, but the sun was partially obscured: from then until 1.55 p.m. the sun shone brightly in a clear sky, with cumulus coming up on S.W. horizon, and wind freshening slightly from the west. At 1.55 p.m. a very thin sheet of high cloud passed over the sun but barely obscured it. The sea surface was calm, with slight swell and lop.

SERIES I. 2 miles East of Eddystone.

Six nets fished together on 75 metres of wire: nets 15 metres apart. Depth recorder and 5 weights (*ca.* $9\frac{1}{4}$ lb. in air) each one metre below nets. Nets= coarse silk international without front meshing.

The sky was quite cloudless for the whole haul, almost over the whole sky except the horizon.

2.24–2.54 p.m.

Average depths of nets. Surface, 7·2, 14·3, 21·4, 28·5, and 35·6 m. Nets took 4 min. 35 secs. shooting; and 4 min. 6 secs. hauling.

3.45 p.m. Cloudless sky. 5.23 p.m. Almost cloudless sky except for a little wispy cirrus. 5.38 p.m. Sun going behind a cloud.

SERIES II. By this time we had drifted to near L4, half-way between Breakwater and Eddystone.

5.54 p.m.–6.24 p.m.

Six nets as in Series I, fishing at average depths of surface, 7·9, 15·7, 23·5, 31·3, and 39·1 m.

At 5.58 the sun came out clear again.

Nets took 3 min. 35 secs. shooting ; and 2 min. 38 secs. hauling.

Sun was shining all the time after 5.58 p.m.

July 22*nd*, 1931.

8 a.m. Very dull and patches of fog. 10.45 a.m. Clearing and sun shining enough to throw shadows. Had been dull up to now. 11 a.m. Sun shining fairly fully through thin sheet of low cloud.

SERIES III. 2 miles East of Eddystone : sea choppy. Six nets fished as in previous series.

11.11 a.m.–11.41 a.m.

Nets fished at average depths of surface, 8·1, 16·1, 24·1, 32·1, and 40·1 m.

Nets took 2 min. 37 secs. shooting ; and 1 min. 59 secs. hauling.

1 p.m. Secchi disc 9 m. on windward side : 8 m. on leeward side. Temperatures of sea : surface, 14·5° C. ; 5 m., 13° C. ; 10 m., 12·8° C. ; 15 m., 12·4° C. ; 25 m., 12·2° C.

July 29*th*, 1931.

S.W. wind : slight lop. It had been dull with the sun covered all morning. Cloud-sheet was of uneven thickness, so that the light was variable.

SERIES IV. 2 miles East of Eddystone.

Six nets fished as previously.

11.39 a.m.–12.9 p.m.

Nets fished at average depths of surface, 7·1, 14·4, 21·7, 29·0, and 36·3 m. Nets took 2 min. 23 secs. shooting and 2 min. 18 secs. hauling.

Secchi disc : 7 m. on weather side ; 8 m. on leeward side. The sun was covered the whole time but the cloud-sheet was of very uneven thickness.

August 5*th*, 1931.

It had been dull with thick low clouds all morning ; at 9.55 the sun was trying to show through a slight break in the clouds. Calm. S.E. breeze.

In shooting lost one net so started again with five.

SERIES V. 2 miles East of Eddystone.

11.19–11.39 a.m.

Nets fished at average depths of surface, 7·1, 14·4, 21·7, and 29 m. Nets took 2 min. 5 secs shooting ; and 1 min. 46 secs. hauling.

Secchi disc : 10 m. on weather side ; 12 m. on leeward side.

August 12*th*, 1931.

Sea calm at first ; clouds all over sky ; low nimbo-cumulus type at about 1500 ft.

SERIES VI. 2 miles East of Eddystone.

10.55 a.m.–11.25 a.m.

Nets fished at average depths of surface, 7·5, 14·9, 22·3, 29·7, and 37·1 m. Bottom net touched bottom while shooting. Nets took 3 min. 8 secs. shooting ; and 2 min. 50 secs. hauling.

Secchi disc : 12½ m. on weather side ; 15 m. on leeward side.

1·45 p.m. Temperatures of sea. Surface 15·1° C. ; 5 m., 15·1° C. ; 10 m., 15·04° C. ; 15 m., 15·0° C. ; 20 m., 13·7° C. ; 30 m., 13·4° C.

2.30 p.m. Sun shining through clouds.

SERIES VII. 2 miles East of Eddystone.

3.7–3.32 p.m.

Nets fished at average depths of surface, 7·0, 13·8, 20·6, 27·4, and 34·2 m. Nets took 2 min. 49 secs. shooting ; and 2 min. 30 secs. hauling.

3.25 p.m. Secchi disc 15 m. on leeward side.

Haul ended about 4 miles E.N.E. of Eddystone.

TABLE II.

NUMBERS OF CALANUS FEMALES AND MALES IN EACH CATCH.

D, average depth of each haul. S, surface.

	SERIES I. July 21st, 1931.			SERIES II. July 21st, 1931.			SERIES III. July 22nd, 1931.	
D.	♀	♂	D.	♀	♂	D.	♀	♂
S.	22,726	186	*S.*	70,000	6,088	*S*	980	–
7·2	11,669	5,321	*7·9*	4,880	5,108	*8·1*	4,233	2,568
14·3	4,822	7,360	*15·7*	4,315	3,377	*16·1*	1,952	3,355
21·4	6,384	7,310	*23·5*	9,555	10,221	*24·1*	1,674	3,648
28·5	7,420	8,283	*31·3*	8,986	11,520	*32·1*	1,373	3,432
35·6	5,038	7,563	*39·1*	8,076	4,814	*40·1*	690	3,698

	SERIES IV. July 29th, 1931.			SERIES V. Aug. 5th, 1931.			SERIES VI. Aug. 12th, 1931.			SERIES VII. Aug. 12th, 1931.	
D.	♀	♂	D.	♀	♂	D.	♀	♂	D.	♀	♂
S.	5,010	53	*S.*	7	–	*S.*	26	1	*S.*	127	3
7·1	6,592	1,071	*7·1*	1,215	100	*7·5*	8,664	1,655	*7*	2,179	204
14·4	3,290	1,128	*14·3*	854	214	*14·9*	3,300	1,620	*13·8*	3,270	1,357
21·7	2,401	1,449	*21·4*	801	378	*22·3*	5,478	3,087	*20·6*	3,697	2,418
29·0	2,164	1,047	*28·5*	579	322	*29·7*	5,170	2,902	*27·4*	3,834	1,952
36·3	1,118	221							*34·2*	1,825	1,460

TABLE III.

LENGTHS OF CALANUS IN MILLIMETRES AS MEDIAN (Q_2), AND UPPER (Q_3) AND LOWER (Q_1) QUARTILES.

		FEMALES.			MALES.		
		Q_1	Q_2	Q_3	Q_1	Q_2	Q_3
July 21st.	Ser. I	3·102	3·186	3·275	2·955	3·034	3·119
,, 21st.	,, II	3·068	3·169	3·266	2·973	3·043	3·125
,, 22nd.	,, III	3·079	3·170	3·259	2·984	3·060	3·136
,, 29th.	,, IV	3·045	3·141	3·227	2·875	2·987	3·066
Aug. 5th.	,, V	2·958	3·068	3·171	2·840	2·943	3·055
,, 12th.	,, VI	2·921	3·000	3·127	2·768	2·837	2·943
,, 12th.	,, VII	2·899	3·013	3·117	2·776	2·873	2·965

TABLE IV.

Measurements of Total Lengths of Calanus in Millimetres.

	Females.							Males.						
	I.	II.	III.	IV.	V.	VI.	VII.	I.	II.	III.	IV.	V.	VI.	VII.
Mm.	July 21st.	,, 21st.	,, 22nd.	,, 29th.	Aug. 5th.	,, 12th.	,, 12th.	July 21st.	,, 21st.	,, 22nd.	,, 29th.	Aug. 5th.	,, 12th.	,, 12th.
2·53	–	–	–	–	–	1	–	–	–	–	–	–	–	–
2·585	–	–	–	–	–	1	–	–	–	–	1	1	2	3
2·64	1	1	–	1	–	2	–	–	–	–	–	2	5	2
2·695	–	–	1	–	2	5	2	–	1	2	–	1	4	5
2·75	–	–	1	2	1	6	13	6	1	1	3	5	13	13
2·805	2	2	2	6	7	12	17	6	6	9	7	6	19	23
2·86	5	7	4	12	20	24	33	13	7	8	15	10	18	16
2·915	9	9	–	11	23	30	38	29	15	16	11	11	22	23
2·97	11	16	8	25	27	36	40	28	21	25	14	13	14	18
3·025	29	15	19	34	37	55	52	62	45	48	26	11	10	15
3·08	34	34	18	56	40	50	48	47	36	60	16	7	4	8
3·135	61	39	31	67	41	38	–	53	36	56	13	5	6	4
3·19	85	50	34	83	37	35	27	34	27	31	8	9	2	3
3·245	71	41	33	56	33	16	22	15	11	22	2	1	–	1
3·30	70	42	29	47	11	16	18	8	5	12	–	1	–	–
3·355	41	27	19	27	10	6	5	2	2	1	2	1	–	–
3·41	25	9	6	7	4	3	1	–	1	1	1	–	–	–
3·465	9	7	4	6	1	1	2	–	–	–	–	–	–	–
3·52	6	4	–	5	–	1	–	–	–	–	–	–	–	–
3·575	–	3	1	–	1	–	–	–	–	–	–	–	–	–
3·63	2	–	–	–	–	–	–	–	–	–	–	–	–	–
Totals	461	306	210	445	295	338	366	303	214	292	119	84	119	134

Seasonal Changes in Biomass of *Calanus finmarchicus* in the Plymouth Area in 1930.

By

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With 8 Figures in the Text.

THIS paper deals with seasonal changes in the biomass of the copepod, *Calanus finmarchicus*. The work was carried out at the end of 1930 in the Laboratory of the Marine Biological Association at Plymouth with all the material of 1930 at my disposal.*

I take this opportunity of expressing my sincere thanks to the Director of the Plymouth Laboratory, Dr. E. J. Allen, for his ready assistance and for permission to work in the laboratory. I am much indebted, too, to E. Ford, V. A. Jaschnov, L. A. Zenkewitch for their valuable advice; particularly my heartiest thanks are due to F. S. Russell for supplying me with material and for the great assistance he has invariably given me throughout the present work.

"By biomass (Demoll) we term the quantity of substance in living organisms per unit of surface or volume. The biomass may be considered at some particular moment, the average yearly, seasonal, monthly, etc." (L. A. Zenkewitch, 1931.)

Weighing is the main method of obtaining the biomass. The conception "biomass" may be applicable also to the quantity of substance, characteristic for a given species at its different stages of development; it may even be applied to a single specimen. It is to be understood, then, that by biomass of a species or organism I mean here the quantity of substance in a living organism at a given moment. This quantity of substance is a characteristic of a given species just as are its size and morphological characters. The variations of biomass with seasons, locality, or in connection with age or different conditions of the medium, and the quantity of substance available for the species and the fluctuations of this quantity from stage to stage, form a definite complex, the study of which is a great problem.

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* Interesting papers by Marshall and Nicholls have appeared recently in the Journal of the Marine Biological Association (Vol. XIX, No. 1, August, 1933) in which some of the questions discussed in the present paper are considered and confirmed.

The determination of the biomass of plankton organisms is of no small importance as a means for the quantitative investigation of the biomass of the plankton. At present quantitative investigations on the biomass of the plankton must be conducted so as to show the weight value of separate components in the total biomass of the plankton, or in the food ration of the plankton-feeding organism (consumption of plankton). The solution of this problem depends on a knowledge of the fluctuation of the biomass, since the plankton community is exceedingly changeable both in time and space. The same quantity of biomass may be formed of different components. One efficient method is to use the average weight, i.e. *the biomass of a given species of plankton organism*, as a coefficient for finding the weight, when the number of specimens is known. Thus we obtain the biomass of each component and of the whole plankton sample, and the relation of the given component to the total biomass. This relates equally to the food of plankton-consuming organisms. Thus plankton in any sea area or fresh-water basin and plankton as food are comparable—both sides of the investigation of the plankton biomass being solved by making use of the same coefficients (average value of the plankton organism's biomass).

Attempts to estimate the weight of plankton organisms were made long ago. Apstein (1896) gives a number of determinations for specimens of the fresh-water plankton; Hensen (1887) records data on marine plankton; Vernadsky and Vinogradov (1927) have emphasized the necessity of characterizing each species by average weight. But these attempts were not systematic; moreover they have not been applied to investigations of the plankton biomass in order to elicit the role of the separate components. Therefore the investigation of the biomass of plankton lags behind similar investigations on the benthos and the feeding of the benthos-consuming organisms. It is impossible to apply the methods used in the study of benthos to plankton investigations for purely technical reasons. The examination of each plankton sample, or food supply, of a plankton-consuming organism, would take too much time; the selected quantity of each species also does not guarantee the possibility of weighing it on account of its minute weight.

Therefore, without finally deciding on the method of estimating the average biomass of the species, whether it be selection of great quantities of a given species in the case of the larger forms, or the weighing of whole cultures of the smaller forms, especially in phytoplankton, or the estimation of the biomass of the organism on the basis of body-volume—I myself consider the method of estimating plankton biomass described above as fundamental if the question is to be attacked from the view-point of dynamics.

The apparent technical difficulties of obtaining the biomass of the plankton organism are in fact not so difficult to overcome. The advantage of such determinations—the biomass having been once found for the organisms of a given area—lies in the possibility of applying the obtained values to further investigations, connected with the estimation of the quantity of substance (biomass). Also old quantitative data on the plankton may be used. This calculation may be made at present in round figures, using the range of the quantity of the biomass of the plankton organism so that the different fluctuations in the biomass of any organism do not affect the total biomass of the whole plankton and its separate groups. It is, however, of considerable interest for further detailed estimations of the plankton biomass in that it raises various questions of the actual problem of " organism and medium."

MATERIAL.

The material was obtained by regular half-hour oblique hauls with the 2-metre stramin ring-trawl two miles east of the Eddystone Lighthouse during 1930. Since the hauls were made with a large-meshed net only the largest copepodite Stages IV, V, VI males and females of *Calanus finmarchicus* were caught ; Stage IV was barely represented.

The material upon which I worked was collected on the following dates : February : 12th, 19th, and 26th. March : 5th, 12th, and 27th. April : 11th, 16th, 24th. May : 7th, 15th, and 22nd. June : 10th, 19th, and 26th. July : 4th and 9th. August : 7th. September : 3rd and 16th. October : 1st, 14th, and 16th. November : 13th and 26th ; and December : 3rd, 10th, 17th, and 22nd.

METHODS.

I made the following determinations : raw weight ; dry weight ; and length of the body.

The weighing of live specimens presents a number of difficulties, and fixed specimens were used instead. Our material was fixed in formalin. The use of other fixatives may strongly affect the material (Vinogradov, 1927).

1. *Raw weight* was determined according to the quantity of material available in the following manner :

(*a*) When material was scarce (up to 300 specimens per sample) all copepodid stages in the sample were selected separately ; the selected quantity was then divided into 2–3 portions according to the number of specimens of a given stage, and each portion was weighed separately.

(*b*) When a given stage was numerous five portions were taken, each containing not less than 100 specimens of each stage.

The preparation of specimens for raw weighing is of paramount importance. To obtain the raw weight all the moisture must be taken off the body; this is no easy task. The usual method of drying in filter-paper (Bogorov, 1933) depends greatly on the individual capacities of the worker and on the conditions under which the weighing is performed; thus the results obtained are not always suitable for comparison, being no more than an index of the range of value of biomass. These deficiencies in the filter-paper method stimulated the working-out of more efficient methods, and I worked out such a method with the kind help of E. M. Kreps.

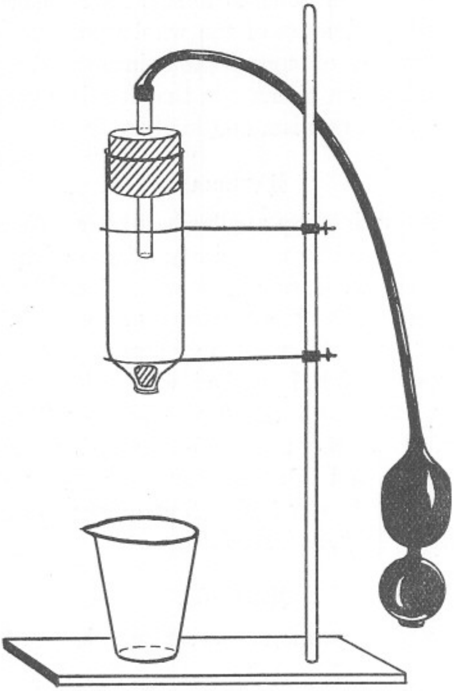

Fig. 1.—Device for "liquid" drying, to drive away water from the body-surface.

This method was based on the driving away of the moisture of the body surface by means of a dripping liquid. A device was constructed as follows: A small test-tube, not over 10 c.c., with a conical bottom and a hole in the apex of the cone, is fixed in a support. A glass ball, closing the lower aperture is placed at the bottom of the test-tube. The sides of the ball are somewhat flattened, forming facets, so as to let the liquid run freely out of the tube; but these facets must be of such a size that none of the specimens are washed out of the tube with the dripping liquid. This test-tube is stopped at the top by a cork, with a glass tube connected by rubber tubing with an air-pumping balloon (Fig. 1).

A weighed portion of the organisms was placed at the bottom of the tube; after all the water, brought with the portion, had been driven down the aperture of the tube, 1 c.c. of 90% alcohol was poured into the test-tube which, running down in a few seconds, brought away all the moisture of the body surface. Then 1 c.c. of ether was poured into the test-tube; the ether, running down rapidly, drove away the remaining alcohol. Then the test-tube was stopped, and air pumped through it for 30–60 seconds, according to the quantity of specimens, to drive out the ether vapour. The degree of dryness was decided arbitrarily, drying being continued until no apparent signs of liquid were left on the surface of the body. When immersed in water most of the specimens sank to the bottom. The exact degree of drying is somewhat indefinite, but after a short training some homegeneity is obtained. The use of measured quantities of fluid gives this method an appreciable advantage over the filter-paper drying method.

As is well known, alcohol extracts a good many substances (Vinogradov, 1927), over 10% in weight. In order to evaluate the method and to find the amount (in weight) of substances extracted by the rapid flow of alcohol and ether in our device, the resulting liquor was analysed. It was found to contain a negligible quantity of extracted substances, fluctuating from 1–2%. As compared to the filter-paper drying method the weight after " liquid " drying is somewhat smaller, but the range of fluctuation between separate weighings is clearly in favour of " liquid " drying.

2. *Dry weight.* The study of specimens by dry weight has many advantages over that by raw weight as it is evidently more accurate and supplies data of actual weight of the body-substance. The dry weight is thus a better characteristic of biomass and it should become the main unit in the determination of biomass.

The raw weight data depend chiefly on the quantity of water contained in the body, not on the quantity of substance of an organism, and the quantity of water in the body of different organisms is variable and depends on different conditions.

To find the dry weight a dessicator containing calcium chloride was used. After obtaining the raw weight the same organisms were placed on the grid of a dessicator on a weighed cover-slip. The material remained in the dessicator usually for two or three days, and weighing was repeated not less than three times at one-day intervals. If the last two weighings were equal the material was considered sufficiently dried and the counts were made.

The figures of dry weight thus obtained are not figures of *constant* dry weight. To obtain the latter the method must be considerably improved by drying in a high-temperature thermostat, or for a very long time. Yet this method gives figures, which, although not of absolute constant dry weight, are still constant to some degree, and fit for comparison, giving a much truer picture of the quantity of substance of an organism than does raw weight. The simplicity of operation, the little time needed, the portability and accessibility of the applied method and the comparative exactitude of the data obtained, tend to uphold dry weight as the best method for obtaining the biomass.

Both dry and raw weights were obtained on the Sartorius analytical balance.

3. The *length measurements* were made with a micrometer eyepiece. The total length was measured from the front edge of cephalothorax to the end of caudal furcæ, the furcal setæ being excluded.

RESULTS.

The results of weighing and measurement clearly show that both biomass and size of Calanus throughout the year are not constant but undergo changes, which so far as weight is concerned may be as great as twice their value.

The data show that the maximum of raw weight (Table I) was observed in May. Stage V (7th May), 0·7 mg. ; adult males (15th May), 1·13 mg. ; and females (15th and 22nd May), 1·10 mg.

The minimum weights were for Stage V, 0·35 mg. (14th October and 13th November) ; adult males, 0·50 mg. (13th November) and females, 0·41 mg. (16th October). The maximum range of fluctuation was for Stage V, 0·35–0·70 mg. ; for adult males, 0·50–1·10 mg. ; for females, 0·41–1·10 mg.

The maximum dry weight for all stages (see Table II) occurred on 15th May : Stage V, 0·252 mg. ; adult males, 0·259 mg. ; and females, 0·256 mg. The minimum dry weights were for Stage V, 0·078 mg. (1st October) ; for adult males, 0·100 mg. (16th October) ; and for females, 0·100 mg. (16th October and 26th November).

TABLE I.

Raw Weight in Milligrams.

Months.	February.			March.			April.	
Dates.	12	19	26	5	12	27	11	16
V	0·40						0·44	0·48
VI ♂	0·58	0·61						0·64
VI ♀	0·69	0·58	0·56	0·78	0·59	0·58	0·64	0·89

Months.	May.			June.			July.		August.
Dates.	7	15	22	10	19	26	4	9	7
V	0·70	0·68	0·62	0·50	0·66	0·43		0·57	0·55
VI ♂	0·85	1·13	0·90	0·69	0·74		0·74	0·74	0·72
VI ♀	1·05	1·10	1·10	0·84	0·93	0·80	0·86	0·88	0·89

Months.	September.		October.		Nov.	December.			
Dates.	3	16	14	16	13	3	10	17	22
V	0·61	0·39	0·35	0·40	0·35	0·45	0·39	0·40	0·39
VI ♂	0·83		0·73		0·50	0·55	0·59	0·55	0·53
VI ♀	0·93	0·81	0·53	0·41	0·50	0·56	0·62	0·55	0·48

TABLE II.

Dry Weight in Milligrams.

Months.	February.			March.		April.		May.		
Dates.	12	19	26	5	27	11	16	7	15	22
V		0·132				0·116	0·119	0·248	0·252	0·216
VI ♂		0·128					0·158	0·256	0·259	0·250
VI ♀	0·100	0·122	0·118	0·130	0·138	0·126	0·175	0·254	0·256	0·252

Months.	June.			July.		August.	September.	
Dates.	10	19	26	4	9	7	3	16
V	0·150	0·190	0·166	0·184	0·196	0·196	0·134	0·139
VI ♂	0·184	0·206		0·200	0·174	0·154	0·170	0·163
VI ♀	0·186	0·224	0·172	0·172	0·214	0·214	0·210	0·177

Months.	October.			November.		December.			
Dates.	1	14	16	13	26	3	10	17	22
V	0·078	0·116	0·112	0·128	0·116	0·106	0·128		0·138
VI ♂		0·120	0·100	0·110		0·118	0·141	0·131	0·109
VI ♀	0·134	0·110	0·100	0·124	0·100	0·110	0·126	0·120	0·141

TABLE III.*

Median Length (Q_2) in Millimetres.

Months.	February.			March.			April.		
Dates.	12	19	26	5	12	27	11	16	24
V		2·72					2·89	2·98	
VI ♂	3·01	3·02					3·30	3·27	
VI ♀	2·98	2·98	2·97	3·00	2·96	2·98	3·07	3·40	3·53

Months.	May.			June.			July.		August.
Dates.	7	15	22	10	19	26	4	9	7
V	3·15	3·09	2·96	2·88	2·86	2·75	2·86	2·81	2·84
VI ♂	3·54	3·59	3·52	3·30	3·30		3·20	3·14	3·19
VI ♀	3·57	3·58	3·61	3·37	3·37	3·27	3·24	3·25	3·30

Months.	September.		October.			November.		December.			
Dates.	3	16	1	14	16	13	26	3	10	17	22
V	2·85	2·75	2·67	2·61	2·69	2·74	2·67	2·56	2·70	2·63	2·75
VI ♂	3·24	3·14	2·95	2·80	2·84	2·90	2·85	2·98	3·09	3·01	2·99
VI ♀	3·38	3·24		2·93	2·83	2·90	2·84	2·94	2·87	2·90	2·85

From the measurements for Stages V and VI males and females were calculated the quantities Q_1, Q_2, and Q_3, Q_2 being the median size (see Tables III and V, and Fig. 3).

Stage IV was very scarce owing to the large-meshed net employed. Measurements gave the following results : April 11th, 2·28 mm. and 16th 2·07 mm. ; May 7th, 2·39 mm. ; June 10th, 2·10 mm. ; July 4th, 2·10 mm

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* In the table are not included data of days when quantity of sampled material was too small to allow computation of average size (Q_2).

and 9th, 2·13 mm.; September 16th, 2·15 mm. and 24th, 2·20 mm.; October 1st, 2·06 mm. and 14th, 2·11 mm.

The maximum average length of the body occurred in May: Stage IV, 2·39 mm.; Stage V, 3·15 mm.; Stage VI males, 3·59 mm.; and Stage VI females, 3·61 mm. The minimum average size occurred in October: Stage IV, 2·06 mm.; V, 2·61 mm.; VI males, 2·80 mm.; VI females, 2·83 mm.

In spite of the great changes of biomass and size during the year we see that for certain periods (see Figs. 2, 3, and 4) both biomass and size remain nearly constant. Three such seasons may be observed:

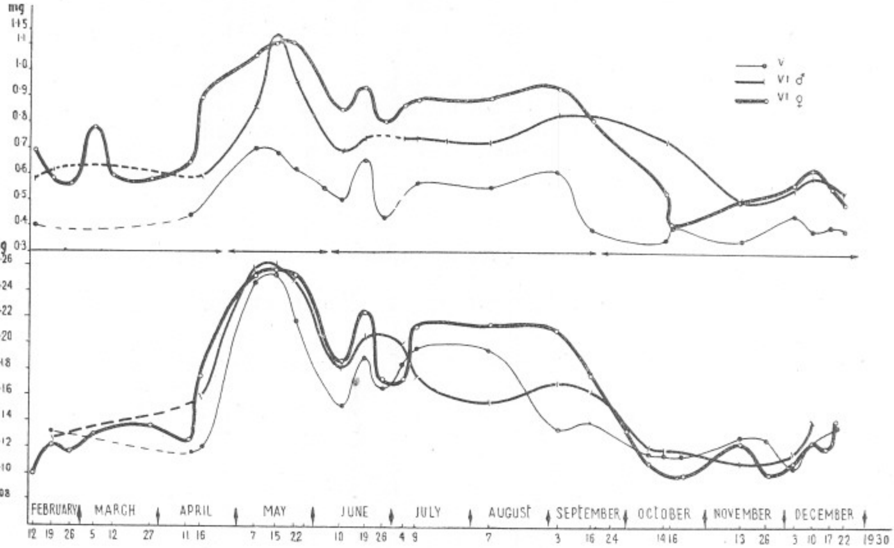

FIG. 2.—Seasonal changes of biomass in *Calanus finmarchicus* (copepodite Stages V, VI males and females) in the Plymouth area in 1930.

Upper part of the graph—curves for variations in average raw weight. Lower part of the graph—curves for variations of average dry weight. Horizontal line with arrows—period of predominance of a given generation.

The first season—"autumn–winter"—from end of September to middle of April; the second season—"spring"—from end of April to June; the third—"summer"—from June to middle of September. As may be seen the seasons differ greatly in duration; and do not coincide with calendar seasons. But yet they are well differentiated in the biomass and size of Calanus. Small fluctuations in the curves during each season are possibly due to faulty methods in preparing and sampling of material.*

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* Marshall (1933) has since shown that this may possibly be due to differences in size between the first and last born in any generation, the former being slightly larger than the latter.

The length of the season is given in Figure 2 by horizontal lines. Our seasons may also be well characterized from the hydrographic view-point (Harvey, 1930) especially according to temperature. The "autumn–winter" season is characterized by homogeneousness of temperature from surface to bottom, the temperature value decreasing from month to month. Towards the end of the "spring" season a discrepancy appears between surface and bottom temperature, that of the surface getting warmer. The "summer" season is characterized by a marked stratification of temperatures and a strong warming of the whole mass of water, especially of the surface layers, the warmest time being towards the end of August and the bottom water attaining its maximum in September.

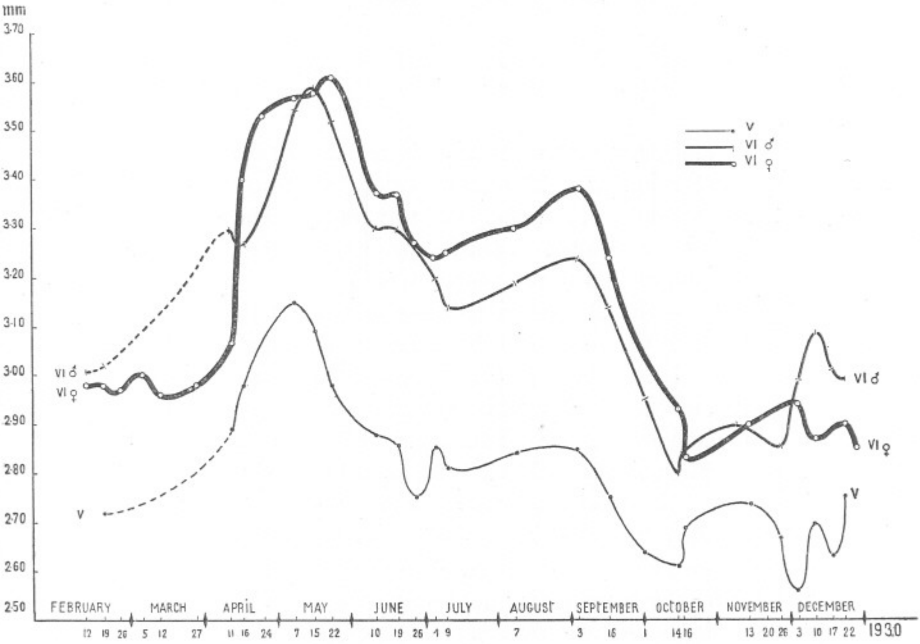

FIG. 3.—Seasonal changes in average size (Q_2) of *Calanus finmarchicus* (copepodite Stages V, VI males and females) in the Plymouth area in 1930.

The salinity in the Plymouth area is subject only to slight fluctuations, its value being about $35^\circ/_{\circ\circ}$. The main source of the water supplied to the English Channel is the Atlantic. In the course of the year the main current of the English Channel is unstable in strength and partly in direction.

To characterize our seasons by biomass and size I have summed up data of Tables I, II, and III. In this way I obtained the following average values for biomass and size (Table IV):

TABLE IV.

	Stages.	Seasons.			Yearly average.	Ratio of Spring/ Autumn-Winter.
		Autumn, Winter.	Spring.	Summer.		
Raw weight mg.	V	0·40	0·67	0·53	0·53	1·7
	VI males	0·59	0·98	0·74	0·77	1·66
	VI females	0·60	1·08	0·87	0·85	1·8
Dry weight mg.	V	0·117	0·239	0·169	0·174	2·04
	VI males	0·124	0·255	0·179	0·186	2·06
	VI females	0·123	0·254	0·196	0·191	2·06
Average size mm.	V	2·72	3·07	2·82	2·87	1·13
	VI males	3·00	3·57	3·22	3·26	1·19
	VI females	2·96	3·57	3·30	3·28	1·21

Stage IV, which was very scarce, is not included in this table. The table shows that the minimum of biomass in the "autumn–winter" season is about as much smaller than the yearly average as the maximum of the "spring" season is greater. Values characteristic for "summer" forms are approximately equal to the yearly average.

The picture of the change in biomass and size during the year is as follows: Early in the year (from February to mid-April) the biomass and size are small. In April the picture begins to alter and in the material of April 16th occur big forms (see Fig. 4) and we observe a decided rise of the average for biomass and size. The big organisms prevail from the end of April and throughout May, the average value of biomass and size being at its maximum, which is characteristic for our "spring" season. From the end of May (May 22nd) begins a decrease in biomass and size, slight for adults and considerable for Stage V, continuing to the first decade of June. During the subsequent months, to the middle of September, the values of biomass and size remain stable, which is characteristic for our "summer" season. From the middle of September for adults, and the end of August for Stage V, biomass and size begin to decrease, the values reaching their lowest level in October and slightly rising again in the subsequent months, but still being very low and deviating greatly from those of the "spring" and "summer" seasons, which is characteristic for the "autumn–winter" season, from end of September to the middle of April.

August and September are intermediate months (see Fig. 4) containing forms, characteristic for different "adjacent" seasons, some organisms gradually replacing others in the course of the month. Evidently the same may be expected in June, but here the replacing of "spring" organisms by "summer" ones is much more rapid and does not show clearly in our material.

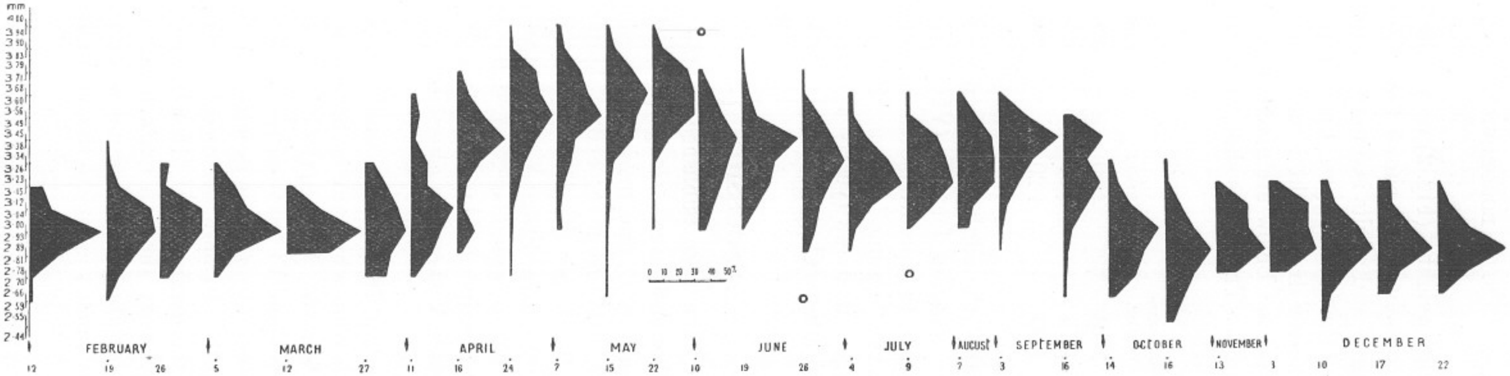

FIG. 4.—Seasonal changes in the percentage size distribution of *Calanus finmarchicus* (Stage VI females) in the Plymouth area in 1930.

In the curves for " dry weight " (Fig. 2) we see the stage-curves following one another very closely. This shows that the difference in " raw weight " between Stage V and adults is due to the difference in quantity of water in specimens of these two stages. Calculation has shown that the surplus of raw weight over dry weight is not constant throughout the year or for different stages. Below are given data showing the ratio of raw weight to dry weight. (The figures show how many times raw weight is greater than dry weight.)

	Seasons.			
Stages.	Autumn–Winter.	Spring.	Summer.	Yearly average.
V	3·40	2·80	3·10	3·10
VI ♂	4·75	3·80	4·10	4·22
VI ♀	4·90	4·20	4·40	4·50

These figures show that the adults contain more water than Stage V, the greatest quantity being in females (VI ♀), and that during the " autumn–winter " season the quantity of water is at its maximum, the minimum occurring in the " spring " season. If the quantity of water be expressed in percentages, it shows (yearly average data) that Stage V contains 65% of water ; adults VI males, 76% ; and VI females, 78%.

DISCUSSION.

No exhaustive data have been published on the biology of *Calanus finmarchicus* in the Plymouth area. Gough (1905), Lebour (1917), and others record the presence of *C. finmarchicus* all through the year and its predominance (Lebour, 1917) from the end of April to the beginning of November. Russell (1928) was the first to give quantitative data for Calanus in the Plymouth area (Stage V and adults, males and females) for a period from April 9th to September 22nd, 1926. His results show that the adults exhibit two maxima in abundance, the first in May–June, the second in August. Stage V shows an alternating decrease and increase in quantity each month.

Russell (1933, Table I, p. 76) gives the total numbers of Calanus in the half-hour oblique hauls from which my material was obtained, and these results are plotted in Figure 5. Early in the year *C. finmarchicus* was very scarce. In March Stages V and VI♂ were entirely lacking. At the beginning of April the quantity began to increase rapidly showing enormous figures to the end of the month. In May the quantity increased still further, reaching on May 7th the maximum of 318,450 specimens in a half-hour haul. In June the quantity shows a marked fall, still remaining at a comparatively high level (about 1000 specimens for a half-hour haul) and keeps stable during the whole summer to the beginning of August. From the end of September the number begins to decrease rapidly (about 100 specimens per haul) becoming quite small in the middle of October and remaining so through all the "autumn–winter" period. There are occasional marked decreases in quantity, e.g. at the end of April, or in summer, but the general trend of the curve remains constant.

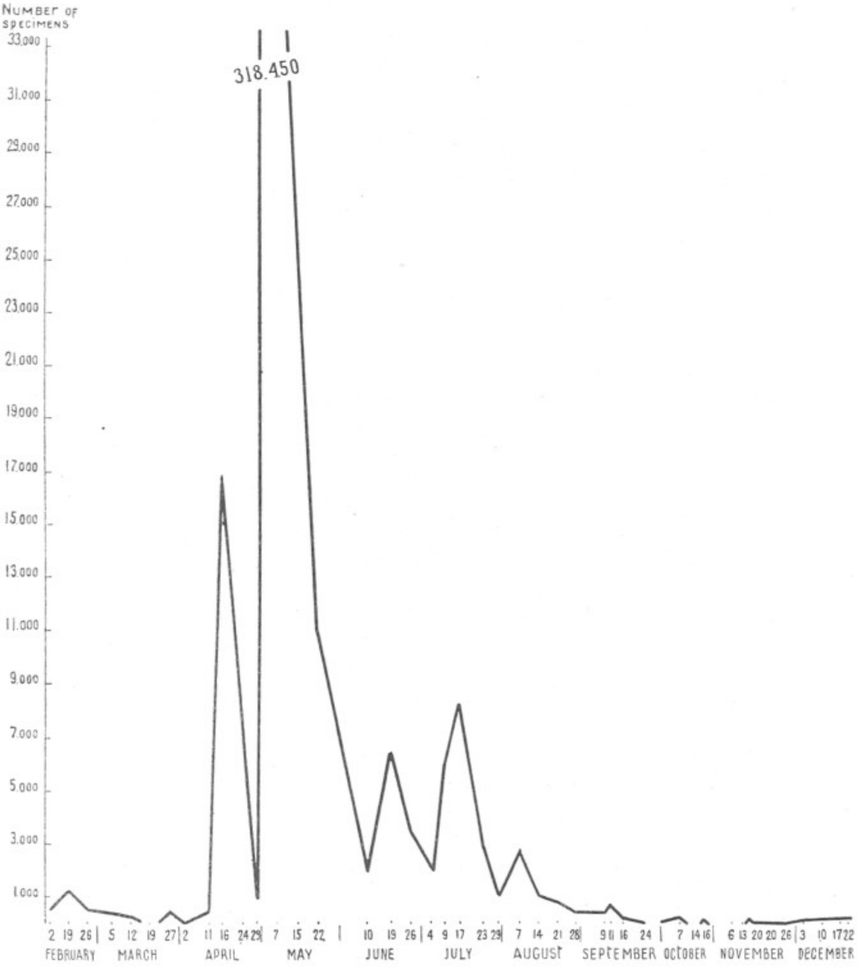

FIG. 5.—Seasonal changes of total number of *Calanus finmarchicus* (copepodite Stages IV, V, VI—males and females) in the Plymouth area in 1930.

Number of specimens caught during a half-hour oblique haul with a 2-metre stramin ring-trawl. Mostly composed of Stage VI females.

The same picture is given by other authors for different parts of the North Sea and the adjoining areas: Paulsen (1906), Damas (1905), Gran (1902), Marshall (1924), Farran (1920, 1927), Johnstone, Scott, and Chadwick (1924), Runström (1932), and others.

The observed times of reproduction of *Calanus finmarchicus* in different parts of the North-European seas are as follows :* Gran (1902) states that the period of reproduction is April–May for the North-Western coast of Norway ; Damas (1905), June for the Norwegian Sea ; May and June for the Faroe Islands. Paulsen (1905), from the end of March up to June for Southern Iceland. Damas and Koefoed (1907), end of June for Norway and Spitzbergen. With (1916), June for Danish current ; May, for Southern Iceland ; June and July, for Western Greenland, and the end of June for Eastern Greenland. Johnstone, Scott, and Chadwick (1924) assign the time from June to August and from September to October as the periods of reproduction for the Irish Sea in the area of Port Erin, whilst Farran (1927) considers April and May as the main period of reproduction for the given area.

The occurrence of both males and females of *C. finmarchicus* all the year round in these regions gives rise to the suggestion that there may be several periods of reproduction and hence several generations in the course of a year.

Paulsen (1905) suggests two periods of reproduction for Iceland area : early spring and end of summer. Ruud (1929) points out the occurrence of a great number of nauplii in the Möre area in March–April and June–July, indicating that there may be two periods of reproduction in this area, in spring and in summer ; the suggested time of spawning for the first period is February–March, for the second, May–June.

In Runström's (1932) tables on page 58–59 we see that the great quantities of *C. finmarchicus*, occurring from March to September, are interrupted by smaller quantities in July. This may be explained by the existence of two periods of reproduction.

Russell (1928) on the basis of measurements states that the great number of *C. finmarchicus*, appearing at the end of April, were hatched in March. This brood is marked by its large size and is termed by the author as " large " brood. This " large " brood is short-living and in the course of May reproduces individuals of a smaller size, " small " brood, and soon dies off. Throughout the summer months, July and August and presumably in September, intermittent spawning occurs, resulting in a new generation, which tides over the winter months to spawn early in the next spring and reproduce once more a brood of large individuals. Females carrying spermatophores occur throughout the year ; in April the number of spermatophore-carrying females is greater than in the following months of May and beginning of June ; then it rises again, reaching the April value in August.

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* Most authors have no yearly material available, which is a drawback.

Thus we may consider that Russell records three periods of reproduction throughout the year, the first period being March–April; the second, May; and third, July–August.

In other regions, too, several periods of reproduction are recorded. Bigelow (1926) records two periods of reproduction for the area of the Gulf of Maine—spring (May) and autumn (September). The first period gives rise to abundant masses of *C. finmarchicus* in spring and summer months; the second period gives smaller quantities, but constantly occurring in the winter months and reproducing again great quantities in spring.

Farran (1927) finds that in the area south of Ireland the young of the previous year become adult in January, February, and March, and that there is a big outburst of reproduction in March–April, reproduction then going on irregularly throughout the rest of the summer.

We have the right to presume the existence of only one generation for Arctic seas, where males occur in a definite short period of time, being quite rare in the plankton (Bogorov, 1932); whereas in those regions, where both sexes occur throughout the year, we have full reason to presume the existence of several periods of reproduction.

My Plymouth material, though not supplying data on young stages and on the presence of spermatophore-bearing females, leads me, nevertheless, to conclusions approaching those of Russell; I endeavoured to complete these data with winter material and to complete the picture of yearly changes in the biomass.

Taking the period of development of Calanus from egg to adult as averaging two months (Lebour, 1916), the rate of the process being different at different seasons, we may presume that the appearance of great masses of Calanus at the end of April and especially in May is due to their reproduction early in the year. These individuals differ appreciably in size and weight from those occurring in winter catches (see Fig. 4). They are considerably greater and heavier; VI females, size, 3·57 mm.; raw weight, 1·08 mg.; dry weight, 0·254 mg. (see Table IV), whereas the size and weight of the "autumn–winter" individuals, having produced the above mentioned is: VI females, size, 2·96 mm.; raw weight, 0·60 mg.; and dry weight, 0·123 mg. The generation of big individuals predominates in the adult stage for a very short time, from end of April to beginning of June, after which, as Figure 4 shows, it disappears, giving place to smaller and lighter individuals, resulting from a generation, produced from big individuals of the end of May. This new generation predominates from June to the beginning of September and is characterized by its size: VI females, 3·30 mm.; raw weight, 0·87 mg., and dry weight, 0·196 mg. In September occurs a rapid disappearance of the generation in question, and a replacement by smaller individuals. The latter generation results from intermittent reproduction throughout the summer season, as pointed out by Russell.

It may be supposed that the end of August and beginning of September is the last period of summer reproduction, the resulting generation tiding over the autumn–winter period. Such intermittent reproduction makes both biomass and size unstable in the autumn and winter periods. However both biomass and size show a slight marked tendency to increase in the course of the period. This is clearly shown by changes in the monthly average.

Stage.	Raw weight.					Dry weight.					Size.				
Months.	Oct.	Nov.	Dec.	Feb.	Mar.	Oct.	Nov.	Dec.	Feb.	Mar.	Oct.	Nov.	Dec.	Feb.	Mar.
V	0·38	0·35	0·41	0·40		0·102	0·122	0·124	0·132		2·66	2·71	2·66	2·72	
VI ♂	0·73	0·50	0·56	0·60		0·110	0·110	0·125	0·128		2·86	2·88	3·02	3·02	
VI ♀	0·47	0·50	0·55	0·61	0·65	0·115	0·112	0·124	0·113	0·134	2·88	2·87	2·89	2·98	2·98

Hence biomass and size in February and March are greater than in October, November, and December. This is probably due to the dying-off of the early born individuals ; Stage V being the source from which adults are drawn (recorded by Farran, 1927) up to the end of February, at which time all the Stage V pass into adults. This coincides with the disappearance of adult males, and supports the suggestion that fertilization had taken place not long before, after which appears a new generation. Several months may elapse before the laying of eggs and hatching of nauplii as pointed out by Farran (1927).

It is worthy of notice that during the " autumn–winter " season males are much more abundant than females, which is just the reverse in other periods.

We would be justified in considering the *C. finmarchicus* of different sizes occurring at different seasons as separate generations if we had proof enough that they actually originated from one another, and that the waters of the region investigated were of the same origin. To decide the first question we need information on the occurrence of the different stages of development throughout the year (viz. eggs, nauplii, and all copepodid stages). Unfortunately I have no available material of that kind, but the literature data, especially those supplied by Russell (1928) and the hydrographical conditions of the waters of the English Channel, strongly support the opinion that several generations may occur here, the waters being from a homogeneous source, namely, the Atlantic.

For lack of material I can give no definite answer to the essential question, whether the Calanus in the Plymouth area are constant inhabitants or whether they are brought here by water currents. But even if these masses of Calanus are brought from another region, our considerations hold true and we have only to make allowance for the time of migration of these masses and for the areas of reproduction of Calanus, from which the main source of supply in the Plymouth region is drawn.

As a result of the present investigation we have the following " generations," which I have named according to the seasons in which they predominate.

The " spring " generation—resulting from reproduction in February–March. Adults predominate in the plankton for about a month and a half (from end of April to May). Value of biomass and size is greatest compared to that of other seasons (Table IV, Figs. 2 and 4).

The " summer " generation—resulting from May reproduction. Adults prevail for about 3½ months from June to mid-September. In biomass and size they are smaller than those of the spring generation.

The " autumn–winter " generation—resulting from intermittent reproduction during the summer months from June to August. The adults prevail during eight months from end of September to mid-April. In biomass and size this generation is the smallest.

What are the causes of seasonal changes of biomass and size ? In Figure 6 are given changes in temperature (from Russell, 1932) and in the size of Calanus for the year 1930. The salinity in the Plymouth area is not subject to any appreciable changes in the course of the year ; the source of water supplied into the Channel remains the same, namely the Atlantic.

While it must be realized that many factors influence biological phenomenon it is evident that temperature is of great importance, reflecting as it does, other environmental changes.

Considering the two-months period, which Calanus takes for developing from the egg to the adult, we see that the " spring " Calanus hatched and developed in cold winter water at the temperature of 8–9° ; the " summer" Calanus grew up in the warmer water of spring and early summer at 10·5 –14·5° ; and the " autumn–winter " Calanus developed in still warmer water of the end of summer at 15–16° C. Plotting on the same graph (Fig. 6) the curve of change of biomass, characteristic for the given season (Table IV) and that of temperature conditions characteristic for the moment of reproduction and beginning of development, i.e. two months previously, we obtain evidence of the interrelation between temperature conditions at the beginning of development and the value of biomass and size of the adults. We see that big organisms with large biomass and size are generated under low temperature conditions and *vice versa.* If we follow the changes in biomass and size during the " autumn–winter " season we observe, as stated above (page 600), that the value of both increases from month to month, the temperature falling respectively. Again we see here the same interrelation, i.e. falling of temperature producing increase in biomass and size.

In contrast to the above we have to deal here with the long-living Stage V, which gradually passes into the adult stage (as recorded by Farran, 1927). Resulting from such lengthy development under conditions of continually decreasing temperature we obtain, in February–March, organisms marked by their greater size in comparison with individuals of the same generation, which have passed a shorter cycle of development and reached the adult stage in October–December. Thus the influence of temperature, which affects later stages of development, is noticeable in the size of adult organisms just as much as if it had occurred in earlier periods of growth.

Investigations on the yearly changes in size of marine and fresh-water copepods have been made by a number of workers; amongst these the following may be quoted, Adler and Jespersen (1920), on Calanus, Pseudocalanus, and Temora; Gran (1902) on Calanus; Rzoska (1927) on *Cyclops strenuus*; Störmer (1929); Ruud (1929); Gardiner (1933); and Russell (1928) on Calanus.

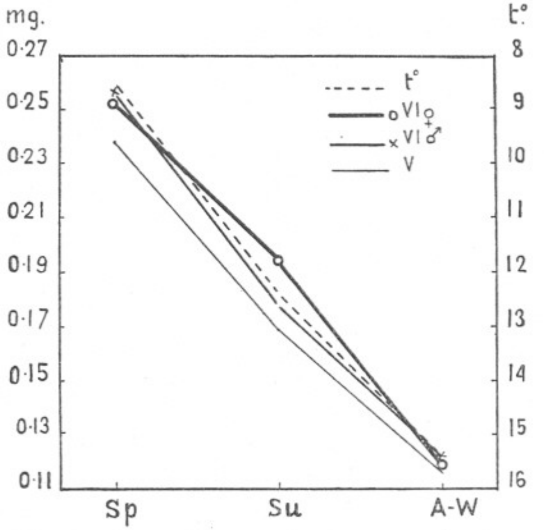

FIG. 6.—Average biomass of a generation of a given season; temperature at time of hatching and beginning of development of a given generation. Sp. = Spring; Su. = Summer; A.-W. = Autumn–Winter.

Comparing our results of 1930 with those of Russell (1928) for 1926 we plotted a graph (Fig. 7) where the thick line shows our results and the thin one those of Russell. We see that in the main 1930 results are characterized by lower temperature and greater size while in 1926 we observe the reverse phenomenon. The graph as a whole, as well as in detail, is very convincing. The " spring " Calanus of May 1930 is larger than that of

1926, temperature conditions at the time of hatching and development (February–March) in 1930 being colder than in 1926. In June and beginning of July the size-curves of 1930 and 1926 follow one another very closely, showing even a smaller size in 1930, but the temperature conditions of May, when the generation in question was developing, were warmer in 1930 than in 1926. Further, the summer of 1930 was colder than in 1926, resulting in the greater size of Calanus of 1930. Finally, in early autumn the temperatures of 1930 and 1926 become similar, which is reflected in the close coincidence of the curves.

It is interesting that the size-curve of summer 1930 is repeated as it were by the temperature curve. Thus we see that the forms in September are larger than those in July. This discrepancy with the basic data is not essential as far as biomass (Fig. 2) is concerned, and the sizes of 1926 Calanus do not exhibit such a picture. It is worthy of notice that the discrepancy between the sizes of 1930 and those of 1926 at the same time is as great as the difference in temperatures of June and early July, which fact, considering the time of development of *C. finmarchicus*, is another proof of the definite dependence between temperature and size of organisms.

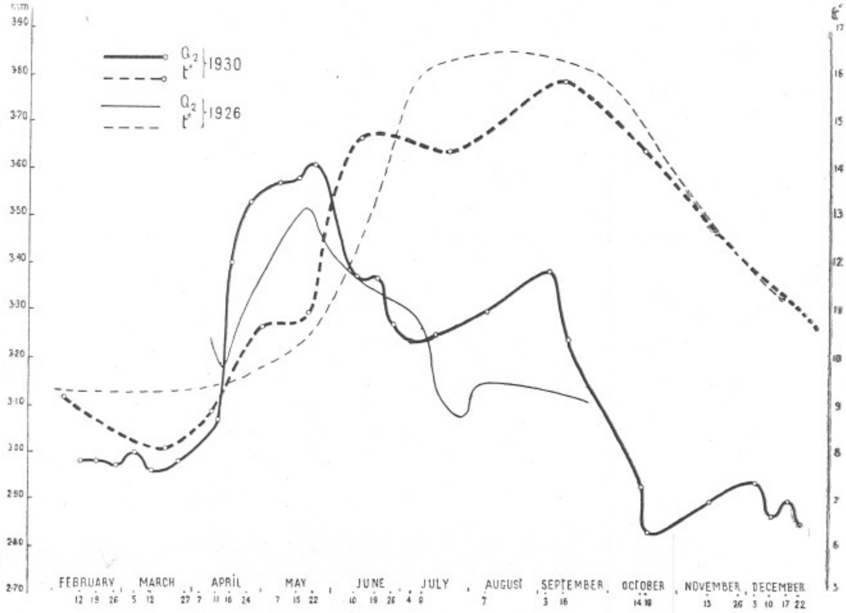

FIG. 7.—Comparison of seasonal changes of size of *Calanus finmarchicus* (Stage VI females) and of temperature in the years 1930 and 1926 in the Plymouth area.

Thick line, 1930; thin line, 1926; continuous line, size of females; broken line, temperature.

In order to elicit the correlation of temperature and size of organism I drew a correlation table (Fig. 8), (*a*) for comparing the biomass and length of organism and the temperature of the medium (Nos. 1 and 3), this

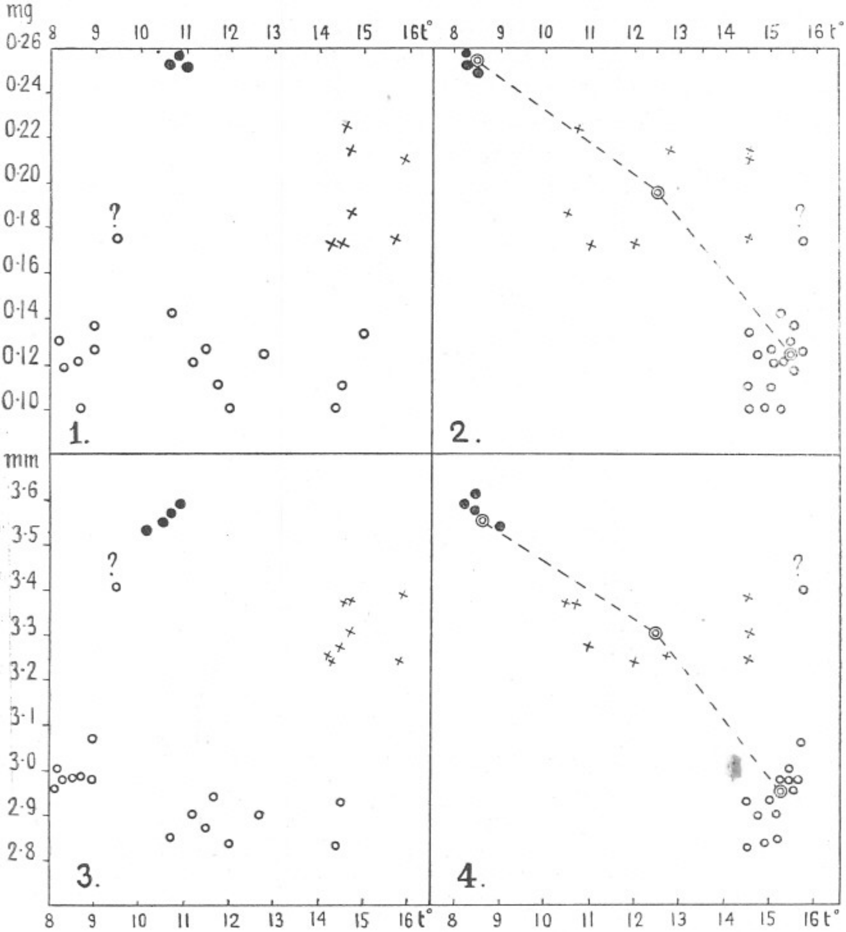

FIG. 8.—Correlation table. Comparison of size and biomass of *Calanus finmarchicus* (females) with temperature.

Nos. 1 and 3—Comparison of biomass (dry weight) and size with temperature of medium. Nos. 2 and 4—Comparison of biomass and size with temperature at time of hatching of given generations.* (● = Spring generation ; × = Summer generation ; ○ = Autumn–Winter generation.)

being the static moment; and (*b*) for comparing the temperature of the period of reproduction with the biomass and length of the resulting generation (Nos. 2 and 4), this being the dynamic moment. In order to

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* In Nos. 2 and 4, average values of a given generation are connected by a straight line.

facilitate reading I have put different signs for different generations. The correlation table shows clearly that firstly (Nos. 1 and 3) small and large organisms occur at all possible temperatures, and secondly (Nos. 2 and 4) all points are strictly within definite temperature limits; if a line be drawn from small to large organisms it will show that low temperature throughout the period of development is the greatest stimulant to growth and *vice versa*.

The graph shows also that in studying the correlation of temperature and size the question is to be regarded from the point of view of dynamics.

A number of investigations on origin of forms in Copepoda show that different geographic-hydrological areas are inhabited by different species and more minute taxonomic subdivisions, low temperature areas being characterized by species and forms of larger size, whereas the warm tropical waters are inhabited by small-sized forms. In a series of papers Steuer (1923 and 1931) has shown on the genus Acartia, Pleuromamma, and Rhincalanus that, for example, the large-sized species *Rhincalanus gigas* is abundant in the cold waters of the Antarctic. The medium-sized *R. nasutus* is widely known in all oceans, but in the colder waters. The small-sized *R. cornutus* is met with in the warm surface water of the Atlantic and Indian Oceans.

By comparing the size of *C. finmarchicus* in the Barents Sea with that of this species in the Plymouth area I found (1933) that the former was much larger. The temperature conditions of Barents Sea waters are much colder than those of the Plymouth area, which accounts for the difference in size of the Calanus.

Many of the above-mentioned authors—Adler and Jespersen (1920), Ruud (1925), Störmer (1929), and others—give the same data. Later investigations in Barents Sea (Bogorov and Preobrajenskaya) have shown, that in different areas of the Barents Sea, which is heterogeneous in its hydrographical conditions, both biomass and size of *C. finmarchicus* vary also, being larger in cold-water than in warm-water regions.

It would be interesting to make an attempt to find the interdependence between biomass of the plankton organism and the temperature differences.

The difference in temperature between the times of hatching of "spring" and "autumn–winter" generations of *C. finmarchicus* in the Plymouth area is about 8°. In biomass the "spring" Calanus are twice as large as the "autumn–winter" ones. The difference of temperature of the English Channel and the Barents Sea* is about 10°; average biomass in *C. finmarchicus* of the Barents Sea is about twice the value of

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* In both cases we compare the temperature for time and locality of sampling of *C. finmarchicus*, hence our average data are not the averages for the whole English Channel or the Barents Sea.

that of *C. finmarchicus* in the English Channel. But the comparison of the northern part of the Barents Sea with the southern one showed that 5° difference in temperature brought forth a threefold difference in biomass. Hence the value of the difference in temperatures depends on its place on the temperature scale, the influence of smaller differences in temperatures, under lower temperatures having a greater effect than large differences at higher temperatures. This means that the size of an organism (biomass) is no simple function of one single factor, even if it be such an important one as temperature, and that there is in different cases the combined influence of various conditions, forming altogether the physico-chemical and biological complex of conditions of existence of the organism. It is quite evident, nevertheless, that temperature conditions are of paramount importance in this complex.

We stated above that the *C. finmarchicus* of the Barents Sea produces only one generation in the course of the year while that of Plymouth area gives three generations. Thus the Calanus of the Barents Sea lives longer than that of Plymouth area, its biomass also being respectively greater. This leads to the conclusion that organisms in cold-water regions have the advantage of greater biomass, whereas warm-water organisms can produce more generations. It is interesting to note that when summed up, the biomass of three generations of *C. finmarchicus* in the Plymouth area (adult females—2·55 mg. raw weight and 0·574 mg. dry weight) approximately equals the average biomass of Calanus in the Barents Sea (adult females—2·18 mg. raw weight, 0·670 mg. dry weight).

These results lead up to the general problem of the relations between temperature, development, and length of life, feeding and metabolism, and growth in size. Amongst others the following workers may be cited: Rzoska (1927) on Cyclops; Russell (1932) on Sagitta; Mielck (1919, cited from Samojloff, 1926) on Arctic fishes; Loeb (1910); and Adler and Jespersen (1920). No decisive answer, however, can be found until we know exactly the quantitative and qualitative variations in the food consumed throughout the year. The food of Calanus has been investigated by Marshall (1924), but in insufficient detail for our purpose. It is interesting that the spring and summer Calanus are reddish yellow with abundant fat inclusions, while the winter specimens are greenish white, and lacking fat inclusions or with very slight ones, presumably due to reduced winter nutrition. Samojloff (1926) has suggested a knowledge of the age to which fossil animals lived will help towards obtaining the temperature conditions of bygone times.

Before concluding I should like to emphasize one particular point I recorded above that the maximum number of specimens fell in with the maximum value of biomass and sizes in spring and *vice versa*, the minimum quantity occurring during the period of the minimum of biomass and size in autumn and winter. This is clearly seen from the details; thus in June (Figs. 2 and 5) we observe, as it were, a pulsation of quantity, reflected by a similar pulsation in biomass—greater biomass and greater number of individuals occurring simultaneously. I suppose this must be explained by the fact that conditions, favourable for the rise in biomass, are at the same time optimal ones for the development of great numbers of individuals. This result is of great biological importance, being contrary to the generally accepted view that the larger-sized organisms are more easily formed in regions with scarce population, where the density of life (number of individuals per definite volume) is smaller.

All the factors mentioned affect to some greater or smaller degree the size of an organism dependent on different combinations of life conditions and forming in their complex the essential problem of "organism and medium." In this complex of various conditions the temperature is the most important, biomass and size of organism being reversed in proportion to temperature conditions during the time of growth.

SUMMARY.

1. The present paper deals with changes of biomass and size of *Calanus finmarchicus* throughout the year in the Plymouth area.

2. The material was supplied by regular oblique hauls during 1930; Stage V and adult males and females having been examined. *Calanus finmarchicus* occurred throughout the year reaching its maximum value in May, being abundant from the middle of April to the middle of September.

3. *Methods.* The study of the material was based on the determination of *raw weight*, *dry weight*, and *length measurements*. For determination of *raw weight* a special method was worked out consisting of "liquid" drying of the body surface with alcohol and ether flowing through a special device, air being pumped through eventually for driving away the ether vapour. This method supplies data more suitable for comparison than those obtained by filter-paper drying. *Dry weight* was determined after drying in a desiccator. The data of *dry weight* are more exact and reliable than those of *raw weight;* dry weight also gives a better idea of quantity of substance, i.e. biomass of the plankton organism. *Raw weight* depends chiefly on the quantity of water in the organism.

Total length of the body was determined.

4. In the course of the year both biomass and size vary appreciably, the size of an organism being, however, approximately constant for a given period of time. Three such seasons are adopted; the first—"spring"

season—May; the second "summer" season—June, July, August, September; and the third—"autumn–winter"—from October to April.

5. These seasons are markedly differentiated in biomass and size, which are characteristic for each season (see Table IV): thus the maximum biomass for all stages occurs in the spring season, decreasing in the summer season and reaching then the yearly average. In the autumn–winter season we have the minimum biomass. Size varies similarly.

6. For the area under investigation we think it possible to specify three periods of reproduction, hence three generations of *Calanus finmarchicus*, named in respect to their time of living "spring," "summer," and "autumn–winter."

The length of life of each generation depends on the length of a given hydrological regime, a new generation growing up at the time of basic change in the regime, the old one dying off.

7. A definite relation is obvious between size of organism and hydrological conditions, the main factor being temperature, particularly during the period of development. Thus the large sized "spring" generation was hatched at 8–9° C. of temperature; the smaller-sized "summer" generation at 10·5°–14·5° C.; the very smallest "autumn–winter" hatched at the warmest temperature of 15–16° C. (see Figs. 7 and 9). We are justified in presuming that the size attained and the temperature conditions during development are inversely proportional.

8. Interrelation between temperature and size of Copepoda has been recorded by many authors, size being largest at low temperatures and *vice versa*. This phenomenon is widely known and used in comparisons of all kinds: geographical, regional, seasonal, vertical (from surface to bottom), sectional (crossing water with different temperature conditions), yearly (comparing years having different temperature conditions).

9. Generations differ from one another not only in size but in physiology (F. S. Russell).

10. Data of dry weight show that the body of adult females contains a greater percentage of water, the water-content varying with seasons, being at its minimum in spring and reaching the maximum in winter.

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TABLE V.

MEASUREMENT OF TOTAL LENGTH OF FEMALE CALANUS (STAGE VI ♀) IN MILLIMETRES, 1930.

mm.	February 12	February 19	February 26	March 5	March 12	March 27	April 11	April 16	April 24	May 7	May 15	May 22	June 10	June 19	June 26	July 4	July 9	August 7	September 3	September 16	September 24	October 1	October 14	October 16	November 13	November 20	December 3	December 10	December 17	December 22
4·00												1																		
3·97									1																					
3·94										1	1	1	1																	
3·90									1		2																			
3·86									2	2	3	8		1																
3·83									2	4	9	7																		
3·79									8	3	12	8																		
3·75								2	13	8	23	23	1	1																
3·71								1	5	6	15	14	1	2	1															
3·68								2	10	8	26	25	4	3		1		1	1											
3·64								3	14	7	22	10	3	1		1			1											
3·60							1	5	19	8	30	18	3	2	1	5	2	3	1											
3·56								7	25	16	29	28	5	4	2	2	2	9	8	1										
3·53							2	6	19	8	13	17	10	5	4	1	1	8	11	2										
3·49								10	18	10	16	8	3	3	5	5		8	12	3										
3·45								14	15	5	14	10	9	9	4	5	6	17	23	5		1								
3·41							1	15	10	5	16	6	6	10	3	13	6	19	29	5	1									
3·38		1						16	13	3	21	7	14	25	14	12	12	12	21	13										
3·34			1				4	8	9	7	5	1	9	8	4	16	9	23	13	5			1							
3·30				1		2		8	7	3	7	1	10	11	7	22	11	16	18	6			1							
3·26		2	2	1				3	5		3	1	3	6	16	22	10	12	11	3			1					1		
3·23		1		3	1	1	1	2	5	1	2	1	9	9	8	37	12	20	13	9	1	1	2	1						
3·19	1	5	1	3		1	1	6	3	3	5		3	7	3	22	13	18	8	4			5	1	1	1	1	1	2	1
3·15	2	2	1			3	2	1	5	1	1	1	5	5	7	21	9	13	4	8	2	2	1				2	2	4	
3·12	1	9	3	1		2	3	1	2	2	1	1	3	2	6	9	10	6	6	2		2	5	1			5	2	1	1
3·08	3	11	2	1	3	3	5	3			2		5	2	2	15	5	8	3	8		2	9	1	2		2	2	4	2
3·04	1	8	10	7	2	3	2	1	2		2	1	1		3	12	6	7	2	3		1	4	4	6		5	1	2	1
3·00	6	10	6	9	4	3	3	5	1	1	2	1	2		5	7	1	9	1	4	1	1	9	5	3	1	5	6	8	5
2·96	3	8	5	4	2	2	1	7	1				2	1	2	4		4	3	1	1	1	10	3	1		2	3	8	3
2·93	7	13	4	5	5	5	3	2	2	2			1		1	1	2			1			13	5	4	1	5	5	5	2
2·89	2	5	3	1	4		2	1	1		1				3				3	1		1	5	5	4		4	6	6	5
2·85	1	8	13	1	1	3		1			2					1				1	1	2	13	6	3	2	4	8	13	7
2·81	4	6	2	4	1	3	3									1				1		1	7	9	5	2	6	9	4	10
2·78		2	1			2															1	1	9	8	2	1	3	2	2	2
2·74		4	1	1		3			1											2			6	3	1		1	4	3	3
2·70	1	2	1			1	1				1						1				1		5	2	2		1	4	5	5
2·66	1																			1	1		3	2		1		2	2	1
2·63		1									1				1					1			2	4				1	1	1
2·59																							1	2		1		1	2	
2·55																								3				1		
2·52																									2					
2·48																														
2·44																									1					
2·40																														
Total number	33	98	56	42	23	36	35	130	219	114	287	199	113	117	102	235	118	213	192	90	10	16	112	66	37	9	46	61	72	49

On the Biology of *Calanus finmarchicus.* Part IV. Seasonal Changes in the Weight and Chemical Composition in Loch Fyne.

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With 5 Figures in the Text.

THE value of the zooplankton as a fish food depends not only on its distribution and numbers but also, to a large extent, on its chemical composition. Analyses of the marine plankton have already been made by Brandt (1898), Brandt and Raben (1919–22), Meyer (1914), Moberg (1926) and Wimpenny (1929). These authors worked on tow-nettings containing mixed plankton, both plant and animal. In the analyses of Brandt and of Brandt and Raben an attempt was made to assess the value of the zooplankton and of the phytoplankton apart from one another. Seasonal variations have apparently been dealt with only by Wimpenny and Moberg who had the disadvantage of dealing with mixed catches ; but the variation shown in some of the analyses given by Brandt and by Brandt and Raben suggests that seasonal variations in chemical composition take place.

The analyses given by the above authors, with the exception of those by Moberg and Wimpenny, were made on preserved material and no separation of individual species of plants and animals was possible ; in any case, the large numbers they had to deal with would have made such an attempt extremely laborious even if the method of preservation adopted had allowed of it. However, by analysing a number of catches in which certain species of plants or animals predominated, Brandt, and Brandt and Raben, were able to give an approximate figure for the chemical composition of certain groups or species.

The results in the following pages record an attempt to measure the variations in the composition of *Calanus finmarchicus* by itself. *C. finmarchicus* is an important food of certain fish and is widely distributed. In the Clyde Sea-Area it constitutes a considerable percentage of the zooplankton as a whole. The object of the work was to ascertain, in conjunction with the observations on size and distribution by Marshall (1933) and Nicholls (1933) recorded in Parts I and II of this series, what changes in weight and chemical composition took place throughout the year. Although Calanus predominated in all the catches, it was not considered that analyses of the catches as a whole would be of sufficient value and it was decided to separate the Calanus from other species. In addition, since it seemed possible that differences between male, female and the later copepodite stages of Calanus might exist, these were separated before analyses were made. Only living Calanus were used throughout. No stages younger than the fifth copepodite were dealt with largely because of the labour involved in their separation, but also because in actual weight they are relatively unimportant. The collection of material was made by Dr. A. G. Nicholls during the fortnightly visits to Loch Fyne. Very considerable help in the picking out of the Calanus was given by Miss S. M. Marshall and Dr. A. G. Nicholls. All the measurements were made by Miss S. M. Marshall. I have to thank both for making the work possible.

METHODS.

Collection of Material.

Vertical hauls with a 1-metre stramin net were made in the deep water off Strachur in Loch Fyne and the catch suitably diluted and brought to the laboratory. When sufficient numbers could not be obtained by the vertical hauls a horizontal haul was made in deep water. Vertical hauls were preferred since the material was then more likely to be similar to that used for size determination by Marshall (Part II). In the laboratory the Calanus generally lived well and could be kept for several days if the dilution was sufficiently great. If not well diluted the Calanus died off rapidly owing to oxygen depletion and decomposition of the dead ones. In addition, fat globules formed on the surface of the water and this would have vitiated fat analyses. Usually on the day following capture a series of samples of Calanus was taken from the diluted tow-nettings and separated into males, females and Stage V Calanus. Younger stages than this were rejected as it would have required a very large number for analysis and also because their occurrence was less frequent. After some practice the separation can be effected by the naked eye, but in all cases they were finally examined under the microscope. As is shown in the foregoing paper by Nicholls (Part I), the Calanus taken at Strachur consisted generally of a number of stages. At certain times males and females were scarce; sufficient for analysis could not then be obtained since it involved the examination of very many thousands of individuals. While this is to be regretted, it should be noted that at these times the very fact that they were scarce made them unimportant as a fish food. Stage V was nearly always present in sufficient numbers for analysis and except during breeding periods Calanus in this area seem to live longer in this stage than in any other (Nicholls, Part I).

SIZE AND WEIGHT.

Two samples of about 100 Calanus were measured under the microscope (see Marshall, Part II), each individual in a separate small drop of sea-water on a slide, and transferred alive to a small quantity of filtered sea-water. They were then collected in a sintered glass Gooch crucible, filtered free from sea-water under pressure and given several (generally three) washes with small quantities of distilled water. They were then dried to constant weight at 110° C. Washing with distilled water was necessary to get rid of the adherent sea-water but the washing should not be prolonged or the Calanus may lose some salts or may even lose some fat. Washing was usually completed in two or three minutes. The weight of the dried Calanus was measured to the nearest 0·1 mg. and was generally between 10 and 25 mg. On ignition the weight of ash was less than 1 mg. showing that the washing had been sufficiently good. On the other hand, the weight of ash was too small to be sufficiently accurate for ash determination. Drying at 110° C. was made as short as was consistent with complete removal of water since continued heating at this temperature results in a slight loss of volatile organic material.

Samples used for weight determination could not be used for any other estimations and the weight of these samples was used for determining the protein and fat percentages on separate samples. Transference (after washing with distilled water) of the undried Calanus from a Gooch crucible to a coverslip for subsequent weighing and fat or protein determination was attempted on several occasions but a loss of 1–3 mg. occurred, largely owing to splitting off of fat globules from the Calanus.

ASH.

Ash was determined on a large number of Stage V Calanus on one occasion only, the males and females being insufficient in numbers. The dry weight was obtained as above and the dry Calanus ignited to a white ash at red heat with the Bunsen burner. This procedure is likely to have resulted in a certain amount of loss by volatilisation of sodium and potassium chlorides and the ash percentage given is a minimum value for the time of year at which the estimation was made. A more elaborate procedure was not advisable with the small quantity of material available and in any case the loss is not likely to have been great.

PROTEIN.

Protein was estimated from the total nitrogen content. Duplicate samples of 100 Calanus were combusted with sulphuric acid in the presence of potassium sulphate and a trace of copper and the ammonia formed estimated by Folin's micro-aspiration method (Plimmer, 1920). In the calculation of protein content the customary factor (N × 6·25) has been used. No allowance has been made for the presence of chitin which contains only about 6% N, whereas protein contains about 16% N. Chitin analyses could only be made on large numbers of Calanus (see below) and sufficient numbers could not be obtained regularly. Since Calanus varies in weight considerably in the course of the year, it is unsafe to make a constant correction for chitin nitrogen throughout.

Fat.

Fat was estimated by Stoddard and Drury's saponification method (1929) with some slight modifications. Duplicate samples of 100 Calanus were transferred from the microscope slide to a small basin and there ground up with the alcohol-ether mixture. The whole was then transferred to a 100 c.c. flask with the alcohol-ether mixture. The subsequent treatment was then similar to that described by Stoddard and Drury with the exception that a fat-free filter paper was used instead of the Gooch crucible suggested by them (see Stewart, Gaddie and Dunlop, 1931) and phenolphthalein was used as indicator. The factor used for conversion of titration value to fat was that for triolein. This was used by Brandt and Raben (1919–22) and is within the range given for Calanus in a recent paper by Klem (1932).

Chitin.

A large number (1000) of Stage V Calanus was treated for a short time with dilute hydrochloric acid and then for a considerable time with 15% caustic soda at 100° C. When clean, the residue was collected on a sintered glass Gooch crucible, washed successively with water, alcohol and ether, dried at 110° C. and weighed. The quantity of chitin present was small even in 1000 Calanus and the weight of the ash of the chitin on ignition lay within the experimental error of weighing.

No determinations of carbohydrate were made since a direct estimation would have involved a large number of Calanus and the indirect method of estimation employed by Brandt (1898) and others could not be adopted.

RESULTS.

Size and Weight.

The seasonal variation in the weight of male, female and fifth copepodite Calanus is shown in Figure 1 and Tables I, II and III. As has been mentioned, only Stage V Calanus could be obtained in sufficient numbers regularly and the curves for male and female Calanus are incomplete.

Adult male Calanus were obtained in sufficient numbers for analysis on only four occasions and the dry weight varied from 23·5 mg. to 18 mg. per 100 Calanus. There was a gradual fall in weight from February to May which is related directly to a decrease in size during that time. They were also largest and heaviest during their period of maximum abundance for the year.

Adult female Calanus were obtained fairly regularly from the beginning of March till the end of August. The weight of 100 Calanus varied from 19·5 mg. to about 11 mg. The variation in weight is irregular with a pronounced high peak in May and a fall thereafter. The curve for weight again shows a relation to size especially in the pronounced high peak in May. There is, however, only a slight correspondence between weight and numbers ; the May peak in weight and size is associated with a very small increase in numbers of females.

Stage V Calanus show greater variations in weight than either males or females and they were available over a much longer period. In the winter of 1931 the greatest weight was 28 mg. per 100 Calanus. This was associated with their presence in very large numbers at this time. During the period from January to April the weight of 100 Calanus rapidly fell and the minimum was reached early in May when 100 Stage V Calanus weighed only about 10 mg. which is approximately a third of the winter value. After this the weight increased rapidly and reached the maximum for the autumn of 1932 in August and September at 23·5 mg. per 100 Calanus. There is a certain correspondence between numbers of Stage V Calanus and weight. The spring decrease in weight is coincident with the rapid disappearance of the large winter stock of Stage V Calanus. According to Nicholls (Part I) the first breeding period of Calanus for the year began early in March so that the nadir of the weight curve (May 2nd) came on a date when the Stage V Calanus would be expected to consist of individuals belonging to the end of this breeding period. Sufficient numbers for weight determinations were not obtained between the beginning of March and the beginning of April so that the weights during this period could not be obtained. Even on May 2nd only 60 individuals were available for weighing and some doubt exists as to the true state of affairs during this period. With the arrival of the second brood, weight rose rapidly though it was still well below winter values. The increase in weight continued thereafter, but the values ultimately reached were considerably lower than those of the previous winter. This again appears to correspond with numbers to some extent for the stock of Calanus late in 1932 was much lower than that of the winter of 1931–32. The relation of size to weight for Stage V Calanus is not so marked as with males and females but there is a general correspondence of the curves. As has already been mentioned, the catches used for analysis were not the same as those used by Marshall (Part II) for size determination and, as might be expected, the relation between weight and size in the samples actually weighed is closer than that between weight and size in the samples measured and recorded by Marshall (Part II). This is to be explained partly by the fact that the stramin net used for the capture of specimens for analyses probably exerts a certain selection on fifth copepodite Calanus; in addition the samples used for weight determination were measured alive while those used for size measurement by Marshall (Part II) were preserved in formalin which causes a slight swelling of the Calanus.

Although it has been shown that when taken separately, there is a relation between size and weight in male, female and Stage V Calanus, the curves (Fig. 1) demonstrate clearly that the weight depends chiefly on the kind of Calanus being dealt with (male, female or Stage V) and the time of year. Thus, for example, on August 22nd the average size of 100 female Calanus was 2·34 mm. and the weight 11·3 mg.; on the same date 100 Stage V Calanus had an average size of only 2·24 mm. (0·10 mm. *less* than that of the females) and yet the weight (23·5 mg.) was more than *double* that of the females. This anomalous relationship of size to weight between female and Stage V Calanus held from late May till the end of August and probably continued later in the season when females were scarce. It is probably to be accounted for by differences in water content.

During the period from March to May when Stage V Calanus were very light, both males and females were from 50–100% heavier than they; males were somewhat lighter than Stage V Calanus in May in spite of the fact that they were definitely larger. So far as can be said from the small number of observations available, male Calanus are heavier than female Calanus in spite of the fact that the latter are generally larger.

From the above remarks it is obvious that dry weight determinations on a catch containing males, females and Stage V Calanus without a preliminary separation of these, must lead to results which are of little value. It is also apparent that the food value of Calanus does not depend entirely on the numbers present but is influenced very considerably by the dry weights of the different stages at different times of the year.

It was unfortunate that the collection of samples for analysis was limited to Loch Fyne, for, as is shown by Nicholls (Part I), the catches there showed less numerous fluctuations and the variations in the sizes of the different broods were also small (Marshall, Part II).

Hitherto no direct weighings of dried Calanus have been available but some estimations of the weights of copepods without reference to species have been made by Brandt (1898). According to him one gram of dry material is contained in between 3×10^5 and 7×10^5 copepods with a probability that the range is only from 3×10^5 to 5×10^5. In the observations on Calanus from Loch Fyne, the numbers per gram dry weight were

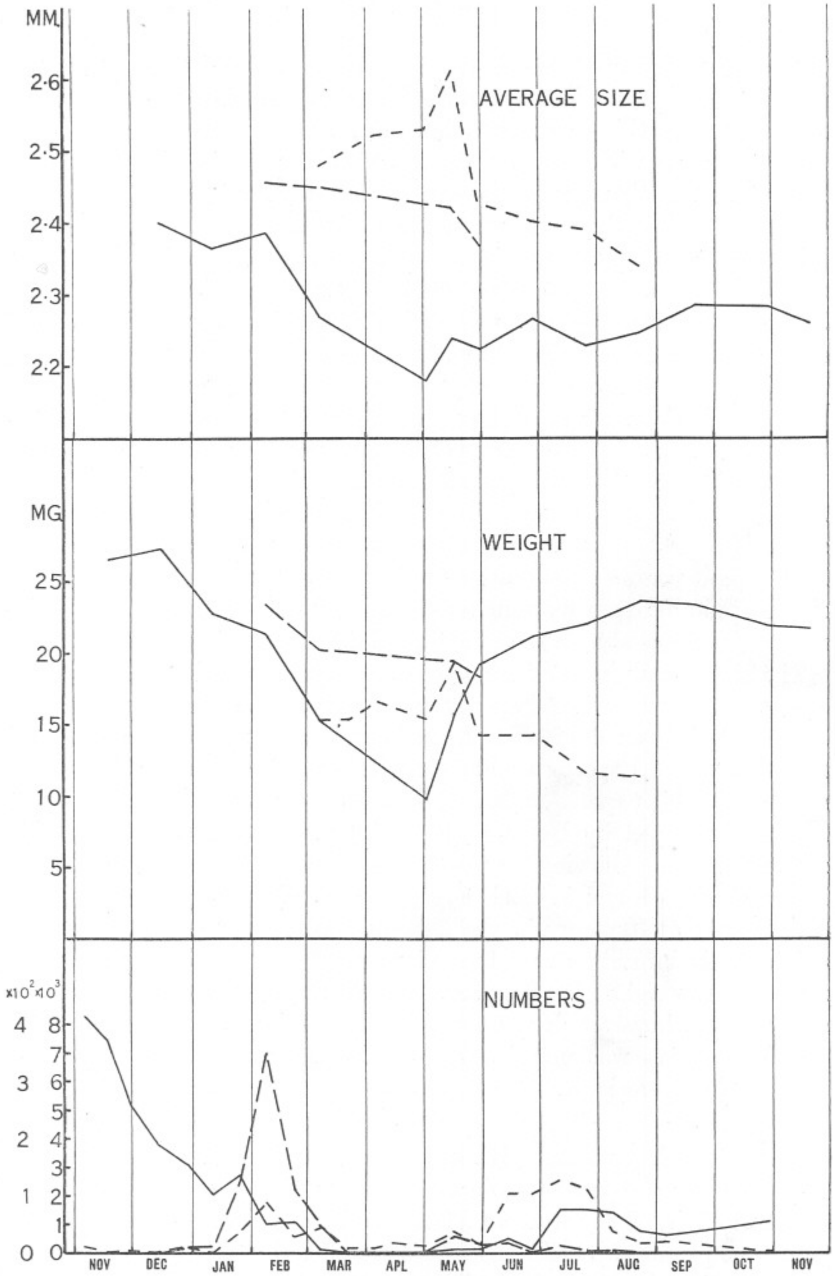

FIG. 1.—Size, weight and numbers of Calanus from Strachur, Loch Fyne.
——— StageV, — — — VI ♂, - - - - - - VI ♀.
Average size in mm. of ca. 100 individuals.
Weight in mg. per 100 individuals.
Numbers taken in one vertical haul (Part I) (V, $\times 10^3$, VI ♂ and VI ♀, $\times 10^2$.).

found to be very much smaller; one gram dry material was contained in 3500 Calanus as a minimum and in 10,000 as a maximum. It should be remembered in this connection, however, that *Calanus finmarchicus* is large compared with the average size of the copepods of the southern North Sea and that the earlier copepodite stages of Calanus have not been dealt with in the analyses from Loch Fyne.

Estimations of the wet weight of Calanus from the Barents Sea have recently been made by Bogorov (1933). The method of weighing adopted by this author (fixation in formalin and drying with filter paper) does not allow of a high degree of accuracy, but is useful in comparing the changes in weight through the copepodite stages to adult. His results showed that adult female Calanus were lighter than Stage V Calanus as has also been found in this area. In the Barents Sea, however, the females were *smaller* than the Stage V Calanus indicating that in this case the females which were lighter probably belonged to a different brood. A close comparison of the results is not possible since his observations were based on a single haul and no seasonal observations were made. His results show that to obtain a suitable quantity of material for analyses of the earlier copepodite stages of Calanus several thousand individuals would be required.

The size measurements in the present paper are those of the length of the cephalothorax while Bogorov measured the length from the head to the tips of the caudal furcæ. It has been found (by Miss S. M. Marshall) that this makes Bogorov's measurements some 20% greater than those recorded in this paper. As has already been mentioned, the method of fixation employed by Bogorov (formalin) may cause a slight swelling of the Calanus. Allowing for these corrections, the largest Stage V and female Calanus found in Loch Fyne are only about 90% of the size of those found by Bogorov in the Barents Sea. If we compare the dry weight of the largest Calanus found in Loch Fyne with the wet weight of the Calanus weighed by Bogorov, we find that about 80% consists of water. This, however, is not a reliable figure for the degree of drying used by Bogorov was empirical and the effect of the formalin on weight may also be appreciable.

ASH.

Since the ash percentage is low, a large number of Stage V Calanus (over 1500) were separated from a catch and collected on a sintered glass Gooch crucible. They were washed several times with distilled water as rapidly as possible and then dried to constant weight at 110° C. The dry mass was then gently ignited till free from carbon, cooled and weighed. The ash was white and weighed 12·9 mg. which was 3·6% of the dry weight of the Calanus. No estimations could be made on male or female Calanus as they were relatively scarce. No analyses of the inorganic constituents of the ash were made.

Figures for the percentage of ash in the plankton have already been given by Brandt (1898), Brandt and Raben (1919–22), Moberg (1926) and others. For a haul rich in copepods, Brandt gives a corrected figure of 7·12% and an average for copepods of 9·3%; Brandt and Raben in their tables give values of 4·24 and 6·42% which are fairly close to those obtained by using *Calanus finmarchicus* alone. Moberg, using material from tow-nettings taken 10 miles off La Jolla, obtained a minimum value of 4% but does not state the composition of the catch. The inshore values obtained by Moberg are very high and are no doubt caused by the silt present.

While the value found (3·6%) in Stage V Calanus probably holds for the major part of the winter, it is possible that there will be changes in ash content associated with the changes in weight.

FAT.

Analyses on adult males and females were limited owing to the difficulty in obtaining specimens in sufficient numbers. Stage V, however, were obtained more regularly. The results of the fat determinations on these are shown in Table III and Figures 2 and 3. The fat content follows the weight curve in general with two exceptions. At the beginning of March with Stage V Calanus the fat content was considerably higher than would be expected had it followed the weight curve and this is shown more clearly on the curve for fat percentage. The lowest value for fat coincided with the lowest point on the weight curve but the lowest percentage of fat was a fortnight later. It is not possible to say whether the peak in fat in March is associated with the spring increase in the phytoplankton, but the fact that the fat content was lowest during the summer when diatoms though not abundant are rarely absent does not support this conclusion. The agreement with the weight curve is to be expected though the high average value for fat content in the autumn and winter is puzzling when we consider that at that time plant food is scarce. Further work will be necessary before the relationship if any of the fat content of Calanus to abundance of phytoplankton can be found.

Analyses of female Calanus were not sufficiently numerous to show whether or not the fat content varied with the state of maturity. They do show, however, that contrary to expectation, female Calanus were less rich in fat than either male or Stage V Calanus.

The results recorded in the present paper are considerably higher than those given by Brandt and by Brandt and Raben for mixed plankton catches in the southern North Sea. They are considerably higher than those of Wimpenny who also worked on mixed catches. A possible objection to the method adopted in the present paper is that the assumption is made that the samples of 100 Calanus used for fat determination have the same weight as the samples used for weight determinations. The difference in weight in duplicate samples taken from a single tow-netting is seldom great (Tables I, II and III) and only exceeded 2 mg. on one occasion (8% error) so that this is not the explanation of the difference. The explanation more probably is that in the present work one stage of a single species is dealt with while the above-mentioned authors dealt with mixed catches.

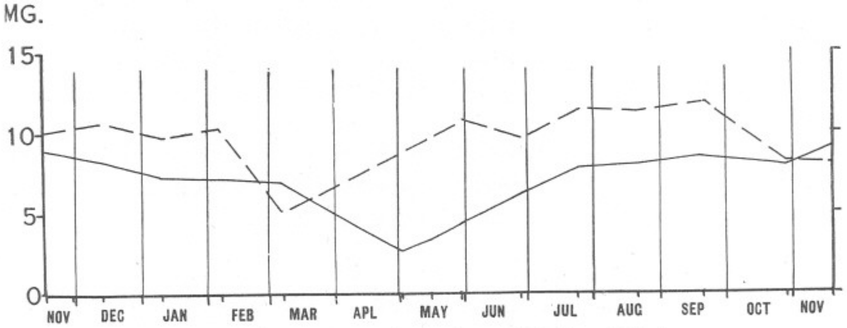

FIG. 2.—Weight of fat and protein per 100 Stage V Calanus.
Fat ———. Protein — — —.

Seasonal observations have been made by Wimpenny (1929) and he records his results as mg. fat per 1000 zooplankton individuals. The maximum fat content in the North Sea was found in August and the minimum in October. Stage V Calanus in the Clyde Sea-Area on the other hand had its maximum fat content in March while the results in spring and autumn were uniformly high. Wimpenny's results, however, are based on the weight of fat per 1000 individuals; since he dealt with mixed catches of varying composition and since as shown in the present

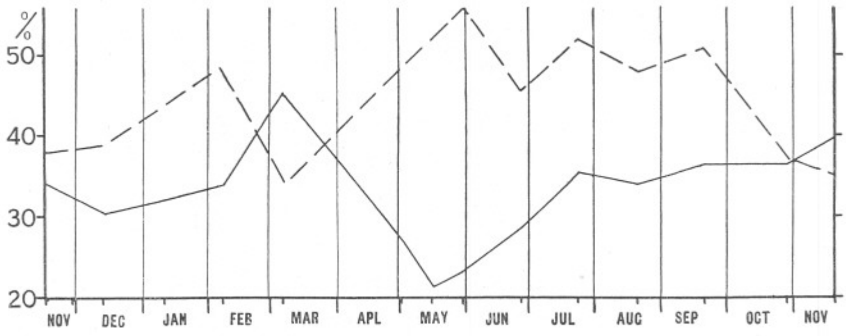

FIG. 3.—Percentage of fat and protein in Stage V Calanus.
Fat ———. Protein — — —.

paper the weight of a given number of individuals may vary considerably in the course of a year, his results should be interpreted with caution.

There is no obvious relation between the percentage of fat in Stage V Calanus and the different broods throughout the year. The first brood of Stage V Calanus had low fat values and thereafter later broods were fatter till the autumn-winter brood with the usual high fat values appeared. Stage V Calanus appears, in the Clyde Sea-Area at any rate, to be the most numerous stage of this important fish food for the major part of the year (Nicholls, Part I) and in view of the results of other authors on mixed plankton catches, it must be classed as one rich in fat.

The results of fat determinations on adult male and female Calanus are not numerous enough for any seasonal changes to be deduced. In adult male Calanus the value fluctuated between 18 and 34% and in adult females between 11 and 30%. Both are less fat on the whole than Stage V Calanus. The low fat values in females were unexpected and the changes recorded showed no relationship to the breeding periods recorded by Nicholls (Part I).

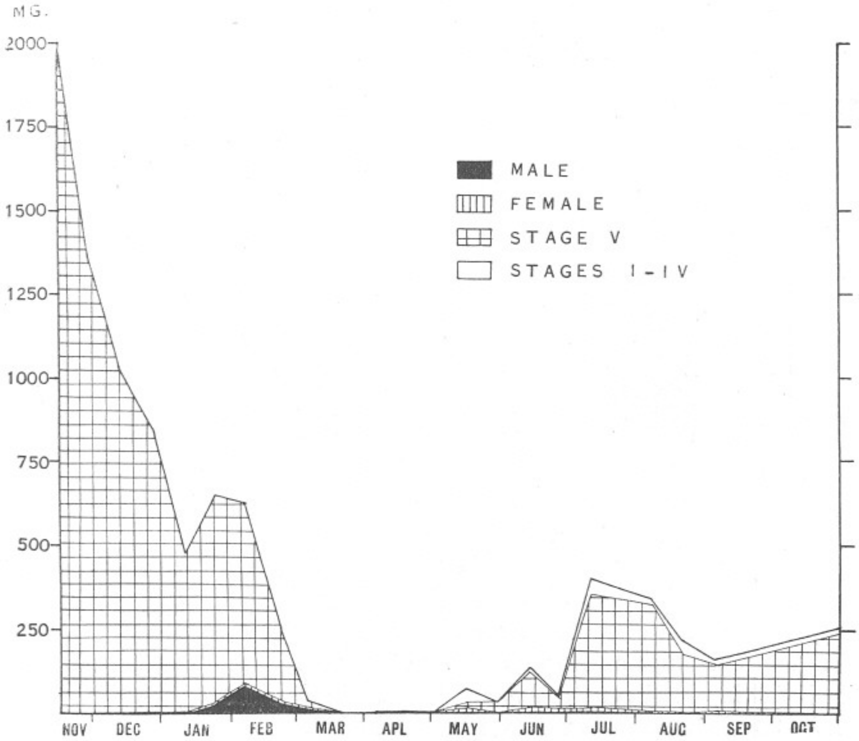

FIG. 4.—Calculated dry weight in mg. of vertical hauls throughout the year showing weight of different sexes and stages.

PROTEIN.

Like fat estimations, nitrogen determinations could only be made on a few occasions with adult male and female Calanus. Even with Stage V Calanus more numerous estimations would have been desirable. The results are shown in Tables I, II and III, and Figures 2 and 3. No reliable estimations could be obtained between February and May when the changes in weight and fat content were most marked. Protein values generally amounted to about 50% of the dry weight of the Stage V Calanus and fluctuated between 35 and 55%. A low value was obtained in the beginning of March on the same date as that on which the fat content was unusually high and in the autumn of 1932 values fell from 50 to 35%. This fall in protein content was not shown in the autumn and winter of 1931–32 when numbers were very much higher.

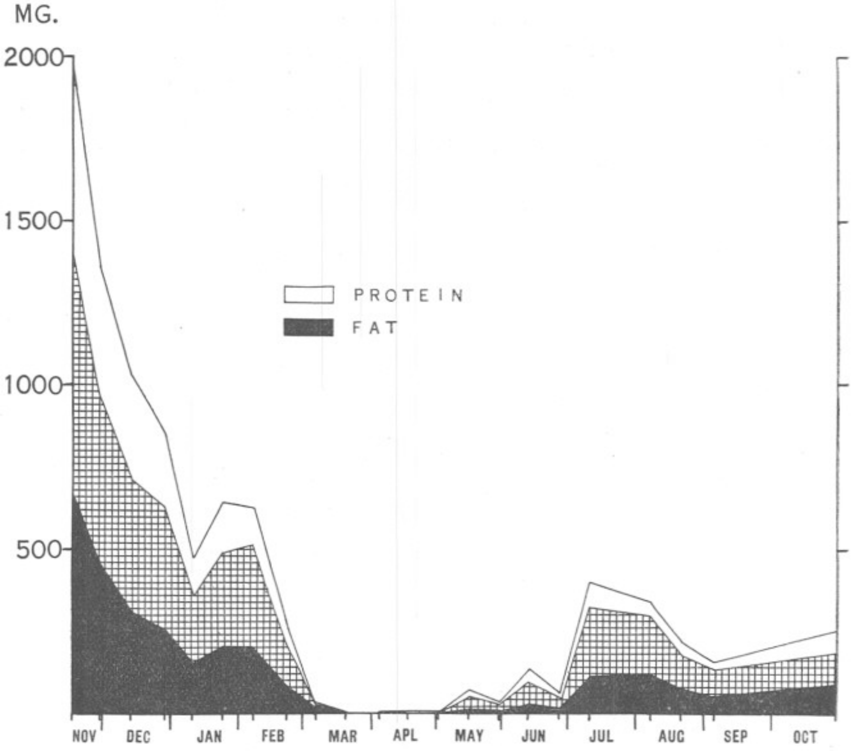

FIG. 5.—Calculated weight of protein and fat per vertical haul.

Adult female Calanus were richer in protein than Stage V Calanus and the level remained high (75%) on all four occasions on which estimations could be made. Adult male Calanus were much the same as Stage V with values varying from 40–70%.

The figures given for protein content of Calanus are considerably lower than those recorded by Brandt and by Brandt and Raben. The explanation of this discrepancy lies apparently in the fact that Calanus is richer in fat than the mixed plankton catches analysed by these authors. No seasonal observations have hitherto been recorded in protein content of plankton.

In the figures given above and in Tables I, II and III no correction is made for the nitrogen present in the chitinous parts of the Calanus.

CHITIN.

An analysis of the chitin was made on only one occasion and on Stage V Calanus alone since it was necessary to use at least 1000 individuals. The Stage V Calanus used for the determination were from the winter stock and the chitin content is probably fairly constant then since they do not moult till early in the year. The amount of chitin in 1000 Stage V Calanus was 6·1 mg., equivalent to 2·98% of the dry weight of the Calanus. This is somewhat lower than the figures given by Brandt and Raben (1919–22) which are 4·37% and 5·02%.

The object of the chitin determination was to find out what fraction of the organic material could definitely be classed as indigestible. Only a comparatively small number of animals is able to digest chitin and with most animals it appears to be excreted unchanged.

THE FOOD VALUE OF CALANUS IN LOCH FYNE IN 1932.

In Figures 4 and 5 and Table IV is shown the calculated total dry weight of the Calanus in the tow-nettings made by Nicholls (Part I) at Strachur in Loch Fyne. Figure 4 shows the weight composition of the catch as male, female, Stage V and Stages I–IV Calanus. The weights have been calculated from the dry weight determinations on 100 individuals except for Stages I–IV when the calculations have been based on Bogorov's (1933) figures making allowance for the water content. According to his figures,

1 Stage V Calanus equals in dry weight about 1·8 Stage IV.
1 ,, V ,, ,, ,, ,, ,, 11 Stage III.
1 ,, V ,, ,, ,, ,, ,, 42 Stage II.
I ,, V ,, ,, ,, ,, ,, 60 Stage I.

The weight figures for Stages I–IV are probably not very accurate but the diagram (Fig. 4) shows that they are relatively unimportant. The nauplius stages of Calanus and the eggs must weigh very much less individually and even the very high numbers met with at times (Nicholls, Part I) will have but little effect on the total weight curve.

Stage V Calanus is responsible for the bulk of the weight except for a short period from the middle of March to the end of April when the total weight of the catch was also very low ; males and females were of importance only spasmodically. During the autumn and winter practically the whole weight of the catch was due to Stage V Calanus. In the winter of 1931 they were very much more numerous and also somewhat heavier than in the winter of 1932 which suggests that there may be considerable fluctuations from year to year.

In Figure 5 and Table IV are shown the weights of fat and protein in the catch throughout the year. The curves for these run fairly parallel to the total weight curve. The fraction unaccounted for will consist partly of ash and chitin and probably to a large extent of carbohydrate (Brandt, 1898). The net used filtered an area of 0·196 sq.m. so that the figures represent the weight of Calanus and of protein and fat below each 0·196 sq.m. of surface. The average depth at Strachur was 130 m. so that the material was distributed through 25·5 cubic metres of water.

SUMMARY.

1. The dry weight of 100 male, female and Stage V Calanus in Loch Fyne fluctuated throughout the year. 100 Stage V Calanus in May weighed only about $\frac{1}{3}$ of what they did in December. Male and female Calanus also fluctuated considerably in weight.

2. Stage V Calanus is usually largest and heaviest when it is most abundant. With male and female Calanus size and weight are related.

3. Stage V Calanus, in spite of being smaller than female Calanus, was from the beginning of June till the end of August considerably heavier (over 100%). When Stage V Calanus was at its lightest and smallest, it weighed less than female Calanus at the same time.

4. The weight of Stage V Calanus fell during the spring and did not increase again till after the end of the first breeding period.

5. The fat and protein content of Calanus depends chiefly on dry weight. The values obtained for fat content were considerably higher than those hitherto recorded for zooplankton and those of protein lower.

6. The ash content is about 3·6% and the chitin content about 3% of the dry weight.

7. Stage V Calanus accounted for by far the most important part of the total weight of the catch throughout the year.

8. The total food value of the Calanus in Loch Fyne probably varies very considerably from year to year.

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TABLE I

Weight and Composition of Male Calanus.

Date.	Dry weight of 100 in mg.	Average length in mm.	Fat %.	Protein %.
8.2.32 . .	22·5	2·45	21·9	56
	24·0	2·46	–	53
7.3.32 . .	20·2	2·45	33·7	–
	20·3	2·45	31·7	–
	20·1	2·45		
16.5.32 . .	19·4	2·42	19·6	69
			18·0	–
30.5.32 . .	18·8	2·36	22·9	59
	17·8	2·37	23·5	54

TABLE II.

Weight and Composition of Female Calanus.

Date.	Dry weight of 100 in mg.	Average length in mm.	Fat %.	Protein %.
7.3.32 . .	15·2	2·48	29·6	–
		2·48	24·3	–
21.3.32 . .	15·2	2·51	16·3	–
	15·5	2·49	16·3	–
5.4.32 . .	17·7	2·54	11·4	74
	15·5	2·51	12·6	73
2.5.32 . .	15·4	2·53	21·4	–
16.5.32 . .	19·4	2·61	12·4	–
			12·9	–
30.5.32 . .	14·6	2·41	21·1	77
	13·9	2·44	17·6	74
27.6.32 . .	14·2	2·40	13·3	79
	14·3	2·40	10·5	69
25.7.32 . .	11·7	2·39	15·6	77
	11·3	2·39	–	–

TABLE III

Weight and Composition of Stage V Calanus.

Date.	Dry weight of 100 in mg.	Average length in mm.	Fat %.	Protein %.
17.11.31	25·4	–	34·4	32
	27·5	–	33·6	44
14.12.31.	26·6	2·40	28·9	42
	28·0	2·40	31·5	36
11.1.32	22·9	2·36	31·2	44
	22·5	2·37	33·0	44
8.2.32	21·0	2·39	34·4	48
	21·5	2·38	33·4	49
7.3.32	15·2	2·27	46·6	34
			44·1	–
2.5.32	9·7	2·18	26·8	–
16.5.32	15·7	2·22	22·7	–
	15·2	2·25	20·1	–
30.5.32	19·1	2·20	23·1	56
	–	2·25	–	–
27.6.32	21·7	2·27	26·1	46
	20·4	2·26	31·3	45
25.7.32	22·2	2·24	35·5	52
	21·7	2·22	–	–
22.8.32	23·4	2·25	34·9	46
	23·6	2·24	32·8	50
21.9.32	23·6	2·28	33·9	51
	23·0	2·29	38·6	–
30.10.32	21·6	2·26	36·8	30
	21·9	2·30	35·8	44
21.11.32	22·1	2·24	39·8	35
	23·1	2·28	–	35
	20·4			

TABLE IV.

WEIGHT AND COMPOSITION OF VERTICAL HAULS TAKEN IN LOCH FYNE.

Date.	No of individuals per vertical haul.	Calculated total weight per vertical haul in mg.	Calculated weight of protein per vertical haul in mg.	Calculated weight of fat per vertical haul in mg.
17.11.31 . .	V. 7420	1962·6	747·6	668·5
	IV. 30	4·4		
		1967		
30.11.31 . .	♀ 5	0·8	0·6	0·2
	V. 5120	1354·2	515·4	461·2
	IV. 15	2·3		
		1357·3	516·0	461·4
14.12.31 . .	V. 3750	1023·8	401·5	310·3
	IV. 30	4·5		
		1028·3		
29.12.31 . .	♂ 10	2·3	1·3	0·5
	♀ 10	1·5	1·1	0·4
	V. 3087	842·8	369·2	254·8
	IV. 7	1·0		
		847·6	371·6	255·7
11.1.32 . .	♂ 10	2·3	1·3	0·5
	♀ 4	0·6	0·4	0·2
	V. 2070	469·9	205·7	150·8
	IV. 2	0·3		
		473·1	207·4	151·5
25.1.32 . .	♂ 128	29·8	16·2	6·5
	♀ 37	5·6	4·1	1·5
	V. 2685	609·4	267·1	195·9
	IV. 8	1·0		
		645·8	287·4	203·9
8.2.32 . .	♂ 348	80·9	44·1	17·7
	♀ 58	8·8	6·5	2·4
	V. 2515	534·4	261·9	181·4
	IV. 10	1·2		
		625·3	312·5	201·5
23.2.32 . .	♂ 113	26·3	14·3	5·8
	♀ 28	4·6	3·4	1·2
	V. 1056	224·4	109·8	76·1
	IV. 2	0·2		
		255·5	127·5	83·1

Date.	No. of individuals per vertical haul.		Calculated total weight per vertical haul in mg.	Calculated weight of protein per vertical haul in mg.	Calculated weight of fat per vertical haul in mg.
7.3.32	♂	48	9·7	5·2	3·2
	♀	46	7·0	5·1	1·9
	V.	142	21·6	7·4	9·8
	I.	1	0·0		
			38·3	17·7	14·9
21.3.32	♂	6	1·2	0·7	0·4
	♀	8	1·2	0·9	0·2
	V.	7	1·1	0·4	0·5
	IV.	1	0·1		
			3·6	2·0	1·1
5.4.32	♂	3	0·6	0·3	0·2
	♀	8	1·3	0·9	0·2
	V.	8	1·2	0·4	0·6
	IV.	1	0·1		
	II.	1	0·0		
	I.	10	0·0		
			3·2	1·6	1·0
18.4.32	♂	3	0·6	·3	0·2
	♀	17	2·8	2·1	0·3
	V.	22	3·3	1·4	1·9
	IV.	10	0·8		
	III.	2	0·0		
	II.	3	0·0		
			7·5	3·8	2·4
2.5.32	♂	2	0·4	0·3	0·1
	♀	13	2·0	1·4	0·4
	V.	21	2·0	2·3	1·1
	IV.	38	2·0		
	III.	5	0·0		
	II.	1	0·0		
	I.	6	0·0		
			6·4	4·0	1·6
16.5.32	♂	28	5·4	3·7	1·0
	♀	38	7·4	5·4	0·9
	V.	122	18·8	32·3	12·3
	IV.	314	26·8		
	III.	796	10·9		
	II.	187	0·7		
	I.	56	0·1		
			70·1	41·4	14·2
30.5.32	♂	13	2·4	1·4	0·6
	♀	16	2·3	1·7	0·4
	V.	132	25·2	17·1	7·0
	IV.	39	4·1		
	III.	44	0·7		
	II.	53	0·2		
	I.	22	0·1		
			35·0	20·2	8·0

Date.	No. of individuals per vertical haul.		Calculated total weight per vertical haul in mg.	Calculated weight of protein per vertical haul in mg.	Calculated weight of fat per vertical haul in mg.
13.6.32 . .	♂	17	3·1	1·8	0·7
	♀	102	14·5	10·9	2·8
	V.	501	105·4	53·1	26·7
	IV.	80	9·3		
	III.	30	0·6		
	II.	40	0·2		
	I.	70	0·2		
			133·3	65·8	30·2
27.6.32 . .	♂	3	0·5	0·3	0·1
	♀	102	14·5	10·9	1·7
	V.	177	37·3	20·2	12·6
	IV.	36	4·2		
	III.	93	1·7		
	II.	93	0·5		
	I.	60	0·2		
			58·9	31·4	14·4
11.7.32 . .	♂	13	2·4	1·4	0·6
	♀	127	18·1	13·4	2·2
	V.	1537	337·4	196·7	108·8
	IV.	326	39·5		
	III.	104	2·0		
	II.	21	0·1		
	I.	13	0·0		
			399·5	211·5	111·6
8.8.32 . .	♂	3	0·5	0·3	0·1
	♀	36	4·1	3·1	0·6
	V.	1442	316·5	174·3	119·2
	IV.	160	19·3		
	II.	1	0·0		
			340·4	177·7	119·9
22.8.32 . .	♂	2	0·4	0·2	0·1
	♀	16	1·8	1·3	0·3
	V.	743	174·6	103·0	72·7
	IV.	311	40·4		
	III.	2	0·0		
			217·2	104·5	73·1
5.9.32 . .	♂	2	0·4	0·2	0·1
	♀	19	2·1	1·6	0·3
	V.	609	141·9	78·8	52·0
	IV.	90	11·6		
	III.	2	0·1		
	II.	4	0·0		
			156·1	80·6	52·4
30.10.32 . .	♂	1	0·2	0·1	0·0
	♀	5	0·5	0·4	0·1
	V.	1110	241·4	93·6	91·9
	IV.	96	11·5		
			253·6	94·1	92·0

Development of *Scolecolepis fuliginosa* (Claparède).

By

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Department of Oceanography, University of Liverpool.

With 16 Figures in Text.

CONTENTS.

INTRODUCTION.

MUCH is already known of Spionid larvæ from descriptions of planktonic forms, but very few species have been reared from the egg through the larval stages to metamorphosis. The egg and early stages of Scolecolepis are figured by McIntosh (1915) and by Claparède and Micznikow (1868), but there is no complete account of the development to be found in the literature. By the courtesy of the Director of the Marine Laboratory at Plymouth I was able to undertake this work, and I am indebted both to Dr. Allen and Mr. D. P. Wilson for advice and help during the course of the research.

In the arrangement of the paper the aim has been to describe fully certain stages in the life history, and to give as concise an account as possible of the development from one stage to the next.

METHODS.

Scolecolepis fuliginosa (Claparède) lives in black mud containing a large percentage of decomposing organic matter, and though localised, the worms are plentiful. At Plymouth they were obtained near the high-tide mark at Rum Bay, where they are covered by the tide for only two to three hours out of the twelve. The oxygen content of this mud is probably low. The worms live in sandy tubes lined with mucus, and the specimens were obtained by lifting loose stones and examining the mud beneath.

The mature worms were carried to the laboratory with the mud in which they live, and there allowed to clean themselves in sea-water. As it is impossible to ascertain the sex without injury to the worm, the whole sample was placed in a finger-bowl, where eggs and sperm were slowly extruded. Half an hour later, the eggs were removed with a pipette, washed free from sperm and placed in a sterilised finger-bowl with filtered sea-water. As soon as the young larvæ had begun to swim, the unfertilised eggs were removed and a few drops of Nitzschia culture, kindly supplied by Dr. Allen, were added as food. When the larvæ were found to be healthy, most of them were transferred to a plunger-jar, the remaining few being retained for continuous observation in the finger-bowl. These latter did not grow as quickly as those in the plunger-jar. From time to time, larvæ were removed and trapped on a cavity slide for observation, care being taken that they were not distorted by pressure; others were killed at various ages by squirting hot Bouin on to them when swimming in a watch-glass. Bouin between 60° and 70° C. was found most suitable. Before sectioning they were first orientated on a piece of stained Ulva, to which they were attached by a solution of collodion in clove oil, which is hardened in equal parts of xylol and chloroform. This is a modification of the process recommended by N. Yatsu (1903). In general, the methods employed were those of Mr. D. P. Wilson.

LARVAL DEVELOPMENT.

The unfertilised egg (Fig. 1) is very similar to that figured by Cunningham and Ramage (1888), Pl. XXXVI for Nerine. It is ellipsoidal, averaging 160μ long and 100μ broad, but size and shape are both variable. The cytoplasm is brown both by transmitted and reflected light. The margin of the egg is lobulated and there is a pale germinal vesicle near the centre, the whole being enclosed by an egg-membrane which appears to be very thick on account of its curious folds, which give the surface the appearance of a honeycomb. This membrane is punctate both internally and externally, the depressions on the one side corresponding to the elevations on the other.

About two hours after fertilisation the germinal vesicle and the lobulated margin are lost, and the cytoplasm rounds off within an inner fertilisation membrane (Fig. 2). Between the rigid egg-membrane and the contracted mass of cytoplasm a space is left and in this cavity several transparent spherical vesicles are to be seen; these originate on the inner surface of the egg-membrane. Their function is not apparent and they are soon lost in the succeeding cleavage stages. The first cleavage is horizontal, the two cells so formed being unequal in size. Later a four-cell, an eight-cell, and between nine and ten hours after fertilisation a sixteen-cell stage is reached, with four large yolk-laden macromeres and smaller and paler micromeres (Fig. 3). Gastrulation follows by epiboly.

Thus far the egg-membrane remains unchanged, but as the developing mass of cells increases in volume, the membrane is pushed out before it. This change in shape is not due to actual stretching of the egg-membrane, but rather to flattening and broadening of the papillæ on its surface. In cases of abnormal development, one part of the egg-membrane may be completely flattened so that a bubble appears on the surface of the larva.

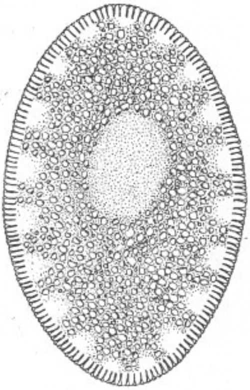
FIG. 1—Unfertilised egg.
× 320.
Actual length 160μ.

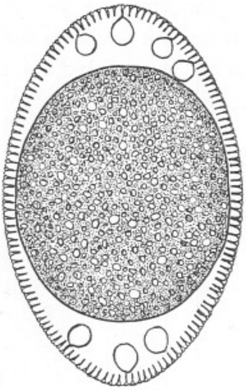
FIG. 2.—Fertilised egg.
× 320.
Actual length 160μ.

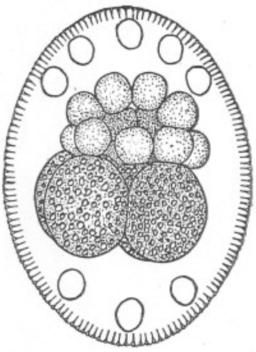
FIG. 3.—Sixteen-cell stage.
× 320.
Actual length 142μ.

The Trochophore.

The first trochophore (Fig. 4) becomes active and begins to swim less than twenty-four hours after fertilisation. It is about 200μ long, roughly coffin-shaped and dorsoventrally flattened. The colour is brown with a darker area where the gut is foreshadowed by the presence of yolk granules. There is a transparent space between the rigid egg-membrane and the developing mass of cells.

The prototroch is not a continuous line but as in Nerine, it is broken into groups of cilia. In this species there are fourteen groups well separated by longitudinal ridges of protoplasm and the containing egg-membrane. There are eight dorsal groups divided by a very broad median dorsal ridge into two groups of four. On the ventral surface there are six groups, three on either side of the mid-ventral line. The cilia of each group come through a single elongated slit in the egg-membrane.

A group of five very fine cilia form the apical tuft. It is probable that each of these cilia comes through a separate hole in the egg-membrane, for in later stages the apical cilia become separated. There is a single pair of eyes set wide apart on the dorsal surface, at first red but later black. The mouth and anus are formed later.

Development of the Trochophore.

As the larva grows the wrinkled membrane is slowly flattened out, the papillæ becoming broader, the depressions shallower and the whole more closely approximated to the ectoderm.

The head becomes flattened anteriorly, the prototroch ridge forming prominences on either side. A second pair of eyes and then a third are formed on the dorsal surface between the first two, which take up a lateral position anterior to the prototroch. Like the first pair, the second and third are at first red but soon change to black.

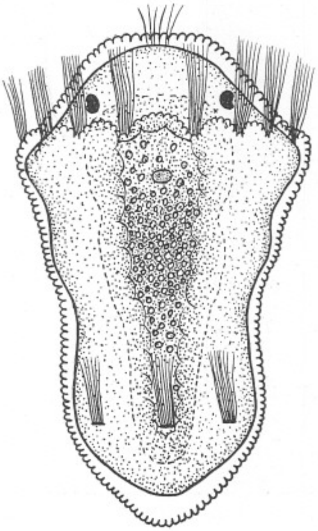

FIG. 4.—Ventral view of the trochophore, 36 hours old. × 320. Actual length 200μ.

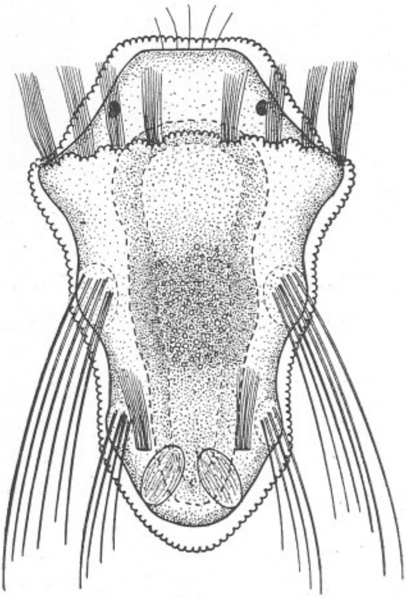

FIG. 5.—Dorsal view of the trochophore, 48 hours old. × 320. Actual length 206μ.

A rounded depression on the ventral surface foreshadows the position of the mouth. The egg-membrane dissolves at this point and the larva begins to feed. The circular mouth soon elongates and appears T-shaped with two anterior grooves. Meanwhile the outline of the gut becomes distinct and the dark yolk-granules are restricted to a rectangular area in the middle of the larva which lengthens and develops into the pigmented stomach-intestine or mid-gut. The anus is formed soon after the mouth.

Thirty-six hours after fertilisation the telotroch is formed, and like the prototroch is not continuous but appears as five separate groups. Two of these groups are dorsal and three are ventral. As the prototroch and telotroch develop, however, each cilia group broadens and the ridges between them disappear, so that the final result is a continuous line of cilia. The dorsal groups of the prototoch move round, and all except one on each side increase in size to form the swimming cilia of the prototroch. The ventral six groups remain small and are soon indistinguishable from the oral cilia which are formed on the sides of the mouth and extend to the ventral surface of the first setiger. The telotroch cilia increase equally in size, forming a continuous line ventrally and laterally, but leaving the broad dorsal gap that is characteristic of Spionid larvæ.

The provisional or larval bristles can first be seen as two minute structures within the prominences behind the prototroch ridges. At an age of two days the first bristle bundles are well developed, each with about four bristles, the largest is 150μ long, and reaches to the end of the larva (Fig. 5). All bristles are slightly curved and beset with spinules on the anterior margin (Fig. 14*a*). A second group and later a third are formed in the lateral elevations which become the parapodia of the second and third setigers. The larval bristles in these and succeding setigers are always slightly shorter than those of the first setiger.

At the time when the bristles of the third setiger become visible, a single pair and later numerous glandular cells are formed below the anus. They are large pale cells probably filled with mucus. Their openings to the exterior are on papillæ on the ventral and lateral surfaces of the anal segment. The function of these mucus cells is not apparent.

The Three-Setiger Larva.

When the larva is three days old the first three bristle bundles are fully formed. The larva is some 250μ long and having lost its coffin-like shape it has become more evenly cylindrical (Fig. 6). The egg-membrane is completely flattened and fused with the ectoderm, forming a persistent cuticle. The colour of the larva is pale brown with a darker area which extends from the beginning of the second setiger to the end of the third indicating the position of the mid-gut.

The head is square in front, a shoulder on each side bearing the swimming cilia of the prototroch. The three pairs of eyes are fully developed, two pairs being dorsal and a larger pair lateral. All three pairs lie on a transverse line across the head, anterior to the prototroch ridge.

There are five well-separated apical cilia. The swimming cilia of the prototroch are very large and like the telotroch cilia, are curled against the sides of the head when not in use. A single prototroch group on the dorso-lateral surface of the head remains small, while ventral groups form the anterior margin of the oral cilia, which now cover the lips and most of the ventral surface of the head (Fig. 6). The oral cilia taper into a neurotroch which extends on to the second setiger. The cilia of the median ventral group of the prototroch have become longer and with the enlarged oral cilia of this region, form an efficient feeding organ. As shown by Wilson (1928) in the development of Polydora, large cilia appear which move independently of the others and probably have a sensory function. They are not as well developed in Scolecolepis as in Polydora, but even at this stage three paired groups are visible, one on the anterior margin of what will become the prostomium, the second in line with the ventral part of the prototroch and the third on the lateral margin of the oral cilia. As has been shown, the oral cilia are continued posteriorly as a neurotroch; this line of cilia ends on the ventral surface of the second setiger in a depression or "pit," on the margins of which are two or three large sensory cilia. The exact structure of this organ is described in the chapter on the fourteen-setiger larva (see Fig. 15). Paired groups of cilia later appear on the ventral surfaces of the first and second setigers.

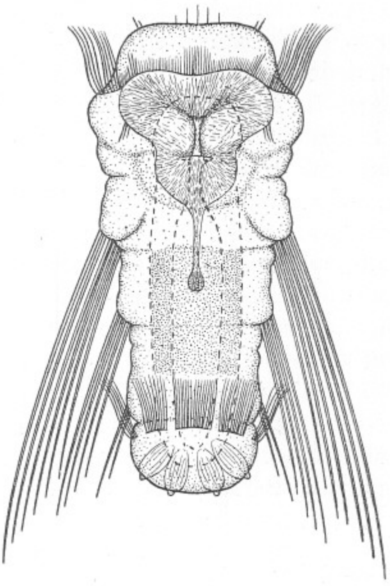

FIG. 6.—Ventral view of the three-setiger larva 4½ days old. × 250. Actual length 250μ.

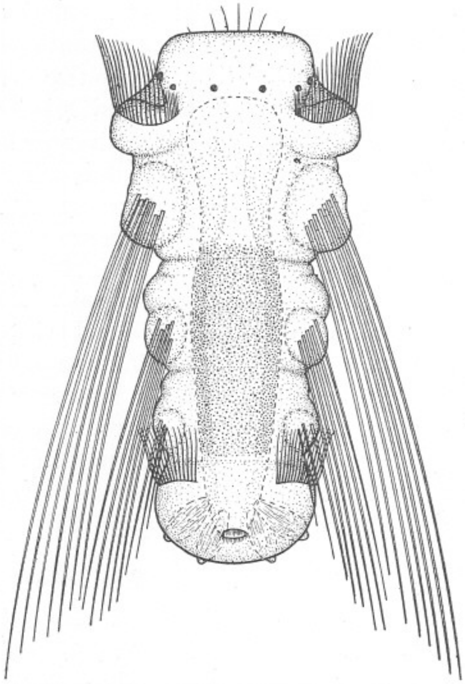

FIG. 7.—Dorsal view of the three-setiger larva, 7 days old. × 250. Actual length 280μ.

The mouth opens into a ciliated vestibule, on either side of which are projecting lips. These lateral lips are separated from a third anterior lip by oblique grooves running from the anterior end of the slit-like mouth. When not feeding a fourth lip projects over the posterior portion of the mouth. But when actively swimming, the mouth is held open, and the shape of the lips is difficult to discern. The narrow gullet is followed by the stomach-intestine, which is characterised by the dark pigment cells that line it. This pigmented portion extends from the second to the end of the third setiger. The last portion of the intestine, the rectum, is pale, and the anus is ciliated.

The segments of the body are marked by projecting seta-sacs (Fig. 7). There are 8 or more larval setæ in the first bristle bundle, the longest of which is 200μ and extends considerably beyond the end of the body. In the second setiger there are 6 and in the third 4, but these numbers are soon augmented.

In the pygidium, the anal glands have increased to 4, each with a distinct papilla on the surface.

Development. With the attainment of the third setiger, growth is apparently less rapid. Though the larva continues to feed, it is not until the 9th day that the fourth setiger is formed. Meanwhile the structures already present increase in size, and the cilia groups develop greatly. The sides of the mouth become slightly pigmented, and the lips more prominent. The larval setæ increase in number as well as length. Finally with the advent of the bristles of the fourth setiger, paired groups of cilia appear on the third setiger which develop into a gastrotroch.

The Four-Setiger Larva.

The larva (Fig. 8) is about 400μ long, with a breadth of 160μ at the first seta-sac. The segments of the body are well marked off by constrictions, and a characteristic mark now forms on that part of the third setiger which becomes the ventral ramus of the parapodium. Pigment is also seen in the dark stomach-intestine, and pale variable marks sometimes appear on each side within the prototroch ridge, as well as a band of brown pigment on the anal segment.

The head is relatively smaller, being no broader than the other segments. The lateral pair of eyes are slightly larger than the others. The prominences of the lateral lips is accentuated, but their general shape remains the same.

The swimming cilia of the prototroch measure 60μ and the cilia of the telotroch 40μ. A single dorsal group of the prototroch remains small (Fig. 9), while the ventral groups have long since merged with the oral cilia. The cilia of the anterior lip and those in the oblique grooves as well as those on the sides of the mouth have enlarged or fused to form broad, plate-like structures which sweep food-particles into the mouth. There are four paired groups of tactile cilia, the newly developed pair being on the posterior edge of the oral cilia. The neurotroch has become broader, the pit deeper, and the sensory cilia which surround it more numerous. There are paired gastrotroch groups on the first three setigers, two small groups on the first, one lateral and one ventral, a single pair on the second and two paired groups on the third.

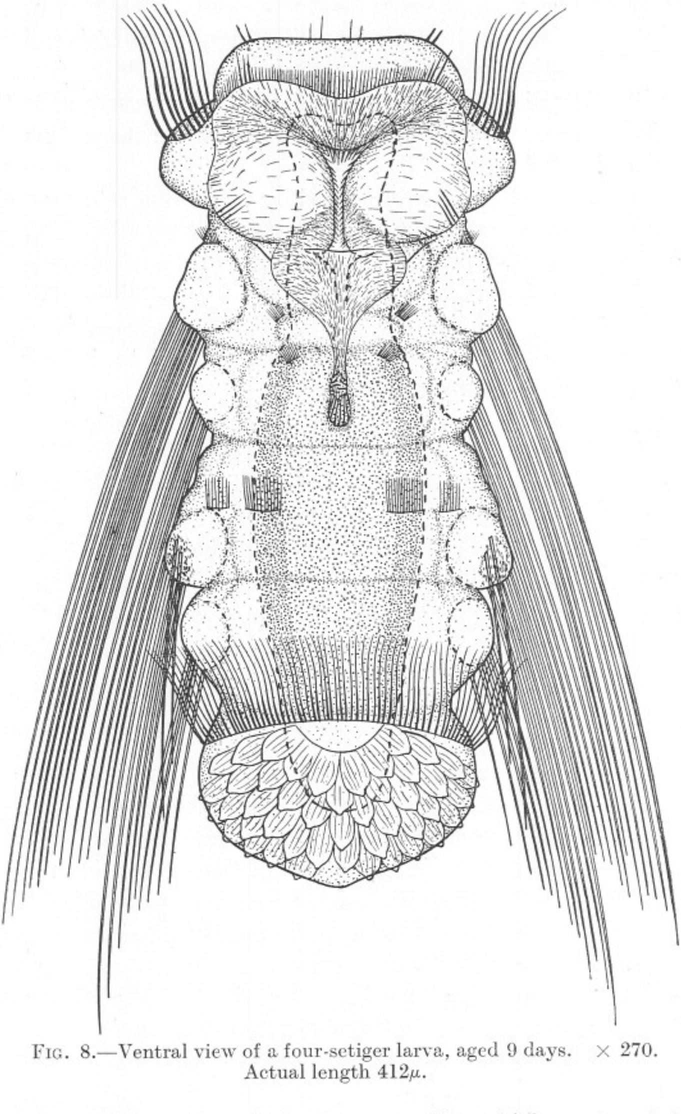

FIG. 8.—Ventral view of a four-setiger larva, aged 9 days. × 270. Actual length 412μ.

The mouth has not changed in shape but the granular pigment has increased on the inner surfaces of the lips ; the stomach-intestine is quite black, and anus is now dorsal in position.

The parapodial prominences show slight division into neuropodia and notopodia. The neuropodial part of the third setiger is slightly pigmented. The number of setæ in the four setigers is respectively 10, 8, 6, 4.

Glands in the anal segment are numerous.

Development. From now on the head remains unaltered, except that in late larval development palpi appear. There is also one more group of tactile cilia formed anterior to the pit on either side of the neurotroch. New segments are added in front of the pygidium, and gastrotroch groups appear on the fifth and later the seventh and ninth setigers, which, with those on the third become important swimming organs. Nototrochs are seen at the six-setiger stage, first on the third setiger and later on the succeeding setigers as well as on the second. In each case six groups unite to form a line across the dorsum. Finally there is the development of the ventral group of larval setæ and the elaboration of the parapodia. The pigment in the ventral ramus of the third setiger is repeated in succeeding setigers, but is not so striking.

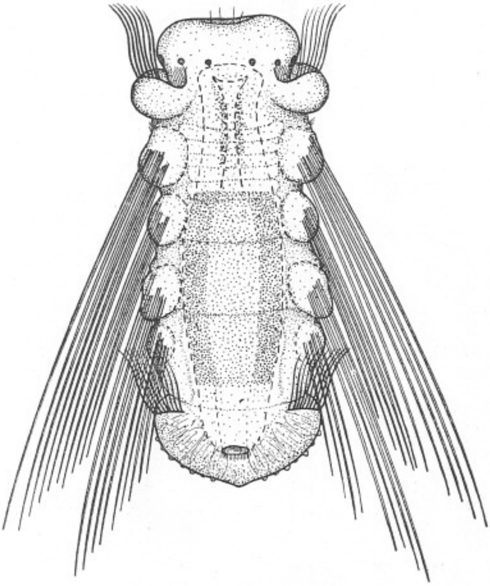

FIG. 9.—Dorsal view of a four-setiger larva, aged 9 days. × 150. Actual length 412μ.

From the four-setiger stage onward it is noticeable that the centre of growth seems to be the third setiger. It is as though growth had previously centred in the head segment and at this stage had shifted back to the third setiger. Later important segmental structures arise first on the third setiger. For example, the differentiation of the parapodia is more advanced in this segment than in preceding or succeeding segments. The ventral groups of larval bristles, the nototrochs and the first group of adult bristles are first seen in this segment. As will be shown this pre-eminence of the third setiger is also evident during metamorphosis.

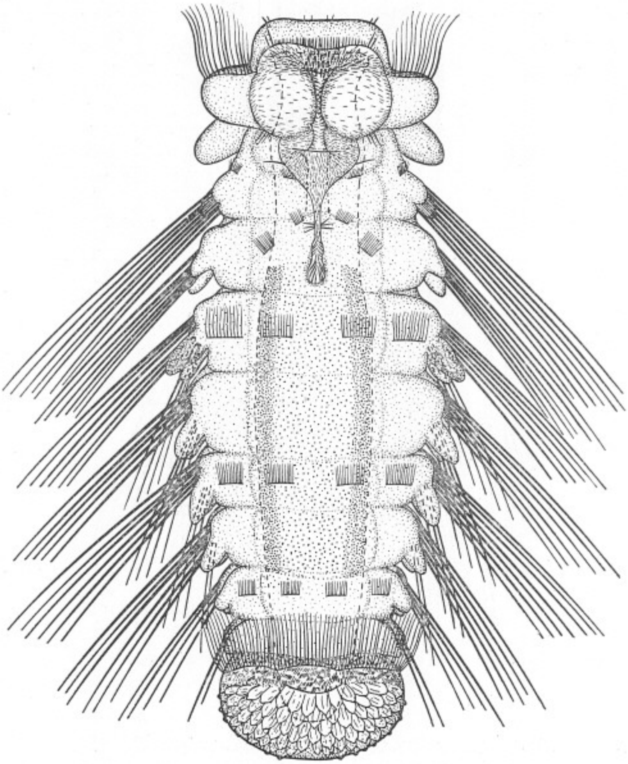

FIG. 10.—Ventral view of an eight-setiger larva, aged 20 days. × 125. Actual length 776μ.

The Eight-Setiger Larva.

The larva at an age of 18 days to three weeks is about 776μ long and has 7–9 setigers (Fig. 10). Larvæ collected from the plankton in Plymouth Sound at this time showed the same development. The body has grown considerably larger with the addition of the new segments. All the structures connected with the larval state are present, and further growth consists in the elaboration of these structures and the addition of new segments.

The body is fairly broad, the parapodia well developed and the head slightly narrower than the rest of the body, except at the prototroch ridge. The only important new pigment marks are pairs of dense black spots on the dorsal surface of the third, fourth, fifth and sixth setigers (Fig. 11). These appear white in reflected light. There is granular pigment on the dorsal surfaces of the succeeding segments, but as these marks are variable they are unimportant for diagnosis. The pigment in the ventral ramus of the third parapodium is now a prominent distinguishing character.

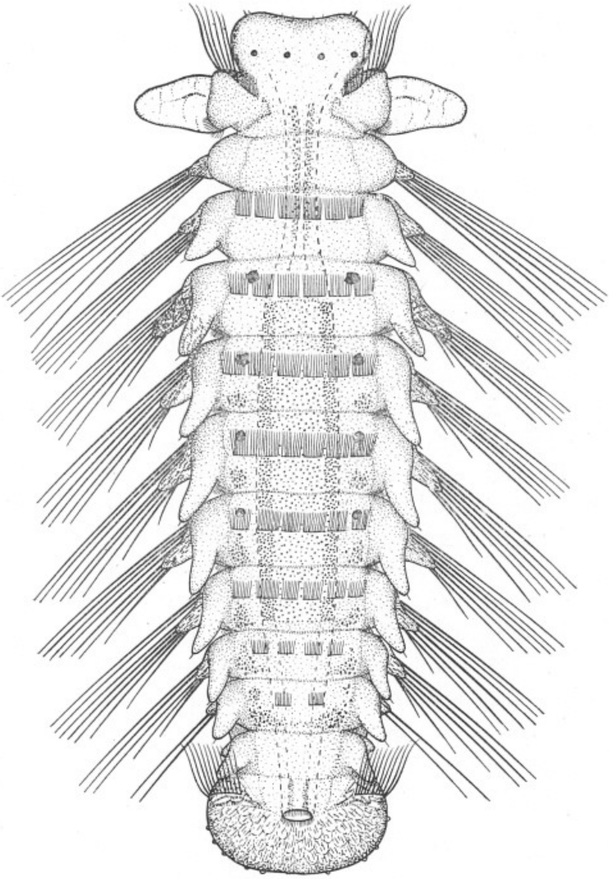

FIG. 11.—Dorsal view of a ten-setiger larva, aged 24 days. × 125. Actual length 0·874 mm.

The head shows little advance, except for the palpi, which appear on the prototroch ridges posterior to the swimming cilia (Fig. 10) and quickly develop into broad stumpy organs, ciliated on both the anterior and posterior margins (Fig. 11). Though called palpi by Fauvel and Ehlers, they are identical with the tentacles described by McIntosh and others. In Wilson's paper on the development of Polydora (Wilson, 1928) they are called tentacles.

The prototroch and telotroch show no advance. The cilia associated with the head have grown longer but no new structures have been formed. In later stages a well-defined row of cilia becomes evident at the base of each palp (Fig. 11) where it arises from the prototroch ridge ; scattered cilia cover the surfaces of these organs. The neurotroch with the associated pit cilia and the gastrotrochs on the first and second setigers show no advance. There is an extra group of tactile cilia on either side of the neurotroch near the pit. The gastrotrochs on the third, fifth and seventh setigers grow very large and extend transversely across the ventral surfaces of these segments. Nototrochs have been developed on the dorsal surfaces of all segments from the second to the sixth setiger. These structures never grow large, and though possibly of use in swimming, this is not their main function. They are not lost at metamorphosis and are probably precociously developed adult structures, in which stage they have an important function as will be shown later.

The shape of the mouth has not altered, but the gullet is more strongly pigmented. In each segment the parapodia are prominent, the notopodia and neuropodia well marked, and each notopodium is divided into a branchial and a setigerous region. The larval setæ have reached their maximum development. These number 12 to 14 in the first setiger and have a maximum length of 285μ. In the succeeding segments there are fewer setæ of a smaller size. Thus the third setiger has 8 with a maximum length of 250μ. The adult setæ now appear, but are extremely difficult to distinguish. They are first formed in the dorsal bundle of the third setiger, where a few, short, smooth and more definitely tapered structures indicate their presence.

Development proceeds steadily till metamorphosis, by the addition of new segments in front of the pygidium. About the time that the palpi appear, small groups of cilia arise on the dorsal surface between the parapodia (Fig. 11). These have been called " intersegmental cilia," and are probably homologous with similarly placed, though larger cilia in Polydora, which Wilson (1928) has named " grasping cilia," from their function of holding the larval bristles in place during swimming. These groups, like the nototrochs are precociously developed adult structures which remain small in the larval state. A little later hooded acicular bristles are developed in the neuropodial bundle of the eighth and succeeding setigers. Another pair of gastrotroch groups is formed on the ninth setiger. On the dorsal surface of the pygidium two pairs of small anal cirri are developed.

A résumé of the larva with fourteen setigers and ready to metamorphose is given at this stage.

The Fourteen-Setiger Larva.

At an age of 34–36 days most of the larvæ are about 1·0 mm. long and have fourteen setigers. The body (Fig. 12) is slightly flattened dorso-ventrally, and somewhat broader at the third setiger than elsewhere. The colour is a general pale brown, with scattered chromatophores on

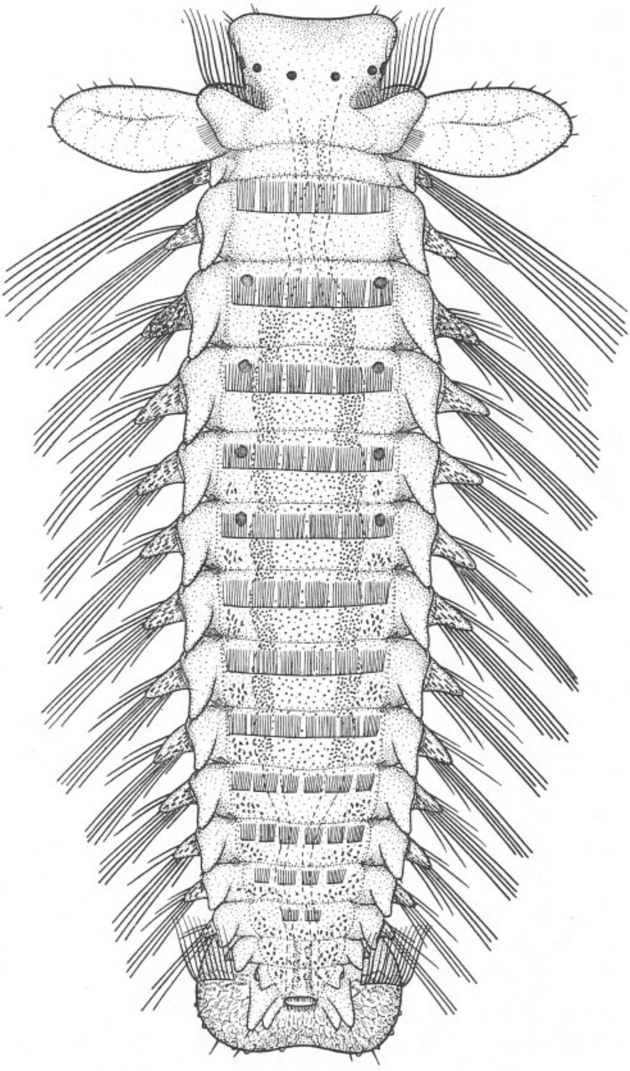

FIG. 12.—Dorsal view of a fourteen-setiger larva, aged 34 days. × 152. Actual length 1·062 mm.

the posterior segments. The neuropodium of the third setiger is dark brown and the third, fourth, fifth and sixth setigers have dense pigment spots. There is granular pigment in the œsophagus and the stomach-intestine is black. That part of the pygidium which bears the telotroch is brown and the posterior, glandular part is bluish.

The prostomium is square in front with a slight median depression. The three pairs of eyes form an inverted crescent across the dorsal surface, the outer pair being almost hidden by the prototroch ridge, which forms the base of the palpi. From now on this part of the head will be called the palpophore. The palpi themselves are broad and flattened.

The swimming cilia of the prototroch are now 68μ long and the telotroch cilia 55μ. The other cilia structures associated with the head and the neurotroch are unchanged. The gastrotroch groups on the anterior segments remain small, but those on the third, fifth, seventh and ninth setigers are large swimming organs. Although Wilson has found that the position of the gastrotrochs is variable in Polydora, in Scolecolepis they seem constant. All setigers from the second onwards bear nototrochs and intersegmental cilia.

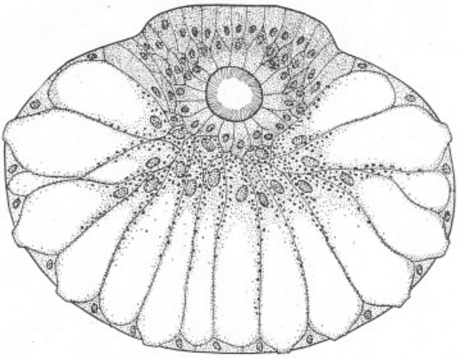

FIG. 13.—Transverse section through the anal segment of a fourteen-setiger larva. × 400.

The structure of the pit is shown in Figure 15, which represents a longitudinal section through a slightly contracted larva. As the histology of the larva otherwise conforms with the general Spionid type, only the remarkable pit is described here. It is an invagination of the ectoderm lying just behind the fold of the contracted lip. The edges are ciliated, but the cavity itself is unusual in that the contents are apparently non-cellular and do not stain. In cross section the pit is reminiscent of a vertebrate notochord. The suggestion that the pit has a sensory function is upheld by its location between the circumœsophageal nerve cords. The first commissures of the double ventral nerve cord (in the second setiger) are shown just behind the pit. Thus the latter is almost entirely surrounded by nervous tissue. The neurotroch in front of the pit is composed of short cilia and commences at the infolding of the posterior lip. There are two groups of strong cilia behind the pit, and it is these that have been referred to as the pit cilia. The third posterior group shown is part of the gastrotroch of the third setiger. It is possible that the function of this organ is similar to that of a statocyst, though no sense organ similar to this is figured in the literature consulted.

Though the shape of the mouth and vestibule remains the same, the œsophagus and rectum are now sinuous in outline, and the stomach-intestine itself is swollen between the septa. The proctodæum is ciliated for a considerable distance internally.

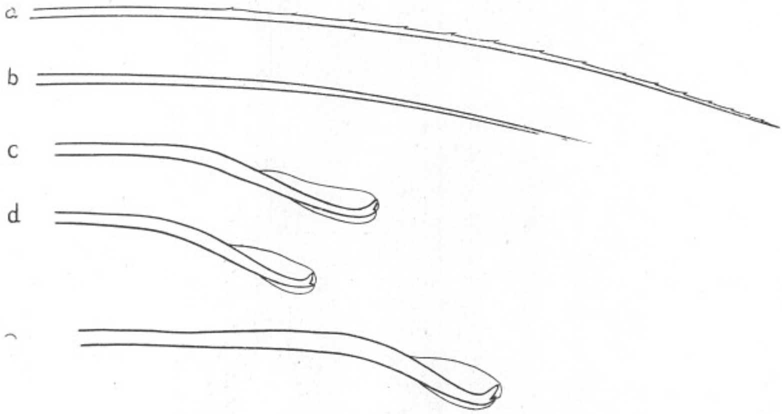

FIG. 14.—(*a*) Larval bristle from a fourteen-setiger larva.
(*b*) Adult type of bristle from the same larva.
(*c*) Crotchet from the 8th parapodium of the same larva.
(*d*) Crotchet from the 10th parapodium of the same larva.
(*e*) Crotchet from the 22nd parapodium of the adult worm.

The parapodia are slightly flattened and there are elongated branchiæ dorsally. In all setigers, with the possible exception of the first, adult setæ (Fig. 14*b*) are present in both the dorsal and ventral bundles. From the eighth setiger onward, crotchets are present in the ventral bundle as well. It is noteworthy that the first crotchets to appear, those in the 8th setiger (Fig. 14*c*) are slightly different from those in the succeeding setigers (Fig. 14*d*), while both are different from the adult type (Fig. 14*e*). The larval bristles (Fig. 14*a*) fall out readily when the animal is trapped on a slide.

The pygidium is short, broad and flattened posteriorly. There are two pairs of anal cirri, which, like the glandular part of the segment and the parapodia, possess tactile cilia. Figure 13 shows a cross section through the anal segment anterior to the anus itself. The large vacuolated cells contain mucus, the limited cytoplasmic contents having large brown chromatophores. These mucus cells, which are themselves ectodermal in origin, open on papillæ which project through the thin ectoderm covering the surface.

From now on growth proceeds slowly and at the end of another week,

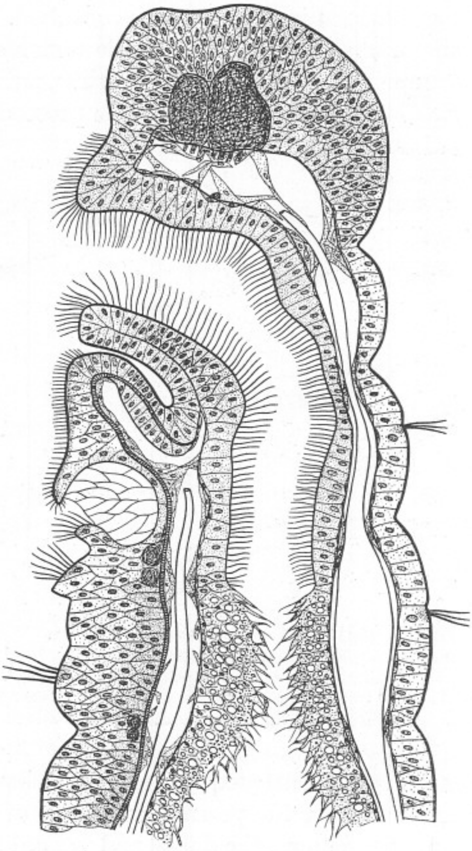

FIG. 15.—Anterior part of a longitudinal section through a fourteen-setiger larva, showing the ciliated pit. × 400.

only a few individuals develop a fifteenth setiger. As will be shown in another paper (Day and Wilson, 1934), experiments were started at this time which show that when kept in conditions unfavourable to metamorphosis larvæ do grow, but so slowly that in another month only four new setigers are added.

In the meantime, some of the largest larvæ were put into a vessel containing purified silver sand and filtered sea-water, to which Nitzschia culture had been added. The larvæ were at this time thirty-four days old. Though they at first explored the bottom, they soon started swimming again, showing a preference for the lighted side of the vessel. After twenty-four hours, however, two of the largest attempted without success to burrow below the surface. It was evident that the sand was too coarse.

A finer sandy mud was obtained, purified by boiling, and placed in a finger-bowl, to which the filtered sea-water and larvæ had been transferred. After crawling on the sand for an hour, the larvæ began to burrow below the surface and to metamorphose.

Metamorphosis of the Young Worm.

The actual process of metamorphosis is not easy to follow, since the larvæ first secrete mucus to which sand grains adhere, making observation difficult. These notes are compiled from the examination of larvæ at different stages of metamorphosis. Fortunately the changes cannot be described as "cataclysmic" so that it is possible to obtain a fairly complete picture by removing larvæ from their tubes and trapping them under a cover-slip on a ringed slide.

When a suitable place has been found, the head is bent down, and with its palpi held forward, the larva jerks from side to side, burrowing below the surface. While crawling the larva secretes mucus, by means of which sand grains adhere to the body, but as the larva burrows further sand grains and larval setæ are left behind in a trail of mucus. Not all the larval setæ are lost at once, for those of the first setiger persist till much later.

Possibly under the influence of burrowing, the palpi soon change both in shape and position. The sides of the palpophores grow unequally, so that the palpi are directed forwards, increasing in length and slenderness. Sooner or later the metamorphosing larva constructs a tube of sand grains and debris loosely stuck together with mucus. Here it remains fairly quiet, with its head at the mouth of the tube and the palpi waving freely in the water.

While in this position many changes occur, some gradual, some rapid. A sudden change such as the loss of the gastrotrochs is easily noted, but others such as the gradual development of the antennæ proceed slowly and continuously, so that it is impossible to say definitely whether the antennæ are developed before or after the loss of the gastrotrochs. This point should be held in mind in the perusal of this chapter. Cataclysmic changes—if the loss of the different larval organs can be called such—are recorded in their true succession, but a more correct picture of the metamorphosis is obtained if these superficially striking changes are regarded merely as milestones in the gradual evolution of the adult organs.

Most of the cilia that are functional only during larval existence are now lost. In this category are included the gastrotrochs, the neurotroch and pit, the telotroch and the prototroch. These disappear in the above order, though the telotroch and prototroch persist long after the others have gone. The other groups of cilia, the nototrochs, intersegmental cilia, oral, anal and tactile cilia may change in character but are never lost for they are functional in the adult as well as in the larval stage. The gastrotrochs go first. The actual loss of the cilia is difficult to follow, for when a larva is isolated on a slide for long periods, metamorphosis either stops or proceeds more slowly, and in the meantime plasmolysis takes place. It was ascertained in many cases, however, that when a group of cilia is about to disappear, most of the protoplasm of the cilia is withdrawn into the body of the larva so that a mere wasted shell remains. Whether this falls off or is also absorbed could not be determined with certainty, but it seemed as though a part appreciably shorter than the original was thrown off. The former position of a cilia group can be detected for a few hours by the presence of a paler mark on the surface of the body.

Just before the pit closes, a lump arises on either side, then lengthens out and the depression fills in. The neurotroch is then lost, and within six hours no trace of the pit can be found externally. The prototroch and telotroch, which up to this time are functional when the larva is forced to swim, now disappear. Changes in the shape of the head and the body generally, become visible. The notch in the middle of the prostomium is accentuated and the prominences on either side foreshadow the future antennæ. The lateral lips grow forward, bringing the reduced posterior lip with them, thus covering part of the mouth so that the opening is V-shaped and anterior. The oral cilia are restricted to the sides of the mouth and the surface of the posterior lip. The two dorsal pairs of eyes form a rectangle, the third pair remaining unchanged laterally. The body meanwhile increases in length, becoming more slender and rounded. The pygidium narrows and the anal cirri grow longer.

Twelve hours after the commencement of burrowing the only larval features which remain are the third pair of eyes, the temporary ventral hooks, and the dark pigment of the mid-gut, of the neuropodium of the third setiger, and of the posterior part of the anal segment. These features persist long after metamorphosis is otherwise complete, and disappear gradually in the life of the young worm.

Development proceeds with the further modification of larval structures. The mouth, lips, antennæ, palpi and eyes change in the manner already indicated and soon conform to the adult type. The rami of the parapodia are further flattened, while the branchial portion of the notopodium becomes more distinct. With the lengthening of the setigerous segments, a corresponding change occurs in the pygidium. The two superior pairs of anal cirri grow considerably, but whereas they were colourless from the start, the third pair arising from the division and prolongation of the glandular region of the segment, contain the bluish pigment which characterised it. In the adult worm, however, they can be distinguished only by their larger size. Twenty-four hours after metamorphosis the young worm has reached a stage shown in Figure 16. As there are still differences between this and the adult a brief résumé of its characters is given.

Characters of the Recently Metamorphosed Worm.

The general shape of the body is similar to that of the adult. When forced to swim it does so with a serpentine motion, using its fan-like setæ and flattened parapodia as oars. The young worm is considerably paler and more transparent than the larva, and except for the scattered pigment granules on the head and dorsum, the few dark patches are the remains of the larval pigment. The mid-gut is brown, as is also the neuropodium of the third setiger. The posterior part of the pygidium and the ventral urites are bluish. The bands of yellowish pigment, seen on the palpi of the adult, are not yet developed.

The prostomium is sharply defined. It is roughly oval, slightly notched in front and rounded posteriorly. The antennæ are conical, but soon grow longer and more regularly cylindrical. The palpophores are short, and the palpi which are long, tapered and slightly grooved dorsally, project beyond the antennæ. There are three pairs of eyes, two dorsal, and a lateral pair hidden by the palpophores.

The large lateral lips are protuberant, and curve posteriorly to enclose the V-shaped mouth. There is an indefinite posterior lip and a larger anterior lip that is separated from the laterals by oblique grooves. The opening of the mouth is anterior and ventral, the pharynx is contractile and the œsophagus is thrown into folds by the contraction of the body. The dark stomach-intestine begins about the third setiger and continues till the fourth from the anus; this pigmented part of the gut is characterised by segmental swellings between the septa. Posteriorly the rectum is again folded, and the proctodæum is ciliated for a considerable distance internally.

The lips are beset with short cilia and the antennæ and palpi are sparsely covered with short tactile cilia. In addition there are rows of cilia at the base of the palpi. All setigers except the first, and those that are undeveloped posteriorly have nototrochs and intersegmental groups of cilia. The gills and the anal cirri possess only a few tactile cilia.

The parapodia are of the adult type, but the branchial part of the notopodium is short and does not as yet arch over the dorsum. Both

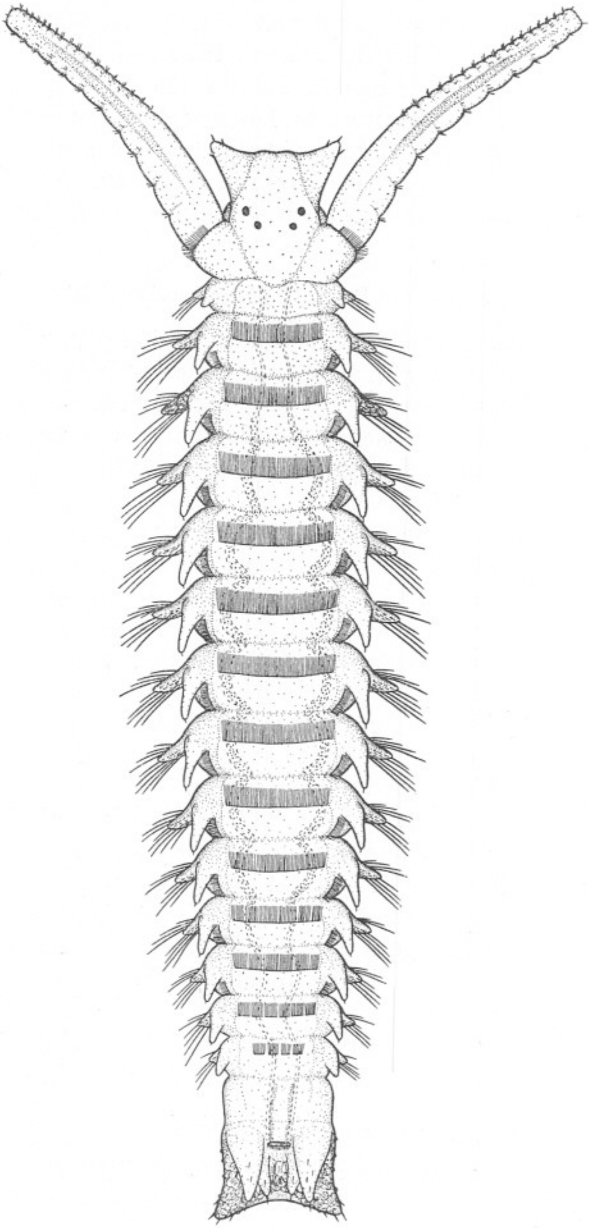

FIG. 16.—Dorsal view of a recently metamorphosed worm. × 104. Actual length 1·367 mm.

the dorsal and the ventral bristle bundles arise on the anterior side of the flattened parapodia and project outwards like a fan. From the eighth setiger onwards, hooded crotchets as well as capillaries are present in the neuropodial group, but these are only temporary, and in the adult crotchets are found only in the twentieth and succeeding setigers.

The pygidium is long and transparent and pigment is restricted to the ventral pair of anal cirri.

From now on the worm grows rapidly. The third pair of eyes are first hidden and then lost. Pigment disappears from the mid-gut, the third parapodia and anal segment. The anal cirri, antennæ and palpi increase greatly in length. As the gills grow longer, they become richly ciliated and arch over the dorsum, and the function of the cilia groups now becomes obvious. Normally the worm rests with its head at the entrance of its mucus-lined tube, the antennæ and long palpi waving freely in the water. In this position there is a free passage between the dorsum and the arched gills, and the motion of the nototrochs, intersegmental cilia and the rows of cilia on the branchiæ draws a current of water down along the dorsum. Part of this current is diverted ventrally at each segment by the action of the intersegmental cilia, thus ensuring a complete circulation of fresh water along the whole length of the body.

SUMMARY.

1. The development of *Scolecolepis fuliginosa* (Claparède) is described from the egg to the young worm for the first time.

2. Comparison of reared larvæ with larvæ from the plankton did not reveal any important difference.

3. The eggs are pelagic, and are similar to those of Nerine.

4. A description is given of the histological structure of a ciliated pit which arises in early larval existence and disappears at metamorphosis. The structure of the glandular region of the pygidium is also described.

5. It is apparent that from the attainment of the fourth setiger onwards, the centre of differentiation is located in the third setiger, so that segmental structures arise first in this segment and then appear in the first and second setigers as well as in the succeeding ones.

6. The larva of Scolecolepis has three pairs of eyes, the third pair disappearing in the young worm long after metamorphosis is otherwise complete.

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On the Relation of the Substratum to the Metamorphosis of *Scolecolepis fuliginosa* (Claparède).

By

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INTRODUCTION.

WHILE investigating the Mitraria larva of *Owenia fusiformis* one of us (Wilson, 1932) obtained striking evidence of the important part played by the nature of the bottom in the metamorphosis of that larva. In the hope that a similar behaviour would be shown by a less specialised type of larval Polychaete experiments were undertaken by us in collaboration. The larvæ used were those of *Scolecolepis fuliginosa.* They were forty days old and were known to be ready to metamorphose given suitable conditions. These larvæ had been reared from the egg by J. H. D., who gives an account of the development in another paper (Day, 1934). Only a limited number were available for experiment but these have proved sufficient to yield a definite result. The major portion of the work was done in the Plymouth Laboratory, but the sands were analysed in the Department of Oceanography, University of Liverpool.

Two initial tests were first made and these giving positive indications that the grade of the bottom deposit is an important factor in metamorphosis a larger experiment was arranged. During these tests a sandy mud had been found in which the larvæ metamorphosed readily. This sandy mud and two other grades of bottom, coarser and finer, were selected and after the first day a fourth grade, a fine clean sand, was also used. A clean glass control dish with rounded corners was included, but it should be noted that in experiments of this kind the ideal control in which the larvæ could not come into contact with any surface whatever is an impossibility.

At the end of the experiment the sands and muds used were examined microscopically (by J. H. D.) and the average size of particles estimated. The sands and muds were then dried and incinerated to obtain a rough estimate of the organic content, which is expressed as a percentage of the dry weight. Care was taken that these results were not falsified by the loss of carbon dioxide from the calcium carbonate present. While it is not suggested that this method of determining organic content is accurate, the results obtained provide comparative values which are important and particularly striking in the mud D.

These results are tabulated below :—

Vessel.	Substratum.	Average diameter of particles.	Limits of variation.	Approximate Organic Content.
A	Smooth glass			
B	Silver sand	0·264 mm.	0·44–0·17 mm.	0·2%
C	Sandy mud	0·047 mm.	0·34–0·03 mm.	6·9%
D	Mud	0·063 mm.	0·15–0·02 mm.	30·0%
E	Fine sand	0·086 mm.	0·10–0·05 mm.	3·0%

The silver sand B consisted of clean well-rounded grains not differing greatly in size. The fine sandy mud C was a mixture of fine particles with organic matter and a few larger sand grains. D was composed largely of organic debris but with a few sand grains, sponge spicules and diatom frustules. E had been elutriated and the variation in size of particle was small. It was dark in colour and contained about 20% calcium carbonate in the form of broken shells. On the whole the grains were sharper and more angular than those of B.

Account of the Experiment.

The experiment, details of which are tabulated on page 662, is divided into two parts. The first part extends from noon on April 30th to noon on May 1st, 1933, when certain changes were made and thereafter continues as the second part.

First Part.

Ten larvæ picked at random from the plunger-jar were put into each of four small vessels (30 c.c. capacity) about half-filled with filtered sea-water. These were the vessels A, B, C, and D, and the amount of sand or mud placed in the last three was just sufficient to cover the bottom with a thin layer. If too much is used it is very difficult to find burrowing larvæ when counting. A little Nitzschia was added to the water in the vessels and they were stood on black paper and covered with dark red glass discs to exclude excess light.

In all cases the larvæ explored the vessel, crawling over the bottom and attempting to burrow. If the bottom proved suitable they metamorphosed, otherwise they alternately burrowed and swam. After six hours the only change was in vessel C where all except two had either secreted mucus or metamorphosed. The two swimming larvæ were smaller than the rest and had possibly not reached the stage when metamorphosis can take place. In less than twenty-four hours all the larvæ in C, except the two mentioned, had become young worms, whilst no larva in the other vessels showed any sign of metamorphosis; they were all swimming actively.

Second Part.

The experiment was continued with two objects in view, first to show that the larvæ in vessels A, B, and D were ready to metamorphose, second to determine what eventually happens when larvæ are kept for long periods in conditions unfavourable to metamorphosis.

The 8 young worms in vessel C were removed and 5 of the 10 larvæ in each of the vessels A, B, and D transferred to C. These with the 2 left made a total of 17. The numbers in A, B, and D were made up to 10 by adding 5 fresh larvæ to each. The fifth vessel E containing 10 fresh larvæ was added to the experiment.

At the end of twenty-four hours all the larvæ in C except 4 had metamorphosed. Most of these had changed within three hours, and all but the 4 small larvæ mentioned had burrowed into the sand at the end of five hours. In vessels B, D, and E nothing had occurred, but in A 4 larvæ had metamorphosed. They were, however, unhealthy and soon died.

Since the course of the experiment covers several weeks the account will be more coherent if each vessel is now considered separately for its whole duration. Comparisons may be made from the table. In the accounts the transition from the first to the second part of the experiment may not be specially referred to although it should be borne in mind.

Vessel A. Four larvæ metamorphosed within forty-eight hours. Some diatoms and a little dust had collected at the bottom of the dish and adhered to the mucus tubes of these unhealthy worms which soon died. Meanwhile the 6 swimming larvæ were transferred to a clean vessel A′ where 3 of them became unhealthy and the other 3 were again transferred to a similar clean vessel A″. One of the unhealthy larvæ in A′ died, but the other 2 lived to become abnormal worms, the first at the end of a week, the second after three weeks. These larvæ showed no appreciable increase in size. Of the healthy larvæ in A″ one became a normal worm at the end of a week, a second after eighteen days, while the third died unmetamorphosed after six weeks without showing any appreciable growth.

Vessel B. The first larva metamorphosed on the fourth day. Four of the remaining 9 larvæ were transferred to C′ to see if they would metamorphose given favourable conditions, which they did. Of the 5 left the 2 largest metamorphosed at the end of a week, another 2 within two weeks, and the last within three weeks. All worms were healthy and lived for a considerable time.

Vessel C. At the end of the first day 8 larvæ had metamorphosed. The 8 worms were removed and 15 swimming larvæ (5 from each of vessels A, B, and D) added. Twenty-four hours later all but 4 of the 17 larvæ had metamorphosed and these did so four days later. The young worms were sent to Liverpool on May 12th. Half of them survived the journey, and 6 were still alive at the end of three months, when they varied in length from 3 to 14 mm. The largest had lost all larval characteristics, but the smaller ones still retained the larval pigment in the anal cirri and third parapodium.

Vessel C′. This had the same kind of bottom as C and was used to test whether larvæ in vessels B and E could metamorphose. When larvæ were transferred from these vessels on May 3rd three were unfortunately lost. Five out of the remaining 6 metamorphosed within three days and the last by the seventh day. Later 2 larvæ were transferred from E and they immediately began to metamorphose.

Vessel D. Three larvæ died on the third day. On the same day 2 metamorphosed followed by 2 more the next day. At the end of the first week there were 6 worms and 1 larva. Two days later this larva had also metamorphosed.

Vessel E. As there was no change after forty-eight hours 5 of the larvæ picked at random were transferred to vessel C′ where they soon metamorphosed. The remaining 5 still showing no change at the end of a week another 2 were then tested. These also metamorphosed in C′. No larva metamorphosed in E until the end of the third week when 2 of the remaining 3 larvæ became young worms. The last larva was transferred to a similar vessel E′. For nine weeks this individual appeared to be in perfect health, sometimes resting on the bottom, sometimes swimming vigorously. At the end of this period it underwent what seemed to be an attempt at metamorphosis during which it became unhealthy and died. These last three larvæ all grew and gained new setigers, the first two metamorphosed with 16 and 18 setigers, and when the last one died it had between 18 and 20 setigers.

DISCUSSION.

It is evident from these results that the muddy sand in vessel C was a very suitable bottom for metamorphosis. This muddy sand was of a very similar nature to that in which the adult worms are found. The silver sand in B and the mud in D were evidently not so suitable ; there was a delay before the larvæ metamorphosed. Since the larvæ were taken at random from the plunger-jar there is only a very slight possibility that those in C were more advanced than those in the other vessels. This possibility is, however, discounted by the result obtained when larvæ from B and D were transferred to C at noon on May 1st. Conclusive evidence of delay on an unsuitable bottom is however furnished by vessel E where there is no possibility of explaining the results there obtained by assuming that the larvæ were in any case not quite ready to undergo their critical change. The delay is far too great and moreover by the time the last three larvæ metamorphosed or died they had more setigers than the stage at which the larvæ first come into a condition when metamorphosis is possible. The larvæ tested by transference to a suitable substratum on the three dates, May 1st, 3rd, and 10th gave as good a proof as could be obtained that the larvæ in this dish were ready to metamorphose during the whole period. Why two of them actually metamorphosed on this bottom on May 22nd is not clear, but the fact that they did so successfully and continued to grow until they were fixed over a month later demonstrates that the bottom itself was not an impossible one for the young worms to live in, at least under laboratory conditions. During this time one had attained 72 setigers and the other 48. The only larval features that remained were the pigment patches on the third parapodia and the anal cirri, as the third pair of eyes had disappeared and the hooded crotchets did not commence till the 23rd setiger. On the shore adults of this species are to be found rarely, if at all, in fine clean sand of this nature.

It is interesting to note that the sand in vessel E which proved so unattractive to Scolecolepis larvæ was of the character that would have readily induced metamorphosis in the Mitraria larva of *Owenia fusiformis*, while the muddy sand in vessel C would probably have proved unsuitable for that species.

Vessel A yields little information. As remarked above it is not an ideal control. We are unable to explain why some of the larvæ became unhealthy after the first two or three days.

GENERAL CONCLUSIONS.

While admitting that it would have been desirable to have used a larger number of larvæ had they been available we are of the opinion that it is possible to draw conclusions of considerable ecological interest. These are as follows :—

1. *Scolecolepis fuliginosa* larvæ do not metamorphose until they have reached the fourteen-setiger stage attained after six weeks of free swimming existence assuming the rate of development in the sea to be the same as in the laboratory.

2. When this stage is reached they make their way to the bottom and begin to burrow as soon as suitable ground is found.

3. They do not metamorphose in the plankton in mid-water and then sink to the bottom to take up adult life.

4. Metamorphosis may be complete in twelve hours or less.

5. The suitability of the substratum evidently depends to some extent at least on the grade of the bottom deposits, a sandy mud being most suitable. Other factors, such as the organic content, may also determine the suitability.

6. Should a suitable locality not be found immediately the larva is able to postpone metamorphosis for a period that may be as long as several weeks. In the meantime the larva still actively swimming, grows slowly with the addition of new setigers.

7. If the right kind of ground is never reached an attempt is made at metamorphosis which may or may not produce a normal worm. This point is not clear and needs further investigation.

8. This ability to delay metamorphosis must greatly increase the larva's chance of reaching suitable ground, and is therefore of the utmost importance as a survival factor.

Apart from those details that are obviously specific for *Scolecolepis fuliginosa* these conclusions are in the main the same as those already formulated for the Mitraria larva (Wilson, 1932, p. 309). They are probably general for other species as well. The account one of us has given of the settling down and metamorphosis of the very similar larva of *Polydora hoplura* (Wilson, 1928b, pp. 583–585) is very suggestive that these postpone metamorphosis until they have found a suitable crevice in which to settle and begin adult life. Species that when adult are sedentary attached to rocks, shells, etc. (e.g. Pomatoceros, Sabellaria) may also suspend metamorphosis for a while until they reach some hard object on the sea bottom. In such cases, however, it would be exceedingly difficult to devise laboratory experiments to show this, as the side of any containing vessel is a suitable substratum for such larvæ. Worms that have a post-larval pelagic stage in a secreted tube (Lanice, Loimia, Arenicola, Pectinaria) will almost certainly be able to live and grow for some time after the stage at which they would normally become benthonic. Monro records (1930 and 1931) some interesting specimens of pelagic Loimia worms belonging, apparently, to the species *L. medusa*, especially one that was obtained between 250 metres and 100 metres in the middle of the South Atlantic. This specimen was at a much more advanced stage than that at which young pelagic *Loimia medusa*, given the opportunity, will start building their sandy tubes (Wilson, 1928a). Probably this worm had failed to reach the bottom at the usual time but had continued to grow normally in spite of an unusually long pelagic existence.

It is hoped to continue investigations along these lines whenever opportunity permits. It is scarcely necessary further to stress the ecological importance of such observations and their bearing on the distribution of ocean life.

SUMMARY.

Laboratory experiments indicate that larvæ of *Scolecolepis fuliginosa* when ready to metamorphose, are able, if necessary, to postpone metamorphosis until a substratum suitable for adult life is reached, meanwhile continuing to swim and grow for a period that may be as long as several weeks.

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EXPLANATION OF THE TABLE.

The main results of the experiment are here tabulated to facilitate comparison between the time of metamorphosis in the different vessels. Only essential dates are recorded. The following abbreviations are used :—

a, abnormal. b, burrowing larva beginning to metamorphose. d, dead. l, accidentally lost. s, swimming larva. u, unhealthy. w, young metamorphosed worm.

The following symbols denote changes in the different vessels.

* 5 larvæ removed to C and 5 fresh swimming larvæ added.

[1] 8 worms removed.

[2] 15 larvæ, 5 from each of A, B and D were added, making with the 2 already present a total of 17.

[3] 6 larvæ transferred from A to A′.

[4] 3 healthy larvæ transferred from A′ to A″.

[5] 4 larvæ transferred from B to C′.

[6] 5 larvæ transferred from E to C′.

[7] 2 larvæ transferred from E to C′. They started to burrow immediately.

[8] 1 larva transferred from E to E′.

[9] Contents of the vessel sent to Liverpool. On arrival 8 worms were still living.

Date.		A Clean Vessel.	A′ Clean Vessel.	A″ Clean Vessel.	B Silver Sand.	C Sandy Mud.	C′ Sandy Mud.	D Mud.	F Fine Sand.	F′ Fine Sand.
April 30	Noon	10s			10s	10s		10s		
,,	1.30 p.m.	,,			,,	2s, 8b		,,		
,,	6 p.m.	,,			,,	2s, 5b, 3w		,,		
May 1	10 a.m.	,,			,,	2s, 8w[1]		,,		
,,	Noon	10s*			10s*	17s[2]		10s*	10s	
,,	1 p.m.	,,			,,	13s, 4b		,,	,,	
,,	2.30 p.m.	,,			,,	10s, 7b		,,	,,	
,,	5 p.m.	,,			,,	4s, 13b		,,	,,	
,, 2		6s[3], 4uw	6s[3]		,,	4s, 13w		,,	,,	
,, 3		4dw	3s[4], 3us	3s[4]	9s[5], 1w	,,	4s[5], 5s[6]	5s, 2w, 3ds	10s[6]	
,, 4			2us, 1ds	,,	5s, 1w	,,	2s, 2b, 2w, 3l	3s, 4w	5s	
,, 6			,,	2s, 1w	3s, 3w	17w	1s, 5w	1s, 6w	,,	
,, 8			1us, 1aw	,,	,,	,,	,,	7w	,,	
,, 10			,,	,,	,,	,,	6w, 2b[7]	,,	5s[7]	
,, 12			,,	,,	,,	8w[9]	8w	,,	3s	
,, 15			,,	,,	1s, 5w	,,	,,	,,	,,	
,, 19			,,	1s, 2w	6w	,,	,,	,,	,,	
,, 22			2aw	,,	,,	6w, 2dw	,,	?	1s[8], 2w	1s[8]
,, 29			,,	,,	,,	6w	,,	Dead	2w	,,
June 6			2dw	1us, 1w, 1dw	,,	,,	7w, 1dw		,,	,,
,, 11				Dead	?	,,	?		,,	,,
,, 28					2w, 4dw	,,	Dead		2w	,,
July 3						,,				1ub
,, 4						,,				,,
,, 26						6w				

The Habitat of *Procerodes ulvæ*.

By

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THE relation of *Procerodes ulvæ* (*Gunda ulvæ*) to its environment has recently been studied by Pantin. In a series of papers (Pantin, 1931 (1) and (2); Weil and Pantin, 1931) a number of interesting facts have been brought out, which can be summarised as follows: This turbellarian is one of a very small number of marine forms which successfully colonise a region where there are large abrupt changes in osmotic pressure. It is found under stones in the intertidal zone and mainly where a stream of fresh water flows down the beach, though it occurs elsewhere too. In this habitat it is immersed in sea-water at high tide but between tides it is in perfectly fresh water (less than 0·01% sea-water). Procerodes is not water-tight, but swells up in fresh water. The swelling is controlled, however, and the animal loses salts in the process. The animal does not come into osmotic equilibrium with fresh water, as it does with sea-water, but can maintain a " steady state " for a time by means of an increased expenditure of energy as shown by increased oxygen intake (Beadle, 1931). The steady state is much better maintained and the swelling controlled in the presence of an appreciable concentration of calcium salts. The particular stream examined by Pantin, at Wembury near Plymouth, contains 58–65 mgm. of calcium per litre. For comparison sea-water contains 420 mgm. Ca per litre. Very hard spring water may contain as much as sea-water, while upland surface water may contain as little as 1 or 2 mgm. per litre.

The question now arises, is Procerodes confined to regions of hard water streams or if it lives in soft water streams is it driven further down the beach, where it has a shorter interval in fresh water? With a view to answering this question I have examined many miles of coast in different parts of the country and, though I never failed to find Procerodes wherever conditions were suitable, for a long time I failed to find a soft water stream on the coast. Whatever the nature of the underlying rock, surface water from cultivated land contains 20 mgm. or more of Ca per litre, generally more. The amount will vary of course with the weather, time of year, and treatment of the soil, and immediately after heavy rain may sink to quite low values. Even where there is no cultivation concentrations between 10 and 20 mgm. are likely. But lower values have been found in two regions, one in the Isle of Man, the other in Morar, Invernesshire.

Place.	Date.	Calc. mgm. per litre.
West of St. Ives, Cornwall (2 streams)	15.7.32	12, 15
St. David's Head, Pembroke	2.7.31	14
South of Carmel Head, Anglesey (2 streams)	13.9.32	17, 18
Bay Fine, Southern end of Isle of Man	8.4.32, 24.9.32	19, 16
Bay Stacka ,, ,, ,, ,,	10.4.32, 25.9.32	18, 13
Near Fleshwick Bay, W. coast of Isle of Man	18.5.33	6
The Stacks, W. coast of Isle of Man	24.9.32, 17.5.33	5, 4
Loch nan Ceall, Morar	19.8.33	5
Bourblach House ,,	19.8.33	5
Sgeir Mhor ,,	19.8.33, 13.9.33	5, 12
Boagha Dearg ,,	13.9.33	8

None of these waters were acid. The Morar waters, though coming from deep peat and coloured with it, were alkaline (pH 7·2 to 7·6) and had an appreciable alkali reserve (combined CO_2). This is presumably the result of active vegetation ; in winter the results might be different. The nearest approach to pure water is that found at The Stacks, Isle of Man. This place is perhaps worth a fuller description.

About 3½ miles north of Port Erin a stream is marked on the One-Inch Ordnance Map entering the sea near a point marked " The Stacks." The stream drains quite uncultivated land, covered with a scanty growth of heather and gorse. The soil is thin and somewhat peaty. The stream drops 500 feet in the course of a quarter of a mile. About half-way down it falls over a small cliff into a shallow ravine where there is much loose soil and stones. Above the ravine the water was found to contain 2–3 mgm. Ca per litre, at the beach 4–5 mgm. Evidently it picks up some from the soil on the way down. The beach is sheltered by outlying rocks and consists of large stones. It is an excellent habitat for Procerodes, which is abundant at all levels.

There is another more accessible stream with low calcium content near Fleshwick Bay, but here the upper beach is shingle and devoid of life so that Procerodes is confined to the lower levels. The Morar beaches are more accessible and have the advantage that High Water at Neaps occurs at less awkward times of day than in the Isle of Man. Observations of the upper limit of Procerodes have been made in both places but before discussing them something ought to be said about what in general constitutes a suitable habitat.

Procerodes lives on the undersides of stones that are large enough or well enough imbedded to be seldom moved. But it needs clean well aerated conditions so that the underside should be on rock, gravel, or coarse sand. Consequently it is scarce or absent in really sheltered waters where the beaches are usually muddy. It is always to be found on beaches of the open coast where the conditions are suitable. In general the best habitat is where the stream is small so that there is not enough flood water to move stones about and where it runs down a gully in rocks or down a beach of large stones in a cove with some shelter from outlying rocks or big boulders. I have found Procerodes flourishing at an exposed part of the southern coast of the Land's End peninsula, where there is a " beach " of huge granite boulders firmly pounded and wedged together by the seas. Underneath the boulders are pools with stones and coarse gravel evidently quite sheltered from the heavy seas of this coast.

On many beaches the higher part from the level of Spring High Water down to the Neap High Water level or lower is shifting gravel or shingle where nothing can live, so that only the lower part of the beach is suitable for Procerodes and other intertidal forms. Where there is a question of the upper limit of Procerodes it is necessary to consider only places where the upper zones are physically suitable.

It is noticeable that, where a stream runs down, the beach is cleaner and less liable to contain putrefying algal detritus. This fact and the fact that the stream keeps things cool and moist makes the region of the stream a better habitat in other respects than the rest of the beach for an organism that can endure large osmotic changes. In the middle of the tidal zone Procerodes is often to be found well away from the stream but higher up it is confined to it. Elsewhere the underside of stones high up the beach will dry up and warm up between tides and may be sticky with decayed weed. Gammarus and a few Isopods can flourish there but nothing else.

Pantin (1931, 1) found Procerodes at Wembury living up to about the level of High Water Neaps, and it was clear from an examination of many beaches that the upper limit is somewhere in this region, but further observation was evidently necessary. When I examined the beach of the Stacks, I.O.M., at Neap High Water of May 17th, 1933, it was surprising to find that the highest Procerodes were more than a foot above the highest point reached by the sea. There was a light offshore wind and the splash zone was quite small. By approximate calculation from the tide tables it was clear that on this beach the uppermost Procerodes were liable to be in pure stream water containing only 5 mgm. Ca per litre for 3 days, possibly 5 days, if there was calm weather with a Neap Tide period, and it had been seen that they could stand at least 2 days without harm. In rough weather of course they would always get splashed. Observations were also made at Bay Stacka using a tape dyed with silver chromate which is stained white by salt water. The highest Procerodes there were at a similar level above high water and they were found alive after 3 days without sea-water in water containing 13–18 mgm. Ca per litre.

It was noticed on these two beaches that the upper limit of Procerodes was very close to the upper limit of *Fucus spiralis* on adjacent rocks. As the line is very sharp and as the upper limit of *Fucus spiralis* is also the lower limit of *Pelvetia caniculata* these two weeds provide an excellent point of reference which may be taken as marking the same tidal level on all beaches, i.e. about Mean High Water Neaps (Colman, 1933).

The Morar coast was visited in August, 1933, and a region for observation was found on the coast below Bourblach Hill to the west of the road to Mallaig just north of the estuary of Morar River (*cf.* One-inch Ordnance Map). This region is entirely uncultivated and the soil is peat. It contains several small streams, of which two are specially suitable. One just north of Sgeir Mhor runs down a cleft in the rocks forming shallow pools with stones. The other is further north, by Bogha Dearg, where a stream is marked on the map. This stream runs down a very gently shelving stony beach sheltered by outlying rocks. A third stream running into the Morar estuary just below Bourblach House with some slight cultivation on its course, was also examined. Although in shelter the beach is clean and suitable for Procerodes. In this region Procerodes is not abundant but is found in all suitable places, the upper limit was seen to be very close to that of *Fucus spiralis* in all three places.

Further observations were made at the low Neap Tides in September (lowest on September 13th). From the data in the Admiralty Tide Tables it is clear that the predictions for Stornoway can be applied to this coast without appreciable correction for height. Fortunately there was a spell of fine weather with calm sea and mainly offshore winds at this time, so that the splash zone was small.

At all three stations the upper limit of Procerodes coincided very closely with that of *Fucus spiralis*, it was certainly not lower. The high water of the afternoon of the 13th (9·4 ft.) was more than a foot below this line at Sgeir Mhor and that of the afternoon of the 14th (10·0 ft.) at least a foot below at Sgeir Mhor and Bogha Dearg. The morning tide of the 14th was predicted as 9·2 ft. so that it was not necessary to make an observation of it. The morning tide of the 15th (9·9 ft.) was observed at Sgeir Mhor by means of silver chromate tape. The wind was S.W. and freshening, raising some sea. Although the splash zone was now considerable the highest Procerodes pool cannot have been reached by sea-water. On this morning (September 15th) the Procerodes at Sgeir Mhor and Bourblach House, which cannot have been in sea-water since the night of September 10th to 11th (10·8 ft. tide) and possibly not since the previous night, were mobile and apparently in good condition if a little swollen. There was no time to visit Bogha Dearg again, but the Procerodes there were alive on the afternoon of the 14th. The afternoon tide of the 15th (10·8 ft.) almost certainly covered the whole Procerodes zone, with the onshore wind then blowing, but if the weather had been calm might have barely reached the upper limit.

It was disappointing to find that the calcium content of the Morar waters was higher than in August, presumably owing to the dry weather. However, the quantities, 8 and 12 mgm. per litre, were not excessive.

For comparison with Morar, the coast to the east of St. Andrews Bay, Fife (Kinkell Braes), was examined on September 11th. A number of small streams partly from springs in the sandstone and partly drainage of cultivated land occur here. In many places the upper beach is pure shell sand and not suitable for Procerodes, but one excellent place was found just west of Kinkell Ness. The water here contained 39 mgm. Ca per litre and Procerodes was living up to the line dividing *Fucus spiralis* and *Pelvetia caniculata*. By reference to these algæ there was no perceptible difference between the upper limit here and in Morar, or in fact in any region examined.

It must be concluded (1) that Procerodes is not limited in its distribution by the calcium content of the fresh water stream it colonizes down to a minimum of 5 mgm. Ca per litre : (2) that it can survive about 5 days without sea-water, a contingency that may occur whenever a low neap tide period coincides with calm weather. It has been pointed out by Orton (1933) that the combination of neap tides, calm sea, and hot weather may be very lethal to the population of the upper part of the tidal zone (i.e. above the lowest Neap High Water level). The habitat chosen by Procerodes has at least the advantage that it is never exposed to high temperature or dessication, and the animal is not confined to short and uncertain periods of immersion in sea-water for obtaining its food.

In the laboratory Procerodes does not seem able to survive more than about 2 days in pure water ; but it must be remembered that laboratory conditions are probably much severer than its natural habitat on account of high temperature, exposure to strong light, and absence of food supply. So that it is not altogether surprising that it should succumb more quickly.

SUMMARY.

Procerodes ulvæ has been found living in streams with calcium content as low as 5 mgm. per litre. Its upper limit does not appear to be affected by the calcium content of the water. The animals at the upper limit are liable to about 5 days' exposure to fresh water if calm weather coincides with Neap Tides. Animals living in water of 8–12 mgm. Ca per litre have been found alive at the end of such a period.

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Two Parasites of the Common Cockle *Cardium edule;* a Rhabdocoele *Paravortex cardii* Hallez and a Copepod *Paranthessius rostratus* (Canu).

By

D. Atkins, B.Sc.

CONTENTS.

IN view of the serious mortality reported among *Cardium edule* in the summer of 1933 (Orton) the following account of British parasites of this species may be of interest.

PARAVORTEX CARDII HALLEZ.

Apparently healthy cockles in the Plymouth area are very generally infected with a viviparous Rhabdocœle, *Paravortex cardii* Hallez (Hallez, 1909). In a passing reference to this parasite in a recent paper (Atkins, 1933, p. 250) I incorrectly referred to it as *Graffilla gemellipara* Linton, a species known as a commensal of *Modiolus demissus* at Woods Hole, America (Linton, 1910).* While my paper was still in the press, but too late for correction, I chanced upon Hallez's paper on *Paravortex cardii*, a species of Rhabdocœle parasitic in *Cardium edule* from Le Portel, Boulogne-sur-Mer. Examination of the parasite of cockles from the Plymouth area showed it to be this species, and not *Paravortex* (=*Graffilla*) *gemellipara* (Linton).

The characteristics of *P. cardii* as given by Hallez (1909, pp. 430–1) are as follows : " Vorticide pourvu de deux ovaires, de deux glandes lécithogènes réticulées et anastomosées et de deux testicules globuleux ; dépourvu

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* Leigh-Sharpe (1933) in a note on the occurrence of a Turbellarian in a *Cardium edule* from Millbrook, Plymouth, also appears to have wrongly identified it as *Graffilla gemellipara*. The animal he figures has the appearance of being somewhat compressed.

de bourse séminale. Orifice génital ventral situé près du pharynx en arrière, à l'extrémité du premier quart du corps. Organe copulateur mâle musculeux, dépourvu de pièces chitineuses et portant deux lobes papillifères. Pharynx doliiforme. Bouche ventrale vers l'extrémité antérieure du corps. Corps cylindrique, à extrémité antérieure plus amincie que le reste du corps, uniformément cilié, blanc légèrement jaunâtre, transparent, dépourvu de rhabdites, très contractile, ordinairement courbé en arc et tournant sur place en décrivant un cercle. Deux yeux noirs réniformes au niveau du pharynx. Longueur maxima, 1 mm.; largeur, 0·3 à 0·4 mm. Vivipare. Nombreuses coques molles (jusqu'à 40) renfermant chacune un à quatre embryons et disséminées dans le tissu conjonctif. Les coques vides et recroquevillées restent dans le corps de la mère. Vit dans l'estomac du *Cardium edule*."

The reproductive organs, so far as can be seen in the living animal, are on the plan described and figured by Hallez (1909, Pl. XXVII, Fig. 20). The atrium was rarely distinguished satisfactorily. The general presence of sperm in the female atrium and oviducts and in the vesicula seminalis renders these parts of the generative apparatus clearly visible; when empty, however, the female atrium and oviducts are distinguishable with difficulty.

Ball in 1916 (p. 455) added to Linton's description of the Rhabdocœle commensal with *Modiolus demissus*, and (p. 459) referred it to the genus Paravortex. He (pp. 459–60) sums up the likenesses and differences of the two species as follows: "Linton's species and *P. cardii* are closely similar both in structure and habits. Both have essentially the same colour and the same shape of body. Both have similar digestive, sensory and glandular organs; both give birth to living young which develop in capsules within the mother's body; both show the same peculiar movements when taken from their host and placed in sea-water.

"The two species differ, however, in that the American form attains twice the size of *P. cardii;* the genital pore is situated farther posteriorly and the ovaries are longer in the latter;* an atrial canal in *P. cardii* leads from the dorsal part of the atrium backward to the antrum femininum, while in the American species there is no distinct canal but rather the antrum femininum extends backward from the middle of the posterior atrial surface and its opening into the latter is strongly constricted by a sphincter muscle; the openings of the shell glands in *P. cardii* are distributed along the entire ventral wall of the atrial canal and antrum femininum, while in Linton's species they all open at the anterior end of the antrum just back of the atrium; the vitello-oviducts

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* This is evidently an error for "former," for the genital opening of *P. cardii* is at the end of the first quarter of the body (Hallez, 1909, p. 431); that of *P. gemellipara* is at the end of the first third (Ball, 1916, p. 455).

of *P. cardii* are the longer. Linton's species lives as a commensal in the mantle cavity of the ribbed mussel, *Modiolus demissus ; P. cardii* is parasitic in the stomach of *Cardium edule.*

"Linton's species resembles *Paravortex scrobicularia* rather than *P. cardii* in the form of the ovaries, i.e., they are elongated in the first two and shorter in *P. cardii.*"

Linton (1910) the discoverer of *P. gemellipara* stated that it was a commensal, but Patterson (1912, pp. 174–5) concluded that it lived chiefly in the kidney. Ball (1916, pp. 462–3), however, failed to find any evidence that it was other than a commensal.

Occasionally specimens of *P. cardii* from Cardium from the Plymouth area are somewhat larger than the maximum length given by Hallez, reaching at least 1·2 mm., but measurements are difficult to make owing to the animals being very contractile, and no really satisfactory narcotic being discovered. Cocain—used by Hallez—was not obtainable ; stovain and chloretone were not successful ; isotonic magnesium chloride gave fairly good results, but caused shedding of the ectoderm in a short time. The maximum length of *P. gemellipara* is given as 2·0 mm. (Linton, 1910, p. 372).

The greatest number of capsules containing embryos observed by Hallez in a single individual was 40. However, a specimen, about 1·2 mm. long, from a Yealm Estuary Cardium, contained 47 full capsules (20 with embryos with eyes developed), while one from Neille Point had 50 to 60 full capsules, many with embryos with eyes developed. Capsules with more than 2 embryos have not been observed, though some 30 capsule-containing specimens have been examined.

According to Hallez (1909, pp. 438, 446) the adult parasites are always found in the stomach of their host. The embryos escape from the body of the parent and pass into the intestine of the host, where they attain their development in some three or four days (this being the time necessary for the emptying of the gut in cockles deprived of food) and pass out by the exhalent siphon. He believes that copulation takes place normally in the intestine, but perhaps exceptionally during the free-living period. Immediately after copulation there occurs migration into the stomach of another Cardium, where the parasite completes its life history.

Hallez (1909, pp. 438–443) notes that exceptionally the formation of capsules may begin while the Rhabdocœle is in the intestine of the host. While the intestines of few Cardium were examined at Plymouth, it was found that of 14 Paravortex, the largest of which was about 0·9 mm. long, taken from this position from 5 hosts, 7 contained 1 to 10 capsules.

The quantity of sperm in the female atrium and oviducts of young specimens is frequently much less than in large ones with many capsules : it would seem, therefore, that copulation occurs more than once, unless self-fertilisation takes place as Hallez supposed possible (1909, p. 444). It is of special interest that a Paravortex from a Neille Point cockle was crowded with numerous capsules the contents of which were degenerating. It seems probable that this was due to the ova being unfertilised; the only sperm visible was a minute quantity of immobile sperm in the vesicula seminalis.

Distribution in the Plymouth Area.

Estuaries of the Hamoaze. Infected cockles have been obtained from several localities.

(*a*) Millbrook. Of those procured on October 12th, 1933, the stomachs of the ten examined were all infected with Paravortex; the intestines were not examined. Single individuals were found respectively with: 27 parasites, all small and none carrying embryos; 23 (7 with capsules); 20 (6 with capsules); 14 (12 with capsules); 10 (4 with capsules); 4 (one being large, with many capsules, and 3 tiny); while four individuals contained two each (all with capsules). A peculiarity of this batch was the number of small individuals.

(*b*) St. John's, St. John's Lake. Three small cockles, 11·0 to 18·0 mm. long, gathered on July 27th, 1933, proved to be infected. From one of these thirteen Paravortex were taken, four having 1 to 14 full capsules. Six of them, including one with 4 capsules, were taken from the intestine. The second Cardium yielded nine parasites, 4 carrying 1 to 4 full capsules. Two of them, each with a single capsule, were taken from the intestine. From the third Cardium eight Paravortex were taken, only one having capsules (8); a tiny one came from the intestine.

(*c*) Saint German's on the Lynher River. Twelve out of fourteen cockles (85·7%) obtained on August 25th, 1933, proved to be infected. The stomachs were examined but not the intestines. Five cockles had one Paravortex each—one being also infected with the sporocysts and cercariæ (Bucephalus) of Gasterostomum;—one had 3; one had 4; one had 5; two had 7; and one had 11.

(*d*) Neille Point, near the junction of the Tamar and Tavy. Four out of ten Cardium (40%) examined on August 3rd, 1933, proved to be infected, one large Paravortex being taken from the stomach of each (the intestines were not examined). The number of full capsules present in these individuals was 22, 26, 50 to 60; in one they were too numerous to count.

(*e*) Stonehouse Pool. Twelve out of thirteen cockles (ca. 92%), examined on August 8th, 1933, were infected. The stomachs only were examined: five individuals had 1 parasite each; one had 3; one had 4; two had 5; one had 6; one had 8; and one had 14.

Yealm Estuary. Cardium from this locality are very generally infected;

of five small individuals especially examined in July, 1933, four were parasitised. Details of the infection are as follows : From one cockle, 23 Paravortex were obtained, 3 only being without capsules. The number of full capsules varied from 3 to about 30 in different individuals, 13 having 10 or more. Escaped young were found in the watch glass with these adults. Seven specimens were a millimetre and more in length. From a second Cardium 17 *P. cardii* were taken, 11 having 2 to 16 full capsules. Five individuals were a millimetre and more in length. From a third Cardium 7 parasites were taken, 3 with 1 to 10 full capsules. Two were a millimetre and more long. From a fourth cockle 3 parasites were taken. Of two, about 1·2 mm. long, one had 47 full capsules, the embryos of 20 having eyes already formed, and the other 31 full capsules, 17 containing embryos with eyes formed. The third specimen, about 0·9 mm. long, had 2 capsules with young embryos.

Salcombe Estuary. Parasitised cockles have been obtained from Kingsbridge. Four out of seventeen (ca. 23%) examined from this locality on August 11th, 1933, were infected. The number of *P. cardii* in a host was small, 3 having 2 each and the fourth a single specimen.

From Millbay, near the mouth of the Estuary, 6 cockles, gathered from the surface on September 5, 1933, had no Paravortex. One at least had the interlamellar spaces of the gills swarming with an Ancistrum type of Ciliate.

From these few examples it would seem that infection varies considerably in different localities, being heaviest in cockles from Millbrook, St. John's Lake, St. German's, Stonehouse Pool and the Yealm Estuary. From these five localities 31 out of 41 hosts had more than one parasite, and one had as many as 27. The infection is heavier than Hallez found at Le Portel, for he writes (1909, p. 437) : " Il est à noter que le nombre des Cardium qui n'hébergent qu'un seul individu est très élevé (43 à 52%) et qu'il est relativement rare de trouver plus de quatre parasites dans le même estomac."

P. cardii would seem to have a wide distribution in the British Isles. Nicoll (1906, p. 154 and Pl. IV, Fig. 7) described as a Trematode sporocyst in *C. edule* at St. Andrews, Scotland, a form which is almost certainly this Rhabdocœle. Dr. M. V. Lebour, to whom I am indebted for the reference both to Linton's and to Nicoll's paper, has pointed out to me that she (1904, pp. 83–84) also described as a Trematode sporocyst in *C. edule* from Budle Bay, Northumberland, a form which is no doubt identical with the Rhabdocœle from South Devon and Cornwall. Lebour (1904, pp. 83, 84) found the parasite in about 75% of the cockles examined. Nicoll (1906, p. 154) states : " Rarely were there more than half a dozen in one cockle, and only in about 20% were they entirely absent." Hallez (1909, pp. 435, 436) found at Le Portel, Boulogne-sur-Mer that 141 out of 300 (47%) *C. edule* examined during August, September, October and November were infected, the number of parasites in a host varying from one to twenty ; 43% contained one only. In December about 43% were infected ; in February about 46%. He therefore concludes that the winter has no influence on the percentage, which remains very much the same as during the summer and autumn. Analogous results were obtained in the spring. At Dannes-Camiers he found the percentage infected to reach 67%.

PARANTHESSIUS ROSTRATUS (CANU).

Paranthessius (=*Herrmannella*) *rostratus* (see Canu, 1892, pp. 235–7, Pl. XXIV, Figs 1–13 ; Monod and Dollfus, 1932, pp. 143–6) has been obtained from the mantle cavity of Cardium from several localities in the Plymouth area. From Neille Point, near the junction of the Tamar and Tavy, the mantle chambers of ten cockles examined on August 3rd, 1933, were aswarm with the copepod. Thirteen cockles from Stonehouse Pool on August 8th, were all infected with Paranthessius, but not heavily. Fourteen Cardium obtained from near Saint German's on the Lynher River, on August 25th, all proved to be heavily infected : females carrying egg-sacs were numerous. Ten cockles examined of those obtained from Millbrook on October 12th were all infected : some of the adults carried egg-sacs.

From Kingsbridge on the Salcombe Estuary seventeen cockles, obtained on August 11th, were all rather heavily infected : many of the copepods carried egg-sacs. On September 5th six cockles from Millbay, near the mouth of the estuary, all proved to be infected : some of the copepods carried egg-sacs.

This copepod was first recorded in the British Isles from *C. edule* from Morecambe Bay, Lancashire, by Fraser (1932). Leigh-Sharpe (1933a, pp. 113–4) has since recorded it from the testis of Cardium from Millbrook, near Plymouth.

Paranthessius is a semi-parasite only (see Canu, 1892) and has been taken in tow-nettings from gulleys on the cockle beds in Morecambe Bay by Fraser (1932).

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Studies in Sublittoral Ecology. I. A Submarine Gully in Wembury Bay, South Devon.

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With 2 Figures in the Text.

CONTENTS.

I. INTRODUCTION.

BOTH the intertidal region of the shore, and the sea-bottom at depths of anything over three or four fathoms, have been comparatively well explored biologically; but that part of the sea coast which lies just below the level of low water spring tides is—around the British Isles—almost unknown. It is out of range of ordinary shore-collecting, and yet much of it is also unsuitable for detailed investigation from a boat. This is especially true of steep, rocky shores, where a large part of the sublittoral region consists of ledges and vertical or even overhanging rock faces, which would be quite inaccessible even if work from a small boat were attempted. In Sweden Gislén (1930), who employed a professional diver, has made an extensive general survey of the plant and animal associations characteristic of a rocky bottom in the Gullmar fiord. But for the British Isles previous knowledge relates only to the distribution of the larger and more conspicuous algæ (Cotton, 1912); although the flora of the German warships which were sunk in Scapa Flow has been investigated more closely by Miss Lyle (1929), also with the help of a professional diver.

In the summer of 1931, at the suggestion of Mr. G. A. Steven, of the Plymouth laboratory of the Marine Biological Association, the writers decided to test the possibility of carrying out a detailed investigation of this hitherto unexplored region by means of a diving helmet (see below). Such a helmet has been used by many workers in the tropics, but has not previously been tried in temperate waters, in view of certain supposed difficulties. Chief of these were :—

(i) Water too cold for an unprotected diver.
(ii) Poor visibility.
(iii) Excessive interference by rough weather.

These difficulties were found to be either not effective, or else easily surmountable, and are discussed in detail below.

(i) *Cold.* In July and August near Plymouth we found that we could each stay down for about a quarter of an hour at a stretch fairly comfortably, and at most for twenty minutes. We compensated ourselves for this shortness of time below water by working as a team generally of four people, of whom each went down in his turn; so that an hour's work could be done below water on any one day, and in favourable circumstances more. We found that the use of grease was of little help in combating the cold. Frequent diving led to a greatly increased appetite for sugar and treacle.

(ii) *Visibility.* There has always been plenty of light at the depths at which we have worked (down to six fathoms on the west coast of

Scotland). After rough weather the water was often turbid with silt in suspension, but even so with a sandy* bottom it was always possible to see clearly objects not more than two feet away.

(iii) *Rough weather.* On shores open to the English Channel the helmet could only be used with safety when the sea was moderately calm. A heavy " ground " swell makes diving impossible, even though the water is otherwise smooth, as it breaks with violence on the rocks. For this reason on an Atlantic coast diving would be difficult, but might be done from a boat. We were able to work under water on about half of the number of days during which operations were in progress, but in settled summer weather it should be possible to dive every day.

In this paper are presented the results of an ecological survey of a small area on the coast near Plymouth, extending from Low Water of Ordinary Spring Tides down to a depth of about 10 feet below this level. The survey was carried out between July 14th and August 14th, 1931, and between July 1st and August 3rd, 1932.

II. Apparatus and Methods.

As the methods employed were modified to suit conditions in our seas, a moderately full account of them is given below.

1. *The Diving Helmet and Pumps.*

The helmet which we used is similar to that described and figured by Beebe (1926), with the difference that, on the advice of Professor C. M. Yonge, in order to avoid " seeing double," we had only one window. Such a helmet fits loosely over the diver's shoulders, and the pressure of air inside it, which is maintained from above by means of pumps (see below), keeps the water out. A helmet of this type is comparatively light and easy to handle, and below water it restricts the movements of the diver very little. It is therefore suitable for use when working in crevices and on steep rock faces. Further, its use requires no previous experience, and the diver, who is in no way attached to it, can easily leave it and swim to the surface if anything goes wrong.

A steady supply of air was provided for the diver from two foot motor-tyre pumps, which were connected through Schræder valves to a T-piece ; this last was connected through about 150 feet of garden hose with the helmet. One pump alone could in emergency supply sufficient air for the diver.

2. *The Telephone.*

A telephone system was installed, which enabled conversation to go on between the diver and those on shore. The system for speaking from the

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* In a Scottish loch with a muddy bottom it was impossible to see at all once the mud was stirred up.

shore to the diver consisted of an ordinary microphone and ear-phone circuit. But since carbon granule microphones are liable to give trouble if they get damp, a different system was used for speaking in the reverse direction. The diver spoke into a high-resistance ear-phone, which was connected at the land end through a transformer to a one-valve amplifier. The output from this was fed into a pair of wireless headphones. In order to keep out the sea-water, the ear-piece and acting microphone were each nearly filled with paraffin wax and covered with a thin rubber toy balloon.

3. *Guide Ropes and Safety Lines.*

(i) In order to recover the helmet should the diver find it necessary to leave it and come to the surface, and in order to take the weight of the helmet off the diver's shoulders while he was entering or leaving the water, a rope was attached to the top of the helmet itself.

(ii) A rope, securely belayed to the rock at its shore end, and attached to a fairly heavy stone at its free end, was thrown out in the direction in which the diver was intending to go. On this the diver lowered himself and hauled himself up. It also assisted him in finding his way to the required spot, and enabled him to work against a rock wall, suspended at any depth.

(iii) A third rope was used for lowering collecting bags to the diver.

4. *Methods of Collecting.*

It seemed essential that data should be quantitative. Accordingly, (*a*) complete collections were made of all animals and plants from small selected areas of rock surface; and (*b*) observations were made of the general distribution of those types of biological community of which the areas were considered typical. In 1931 (July 14th–August 14th) the selected areas were scraped clean with a strong knife into jars. This was a very slow process, and great care was needed to avoid loss of material. Therefore in 1932 (July) we used large bags with folding metal frames in the mouths. These frames were 1 foot × 1 foot or 2 feet × 1 foot, and when closed could be clipped together so as to keep the bags shut. Areas were scraped into these with a paint-scraper. With each of these methods there were some fast-moving animals (e.g. prawns, small fish) which must have escaped; but as this work was directed mainly towards sedentary or slow-moving forms, which make up by far the greater part of the community, this does not matter much. Encrusting Coralline Algæ could seldom be scraped off the rock, and boring animals would not have been collected by this method, so that the collections must be considered incomplete in respect of these types. Although a standard size and shape of area would have been advantageous, we had in practice to take whatever areas were allowed by the configuration of the rock surface.

III. Description of Environment.

1. *Geographical Account.*

The locality chosen for a detailed survey by means of diving was in Wembury Bay, South Devon; and the work was done in the gully on the S.E. side of the reef next to and S.E. of "Tomb Rock" (Ordnance Survey, 1913). This gully runs approximately N.E. and S.W., and is formed in the Dartmouth Slates (Ussher, 1912). It has on its N.W. side a nearly smooth rock wall, which is at about 15–20° from the vertical,

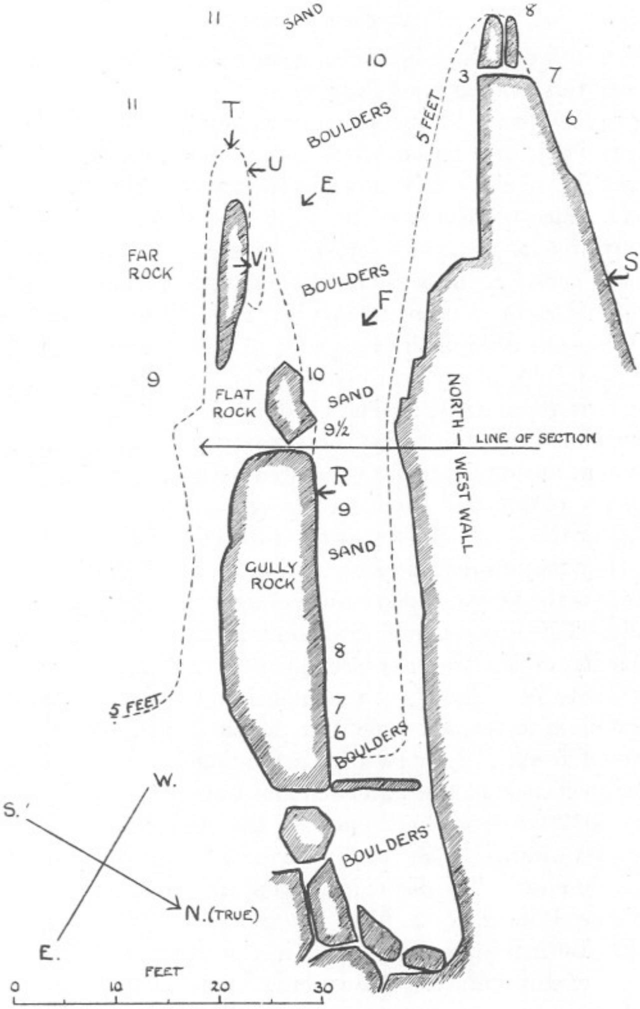

Fig. 1.—Chart of the Gully.

All depths are marked in feet below chart datum.

facing upwards. On the S.E. side the rock surface is irregular and in most places overhanging (see section, Fig. 2). This gully is one of a series of similar parallel gullies which have been eroded in this particular way owing to the high angle of dip of the strata. The middle part of the gully (see Fig. 1) has a sandy bottom at a depth of 10 feet below the level of low water of ordinary spring tides. At the two ends of the gully the bottom is strewn with large boulders. At the S.W. end, beyond the boulders, the gully opens out to join the even sandy bottom which is characteristic of that part of Wembury Bay.

2. *Ecological Factors.*

The chief environmental influences which are likely to affect the flora and fauna of this gully are as follows :—

(i) *Slope of Surface.* This is believed to be of great importance (see p. 694), and has obvious connexions with illumination and with the settling of silt. It is shown in the section (Fig. 2).

(ii) *Light.* Measurements of the light intensity at various positions in the gully were made by Dr. Atkins by means of two cuprous oxide photoelectric cells. A full account of these cells, including the methods of use and the corrections to be applied, is given by Atkins and Poole (1933). While one cell remained exposed to the full light in air, the other was placed or held in any required position below water by the diver. The diver took precautions against shading his cell himself, and when it was in position he notified the shore party by telephone. Thus the illumination at any position was compared with that in air. A full table of the figures obtained is given in the Appendix. While such figures only represent the light intensity at one time of day and state of weather and tide, they may nevertheless be used as a basis for comparison. The chief feature is the very low percentage of light which reaches the bottom of the gully. This is due partly to shading by the gully walls, and partly to the opacity of the water, especially near the bottom. The lowest figure obtained—less than 1% of the intensity in air—was from a position in the Laminaria forest (see p. 685) at the base of the plants, below the "canopy" of fronds. In view of the shading by the gully walls, the absorption coefficient of the water remains uncertain, but in any case it must vary greatly, depending much on the roughness of the sea, and increasing downwards. The upper layers at high tide are probably comparatively clear. The biological significance of illumination in this gully is discussed later (see p. 694).

(iii) *Silt.* Both the presence of silt in the water, and the settling of silt, may be of importance. The amount of silt in the water was very variable, but was greater near the bottom. Sometimes the bottom foot of water was thick with seaweed remains. Silt carried along in the water by waves probably has a scouring action, especially near the bottom. The amount of silt which settles will depend partly on the slope of the rock surface, and partly on changes in the turbulence of the water.

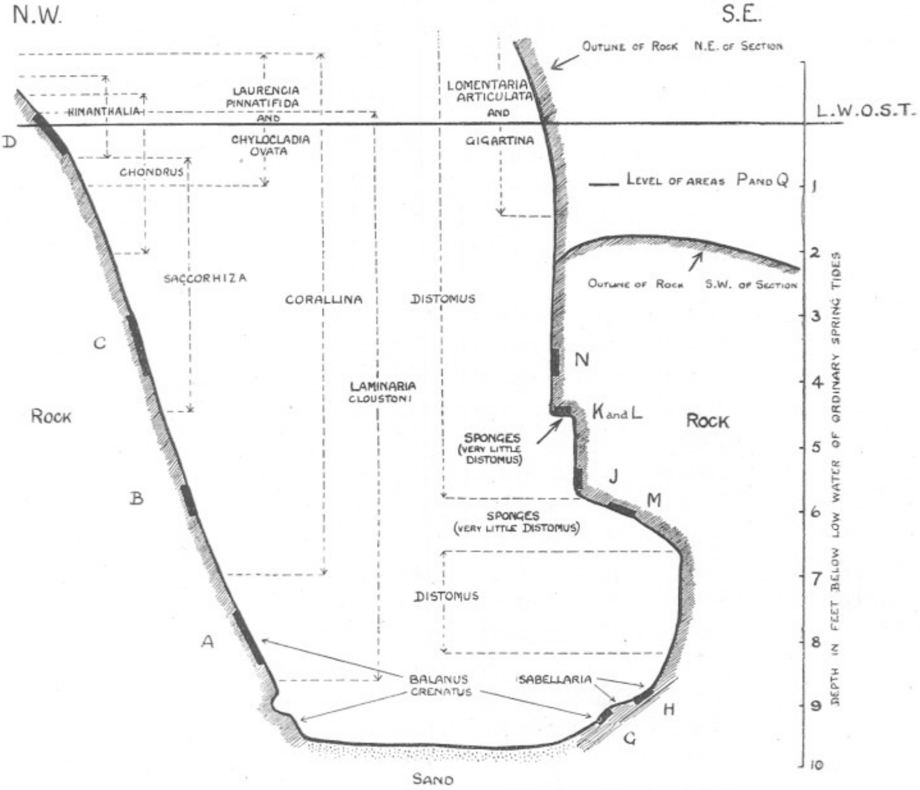

Fig. 2.—Section of the Gully.

L.W.O.S.T. Low Water of Ordinary Spring Tides has been taken as equal in level with Chart Datum. This latter was estimated by comparisons of the level of the water in calm weather with the level predicted for Devonport.

L.W.E.S.T. Low Water of Equinoctial Spring Tides is variable in level, but is generally between a half and two feet below Chart Datum.

We hope in a future investigation to be able to obtain some comparative measurements of the turbulence in different parts of the gully.

(iv) *Wave action.* This part of Wembury Bay is exposed* to weather

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* Some indication is given of the degree of exposure to wave action by the fact that in the intertidal region *Balanus balanoides*, *Chthamalus stellatus* and *Fucus vesiculosus evesiculosus* are present,—the last in small patches only, and poorly grown; while Pelvetia, *Fucus platycarpus* and Ascophyllum are absent. This combination is indicative of moderate exposure. It is hoped that later it may be possible, at any rate on some parts of the coast, to use certain common intertidal plants and animals as indicators of the degree of exposure to waves of a locality.

from S.W. by W. to S., and heavy storms occur in winter. It is possible that wave action is more intense on the N.W. wall than elsewhere, owing to the fact that waves rush up the intertidal slope above it, and then fall back with great force. It was observed during diving that the effects of a short choppy sea could scarcely be felt more than a few feet below the surface. But this part of the coast is much more subject to a comparatively long sea or swell, the influence of which extends to the bottom.

(v) *Exposure to the air.* This factor is not operative except in the intertidal region, which was studied in its lowest part only, merely for comparison with the contiguous infra-tidal region. Exposure to air may subject organisms both to desiccation and to rise in temperature.

(vi) *Variations in oxygen-content of the water, and other chemical factors.* These were not measured, as it is unlikely that areas in a region of so much water movement differ greatly in this respect. It is, however, possible that the fronds of the larger Algæ cause sufficient stagnation around their bases to produce an appreciable reduction in oxygen tension. It remains to be seen* to what extent the growth of various animals and plants upon the fronds and stipes of some of the larger algæ is to be ascribed to the presence of an environment more favourable than the rock surface itself (e.g. in oxygen tension, temperature, light, silt, turbulence), and to what extent it represents merely an overflow from the normal rock-surface community, induced by the struggle to gain a foothold.

(vii) *Temperature.* This rises near the surface on a calm warm day, but owing to unfavourable weather no adequate data were obtained. A discussion of this matter must therefore be withheld, although it is unlikely that temperature differences have any great significance.

IV. Distribution and Analysis of Types of Community.

There were two main associations in the gully, the " Laminaria forest association " (including the " Laminaria association " and the " Himanthalia association " of Cotton (1912)) and the " Distomus-Halichondria association." In this description only the most important species are mentioned ; many others occurred and are given in the full lists in the appendix. The nomenclature followed is for algæ that used by Newton (1931), and for animals that given in the Plymouth Marine Fauna (Marine Biological Association, 1931), unless it is stated otherwise.

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* It is hoped to obtain data relating to this question during the course of a survey at present in progress on the W. coast of Scotland. A discussion of the influence of illumination on epiphytism is given by Børgesen (1908).

1. *The Laminaria Forest Association.*

This covered all the N.W. wall, and the boulders at the bottom of the gully. It occurred on all upward-facing rock surfaces in this and neighbouring gullies. When fully developed it consisted of :—

(*a*) A " canopy " layer formed by the fronds of one or more species of large brown alga (generally a Laminaria).
(*b*) An undergrowth of Corallina and other algæ.
(*c*) Species associated with the canopy.
(*d*) Species inhabiting the undergrowth and the holdfasts of the larger algæ.

(*a*) *The Canopy-forming Algæ.*

Himanthalia lorea was dominant in a narrow belt about a foot wide around the level of low water of ordinary spring tides. It occurred along the N.W. wall, on the E. side of " Gully " and " Far " rocks, and on the top of " Flat " rock (here above its more usual level). Corallina was present as a thick undergrowth. Himanthalia " buttons " were seen at lower levels, but never the reproductive parts. *Laminaria Cloustoni* was also present in this zone.

Saccorhiza bulbosa was dominant in 1931 in a belt just below the Himanthalia zone on the N.W. wall, and also on the boulders at the S.W. end of the gully. In 1932* it was almost completely absent from the gully except at the mouth, its place as dominant being taken by *Laminaria Cloustoni.*

Laminaria digitata was confined to the top of Far Rock (at L.W.E.S.T. level) and to ledges at L.W.E.S.T. level on the E. side of Far Rock and at the seaward end of the N.W. wall.

Laminaria saccharina was dominant in a small patch on the S.W. boulders in 1932.

Laminaria Cloustoni was dominant in all parts of the Laminaria forest association except for the above-mentioned places, and even in these (except for places occupied by *Laminaria digitata*) it was present. On the N.W. wall it was graded in size, being larger (up to 340 grams) near the top. Only small specimens (up to about 60 grams) were found near the bottom. On the boulders however it reached up to 280 grams or more ; and it was very large (up to 1800 grams) and covered with other growths (*Distomus variolosus* on the holdfast, *Rhodymenia palmata*, other red algæ and *Sertularia operculata* on the stipe) on the top of the narrow ridge N.W. of Far Rock.

Desmarestia aculeata and *Desmarestia ligulata* occurred fairly plentifully

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* In 1933 (September) it was observed that *Saccorhiza bulbosa* had reappeared both on the boulders and on the N.W. wall.

in 1931, but were scarce in 1932. The former was most common on the N.W. wall at about 5 feet from the bottom, while the latter was commoner above this level.

(*b*) *The Undergrowth.*

Corallina spp. formed a dense growth all over the N.W. wall except at the bottom. (Upper limit, 1 foot above low water of ordinary spring tides and higher in cracks.) In places it was to some extent embedded in *Halichondria panicea.* From an examination of the samples collected, it appears that *C. squamata* predominated in the Himanthalia zone, but that lower down it was replaced by *C. officinalis.*

Chondrus crispus, *Chylocladia ovata*, and *Laurencia pinnatifida* were common in the zone of reproductive Himanthalia, and extended down to 1 or 2 feet below the bottom of this zone (see section). (Upper limit, 1 foot above L.W.O.S.T.) *Gigartina stellata* was locally plentiful in this zone.

Rhodymenia palmata was widely distributed (growing on the rock as well as on stipes of *Laminaria Cloustoni*).

Cladostephus verticillatus was locally abundant on the boulders.

(*c*) *The Population of the Canopy Layer.*

Rhodymenia palmata and *Sertularia operculata* grew on the stipes of the larger plants of *Laminaria Cloustoni.*

Obelia lucifera and *Gibbula cineraria* occurred on the fronds of some plants of *Laminaria Cloustoni.*

Patina pellucida (small* individuals only) occurred feeding on fronds and stipes of Laminaria spp., Saccorhiza, and Himanthalia.

Membranipora membranacea was nearly always present on fronds of *Laminaria digitata*, but only occasionally on those of *L. Cloustoni.*

(*d*) *The Population of the Undergrowth.*

Sessile forms (dealt with approximately in order from the rock outwards) included :—

An encrusting corralline alga forming a continuous coating over the tops of many of the boulders, and over the bottom of the N.W. wall. It may have extended upwards, but if so it was concealed by other growths.

Pomatoceros triqueter, widely distributed, and reaching as far as the upper limit of Corallina ; and *Umbonula verrucosa*, occasional. Both of these were fixed to the rock.

Balanus crenatus, at the bottom of both walls of the gully,—fixed to the rock.

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* Large individuals were occasionally found inside cavities, which they had no doubt themselves eaten out, in the holdfasts of large plants of *Laminaria Cloustoni.*

Hiatella arctica, at base of undergrowth and probably burrowing in the rock, but this was not observed.

Sabellaria spinulosa, occasional on the N.W. wall, but often filling the holdfasts of *Laminaria Cloustoni* growing on the boulders. On low horizontal ledges at the foot of the S.E. wall—ledges on which there were a few scattered and small plants of *Laminaria Cloustoni*—Sabellaria tubes formed a continuous coating to the rock.

Mytilus edulis (very small) and *Heteranomia squamula* on and among the undergrowth, but chiefly fixed to Laminaria holdfasts and Corallina.

Schizoporella hyalina, chiefly in small patches on holdfasts of *Laminaria Cloustoni*.

Membranipora pilosa, on holdfasts of *Laminaria Cloustoni* and on the fronds of red algæ.

The vegetative " buttons " of Himanthalia—which may be treated as part of the undergrowth—were always at least partly covered with Polyzoa (*Schizoporella hyalina* and *Membranipora pilosa*) on their undersides. On the other hand polyzoa and algæ were never found growing on the upper side of the " button," or on the fertile frond, of a healthy Himanthalia plant; although on one occasion a dead " button " was found to be covered all over with *Membranipora pilosa*.

Bunodactis verrucosa and *Spirorbis borealis* on Corallina.

Grantia compressa and *Sycon coronatum* attached to the undergrowth at random.

And motile forms :—

Nereis pelagica and *Platynereis dumerili*, the largest specimens being mostly inside holdfasts ; and many other Polychæta errantia.

Jassa spp.

Elasmopus rapax.

Eurystheus maculatus (in areas " C " and " Z " this occurred in considerable numbers inside the holdfasts of *Saccorhiza bulbosa*) ; and many other Amphipoda.

Amphipholis squamata.

2. *The Distomus-Halichondria Association.*

This covered those parts of the S.E. wall which were overhanging, and all overhanging walls in a neighbouring gully. It ranged upwards above the level of L.W.O.S.T. in places. It consisted of :—

(*a*) A carpet-like growth of *Distomus variolosus* or of various sponges.
(*b*) Certain species (chiefly red algæ) projecting through (*a*) but with their bases embedded in it.
(*c*) Species living on or among the " carpet."
(*d*) Species associated with (*b*).

(*a*) Carpet-forming species.

Distomus variolosus was dominant on vertical or slightly overhanging rock faces. It formed in many places a continuous sheet. (Upper limit, about 2½ feet above L.W.O.S.T.)

Stolonica socialis was locally dominant at the seaward end of "Far Rock" in the region of transition from the Distomus-Halichondria association to the Laminaria forest association.

Sponges became more important the more the rock face overhung. On surfaces at an inclination of about 60° from the vertical, and facing downwards, sponges (especially *Halichondria panicea*, but also other species) were dominant, and Distomus was almost absent except where the inclined part adjoined a vertical Distomus-covered part.

(*b*) Projecting species.

Red algæ such as *Rhodymenia Palmetta*, *Cryptopleura ramosum*, and *Myriogramme Bonnemaisoni* were widespread below L.W.E.S.T. level on vertical or slightly overhanging surfaces, but they did not grow on the more steeply overhanging rock faces.

Gigartina stellata, *Laurencia pinnatifida*, and *Lomentaria articulata* were plentiful at and above the L.W.E.S.T. level, and in places grew thickly. (Upper limit 2½–3 feet above L.W.O.S.T.)

Hydroids, especially *Aglaophenia pluma* and *Sertularia operculata*, were common.

(*c*) The Population of the Sponge-Distomus "carpet."

Sessile species included :—various Cirripedia, *Umbonula verrucosa*, *Pomatoceros triqueter*—all growing on the rock surface, and generally much overgrown. *Pomatoceros triqueter* was very common at about 1 to 2 feet above L.W.O.S.T., under overhanging rocks, and near the upper limit of the carpet-forming species. The upper limit was 3 feet above L.W.O.S.T.

Hiatella arctica, *Sabella pavonina*, *Dasychone bombyx*, and other Polychæta sedentaria embedded in the sponges or Distomus.

Corynactis viridis, commonest under shelves in the sponge-covered areas.

Mytilus edulis.

Heteranomia squamula.

And motile species :—

Many Polychæta errantia, including *Nereis pelagica* and *Platynereis dumerili*.

Many Amphipoda, including Jassa spp., *Elasmopus rapax*, *Apherusa jurinei*, and various Caprellidæ.

Amphipholis squamata.

(*d*) The Population of the Projecting species included :—

Membranipora pilosa, growing in great profusion on red algæ, especially on *Gigartina stellata.*

Schizoporella hyalina, also very plentiful on red algæ, especially on *Rhodymenia Palmetta.*

Parajassa pelagica, nesting in the branches of *Sertularia operculata.*

Caprellidæ.

3. *Undergrowth Layers.*

More detailed examination of the undergrowth of the two sides of the gully leads to the subdivision of that of the Laminaria forest association into :—

- (i) Outer undergrowth layer, consisting of larger undergrowth algæ such as *Rhodymenia palmata*, *Chondrus crispus*, etc., and generally rather loosely packed or sparse.
- (ii) A middle layer of Corallina and holdfasts of Laminaria, which is dense.
- (iii) A basal layer of species which are completely adherent to the rock surface, such as *Balanus crenatus*, *Pomatoceros triqueter*, and *Umbonula verrucosa.*

The "carpet" layer of the Distomus-Halichondria association corresponds with the middle layer of the Laminaria forest undergrowth, and it is this layer which harbours most of the animal species. The projecting species of the Distomus-Halichondria association correspond with the outer layer of the Laminaria forest undergrowth ; this layer is generally populated chiefly by Polyzoa, and is too loosely packed to give shelter to many motile animals. This detailed analysis is summarised in Table I.

TABLE I.

Layer.	Fully developed Laminaria forest association.	Distomus sub-association.	Halichondria sub-association.
Canopy	Present	None	None
Outer Undergrowth	Present	Present	Reduced
Middle Undergrowth	Present	Present	Present
Basal Undergrowth	Present	Present	Present

TABLE II.

All Quantities have been Reduced to Numbers per Square Foot.

Area.	Canopy Layer.	Undergrowth.	*Pomatoceros triqueter.*	*Umbonula verrucosa.*	*Balanus crenatus.*	*Bunodactis verrucosa.*	*Spirorbis borealis.*	*Nereis pelagica.*	*Platynereis dumerili.*	Other Polychæta errantia.	*Elasmopus rapax.*	*Eurystheus maculatus.*	Jassa spp.	*Caprella acanthifera.*	Other Amphipoda.	*Mytilus edulis.*	*Heteranomia squamula.*	Total No. of animal species in area.	Total No. of plant species in area.
D	Himanthalia (dominant). Some *Laminaria Cloustoni*.	Corallina, Chondrus, Laurencia, Chylocladia.	5	¾ to 1 sq. in.	0	54	49	11	0	10	3	0	2	0	2	216	16	26	8
C	Saccorhiza (dominant). Some *Laminaria Cloustoni*.	Corallina.	8	0	0	51	31	7	17	22	14	43	43	9	22	85	17	66	10
B	*Laminaria Cloustoni* (dominant).	Corallina (a little).	17	0	14	31	12	5	2	22	0	0	0	0	12	804	5	26*	4*
A	Very small plants of *Laminaria Cloustoni*.	Practically none (excluding holdfasts).	79	1 to 2 sq. ins.	872	0	0	12	2	5	0	0	5	2	6	265	17	30	4

* These values are probably too low, as area B is smaller than the other areas.

V. Analysis of Lists.

1. *Areas from Laminaria Forest Association.*

Areas A, B, C, D were taken from the N.W. wall. The basal part of the wall, from which Area A was collected, is very poorly illuminated (see Table VIII), and in the water around it there is much suspended matter, which probably has a scouring action. To one or both of these influences may be attributed the lack of undergrowth. The fauna of A differs from that of Areas B, C, D, which are higher up the wall, in the following respects (see Table II) :—

(i) Absence of *Spirorbis borealis* and *Bunodactis verrucosa*, which may be attributed to the absence of Corallina (or possibly to the presence of so much silt).

(ii) Abundance of *Balanus crenatus* and *Pomatoceros triqueter*, and

TABLE III.

Species Confined to or Characteristic of the Laminaria Forest Association.

- Algæ.
  - Desmarestia aculeata.
  - Desmarestia ligulata.
  - Cladostephus verticillatus.
  - Laminaria digitata.
  - Laminaria saccharina.
  - Laminaria Cloustoni
  - Saccorhiza bulbosa.
  - Himanthalia lorea.
  - Corallina officinalis.
  - Corallina squamata.
  - Chylocladia ovata.
- Cœlenterata.
  - †Obelia lucifera.
  - †Bunodactis verrucosa.
- Polychæta.
  - †Spirorbis borealis.
- Crustacea.
  - Anthura gracilis.
- Mollusca.
  - Paphia pullastra.
  - †Patina pellucida.
  - †Gibbula cineraria.
  - Tricolia pullus.
- And other rarer species.

TABLE IV.

Species Confined to or Characteristic of the Distomus-Halichondria Association.

- Algæ.
  - Myriogramme Bonnemaisoni.
  - Rhodymenia Palmetta.
  - Lomentaria articulata.
- Porifera.
  - Leucosolenia coriacea.
  - Leuconia nivea.
  - Leuconia gossei.
  - Amphilectus fucorum.
  - Myxilla rosacea.
  - Anchinoe fictitia.
- Cœlenterata.
  - Myriothela cocksi.
  - Dynamena pumila.
  - Sertularella polyzonias.
  - Sertularia operculata.
  - Plumularia setacea.
  - Aglaophenia pluma.
  - Corynactis viridis.
- Nemertini.
  - Œrstedia nigra.
- Polychæta.
  - Syllis prolifera.
  - Syllis variegata.
  - Eusyllis blomstrandi.
  - Sabella pavonina.
  - Dasychone bombyx.
- Crustacea.
  - Verruca strœmia.
  - Balanus perforatus.
  - Stenothöe marina.
  - Nototropis swammerdami.
  - Lembos websteri.
  - Caprella acutifrons.
  - Caprella tuberculata.
- Mollusca.
  - Kellia suborbicularis.
- Bryozoa.
  - Schizoporella linearis.
- Tunicata.
  - Distomus variolosus.
  - Amaroucium punctum.
  - Diplosoma listerianum.
- And other rarer species.

TABLE V.

SPECIES COMMON TO BOTH ASSOCIATIONS.

- Algæ.
  - Cryptopleura ramosum.
  - Laurencia pinnatifida.
  - Chondrus crispus.
  - Gigartina stellata.
- Porifera.
  - Sycon coronatum.
  - Grantia compressa.
  - Halichondria panicea.
- Polychæta.
  - Lepidonotus clava.
  - Eulalia viridis.
  - Eulalia sanguinea.
  - Syllis gracilis.
  - Trypanosyllis zebra.
  - Leptonereis glauca.
  - Nereis pelagica.
  - Platynereis dumerili.
  - Lysidice ninetta.
  - Sabellaria spinulosa.
  - Pomatoceros triqueter.
- Crustacea.
  - Balanus crenatus.
  - Janira maculosa.
  - Lysianassa ceratina.
  - Apherusa jurinei.
  - Apherusa bispinosa.
  - Gammarellus angulosus.
  - Elasmopus rapax.
  - Microdeutopus sp.
  - Eurystheus maculatus.
  - Jassa falcata.
  - Jassa dentex.
  - Parajassa pelagica.
  - Unciola crenatipalma.
  - Caprella acanthifera.
  - Porcellana longicornis.
- Pycnogonida.
  - Pycnogonum littorale.
  - Ammothea echinata.
- Mollusca.
  - Acanthochitona crinitus.
  - Heteranomia squamula.
  - Mytilus edulis.
  - Musculus marmoratus.
  - Hiatella arctica.
  - Rissoa parva.
- Bryozoa.
  - Membranipora pilosa.
  - Umbonula verrucosa.
  - Schizoporella hyalina.
- Echinodermata.
  - Ophiothrix fragilis.
  - Amphipholis squamata.
- Tunicata.
  - Aplidium pallidum.

presence of a considerable amount of *Umbonula verrucosa*. This is probably connected with the absence of undergrowth such as would cover them up. Area C, from the Saccorhiza zone, contains the largest number of animal species, and the largest numbers of individuals of most of the species.

Areas E, F, and Z were collected from the S.W. boulders, where the illumination is very poor under the Laminaria and Saccorhiza fronds (see Table VIII) and where there is at times a great amount of sediment and algal débris in the water. As in Area A, there is very little undergrowth, but Laminaria and Saccorhiza holdfasts, which function as undergrowth, are present. These areas are fairly poor in undergrowth inhabiting species, although the fauna is in most respects similar to that of B, C, D. The absence of *Balanus crenatus* is noticeable.

Areas G and H are from the base of the S.E. wall. Area G corresponds in position to some extent with Area A on the N.W. wall, and resembles it in its large number of *Balanus crenatus*. Area H, from a flat sandy ledge near the bottom of the S.E. wall, contains many individuals of *Sabellaria spinulosa*.

A list of species confined or nearly confined to the Laminaria forest association is given in Table III. The only five animals (marked with daggers) on this list which are common are associated especially with algæ peculiar to the association. It is not surprising that of the species common to both associations (Table V), all belong to the undergrowth.

2. *Areas from the Distomus-Halichondria Association.*

Areas R and S were collected about 1 foot above the level of L.W.O.S.T., and from their fauna it is clear that many species which are characteristic of the sub-littoral region extend upwards above the L.W.E.S.T. level on vertical or overhanging surfaces. These areas also contain several Tunicata which were not collected elsewhere. Apart from this a detailed study of the separate areas of this association does not reveal more than has already been noted in the preceding section from general observations.

Among the species confined to this association (see Table IV) the importance of Porifera, Cœlenterata, and Tunicata is remarkable,—and so in a lesser degree is that of Polychæta sedentaria, Cirripedia, and Caprellidæ.

3. *Transitional Areas.*

Areas T and U are to a large extent intermediate between the Laminaria forest and Distomus-Halichondria associations. Their fauna may be analysed as follows :—

TABLE VI.

	Species found in T and U.			T only.			U only.		
	C.	LF.	DH.	C.	LF.	DH.	C.	LF.	DH.
Algæ	–	1	–	–	1	–	–	–	2
Porifera	1	–	–	–	–	–	–	–	2
Cœlenterata	–	–	1	–	–	–	–	–	2
Polychæta	4	1	1	1	–	–	1	–	1
Crustacea	5	–	–	5	–	1	–	–	–
Mollusca	2	–	–	1	2	–	–	–	–
Bryozoa	2	–	–	1	–	–	–	–	–
Echinodermata	2	–	–	–	–	–	–	–	–
Tunicata	–	–	1*	–	–	–	–	–	–†
TOTAL	16	2	3	8	3	1	1	0	7

* Also one species found nowhere else.
† Two species found nowhere else.
Column C=species common to both associations.
LF=species of the Laminaria forest group.
DH=species of the Distomus-Halichondria group.

Only species which occur in sufficient areas (i.e. at least two) and in sufficiently large quantities to be grouped in Tables III, IV and V have been considered in this analysis.

It will be seen that U shows a marked predominance of species from the Distomus-Halichondria association, as compared with T, which shows a less marked one of " Laminaria forest " species, and a great number of " common " species. A detailed study of the intermediate region might reveal an interesting transitional zonation, especially in the tunicates.

4. *New Records for Plymouth.*

Twelve animal species (see Table VII in the Appendix) were found which are not listed in the Plymouth Marine Fauna (Marine Biological

Association, 1931), and of these six are Porifera from the overhanging S.E. wall. This is explained by the fact that hitherto such localities have been very difficult of access.

VI. Discussion.

The differences between the various associations and sub-associations are so sharply marked, and show such close correlation with the differences in the external conditions of the habitat, as to suggest that the nature of these associations is rigorously controlled by environmental factors. The principal difference between the regions colonised by the two main associations is the slope of the rock surface, which will react on the fauna and flora in several ways, viz. :—

(i) *Ability of spores or larvæ to settle or develop.*

It is possible that some spores or larvæ may be unable to settle on overhanging rock surfaces, or that such positions may be unsuitable for their further development into adult organisms. The possibility that some such unknown factor excludes the larger brown algæ* from overhanging surfaces must not be ignored. The fact that the areas scraped clear in 1931 were almost all unrecognisable in 1932 shows that no such difficulty operates against the dominant members of the Distomus-Halichondria association, and that any given area continues to support a similar community even after such drastic interference. This was perhaps to be expected, since depopulation by storms must be a fairly frequent event.

(ii) *Settling of silt.*

It is noticeable that the most important of the species confined to the Distomus-Halichondria association are such as might be damaged by excessive deposition of silt. Unless they are excluded from the Laminaria forest association by competition or by some adverse effect of light, silt may be the responsible factor. It is possibly significant that whereas the stalked sponges were found plentifully on both walls of the gully, the encrusting species were confined to, or only flourished on the vertical or overhanging parts of the S.E. wall. The fact that hydroids were not found on the N.W. wall except on Laminaria fronds suggests that they may require to be held further off the rock face into a position where the water is more turbulent and silt-deposition less.

(iii) *Illumination.*

Laminaria Cloustoni occurred, though poorly and sparsely, on the Sabellaria ledge ; but on the upper part of the S.E. wall—a position which

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* Intertidally Pelvetia and *Fucus platycarpus* are usually absent from overhanging rock surfaces.

is better illuminated (see Table VIII)—it did not grow at all. While its poorness of growth on the former may possibly have been due to a deficiency of light, its absence from the latter cannot be attributed to this cause. Unless *Laminaria Cloustoni* is unable to gain a foothold among or compete with the members of the Distomus-Halichondria association, its absence from the upper part of the S.E. wall must in some way be connected with the slope of the surface. The grading in size of Laminaria plants on the N.W. wall may be due to the greater illumination near the surface ; they probably often get torn off by storms, and the Laminaria forest would be regenerated more quickly where the illumination was greater. But there may also be some adverse factor such as silt in suspension affecting those near the bottom. The absence of *Saccorhiza bulbosa* in 1932 may probably be attributed to its being torn off by storms. The Sabellaria ledge at the bottom of the S.E. wall may be regarded as potential Laminaria forest which has failed to develop properly—possibly owing to inadequate illumination.

Of the large brown algæ *Saccorhiza bulbosa* with its capacious holdfast supported by far the largest fauna, as regards both number of species and number of individuals ; these included not only many small forms such as amphipods and polychætes, but also small fish and young echinoderms. *Laminaria Cloustoni* had a moderate fauna ; but Desmarestia spp. and Himanthalia, which have small holdfasts, were in this respect unimportant.

The same types of community which are found below the low water of equinoctial spring tides reach a little way above this level, especially under ledges where there is protection from the adverse effects of being left high and dry. Colman (1933) has pointed out that at any time the belt of sea-shore which is within reach of the splashing of waves may be considered as being, for biological purposes, submerged. Thus infra-tidal conditions extend upwards above the level of L.W.E.S.T. by the width of the " splash zone." Many species found at this level may be regarded as really belonging to the infra-tidal region, and as having ranged upwards as far as conditions have allowed. Certain algæ, on the other hand (notably Himanthalia and Laurencia), belong properly to the lowest part of the inter-tidal region, and do not flourish below it. It is possible that illumination is the limiting factor. Strong evidence has been brought forward by Gail (1918) that insufficient illumination limits the downward distribution of Fucus in Puget Sound.

The part played by the basal undergrowth layer (encrusting Coralline algæ, barnacles, *Pomatoceros triqueter*, and *Umbonula verrucosa*) is especially interesting. The occurrence of barnacles both in the inter-tidal region and at the bottom of the N.W. and S.E. walls suggests that they are only able to live where they are free from competition with various other species. They are able to endure conditions which other species cannot endure, but in open competition become overgrown and smothered. The same is probably true to a less extent of other species of the basal undergrowth layer. Pomatoceros occurred most plentifully at the bottom of the N.W. wall and on vertical or overhanging faces in the lowest part of the inter-tidal region (up to 3 feet above L.W.O.S.T.), near the upper limit of the distribution of the main carpet-forming species. Unlike the barnacles, it is prevented, no doubt by the effects of exposure to air, from colonising the corresponding inter-tidal levels on the upward facing N.W. wall. From the occurrence of barnacle remains under *Distomus variolosus* and other carpet-forming species, and from an examination of the fauna of Area J(2),—an area which was scraped on the same site as the Area J(1) of the previous year—it seems that *Balanus crenatus* is (at any rate in some cases) an early coloniser of any available space, but that it later succumbs owing to competition. Our inability in 1932 to find any trace of the previous year's scrapings shows that recolonisation is very rapid.

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SUMMARY.

1. A diving helmet can be used successfully on British coasts.

2. An ecological survey, extending to a depth of 10 feet below low water of ordinary spring tides, has been made of a small area in Wembury Bay, S. Devon.

3. Below low water of ordinary spring tides upward facing rock surfaces were occupied by a " Laminaria forest association."

4. Below L.W.O.S.T. vertical or overhanging rock surfaces were occupied by a " Distomus-Halichondria association."

5. Large brown Algæ are excluded from the Distomus-Halichondria association by some factor connected with the slope of the rock surface, other than inadequate illumination.

6. Freedom from silt deposition may be responsible for many of the peculiarities of the Distomus-Halichondria association,—in particular for the importance of sponges, cœlenterates, and tunicates.

7. Barnacles play an important part in the recolonisation of bare rock surfaces.

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APPENDIX.

The following is a list of species recorded here for the first time at Plymouth :—

TABLE VII.

Porifera.	Examined by	Area of occurrence.
Leuconia nivea Grant [*Bowerbank*, 1874, 3, p. 11] .	M. Burton	K, L, M, U.
Leuconia gossei (Bowerbank) [*Bowerbank*, 1874, 3, p. 13]	M. Burton	M, S, U.
Ute glabra (Schmidt) [*Schmidt*, 1864, p. 23] . . .	M. Burton	L.
Halichondria albescens (Bowerbank) (*Bowerbank*, 1874, 3, p. 265]	M. Burton	K.
Amphilectus fucorum (Johnston) [*Bowerbank*, 1874, 3, p. 142]	M. Burton	M, R,S.
Anchinoe fictitia (Bowerbank) [*Bowerbank*, 1874, 3, p. 265]	M. Burton	K, P, V.

POLYCHÆTA.	Examined by	Area of occurrence.
SYLLIS (EHLERSIA) FERRUGINA (Langerhans) [*Fauvel*, 1923, p. 269]	D. P. Wilson	E, K.
HETEROCIRRUS BIOCULATUS (Keferstein) [*Fauvel*, 1927, p. 96]	D. P. Wilson	J(1).
ISOPODA.		
HETEROTANAIS SP. ? ÖRSTEDI Kröyer [*Sars*, 1899, p. 14]	H. G. Jackson	U.
CYATHURA CARINATA (Kröyer) [*Barnard*, 1925, p. 140]	H. G. Jackson	S.
IDOTEA GRANULOSA Rathke [*Collinge*, 1917, p. 742]	H. G. Jackson	R.
AMPHIPODA.		
GAMMARELLUS ANGULOSUS (H. Rathke) [*Chevreux et Fage*, 1925, p. 204]	G. A. Steven	B, Q, T, S.

N.B.—Details concerning the areas of occurrence are given in Table IX.

MEASUREMENTS OF LIGHT INTENSITY.

The following measurements of light intensities were made on August 3rd, 1932, between 12 noon and 1 p.m., G.M.T., and the under-water values are expressed as percentages of the illumination in air. The illumination in air varied from 40·0 to 127 k.m.c. (thousands of metre-candles). In cases when the sun was shining an approximate correction ($\times \frac{\text{total light}}{\text{diffuse light}}$) has been applied, owing to the fact that the walls of the gully shaded the gully from direct sunlight. By means of this correction the under-water values are expressed as percentages of the diffuse light, and such corrected figures are shown in the table in brackets. The water was 12 feet deep when the measurements were made. The submarine photometer was held facing away from the rock, in such a way as to receive the maximum illumination.

TABLE VIII.

Position.	Illumination in air (k.m.c.).	Illumination in water (k.m.c).	$\frac{\text{Water}}{\text{Air.}}$
Just below surface	44·4	29·0	65%
N.W. wall, just below Himanthalia zone	40·9	8·10–15·2	20–37%
N.W. wall just below Himanthalia zone	50·0	10·8–18·9	22–38%
N.W. wall, bottom	122	1·36	1·1% (2·4%)
Middle of gully, 6ft. above bottom	127	15·2–18·3	12–14% (30%)
Middle of gully, 3 ft. above bottom	127	6·49	5·1% (12%)
S.E. wall, bottom	57·7	1·36	2·4%
S.E. wall, bottom	55·5	1·60	2·9%
S.E. wall, bottom	88·9	2·18	2·5% (3·9%)
S.E. wall, Sabellaria ledge (Area H)	57·7	1·40	2·4%
S.E. wall, Area J	40·0	1·49	3·7%
S.E. wall, Area K	39·7	0·65	1·6%
S.E. wall, Area N	38·5	3·24	8·4%
Ravine, Area V	38·9	1·60–3·77	4·1–9·7%
S.W. boulders, Laminaria forest, above fronds	40·8	2·18	5·3%
S.W. boulders, Laminaria forest, below fronds	42·2	0·27–0·44	0·64–1·0%

TABLE IX.

List of Sample Areas.

Area.	Dimensions in inches.	Depth above (+) or below (−) L.W.O.S.T. in feet.	Slope of Surface.	Position.	Date of collection.
A	12 × 15	− 8	60–70° from horizontal ,facing upwards	near bottom of N.W. wall	Aug. 3, 1931
B	6 × 10	− 6		on N.W. wall	Aug. 3, 1931
C	12 × 14	− 3½		on N.W. wall	Aug. 4, 1931
D	8 × 11	0		on N.W. wall	Aug. 7, 1931
E	Two separate squares each 12 × 12	− 10	horizontal	on S.W. boulders	July 16, 1932
F	15 × 15	− 10	horizontal	on S.W. boulders	July 18, 1932
G	4 × 4	− 9½	40°–50° from horizontal	at base of S.E. wall, in section	Aug. 12, 1931
H	6 × 10	− 9	nearly horizontal	on Sabellaria ledge, in section	Aug. 7, 1931
J(1)	6 × 9	− 5½	vertical	on S.E. wall, in section	Aug. 7, 1931
J(2)	4 × 4	− 5½	vertical	on same site as J(1)	July 18, 1932
K	5 × 14	− 4½	horizontal, facing downwards	on S E wall, in section	Aug. 9, 1931
L	2½ × 5	− 4½	horizontal, facing downwards	close to L	Aug. 9, 1931
M	6 × 20	− 6	overhanging, at about 40–50° from vertical	on S.E. wall, in section	July 18, 1932
N	5 × 9	− 3½ to − 4	vertical	on S.E. wall, in section	Aug. 13, 1931
P	9 × 8	− 1	vertical	at S.W. end of Gully Rock, in section	Aug. 13, 1931
Q	2½ × 4	− 1	vertical	close to P	Aug. 13, 1931
R	12 × 12	+1	vertical	on Gully Rock, facing N.W., in Gully	July 7, 1932
S	12 × 12	+1	overhanging at about 40–50° from vertical	in next gully, see chart	July 18, 1932
T	12 × 12	− 7	nearly vertical	at S.W. end of Far Rock	July 23, 1932
U	12 × 12	− 7	vertical	near S.W. end of Far Rock	July 16, 1932,
V	10 × 10	− 4	vertical	inside vertical cleft, about 3 feet wide, on N.W. side of Far Rock	Aug. 2, 1932
Z	–	− 10	horizontal	3 plants of Saccorhiza bulbosa, collected in a bag	Aug. 7, 1931

N.B.—The depths are taken to the middle of the Areas.

NOTES TO TABLES X AND XI.

In Tables X and XI the following abbreviations and signs have been used :—

fr. = fragment.
indiv. = individual.
s.q. = small quantity.
(?) identification not absolutely certain, owing to inadequacy of specimen.
(a) 13 of them very small.
(b) mostly *Corallina squamata*.
(c) quantity approximate.
(d) from holdfast of *Saccorhiza bulbosa*.
(e) on Corallina.
(f) +1 dead one.
(g) +2 dead ones.
(h) family inside *Verruca strœmia*.
(j) a few small colonies.
(k) degenerating.
(l) breeding.
(m) probably *Dendrodoa grossularia*.
(n) breeding in July, 1931.
(p) 1 ♀ was also found intertidally on Gully Rock.
(q) 38 of them from holdfast of *Saccorhiza bulbosa*.
(r) = 7 or 8 plants.
(s) small specimen or specimens.
(t) for nomenclature see Lebour (1933).
(u) *O. lucifera* includes *O. dichotoma* and *O. geniculata* in the Plymouth Marine Fauna.
(v) on *Gigartina stellata*.
(x) frond not collected.

The quantities of most Porifera have been estimated by volume (after preservation in alcohol). Rough plasticine models were made of the sponges, and the volumes of water displaced by the models were found. It is recognised that the sponges may have shrunk in the preservative.

TABLE X.

AREAS FROM "LAMINARIA FOREST" ASSOCIATION.

	Unit measured.										Transitional Areas.	
		A	B	C	D	E	F	G	H	Z	T	U
Ectocarpus tomentosus	plant	–	–	–	–	1	–	–	–	–	–	–
Ectocarpus sp.	plant	–	–	–	–	–	1	–	–	–	–	–
Desmarestia aculeata . .		–	–	–	–	fr.	–	–	–	–	–	–
Desmarestia ligulata . .		–	–	–	–	fr.	–	–	–	–	–	–
Cladostephus verticillatus .	plant	–	2	–	–	–	–	–	–	–	–	–
Laminaria saccharina . .	plant	–	1 (s)	1	–	–	7	–	–	–	–	–
Laminaria Cloustoni . .	plant	7 (s)	5	4 (x)	2 (x)	22	5 (s)	–	–	–	–	–
Saccorhiza bulbosa . .	plant	–	–	1 (x)	–	1 (s)	–	–	–	3	–	–
Dictyota dichotoma . .	frond	–	–	–	–	–	1	–	–	–	–	–
Fucus serratus . . .	plant	–	–	1 (?)	–	–	1 (s)	–	–	–	–	–
Himanthalia lorea (fertile) .	plant	–	–	–	8	–	–	–	–	–	–	–
Himanthalia lorea (sterile) .	plant	–	–	5	7	–	–	–	–	–	–	–
Lithophyllum incrustans .	sq. ins.	–	–	½ (c)	2–3	–	–	–	–	–	–	–
Corallina officinalis . .	gram	–	5	13	35 (b)	1	–	–	–	–	9	2 (?)
Corallina squamata . .	gram	–	–			–	–	–	–	–	–	–
Delesseria sanguinea . .	frond	1 (s)	–	–	–	–	–	–	–	–	–	–
Membranoptera alata . .	plant	–	–	–	–	–	1	–	–	–	–	–
Myriogramme Bonnemaisoni		–	–	–	–	–	–	–	s.q.(s)(?)	–	–	fr.
Phycodrys rubens . .	frond	–	–	–	–	1	6	–	–	–	–	–
Polyneura Gmelini . .	frond	–	–	–	–	–	–	–	3 (?)	–	–	–
Cryptopleura ramosum . .	frond	–	–	4	–	–	–	–	2	–	8	3
Laurencia pinnatifida . .	frond	–	–	–	5	–	–	–	–	–	–	–

	Unit measured.	A	B	C	D	E	F	G	H	Z	Transitional Areas.	
											T	U
Polysiphonia nigrescens	plant	–	–	–	–	–	1	–	–	–	–	–
Heterosiphonia plumosa	plant	–	–	–	–	–	1	–	–	–	–	–
Ceramium rubrum	plant	1	–	–	–	–	–	–	2	–	–	–
Ceramium acanthonotum	tuft	–	–	1	6	–	–	–	–	–	–	–
Chondrus crispus	frond	–	–	–	5	–	–	–	–	–	–	–
Gigartina stellata	frond	–	–	–	–	–	2	–	–	–	–	–
Rhodymenia palmata	frond	–	–	–	–	1	–	–	–	–	–	–
? Rhodymenia	frond	6 (s)	–	–	–	1	3	–	s.q. (s)	–	–	–
Lomentaria articulata	gram	–	–	–	–	–	½	–	–	–	–	–
Chylocladia ovata	gram	–	–	–	2 (r)	–	–	–	–	–	–	–
Plocamium coccineum	plant	–	–	–	–	–	1	–	fr.	–	–	–
Sycon coronatum	indiv.	18	–	3	–	–	–	–	3	1	–	–
Grantia compressa	indiv.	6	–	6	5	–	–	–	3	–	–	–
Halichondria panicea	c.c.	–	5	10–12	¼	–	–	–	–	–	14	4
Obelia lucifera (u)	colony	–	–	50 (c)	–	–	–	–	–	–	–	–
Aglaophenia pluma	plume	–	–	–	–	–	–	–	–	5	–	–
Bunodactis verrucosa (?)	indiv.	–	13	59	33	1 (?)	–	–	–	–	–	–
Zoantharia sp.	indiv.	–	–	–	–	–	–	–	1	–	–	–
Lepidonotus clava	indiv.	–	–	1	–	–	–	–	–	–	–	1
Harmothoe sp.	indiv.	1	–	1	–	–	–	–	–	–	1 (?)	1
Phyllodoce maculata	indiv.	–	–	1	–	–	–	–	–	–	–	–
Eulalia bilineata	indiv.	–	–	1	–	–	–	–	–	–	–	–
Eulalia viridis	indiv.	–	–	4	1	–	–	–	2	–	–	–
Eulalia tripunctata	indiv.	–	1	–	–	2	–	–	–	–	–	–
Eulalia punctifera	indiv.	–	–	–	–	–	–	–	1	–	–	–
Eulalia sanguinea	indiv.	–	–	2	–	–	–	–	1	–	–	–
Eulalia sp.	indiv.	–	4	2	2	–	–	1	–	–	–	–
Eteone picta	indiv.	–	–	–	–	–	–	–	1	1	–	–
Phyllodocid sp.	indiv.	2	1	3	–	–	–	–	–	–	–	–
Kefersteinia cirrata	indiv.	–	–	1	–	–	–	–	–	1	–	–
Syllis gracilis	indiv.	–	–	3	1	–	–	–	1	–	–	–
Syllis armillaris	indiv.	–	–	–	–	–	–	–	1	–	–	–
Syllis cornuta	indiv.	–	–	1	–	–	–	–	–	–	–	–
Syllis ferrugina	indiv.	–	–	–	–	1	–	–	–	–	–	–
Trypanosyllis zebra	indiv.	2	1	–	–	–	–	–	1	–	–	–
Syllid sp.	indiv.	–	–	1	1	–	–	–	1	–	–	1
Leptonereis glauca	indiv.	1	–	–	–	–	–	–	1	–	–	–
Nereis pelagica	indiv.	14	2	8	7	8	1	–	2	3	1	1
Platynereis dumerili	indiv.	2	1	15	–	4	–	–	9	5	5	3
Nereid sp.	indiv.	–	1	–	–	–	–	–	1	–	–	–
Eunice harassi	indiv.	–		2	–	–	–	–	–	–	–	–
Lysidice ninetta	indiv.	–	1	3	1	1	–	–	–	–	1	2
Eunicid sp.	indiv.	–	–	–	–	–	–	–	1	–	–	–
Dodecaceria concharum	indiv.	–	–	–	3	–	–	–	–	–	–	–
Sclerocheilus minutus	indiv.	–	–	–	–	–	–	–	1	–	–	–
Sabellaria spinulosa	indiv.	5	7	21	–	24	1	1	90	1	1	–
Amphitrite gracilis	indiv.	–	–	1	1	–	–	–	–	–	–	–
Polymnia nebulosa (s)	indiv.	–	–	1	–	–	–	–	–	–	–	–
Polymnia nesidensis (s)	indiv.	–	–	4	–	–	–	–	–	–	–	1
Nicolea venustula	indiv.	–	–	1	–	–	–	–	–	–	–	–
Polycirrus sp.	indiv.	1	–	1	–	–	–	–	1	–	–	–
Terebellid sp.	indiv.	–	–	fr.	–	–	–	—	fr.	–	–	–
Dasychone bombyx	indiv.	–	–	–	–	–	–	–	3	–	–	2
Pomatoceros triqueter	indiv.	99	7	9	3	6	–	–	3	1	1	1
Spirorbis borealis	indiv.	–	5 (e)	36 (e)	30 (e)	–	–	–	–	–	163 (e)	4 (e)
Balanus crenatus	indiv.	1009	6	–	–	–	–	56	–	–	13	–
Balanus balanoides	indiv.	–	–	–	5	–	–	–	–	–	–	–
Anthura gracilis	indiv.	2	–	3	–	–	–	–	–	–	–	–
Gnathia maxillaris	indiv.	–	–	1♀	–	–	–	–	–	–	–	–
Janira maculosa	indiv.	–	–	4	–	–	–	–	–	–	–	–
Lysianassa ceratina	indiv.	1	–	–	–	–	–	–	1	–	1	5
Apherusa jurinei	indiv.	–	–	1	–	–	–	–	–	–	5	–
Apherusa bispinosa	indiv.	1	–	1	–	–	8	–	–	–	14	–
Nototropis swammerdami	indiv.	–	–	–	–	–	–	–	–	2	2	–
Gammarellus angulosus	indiv.	–	2	–	–	–	–	–	–	–	1	–
Elasmopus rapax	indiv.	–	–	16	2	1	–	–	–	–	1	2
Hyale ? nilssoni	indiv.	–	1	–	–	–	–	–	–	–	–	–
Microdeutopus damnoniensis ♂	indiv.	1	–	–	–	–	–	–	–	–	1	–
Microdeutopus chelifer ♂	indiv.	1	–	5	–	–	–	–	–	1	–	–
Microdeutopus sp.	indiv.	2	1	8	–	–	–	1	1	–	–	1
Aorid sp.	indiv.	–	–	–	–	–	–	–	–	1♀	–	–
Photis longicaudata	indiv.	–	–	1	–	–	–	–	–	–	–	–
Eurystheus maculatus	indiv.	–	–	50 (q)	–	–	–	–	–	10	8	2
Amphithöe rubricata	indiv.	–	–	4	–	–	–	–	–	2	–	–
Jassa falcata ♂	indiv.	1	–	4	–	–	2	–	–	–	–	–
Jassa dentex ♂	indiv.	1	–	6	–	–	–	–	–	–	–	–
Jassa sp.	indiv.	4	–	40	1	1	13	–	4	–	3	–
Parajassa pelagica	indiv.	–	–	–	1	–	–	–	–	–	–	–
Unciola crenatipalma	indiv.	–	1	–	–	–	–	–	3	–	1	–

	Unit measured.	A	B	C	D	E	F	G	H	Z	Transitional Areas.	
											T	U
Corophium bonelli	indiv.	–	–	–	–	–	–	–	2	–	–	–
Podocerus variegatus	indiv.	–	–	2	–	–	–	–	–	–	–	–
Caprella acanthifera	indiv.	2	–	10	–	–	–	–	1	2	12	1
Fragmentary Amphipoda	indiv.	2	–	10	–	–	–	–	1	5	–	–
Praunus inermis	indiv.	–	–	–	–	6	–	–	–	–	–	–
Fragmentary Mysidæ	indiv.	–	–	–	–	2	–	–	–	–	–	–
Porcellana longicornis	indiv.	–	–	1 (?)	–	1	–	–	–	–	–	–
Cancer pagurus	indiv.	–	–	–	–	–	–	–	–	3 (s)	–	–
Pilumnus hirtellus	indiv.	–	–	–	–	3	–	–	1	–	–	–
Pycnogonum littorale	indiv.	–	–	2	–	1	–	–	–	–	–	–
Nymphon gallicum	indiv.	–	–	–	–	–	1	–	–	–	–	–
Ammothea echinata	indiv.	2	1	–	–	–	–	1	–	–	–	–
Acanthochitona crinitus	indiv.	2	–	3	1	–	–	–	–	–	–	–
Heteranomia squamula	indiv.	21	2	15	10	9	–	–	6	–	15	22
Mytilus edulis (s)	indiv.	331	335	99	132	7	5	1	5	10	5	–
Musculus marmoratus	indiv.	1	–	3	–	–	–	–	–	–	1	7
Chlamys opercularis	indiv.	–	–	2 (s) (d)	–	–	–	–	–	–	–	–
Paphia pullastra	indiv.	–	–	2	2	5	–	–	–	2	–	–
Hiatella arctica	indiv.	–	5	10	8	–	–	–	2	–	–	–
Patella vulgata	indiv.	–	–	–	1	–	–	–	–	–	–	–
Patina pellucida	indiv.	–	–	3+	25	5	–	–	–	95	3	–
Gibbula cineraria	indiv.	–	–	–	–	1	2	–	–	8	–	–
Tricolia pullus	indiv.	–	–	1	–	1	–	–	–	–	2	–
Littorina littoralis	indiv.	–	–	–	–	–	–	–	3	–	–	–
Littorina ? rudis	indiv.	–	1 (s)	–	–	–	–	–	–	–	–	–
Rissoa parva	indiv.	1	1	7	1	2	–	–	–	1 (?)	–	–
Onoba candida	indiv.	–	–	–	–	1	–	–	–	–	–	–
Trivia sp.	indiv.	–	–	–	–	1	–	–	–	–	–	–
Nucella lapillus	indiv.	–	–	1	–	–	–	–	–	–	–	–
Nassarius incrassatus	indiv.	–	–	–	–	1	–	–	–	–	–	4
Retusa mammillata	indiv.	–	–	–	–	1	–	–	–	1	–	–
Membranipora pilosa	sq. ins.	–	–	< ½	–	½	1	–	s.q.	½ (c)	4	–
Umbonula verrucosa	sq. ins.	1–2	–	–	½	s.q.	–	–	–	–	1–2	½
Schizoporella hyalina	sq. ins.	–	–	½ (c)	s.q.	1 (c)	½	–	s q	½ (c)	½	1(c)
Tubulipora lobulata		–	–	–	–	–	–	–	–	s.q.	–	–
Marthasterias glacialis	indiv.	–	–	1 (d) (s)	–	–	–	–	–	–	–	–
Ophiothrix fragilis	indiv.	–	1	7	–	7	4	–	–	6	6	11
Amphipholis squamata	indiv.	1	1	20	–	1	–	–	–	3	2	3
Cucumaria saxicola	indiv.	–	–	1 (d) (s)	–	–	–	–	–	–	–	–
Styelid sp.	zooid	–	2	–	–	–	–	–	–	–	–	–
Aplidium pallidum	colony	–	–	20–30 (e) (l)	–	–	–	–	–	–	–	–
Liparis sp.	indiv.	–	–	–	–	–	–	–	–	1 (d)	–	–

Transitional Areas (continued from above)

		T	U
Laminaria sp.	plant	2 (s)	–
Cystoclonoum purpureum	plant	1	–
Rhodymenia Palmetta	frond	–	3
Leuconia nivea	c.c.	–	5
Leuconia gossei	c.c.	–	1–2
Halisarca dujardini	c.c.	–	1
Myriothela cocksi	indiv.	–	1
Sertularella polyzonias	colony	–	1
Corynactis viridis	indiv.	1	2
Harmothöe impar	indiv.	–	1
Lumbriconereis sp.	indiv.	–	1 (s)
Sabella pavonina	indiv.	1 (s)	2 (s)
Heterotanais ? örstedi	indiv.	–	1

		T	U
Synisoma lancifer	indiv.	1♂ (p)	–
Aora typica	indiv.	2	–
Plœnexes gammaroides	indiv.	1	–
Hippolyte varians	indiv.	2	–
Trivia arctica (t)	indiv.	–	1
Goniodoris nodosa	indiv.	2 (s)	1
Scrupocellaria reptans	colony	–	100 (c)
Bugula turbinata	colony	2	–
Polycarpa sp.	zooid	–	2
Styelid sp. ? Dendrodoa		–	s.q.
Stolonica socialis	zooid	55 (c)	200 (c)
Distomus variolosus	zooid	100 (c)	100 (c)

TABLE XI.

AREAS FROM DISTOMUS-HALICHONDRIA ASSOCIATION.

	Unit measured.	J (1)	J (2)	K	L	M	N	P	Q	R	S	V
Dictyota dichotoma .	frond	–	–	–	–	–	–	–	–	20 (c)(s)	2	–
Corallina officinalis .	gram	–	–	–	–	–	–	–	–	–	–	2 (?)
Corallina squamata .	gram	–	–	–	–	–	–	–	–	3	1	–
Nitophyllum punctatum	frond	–	–	–	–	–	–	–	–	–	–	3
Myriogramme Bonnemaisoni .	frond	–	–	–	–	–	–	–	–	–	5	3
Cryptopleura ramosum	frond	–	–	–	–	–	–	–	–	–	–	1
Laurencia pinnatifida .	frond	–	–	–	–	–	–	–	–	40 (c)	–	–
Pterosiphonia parasitica	plant	–	–	–	–	–	–	–	–	–	1	–
Brongniartella byssoides	plant	–	–	–	–	–	–	–	–	1	–	–
Heterosiphonia plumosa	plant	–	1	–	–	–	–	–	–	–	–	–
Halurus equisetifolius .	plant	–	–	–	–	–	–	–	1	–	–	–
Ceramium circinatum .	plant	–	–	–	–	–	–	s.q.	1	–	–	–
Ceramium echionotum .	plant	–	–	–	–	–	–	–	1	–	–	–
Chondrus crispus .	frond	–	–	–	–	–	–	12 (s)(?)	–	–	–	–
Gigartina stellata .	frond	–	–	–	–	–	–	5 (s)	50 (c)	1	–	–
Phyllophora epiphylla .	frond	–	–	–	–	–	–	–	–	–	–	– 12 (c)
Rhodymenia Palmetta	frond	16	–	–	–	–	9 (?)	–	–	–	–	3
? Rhodymenia . .	frond	–	5 (s)	–	–	–	–	–	–	–	–	–
Lomentaria articulata	gram	–	–	–	–	–	–	fr.	–	75 (c)	1	–
Plocamium coccineum .	plant	–	–	–	–	–	–	–	–	–	–	5
Leucosolenia coriacea .	c.c.	–	–	27	–	–	1	–	–	–	–	–
Sycon coronatum .	indiv.	–	–	–	–	1	–	–	–	–	–	–
Grantia compressa .	indiv.	2	2	3	4	15	–	7	–	–	1	14
Leuconia nivea . .	c.c.	–	–	3	3	5	–	–	–	–	–	–
Leuconia gossei . .	c.c.	–	–	–	–	½	–	–	–	–	½	–
Ute glabra . . .	c.c.	–	–	–	1	–	–	–	–	–	–	–
Halichondria panicea .	c.c.	11	–	–	10	150	–	1	–	9	40	½
Halichondria albescens	c.c.	–	–	2	–	–	–	–	–	–	–	–
Halichondria bowerbanki . .	c.c.	–	–	–	–	–	–	–	–	–	1	–
Hymeniacidon sanguinea . .	c.c.	–	–	–	–	–	–	–	–	4	5	–
Amphilectus fucorum .	c.c.	–	–	–	–	3	–	–	–	1	4	–
Myxilla incrustans .	c.c.	–	–	–	–	20	–	–	–	–	–	–
Myxilla rosacea . .	c.c.	–	–	–	–	2	25 (c)	–	–	–	–	–
Anchinöe fictitia .	c.c.	–	–	5	–	–	–	25 (c)	–	–	–	15
Chalina cinerea . .	c.c.	–	–	–	–	–	–	–	–	–	2	–
Myriothela cocksi .	indiv.	1	–	–	–	–	–	–	–	–	3	–
Dynamena pumila .	colony	–	–	–	–	–	–	–	–	20 (c)	–	25 (c)
Sertularella polyzonias	colony	–	–	–	4	8 (c)	–	–	1	–	–	1
Sertularia operculata .	colony	–	–	1	–	–	–	10	45 (c)	–	1	6
Kirchenpaueria pinnata	colony	–	–	–	–	–	–	–	18	–	–	–
Plumularia setacea .	colony	–	–	–	–	4	–	–	10 (c)	–	5 (c)	–
Aglaophenia pluma .	plume	1	–	40 (c)	1	–	24	250–300	–	1	–	–
Metridium ? senile .	indiv.	–	–	–	–	–	1 (?)	–	–	–	–	–
Corynactis viridis .	indiv.	5	–	26	15	38	15	–	–	–	–	7
Œrstedia dorsalis .	indiv.	–	–	–	–	–	–	–	–	–	–	3
Œrstedia nigra . .	indiv.	1	–	2	–	–	8	–	–	–	–	–
Lepidonotus clava .	indiv.	–	–	–	–	–	–	1	–	–	1	–
? Eunöe nodosa . .	indiv.	–	–	–	–	–	1 (s)	–	–	–	–	–
Harmothöe impar .	indiv.	–	–	1	–	–	–	–	–	–	–	–
Harmothöe sp. . .	indiv.	–	–	–	2	3	2	–	–	1	1	–
Lagisca extenuata .	indiv.	–	–	–	–	–	–	–	–	–	–	1 (?) (s)
Eulalia viridis . .	indiv.	2	–	–	–	–	–	–	–	–	–	–
Eulalia sanguinea .	indiv.	1	–	2	1	2	–	–	–	–	1	–
Eulalia sp. . . .	indiv.	–	–	–	–	–	–	–	–	–	1	–
Syllis gracilis . .	indiv.	1	–	–	–	–	–	–	1	–	1	–
Syllis ferrugina . .	indiv.	–	–	1	–	–	–	–	–	–	–	–
Syllis prolifera . .	indiv.	1	–	–	–	–	–	–	1	–	–	–
Syllis variegata . .	indiv.	4	–	–	1	–	–	–	–	–	–	–
Syllis armillaris . .	indiv.	–	1	2	–	–	4	–	–	–	–	–
Syllis sp. . . .	indiv.	–	1	–	–	1	–	–	–	–	–	–
Trypanosyllis zebra .	indiv.	2	–	1	2	1	1	2	–	–	1	–
Eusyllis blomstrandi .	indiv.	1	–	1	–	–	–	–	1	–	–	–
Grubea pusilla . .	indiv.	–	–	–	–	–	–	–	–	–	1	–
Autolytus pictus .	indiv.	–	–	1	–	–	–	–	–	–	–	–
Autolytus sp. . .	indiv.	–	–	2	–	–	1	–	–	–	–	–
Syllid sp. . . .	indiv.	2	–	1	–	–	4	1	–	–	–	–
Leptonereis glauca .	indiv.	–	–	1	–	–	–	–	–	–	–	–
Nereis pelagica . .	indiv.	2	–	5	1 (s)	7	5	2	–	1	11	5
Platynereis dumerili .	indiv.	11	1	–	–	5	1	–	1 (?)	–	16	10
Nereid sp. . . .	indiv.	–	–	–	–	–	1	–	–	2	1	2
Lysidice ninetta . .	indiv.	2	–	1	1	1	1	–	–	1	3	1
Eunicid sp. . .	indiv.	–	–	1	1	–	–	–	–	1	–	1 (?)
Heterocirrus bioculatus	indiv.	1	–	–	–	–	–	–	–	–	–	–
Arenicola sp. . .	indiv.	1 (s)	–	–	–	–	–	–	–	–	–	–
Sabellaria spinulosa .	indiv.	9	2	1 (?)	1	1	–	–	fr. (?)	1	–	1
Nicolea zostericola .	indiv.	–	–	1	–	–	–	–	–	–	–	–
Sabella pavonina .	indiv.	2 (s)	–	3 (?) (s)	–	5 (s)	1 (s)	1 (?) (s)	–	–	38 (s)	–

	Unit measured.	J (1)	J (2)	K	L	M	N	P	Q	R	S	V
Potomilla reniformis .	indiv.	1 (s)	–	–	–	–	1 (s)	–	–	–	–	–
Dasychone bombyx .	indiv.	–	–	–	1	2	–	–	–	–	–	1
Fabricia sabella . .	indiv.	–	–	–	–	–	15	–	–	–	1	–
Sabellid sp. . .	indiv.	1	–	–	–	1	–	–	–	–	–	–
Pomatoceros triqueter .	indiv.	6	1	–	–	7	2	2	4	11	46	–
Spirorbis borealis .	indiv.	–	–	–	–	–	–	–	–	–	–	10 (e)
Verruca strœmia .	indiv.	–	–	1	1	2	–	–	1	–	1	–
Balanus crenatus .	indiv.	17	116 (s)	1	1	11	17	4	10+	15+	1	1
Balanus perforatus .	indiv.	–	–	–	–	–	–	–	– (f)	2 (g)	1 (g)	–
Balanus improvisus .	indiv.	–	–	–	–	–	–	–	–	1	–	–
Cypris larva . .	indiv.	–	–	–	–	1	–	–	–	–	–	–
Cyathura carinata .	indiv.	–	–	–	–	–	–	–	–	–	1	–
Gnathia maxillaris .	indiv.	–	–	–	–	–	–	–	–	–	(h)	–
Næsa bidentata . .	indiv.	–	–	–	–	–	–	–	–	1	–	–
Idotea granulosa .	indiv.	–	–	–	–	–	–	–	–	6	–	–
Janira maculosa . .	indiv.	2	–	15	7	2	9	6	–	–	2	2
Lysianassa ceratina .	indiv.	4	–	–	–	1	–	–	–	–	–	–
Leucothöe spinicarpa .	indiv.	–	–	–	1	–	–	–	–	–	–	–
Stenothöe marina . .	iodiv.	–	–	–	1	–	–	1	–	–	4	–
Apherusa jurinei .	indiv.	–	–	–	–	–	3	8	2	11	16	–
Apherusa bispinosa .	indiv.	–	1	1	–	1	–	–	–	–	–	2
Nototropis swammerdami .	indiv.	–	–	1	–	1	1	–	–	–	–	–
Gammarellus angulosus	indiv.	–	–	–	–	–	–	–	4	–	5	–
Elasmopus rapax .	indiv.	5	–	6	2	1	1	6	–	–	5	1
Microdeutopus sp. .	indiv.	–	–	–	5	2	1	–	–	–	–	3
Lembos websteri . .	indiv.	1	–	1	1	1	–	–	–	–	–	2
Eurystheus maculatus .	indiv.	1	–	–	3	1	–	–	–	–	–	3
Jassa falcata ♂ . .	indiv.	–	–	–	–	–	2	–	1	–	3	–
Jassa dentex ♂ . .	indiv.	–	–	–	1	–	–	–	–	–	–	–
Jassa sp. . . .	indiv.	4	–	46	–	1	57	3	4	2	16	1
Parajassa pelagica .	indiv.	1	–	93	–	–	1	83	142	3	–	–
Unciola crenatipalma .	indiv.	–	–	2	–	–	1	–	–	–	–	–
Corophium bonelli .	indiv.	–	–	1	–	–	–	–	–	–	–	1
Podocerus variegatus .	indiv.	–	–	–	–	–	–	–	1	–	–	–
Pseudoprotella phasma	indiv.	–	–	–	–	–	1	–	–	–	–	–
Caprella acanthifera .	indiv.	–	–	2	–	–	5	–	–	–	1	2
Caprella acutifrons .	indiv.	–	–	–	–	–	9	7	1	1	–	–
Caprella tuberculata .	indiv.	–	–	61	4	–	4	–	–	–	–	–
Fragmentary Amphipoda . .	indiv.	–	–	12	–	2	1	5	–	–	–	1
Hippolyte varians .	indiv.	–	–	–	–	–	–	–	–	–	–	2
Porcellana longicornis .	indiv.	–	–	–	–	–	–	–	–	–	–	1
Cancer pagurus . .	indiv.	–	–	–	–	–	–	–	–	–	1 (s)	–
Pycnogonum littorale .	indiv.	–	–	–	–	–	–	–	–	–	1	–
Ammothea echinata .	indiv.	–	–	–	–	–	–	1	–	–	–	–
Acanthochitona crinitus	indiv.	–	1	–	–	1	1	1	–	2	2	1
Heteranomia squamula	indiv.	16	13	10	7	20	1	7	–	3	1	5
Mytilus edulis (s) .	indiv.	–	–	2	–	1	1	12	25	39	65	–
Musculus marmoratus .	indiv.	4	1	3	–	1	–	–	–	–	3	5
Kellia suborbicularis .	indiv.	1	–	1	2	–	–	–	–	–	–	–
Hiatella arctica . .	indiv.	4	–	1	1	–	1	–	–	3	10	–
Patina pellucida .	indiv.	–	–	–	–	–	–	–	4	–	–	–
Calliostoma zizyphinum	indiv.	–	–	–	–	–	–	–	–	–	–	1
Littorina littoralis .	indiv.	–	–	1	–	–	–	–	–	–	–	–
Littorina sp. . .	indiv.	–	–	–	–	–	–	–	–	–	–	1 (s)
Rissoa parva . .	indiv.	1	–	–	–	–	–	1	–	–	–	–
Lamellaria perspicua .	indiv.	–	–	–	–	1	–	–	–	–	–	–
Nassarius incrassatus .	indiv.	–	–	–	–	–	–	–	–	–	–	1
Polycera quadrilineata .	indiv.	–	–	–	–	–	–	–	1	–	–	–
Scrupocellaria reptans .	colony	1	(j)	–	–	–	–	–	–	–	–	–
Bugula turbinata .	colony	–	–	–	–	2	–	–	–	–	–	–
Membranipora pilosa .	sq. ins.	s.q.	–	–	–	s.q.	–	1–2 (v)	3½–4 (v)	s.q.	½	3
Umbonula verrucosa .	sq. ins.	–	–	s.q.	–	s.q.	–	–	–	7 (c)	4	–
Schizoporella hyalina .	sq. ins.	8–9	s.q.	–	–	–	25 (c)	–	–	s.q.	s.q.	2
Schizoporella linearis .		s.q.	–	–	s.q.	s.q.	–	–	–	–	–	–
Alcyonidium hirsutum		–	–	–	–	–	–	–	–	s.q.	–	–
Ophiothrix fragilis .	indiv.	1	–	1	1	2	1	1	–	–	–	1
Amphipholis squamata	indiv.	–	–	–	–	–	–	–	–	–	1	–
Dendrodoa grossularia	zooid	–	–	–	–	–	–	–	–	–	1	–
Distomus variolosus (n)	zooid	850–1000	10	–	–	200 (c)	400–500	1500 (c)	80–100	200 (c)	1500–2000	600–700
Styelid sp. . .		–	–	–	–	–	–	–	–	–	s.q. (s)	–
Sidnyum turbinatum .	colony	–	–	–	–	–	–	–	–	1 (s) (l)	–	–
Amaroucium punctum		–	–	–	–	–	–	–	–	s.q.	s.q. (l)	–
Amaroucium nordmanni	colony	–	–	–	–	–	–	–	–	2	–	–
Aplidium pallidum .	colony	–	–	–	–	1 (s) (l)	–	–	–	s.q. (l)	2 (l)	–
Morchellium argus .	colony	–	–	–	–	–	–	–	–	–	1 (s)	–
Diplosoma listerianum	sq. ins.	–	–	2–3 (l)	–	–	1	–	–	s.q.	s.q.	–
Trididemnum tenerum .		–	–	–	–	–	–	–	–	–	s.q. (l)	–
Didemnid sp. . .		–	–	–	–	–	–	–	–	–	s.q. (k) (l)	–

Studies on *Stylonethes sterkii* sp. nov. I. Morphology and Systematic Position.

By

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With Plates I and II, and 1 Text-figure.

WHILE studying some of the ciliates found in the region of the Marine Biological Laboratory at Plymouth, England, from January to May, 1929, the author collected from Chelson Meadow a hypotrich which undergoes binary fission only during encystment. This interesting behaviour, which appears to be rare among the Hypotrichida, led to a study of the morphology of the free-swimming form; preliminary to further investigations, including a study of both protective and reproductive cysts.

The organism has been named *Stylonethes sterkii*, reasons for which are presented in this paper.

Acknowledgment.

This investigation was begun when the author was a Fellow of the Oregon Division of the American Association of University Women, in the year 1928–29. She wishes to extend thanks to Dr. E. J. Allen, F.R.S., Director of the Marine Biological Laboratory of the United Kingdom, Plymouth, England, for the use of a table and for the collecting assistance and equipment put at her disposal during her stay at the laboratory; to Dr. Harold Kirby, Jr., of the University of California at Berkeley, for criticizing the manuscript; and to Dr. C. V. Taylor of Stanford University, for his many kindnesses and helpful suggestions. The writer is also indebted to Dr. C. A. Kofoid of the University of California, for the use of his extensive library.

TECHNIQUE.

Culture.

Both protective and reproductive cysts of *S. sterkii* remain viable when dried. This discovery made possible a transfer of the new hypotrich in May, 1929, from Plymouth to Stanford University, where the strain has been continued to the present time (July, 1933).

The following wheat infusion method of culturing was used exclusively. Twenty grains of wheat were cracked and then boiled in 15 c.c. of glass distilled water for from three to five minutes. The fluid containing numerous starch grains was used immediately after cooling and was transferred to the culture by means of a pipette having a bore of 1·5 mm.

Experiments have shown that thriving cultures are most easily maintained when complete evaporation of the medium takes place at intervals. Consequently, the organisms were grown in watchglasses holding conveniently about 4 c.c. of fluid. These were ordinarily enclosed in Petri dishes to prevent evaporation and to facilitate handling, but when mass encystment and complete evaporation of the medium was desired, the cover was removed. Or, the cover may be partly removed so that it protects the watchglass from dust but leaves a wide open gap between the two dishes. Within 8–10 hours, at a temperature varying from 15–22° C., the cultures were completely dried out.

New cultures were started daily when free-swimming individuals were wanted for study. By means of a mouth pipette twenty organisms from a thriving culture were transferred to a watchglass containing 4 c.c. of tap water and a drop of fresh wheat infusion. A drop of infusion was added daily to old cultures until protective cysts began to appear (2–4 days). Then they were allowed to dry out. Thus it can be arranged that there are always on hand about as many new cultures as old ones, and a reserve supply of dry cysts. If the study of active organisms is to be suspended for a few days or weeks, it is safe to rely upon the stock of dry cysts to begin new cultures, as was proved by the transfer of cysts in watchglasses from England to California. These cysts were about three weeks old when they arrived. Excystment occurred in three to four hours after distilled or tap water had been added.

Methods of Preparation.

The following description of *S. sterkii* is based mainly on observations made upon the living organism, although for purposes of confirmation and for study of fine details of structure, permanent mounts were made. The iron-alum-hæmatoxylin method of staining was most frequently used, after killing and fixing in Bouin's or Schaudinn's fluid (without acetic acid), the latter being better for the free-swimming forms, and the former for the cysts. Bresslau's (1921) China blue relief staining method was found to be excellent for a comparative study of external structures.

It is a difficult task to observe this form under the high powers of the microscope in living condition for the two following reasons: Rapid evaporation of the medium bursts the pellicle very easily, and the organisms encyst if evaporation proceeds slowly. However, with patience it is possible to acquire skill in manipulation whereby the living organism may be observed for two hours, or even longer in some cases. The locomotor organelles sooner or later stop beating, and after a quiescent period they sometimes function again just before death and disintegration. A minute drop of 10% alcohol, added to the hanging drop by means of a fine pipette, retards the movement of the organisms within a shorter time, and if evaporation is gradual the protoplasm eventually coagulates without much distortion, so that even after death the structures stand out quite clearly. A 1% solution of eurythane was also tried with some success.

General Morphology.

The body form of *Stylonethes sterkii* (Plate I, Fig. 1) may in general be described as an elongated ellipsoid, with a shallow excavation in the anterior portion of the left side. The ventral surface is slightly concave, the periphery is rounded, and the dorsal surface is broadly arched, the body being thickest centrally.

A thin and elastic pellicle, however, permits considerable modification in form. Especially is this apparent when the animal is gorged with food. The dorsal surface is then highly arched, and the anterior end is smaller than the broadly rounded posterior end. Individuals containing few food vacuoles sometimes are bluntly pointed posteriorly.

The structure of the anterior extremity is extraordinarily complex. Ventrally it terminates in a narrow and inconspicuous projecting lip of uniform width. Dorsally it gives rise to a series of typical membranelles, which extend from the anterior end of the right median ventral row of cirri (described below) to the extreme left side of the body, where they pass ventrally and posteriorly to form the left border of the peristome.

The longest membranelles are found at the most anterior point of the body, and they become shorter gradually away from this point in either direction. The bases of the first twelve or thirteen membranelles, beginning at the right, slope downward on the lip. The turn to the ventral surface is accomplished by the next six or seven membranelles, and posterior to these the bases slope gently downward from the margin of the peristome toward the periphery of the body. The peristomal membranelles gradually come to point ventrally and finally they project toward the midline. The number of membranelles varies. From 25 to 48 have been counted, the number being smaller in small individuals, and larger in large individuals.

Thus far the membranelle region is essentially the same as that described in many other members of the Hypotrichida, such as *Holosticha rubra* Ehrenberg (Wallengren, 1900) and *Euplotes patella* Ehrenberg (Taylor, 1929). However, in *S. sterkii* additional and unique structures are situated between the bases of the membranelles.

In the first place, small elevations, within which are found deeply staining spherules, arise in these narrow spaces (Plate II, Fig. 2). The spherules are most conspicuous in the first seven or eight inter-membranellar spaces, beginning at the right, and in size (largest about $\cdot 6\mu$) form a closely graded series so that the tenth or eleventh is barely visible. Beyond this point none can be seen, and if present they must be exceedingly small. Careful focusing from the dorsal surface or a frontal view reveals the fact that the first seven or eight spherules are double. The remainder appear to be single. Considerable variation in respect to number was noted. A small individual may have as few as eight. However, without exception, these spherules are clearly evident in organisms killed in Schaudinn's fluid (without acetic acid) and stained with Heidenhain's hæmatoxylin. This is true even when the preparation is greatly de-stained, thus showing exceedingly strong affinity for the dye. They were seen also in the living state as rounded bodies of greater density than that of the surrounding cytoplasm. The function of these unusual structures is not known.

Interpolated between the right side of each membranelle (except the first) and the left side of the elevation is a small, slender motile structure, which at rest is directed at an angle toward the apposing membranelle; that is, in a direction away from the peristome. Its base is about two-thirds the length of the membranelle base and so inserted that both proximal and distal ends of the membranelle base extend beyond it. This observation is most easily made in China blue preparations and in those individuals which have rounded up so that the frontal surface is uppermost. The length of this small organelle measures about 3·5 microns in living condition. As observed in China blue preparations, it was found

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EXPLANATION OF PLATES.

All figures were drawn with the aid of the camera-lucida.

PLATE I.

Fig. 1.—*Stylonethes sterkii* sp. nov., ventral aspect. Semidiagrammatic drawing of living organism. × 800.

PLATE II.

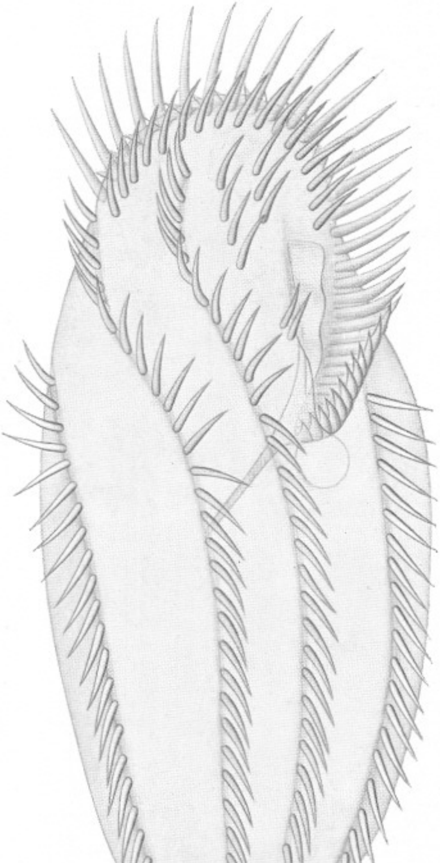
Fig. 2.—Anterior extremity, dorsal view, showing position of membranelles, inter-membranelles, and spherules within elevations. Semidiagrammatic. Heidenhain's hæmatoxylin stain. × 1896.

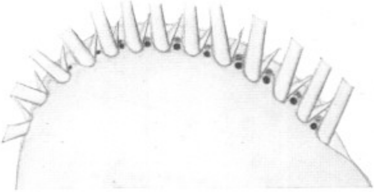
Fig. 3.—Right end of membranelle series. Membranelles, inter-membranelles, and cirri of transverse row are fimbriated. Light line between membranelles and cirri indicates lip, which was flattened in preparation. China blue relief stain. × 1290.

Fig. 4.—Dorsal aspect, showing three longitudinal rows of cilia. Living organism. × 750.

Fig. 5.—Note accumulation of granules at anterior end. Dorsal view. Heidenhain's hæmatoxylin stain. × 750.

Fig. 6.—Macronuclei and micronuclei, ventral view. Heidenhain's hæmatoxylin stain. × 750.





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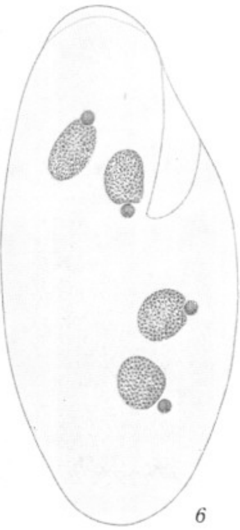

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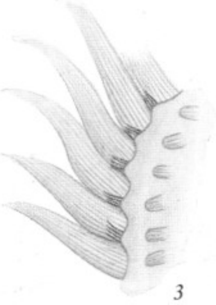

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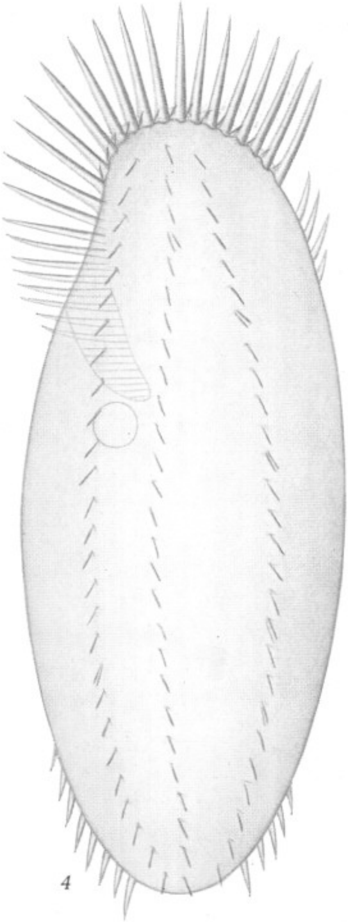

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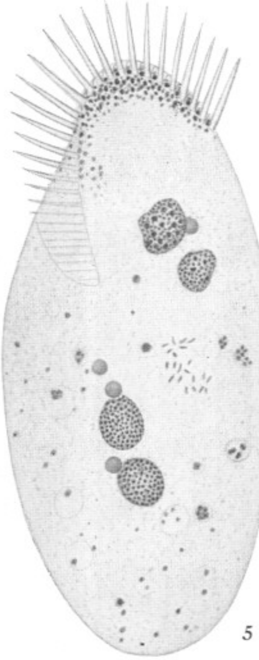


5

zugekehrten Seite noch eine weitere kleine Nebenmembranelle entwickelt ist. . . . Die Höhe dieser Zwergmembranellen ist gering, aber doch variabel; einmal habe ich in einem Fall mit der regelrechten eine gleich grosse beobachtet. Der Bau und die Bedeutung dieser Nebenmembranellen ist mir unbekannt. Ihre Bewegung wurde auch nicht beobachtet, nur aus der Querschnittsform erschlossen."

Four longitudinal, uninterrupted rows of closely set cirri constitute the most conspicuous feature of the ventral surface. Two are median in position and two are lateral. The median rows are longer than the laterals, extending across the frontal field with a shallow curve to the right. The

to be composed of cilia, similar to cirri, membranelles, and undulating membranes, since it shows fimbriation (Plate II, Fig. 3) when cirri and membranelles in the same specimen are thus separated into their component parts.

These minute inter-membranelles were first seen in the living organism and it was thought that their movement might be a passive one caused by the pressure of the two membranelles upon them, first on the one side and then on the other. This is not the case, however, for when observing an organism in a hanging drop preparation just prior to death due to the evaporation of the water, the larger motile organs, such as the membranelles, may cease movement, while these smaller structures continue vigorous movement. It sometimes happens that both stop functioning at the same time, or, the smaller structures may stop first, but occasions such as described above often occurred. Whether or not these organelles are present between all the membranelles is not known. The largest number counted was found in an individual having 38 membranelles. Beginning at the right, fourteen intermembranelles were clearly evident, and if they are present between the remaining membranelles, they must be very small.

While looking through the literature for recently described genera of the Hypotrichida, the writer encountered the article of von Gelei (1929) in which he briefly described " Nebenmembranellen " or " Zwergmembranellen " in *Spirofilum tisiœ* n. sp., n. gen. (according to Rossolimo (1929), a new species of the genus Hypotrichidium Ilowaisky, 1921). The position of this organelle, according to von Gelei, seems to be similar to that just described for *S. sterkii*, i.e. between the membranelles, but whether or not the structure is the same cannot be determined from the information given. Ilowaisky (Rossolimo, 1929) studied only the living specimens of his new form, *H. conicum*, and did not mention having seen minute organelles between the membranelles. Von Gelei's description (1929, p. 175) is as follows :—

" Mir ist an diesen Membranellen eine merkwürdige Erscheinung aufgefallen, die nämlich, dass neben beiden Organen an ihrer einander zugekehrten Seite noch eine weitere kleine Nebenmembranelle entwickelt ist. . . . Die Höhe dieser Zwergmembranellen ist gering, aber doch variabel ; einmal habe ich in einem Fall mit der regelrechten eine gleich grosse beobachtet. Der Bau und die Bedeutung dieser Nebenmembranellen ist mir unbekannt. Ihre Bewegung wurde auch nicht beobachtet, nur aus der Querschnittsform erschlossen."

Four longitudinal, uninterrupted rows of closely set cirri constitute the most conspicuous feature of the ventral surface. Two are median in position and two are lateral. The median rows are longer than the laterals, extending across the frontal field with a shallow curve to the right. The right lateral row originates at the periphery about one-third of the way back from the anterior end, and from this point posteriorly it becomes set in from the margin, as shown in Plate I, Figure 1. The anterior origin of the left lateral row is posterior to the peristome, about 8·5 microns from the body periphery. With the exception of the left median row, in which about four or five of the most posterior cirri are constantly missing, all the longitudinal rows extend almost to the posterior extremity of the body (Plate I, Fig. 1). Each row is set within a distinct groove in the pellicle, which is most clearly seen at the anterior end of the right lateral row. This groove extends over the rounded periphery to terminate on the margin of the dorsal surface. In individuals with few food vacuoles the longitudinal rows are equidistant from each other, but with increase in food contents, the median rows are slightly closer to each other than they are to the laterals.

The cirri in the longitudinal rows are more closely approximated to each other in some individuals than in others, and the number in each row in different individuals varies. Counts can be made on living specimens, but they can be easily and more carefully made on animals stained with China blue. However, in these preparations only in rare instances are all the four rows visible for their entire length, due to the contraction of the posterior extremity. (See summary below.)

On the ventral surface, posterior in position to the membranelle series, is a semicircular row consisting of a variable number of cirri. The position of the first cirrus at the right is constant—posterior to the first membranelle and opposite the first cirrus of the right median longitudinal row of cirri. Since the spaces between these cirri tend to be equal, the location of the last cirrus and the length of the row depends upon the number of cirri present in this row, which may be from 12 to 22. This interesting departure from the ciliation ordinarily found in the Hypotrichida has also been described by Penard (1922) in *Keronopsis helluo*, and recently by Kahl (1932) in the two species of his new genus Paraholosticha. According to the former investigator, the transverse row extends only about half-way across the anterior end.

Additional frontal cirri are disposed in two short rows to the left of the left median longitudinal row of cirri, the spaces between the three rows being approximately equal to each other. Immediately to the left is the peristomal groove. The number of cirri is variable within each row. From two to six have been found in the right row and from one to five, in the left row ; the smallest number in any one individual is three, and the largest number, ten.

The variation in number of frontal cirri does not indicate that there are races or strains within the species having a constant pattern of frontal cirri. Pure line cultures have been grown and these show all the variations of the frontal cirri pattern found in a mixed culture. The two daughters of a single individual may vary in respect to the number of frontal cirri.

Isolated cirri originate at the right peristomal border posterior to the frontals. Their number varies from one to three.

The following is a summary of cirri counts made upon five living, unstained individuals, together with the number of membranelles and the length of the organism.

	Body Length.	Membr.	Trans. Row.	Frontals R.,	L.	Isol.	Longit. Rows R. to L.
1.	100μ	29	14	3	1	1	23, 29, 23, 20
2.	108	34	15	3	2	1	20, 24, 25, 20
3.	145	48	20	5	4	3	27, 38, 38, 30
4.	148	38	17	4	3	3	29, 32, 29, 27
5.	152	38	18	4	2	2	26, 32, 30, 25

There is no appreciable difference in size among the ventral cirri. Except for the first two or three cirri at the anterior end of the right lateral and right median rows, and the isolated cirri, which appear to be slightly smaller, there is a remarkable uniformity in size of all the cirri of an individual. But the size of the cirri in different individuals varies, as is to be expected. The largest found measured fourteen microns in length.

Three longitudinal rows of cilia are found on the dorsal surface (Plate II, Fig. 4). The cilia are about three microns in length and are placed about five to six microns apart. Frequently two cilia originate at the same point. The dorsal cilia are not immotile (or very slightly movable) spines or bristles as found in *Euplotes worcesteri* Griffin (1910) and many other hypotrichs, but are definitely motile cilia, as can be readily demonstrated.

It has been generally believed that in the Hypotrichida motile organs are confined to the ventral surface (Calkins, 1926; Doflein-Reichenow, 1929; and others). *S. sterkii* then is unique in having cilia on the dorsal surface. On the other hand, careful and complete descriptions have not been made for many species on record, and therefore the presence of cilia may have been overlooked in some cases.

The peristome is a narrow longitudinal groove on the left ventral surface, slightly wider anteriorly than posteriorly. It originates between the left frontal row of cirri and the left end of the transverse row, and extends posteriorly for about two-fifths the length of the body. On the left the peristome is bordered by the membranelles, as already described. An undulating membrane is attached along the right border. The anterior end is often found directly opposite the third cirrus of the right frontal row, that is, when at least three are present in that row. Here the membrane is almost as wide as the peristome, but as it extends backward it gradually tapers to a point. Its posterior extremity extends into the cytopharynx.

The peristome opens into a funnel-shaped cytopharynx (Plate I, Fig. 1). One side of the " cone " is somewhat elongated anteriorly and ventrally it is flattened, forming the thin and transparent floor of the cytopharynx. The posterior portion (or stem of the funnel) extends diagonally across the body within the endoplasm, opening into the interior of the body above the right median row of cirri. The lumen of this posterior cytopharynx is ciliated, and in some specimens stained with hæmatoxylin, the wall appears to be lines with dense strands which retain the dye. Judging from the large size of starch grains often ingested by the organism, the cytopharynx is capable of considerable distension.

The entrance point of food probably accounts for the fact that some organisms were found which are thickest to the right of the main axis. A rapid intake of food, such as takes place after excystment or a period of semi-starvation, would cause the food vacuoles to accumulate there temporarily.

When the body is quite free from food particles, the cytoplasm is pale yellow in colour. The ectoplasm and endoplasm are not visibly differentiated from each other in the living organism. In stained specimens the thin pellicle is apparent, beneath which is a very narrow zone of clear ectoplasm. The remainder of the cytoplasm, or endoplasm, is finely alveolar, and within it lie the food vacuoles.

A conspicuous band of deeply staining granules, irregular in arrangement, sometimes occurs across the entire anterior extremity of the animal (Plate II, Fig. 5). They were seen also within the living organism as coarse refractile granules. The spherules described in connection with the membranelles are quite easily distinguished from them by their definite position and more intense staining property. The significance of the accumulation of these granules in some organisms has not been determined.

In the majority of individuals, four rounded macronuclei lie within the endoplasm. Two are anterior in position and two, posterior (Plate II, Fig. 6). Each has its accompanying micronucleus, which may lie within a distinct depression or near a flattened area of the macronucleus, or free in the endoplasm. The micronucleus is spherical in shape and during its interphase about 2·5 microns in diameter (fixed and stained organism). It is of the massive type.

It must be pointed out here that the free-swimming organisms present a varying picture with respect to nuclei. The process of fission is being studied and will be presented in a later paper. At the present time these studies indicate that each of the two new daughter individuals leaving the cyst wall usually contains four macronuclei and a varying number (2–6) of micronuclei, although frequently four of each type are present. This hypotrich, as stated earlier, divides only during an encysted state and more than one division does not occur. Conjugating individuals have never been encountered.

S. sterkii has one contractile vacuole, located in the endoplasm near the dorsal surface, behind and above the posterior end of the peristome. When the organism is under pressure, a more anterior contractile vacuole may appear in addition to the usual one. An illustration of the elasticity of the pellicle can be seen in connection with the pulsation of this organelle. When the animal is viewed in profile, the expanded vacuole raises the surface like a blister. With contraction the bulge disappears.

The anus is situated at the posterior end of the mid-line. On several occasions, preceding its opening, a vacuole appeared into which an excretory particle was received and then emitted to the exterior.

HABITAT AND BEHAVIOUR.

S. sterkii was collected from a puddle in Chelson Meadow, which, according to Sexton (1924, p. 342), is "a salt marsh near Plymouth reclaimed from the tidal part of the Plym a little more than a century ago, and protected from the tide by an embankment, the accumulation of drainage water being emptied through sluice-gates into the river only at rare intervals." Culture experiments show that the organism thrives equally well in tap water or in brackish water up to a concentration of one part sea-water to one part distilled water. This, of course, is not unusual considering the original habitat just described.

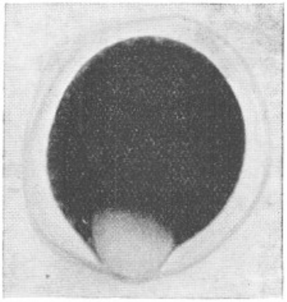
The organism is also otherwise well adapted to life in puddles of short duration. The newly excysted individuals may be exceedingly small, thin, and transparent, but the rate of feeding is so rapid that within a few hours, depending of course upon the amount of food present, their bodies become exceedingly plump. If the first reproductive cyst of an individual of this type is isolated, another division occurs within twelve hours, although the average fission rate seems to be one about every 24 hours. In other words, the organism is able to take advantage of a short favourable period. Further, binary fission takes place at all times within a cyst membrane, and, in many cases at least, the daughter organisms withstand drying.

Protective cysts can be induced at any time by evaporation of the medium, but they may form also when sufficient water is present. The causes of encystment have not been investigated, but even casual observation in connection with the culture of this ciliate convinces one that it is quite sensitive to its environment, and that this sensitivity is often expressed in terms of encystment or excystment.

S. sterkii tends to encyst in groups, as was found to be the case in

Euplotes taylori (Garnjobst, 1928), so that the surface of the watchglass may be sprinkled with grape-like clusters. If complete evaporation of the medium takes place very quickly, or if the medium is removed at once following the formation of a cyst wall, the organism invariably dies. Whether accidental or not, the formation of clusters of cysts would then be of survival value, for cysts more central in position are protected from rapid dessication. This point has not been tested experimentally.

Cyst formation may be observed under the microscope in hanging drop preparations. Both protective and reproductive cysts may be formed if the organisms are chosen at random from a thriving culture. In either case the animal rotates in place until a rounded form is assumed and a cyst wall has been secreted, after which rotation continues for some time within the wall. The reproductive cyst can be recognized while rotation is still in progress, for in these the macronuclei aggregate to form one large central mass, whereas in protective cysts they remain separated from each other. The macronuclear mass soon elongates and this indicates the position of the division plane, which is always at right angles to the elongation. Cytoplasmic division is preceded by the thinning of the macronucleus at its mid-region and final separation into two parts.



TEXT-FIG. 1.—Cyst of *S. sterkii*. Photo-micrograph. Heidenhain's hæmatoxylin stain with very little destaining to show large vacuole. × 638.

Sooner or later ciliary motion within both types of cysts discontinues. Now if the coverslip is placed within a moist chamber for several hours, or overnight, a large fluid vacuole appears, such as is shown in Text-Figure 1. The space between the wall and the dedifferentiated organism is typical also of the living cyst.

Excystment may be induced by the addition of tap or distilled water, either before or after evaporation of the medium, at room temperature. Reproductive cysts which are formed without an accompanying evaporation of the surrounding medium, excyst spontaneously, that is, after the quiescent period ciliary motion again occurs, rotation commences, and in due time two new daughter individuals emerge through the cyst wall.

A detailed description of encystment and excystment will appear in a later paper.

Systematic Position.

In 1878 Sterki outlined a revision of the Oxytrichina instituting seven new genera, among which was Stylonethes which he characterized as follows :—

" Körper vorn verschmälert, hinten gerundet, stark gewölbt. Auf den vordern Hälfte des Stirnfeldes viele (15–20) zerstreute Wimpern, 2 Bauchwimperreihen, keine Afterwimpern. Die linke Randreihe beginnt auf dem Stirnfeld und überspringt das Peristom."

A single species, named *S. tardus*, was placed within the genus, but no description was given, the reason being that the author intended to give complete details in a later paper. This, so far as the writer has been able to learn, has never appeared.

Kent (1881, p. 782) stated that " so far as is at present possible to determine, this single type (Stylonethes) connects the two genera Holosticha and Uroleptus." Bütschli (1889), on the other hand, temporarily assigned *S. tardus* to the genus Uroleptus. In 1888, Gourret and Roeser described a new ciliate which they named *Stylonethes fusiformis*. The validity of this placement will be discussed below. Recently, Kahl (1932) described a new genus, Paraholosticha, including two species which bear a close resemblance to *S. sterkii*.

There are five distinct characters given by Sterki in his brief description of Stylonethes which are found also in the species herein described and in Kahl's *P. herbicola* and *P. muscicola*, namely, (1) four ventral, longitudinal, uninterrupted rows of cirri ; (2) an anterior transverse row of cirri ; (3) differentiated frontal cirri ; (4) no anal cirri ; and (5) a rounded posterior extremity.

Sterki considered the transverse row as an anterior extension of the left marginal row of cirri which is interrupted by the peristome. Since it is not interrupted by a more or less undifferentiated space, as is the case in some species of the genus Oxytricha, but by the highly differentiated region, the peristome, it seems to the writer more convenient and correct to consider this row a separate one. It is true that Sterki did not designate precisely the location of this row, except to state that it begins on the frontal field. However, it is clear that in *S. tardus* there is present an anterior row of considerable length, otherwise Sterki would not have been able to differentiate these cirri from the scattered frontal cirri, which are quite numerous (15–20). Kahl (1932) in his description of *S. tardus* does not include the statement of Sterki, " Die linke Randreihe beginnt auf dem Stirnfeld und überspringt das Peristom."

Whether the anterior transverse row is of generic significance or not, the remaining four characters are sufficient to distinguish the species under consideration from other genera having few, uninterrupted, longitudinal rows of cirri on the ventral surface. These genera are (1) Uroleptopsis Kahl 1932; (2) Holosticha Wrzesniowski 1878, emend. Entz 1884; (3) Amphisia Sterki 1878, emend. Entz 1884; and (4) Uroleptus Ehrenberg 1831, emend. Stein 1859. The following summary illustrates this point:—

	Frontals.	Anals.	Post. Extremity.
Uroleptopsis	None	None	Rounded.
Holosticha	None	Present	Rounded.
Stylonethes	Present	None	Rounded.
Uroleptus	Present	Pres. in some	Tail
Amphisia	Present	Present	Rounded.

Gourret and Roeser (1888) maintain that the characters of their *S. fusiformis* correspond in all respects to those laid down for the genus Stylonethes by Sterki, except that the marginal cirri are entirely lacking. This difference they did not consider sufficient to place the species elsewhere. If this were the only difference their stand might be justifiable, since in the closely related genera Holosticha and Amphisia, as emended by Entz (1884), there is a slight variation in number of ventral rows. However, it is difficult to understand the row of cirri along the right border of the peristome. These must have been considered the frontal cirri by the authors, otherwise the absence of frontals would certainly have been considered a second, if not an important generic difference. But, because of the similarity in position, it is also possible that they mistook an undulating membrane for a row of cirri; or, they are cilia and not cirri. The description of the ciliation of the peristome is as follows: " Des deux côtés de la gouttière, le droit est un peu plus saillant; il porte des cirrhes plus vigoreux que ceux implantés à gauche " (p. 191). No further mention was made of this anterior row of cirri. Figure 13, Plate XIV is not adequate with respect to the ciliation of the peristome and is not convincing with respect to the presence of frontal cirri. For these reasons it seems to the writer that Gourret and Roeser's *S. fusiformis* cannot be placed with certainty within any genus. Kahl (1932) expressed doubt that it is a hypotrich.

S. sterkii and *P. herbicola* Kahl show a striking resemblance and it is not at all unlikely that they are one and the same species. If so, then *S. sterkii* should be called *S. herbicola* (Kahl). On the other hand, there are differences, according to determinations made from the figure and short description of *P. herbicola* (Kahl, 1932, Fig. 88). These are summarized below :—

S. sterkii.	*P. herbicola.*
1. Length, 94–160μ.	1. 150–190μ.
2. All 4 longitudinal rows of cirri, *except* left median row, extending to posterior extremity.	2. All 4 longitudinal rows of cirri extending to posterior extremity.
3. Anterior transverse row with 12–22 cirri.	3. Anterior transverse row with 15–20 cirri.
4. 3–10 frontal cirri, in 2 short rows.	4. 16 frontal cirri, in 2 short rows.
5. Cirri of ventral surface similar in size.	5. Cirri of anterior transverse row and marginals larger.
6. Dorsal cilia, in 3 longitudinal rows.	6. Dorsal bristles or cilia (?) present.
7. Isolated cirri near right peristomal border.	7. No isolated cirri.
8. Intermembranelles present.	8. ?
9. Dorsal contractile vacuole, above posterior end of peristome.	9. Contractile vacuole some distance posterior to peristome.
10. Macronuclei, 4 ; micronuclei, 4.	10. Macronuclei, 2 ; 1 micronucleus.

Some of these differences may be due to oversight on the part of Kahl. Yet this can hardly be said of his observations regarding the larger size of the cirri of the anterior transverse row, " Ganz nahe dem Vorderrand des Frontalfeldes ein Kranz zahlreicher verstärkter Cirren " (p. 545). Figure 88 shows larger cirri in the marginal rows, although no mention is made of it in the text. In Kahl's general description of the Hypotricha (1932, p. 533), the following statement is made of the marginal cirri, " . . . sie sind öfter etwas stärker als die eigentlichen Ventralcirren. . . ."

It seems impossible to the writer that anyone studying *S. sterkii* even for a short period would not have discovered its cysts. Kahl (1932) does not mention cysts. It is of course understood that a key is necessarily limited in matters of detail. However, in the separation of species if it should be found that in addition to minor differences, one species divides only within a cyst wall and the other does not, the character becomes significant as a specific difference.

The writer has already pointed out that in *S. sterkii* the free-swimming forms present a varying picture with respect to nuclei. According to Kahl, *P. herbicola* has two macronuclei with one micronucleus between. This condition is also found in some free-swimming forms of *S. sterkii*.

Kahl maintains that the most important difference between *P. herbicola* and *P. muscicola* is the presence in the former of two macronuclei and one micronucleus, and in the latter, of two to three micronuclei for each macronucleus. Figure 89 shows two macronuclei with reorganization bands, thus it does not represent the nuclear condition at the interphase. There are, however, other differences, (1) in length of organism ; (2) in the arrangement of the ventral, longitudinal rows ; (3) in length of peristomal field ; and (4) the presence of three cirri at the mid-line posterior in position to the frontal transverse row in *S. muscicola.*

It is of no consequence to the writer whether the form herein described is named *S. sterkii* or *S. herbicola.* A detailed description of *S. herbicola* would decide the matter. The key by Kahl (1932) has been available to the writer only very recently through the courtesy of Professor Kirby. Many changes have been made in the genera characterized by few uninterrupted rows of cirri on the ventral surface. The value of these changes can only be determined by those who have a thorough knowledge of the various types involved.

DIAGNOSES.

Credit is due Sterki for having recognized the distinctive characters of the genus which he created, but he also included those which are specific for *S. tardus.* Therefore, it seems desirable to restate the generic characters of Stylonethes briefly as follows :—

Genus STYLONETHES Sterki, 1878

Paraholosticha Kahl, 1932.

Diagnosis : A hypotrich without neck or tail. Ventral surface with four uninterrupted longitudinal rows of cirri. Differentiated frontal cirri present, disposed in rows or scattered. No anal cirri.

STYLONETHES STERKII sp. nov.

Diagnosis : Body highly flexible, elongate-elliptical, anterior end with shallow excavation on left side, widest through middle, width about $\frac{2}{5}$ to $\frac{1}{2}$ of length. Anterior extremity having ventrally, transparent projecting lip ; dorsally, membranelles extending sinistrally from termination of right median ventral row of cirri following peristomal border. Dorsal surface elevated, thickest centrally, periphery rounded ; with 3 longitudinal rows of cilia. Ventral surface slightly concave with 4 (2 median and 2 lateral) uninterrupted rows of closely-set cirri, median ventrals traversing frontal field. Twelve to 22 cirri form a ventral transverse row immediately posterior to membranelle series. Differentiated frontal cirri in 2 rows between the left median ventral row of cirri and peristomal field ; number of cirri in these rows variable—left, 1–5, right, 2–6. One to 3 isolated cirri posterior to frontal cirri and near right peristomal border. Peristomal field narrow, length about two-fifths of body ; undulating membrane on right border. Cytopharynx directed obliquely, opening centrally above right row of median ventral row of cirri ; ciliated. A dorsal contractile vacuole above posterior extremity of peristomal field. Anal opening at mid-line of posterior extremity. Four macronuclei, two anterior and two posterior. Micronuclei 4, position variable. Binary fission in encysted state only. Length 94–160μ; width 38–70μ. Habitat, fresh water or brackish. Locality, Chelson Meadow, Plymouth, England.

STYLONETHES TARDUS Sterki 1878.

Diagnosis: Differentiated frontal cirri scattered, 15–20 in number. Two median ventral rows of cirri probably not traversing frontal field. Species without figures and dimensions.

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Nitrates in Aquarium Water.

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It is known that considerable amounts of nitrates accumulate in sea-water which has been circulating in an aquarium stocked with fish and marine animals. An amount equivalent to 1 gram $NaNO_3$ per litre was found in the Aquarium of the Koninklyk Zoölogisch Genootschap Natura Artis Magistra in Amsterdam.

These amounts of nitrate are never found in natural sea-water and whereas it is not quite certain whether such quantities of nitrates themselves are absolutely harmless, they cause a decrease in pH by substituting CO''_3 and HCO''_3 ion by NO'_3, and they may lead to an undesirable formation of injurious nitrates as is described below.

The rate of production of nitrate and dissolved phosphate was followed in a tank stocked with fish, having a capacity of 1·3 cubic metres. During a month when the water was being continuously passed through a filter at a rate of 20 cubic metres per hour, the production was found to be 12·4 mg. nitrate-nitrogen per litre and 0·87 mg. P_2O_5 per litre. During the following month when the filter was kept out of action and the air supply carefully regulated, the production was found to be 10·6 mg. nitrate-nitrogen and 0·24 mg. P_2O_5 per litre. At the end of the month the water became turbid and had to be filtered.

Provided the water is aerated, the ammonia (which never amounts to more than 0·1 mg. per litre daily) originating from the breakdown of albuminoids is oxidised by nitrifying bacteria to nitrites and nitrates, a process which is stimulated by a small amount of organic matter and is not affected by filtration.

The reverse process—the reduction of nitrate *via* nitrite to nitrogen—is not likely to occur in water nearly saturated with oxygen and containing only a small amount of dissolved organic substances, although denitrifying bacteria are always present.

An experiment was made in which the organic substances suitable as food for the last-mentioned bacteria were increased. A tank stocked with fish, having a capacity of 1·3 cubic metres of sea-water was brought to a pH of 8·2 by the addition of lime, and a quantity equivalent to the addition of 0·6% of sodium lactate dissolved in it. The water in the tank was then kept continuously passed through a filter and was thoroughly aerated. Analyses were made at frequent intervals of the ammonium, nitrite, nitrate, total nitrogen and phosphate content of the water. A measure of oxidisable organic matter present was obtained by titrating with decinormal potassium permanganate. The estimations were made in the water that flows directly from the filter (F) and in the water in the tank (B). F is therefore the purified water, B the water contaminated by the fishes.

After the addition of lactate the water became turbid and a considerable amount of nitrite was found in the water, while the amount of nitrate and of total inorganic nitrogen decreased, as shown in the Table. It is considered that the added lactate caused the denitrifying bacteria to develop. Later, when the lactate had been partly used up, the analyses showed oxidation of nitrite to nitrate to be taking place. The increase in nitrate started some four days after the addition of lactate, when the value for oxidisable organic matter had fallen to about 30. It is considered that an equilibrium is attained at a given moment between the activities of the denitrifying and the nitrifying bacteria and that nitrite appears when the denitrifying bacteria have insufficient lactate left. After a second addition of lactate on the 16th, the remaining nitrite and nitrate rapidly disappeared.

Throughout the experiment the concentration of ammoniacal nitrogen remained low, the ammonia formed being rapidly and almost completely oxidised. Repetition of the experiment after addition of potassium nitrate to the water gave a similar result. It was also found that, instead of lactate, tartrate may be used and that without filtration the water remained turbid and that denitrification was neither so quick nor so complete.

The turbidity is caused by bacteria, both cocci and rods. After the treatment with lactate followed by the disappearance of nitrates, the water supported fish life in a healthy condition.

SUMMARY.

The formation of nitrate in the water of an aquarium tank stocked with fish was followed. As much as 1 gram per litre expressed as sodium nitrate was found.

By adding lactate or tartrate to the water the development of denitrifying bacteria brought about almost complete removal of the nitrates and nitrites in the water.

The experiments form part of an investigation made under the direction of Dr. Jan Smit.

TABLE I.

SEA-WATER FILTERED UNDER ADDITION OF LACTATE.

	Date.	Temp. °C	·pH	Water.	NH_3N mg./L.	NO_2N mg./L.	NO'_3N mg./L.	Total Inorg.N mg./L.	Org.N. mg./L.	P_3O_5 mg./L.	$KMnO_4$ c.c.O.In/L.
F	28.5.32	15·5°	8·2	clear	0·2	0	53·5	58·7			
B			8·2	,,	0·3	trace	59·2	59·5			
F	1.6.32	16°	8·2	,,	0·20	,,	58·5	58·7	0·26	3·96	4·84
B			8·2	,,	0·16	,,	58·5	58·7	0·53	3·96	4.84
→											
F	4.6.32	16·5°	8·2	,,	0·16	,,	37·1	37·3		3·65	40
B			8·2	,,	0·27	0	53·8	54·1		3·65	40
F	6.6.32	16°	8·1	turbid	0·28	4·87	24·7	29·9			58
B			8·1	,,	0·23	2·74	26·9	29·8			80
F	7.6.32	16°	8·1	,,	0·33	12·4	1·3	14·0			30·2
B			8·1	,,	0·51	11·3	2·4	14·2			34·0
F	8.6.32	16°	8·1	,,	0·77	12·2	2·2	15·2		1·90	28·6
B			8·1	,,	0·50	12·2	2·8	15·5		1·90	30·2
F	11.6.32	16·5°	8·1	,,	1·59	12·5	6·9	21·0		2·00	26·5
B			8·1	,,	1·27	12·1	6·6	20·0		2·00	27·5
F	13.6.32	18·5°	8·1	clear	0·80	14·6	7·3	22·7		2·56	26·9
B			8·1	,,	1·06	14·6	7·3	23·0		2·56	27·1
F	15.6.32	18·5°	8·2	,,	0·26	12·3	11·9	24·5	4·44	2·83	24·6
B			8·2	,,	0·22	12·3	10·5	23·0	2·72	2·83	25·1
→											
F	16.6.32	19°	8·2	turbid	0·24	9·6	0	9·8		2·07	96
B			8·2	,,	0·20	11·4	2·7	14·3		2·17	117
F	18.6.32	19°	8·2	,,	0·26	0	0·12	0·38		2·17	109
B			8·2	,,	0·25	0	0·12	0·37		2·17	108
F	20.6.32	17°	8·2	,,	0·17	0	0	0·17	1·22	2·13	55·8
B			8·2	,,	0·16	0	trace	0·16		2·13	56·2
F	22.6.32	16·5°	8·1	clear	0·28	0	0·18	0·46		2·47	58·1
B			8·1	,,	0·39	0	0·07	0·46		2·40	60·3
F	30.6.32	18°	8·1	,,	0·51	0	0·6	0·57		1·82	10·8
B			8·1	,,	0·58	0	0·6	0·64		1·88	11·0

→ Addition of organic substance.
F=filtered water.
B=water in the tank.
(The difference between the values of F and B on the same day is affected by the filtration.)

The Use of a Selenium Rectifier Photo-electric Cell for Submarine Photometry.

By

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and

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With 1 Figure in the Text.

PHOTO-ELECTRIC cells of the rectifier or "Blocking-layer" type possess such manifest attractions from the point of view of convenience that they have come into wide use for the measurement of illumination, especially for artificial light and for use as exposure meters. Several photometers making use either of the cuprous oxide cell of Lange (1930), or of the selenium cell of Bergmann (1931), or of that of Bernheim, the composition of which is as yet undisclosed, are now on the market for such purposes. Many, if not all, of these are graduated on the assumption that the current is related to the illumination by a rectilinear proportion; such a proportionality holds approximately for the relatively feeble illuminations met with indoors, when the galvanometers used are of low resistance. The cells have, however, in several instances been used for measuring daylight in the open without paying attention to the fact that, under such conditions, the illumination–current relationship is not rectilinear. We have already (1933, 1) gone into these and other precautions required in the use of rectifier cells, and have found (1933, 4) that for a Bergmann cell made by the Weston Electrical Instrument Co. the curvature of the illumination–current characteristic could be allowed for with sufficient accuracy by dividing the current in micro-amperes, C, flowing through a 10-ohm galvanometer, by $1-0{\cdot}003\times\sqrt{C}$, the use of a divisor in place of a multiplying factor being more convenient, in this instance, for slide rule working; alternatively, a curve may be constructed from the formula to reproduce that found by experiment. Owing to its great sensitivity the cell, under opal-flashed glass, may give a current of over one milliampere at noon in the open late in January, when set horizontally. This must be divided by 0·905 to correct for curvature of characteristic, so that a current of 1·00 milliampere corresponds to a true illumination of 16·0 thousand metre candles; this would appear to be 14·4 if uncorrected. The figures are given on the " selenium, arc, scale," namely using a carbon arc to standardize the selenium cell. With summer illuminations of 50–100 thousand metre candles the difference between the true and the uncorrected illumination would be more serious.

It follows from this that, if such a rectifier cell be used for the permanent recording of daylight, corrections would need to be applied to the record charts. This effect might be greatly reduced (probably to negligible size) by mounting the cell so that it only received a small fraction of the light transmitted by a diffusing window and by then using a sensitive instrument to record the small currents obtained with this relatively feeble illumination.

The effect is generally negligible with vacuum emission cells, provided sufficient anode potential be applied to ensure saturation in the brightest light.

For measuring under-water illumination, rectifier cells were used by several workers almost simultaneously. We used a cuprous oxide cell (1933, 3) in the summer of 1932, making use of a 10-ohm galvanometer for measuring the current. The galvanometer was on land, the cell being carried by a diver. For use at sea it was proposed to use the potentiometer-telephone method to measure the open circuit voltage, the illumination–voltage relationship for which was found to show a very pronounced curvature. The cuprous oxide cell has since been abandoned as much inferior to the selenium rectifier.

Pearsall and Ullyott (1933) used a Bernheim cell in Lake Windermere, and give a comparison between its readings and those of a thin-film potassium on copper vacuum cell for February 8th. The Bernheim cell has a high sensitivity and a greater blue sensitivity than the selenium cell. A pointer galvanometer was found suitable for work from a small boat on the lake.

The most extensive series of measurements in the open sea with a rectifier cell were those carried out by Utterback and Boyle (1933) upon waters in and outside Puget Sound and up the coast towards Alaska; they worked in a small steamer, and used the Leeds and Northrup marine galvanometer; this is a mirror galvanometer with a specially robust suspension. To provide sufficient sensitivity a very powerful field is used, produced by an electro-magnet. The latter operates from a 6-volt circuit and takes half an ampere. Utterback found this quite satisfactory with the Bergmann-Weston cell, and worked down to 50 m., using colour filters for the various regions of the spectrum and an ingenious electrically operated filter-changing mechanism.

In the Baltic Pettersson and Landberg (1934) used a selenium cell of the Bergmann type, constructed or modified by Lange, which, they state, has a maximum of sensitivity rather in the green than in the yellow orange as usual. This they used with a pointer galvanometer which worked well in their calm water. They found it necessary to use a screen to limit the illumination of their cell in strong light.

Our own work was carried out with two Bergmann-Weston selenium cells, one mounted on the deck-house roof, and the other in the small gun-metal case previously used for the cuprous oxide cell. With this we have made some preliminary measurements of the penetration of light of various colours into sea-water 1–2 miles south-east of Plymouth Breakwater.

THE STANDARDISATION AND USE OF RECTIFIER CELLS.

We have dealt elsewhere with the optical conditions affecting a submerged photometer (1933, 2), and with the testing and behaviour of rectifier cells in bright light (1933, 1). It is only necessary to state here that the reading of a submerged photometer must be multiplied by 1·09 to correct for the nett effect of variations in internal and external reflections at the surface of the opal window, and that we must allow for the curvature of the current—illumination characteristic of the cell, which curvature becomes more pronounced as the resistance in series with the cell is increased. As high resistance also increases the error due to temperature variation of the cell, it is desirable to use a measuring instrument with the lowest possible resistance. The temperature variation error has been fully studied by Lange (1931).

For work on shore in comparatively bright light we have found a Cambridge Unipivot "Versatile" pointer galvanometer very suitable, as its resistance is only 10 ohms and 1 scale division (readable to 0·1) corresponds to 2 micro amperes, i.e. to about 30 metre candles with the opal glass in position. For strong light a special shunt designed to maintain the effective resistance at 10 ohms (1933, 1, p. 538) may be used.

For weak light, however (say below 500 m.c. or 0·5% of full noon sunlight), a more sensitive instrument is advantageous, and this will probably entail a higher resistance. This is not a serious drawback as the curvature of the characteristic is comparatively small in weak light, and can be corrected for if the requisite data for the given galvanometer resistance has been obtained by photometer bench tests (1933, 1) or by comparison with a vacuum emission cell (1933, 3).

We have not so far attempted to use a galvanometer at sea, as the comparatively small currents obtainable in deep or turbid water, especially with colour screens in use, would require a rather costly and sensitive instrument. We found it more convenient to employ our potentiometer-telephone method (1928, 1933, 2) which was available, rather than to attempt to fit up a system of gimbals sufficiently perfect to enable such a galvanometer to be used on board the trawler *Salpa*. We were not at the time aware of the existence of the special marine galvanometer. The only modification required in the apparatus was the reduction of the resistance through which the current from the cell passed, and across which the potential difference was measured by means of the potentiometer. In the measurements described below this resistance was made 10, 100 or 200 ohms according to the brightness of the light to be measured, but subsequent experience has shown that values of 1000 or 10,000 ohms may be used in weak light, provided that suitable calibrations are effected. This means that for bright light with 10-ohm resistance one potentiometer scale division (10^{-4} volt) corresponds to about 150 m.c., while in weak light the sensitivity can be instantly increased as much as 400 times. There is evidently a limit to the gain of sensitivity obtainable in this way, as, even in very weak light, a large resistance reduces the current passing through; in fact the maximum P.D. available is the open circuit P.D. of the cell under the given illumination. This might be used, if desired, to measure very weak light, but this method would not increase the sensitivity greatly above that obtainable with 10,000 ohms in circuit.

A curve for the open circuit P.D. of a cuprous oxide cell has already been given (1933, 3).

It is, however, doubtful whether the rectifier cells available at present can be used at considerable depths in the ocean, such as 180 m. (Clarke, 1933), at which emission cells have been used. This doubt arises from the fact that though on open circuit the rectifier cell is rather more sensitive than the emission cell over 100,000 ohms, yet the latter may be used over 1 or 2 megohms. Furthermore, the potassium cell is most sensitive just where the water is most transparent, whereas the selenium cell has its maximum in the orange yellow.

For a typical Weston cell, with opal window, photometer bench tests have shown that the following resistances are convenient:

For currents up to $2{\cdot}5\mu$a (c. 110 m.c.) 10,000 ohms, giving about $2{\cdot}5 \times 10^{-4}$ volt per m.c.

For currents up to 50 μa (c. 1050 m.c.) 1,000 ohms, giving about $0{\cdot}5 \times 10^{-4}$ volt per m.c.

For currents up to 500 μa (c. 8500 m.c.) 100 ohms, giving about $0{\cdot}06 \times 10^{-4}$ volt per m.c.

For currents over 500 μa (c. 8500 m.c.) 10 ohms, giving about $0{\cdot}006 \times 10^{-4}$ volt per m.c.

The calibration curve corresponding to the cell and the resistance must be used to find the value of the illumination.

For further work we have had constructed, by Messrs. Tinsley & Co., a plug-in resistance set, so arranged that the potential difference measured can be across 10, 100 or 1000 ohms according as a single plug is inserted. This aids rapidity of work, for while the air illumination is measured across 10 ohms the under-water illumination may be across 1000 ohms. Spare terminals and a spare plug-hole permit the use of 10,000 ohms already in the potentiometer-telephone apparatus as part of the subdivided 100,000 ohm set.

The potentiometer method seems to be very suitable for work with rectifier cells. The absence of high potentials removes all insulation troubles, and the lowness of the resistance across which the P.D. is measured, as compared with the high value (100,000 ohms) generally needed with emission cells, renders the potentiometer balance very sharp. It could generally be set to within 0·2 scale division, viz. 20 microvolts, when the light was steady enough.

The surface illumination was measured by a cell mounted (under opal glass) on gimbals on the deck-house roof. This was the actual cell used in the laboratory and sky light measurements already recorded (1933, 1, 4), so its characteristics for various series resistances were known. The cell used under water has not, as yet, been tested in this way, but for these preliminary measurements, under conditions in which great accuracy was hardly attainable, we may, without serious error, take its curvature corrections for various resistances to be the same as those for the " deck " cell. The two were almost the same in sensitivity.

The deck cell had been standardised against a carbon arc by the method already described (1928, p. 460), and also against a standard vacuum lamp at a colour temperature 2360° K.—the former gave 14·4 m.c., and the latter 15·1 m.c. per μa for the cell under opal glass exposed to weak diffuse light. The agreement shows the general similarity that this cell bears to the eye in its estimate of the relative brightness of sources of different colours. This is the first cell that we have found that can be standardised against a bare filament lamp and used to measure daylight without obtaining a scale of values utterly different from the visual one. This is a very great advantage, as the arc cannot be regarded as either a convenient or an accurate standard, though it possesses the advantage of readily providing high intensities. Some preliminary tests have indicated that winter daylight with low sun (February 15th, 1934, 15.30 G.M.T.), which was recorded as 15,850 m.c. by a vacuum potassium cell standardised against the arc, was measured as 12,400 m.c. by the Weston cell standardised against the standard filament lamp. Daylight measurements on what we may briefly call the " Selenium, 2360°, Scale " as used below, should, therefore, be about 78 per cent of the corresponding values on the " Potassium, Arc, Scale " which we have hitherto employed. The ratio of the two scales will, however, depend on the colour of the light, and hence on the relative proportion of direct sunlight, the selenium cell being relatively more sensitive to sunlight and the potassium cell to blue sky light.

SUBMARINE MEASUREMENTS.

One group of five series of readings was made a couple of miles south of Plymouth Breakwater on October 10th, 1933.

The usual procedure was adopted, sets of alternate readings of the deck and sea cells being made with the latter suspended from a spar projecting about 2·2 m. clear of the ship's counter, first with the cell about 1 m. above the surface, where the shading due to the ship was small, and then at depths of 1, 5, 10 and 15 metres. Consistent readings could not be obtained at less than 1 m., and the available depth did not allow of working below 15 m., in fact on two occasions the photometer touched the bottom and had to be hauled up a metre or two.

Series were obtained with the cells covered only by opal glasses, and also with blue, green, yellow, and red, filters placed beneath the opal glasses of each photometer, so that the transmission of each filter was independent of the average obliquity of the incident light. The following are particulars of the conditions under which this group of series was obtained :—

Group W.1., including series W.1, W.1.B., W.1.G., W.1.Y., and W.1.R., October 10th, 1933. Drifting W. from position ½ mile W. of Mewstone. Light variable, blue sky and white clouds, β* about 2·0 at 12.42 G.M.T. Wind E., moderate to fresh. Easterly swell. High water 6.51 G.M.T., tide flows to the W. until 2 hours after low water.

W.1. No colour filters. 11.21–12.01 G.M.T., commencing near Mewstone. Vertical surface illumination 45 to 71·5 thousands of metre candles (selenium, 2360°, scale). Touched bottom at 15 m.

W.1.B. Chance's No. 7 blue filters, 13.05–13.25 G.M.T. (just after low water), commencing near Mewstone. Secchi disc visible to 9·5 m. at 13.11.

W.1.G. Corning "sextant green" filters, 13.41–13.59 G.M.T., commencing near Mewstone. Touched bottom at 15 m.

W.1.Y. Sea cell, Chance's No. 4 orange filter. Deck cell Corning H.R. yellow, 14.9–14.50 G.M.T. Further W. than W.1.G.

W.1.R. Schott R.G.1 red filters, 15.05–15.21 G.M.T. Wind lighter. Further W. than W.1.Y.

The results are plotted in the figure on a logarithmic scale as percentages of the vertical surface illumination of the same colour. It will be noted that they all indicate a somewhat large surface loss, which is not unusual with strong winds. Surprisingly clear water seems to have been

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* As before β denotes the ratio of light from sun plus sky to that from sky alone, receiving surface being set horizontally.

encountered during the 5-m. readings of series W.1.B., otherwise the results are in accordance with what we should expect for inshore waters, where green light is generally found to penetrate best (1933, 2). It is worth noting that the vertical absorption coefficient μ_v for series W.1.B, (1–10 m.) viz. 0·177, agrees almost perfectly with the value 0·179 found by the rough rule $\mu_v = 1·7/D$ which we have previously found applicable as a correlation between μ_v for blue light and D, the maximum depth of visibility of the Secchi disc.

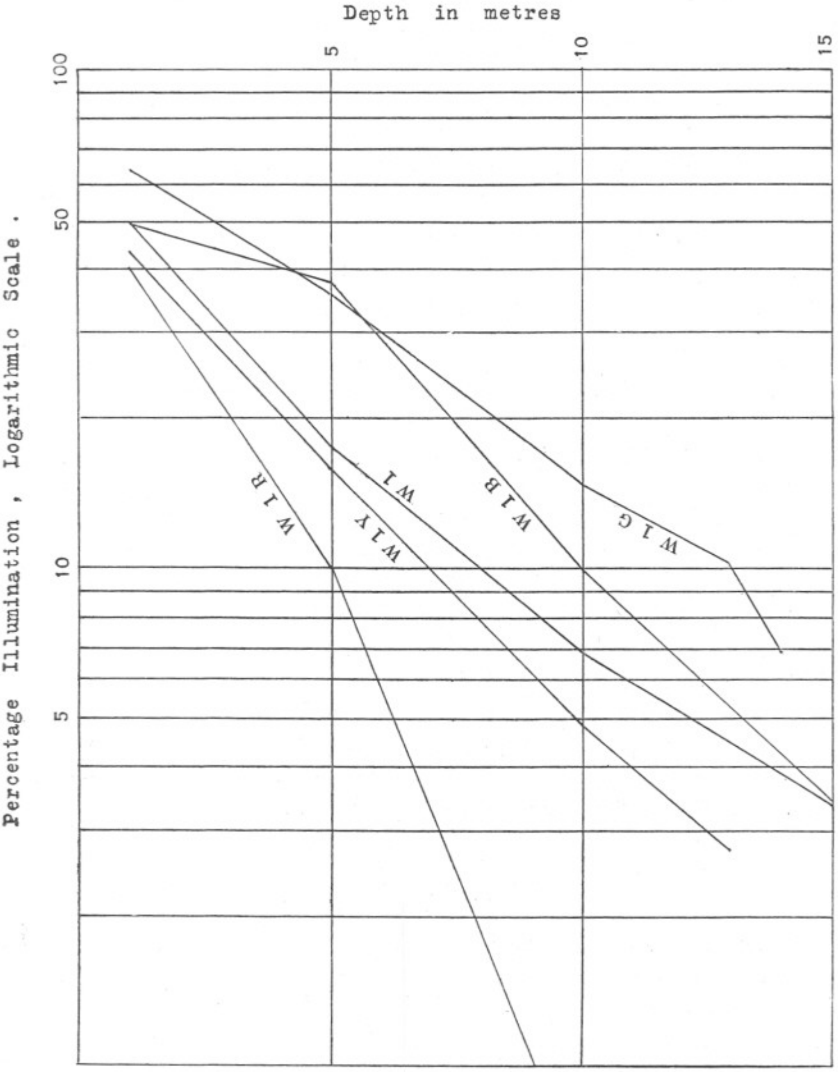

Fig.—Percentage submarine illumination near Mewstone, off Plymouth, October 10th, 1933. The mean vertical absorption coefficients calculated between one and ten metres are: opal only 0·216; blue under opal, 0·177; green under opal, 0·153; yellow under opal (including red), 0·243; red under opal, 0·345.

The results shown in the figure agree well with certain of our previous determinations on inshore waters in 1931, carried out at about 1–2 miles off the shore in Whitsand Bay, to the west of Plymouth Sound. These were made using an emission cell, thin-film caesium type CMV6 with colour filters The table shows that the water was slightly clearer for the August 1931 measurements. The filters were the same for the red and green in each year, and very similar in the other cases.

TABLE I.

SHOWING THE DEPTHS IN METRES AT WHICH THE AIR ILLUMINATION IS REDUCED, IN WATER, TO 10 PER CENT. THE SERIES NUMBERS REFER TO THE 1931 MEASUREMENTS ONLY, SINCE ALL THE 1933 RESULTS ARE GIVEN.

Filter. Series	Blue. 80B	Green. 72G	Yellow. 71Y	Red. 74R	" White." 68H
1931	10·6	14·6	8·0	5·0	7·4
1933	9·9	13·0	7·0	5·0	7·9

Only in the " white " column does the water appear clearer in 1933 than in 1931. This column for 1931 represents the thin-film caesium cell, with a heat-absorbing filter, light green in tint ; this renders its sensitivity nearly uniform over the visible spectrum and absorbs the near infra-red to which this cell is very sensitive. The figures indicate, however, that the selenium cell, which has a maximum sensitivity about 590 mμ, is relatively slightly more sensitive to green light, which penetrates best, than the CMV6 cell with heat-absorbing filter.

The values of percentage illumination given in the table are actual values, read off from the graphs, but as measures of clearness of the water the comparison is not exact, since the surface losses were not the same on the different dates. The general agreement is, however, quite evident.

SUMMARY.

1. Measurements of the penetration of light of various colours into the sea were carried out by means of a selenium rectifier cell. The mean vertical absorption coefficients were : for blue, 0·177 ; green, 0·153 ; " white," viz. no filter, 0·216 ; yellow, 0·243 ; red, 0·345. The results accord well with those obtained under similar conditions with emission cells and show that, for water a couple of miles offshore, green light penetrates best.

2. The current was measured using the potentiometer-telephone method as for emission cells, but determining the drop in potential across

a low resistance, 10, 100, or 1000 ohms. The motion of the ship was too violent to permit of the use of any available galvanometer of adequate sensitivity.

3. Rectifier cells are more convenient to use than emission cells, as the currents to be measured are much larger and the absence of high potentials greatly simplifies all insulation problems. On the other hand the curvature of the illumination–current relation involves additional labour in standardizing and in calculating results.

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Hydrography of the Mouth of the English Channel, 1929–1932.

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With 7 Figures in the Text.

Since 1921 hydrographic data have been collected by the S.S. *Salpa* and several merchant vessels, the records being published in the *Rapport Atlantique* and the *Bulletin Hydrographique* each year. A description of the conditions in the mouth of the Channel—the varying temperature, salinity, and movements of the water masses—during the years 1925–1928 was published in this Journal, Vol. XVI., pp. 791–820, and included a review of the objects of these investigations and the methods used in working up the collected data. This present publication forms a continuation of this. The same methods of dealing with the data have been used.

Temperature Distribution.

Diagrams showing the distribution of temperature with depth at the International Station E1 for the years 1930, 1931, and 1932 are shown below, that for the year 1929 having been included on page 801, Vol. XVI. These three years are not remarkable, except that the water in the autumn of 1931 was warmer than any of the previous years except 1921. This cannot be attributed to an inflow of warmer Atlantic water such as occurred in 1921, because at this time the mouth of the Channel was of unusually low salinity.

Salinity Distribution.

Charts showing the distribution of salinity at the beginning of each month have been prepared from isopleth diagrams of the data as in previous years. A selection of these is reproduced in Figures 3–7, and illustrates changes which have occurred during the four years under review. It has been clear throughout that such charts only give a rough picture owing to the limited intensity of sampling, and, furthermore, that the isohalines are not smooth contours, but that numerous offshoots, lacunæ and isolated patches exist. The data shown in Figure 2 confirm this deduction.

However, in spite of this and the fact that a personal equation comes in when drawing the salinity diagrams, each one gives a consistent generalised picture. A number of such diagrams were drawn for fortnightly intervals, without reference to the diagram for the preceding and subsequent fortnight. Arranged in order these pictures gave a reasonable

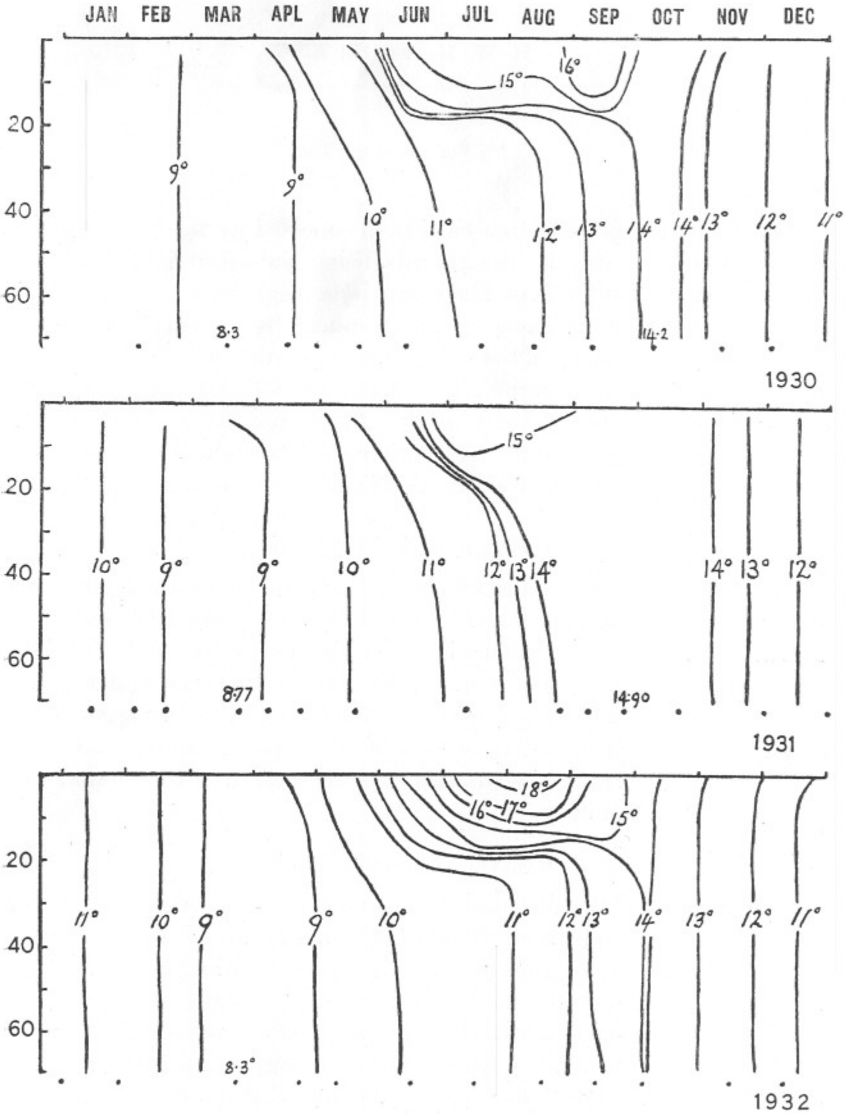


FIG. 1.—Isopleth diagrams showing distribution of temperature with depth (in metres) at Station E, from January, 1930, to December, 1932.

sketch of the general distribution, for if it had been otherwise diagrams for consecutive fortnights would not have been consistent.

The general circulation of the water masses in the area may be outlined. There is usually a slow drift of water through the Channel and out into the North Sea, undergoing gradual dilution as it passes eastward from the Atlantic. This east-going drift is sometimes held up and even reversed by northerly and easterly winds (Carruthers). At times Atlantic water in large quantity enters the mouth of the Channel in the form of a tongue, the water which it displaces moving out north-westward past Lands End. Sometimes the tongue penetrates far up Channel in the east-going drift, either as a ribbon or as patches. More often the high salinity water forming the tongue moves out north-westward past Land's End, its place being taken for the most part by water of lesser salinity from the Atlantic and the west coast of France, and only a small moiety of it passes up Channel. On occasions the mouth of the Channel has filled up with quite low salinity water passing in round Ushant from the west coast of France (April–May, 1928, and again apparently in July, 1931), the water which it displaced having of necessity moved out north-westward for the most part.

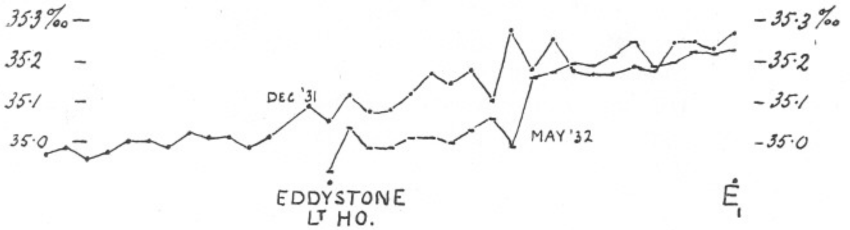


FIG. 2.—Diagram showing salinity of surface samples taken at half-mile intervals on the line Plymouth–Eddystone–International Station E_1, on December 31, 1931, and May 10, 1932.

Throughout the period under review current measurements have been made at the Varne Lightship and the movement of water into or out of the North Sea calculated for each month. I am indebted to Dr. J. N. Carruthers for these data.

The change in salinity distribution indicates during some months a passage of relatively high salinity water up Channel and during others a hold-up or even reversal. It could not be expected that they would every month reflect the nature of movement through the Straits of Dover, although this frequently occurred. The notable exceptions were that in July, 1931, there was a flow through into the North Sea, whereas the salinity distribution suggests a hold-up or reversal ; again it was deduced from the salinity distribution that a flow into the North Sea was resumed during the latter part of October, 1931, whereas this did not happen until the beginning of November.

The changes and deductions may be epitomised as follows, where, for the sake of brevity, water above 35·3°/₀₀ salinity is termed Atlantic water.

1929.

During January and February Atlantic water in the Channel moved out north-westward past the Lizard and also up Channel.

March. Little or no change.

April. Atlantic water moving out north-westward past the Lizard. East-going drift through Dover Straits held up by easterly winds.

May. Atlantic water entering mouth of Channel past Ushant.

June, July, August, September, October, November. Gradual penetration of Atlantic water into mouth of Channel.

December. Notable east-going drift up Channel.

1930.

January. Movement up Channel. A patch of high salinity water 35·3–35·4°/₀₀ occurred north of the Channel Islands during this month.

May. Appearance of high salinity water on the line Land's End–Ushant in the middle of the month and of remarkably high salinity water, 35·5–35·7°/₀₀, at the end of the month.

Water of 35·8°/₀₀ occurred at Seven Stones light vessel at end of month.

A stratum of water with salinity 35·6–35·7°/₀₀ was found by H.M.S. *Beaufort* at 50° 08′ N. 6° 15′ W. at a depth of 50 metres, with water of lesser salinity above and below. A stratum with salinity 35·5–35·59°/₀₀ found by S.S *Muirchu* on May 15 at 50° 55′ N. 9° 56′W. with water of lesser salinity above and below.

June. Gradual penetration of the very high salinity water into mouth of Channel, a patch having salinity 35·75°/₀₀ being encountered early in July on the line Plymouth–Guernsey.

July. Retreat of the very high salinity water, probably north-westward past the Scillies.

August. Penetration of Atlantic water into mouth of Channel; rather marked movement of water through Dover Straits.

September and October. Continuation of the movements experienced in August but less marked; passage of Atlantic water out north-westward past Lizard.

1931.

November, December, 1930, January, February. Atlantic water seems to have been replaced largely by low salinity water moving in past Ushant from the French coast. Patches of Atlantic water meanwhile passing up Channel.

March. Water of relatively high salinity, 35·4–35·58$^{\circ}/_{\circ\circ}$, appeared on the line Land's End–Ushant at the beginning of the month and again towards the end of the month.

April, May, June. Patches of high salinity water passing eastward up Channel. Reappearance of high salinity water on the line Land's End–Ushant at beginning of June.

July, August. Mouth of Channel filled with water of unusually low salinity.

September, October. Passage up Channel and through the Straits of Dover held up or reversed by easterly winds.

November. Water from Atlantic entered mouth of Channel. Passage westward through Straits of Dover resumed.

December. Atlantic water entered mouth of Channel.

1932.

January. Water of 35·4$^{\circ}/_{\circ\circ}$ salinity and greater observed off the mouth of the Channel. Marked passage into North Sea through the Straits of Dover.

February. Water of 34·4–35·5$^{\circ}/_{\circ\circ}$ observed off mouth of Channel. A patch having salinity exceeding 35·5 moved up Channel as far as 3° W. Passage of water into North Sea held up or reversed.

March. Atlantic water moves out from mouth of Channel.

April. High salinity water reappears north of Ushant, 35·5%°, and Atlantic water penetrates into Channel. Passage into North Sea took place.

May, June. Patches only of high salinity water observed within the Channel. During June passage into North Sea held up.

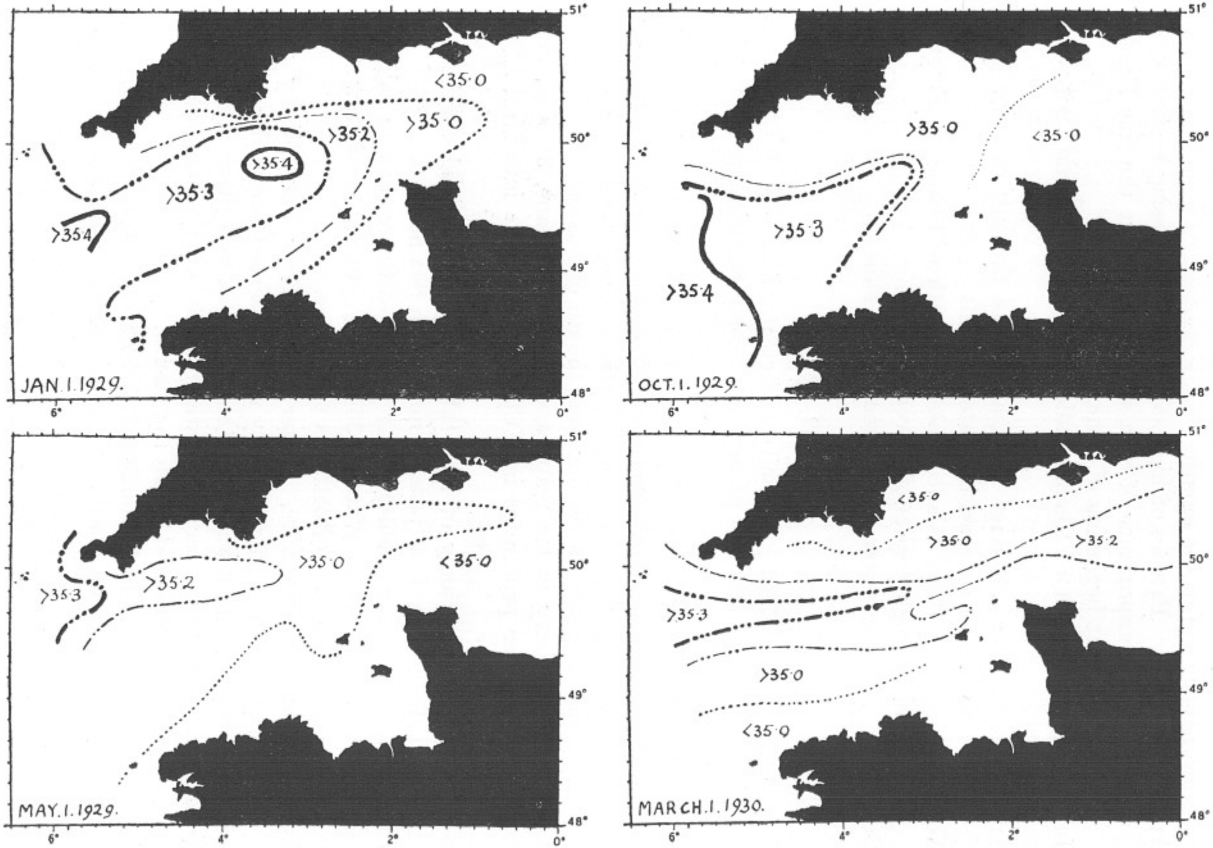
July. Water of lower salinity filling mouth of Channel, high salinity water off the mouth. Water of 35·5–35·6$^{\circ}/_{\circ\circ}$ observed south-west of Ireland. Passage into North Sea took place.

August, September, October. Water of relatively low salinity fills mouth of Channel; high salinity water observed across the mouth. A notable passage of water into the North Sea took place in October.

November. Atlantic water penetrates mouth of Channel and high salinity water observed across the mouth.

December. Water of high salinity, 35·5–35·6$^{\circ}/_{\circ\circ}$, observed at entrance during early part of month. A passage of water into the North Sea took place.

The notable conditions during this period were the relatively low salinities and high temperatures during the latter part of 1931, and the frequent occurrence of unusually high salinity water off the mouth of the Channel at intervals during 1931 and 1932.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>35·4
>35·3
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OCT.1.1929.
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>35·3
>35·4
MAY.1.1929.
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>35·0
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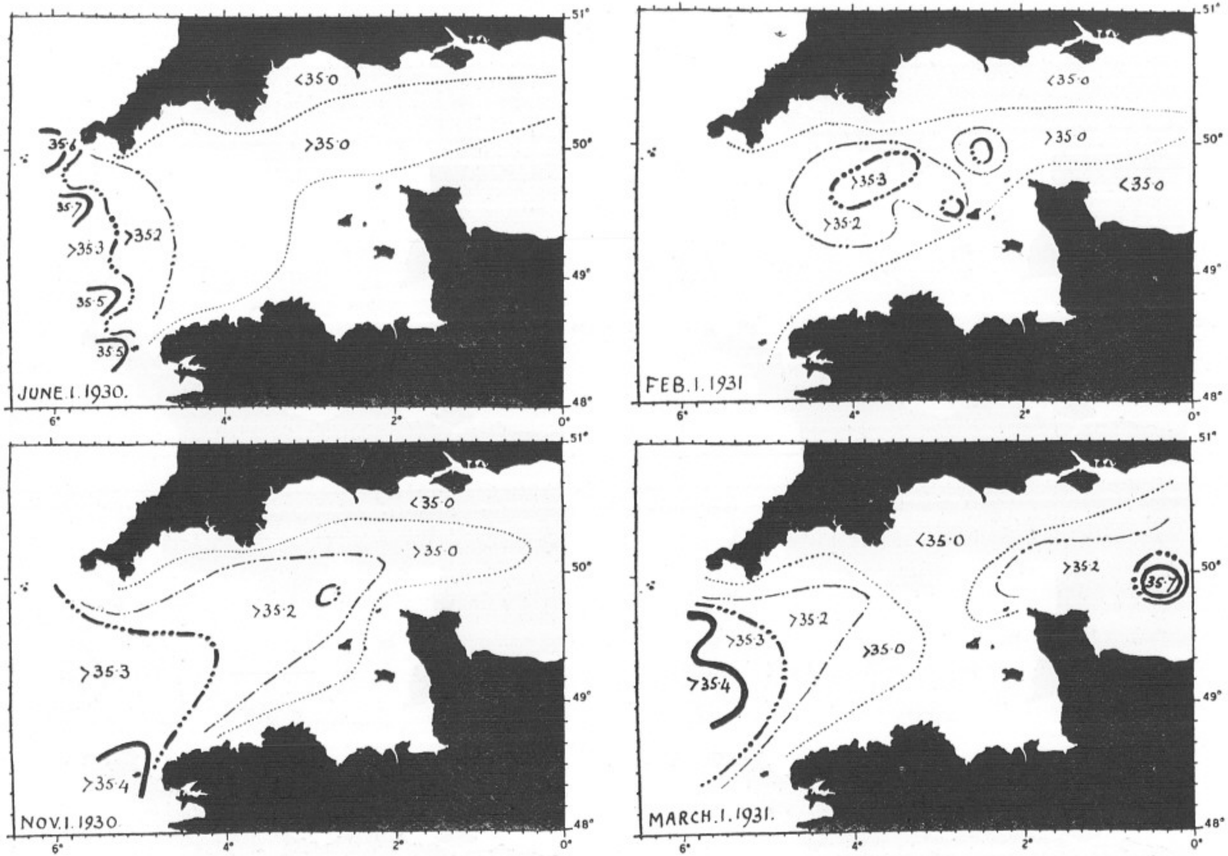
MARCH.1.1930.
<35·0
>35·0
>35·2
>35·3
>35·0
<35·0
51°
50°
49°
48°
6°
4°
2°
0°

FIG. 3.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35·7
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>35·2
35·5
35·5
FEB.1.1931
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>35·0
<35·0
>35·3
>35·2
NOV.1.1930
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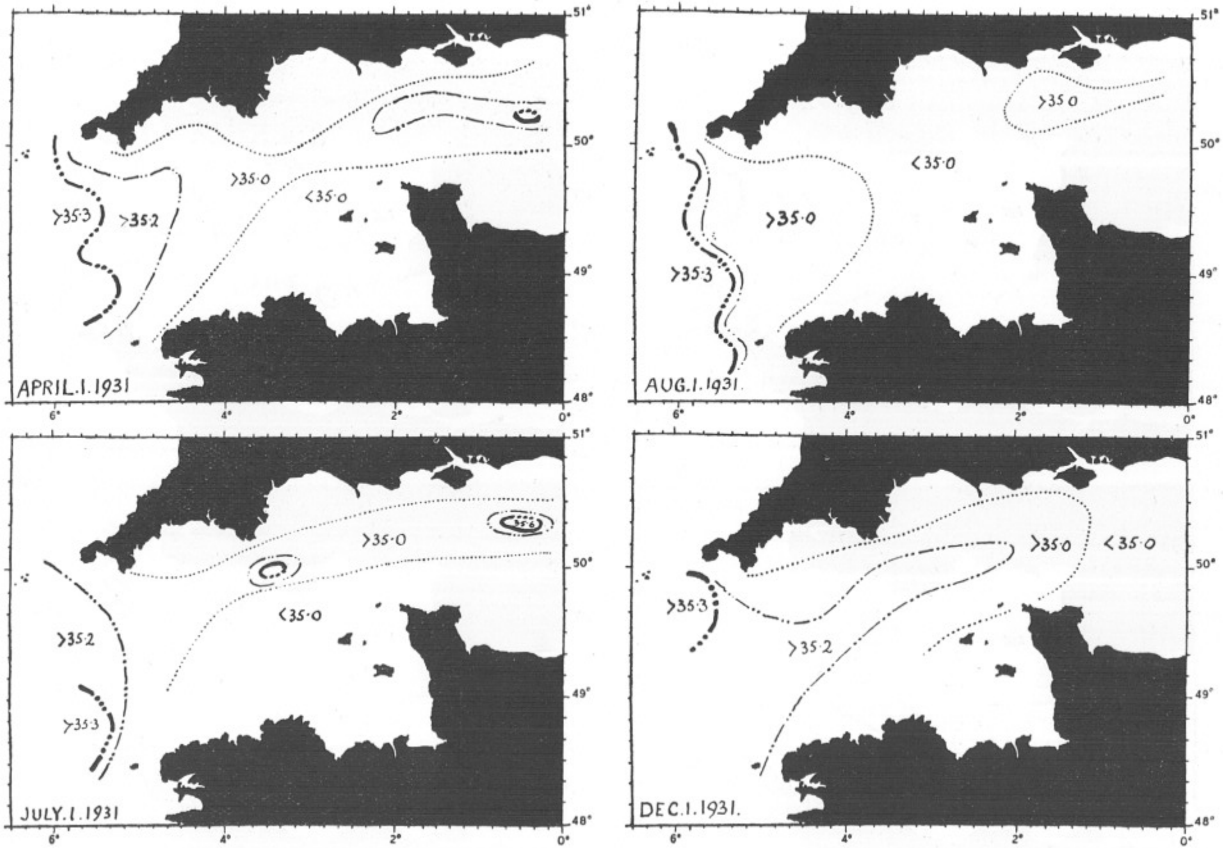
>35·0
>35·2
>35·3
>35·4
MARCH.1.1931.
<35·0
>35·2
35·7
>35·2
>35·3
>35·0
>35·4
51°
50°
49°
48°
6°
4°
2°
0°

FIG. 4.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<35·0
AUG.1.1931.
>35·3
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<35·0
35·6
DEC.1.1931.
>35·3
>35·2
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51°
50°
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48°
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4°
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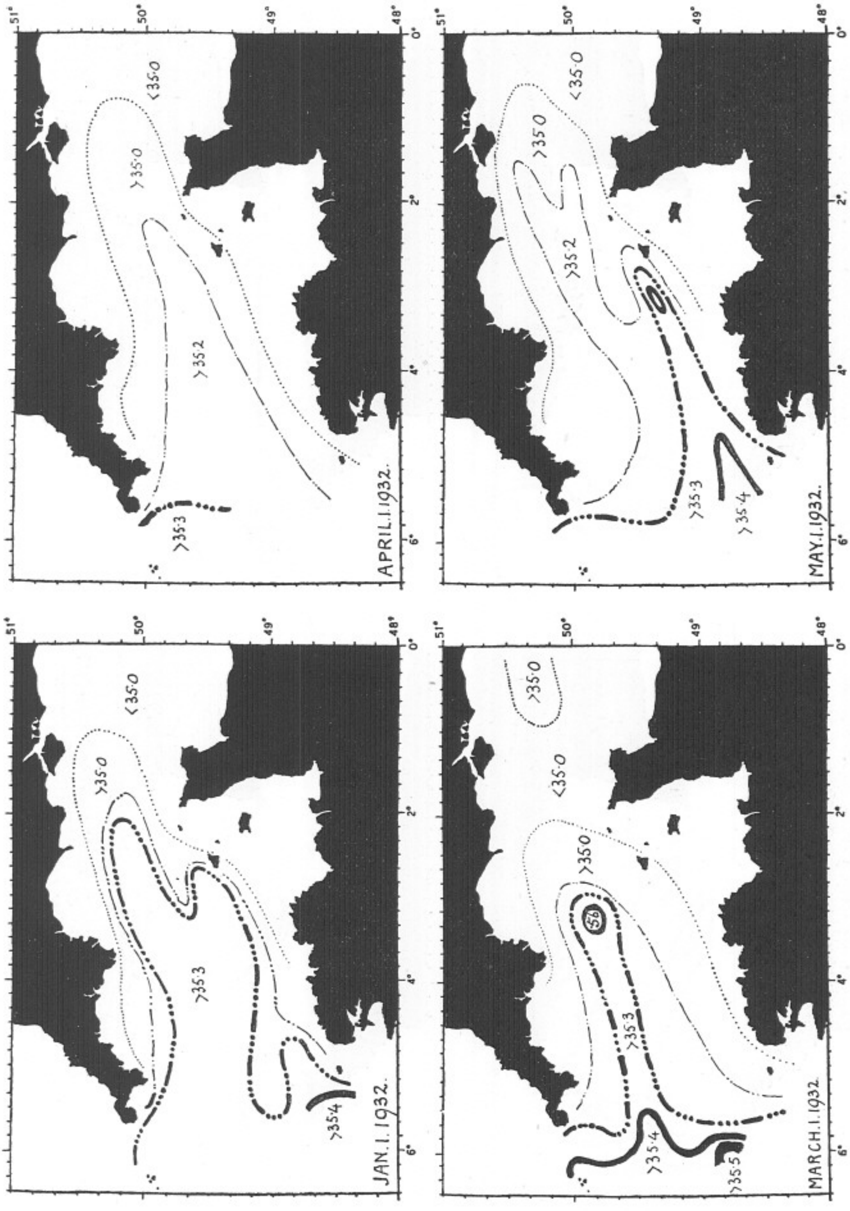
FIG. 5.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50°
49°
48°
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2°
4°
6°
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>35·2
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JAN.1.1932.
<35·0
>35·0
>35·3
>35·4
MARCH.1.1932.
>35·0
<35·0
>35·0
35·6
>35·3
>35·4
>35·5

Fig. 6.

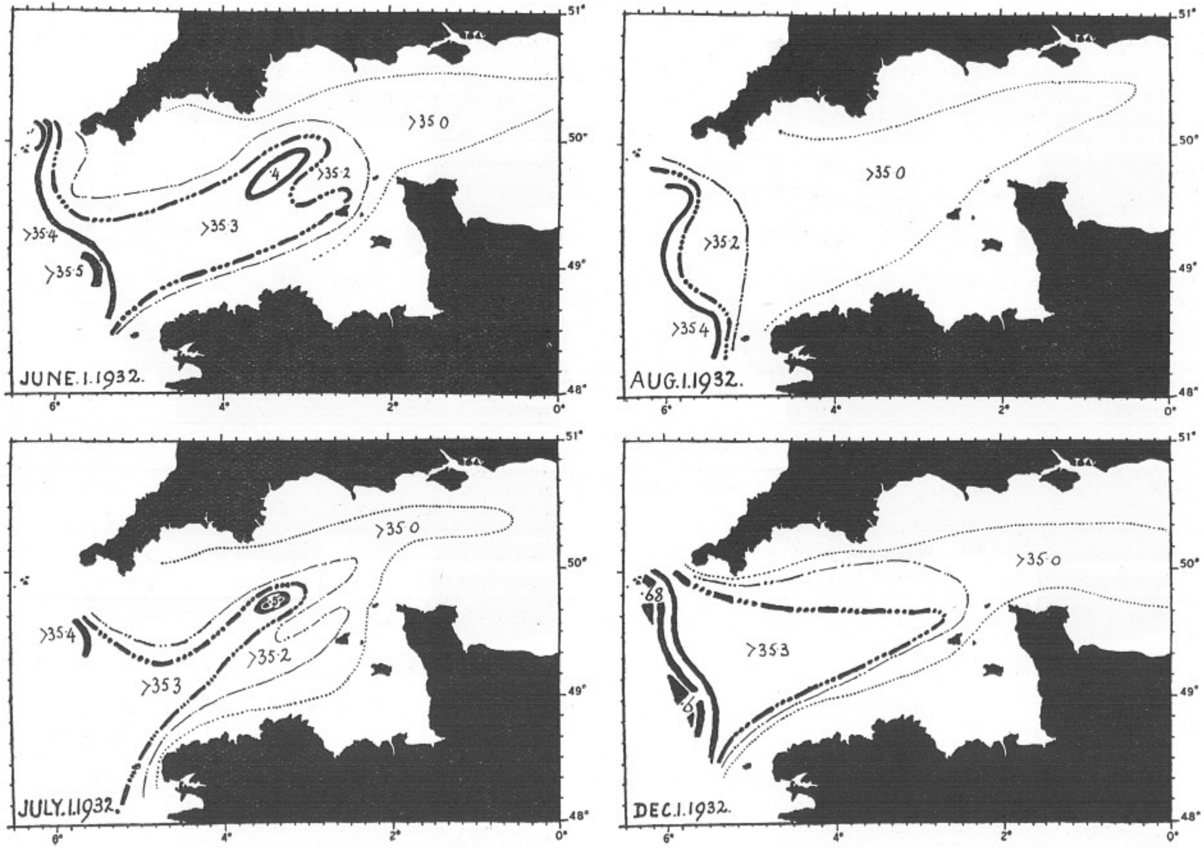
JUNE.1.1932.
>35·0
·4
>35·2
>35·3
>35·4
>35·5
AUG.1.1932.
>35·0
>35·2
>35·4
JULY.1.1932.
>35·0
·55
>35·4
>35·2
>35·3
DEC.1.1932.
>35·0
·68
>35·3
·6
51°
50°
49°
48°
6°
4°
2°
0°

FIG. 7.

The Variation of Excess Base with Depth in the English Channel with reference to the Seasonal Consumption of Calcium by Plankton.

By

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Since excess base or titration alkalinity increases with increasing chlorinity, the ratio, $\frac{\text{excess base}}{\text{chlorinity}}$, termed by Wattenberg the "specific alkalinity," is the most suitable quantity to consider when determining whether or not excess base varies with depth or from time to time. Wattenberg (**5**) has shown that a marked increase occurs in the great ocean depths immediately above the bottom. There is at present no evidence, other than that found by the writer (**2**), for the English Channel in the summer of 1931, to suggest any variation of excess base in shoal water on the continental shelf and away from the influence of large rivers such as appear to affect the Heligoland Bight (Zorell, **6**). The variation found in 1931 was small and of the order of the experimental error of any one pair of observations. To overcome this difficulty, statistical methods were applied to the grouped results obtained from similar depths during the summer and early autumn of 1931. The differences found between the specific alkalinities of the surface and bottom waters were several times the standard errors. The conclusions, however, were open to criticism in that the experimental results were not designed for statistical treatment.

In the summer of 1933 the problem was attacked somewhat differently. From each sample, contained in a number of 170 ml. standard sample bottles, about six to fifteen sub-samples, each 100 ml., were analysed for excess base by the method of Wattenberg (**4**) which had been used in 1931. It is generally recognised that in making a series of consecutive determinations on one quantity, the later results may not be independent of the earlier. Particularly in reading a burette there is a tendency to "adjust" the value read in accordance with the knowledge already gained on the sample. To overcome this, analyses of sub-samples of different samples were carried out in a haphazard sequence in flasks marked by a reference letter only, so that the origin of the sub-samples was at the time unknown. Again, in some analyses the volume of the sub-sample was increased by 1 ml. in order slightly to displace the titration.

The standardisation of the N/20 baryta in terms of 10 ml. of N/20 hydrochloric acid was carried out in quadruplicate and the mean taken as the true value. From this each titration of sea-water was subtracted in order to get the " baryta equivalents " of the excess base. These were then corrected for the error at the temperature of the laboratory of the two 100 ml. pipettes used for measuring the water. On each occasion the pipettes were calibrated by weighing the distilled water delivered under standard conditions. The distilled water had been allowed to attain the temperature of the laboratory and its volume was calculated from its temperature and weight. In any one working day the temperature of the laboratory did not vary by more than 2° C.

For each set of sub-samples, the mean baryta equivalent was found and the sum of the squares of the deviations from the mean gave the variance, $\Sigma\, d_n^2$. The standard error for the sample was then derived from the formula :—

$$\rho_A = \sqrt{\frac{\Sigma\, d_n^2}{n(n-1)}}$$

It must be admitted that owing to their small number the baryta equivalents of the sub-samples do not fall on a typical population curve. The means and standard errors were then multiplied by the baryta normality factor to give the excess base in milliequivalents per litre.

In earlier work the ratio considered for specific alkalinity, Λ, was :—

$$\Lambda_v = \frac{\text{excess base in milliequivalents per litre}}{\text{chlorinity in grams per kilogram}} = \frac{A_v}{Cl}$$

Elsewhere the writer (**3**) has discussed the advisability of replacing this volume/weight ratio by the weight/weight ratio :—

$$\Lambda_w = \frac{\text{excess base in milliequivalents per kilogram}}{\text{chlorinity in grams per kilogram}} = \frac{A_w}{Cl}$$

i.e. a ratio which varies with temperature may be replaced by one which is invariant. The excess base has therefore been converted to milliequivalents per kilogram by dividing by σ_t, the density found from the chlorinity and the temperature of the laboratory.

Since the determinations of chlorinity are relatively considerably more accurate than those of excess base, fewer sub-samples were called for. Indeed, no great error would be introduced by ignoring the standard error of the chlorinity and relying on one determination. The specific alkalinity has then to be found from the expression :—

$$\Lambda \pm \rho_A = \frac{A \pm \rho_A}{Cl \pm \rho_{Cl}}$$

TABLE I.

Date 1933 and temp. of Lab.	Station	Depth metres	EXCESS BASE				CHLORINITY			SPECIFIC ALKALINITY	
			No. of sub-samples analysed	A_v (vol/wt) milli-equiv per litre	A_w (wt/wt)		No. of sub-samples analysed	Cl ‰	Standard Error ρCl	$\Lambda_w \times 10^4$	Standard Error $\Lambda_w \times 10^4$
					milli-equiv per kg.	Standard Error ρA_w					
18/7	L 4	0	7	2.3692	2.3146	0.00207	6	19.323	0.0027	1197.8	1.19
24° C		50	6	2.3850	2.3299	0.00277	6	19.341	0.0038	1204.7	1.45
	L 6	0	12	2.3590	2.3046	0.00178	4	19.314	0.0013	1193.3	0.93
		5	4	2.3623	2.3078	0.00349	3	19.322	0.0036	1194.4	1.82
		25	13	2.3724	2.3176	0.00148	5	19.350	0.0020	1197.7	0.78
		68	15	2.3814	2.3263	0.00242	4	19.359	0.0038	1201.7	1.27
10/8	E 1	0	5	2.3604	2.3051	0.00132	1	19.36	-	1190.5	0.70
22.5° C		69	5	2.3690	2.3134	0.00498	1	19.33	-	1196.8	2.60
19/9	L 4	0	6	2.3582	2.3000	0.00107	4	19.379	0.0013	1186.8	0.56
18° C		50	9	2.3740	2.3153	0.00235	4	19.390	0.0029	1194.1	1.22
	E 1	0	8	2.3617	2.3027	0.00286	3	19.434	0.0021	1184.9	1.47
		69	10	2.3768	2.3181	0.00136	3	19.417	0.0032	1193.8	0.73

The writer is indebted to Prof. R. A. Fisher for the following method of obtaining ρ_Λ from ρ_A and ρ_{Cl}.

$$\text{Let } \Lambda \pm \rho_\Lambda = \frac{A \pm \rho_A}{Cl \pm \rho_{Cl}} = \frac{A(1 \pm \xi_A)}{Cl(1 \pm \xi_{Cl})}$$

Then since, for small variations, the relative variance of the quotient is equal to the sum of the relative variances of the numerator and denominator,

$$\therefore \quad \Lambda \pm \rho_\Lambda = \frac{A}{Cl}\left(1 \pm \sqrt{\xi_A{}^2 + \xi_{Cl}{}^2}\right)$$

$$\therefore \quad \rho_\Lambda = \frac{A}{Cl}\sqrt{\xi_A{}^2 + \xi_{Cl}{}^2}$$

In Table I are first given date, station, depth and the excess base in milliequivalents per litre, A_v, for comparison with earlier work. Then follow excess base in milliequivalents per kilogram, A_w, and chlorinity in grams per kilogram each with their standard error and the number of sub-samples. Finally is given the specific alkalinity, $\Lambda_w \times 10^4$.

Since the mean values and their standard errors are to be used for further statistical calculations, they are given to five significant figures. Although this is not usual in chemical work it is felt that the tests of significance in Table II are thereby rendered more precise.

TABLE II.

Variation of Specific Alkalinity with Depth.

Date 1933.	Station.	Depths compared metres.	Differences in $\Lambda_w \times 10^4$ with standard error.	Difference in Ca. mg./metric ton with standard error.	
18/7	L4	0 & 50	$+6{\cdot}9 \pm 1{\cdot}87$	$+270 \pm 70$	Significant.
	L6	0 & 68	$+8{\cdot}4 \pm 1{\cdot}57$	$+325 \pm 60$	Significant.
		0 & 25	$+4{\cdot}4 \pm 1{\cdot}21$	$+170 \pm 50$	Significant.
		5 & 25	$+3{\cdot}3 \pm 0{\cdot}80$	$+130 \pm 30$	Probably significant.
		25 & 68	$+4{\cdot}0 \pm 1{\cdot}49$	$+155 \pm 60$	Significant.
10/8	E1	0 & 69	$+6{\cdot}3 \pm 2{\cdot}69$	$+245 \pm 105$	Significant.
19/9	L4	0 & 50	$+7{\cdot}3 \pm 1{\cdot}34$	$+280 \pm 50$	Significant.
	E1	0 & 69	$+8{\cdot}9 \pm 1{\cdot}64$	$+345 \pm 65$	Significant.
Mean for all stations and dates.		Surface and bottom.	$+7{\cdot}6$	$+295$	

It will be seen that in all cases the specific alkalinity increases with depth. In Table II will be found the differences in specific alkalinity, $\Lambda_w \times 10^4$, between given pairs of depths. The standard error of the difference is derived from the expression :—

$$\rho_{\Lambda\ \text{diff.}} = \sqrt{\rho_{\Lambda_1}{}^2 + \rho_{\Lambda_2}{}^2}$$

These differences are all positive, that is, the specific alkalinity increased with depth. They are somewhat less than was found in 1931, but owing to the groups of analyses being made each on sub-samples of one sample the standard errors are much less.

There remains little doubt that the variations found in 1931 were real and that small variations in specific alkalinity do occur in the shallow waters of the English Channel.

As a result of Wattenberg's investigations (**5**) on board the *Meteor* in the South Atlantic, it would appear that these variations are in large part due to variations in calcium. According to his data the water in the English Channel is always slightly supersaturated with calcium carbonate (Table III). Since in summer the percentage supersaturation amounts to 30 or 40 per cent, the increase in calcium towards the bottom cannot be attributed to re-solution of bottom deposits; rather must the water be regarded as in unstable equilibrium ready to deposit calcium carbonate on suitable nuclei of calcite (cf. Wattenberg's review of the literature of this subject, **5**).

TABLE III.

PERCENTAGE SATURATION OF CALCIUM AS CARBONATE WITHIN THE RANGE OF pH AND TEMPERATURE FOUND IN THE ENGLISH CHANNEL, (FROM DATA BY WATTENBERG, **5**, TABLE 31).

pH t, °C.	8·0	8·1	8·2	8·3
8°	110	115	121	128
12°	113	119	126	134
16°	117	124	132	140

The lower calcium content of the surface water can be explained by deposition of calcium carbonate in the skeletons of flagellates and calcareous algæ which afterwards die off, falling to the bottom, or are eaten, the calcium going to build up the skeletons of crustaceans and teleosts (see however p. 753).

The presence of calcium and other cations as chlorides in body fluids in concentrations similar to those in sea-water does not affect these calculations. In the main, depletion of calcium in the water may be attributed to its deposition as carbonate or phosphate in the skeletons. Magnesium, in so far as it is concerned in such deposition, is included with calcium for the purposes of this discussion.

The degree of accuracy necessary for the statistical treatment is relative and confined within any one batch of samples analysed at any one time. Analyses made at different times are affected by errors in the standardisation of the baryta by hydrochloric acid, of the hydrochloric acid by sodium carbonate and of any change in the latter standard. These have not been treated statistically. Thus summer determinations of specific alkalinity could not be compared in time with spring determinations even if these existed.

Nevertheless the data of July 18th, 1933, for Station L6 may be used for a very rough calculation of the production of calcareous plankton.

Let us suppose that the bottom layer of water (68 metres) had remained unchanged in its specific alkalinity, Λ_w, since the previous winter. The differences in Λ_w between this layer and the surface, 5-metre, and 25-metre layers are known (Table II), so that with the aid of the procedure outlined in (**1**), p. 723, it is possible to work out the total deficiency in Λ_w for the whole water column of 70 metres depth and one sq. metre cross-section.

$$\delta\Lambda_w \times 10^4 = \delta\frac{A_w}{Cl} \times 10^4 = 212{\cdot}2$$

Regarding Cl as constant and equal to 19·4 g. per kg. or $19{\cdot}4 \times 10^3$ g. per metric ton,

$$\therefore \quad \delta A_w = \frac{19{\cdot}4 \times 10^3}{10^4} \times 212{\cdot}2 \text{ milliequivalents for the whole water column.}$$

For the present purpose the density of the sea-water may be taken as unity, so that $\delta A_w = \delta A_v$;

whence $\delta A_v = 410$ milliequivalents for a column 1 sq. metre in cross-section and 70 metres deep.

If the entire loss of excess base can be attributed to deposition of calcium in plant skeletons, this is equivalent to 8·2 g. Ca beneath each sq. metre or 8·2 metric tons beneath each sq. kilometre. The writer has been unable to find any quantitative data on the amount of calcium in the skeletons of calcareous phytoplankton, but if this is *assumed* to be 10% of the wet weight the production of calcareous algæ works out at 82 metric tons per sq. kilometre of surface. This figure may be compared with the total plankton crops calculated from changes in other constituents in (**2**), p. 744.

Basis.	Minimum production of phytoplankton wet weight, metric tons per sq. km.
CO_2	1,600
O_2	1,000
Phosphate	1,400*
Nitrate	1,500
Silicate	110
Calcium	82

* This figure is corrected from the original (1,200 tons) for the salt error in the determination of phosphate which was ignored.

As was stated in (**2**), p. 744, silica is of no use to animals feeding on diatoms and is probably excreted immediately into the sea-water where it may be quickly redissolved. If the intestinal juices of the zooplankton are alkaline it may even be excreted already in solution. In either case, the silica appears to take part in the life cycle several times in one season.

So far as calcium is concerned, the writer is not clear just how far zooplankton, such as, for example, Limacina and the larvæ of other molluscs, are dependent for calcium on their ingested food or how far they are able to absorb it directly from the sea-water across the body wall, but in either case the net result will be its removal from the water for the life of the animal or until the next moult.

Since a part of the calcium consumption may be attributable to direct assimilation by zooplankton without first passing through the stage of phytoplankton, the above calculation is strictly comparable neither with the silicate nor with the first four of the above nutrient salt data.

The writer is greatly indebted to Prof. R. A. Fisher of the Galton Laboratory, to whom the draft of the paper was submitted, for helpful criticism and advice. The following quotations are taken, with permission, from a letter of his dealing with the validity of the statistical treatment.

" . . . I think that, with the precautions you mention on page 2 (p. 747 of text), as to randomising the flasks in the laboratory, there can be no question of the validity of your conclusion. Reading to three figures, beginning with 5 is equivalent to admitting errors up to ±1 in 1000, or a standard error of observation of about 0·7 in 1200. The fact, however, that you have based each value on not less than four sub-samples reduces this so to speak deliberate error to a half, or in some cases nearly to a quarter of this value. So that there is no theoretical impossibility in your finding, as you have done, differences of 6 or 8 units definitely significant."

Referring to the reporting of data to five significant figures, he says: " Personally I should like to see the five figures retained, as they make the tests of significance definitely more precise, but if it goes against the grain of chemical tradition to publish final figures, which are very unlikely to be exact for the material examined, it might be made clear that such a figure as 1193·3 with a standard error ±0·93 implies that the final figures lie between 1191·4 and 1195·2 with the rather high probability of about 20 to 1, but as among the numbers within this range the value printed, 1193·3, is only the most likely among a number of values of almost equal plausibility. In fact, if you were giving a guarantee, you would probably not take narrower limits than I have stated. But 1193·3 is definitely, though not greatly, more likely than 1193·0, just as at 68 metres 1201·7 is more likely than 1202·0, so that the test of significance appropriate to the comparison of these two most likely values is properly carried out on the difference 8·4, whereas the approximate difference 9·0 would be rather inaccurate for this purpose."

SUMMARY.

In the English Channel in summer a small difference in specific alkalinity between the surface and bottom waters has been established by a statistical method. This is not due to re-solution of bottom deposits of calcium carbonate with which the water is supersaturated. It is attributed to removal of calcium from the surface waters by plankton and an attempt has been made to calculate the production of calcareous plankton.

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The Determination of Phosphorus and Nitrogen in Plankton.

By

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During the course of an investigation on the seasonal changes in phytoplankton (Harvey, 1934), the need arose for analyses of organic phosphorus. The quantities available being very small it was necessary to develop a method of analysis.

Since the plankton consists of many different organisms ranging widely in size and shape and organic content, neither a description of its composition, its volume, nor its wet or dry weight gives a clear indication of its value as food for other animals. It was considered that its phosphorus or nitrogen content, as indicative of protein content, would best serve this purpose and allow comparison to be made between different samples of plankton.

DETERMINATION OF TOTAL PHOSPHORUS IN PLANKTON.

The method of Juday, Birge, Kemmerer, and Robinson for total phosphorus in lake residues as modified by Robinson and Kemmerer (1930) and Titus and Meloche (1931), in which the plankton sample was digested with a mixture of sulphuric, hydrochloric, and nitric acids, was not satisfactory for marine plankton. It proved very difficult to drive off the last of the oxidising agent; which interfered with the subsequent reduction of the phosphomolybdate by stannous chloride. Various modifications of the nitric acid oxidation as well as a number of ignition methods were tried with only partial success. Finally perhydrol (Merck's 30% hydrogen peroxide) in presence of sulphuric acid was found to be the most suitable oxidising agent. For the determination of total phosphorus in sea-water Kreps and Osadchih (1933) used 3% hydrogen peroxide in order to oxidise and hydrolyse the organic matter, and Kalle (1933) for the same purpose used potassium persulphate whose action is essentially the same. Perhydrol has obvious advantages over weaker solutions of hydrogen peroxide. But, when the product of digestion was diluted to 100 ml. and treated with the usual molybdimetric reagents, the colour developed was invariably off shade. Furthermore, halogens set free by the oxidation of sea salts were only driven off completely when attention had been given to the design of an air bath which would enable the fumes to escape from the flask without collecting on its upper walls and running back. The following procedure has proved highly satisfactory.

Method. A suitable volume of the plankton concentrated in a small volume of sea-water, as obtained in the bucket of a tow-net, was filtered through a small disc of bolting silk (200 mesh to the linear inch ; Harvey, this Journal, pp. 770). The first 20–25 ml. of filtrate was again passed through the filter, since it was found to contain some of the smaller plankton organisms. The final filtrate, which was usually clear to the eye, was transferred to a small wash-bottle and used for washing down the sides of the funnel. The filter disc was removed from the funnel and the plankton washed into a 50 ml. Erlenmeyer flask with a jet of distilled water amounting to about 5–10 ml. in all. Concentrated sulphuric acid (0·2 ml.) was added and the liquid was evaporated without boiling during the course of one hour in a covered air bath at 115–120°, and subsequently slowly raised to 160°.

The carbonaceous residue in the flask at 150–160° was treated with Merck's perhydrol, drop by drop. By twirling the flask the perhydrol can be readily spread over the bottom of the flask before decomposing and three to five drops usually sufficed to oxidise the carbonaceous matter. It was found better to re-heat between successive additions of perhydrol. Occasionally the residue remained brown and in such a case it was taken up with 5 ml. of water, re-evaporated, and again treated with perhydrol. Five drops of perhydrol contained only $0{\cdot}1\gamma$ P_2O_5 which could be safely ignored.* Finally the flask was heated for twenty minutes at 180°. After cooling, about 8 ml. of distilled water was added and the solution allowed to simmer gently while the volume fell to about 4 ml. This treatment should have destroyed any persulphate which had survived heating at 180°. It is doubtful if it was of any value, as is sometimes claimed, in hydrolysing to orthophosphate any pyrophosphate which might have been formed [cf. Berthelot and André (1896)]. The good agreement between duplicate determinations and the recovery from trial runs with known amounts of phosphate showed that pyrophosphate was not formed. This agrees with the findings of Titus and Meloche (1931).

In order to remove silica, the acid solution was transferred to a calibrated 10 ml. pointed centrifuge tube and the Erlenmeyer flask washed out with 2–3 ml. of water in all. The acid solutions and washings were thoroughly mixed by a glass rod, their volume noted and centrifuged. Then 5 ml. of the supernatant liquor was pipetted off and made up to 100 ml. Aliquot parts of this were again diluted to 100 ml. and then compared in Hehner cylinders in duplicate with a standard containing, say, 12·5 γ P_2O_5 per 100 ml.* (=125 mg. P_2O_5 per cubic metre).

By this double dilution four advantages were gained : (*a*) the foreign matter which earlier upset the colour match was rendered innocuous, (*b*) when adding the acid molybdate reagent it was unnecessary to allow for the small excess of acid already present, (*c*) the salt error was made negligible, (*d*) two or more determinations could be made on the same digest. A set of analyses on three sub-samples of one sample of plankton is shown in Table I.

TABLE I.

ANALYSES IN TRIPLICATE ON MIXED PLANKTON FILTERED FROM 388 LITRES OF WATER AT STATION L4, BETWEEN THE SURFACE AND 45 METRES ON 12TH FEBRUARY, 1934.

Analysed on 13th and 14th February. Sub-samples each compared colorimetrically in duplicate.

Sub sample.	Phosphorus in Plankton expressed as γ P_2O_5 per cubic metre of sea-water, i.e. as parts per million million.
A	241 230
B	246 249
C	244 245
Mean	242

The reducing agent consisted of a solution of about 0·1 g. of stannous chloride (clear crystals) in 10 ml. of concentrated hydrochloric acid. Two drops of this solution were added to the standard or sample under comparison, which was well shaken before and after adding quickly 2·0 ml. of the usual 2·5% solution of ammonium molybdate in 37·5% (by volume) sulphuric acid. This reversal of the usual order of addition of the two reagents has been found to give more consistent results.

Only one opportunity has presented itself of applying the method, as finally developed, to a catch consisting almost only of plants. The result is shown in Table II, together with a further analysis of a clean sample judged to consist of 70% to 80% plants and 30% to 20% animals. After making allowance for this, the quantity of organic phosphorus

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* $1\gamma = 0·001$ mg. ; thus 1γ per litre = 1 mg. per cubic metre.

works out in both cases at about 0·3 mg. P_2O_5 per 1000 " units of plant pigments " (p. 771). This approximate ratio has already found application (p. 782), and its magnitude has been confirmed by a number of other analyses which have been made in connexion with a research now in progress.

TABLE II.

ANALYSES OF PLANKTON FROM WHICH THE LARGER ORGANISMS HAD BEEN REMOVED.

Date.	Description.	Phosphorus expressed as mg. P_2O_5 per litre of catch.	mg. P_2O_5 per 1000 " units of plant pigments " (p. 771) present.
1/1/34	Almost wholly diatoms	0·089	0·31
7/2/34	70% to 80% diatoms	1·47	0·27 to 0·31*

DETERMINATION OF TOTAL NITROGEN IN PLANKTON.

The standard micro-Kjeldahl method of Parnas and Wagner, as described by Pregl (1930), has proved excellent. When using 5 ml. of N/100 hydrochloric acid to absorb the ammonia liberated, the amount of nitrogen in the sample needs to be between 0·15 and 0·6 mg. Thus about two to three times as much plankton is required as for the phosphorus determination. The plankton sample was washed straight off the silk disc into a micro-Kjeldahl digestion flask and 0·2 ml. of concentrated sulphuric acid added to avoid loss of nitrogen bases during the evaporation of the water. Most of this was removed by boiling off on the Kjeldahl heating stand and the evaporation completed in an air bath or oven at 120°. The digestion with sulphuric acid (1 ml.), mixed potassium and copper sulphates and perhydrol, and the distillation and collection of the ammonia in N/100 hydrochloric acid were carried out exactly as described by Pregl. Duplicate runs on a sample of tow-net plankton gave 1·47 and 1·52 mg. nitrogen per litre of sample, being 2·75 times the quantity of P_2O_5. This ratio is of interest because previous work at Plymouth has shown that the vegetation utilises two and a half times more nitrate-nitrogen than P_2O_5.

In subsequent work time was saved by adding immediately all the sulphuric acid (1 ml.) and the mixed sulphates to the plankton and wash water in the Kjeldahl flask. Evaporation of the water without bumping was assisted by adding occasionally a drop of perhydrol.

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* After deducting 30% to 20% for phosphorus present in animals.

SUMMARY.

Phosphorus in plankton has been determined by digestion with sulphuric acid and perhydrol followed by colorimetric determination.

Nitrogen has been readily determined by the micro-Kjeldahl method of Parnas and Wagner.

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Measurement of Phytoplankton Population.

By

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With 9 Figures in the Text.

It is known that the unicellular plants in the sea are not evenly distributed; not only do quantity and species change on proceeding away from the shore, but more or less extensive fields of some one species or community may be met with in the open seas.

The only strictly quantitative method of sampling the population is to centrifuge a small sample of water and count the plants in it. The amount of sea-water sampled is small, the time consumed in making the count is great, and the resulting list of species and their numbers per litre of water is difficult to interpret in terms of the crop. The species are so different in size and shape and quantity of contained organic matter, that a comparison of such lists of species does not give a clear picture of the relative proportion of vegetable organic matter in the waters. In considering the productivity of the sea, it is the quantity of vegetable food available for the animals rather than the number and kind of individual plants which is of primary interest.

It was the aim of this investigation to devise a rapid method of obtaining a measure of the quantity of vegetable matter in the water so that a number of estimations could be carried out over an area in a limited time. It seemed impracticable to separate the vegetable from the animal plankton, which ruled out any estimation of organic matter. The quantity of green vegetable pigments on the other hand is easy to estimate quickly, and gives a measure of the organic vegetable matter in mixed plankton. It is not supposed that the ratio of pigments to organic matter is constant either for any one species or for different species, but this ratio is probably a great deal more constant than the quantity of organic matter to size of cell and so gives as good a measure of the crop as counting and judging the amount of cell contents under a microscope. Pigment content as a measure of quantities of diatoms was first used by Kreps (1930).

Since it was impracticable to centrifuge sufficiently large samples of water, particularly during the barren months, the finest obtainable bolting silk—200 meshes to the linear inch—was used. This does let through the smallest phytoplankton organisms. Although these may at times be numerous, it is assumed that they do not make up any material proportion of the *volume* of the catch, except in low latitudes and possibly during the height of the summer when the quantity of diatoms is very small. It is also likely that a moiety of any *Skeltonema costatum* would be lost, as would some other small diatoms.

A water meter was constructed and attached as shown in Figure 1 to a net of bolting silk. The gear is drawn through the sea either up and down vertically, obliquely, or hauled horizontally. The water meter measures the volume of sea-water which passes into the net and is filtered through it. The use of a water meter in the mouth of a tow-net had been suggested by Nansen (1915) and a net with meter to measure the water which had actually passed through it was constructed by Dr. E. J. Allen and exhibited at a meeting of the Challenger Society. However, I can find no record of a measuring net having been used to any extent.

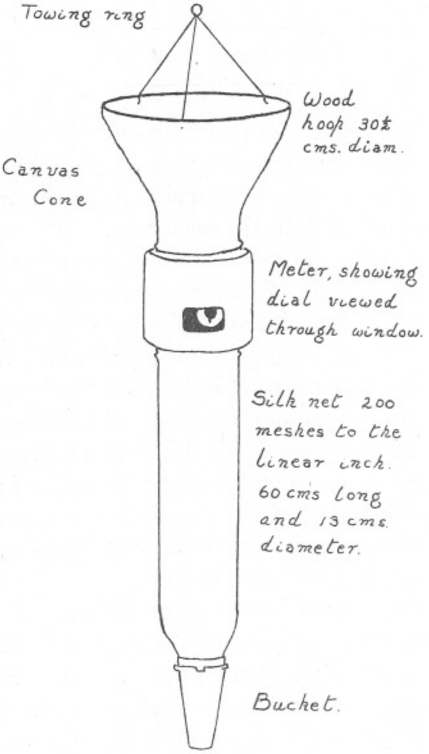

FIG. 1.—Diagram of the measuring net.

The catch is washed into the bucket, its volume measured if it is desired to keep a small aliquot portion for examination and counting, and the rest filtered through a disc of bolting silk about 3½ cm. in diameter. This disc is put into a tube with a few c.c. of 80% acetone which dissolves the yellow-green pigments from the phytoplankton. The quantity of pigment is then estimated by comparing this known volume of acetone solution with colour standards.

The Meter.

The meter is shown in Figures 2 and 3. The rotor consists of a brass spindle revolving freely on agate cups and points. On this a small brass boss 6·5 mm. in diameter is mounted, into which are screwed and soldered six short arms of hard brass wire, 1·7 mm. diameter, to which are soldered vanes of brass foil 0·25 mm. thick, the soldered joint being kept coated with cellulose enamel. A worm gear is cut in the after end of the spindle. It is essential that the rotor be carefully balanced, and this was done by filing from some vanes, adding very small amounts of solder to others, until it revolved quite regularly when drawn very slowly through water and did not tend to stop in any one position.

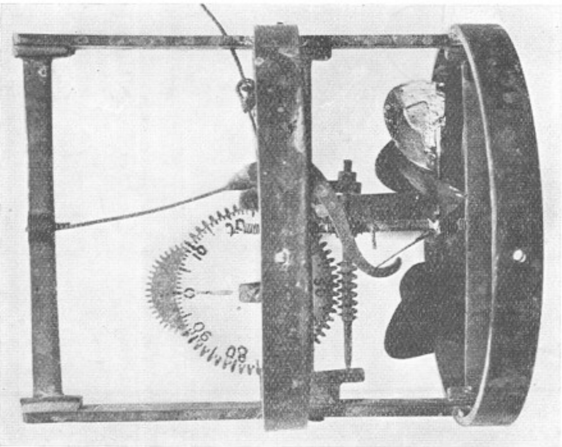

Fig. 2.—Photograph of meter removed from outer casing. The spring arm and cord which stops the rotor revolving is shown.

The shaft carries a pinion wheel having ten teeth which engage with the worm gear on the spindle of the rotor. On the other end of the shaft a second worm gear is cut, and engages with the 60-toothed dial wheel, which is enamelled white on one face with 100 divisions marked in black, every tenth division being numbered. Mounted behind the dial wheel and engaging with a pinion wheel attached to it, a second toothed wheel makes one revolution for every four revolutions of the dial. Quantities up to $4\frac{1}{2}$ cubic metres of water can in this way be recorded.

Calibration of the meter.

The meter in its case was mounted on a partition in a trough through which water was passed in a steady stream (Fig. 4). In order to eliminate air bubbles and reduce swirls the water was led into a preliminary compartment as shown in the figure. After trials in this laboratory, the meter described was calibrated at the National Physical Laboratory, where a larger flow of water and means of accurate measurement were obtainable. The results of this calibration are shown in the following table :—

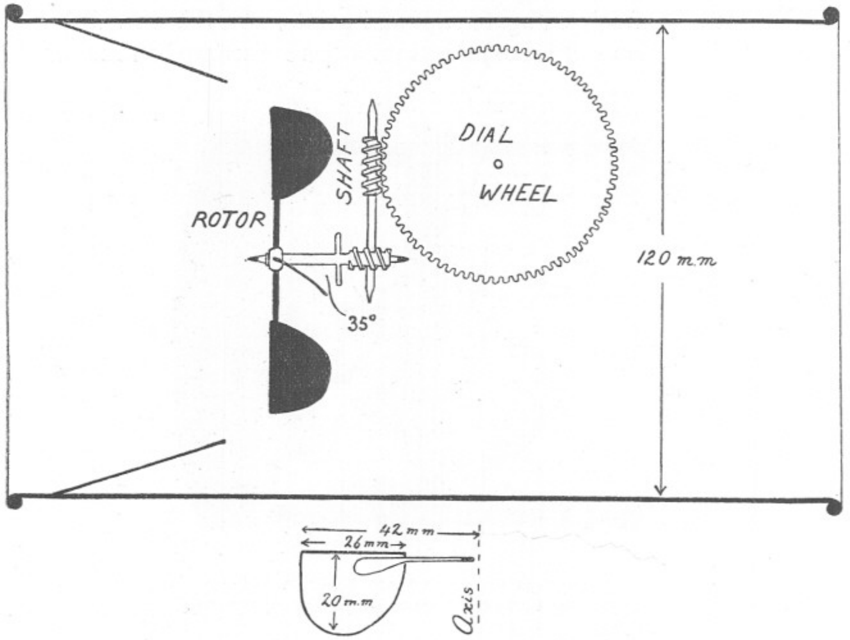

FIG. 3.—Sectional diagram showing meter in outer brass case, and details of vane.

Rate of passage of water through the meter.	Litres of water passed for every unit division on the dial wheel.
47 litres per minute	12·20
79 ,, ,, ,,	11·60
148 ,, ,, ,,	11·40
550 ,, ,, ,,	12.20

For practical purposes it is taken that the passage of 12 litres of water registers one division on the dial, provided the rate of flow lies between 47 and 550 litres per minute. If the net were very heavily clogged, the passage of too little water would be recorded during the latter part of the haul; thus an extraordinarily rich plankton might appear somewhat richer than it really was. Such conditions have not yet been met with.

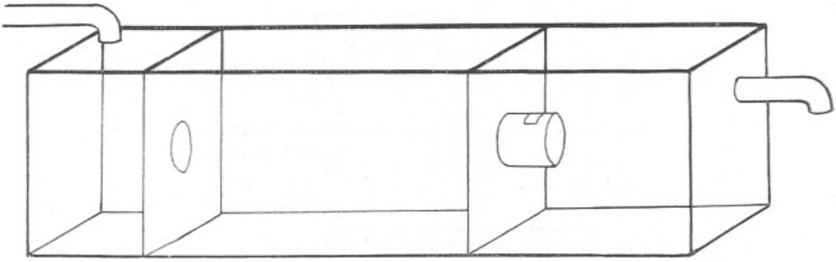

FIG. 4.—Diagram of tank used for calibrating the meter which is shown mounted on the right-hand partition.

As ordinarily fished while making vertical hauls some 120 to 200 litres of water per minute pass through the net.

When the measuring net is drawn out of the sea, and when being lowered on a windy day, the rotor will spin. This necessitates the provision of a stop or brake, which is released when the net is in the water and engaged again before it is drawn out of the water. The photograph shows the spring arm used for this purpose. On pulling the light cord attached to it, it engages with a brass pin mounted on the spindle of the rotor, and on being released it flies back, allowing the rotor to turn.

THE MEASURING NET AND GEAR.

The general arrangement as used when fishing from a boat is shown in Figure 1. The ring on the three wires holding the hoop is attached to a line about 2 metres above a lead. In order that the net may fish equally well when being lowered, hauled up or towed the brass case is surrounded by a wooden jacket so that the meter has but little positive or negative buoyancy when immersed in water.

In order that diatoms caught up at the joint between the silk net and bucket may be washed out into the bucket, the following construction is employed.

The bottom of the silk net ($7\frac{1}{2}$ cm. diameter) is slipped over a brass carrier (Fig. 5) and held by a thin rubber band. A brass band is placed over this as shown in the sketch and screwed up tight. A rubber washer and brass foil washer are attached to the carrier. The brass bucket is pushed against this and by means of a twist held firmly by the four cams. The brass bucket and carrier do not exceed 400 gm. in weight.

From a boat, where one can reach over and release the brake or stop when the meter is in the water and engage it again before drawing the net out of the sea, this arrangement is simple to work. A haul to 40 metres depth may be completed and the contents of the bucket emptied into a jar or a filter in about 4 minutes. However, from a ship, except in very calm weather, the net may twist round the wire or may go down with air entrapped in it. In the earlier work the brake or stop was actuated by means of a "Bowden wire," but a more satisfactory arrangement was finally devised, which not only enables the net to be used in moderate weather provided the ship is not rolling unduly and putting too great a strain on the gear, but also allows vertical hauls to be made between any two desired depths, or horizontal hauls at any desired depth.

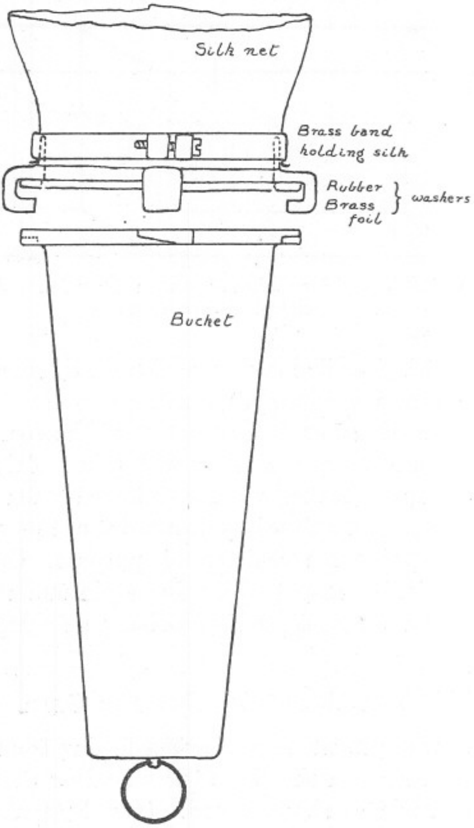

Fig. 5.—Drawing of bucket and attachment to the silk net.

THE THROTTLING GEAR.

The measuring net is lowered with the canvas mouth throttled and a strain on the line actuating the brake or stop. The net is held as shown in Figure 6, A, by means of a wooden frame attached to the meter.

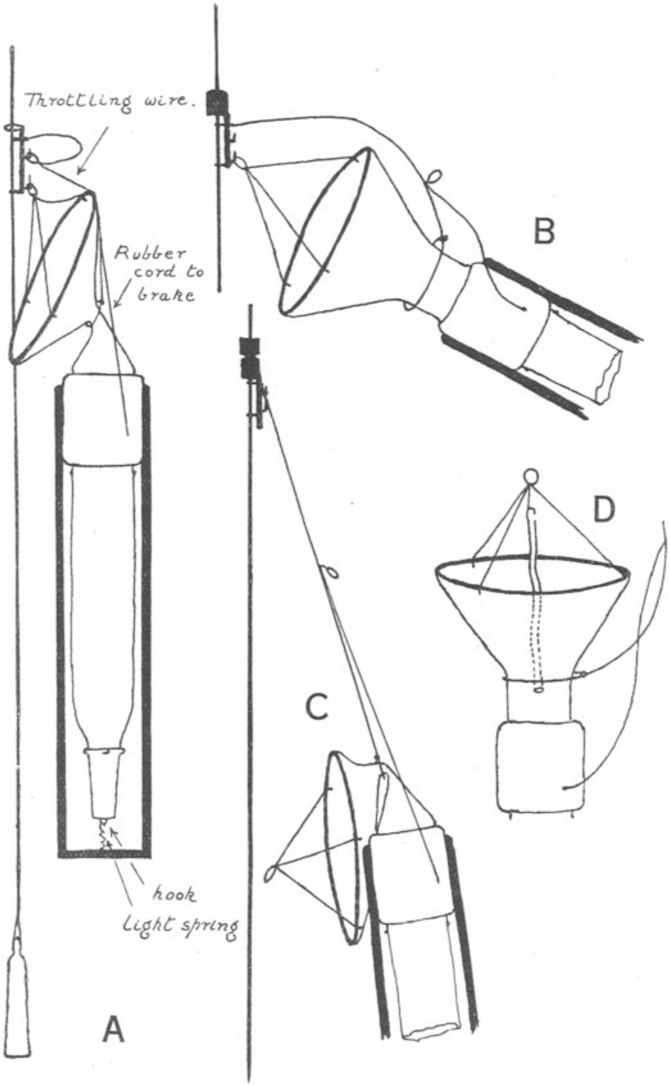

FIG. 6.—Diagram of throttling gear. A, shows net being lowered from ship. B, shows the net fishing after impact of first messenger. C, shows net throttled after impact of second messenger and ready to haul on board.

When the gear has been lowered to the desired depth, a messenger is sent down the wire. This actuates the first release, lets go the throttling line and slacks off the rubber cord attached to the brake. The net then fishes (Fig. 6, B). When it is desired to throttle and haul the net, a second messenger is sent down the line. This releases the ring attached to the wires holding the hoop of the canvas cone, throttles the net and again puts a strain on the brake (Fig. 6, C). The throttling wire is made of extra flexible steel wire 3½ mm. diameter, the rubber cord of "lingerie elastic," the wooden frame of oak 2·5 × 1·4 cm. section, the canvas cone of light duck with a wooden hoop 1·5 × 1·2 cm. section. In order to hasten the escape of air as the apparatus is being lowered into the sea, a short piece of flexible metallic tubing 1 cm. diameter is attached inside the cone, as shown in Figure 6, D.

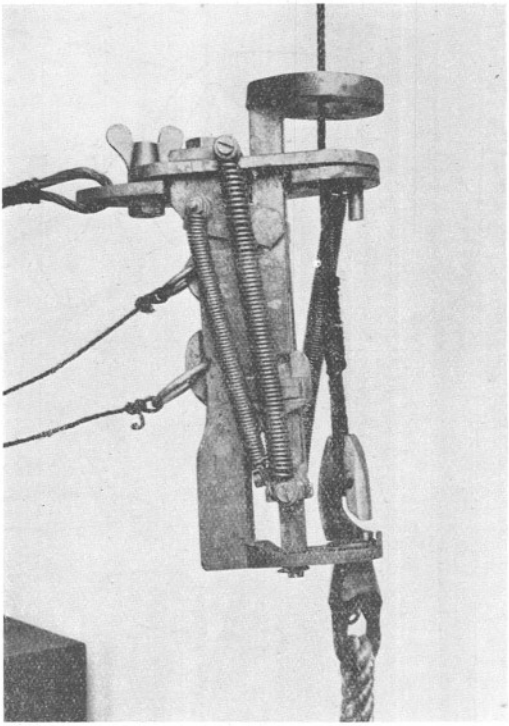

FIG. 7.

The double release is shown in the photograph (Fig. 7) and the principle on which it works in Figure 8. The impact of the first messenger knocks the slide down until it is stopped by the trigger hitting the body of the mechanism (B). A steel ring to which the throttling wire is attached is left free to fall out. Two brass springs, one on each side of the slide, cause it to rise to the upper limit of its travel (C) when the trigger, freed from its guide, is pulled out by a third spring. The impact of a second messenger knocks the slide down to the lower limit of its travel, allowing the second steel ring, to which the canvas cone is attached, to fall out. An attachment to the trigger does not allow the first release ring to be

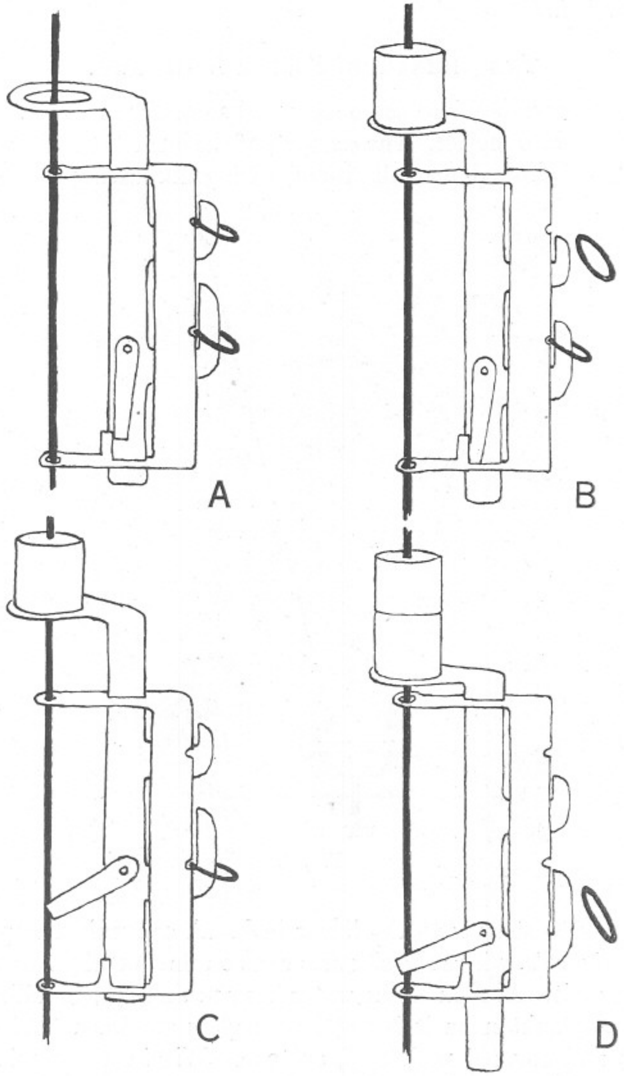

Fig. 8.

put in position unless the trigger is in the up and down position, engaged against its guide. The mechanism is attached to the wire hauling line, and is free to swivel round it. A lead of about 14 lb. is made fast to about 2 metres of light rope, the other end of which is spliced to the swivel on the mechanism.

THE FILTER AND COLOUR STANDARDS.

The catch is washed into the bucket and somewhat reduced in volume by shaking up into the net. The contents of the bucket, or a proportionate part, is passed through a small disc of bolting silk having the same mesh as the net—200 strands to the linear inch. A convenient apparatus is shown in Figure 9, where the silk disc rests on fine metal gauze to reduce any strain on it. As soon as the water has run through, the silk with the wad of wet plankton on it is put into a glass specimen tube (17 mm. diameter) and covered with 80% acetone. Within a few minutes the yellow-green pigment of the plants dissolves, although it is reasonable to allow several hours for complete solution, and necessary in the case of Thalassiosira. If necessary more acetone is then added to reduce the colour to a pale green of such a depth that slight differences in intensity are most readily seen.

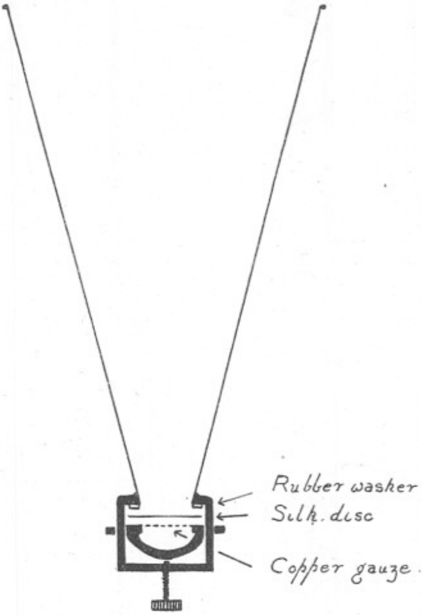

FIG. 9.

It is obvious that the colour comparison may be made in a variety of ways. The use of a spectrophotometer with monochromatic light of wave length within a chlorophyll absorption band would doubtless give the most accurate index. Actually the following very simple technique was employed and found satisfactory unless there were many pigmented copepods and larvæ in the catch, and the diatoms were not abundant. Under these circumstances the values obtained were probably too high.

A green solution was prepared, being an almost exact visual colour match with an acetone extract of diatoms. At first a mixture of chromate and chromium salt was used, later a mixture of potassium chromate and nickel sulphate was found more suitable. A solution in distilled water, made faintly acid, containing 25×10^{-6} gm. potassium chromate and 430×10^{-6} gm. nickel sulphate—$NiSO_4, 6H_2O$—was taken as containing one arbitrary " unit of colour or pigment." A series of specimen tubes, all 17 mm. diameter and stoppered with waxed corks, were filled with concentrations of this mixture containing respectively 2, 4, 5, 6, 8, 9, 10, 12, 14, 16, and 19 " units of pigment per c.c." If the acetone extract of the catch was more coloured than the tube containing 14 " units of pigment " per c.c., it was further diluted to fall within the range of 8–12, the volume of extract measured and the colour comparison made. The method of calculating and expressing the results is shown in the following example : 550 litres of water had been filtered through the net, the dial of the meter having travelled through 46 divisions. The acetone extract measured 9·3 c.c. and matched the standard tube containing 8 units of pigment per c.c. Hence the acetone extract from the phytoplankton in one cubic metre of water would contain $\frac{1000}{550} \times 8 \times 9{\cdot}3$ " units of pigment." The results are thus expressed in units of plant pigments per cubic metre of sea-water.

During the first year's working with this measuring net, and the earlier models which led up to it, it was noticed that materially more water passed through the net when it was dry to start with than when it had been in use and wet for an hour or more. Further, a slight drift of the ship while a vertical haul was being made caused an unexpectedly larger quantity of water to pass through the net. These observations suggest that vertical hauls without the use of a meter do not necessarily give comparable results.

IRREGULAR DISTRIBUTION OF PHYTOPLANKTON ORGANISMS.

A series of vertical hauls to the same depth at or near the same position, that is to say through materially the same body of water, show that the diatoms are not distributed evenly. The following values were obtained near the same position, 5 miles south-west of Plymouth Breakwater.

	Hauls to 20 metres depth.	Hauls to 40 metres depth.	Hauls to 50 metres depth.	
Units of pigment per cubic metre	3800		4800	May 22, 1933.
	2600		4730	
	2850		5180	
	3500		4400	
	3080		5500	
	2280		3500	
	2380		3730	
	2530	Max. deviation 21% from mean.		
Max. deviation 32% from mean				
	less than 50	6400		June 28.
	,, ,, 200	4100		
	300	1280		July 17.
	395	1250		
	1000	940		Oct. 25.
	1310	1260		
		1230		
		1130		
		1380		
	3200			Nov. 23.
	4100			
	3100			
	3850			
	3500			
	2900			
	3540			
	2400			
	3300			
	3100			
	2500			
	3000			
Mean	3200	Max. deviation 25% from mean.		

Although these differences are considerable, particularly during the summer, even if a solitary observation should differ grossly from the mean, it does not obliterate the general picture of crop distribution which is given by this method, the differences in crop from place to place and from time to time being so great.

CORRELATION OF THE "UNIT" OF PLANT PIGMENTS.

During May catches of *Rhizosolenia alata* were obtained, almost free from other diatoms. Counts were made of the number of this diatom per c.c. of catch, and a measured volume filtered and extracted with acetone. A similar assay was made with a culture of *Biddulphia regia*,* in a healthy condition growing in Allen–Miquel enriched sea-water. These showed that one "unit of pigment" was dissolved from

$\left\{\begin{matrix}6950\\7300\end{matrix}\right.$ individual cells of *Rhizosolenia alata*, a small form.

224 ,, ,, *Biddulphia regia.*

SUMMARY.

A meter is described which measures the volume of water which has passed through a silk net which may be either towed or lowered and raised vertically.

A double release gear and throttling arrangement allows the net to be opened and, later, closed at any desired depths.

The catch of phytoplankton, from a volume of water which has been measured by the meter, may be assessed from its content of yellow-green pigments, which readily dissolve in acetone.

A rapid method of measuring the pigment content of the catch in terms of arbitrary units of plant pigment is described. The arbitrary unit is related to numbers of two species of diatoms.

The irregular distribution of phytoplankton in the sea is considered in connexion with representative sampling with this measuring net.

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* For this I am indebted to Miss P. Jenkin.

Annual Variation of Planktonic Vegetation, 1933.

By

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Hydrographer at the Plymouth Laboratory.

With 5 Figures in the Text.

SINCE February, 1933, quantitative hauls have been made at frequent intervals with the measuring net previously described in this Journal, Vol. XIX, pp. 761–773, at the entrance to Plymouth Sound and seaward thereof. The more usual positions are shown in the sketch chart, Figure 1. On passing out of Plymouth Sound the salinity of the water increases more or less rapidly, according to the state of the tide and flow from the rivers, until near the position L_3, after which the increase is gradual. In winter or after heavy weather the water becomes noticeably more transparent in the neighbourhood of L_3.

Although the water at L_4, three miles beyond L_3, is not beyond the immediate influence of the land, it would seem that more or less open sea conditions are reached there. Observations made up to 15 miles farther seaward in March, April, and May showed that the phytoplankton did not remain the same either in composition or abundance, but suggested that observations at L_4 gave a measure of conditions farther to seaward. For this reason, and because it is accessible by motor boat during fine weather, most of the observations of this preliminary first year's survey were made at L_4 and the inshore positions.

In most cases the net was lowered twice to 20 metres depth or once to 40 metres, during which operation it filtered between 200 and 350 litres of water, according to the drift of the ship and the length of time the net had been in use. A small portion of the catch was usually reserved to examine the nature of the plankton, and to note the dominant species of plants. The remainder was used to estimate " units of plant pigment " per cubic metre of water filtered (p. 771). The vertical sections, Figures 2, 3, and 4, show the changing density of population on passing away from the shore and the rapid changes which take place in quite short intervals of time, which are also shown in Figure 5. The values shown in Figures 2, 3, 4 are in many cases the average of a number of observations.

Many of the lesser changes which take place are doubtless due to the mass of water which occupied the area having moved away to be replaced by other water, bringing its own flora with it. The incoming water is usually of similar salinity and has previously occupied similar areas. Any big change in the flora brought in with a new water mass would indicate that the new water came from an area having different conditions for plant growth, and it is therefore probable that such a change would be accompanied by a considerable change in salinity. Provided no marked salinity changes take place it seems justifiable to consider the area as a closed one for the purpose of describing the seasonal changes in plant life within it, although we know that water may be frequently replaced by water of similar history, but the possibility has to be borne in mind that a

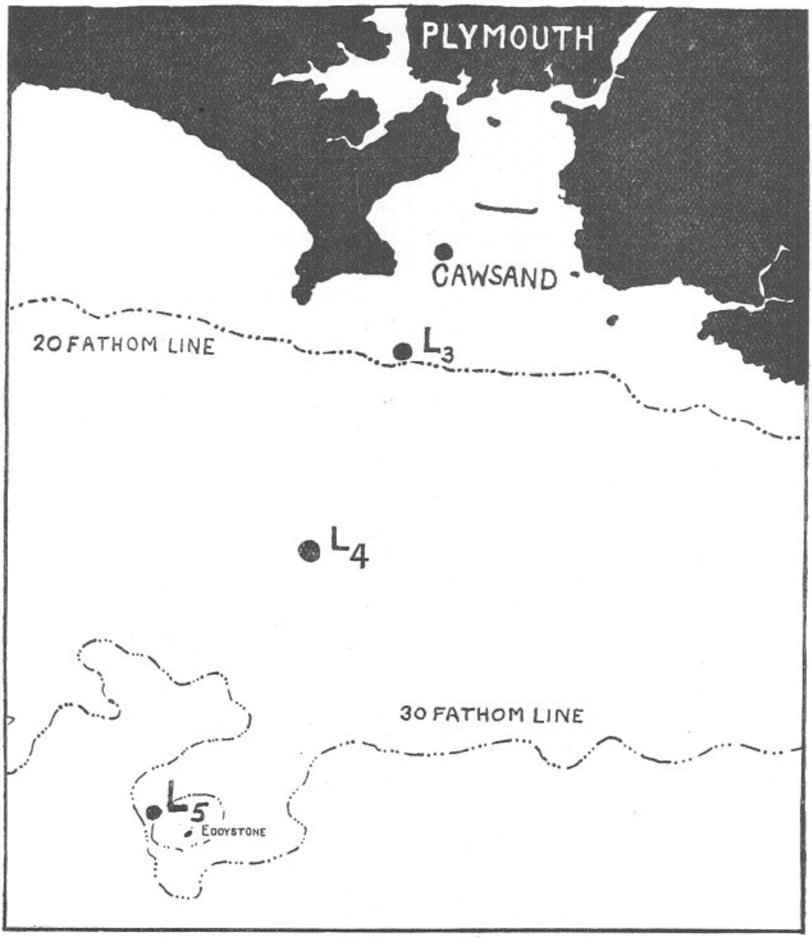

Fig. 1.

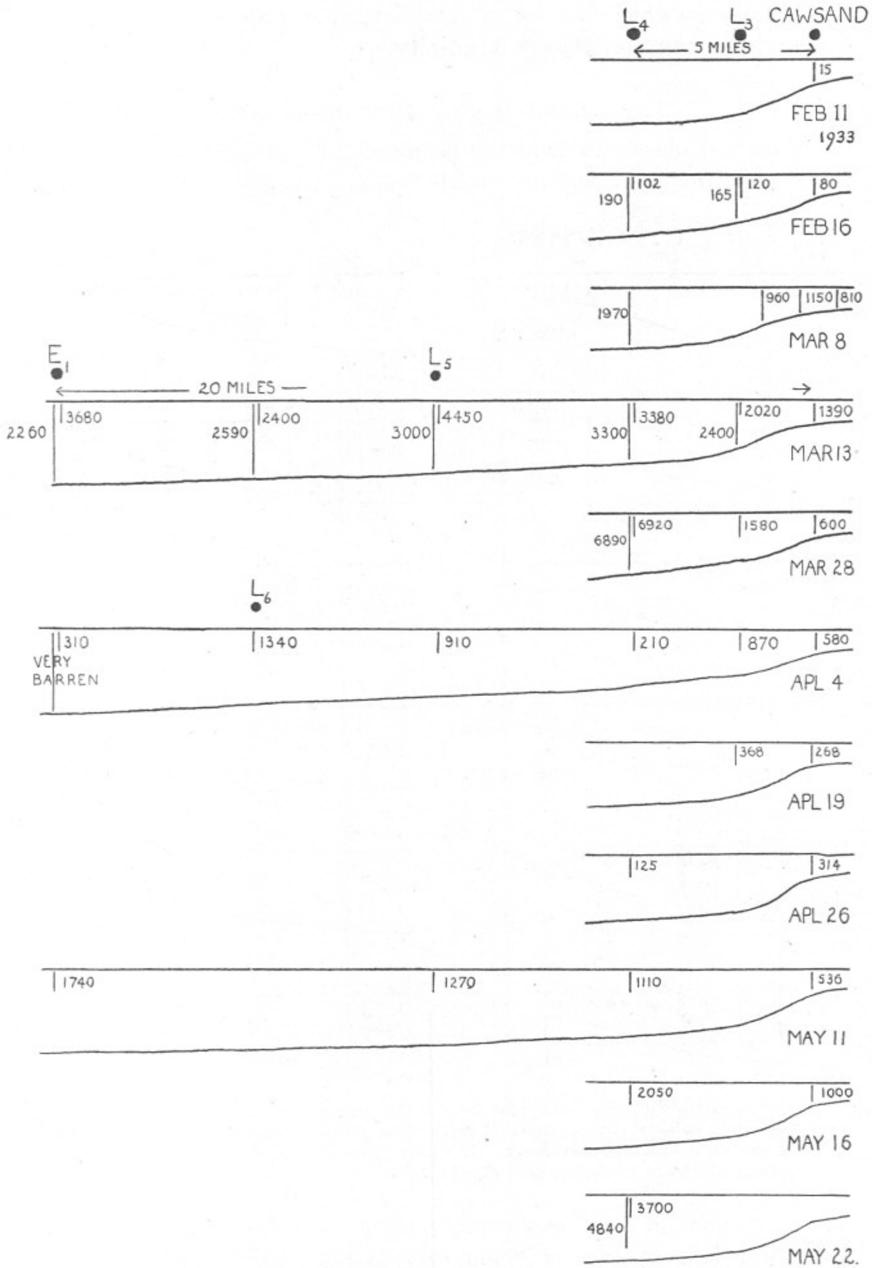

Fig. 2.—Sections showing the plant pigments in the catches, expressed as units of plant pigments per cubic metre of water filtered. The vertical lines indicate the depth to which the vertical hauls were made. In many cases the values shown are the mean value obtained from a number of vertical hauls.

mass of water which has had a very different history may move in, unheralded by any big change in salinity.

The Spring Diatom Outburst, 1933.

The earliest observations at the beginning of February showed a very barren condition close inshore; on February 11th in Cawsand Bay only

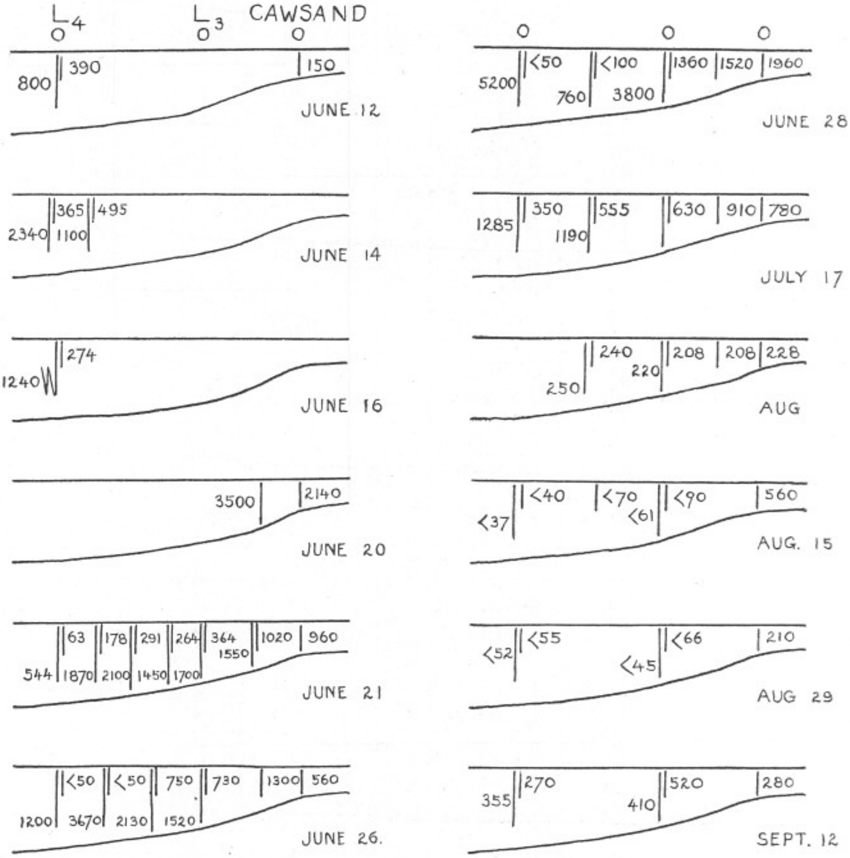

Fig. 3.—Sections showing the plant pigments in the catches, expressed as units of plant pigments per cubic metre of water filtered. The vertical lines indicate the depth to which the vertical hauls were made. In many cases the values shown are the mean value obtained from a number of vertical hauls.

about 15 'units of plant pigments' per m.^{3} were found. After five days with a daily average of 5 hours of sunshine, on February 16th, a series of horizontal and oblique hauls were made farther to seaward, the results of which are expressed in Figure 2.

On March 8th, after 20 lengthening days with an average of 3·8 hours of sunshine daily, a series of vertical hauls showed a tenfold increase since February 16th.

The observations on March 13th after a further five days of sunny weather showed further increase, and a similar density of population

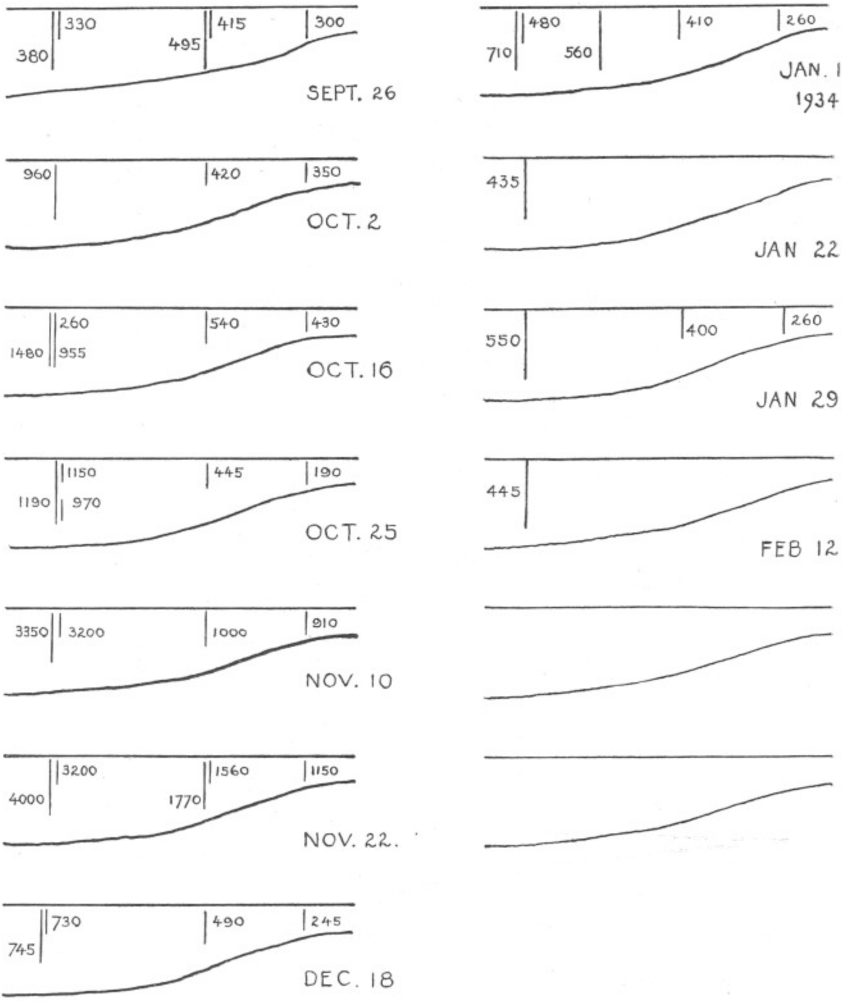

Fig. 4.—Sections showing the plant pigments in the catches, expressed as units of plant pigments per cubic metre of water filtered. The vertical lines indicate the depth to which the vertical hauls were made. In many cases the values shown are the mean value obtained from a number of vertical hauls.

extending 15 miles to seaward beyond the position L_4. The flora was very mixed, many species of diatoms being present. Counts were made, but they only serve to give a general idea of the composition of the catch

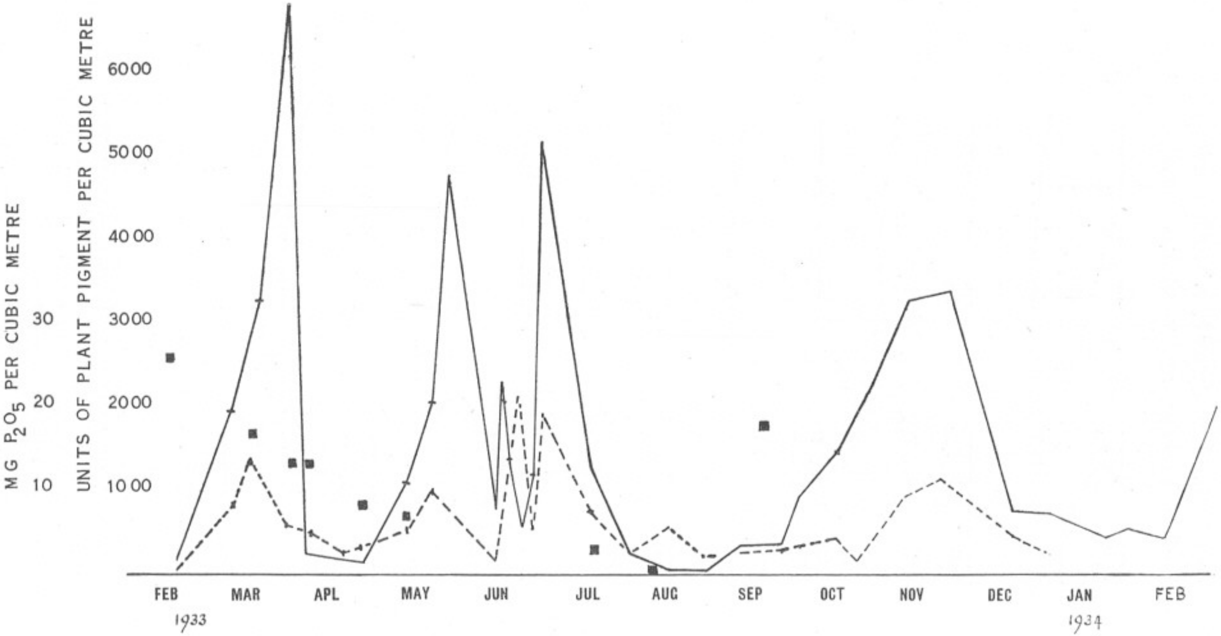

FIG. 5.—Diagram showing the mean content of plant pigments in the column of water at Station L_4 (plain line) and at the inshore station (pecked line). The black squares show the phosphate content of the column of water between surface and bottom at Station L_4.

because too few cells were counted. In fact, it was later concluded that such counts were likely to be misleading unless the diatoms in many fields under the microscope were counted and numbered in all 500 or more. This was not done except on a few occasions where it was desired to link up the pigment content with the number of individual cells. The following table only provides a general indication of the composition of the catches.

TABLE I.

NUMBER OF INDIVIDUAL CELLS PER LITRE, MARCH 13TH, 1933.

	In vertical haul to 60-m. depth at E_1.	In vertical haul to 45-m. depth at L_4.	In vertical haul off Cawsand.
Biddulphia sinensis	110	450	150
Coscinodiscus excentricus	80	200	90
Ditylium brightwelli	90	410	90
Guinardia flaccida	400	—	30
Rhizosolenia stolterfothii	470	—	—
,, færœnse	—	780	—
,, sp.	—	80	—
Thalassiosira gravida	760	240	150
,, nordenskioldii	110	—	—
Thalassiothrix nitzschioides	360	620	—
Lauderia borealis	250	—	90
Chætoceros densus	40	—	30
,, decipiens	510	—	—
Ceratium fusus	10	—	—
Skeletonema costatum	580	—	150
Navicula sp.	—	—	30

After a further period of 15 days, having a daily average of 6·8 hours' sunshine, a series of observations were made on March 28th, when the maximum spring population was found. The composition of the flora had remained much the same except that Guinardia was present in some quantity at L_4.

Throughout this period of increasing diatom population between winter and spring, planktonic animals were not noticeably numerous, quite half the catch in the fine nets appeared to consist of diatoms.

Nevertheless, this maximum population only represents those diatoms which had not been eaten or died during the previous six weeks. Some 7000 units of plant pigment per cubic metre of water does not represent the six weeks' production of vegetable matter, for there is evidence that considerably more had been produced. I am indebted to Dr. L. H. N. Cooper for analyses showing the phosphate content of the water in the area. At L_4 the dissolved phosphate in the column of water from surface to bottom had fallen from 26 to $13\frac{1}{2}$ mg. P_2O_5 per $m.^3$ during this period of six weeks (Feb. 16th–March 28th), indicating that $12\frac{1}{2}$ mg. P_2O_5 had been utilised in the production of diatoms—on the assumption that the water-mass had not changed. Since the sea at the beginning of the period contained an equal quantity of phosphate farther out to sea, and at the end of March rather more than at L_4, and since the water in Plymouth Sound contains more phosphate than at L_4, the likelihood is that any movement of water to the L_4 position brought a little phosphate with it. Hence the value 12½ mg. utilised is if anything on the low side.

These values are expressed in the customary manner, no correction being made for salt error. If this be taken into account, the value 12½ becomes 15½ mg. P_2O_5 per m.^{3}.

I am indebted also to Dr. Cooper for analyses of the total phosphorus contained in a catch of diatoms. These consisted for the most part of *Biddulphia sinensis* and *Thalassiosira sp.* and were nearly free from zooplankton. A description of the method of analysis which was finally employed is published in this Journal, Vol. XIX, pp. 755–759. The pigment content of a part of the catch was estimated directly they were caught, and the remainder divided into three parts to allow analysis in triplicate.

The result showed that a quantity of diatoms containing 1000 units of plant pigment contained phosphorus amounting to 0·31 mg. when expressed as P_2O_5.

Several other catches, consisting mainly of diatoms, were analysed. They were not as free from animals and detritus as in this case, but after making allowance for this, they confirmed the value arrived at as representative for the mixed diatoms which flourish in winter. The assumption is made, pending further investigations, that the value is also more or less representative for summer diatoms.

From this it is deduced that at the time of the diatom outburst, when each cubic metre contained some 7000 units of plant pigment, the diatoms contained some 2 mg. P_2O_5. Since they had utilised over 15 mg. P_2O_5 during the previous six weeks, seven to eight times the quantity of diatoms found on March 28th had been produced. Seven-eights of this estimated six weeks' production had disappeared either by having been eaten, or much less likely by having died.

Neither this estimate, nor any one of those which follow, can by itself be considered as more than indicative. Each is subject to obvious reservations. But, taken as a whole, they present a consistent picture of a well, and often heavily, grazed pasturage of diatoms during the first half of the year.

The increase in population during the twenty-day period between March 8th and 28th at L_4 contained some 5000 units of plant pigment per cubic metre, and hence phosphorus amounting to 1½ mg. P_2O_5. The phosphate in the water utilised during this period amounted to some 7 or 8 mg. P_2O_5 per cubic metre after making allowance for salt error. This quantity of phosphate would be contained in diatoms having 22,000 to 26,000 units of plant pigments, or five times more diatoms than the observed increase in population. During this period of the spring outburst, conditions were clearly satisfactory for diatom growth, there was both sunshine and an ample supply of nutrient salts. It is improbable that diatoms died in any quantity; however, if we imagine that all the phytoplankton present on March 8th died naturally before the 28th, a similar calculation indicates that four to five times the nett increase had actually been produced.

It appears, therefore, that throughout this period of rapid increase the diatoms were being well grazed by the herbivorous animals.

The rate at which the diatoms reproduced is of interest. During the 20 days the mean population or "breeding stock" contained some 4200 units of pigment. The total calculated production lies between 22,000 and 26,000 units of pigment. This points to the breeding stock having divided about six times, or, on the average, once every 3½ days. If the diatoms were not being grazed the actual increase in abundance could be accounted for by less than two divisions during the 20 days.

THE FIRST OUTBURST OF LARVÆ.

As already mentioned the catches consisted of diatoms with only a moderate or small proportion of animal plankton. On April 4th, one week after the observations of maximum diatom population, the catches were equally large or larger, but consisted mostly of larvæ with only a small amount of phytoplankton—most in the inshore water. The catches also contained a great number of small fæcal pellets, most of which were tinted green with plant pigment.

It is concluded that the outburst of planktonic larvæ which occurred during this week had grazed down the pasturage of diatoms. There is no reason to suppose that the diatoms had ceased proliferating, because there was still plenty of phosphate in the water (Fig. 5) and there was an average of seven hours of sunshine daily during the week. There is no evidence that the water mass occupying the area on March 28th had moved away by April 4th to be replaced by water from another area in which there had been different conditions for growth. Neither salinity nor phosphate content had altered materially. The character of the phytoplankton had changed, at the Cawsand position and at L_6 where the diatoms had remained most abundant some of the large *Biddulphia sinensis* and Guinardia remained, at L_4 these seemed to have been eaten, the more spiny Chætoceros and Rhizosolenia remaining, and the peridinians *Ceratium fusus* and *Peridinium depressum* appeared in the catches.

Unfortunately, only one haul was made below 20 metres on April 4th, from surface to near the bottom at E_1. The result showed water very barren of diatoms. This does not support the unlikely possibility that the diatoms had died in the surface layers and had sunk.

Throughout April and early May small diatom-feeding larvæ remained numerous and the phytoplankton sparse. At L_4 on April 26th the catch consisted for the most part of larvæ and numerous fæcal pellets, with *Chætoceros densus* and *Thalassiosira sp.* dominant amongst the few diatoms ; by May 11th *Rhizosolenia alata* had become dominant and the daily production of diatoms considerable.

Although the observations showed that the stock of diatoms at any time was small, the phosphate content of the water continued to fall. A decrease of about 8½ mg. P_2O_5 per $m.^3$ between April 4th and May 11th at L_4 indicates the production of diatoms containing some 27,000 units of pigment in each cubic metre of water, or an average of some 700 units daily. The observations, which are admittedly insufficient, indicate that less than this quantity was present in the water on the average and suggest that the diatoms present had divided as often as twice daily to produce 27,000 units of pigment in 5 weeks.

The rate of production suggested by this calculation appears at first sight excessive. However, Gran (1933) found that Chætoceros at 1½ metres below the surface at Woods Hole, one month after midsummer, made seven divisions in three days and other species five to six divisions. In other words, they produced three times their own weight of vegetation daily. During this period at L_4, two months before the summer solstice, there was an average of 5·8 hours of sunshine daily. Certainly the water at L_4 was poor in nutrient salts compared with that used in Gran's experiments. From this it seems that although the calculated rate of production at L_4 may be excessive, it is not absurdly so.

To sum up, the evidence as a whole indicates that with lengthening days and increasing sunshine the stock of diatoms increased from February to March 28th, producing more daily than was eaten by the herbivores. Then a sudden outburst of larvæ rapidly ate down the stock of diatoms to a low level, and kept it eaten down closely for the following five weeks, during which time the small stock was producing vegetable food for the herbivores. Rough calculation, based on the assumption that water of different origin had not moved into the area, suggests that the stock was producing more than its own weight of vegetable food daily.

At Cawsand on May 11th the catch was composed as follows :—

Rhizosolenia alata	3440 individual cells per litre.
,, *styliformis* . . .	82
Ceratium fusus	41
Guinardia flaccida . . .	20
Gyrosigma sp.	40

comparable in cell contents to some 3900 cells of *R. alata* per litre, and contained 0·536 units of plant pigment per litre. Hence 1 unit of plant pigment was contained in about 7300 cells of *R. alata*.

THE OUTBURSTS OF *Rhizosolenia alata* IN MAY AND OF *R. stolterfothii* IN JUNE.

During the five days between May 11th and 16th the diatom population at both L_4 and the Cawsand station had doubled. At L_4 the diatoms consisted almost entirely of *R. alata*, which allowed another assessment of the unit of pigment to be made in terms of this diatom. A similar value was obtained, one unit of pigment being contained in 6950 individual cells. The species was a small form. At the Cawsand station the same species was dominant with some *Chætoceros densus* and Skeletonema.

On May 22nd an extensive series of hauls were made at L_4 and at positions 2 miles either side in a direction parallel to the coast, in order to investigate the uniformity of the population (p. 772). The diatoms again consisted almost entirely of *R. alata* which had attained a considerable density, over 30,000 cells per litre. The maximum occurred below the 20-metre level and doubtless exceeded 40,000 cells per litre in patches.

It is interesting to compare the density of this species in the Gulf of Maine, when a maximum of 50,000 cells per litre were found on August 4th, 1932, at 26 metres, less above and below, at one station—" a nearly maximal density " (Gran, 1933). The size of the cells may have been much larger, if they were one of the several other " forms " of this species.

By June 12th this population had been grazed down or had died down, much zooplankton and their fæcal pellets being present in the catch. The association of plants had changed to a very mixed plankton with *Ceratium fusus*, *R. alata*, and *styliformis* dominant. On both the 12th and 16th there was a greater density of population below the 20-metre level. On June 16th a haul was made several times up and down between the 20- and 40-metre levels (Fig. 3) which substantiated this vertical distribution, *R. stolterfothii* and *Guinardia flaccida* being dominant in the catch. By this time the upper 20 metres had probably been depleted of nutrient salts.

On June 20th an outburst of these two species was found close inshore, the hauls containing very little zooplankton.

On June 28th considerable quantities of these diatoms, mostly *R. stolterfothii* were found at L_4 below the 20-metre level. The dominance of this species persisted throughout July.

From the middle of June throughout the summer copepods were numerous.

During this period of dominance of *R. stolterfothii*, sporadic outbursts are indicated in the shallow inshore waters—the marked outburst on June 20th occurring at a time when zooplankton was for some reason scarce—and sporadic outbursts farther to seaward in the deeper water. The sections (Fig. 3) suggest that in June the zooplankton may have occurred in swarms, accounting for the uneven distribution of diatoms. Herdman (1922) notes that in the Irish Sea during the diatom outburst there is greater uniformity in adjacent hauls than at other times when a zooplankton was present. There is evidence of a lack of nutrient salts in the upper layers beyond the coast about this time (Fig. 5).

It was noted that zooplankton was relatively sparse, both when *R. alata* was dense in May and *R. stolterfothii* dense later, suggesting that the summer outbursts occur only when and where the demand of the herbivores slackens, and, naturally, where there are enough nutrient salts. I did not realise this early in the summer, and no measurements of the zooplankton were made, so the suggestion can only be put forward as such. The evidence so far accumulated points to the important part played by the herbivorous zooplankton in regulating the vegetable population. If this is not the explanation of why some species of the mixed diatom population in March did not proliferate and use up the remaining nutrient salts, we have to fall back upon some idiosyncrasy of the diatoms themselves, or lack of some unknown constituent in the water which is but slowly reformed, as explanation. Of these we have no real evidence ; certainly cultures of oceanic diatoms tend to die out, but then such cultures are immensely dense compared with conditions in the sea. The suggested explanation can account for smaller outbursts occurring at intervals or sporadically during the early summer while there are still nutrient salts in the water. When it is borne in mind that diatoms can, and do, more than double their weight daily in the sea under optimal conditions, an explanation is necessary to account for some of the numerous species present not increasing in numbers sufficiently to use up the available nutrient salts before the end of the spring.

THE AUGUST SCARCITY.

By August 1st diatoms, of which *R. stolterfothii* remained dominant, had become scarce. On the 15th and 29th they must have been very scarce indeed. Many pigmented copepods were present, which rendered colour comparison of the extracted pigment uncertain, so that all one could do was to obtain a maximum value for the yellow-green plant pigments in the acetone extract. It is probable that these maximum values, small though they are, are themselves considerably greater than the actual. During this period lack of nutrient salts limited the production ; on the 9th the surface water was found free from phosphate and at 49 metres only 2 mg. P_2O_5 per m.^{3}. Since mid-July life had become dependent upon the phosphate and ammonium salts being excreted and reformed from dead organisms.

It is of interest to consider the rate at which nutrient salts are supplied to the water during the summer, although these observations only allow the roughest calculation to be made. If we assume that throughout August phytoplankton in the L_4 water contained no more than 50 units of pigment per m.^{3} and the organisms reproduced daily—the month's production contained 1500 units of colour or 0·47 mg. P_2O_5 per m.^{3}. This suggests that until the end of August and the dying down of the summer zooplankton, only a very small quantity of phosphate was regenerated and used again, and that the phosphorus abstracted from the water in the form of phosphate by the phytoplankton earlier in the year was kept almost entirely locked away as phosphoproteins in the animals until the end of August in this relatively shallow area. However, farther to seaward we have evidence that regeneration of phosphate took place in considerable quantity before the end of July in several previous years (Atkins, 1930).

In the shallow inshore waters, which had probably some nutrient salts available, diatoms were present during August when the water offshore was barren.

THE AUTUMN AND WINTER CONDITIONS.

In September the copepods in the catches decreased and a mixed diatom plankton appeared, *Rhizosolenia styliformis* and *Biddulphia sinensis* being dominant. On the 19th, at both surface and bottom, the water contained 19 mg. P_2O_5 per cubic metre, indicating that death and decay of much of the summer plankton had taken place. There seems to be a possible lag in time between the proliferation of the diatoms and the appearance of a supply of phosphate. This was expected, because in previous years, when analyses of nitrate in the water were made, the regeneration of nitrate was found to have taken place a little later than that of phosphate. No measurements of the quantity of zooplankton in the water were made and no evidence obtained of the date at which great quantities apparently died, nor have we any knowledge of the length of time taken for phosphate to be regenerated from dead zooplankton, a question open to experimental attack. It is thought that rather wholesale death of herbivorous organisms and some of the carnivores dependent upon them for food was brought about at the end of August through starvation.

By the end of September zooplankton was sparse. During October and November there was much sunshine and few herbivorous animals in the catches; the diatoms increased, maximum catches being obtained on November 22nd when the same two diatom species were dominant as in September.

With regard to the autumn outburst Herdman remarks that this only takes place when the weather conditions are satisfactory. With respect to illumination, the autumn of 1933 had considerably more sunshine than normal in September and slightly more than normal in October and November.

The observations made during these two months show an even vertical distribution at L_4, which does not suggest a loss due to diatoms dying and sinking to the bottom, which undoubtedly takes place at some times and in some areas. In fact, no evidence of this has emerged, although it may sometimes occur in this area.

During the winter months of December, January, and February, 1934, considerable quantities of diatoms were present. At no time was the water other than well-seeded with diatoms. The community was very mixed, Biddulphia, Coscinodiscus, and Thallassiosira species being dominant. In one respect these winter months were quite unusual, considerably less phosphate being found in the water than in previous years. In view of this unusual condition it is not possible to judge whether the rather considerable diatom population during the winter was a normal phenomenon.

The Inshore Station.

The quantity of phytoplankton at the inshore station off Cawsand remained low throughout the year (Fig. 5). Except during April and August there was consistently less than farther out to sea. During the winter months this may be due to the lesser transparency of the water; but no reason is obvious for the small quantities found in summer, because in previous years the water here was found to be richer in nutrient salts than farther to seaward.

DISCUSSION.

The first half of the year 1933 was marked by much sunshine, an absence of strong winds, and a rather early spring maximum of diatoms. The seasonal change in dissolved phosphate in the water as it was utilised by the phytoplankton was in no way remarkable. A proliferation and spring maximum of diatoms, their very sudden decrease in numbers *before* all the dissolved phosphate is used up, and secondary maxima in the early summer are quite usual.

The data collected allow a picture to be drawn which accounts for the big changes which occur in the phytoplankton population during the year. The estimates arrived at, upon which this picture of the regime of the vegetation depends, are based to some extent on certain assumptions which are not rigidly true. However, even if some of the true average values are grossly different from those estimated, the same general picture is still presented, only modified in degree. Changes of several hundred per cent are being dealt with, so that errors amounting to 50 or even 100 per cent due to sampling or renewal of the water from elsewhere do not necessarily destroy the general picture.

In the first place it is concluded that several times more vegetation is produced during the few weeks' proliferation than is found at the spring maximum. The decrease in phosphate content of the water during this period was in no way unusual. Atkins records the daily decrease in phosphate at E_1 during spring diatom outbursts as varying between 0·40 and 1·06 mg. P_2O_5 per cubic metre for the whole column of water from surface to bottom. During the few weeks of the spring increase in Loch Strivan, between March 23rd and April 20th, 1926, Marshall and Orr record a fall from 44 to 30 mg. P_2O_5 per m.^{3} in the column of water from surface to bottom, that is a fall of some 20 mg. P_2O_5 per m.^{3} after allowing for salt error. The spring maximum of diatoms at L_4 as found on March 28th may have been less than the average maximum attained, although there is no evidence to suggest this. If we imagine that the true average was even three times the quantity found, it then contained phosphorus amounting to about 6 mg. P_2O_5 per m.^{3}, which is less than half the decrease in dissolved phosphate during the previous six weeks.

It is next concluded that this excess of production over increase in population was eaten and did not die. There was no evidence of dead diatoms in the catches, and an enormous death rate amongst *actively dividing* diatoms is against our present knowledge.

It is then concluded that at the end of March the population was rather suddenly eaten down to a low level. For this to happen would only require a moderate increase in the intensity of grazing by the herbivores, if their activities in eating the greater part of the production prior to the end of March is admitted. We have the general observation of a great increase in the quantity of zooplankton on April 4th, and the very noticeable presence in the catch of great quantities of fæcal pellets tinted green with diatom remains, which by itself is strong circumstantial evidence. If this is not the explanation of the decrease in diatom population, we have not only to fall back upon their death during a time when there was ample illumination and ample nutrient salts in the water, due to some peculiar idiosyncrasy of the plants themselves, but to neglect the evidence of fæcal pellets, of increased zooplankton, and lack of dead diatoms on April 4th.

During the early summer the greater part of the catches consisted of zooplankton, requiring a considerable daily ration of diatoms for their maintenance. If we concede that during March, when the relative proportion of herbivores was much less, a considerable part of the daily production of diatoms was eaten, it follows that during the early summer grazing was very intense. Fluctuations in the numbers of herbivores can readily account for the secondary diatom maxima during early summer.

Such fluctuations amongst copepods, which perhaps make up the greater number of herbivores, are known to occur, cf. *Calanus finmarchicus* (Nicholls, 1933). This provides a simple explanation of a hitherto unexplained occurrence.

During the winter months at the beginning of the year, the amount of sunshine and transparency of the water without doubt keeps the daily production of diatoms from greatly exceeding the herbivores' requirements, in March the lengthening days and greater illumination allow an increase in vegetation. From then onwards the diatom population is regulated by the intensity of grazing, until it has used up the nutrient salts in the water. The utilisation of the nutrient salts and onset of barren conditions would presumably occur in the spring, if the herbivores did not keep the breeding stock of plants eaten down.

It is seen that the available plant food for marine animals varies greatly throughout the year. There is good reason to suppose that the periods of plenty and periods of famine do not occur at the same time in different years. The incidence of sunshine varies greatly, some weeks being bright and allowing considerable growth of the phytoplankton, other weeks dull and so limiting it, particularly between October and April. The density of herbivorous animals—mostly the smaller zooplankton—doubtless varies at any particular time from year to year, on account of there being sufficiency or insufficiency of plant food, of the balance between herbivores and carnivores, and of temperature affecting their breeding time. Shortage of vegetation occurred in April at L_4 during sunny weather when there was plenty of nutrient salts in the water.

An intimate relation or balance exists between the ever-varying populations of carnivores, herbivores, and vegetable food, which in its turn is sometimes controlled and always affected by the available nutrient salts and illumination. If the proportion of carnivorous to herbivorous animals is displaced for a period by an " abnormally " large number of carnivores, then the diatoms are free to flourish and increase their population. If, on the other hand, the balance is displaced for a period by an " abnormally " small proportion of carnivores, then the herbivores freed from their enemies can flourish, keep the breeding stock of vegetation closely grazed, and by so doing limit their own increase. This would automatically delay the utilisation of nutrient salts.

The total productivity of the sea in most northern areas is limited by the nutrient salts available in the illuminated upper layers, for these are entirely or almost entirely utilised before the end of summer. However, in the Southern ocean only a part is utilised before the end of summer. This unexplained occurrence leaves a gap in our present knowledge of the productivity of the sea. In addition to slower rates of proliferation in colder waters, to the diatoms being subject to vertical movements which may carry them rather soon below the range of sufficient light, the herbivorous population grazing upon them will tend to delay the utilisation of the very rich supply of nutrient salts, as it does elsewhere.

SUMMARY.

Vertical hauls were made with a very fine silk net having a meter attached, which measured the volume of water filtered, at positions off Plymouth throughout the year 1933.

The quantity of phytoplankton was assessed from its content of yellow-green colouring matter, and expressed in terms of " units of plant pigments " per cubic metre of water filtered.

The diatom population per cubic metre at Station L_4 on March 28th was estimated to contain phosphorus amounting to 2 mg. P_2O_5, whereas dissolved phosphate amounting to some 15 mg. P_2O_5 had been used from each cubic metre of water by the diatoms during the previous six weeks.

It is concluded that the production of phytoplankton during this period greatly exceeded the quantity found at the height of the spring outburst, and that the excess had been eaten by the herbivorous zooplankton.

Between March 28th and April 4th the phytoplankton decreased to one thirty-fifth, coincident with a noticeable increase in zooplankton. Great numbers of fæcal pellets tinted green and largely composed of the remains of diatoms were found in the catch on April 4th.

It is concluded that the sudden decrease in vegetation after the spring maximum was due to increased intensity of grazing by the increased numbers of herbivorous zooplankton.

Evidence is presented that between April and the end of July the phytoplankton population was regulated by the intensity of grazing by the zooplankton. Two secondary diatom maxima occurred during this period. A rough calculation indicates that the phytoplankton was producing more than its own weight of vegetable matter daily during the first five weeks of this period, the zooplankton meanwhile eating this daily supply of vegetation.

During August the water was almost barren of vegetation, except at the inshore station, coincident with almost complete lack of dissolved phosphate in the water at a short distance offshore.

A well-marked autumn outburst of diatoms occurred in October and November, and during the winter months the phytoplankton was over eight times more than in August.

I take this opportunity of acknowledging the help and co-operation of Dr. L. H. N. Cooper who has carried out all the phosphate analyses and, after developing a suitable method, the analyses of organic phosphorus, of Dr. M. V. Lebour for identifying many diatoms, of my colleagues, particularly Mr. F. S. Russell, for much information and helpful suggestions, of the personnel of the S.S. *Salpa* and M.B. *Gammarus* for patiently hauling the net through several miles of sea.

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On the Biology of *Calanus finmarchicus.* V. Seasonal Distribution, Size, Weight and Chemical Composition in Loch Striven in 1933, and their Relation to the Phytoplankton.

By

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With 9 Figures in the Text and Plates I and II.

CONTENTS.

INTRODUCTION.

THE work on Calanus carried out in 1932 (Nicholls, 1933, Part I) in the Clyde Sea-Area showed that the course of events was very much the same at all four stations worked. It was felt, however, that more frequent observations would be useful for understanding the fluctuations in the population and for relating them to the food available as microplankton. Loch Striven was therefore chosen, primarily for the convenience of its position, and was visited weekly. Previous work (Marshall and Orr, 1927) has shown that this loch, although not so isolated as Loch Fyne, is little affected by ingoing or outgoing currents, and the population can be taken as self-contained. The position chosen, Station VIII (see Part I, Text-figure 1), was situated in mid-loch and had a maximum depth of about 70 metres.

Since it was known that the autumn–winter stock of Calanus starts moulting early in the year, the first visit was made in the middle of January. Weekly visits were then continued until the end of August, by which time the population had returned to its normal autumn–winter state (mainly Stage V). Two further visits in September and October confirmed this.

A series of five vertical hauls was taken each time with the Standard Net described in Part I. Five hauls were taken because of Gardiner's statement (1931) that of a large number of comparable hauls only about one in five is likely to deviate considerably from the average. Any haul which was by inspection a freak, being either much richer or much poorer than the others, was therefore rejected. On three occasions all five hauls were counted separately ; on two of these there was a gradual diminution of numbers from first to last. Although the taking of a number of hauls in this way probably diminished considerably the errors inherent in the method, yet it does not do away with them entirely. The five hauls were taken within such a small area that they are not necessarily representative of the loch as a whole.

From March 27th onwards one haul in every five was taken in two sections (from the bottom to 10 metres and from there to the surface), in order to throw further light on the seasonal changes in vertical distribution. This divided haul was always counted, but when it disagreed noticeably from the average of the other four, in numbers or composition, it was ignored in estimating the average number per haul.

Samples of all the copepodite stages were taken from the standard hauls for measurement. On a few occasions in spring, when adults were scarce, additional vertical hauls were made with a one-metre stramin net to provide sufficient material for measurement. Methods of preservation, sampling, counting, and measurement were the same as described in Part I and Part II (Marshall, 1933).

Further hauls were made with the stramin net to provide material for weight determinations and chemical analyses, and these catches, suitably diluted, were taken home alive in large jars of sea-water. These hauls were usually taken horizontally in deep water, so that the Calanus caught were not necessarily a fair sample of the population. Measurements show that the majority of the Stage V and adult Calanus are caught, but that when they are small a few of the smallest may be lost by passing through the meshes of the net.

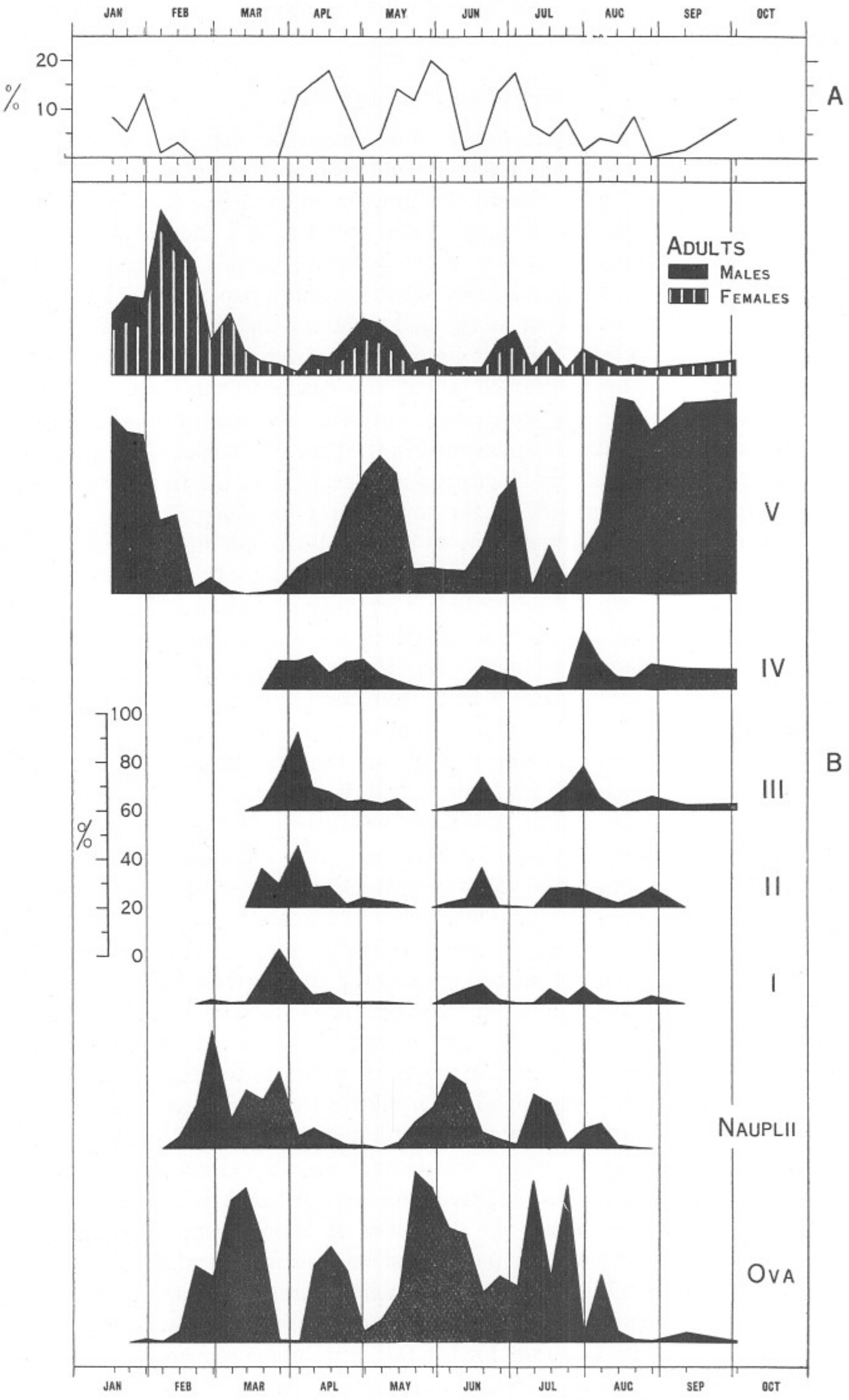
Water samples were taken with the insulating water-bottle at the surface and 30 metres, and the temperature noted. Samples from each were subsequently centrifuged and the number of organisms counted. Although counts made at only two depths do not give a detailed idea of the course of events in the microplankton, yet they are usually sufficient to show whether a diatom increase is present or not.

SEASONAL DISTRIBUTION.

The course of events this year was similar to that found in 1932. The autumn-winter Stage V Calanus moulted into adults through January and February and gave rise to the first brood of eggs. This is clearly seen in Plate I (percentage composition) and Tables I and II, but owing to the low numbers at that time the presence of this breeding period cannot be detected in the diagram showing numbers per haul. The first increase in numbers is seen at the end of March and beginning of April when the Calanus from the first brood of eggs were coming to maturity. One point must be mentioned about the catches from April 17th to May 1st. The number of copepodites present was much too large when we consider the number of eggs found in the previous weeks. The number of copepodites must always be *apparently* larger than the number of eggs which produced them because the copepodites stay longer in each stage than do the eggs, which remain as such only for about 24 hours, but this is not enough to account for the discrepancy. It must be noted, however, that at this time diatoms were very abundant. These would clog the meshes of the net and so reduce the amount of water filtered, particularly in the upper layers where the eggs and nauplii live (p. 814). Further, in the early part of March, from the number of females present one would have expected the number of eggs to be higher.

It will be noticed that the Calanus of the first brood of eggs were accumulating as Stage V in April and May. Only a few of these went straight through to adults and these produced a small brood of eggs during April. These eggs, however, were not followed by any considerable number of nauplii and young stages ; that is, the brood for the most part failed to develop. Only a few of the earliest eggs were found as nauplii. The failure of this brood is clearly seen in Text-figure 1. The Calanus which had accumulated as Stage V during this period moulted into adults about May 22nd and these produced the true second brood of eggs which lasted until about June 19th. This brood went through successfully to adults and these in turn produced another brood, the third, in July. Of the copepodites resulting from this brood many did not go through to the adult state but remained to form the autumn-winter stock of Stage V which was clearly established by August 14th. The few which did moult produced the small subsidiary broods of eggs in August and September, the survivors of which went to swell the stock of Stage V. One other point must be mentioned : the curious fall in numbers on July 17th. This fall is almost entirely in egg numbers since the actual numbers of nauplii and copepodites follow the usual course.

Natural mortality accounts for the fall in numbers after each breeding period and is most marked in the eggs and nauplii.



TEXT-FIG. 1.—A, The percentage of females bearing spermatophores. B, The succession of developmental stages through each breeding period.

Fertilization and Breeding.

From April onwards the female Calanus measured alive for weight determination were examined also for the condition of the ovary. They were divided into four groups (Table V): (i) early state, in which the eggs in the ovary were small and there was only one row of small eggs in the oviduct; (ii) medium state, in which the eggs in the ovary were enlarging and there were several rows of small eggs in the oviduct; (iii) mature state, in which the oviducts were full of large eggs; and (iv) spent state, in which the ovary was degenerating or had disappeared. It was not always easy to distinguish between the four types and a certain amount of overlapping must be allowed for. Rough observations from January to March, before the first breeding period, showed that on February 20th there was a large proportion of the females in the early state. On March 7th the majority were mature and on March 27th a large number was spent. This agrees well with the production of the first brood of eggs. In the same way from April 4th to May 15th there was a large proportion of early and medium state females, those which were about to produce the abortive and the true second brood, and a large proportion again on July 3rd before the third brood. After this mature females always predominated. In September the number of females decreased but the majority still remained in the mature condition. The small number of spent Calanus probably indicates that females die soon after reproduction.

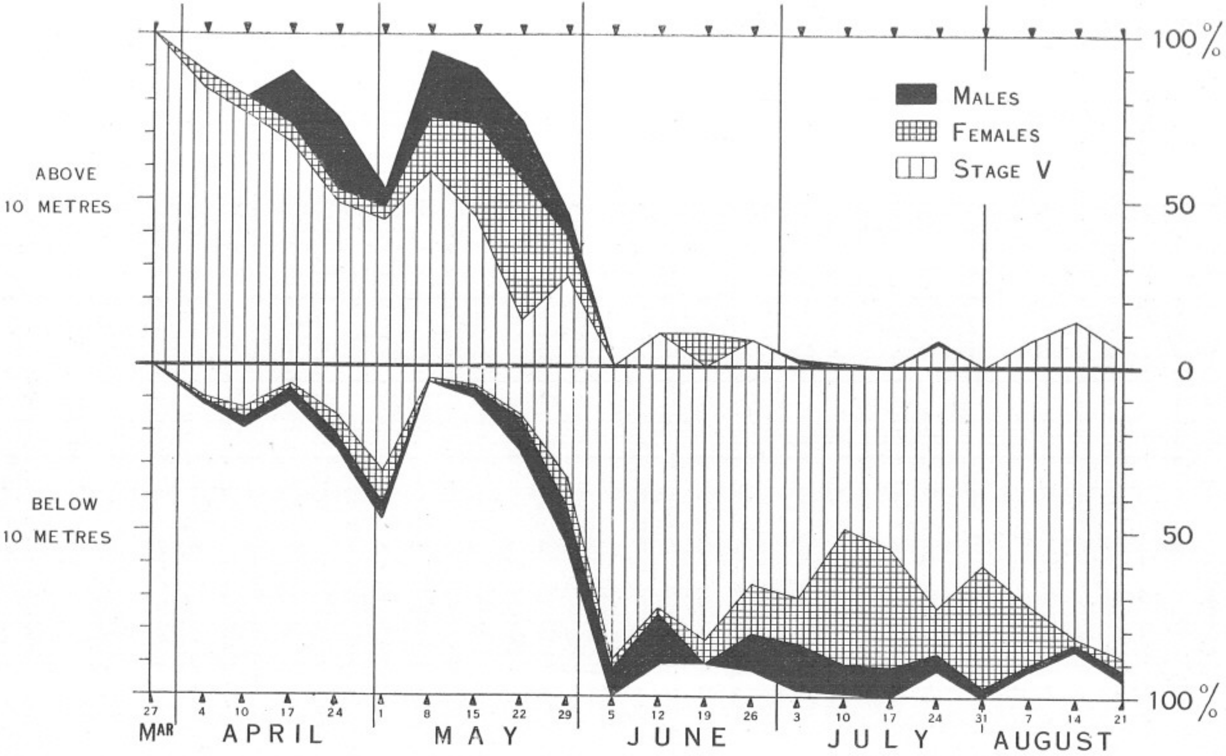
The percentage of females (in the standard hauls) bearing spermatophores rises before each brood of eggs (Table V and Text-figure 1) and is usually greatest when the proportion of males is at its maximum. Thus there is a peak in spermatophore-bearing females on January 30th before the first brood, on April 4th to 17th before the abortive beginning to the second brood, on May 15th to June 5th before and during the true second brood, and from June 26th to July 3rd before the third brood. After this the proportion was never high and the small peaks do not agree with the subsidiary broods. In this area the majority of females carry one spermatophore only, although occasionally two or three or even more are found. The males were never as numerous as the females except in April, but the disproportion is not so great as that described, for instance, in the North Sea (Gibbons, 1933). It is interesting to note that on several occasions Stage V Calanus were found with several spermatophores attached and in one case the number was as high as 13. These were usually distributed indiscriminately over the urosome and caudal furcæ but one or two were found attached to the posterior region of the thorax and fifth pair of swimming feet.

When the state of the ovary in spermatophore-bearing females is examined, it is found that spermatophores are much more frequent in the early stages than in the later. If we take early and medium state females together we find that of the 674 examined 17·4% carried spermatophores, while of the 1473 mature females less than 1% did so. One spent Calanus out of the total number of 38 had a spermatophore attached. These figures indicate clearly that the spermatophore is normally lost at a fairly early stage of development of the ovary. In recently moulted unfertilized Calanus the sacs opening on the genital segment are colourless and apparently empty, but in the great majority of the females found in the plankton they are dark in colour and appear to be full, presumably with the contents of the spermatophores. The spermatophores attached to the females are often empty. It is suggested that the sperm are stored in these sacs until spawning takes place and that some are passed out along with the eggs, but this needs confirmation by experiment. It may, however, be noted in support of this suggestion that in several other copepods the spermatozoa reach the eggs only when these are being spawned (Matscheck, 1909 ; Gray, 1929).

Immediately before the eggs are spawned they swell up and become granular in appearance. They are then squeezed out through the genital aperture as a string of sausage-shaped masses which separate and round off in a few seconds. Numerous females have been thus observed laying eggs on a slide and in several cases the numbers have been counted. The greatest number counted was 70. This agrees with the number suggested in Part I, but it is possibly exceeded at times.

VERTICAL DISTRIBUTION.

It has been shown before (Nicholls, 1933, Part III) that during the day in this area adult and Stage V Calanus normally live in deep water, but that at certain times of the year they may be found near the surface. Text-figure 2 illustrates their vertical distribution during the period from March 27th to August 21st, during which time one haul was divided at 10 metres. Numbers (Table II) above 10 metres were multiplied by six in order to make possible a fair comparison of the density above and below this level, since there was about six times as much water below as above. Young stages were not taken into consideration since their normal distribution is above 30 metres (Part III). It will be seen that from March 27th till May 29th Calanus in Loch Striven were inhabiting the upper 10 metres continuously and almost exclusively. After that date on no occasion were they found above 10 metres to any extent. It is interesting to note that the period in which they were moving down coincided with the transition period between the first and second broods, at which time Stage V and adults from the first brood were dying out



Text-Fig. 2.—The vertical distribution of Calanus in the divided haul during the three main breeding periods. (Based on Table II).

and those from the second brood were appearing in the catches. This indicates clearly that it was the first brood alone which showed this unusual vertical distribution. Gardiner's (1933) results on diurnal migration in the North Sea also showed Calanus more abundant near the surface than below in May. A comparison with last year's results when the hauls were divided at 30 metres shows that this phenomenon is not of regular occurrence. On two occasions in 1932 Calanus were noticeably more abundant above 30 metres than below and these were not restricted to the first brood.

SIZE, WEIGHT AND TEMPERATURE.

Where possible, samples of at least one hundred of each of the six copepodite stages of Calanus taken from the standard hauls were measured. The size-frequency distribution throughout the year is shown in Plate II, and the median lengths of the cephalothorax in Table III and Text-figure 3. The small size of Stages II and III partly accounts for the high values on the size-frequency curves for these two stages. All except Stage I copepodites were measured on the same scale; Stage I were so small that they were measured under a higher magnification. This naturally makes the areas covered by their frequency distribution curves smaller than those of other stages, but the lengths of the base lines are still strictly comparable.

From January to the middle of March only Stage V and adults were present; for most of this time only females were present in numbers sufficient to measure. The sizes fluctuate considerably, but this is partly because the numbers measured were very small.

On March 20th the first of the new brood appeared as Stage I and II copepodites; by March 27th they had developed to Stages III and IV, and by April 4th to Stage V and adults. From April 4th the size of each of these stages increased and the largest Calanus were found on April 24th. The female Calanus found on this date measured 2·82 mm. as compared with 2·41 mm. on March 27th. The females during this time were a mixture of autumn–winter stock and first brood Calanus, and the dying out of the former can be seen in the frequency distribution curves (Plate II). The curves are bimodal and the lower mode corresponding to the small autumn–winter stock gradually disappears. After April 24th

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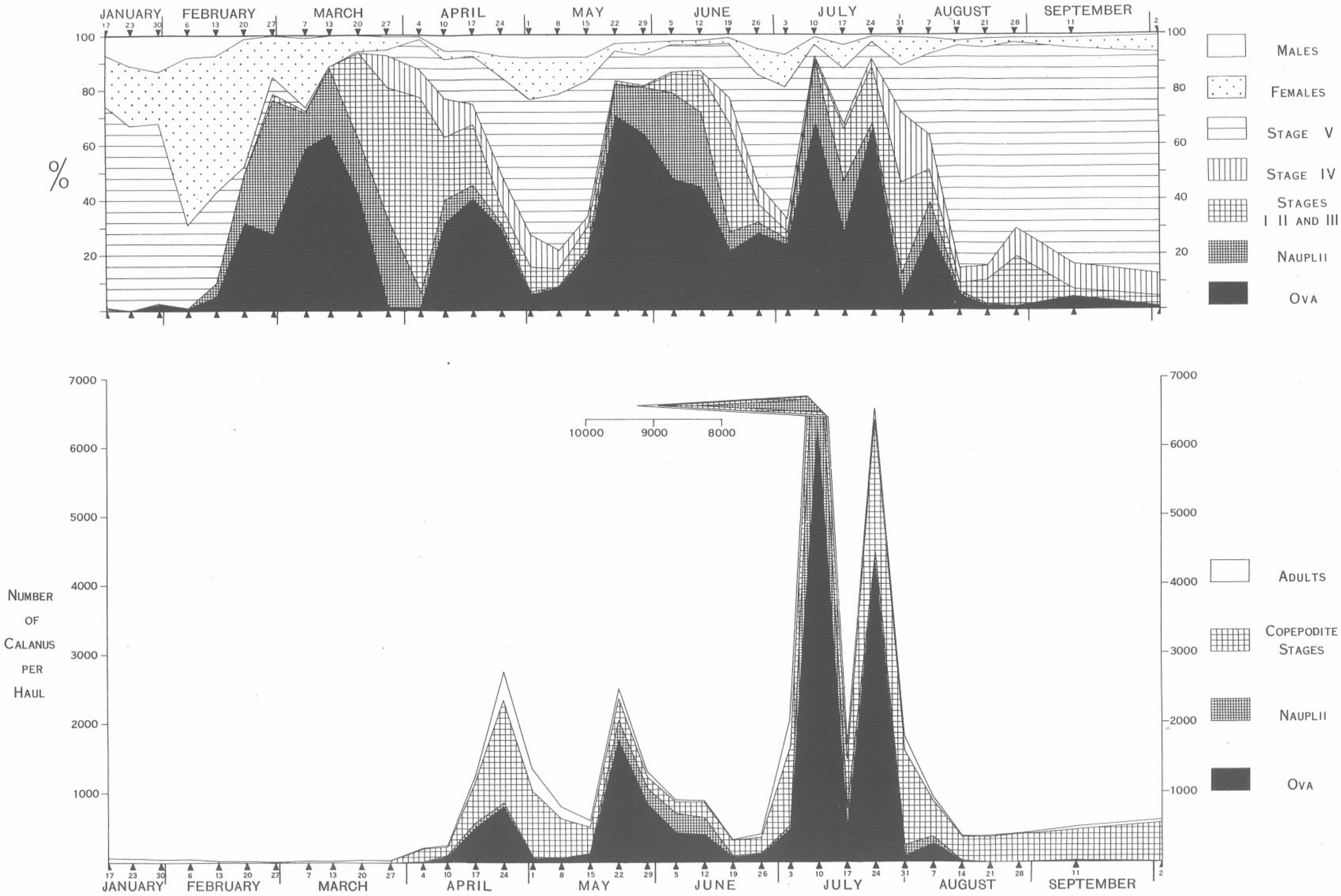
PLATES.

PLATE I.—Chart showing numbers per haul and percentage composition of population of *Calanus finmarchicus* during 1933.

PLATE II.—Curves showing the percentage size distribution of Calanus in Loch Striven, 1933. Left-hand side: thick line, males; thin lines, Stages V, III and I. Right-hand side: thick line, females; thin lines, Stages IV and II.

PLATE I.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29
JUNE
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19
26
JULY
3
10
17
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31
AUGUST
7
14
21
28
SEPTEMBER
11
2
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100
80
60
40
20
MALES
FEMALES
STAGE V
STAGE IV
STAGES I II AND III
NAUPLII
OVA
NUMBER OF CALANUS PER HAUL
7000
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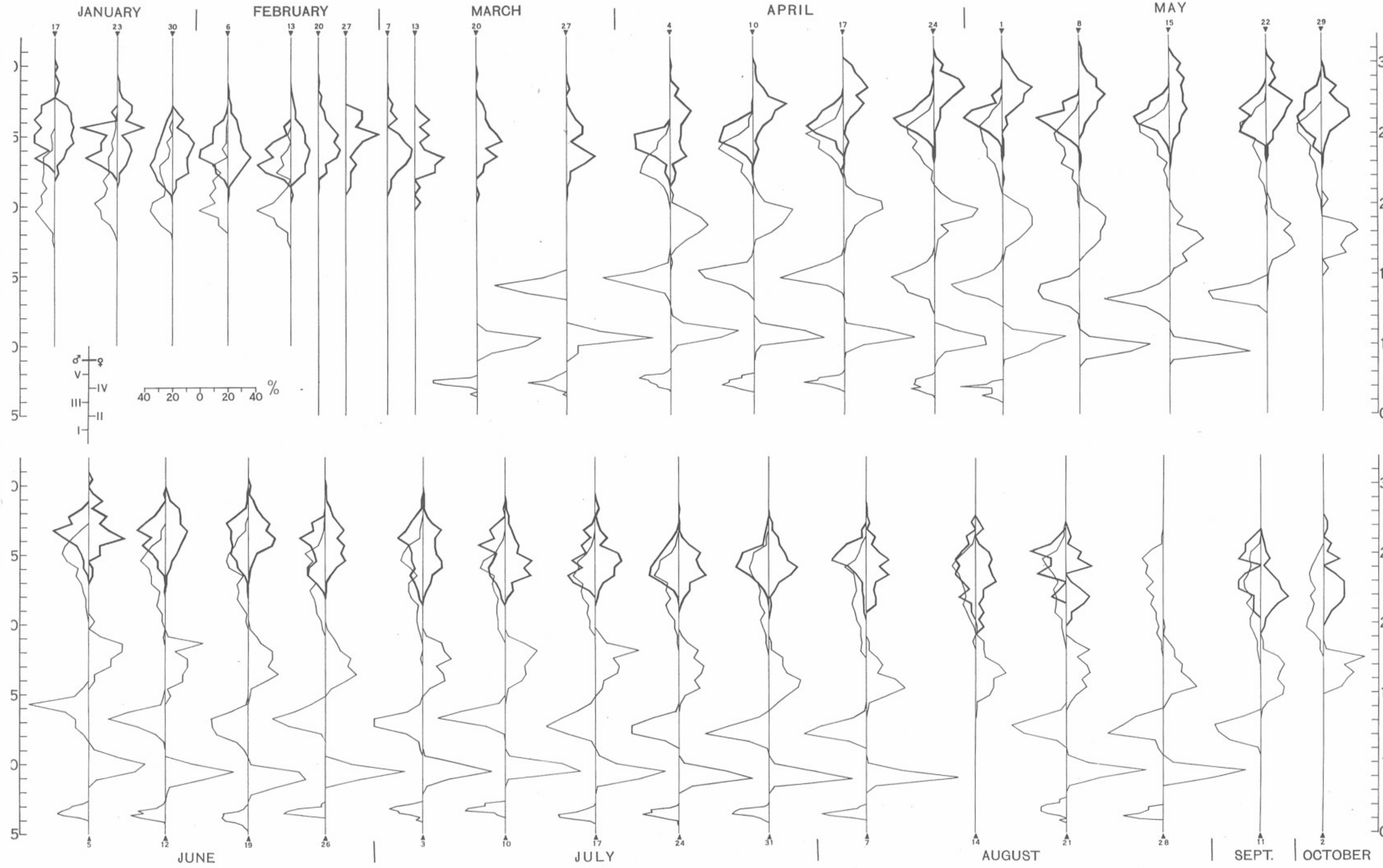
10000
9000
8000
ADULTS
COPEPODITE STAGES
NAUPLII
OVA

PLATE II.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2

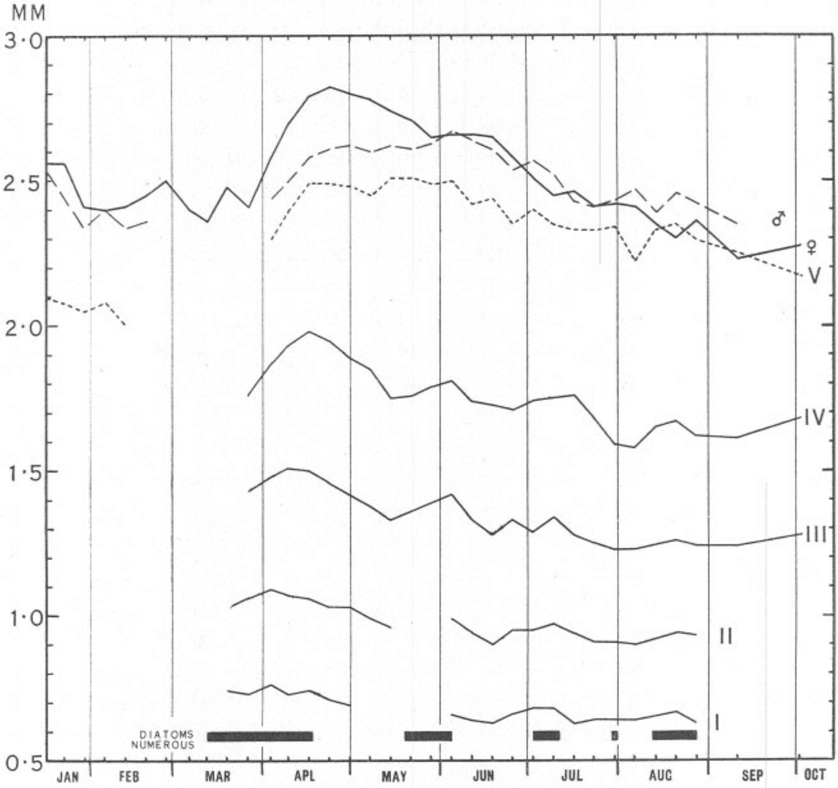
the size of all stages except Stage V and males fell until May 22nd or 29th, when the fall was checked, and in the younger stages the size actually increased a little. This corresponds to the appearance of the second brood. There were not enough of Stages I and II to measure. Males remained fairly constant in size and rose to their maximum for the year (2·67 mm.) on June 5th at the time of the second brood. The Stage V Calanus did not show the gradual fall in size either, but this is probably because in May they were accumulating instead of moulting to adults and the large ones remained to increase the average size of the stock. After the second brood, up to the middle of July, there was again a fall in size in all stages, but this was not regular and showed minor increases. The third brood appeared as Stages I, II, and III on July 10th, as Stage IV on July 17th, and as Stage V and adults, though less clearly, on July 31st. There was an indication of a subsidiary fourth brood towards the end of August. Since only a small proportion of these two broods became adults, a marked increase in adult size is not to be expected. In August and September the sizes of adults and Stage V approached each other, and in some cases the Stage V were actually larger than the females.

It seems certain, then, that while there was a gradual fall in size throughout the summer, this fall was temporarily checked at the time of the production of each new brood. In 1932 (Part II) it appeared that the Calanus from eggs spawned at the beginning of the breeding period were larger than those developing from eggs spawned at the end. This may be true in some cases this year, but it was certainly not so for the first brood in which the young stages (II–V) show that the size first increased and then decreased.

The fluctuations in dry weight of Stage V and adult Calanus are shown in Table V and Text-figure 4A. These weight determinations were made as described in Part IV (Orr, 1934) and usually on 100 individuals. The weight of Calanus naturally depends to some extent on its size, but the relation is not as close as might be expected (see below). Those which were weighed were also measured and the change in size in these samples agreed closely with the weight curves. A comparison of Text-figures 3 and 4B shows that they agreed also with the size samples from the standard hauls, especially the adults.

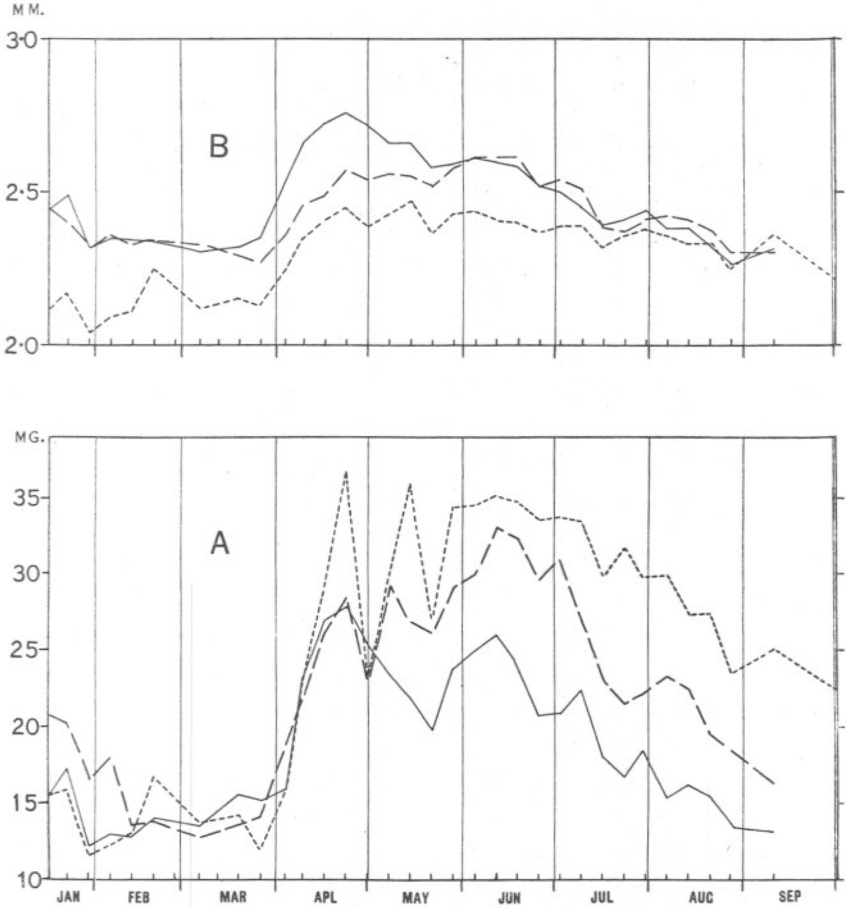
The samples were taken with a stramin and not with a fine silk net, so that one might expect them to be on the whole larger; on the other hand, these Calanus were measured alive and formalin fixation increases the size a little. Allowing for this increase after fixation the size of the adults in the two sets of measurements agrees very well. The main divergences occur in Stage V, but are, however, much larger than can be accounted for in this way, and must be caused by imperfect sampling. Stage V predominated in the catches from April onwards, and though it was often necessary to go through the whole catch to obtain sufficient adults, the required number of Stage V was obtained from one jar which represented only a small fraction of the catch.

From January to March Stage V and adults weighed very nearly the same in spite of Stage V being considerably smaller. At this time the numbers of males and Stage V available for weight determination were occasionally very small (Table V), so that the value may not be very reliable. With the appearance of the first brood in the beginning of April, the weight rose rapidly, especially that of the Stage V Calanus, so that while the weight of 100 adult Calanus, male or female, rose from about 15 mg. on March 27th to 28 mg. on April 24th, 100 Stage V rose from 12 mg. to 37 mg. in the same time. After this, in accordance with size changes the weight of the females fell steadily to the end of May; it then rose to a secondary maximum in the middle of June, corresponding to the appearance of the second brood. There was a small rise in the beginning of July and another (corresponding to the beginning of the third brood) at



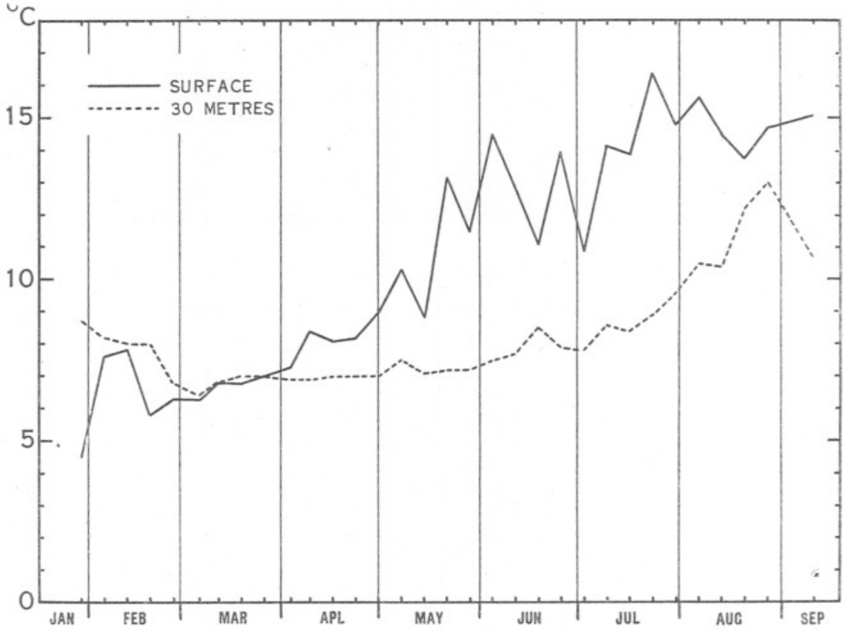
TEXT FIG. 3.—The median lengths of the copepodite stages of Calanus.

the end of July, but otherwise the weight fell gradually until winter values were reached again in September. The weight curve for males follows the size curve for males closely, with a maximum in June. Males were distinctly heavier than females throughout the summer. After the abrupt increase in weight in April Stage V Calanus remained heavier than either male or female for the rest of the summer, apart from several curious deviations in April and May, probably to be explained by imperfect sampling. The weight remained high until mid-July and then fell gradually till September, although even then it was still above winter values.



TEXT-FIG. 4.—Changes in median length and dry weight of 100 Calanus during the year. A, dry weight. B, median length. — — — Males; ———— Females; - - - - - Stage V.

The most striking point is, of course, that the relation of size to weight in female, male, and Stage V Calanus is *inverse*. It is obvious, therefore, that when a Stage V Calanus moults there must, at least during the summer, be a subsequent loss of organic material. It should be noted that the weights referred to above are all dry weights, and the same results do not hold if we compare wet weights. The wet weights of a number of male, female, and Stage V Calanus were determined on two occasions during the summer. About 50 Calanus were put in small drops of sea-water on a slide and the sea-water removed by carefully drying with filter paper. They were weighed after a fixed time, dried at 110° C., and reweighed. The dry weight of 100 individuals, determined in the usual way, acted as a check on this and showed that the adherent sea-water had been almost completely removed by the filter paper. It was found that while Stage V Calanus contained 47 to 50% water, male Calanus had 54% and females 68 to 70%. Thus in the living state females actually weigh more than males, and males more than Stage V. Gardiner (1933) has shown that large Calanus sink more quickly than small, indicating that females have a higher specific gravity than Stage V in spite of their lower dry weight.



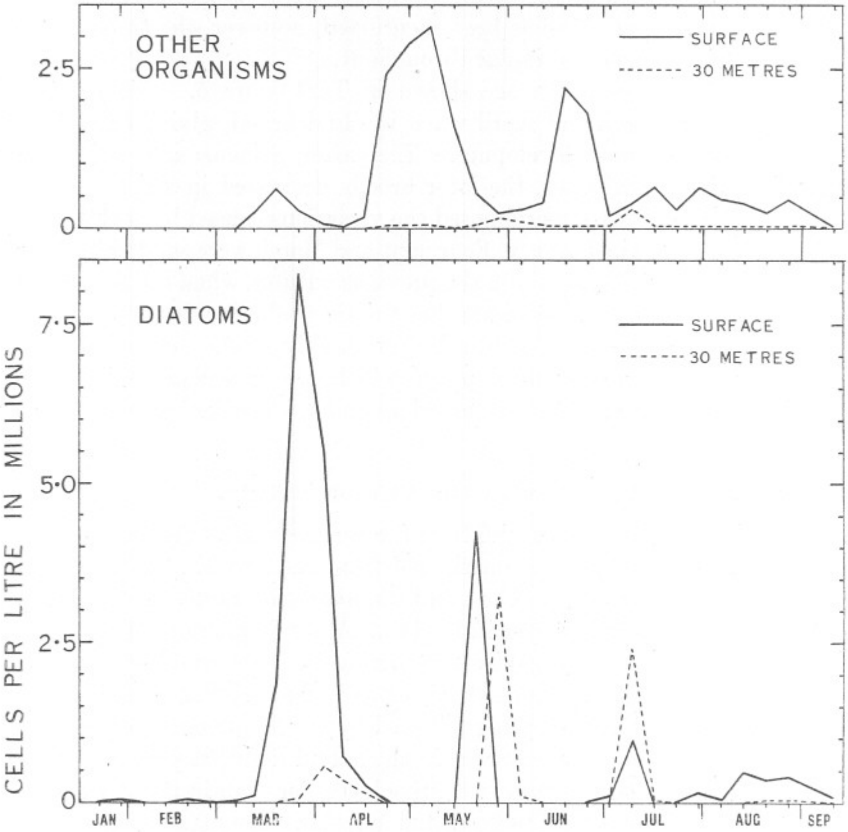
TEXT-FIG. 5.—The sea temperatures at the surface and 30 metres.

Throughout the year there is no constant relation between size and weight for male, female, or Stage V Calanus. In duplicate samples the agreement is good, but Calanus of the same stage and size show differences in dry weight at different times of the year which lie far beyond the experimental error of weighing or measuring. Thus of two lots of 100 Stage V Calanus with a median length of 2·35 mm. the first, on April 10th, weighed 23·0 mg., and the second, on July 24th, weighed 31·7 mg., a difference of 8·7 mg. As has been mentioned, however, the trend of the size and weight curves is similar throughout.

The temperatures taken are shown in Text-figure 5. The sea was coldest during March and April when the first brood, giving rise to the largest Calanus, was developing. Thereafter, concurrently with the warming of the sea-water, the later broods decreased in size. On this gradual fall in size are superimposed the variations caused by each brood. The Calanus found in January, February, and March were small, but these had developed from eggs laid in the previous autumn when the sea was at its warmest. Although it appears that the time taken to develop is about one month for each of the broods yet weekly visits cannot give an accurate figure for time of development which may on account of temperature be a little more for the first brood and a little less for the later ones.

Relation to the Phytoplankton.

The water samples taken weekly at the surface and 30 metres were not preserved, but 20 c.c. were centrifuged from each within 24 hours and all the organisms counted. The numbers, expressed as millions per litre, are shown in Text-figure 6 (see Table IV). Apart from minute flagellates, diatoms were the only organisms occurring in large numbers and the cycle of events was very much the same as is usual in this area, namely, a large diatom increase in spring followed by smaller increases during the summer. The main difference was in the actual numbers present which, for the spring increase at least, were much smaller than in the years from 1926 to 1931 (diatoms were not counted in 1929). The maximum number during the spring increase in these years varied from 15 to 30 million cells per litre ; in 1932, although water samples were not taken regularly, there was apparently no great increase at all, and in 1933 the maximum number was only 8·5 million cells per litre. The summer increases were also small and the year as a whole must be considered poor in diatom growth. The majority of the other organisms (Table IV and Text-figure 6) were minute flagellates which occurred in large numbers during the summer. It is possible that these flagellates are characteristic only of coastal water and would not be found in such numbers in the open sea. Many of them are colourless. Dinoflagellates did not occur in large numbers. Samples taken at only two depths can give but a general idea of the total numbers present, and there may sometimes have been more than the curves indicate. On July 3rd, for instance, the numbers counted were not particularly large at either the surface or 30 metres, but the tow-netting from 10 metres to the surface was very rich in diatoms, indicating that the maximum (which must have been greater than the figures shown at 30 metres in the following week) was a little below the surface.



TEXT-FIG. 6.—The microplankton in Loch Striven in 1933.

Previous work (Lebour, 1922 ; Marshall, 1924) has shown that diatoms form an important part of the food of Calanus throughout the year and it might therefore be expected that the number of Calanus would bear some relation to the distribution of diatoms.

The spring increase this year, which lasted from March 13th to the middle of April, began at the time when the number of eggs was near its maximum and lasted over the period when the nauplii and young stages were developing (Plate I, Text-figure 1). These went through successfully to adults. The end of this increase overlapped the abortive beginning of the second brood which failed to produce more than a few survivors (Text-figure 1). Only the nauplii from the eggs spawned during the first few days of this production had a sufficient food supply. There was a large number of minute flagellates present during this time but they had no effect on the survival.

The second diatom increase, at the end of May, coincided with the appearance of the second brood, but did not last so long. Similarly the increase from July 3rd to 10th provided diatoms when the eggs and nauplii of the first part of the third brood were at their maximum, and these gave rise to the main bulk of the copepodite stages of this brood. Diatoms were very scarce again until July 31st, and this is reflected in the lack of nauplii from the eggs produced at the end of this brood (Plate I). Throughout August and September there was a small number of diatoms constantly present, which may have been responsible for the survival of the subsidiary fourth brood, but by this time most of the developing Calanus were not moulting into adults but remained as Stage V to form the autumn–winter stock.

Earlier work has shown that a large percentage of the diatoms produced during an increase sink to the bottom. Since the Calanus of the first brood were found almost entirely in the upper layers (Text-figure 2) the diatoms when they had sunk into deep water were of no significance to them. With the second and third broods the diatoms would be of value to the young stages when they were near the surface and in deeper water would be available for the older stages. It is curious to note that the minute flagellates, although they would appear to be suitable food, do not seem to be used.

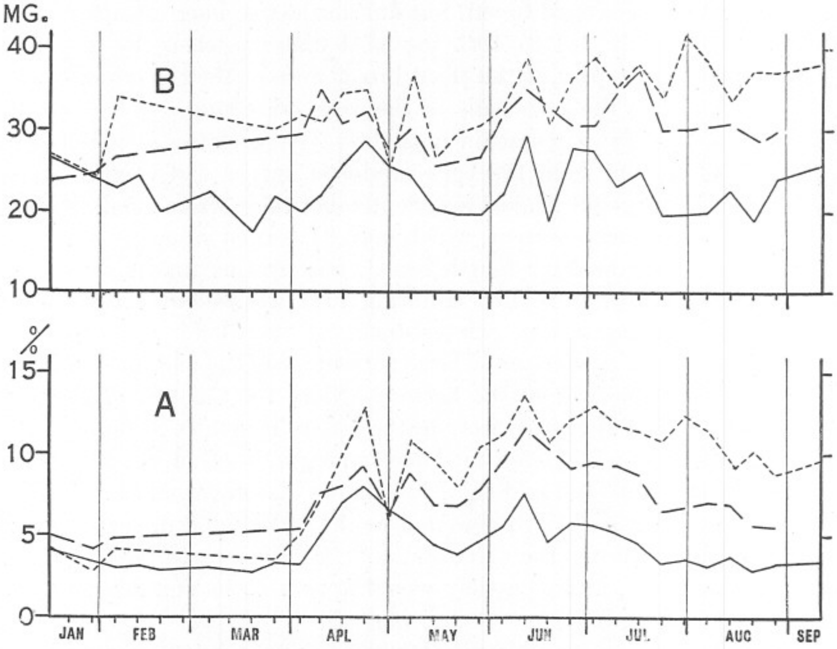
It is, of course, impossible to state what are the actual requirements of a Calanus, but the young stages, being less mobile, will require a richer supply than the later stages and adults. The critical time is therefore the period from egg to early copepodite, and the presence or absence of diatoms in the water then, means the success or failure of a brood.

The coincidence of a diatom increase with egg production (except in the case of the abortive beginning to the second brood) is interesting, but no causal relation is apparent.

In Text-figure 3 the periods when there were over 100,000 diatom cells per litre are marked in black. It can be seen that the size maxima occur shortly after these diatom-rich periods. The size maxima depend mainly on the broods, but it is possible that a rich food supply may also have a direct effect on the size.

CHEMICAL COMPOSITION.

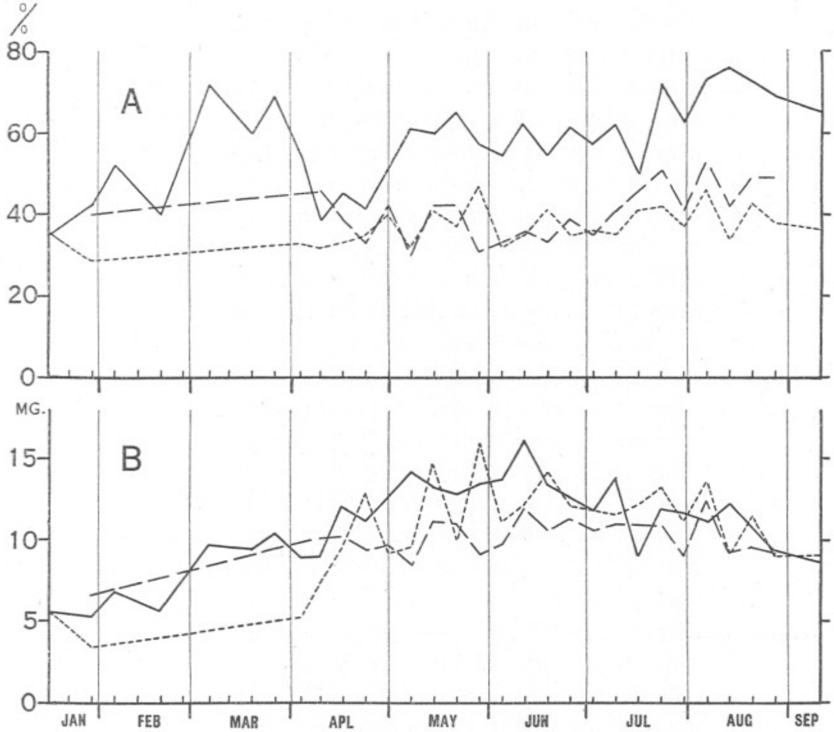
The fat and protein content was estimated from January to September in male, female, and Stage V Calanus. The methods used were the same as described in Part IV, but during 1933 the Calanus were not measured. The samples used for fat and protein analyses could not conveniently be weighed, so that the assumption is made that the samples of 100 Calanus used for these were strictly comparable with those used for weight and size determination. That this is justified is shown by the agreement between the duplicate weight samples and between the curves for weight and fat content.



TEXT-FIG. 7.—Changes in fat content of Calanus during the year. A, Fat percentage. B, Weight of fat per 100 Calanus. — — — Males ; ——— Females ; - - - - - Stage V.

The weight of fat per 100 Calanus and the percentage of fat are shown in Text-figure 7. In the early part of the year male and Stage V Calanus were scarce and it was often difficult to get sufficient for analysis. Corresponding with the low values for weight at this time of year fat content was also low. With the appearance in April of the Stage V and adult Calanus of the first brood there was a rapid increase in fat content; thereafter the curves showing fat content of male and female Calanus agree well throughout with weight and size (Text-figure 4), while that for

Stage V shows a very good agreement except for a short period during July. Thus with male and female Calanus the three broods for the year can be recognised by the change in fat content. With Stage V, as has already been mentioned, the sampling errors are at times significant and the curve for fat content follows that for weight, which has considerable irregularities during the spring. Both the actual content and percentage of fat are lowest in females and highest in Stage V, in agreement with



TEXT-FIG. 8.—Changes in protein content of Calanus during the year. A, Protein percentage. B, Weight of protein per 100 Calanus. — — — Males; ———— Females; - - - - - Stage V.

weight. There is a maximum fluctuation in percentage of fat in male Calanus of 20%, in females of 13%, and in Stage V of 20%. While the curves show that the large increase in the actual fat content in April depends chiefly on the increase in weight, Text-figure 7A shows that the increases in the *percentage* of fat occur at the same time and are therefore related to broods. This is shown most clearly for the first brood of the year, less clearly for the second, and still less for the third, as was the case with sizes. These increases in the percentage of fat suggest that the abundant food provided by the spring diatom increase resulted in a storage of fat.

After the appearance of the third brood there is a general fall in the fat contents of male and female Calanus, which by September have reached approximately the same values as in early spring. The adults then die out. With Stage V, however, the value is still high in the autumn–winter stock in September, being about 6% higher than during the spring.

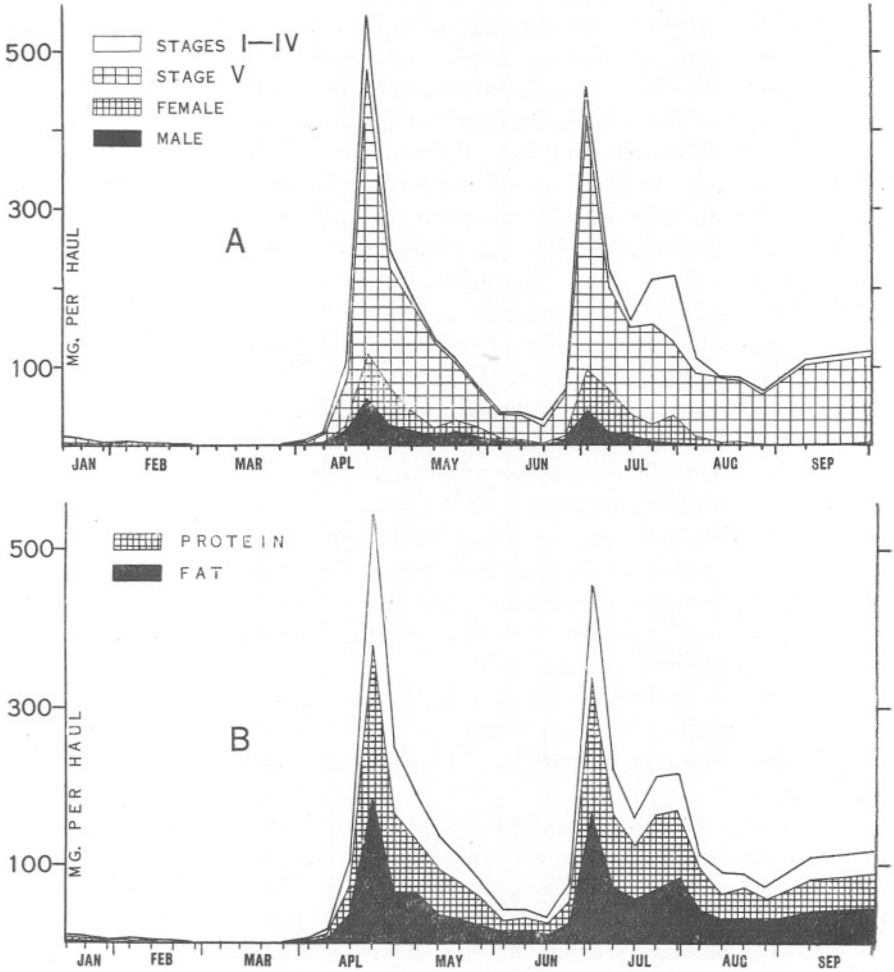
There is little or no relation shown between the fat content of female Calanus and the state of the ovaries. As is shown in Table V, there was always a high percentage of those in the mature condition, so that any changes due to the variations in this must be small and would not be shown in the curves for fat content.

The protein content of Calanus and the protein percentage are shown in Text-figure 8. There is less agreement between weight and protein than between weight and fat content. This is partly because the method of analysis was less accurate, and also because protein was estimated less frequently than fat. The agreement between protein content and weight is shown in the rise to higher values in April corresponding to the first brood, especially in Stage V. During the summer the values remained high and showed at best only a general relation to weight. After the third breeding period in July there was a fall towards winter values again. Text-figure 8B shows that, in contrast to fat, females are richest in protein and Stage V poorest. In the case of protein the difference between females on the one hand and males and Stage V Calanus on the other is more marked than with fat. The curves for protein percentage do not show any relation to the breeding periods with the possible exception of females, and their chief feature is a comparative constancy in male and Stage V Calanus. Thus the great increase of weight in spring is due more to fat than to protein.

On the basis of the weight, fat, and protein determinations, diagrams showing the total dry weight of the copepodite stages and the amount of fat and protein per haul have been constructed (Text-figure 9). The dry weights of the early copepodite stages have been calculated on the basis of Bogorov's figures (1933), while nauplius stages and eggs have been omitted, since although they were at times present in large numbers, their weight will be insignificant in comparison with copepodites and adults. During the winter the total weight (Text-figure 9A) was low because of the small numbers. The increase in the middle of April corresponded to the appearance of copepodites from the first brood. Those from the second brood, in May, caused the second weight peak on July 3rd. The third brood caused a slight increase on July 24th and 31st in which the early copepodites were of considerable importance. Thereafter the curve remained high owing chiefly to the Stage V Calanus which formed the autumn–winter stock.

The fat and protein content and the unidentified constituents of the

Calanus as a whole (Text-figure 9B) follow fairly closely the total weight curve. Of the unidentified constituents ash amounts to about 4% and chitin to about 3% (see Part IV) of the dry weight of the Calanus, while the remainder is probably largely carbohydrate (Brandt, 1898; Brandt and Raben, 1919–1922). At its maximum on April 24th the total dry weight of the copepodite stages was over 540 mg. in the whole column of water filtered (about 70 metres). This corresponds to a concentration of about 40 mg. per cubic metre, but the actual concentration will of course depend entirely on the vertical distribution of the Calanus.



Text-Fig. 9.—Diagram showing dry weight of Calanus per haul. A, Relative weights of different copepodite stages. B, Fat and protein content.

NOTES ON PARASITES.

A striking fact about Calanus is the number found parasitised. Apstein (1911) has already given a list of parasites which occur, and it may be of interest to add a few notes on those found here and their distribution.

Parasitised forms are often recognisable by their colour. Those whose body cavities contain cestode larvæ, trematodes, or dinoflagellates are all coloured red. With cestodes and trematodes the colour seems to be a development of the red pigment present in the chromatophores usually associated with the fat body, and the whole animal may be coloured a brilliant scarlet. In those parasitised with dinoflagellates the colour is associated with the mass of the parasites and varies from a pinkish yellow to bright red. The other parasites do not affect the colour at all.

An isopod of the genus Microniscus occurs occasionally throughout the year.

Two types of cestode larvæ are found, a tetraphyllid and a cyclophyllid. Both occur in large numbers in the body cavity, the cyclophyllid being smaller and more numerous. Apstein has recorded over 2000 of them in one Calanus, but the numbers here have not been more than several hundred. When these parasites were first noticed in this area, about 1924, they were rare, the tetraphyllids much rarer than the cyclophyllids. By about 1930, however, the tetraphyllids had become more numerous and in 1932 and 1933 cyclophyllids were exceedingly rare and tetraphyllids comparatively common. An interesting point about these cestode larvæ is of course the difficulty of explaining how they can occur in such large numbers in a single host.

Trematodes, probably a species of Hemiurus, occur rarely and are found only singly. The most brilliantly coloured Calanus are usually those which contain a trematode. They have also been found in Pseudocalanus.

Nematodes also occur singly in the body cavity but have no effect on the colour. They may be very small, but all sizes are found up to those which are longer than the Calanus which contains them and lie coiled up in the body cavity. These were rare until the spring of 1933, when they became comparatively common. Dr. Baylis has kindly identified this form as Contracæcum sp. At the same time this species was also common in Sagitta.

A species of gregarine is frequent in the gut and is more common in summer than in winter. It appears to have no effect on the Calanus at all.

The most common parasite of all is a species of the dinoflagellate Syndinium which occurs in masses in the body cavity. When such parasitised Calanus are kept in the laboratory they will frequently extrude the parasites as a discrete mass, but the host usually dies soon afterwards. Rarely, they extrude a mass of flagellated swarm-spores. The number of Calanus parasitised by this form is so large that it probably has a considerable effect on the mortality. The Calanus infected are usually found swimming about actively, but they are less resistant than normal specimens and die more quickly in the laboratory.

Another parasite, probably also a dinoflagellate, is *Ellobiopsis chattoni*, which is a pear-shaped body attached by a stalk usually to the antennule or one of the other cephalic appendages. It occurs most frequently in summer and was very common in the summers of 1931 and 1932. It was rare in 1933.

Except for the Syndinium, none of these parasites has much apparent effect on Calanus, which remain as active and lively as normal specimens. If they are examined more closely, however, it is usually found that the ovary remains undeveloped in females containing trematodes, cestodes, nematodes, or Syndinium. Females are found parasitised much more frequently than any other stage. Syndinium is found often in Stage V and sometimes in male Calanus, and the same may be said of nematodes and Ellobiopsis, but it is rare to find cestodes or trematodes in any but adult females.

On the whole infection is much heavier in the autumn–winter stock than in any other. These Calanus have lived much longer than those of other broods and have therefore been exposed to infection for a longer time. It is curious to notice the change which comes with the appearance of the first brood. Whereas out of a catch of a few hundred of the autumn–winter stock there may be 50 or 60 infected Calanus, out of the much larger catches of the first brood it is rare to find more than a dozen parasitised. In a catch taken on March 26th, 1931, out of 363 females, 42 were infected with Syndinium, 27 with tetraphyllids, 3 with cyclophillids, 6 with nematodes, and 1 with Ellobiopsis. Infection such as this probably accounts for a heavy mortality.

DISCUSSION.

A comparison with last year's results (Part I) shows that in general there is close agreement. The three main breeding periods, with one or more subsidiary broods, found at all Stations last year, were repeated in Loch Striven. The abortive beginning of the second brood and the accumulation of Stage V after the first brood delayed both the second and third broods by about a month, so that the autumn–winter stock was not established until August 14th (compared with July 11th in 1932). It is considered therefore that this may be regarded as a true representation of the course of breeding in the Clyde Sea-Area.

If total numbers are considered alone (Plate I) three distinct peaks appear which, except for the first, are caused mainly by large numbers of eggs. The eggs in the first are those of the abortive beginning of the second brood while the copepodites are those from the first brood, the eggs of which appeared in February and March, but were found in relatively small numbers. It has been shown that diatoms coincided with the eggs and nauplii of each brood and so aided their survival, but this will also have affected the number caught, since when diatoms are thick considerable clogging of the net is caused and its fishing capacity largely reduced. This was observed on several occasions, when the net on reaching the surface was seen to be pushing a cushion of water in front of it, and as it was hauled out brought water with it which drained away more or less slowly. This did not happen except when diatoms were very numerous. Thus while an inaccurate sample of the eggs and nauplii might have been taken because of diatoms, by the time they had developed into older copepodites diatoms had disappeared and truer samples were obtained. This applies in general to the later broods, but less to the third, since the number of diatoms at this time probably did not reach such high values as in the two preceding increases.

In the third brood alone were young stages present in sufficient numbers to produce the later copepodites and adults, and a diminution is shown from each stage to the next throughout this brood (except the first copepodites whose peak in numbers may have been missed between two successive weekly visits). In the first and second broods the reverse was the case, there being an actual increase in numbers from one stage to the next, but, as has been shown, this follows the increased efficiency of the net with decrease in diatoms. A similar state of affairs has been ascribed by Gibbons (1933) in the North Sea to immigration. It is, however, very difficult to apply this to Loch Striven. Text-figure 1 shows clearly that no large immigration of any particular stage took place at any time during the year. The broods can be followed in successive weeks from egg up to adult without any break in continuity. Apart from this it is known from previous work that hydrographic conditions in Loch Striven show no violent changes and that the microplankton maintains a more or less independent character, although the same general changes take place there as in the rest of the area.

The resemblances between the course of events in this and other areas have already been pointed out (Part I). Off the south coast of Ireland (Farran, 1927) the first brood appears to be so small that the copepodites resulting from it are negligible in numbers; the second brood in April and May is important and Farran states that thereafter breeding is continuous throughout the summer. His work, however, is based on collections accumulated over a number of years (1913–14 and 1920–26) and data for more than two consecutive months in any year were not obtained. They cannot, therefore, be expected to show distinct broods since these may occur at different times in different years. The recently published work of Gibbons in the North Sea (1933) does not give sufficient data for a comparison to be made. He states, however, that two broods occur, the main one in April and a secondary one in August.

On page 806 it has been shown that the phytoplankton had an effect on Calanus in 1933, mainly on the survival of the broods. In 1932 this connexion was not so obvious. There were then diatoms present during at least part of each spawning period at Stations I and II so that no brood failed completely for lack of food. At Station IV there was only one diatom increase, during May and June, which accounted for the survival of the second and third broods, but did not provide food for the first brood in March which failed. It is interesting to compare the delay in the start of breeding in Loch Fyne in 1932 and the accumulation of Stage V before the second brood in Loch Striven with the absence of diatoms in both cases.

In the open sea diatoms are less numerous than in the Clyde Sea-Area, and as a rule there is a large outburst of growth in spring and a smaller one in autumn (Gran, 1929). The sporadic increases during the summer which occur in the Clyde Sea-Area are absent. It is possible that this may have an effect on the Calanus population by delaying, or at least diminishing, one of the later broods.

In fresh water a relationship between the maxima of Cladocera and those of the phytoplankton has been shown by Krogh and Berg (1931).

It is clear that once breeding starts Calanus takes about a month to develop from egg to adult. The eggs appear after two to four weeks, spawning may last for several weeks, and the adults then die out. This sequence of events results in the production of successive broods during the summer, but owing to differences in survival these may not be apparent when only copepodites are taken into account.

The size curves show very much the same features as in 1932. They are seldom clearly unimodal except at the appearance of a new brood (Plate II, April 10th, July 31st). The Stage V and females have a particularly wide range. Although in 1933 the maxima in size correspond with diatom increases the connexion is probably indirect, for in 1932, although in several cases peaks in size corresponded with peaks in diatoms (Part II, p. 122) yet during the longest continued diatom increase there occurred a size minimum as well as a size maximum. In 1932 the connexion between broods and size was shown most clearly in females and Stage V at Station I. In 1933 it is not so clear and shows mainly in females and young copepodites.

The Stage V Calanus in Loch Striven had a considerably larger range in weight than those from Loch Fyne in 1932 (Part IV). In both cases the lowest values (10–12 mg.) were obtained in spring when numbers were low. Loch Fyne was peculiar in that there was no diatom increase until May and that the first brood was delayed and was unsuccessful. It was probably on account of this that the numbers and weight fell steadily till May and the sudden increase in weight came with the second and not with the first brood. After this the females remained much lighter than Stage V in spite of their greater size, as in 1933. The maximum weight of Stage V for the year was considerably higher in Loch Striven (37 mg. on April 24th) than in Loch Fyne (28 mg. on December 14th, 1931). The values for fat and protein percentage were comparable with those for Loch Fyne though the range was greater there. Females had low fat and high protein percentages compared with Stage V, while males occupied an intermediate position. Owing to the comparatively small numbers of analyses made in 1932, the seasonal cycle was not so well shown in Loch Fyne.

The curves for total weight per haul are very different in the two cases except for the low weights in spring. The stock of Stage V Calanus present in Loch Fyne in the winter of 1931–32 was very high when compared with the 1932–33 autumn–winter stock in Loch Striven. With the onset of breeding in spring, the total weights rose in both lochs, corresponding with the number of copepodites.

SUMMARY.

1. The seasonal changes in the population of Calanus in Loch Striven in 1933 have been investigated.

2. There were three main breeding periods. The first was in February and March, an unsuccessful beginning of the second in April, the true second brood in May to June, the third in July, and subsidiary broods in August and September.

3. Numbers were very low until April when the copepodites of the first brood caused a large increase; there was a second increase in May consisting mainly of the eggs of the second brood, and the maximum for the year came in July. The last and subsidiary broods provided the stock for the autumn and winter of 1933.

4. The reliability of the total numbers is discussed and it is concluded that a study of the percentage composition of the catch gives a reliable indication of the course of breeding.

5. A breeding period is always preceded by a large proportion of females with immature ovaries which gives way to a large proportion of mature females at the time of spawning. Spermatophores are found

chiefly on females with immature ovaries and are usually most numerous when males are abundant.

6. The Calanus of the first brood were almost entirely restricted to the upper 10 metres. This was not so for Stage V and adults of the later broods.

7. The Calanus of the first brood, which developed when the sea was at its coldest, were the largest found during the year. Thereafter there was a gradual fall, corresponding to the warming of the sea. On this fall was superimposed a series of variations caused by each brood. With the first appearance of each brood the fall in size was temporarily checked. This is shown for each copepodite stage.

8. The changes in dry weight followed the broods and changes in size, the most marked change being with the first brood in April, after which there was a general fall. Females, though largest, weighed least and Stage V, though smallest, were heaviest. This is due to differences in water content.

9. There was a spring diatom increase in March–April, followed by smaller increases in May, July and August–September. These coincided with the three main spawning periods so that the resulting nauplii had a rich food supply. The eggs spawned in April lacked diatoms and failed to develop into copepodites. The results indicate that the success or failure of a brood depends on the presence or absence of diatoms during the early stages of development.

10. The remaining constituents of the microplankton (chiefly minute flagellates) although at times numerous show no relation to breeding periods or survival.

11. The fat content of Calanus followed the changes in weight. There was also an increase in the percentage of fat with the appearance of each brood. The percentage of fat was highest in Stage V and lowest in females.

12. The protein content of Calanus followed in general the changes in weight. The percentage of protein was highest in females and lowest in Stage V.

13. The increase in percentage of fat which accompanied the increase in size and weight with the appearance of each brood suggests that a storage of fat can take place when food is plentiful.

14. The total weight of Calanus per haul is largely dependent on the number of Stage V copepodites.

15. The parasites occurring in Calanus are considered. They are most abundant in the females from the autumn–winter stock.

16. A comparison is made with previous work in this and other areas.

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TABLE I.

Calanus in Five Hauls.

Date.	Eggs.		Nauplii.		Copepodites.										Adults.				Total.
					I.		II.		III.		IV.		V.		♀		♂		
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	
Jan. 17	–	–	2	1	–	–	–	–	–	–	1	–	223	73	57	19	22	7	305
,, 23	–	–	–	–	–	–	–	–	–	–	–	–	166	67	54	22	28	11	248
,, 30	3	2	–	–	–	–	–	–	–	–	1	1	104	65	30	19	21	13	159
Feb. 6	2	1	–	–	–	–	–	–	–	–	–	–	76	31	151	61	20	8	249
,, 13	7	5	7	5	–	–	–	–	–	–	–	–	46	33	69	50	10	7	139
,, 20	34	32	19	18	–	–	–	–	–	–	–	–	3	3	50	47	1	1	107
,, 27	13	28	23	49	1	2	–	–	–	–	–	–	3	6	7	15	–	–	47
March 7	83	59	18	13	1	1	–	–	–	–	–	–	2	1	36	26	1	1	141
,, 13	53	64	20	24	1	1	–	–	–	–	–	–	–	–	9	11	–	–	83
,, 20	79	42	39	21	23	12	31	16	6	3	–	–	1	1	11	6	–	–	190
,, 27	2	1	49	32	35	23	15	10	23	15	18	12	3	2	7	5	1	1	153
April 4	9	1	55	5	114	11	262	26	339	33	120	12	113	11	9	1	5	1	1,026
,, 10	387	32	99	8	49	4	104	9	123	10	167	14	174	14	39	3	63	5	1,205
,, 17	2,508	40	325	5	298	5	562	9	504	8	457	7	1,091	18	115	2	349	6	6,209
,, 24*	3,215	29	215	2	95	1	150	1	435	4	1,270	12	3,925	36	815	7	835	8	10,955
May 1	329	5	84	1	74	1	257	4	314	5	819	12	3,232	48	1,014	15	555	8	6,678
,, 8*	256	8	8	–	24	1	92	3	96	3	212	7	1,808	57	428	14	256	8	3,180
,, 15†	243	20	27	2	4	–	26	2	62	5	42	4	591	50	105	9	95	8	1,195
,, 22*	7,015	70	1,155	12	5	–	–	–	30	–	135	1	1,065	11	270	3	295	3	9,970
,, 29	4,168	64	1,120	17	2	–	10	–	11	–	22	–	733	11	279	4	190	3	6,535
June 5*	1,692	48	1,124	32	124	4	66	2	48	1	24	1	364	10	40	1	83	2	3,565
,, 12†	786	45	474	27	112	6	64	4	61	4	29	2	169	10	28	2	31	2	1,754
,, 19*	276	21	94	7	108	8	223	17	179	14	121	9	256	20	28	2	14	1	1,299
,, 26*	447	28	67	4	30	2	18	1	58	4	116	7	646	40	154	10	79	5	1,615
July 3*	1,910	23	180	2	40	1	30	–	140	2	400	5	3,900	48	970	12	585	7	8,155
,, 10*	25,080	68	8,310	23	180	1	85	–	165	–	410	1	1,535	4	985	3	250	1	37,000
,, 17	2,350	28	1,576	19	538	6	671	8	382	5	153	2	1,692	20	726	9	302	4	8,390
,, 24	21,516	66	776	2	709	2	2,709	8	3,225	10	983	3	2,016	6	607	2	150	1	32,691
,, 31	389	4	785	9	683	8	666	7	1,670	19	2,279	25	1,550	17	936	10	72	1	9,030
August 7	1,304	28	489	11	94	2	214	5	254	6	584	13	1,343	29	278	6	52	1	4,612
,, 14	93	5	26	1	8	–	36	2	15	1	105	6	1,540	81	35	2	42	2	1,900
,, 21	25	1	9	1	21	1	81	4	62	3	95	5	1,468	80	60	3	24	1	1,845
,, 28†	8	1	–	–	28	4	67	8	50	6	83	10	543	68	15	2	7	1	801
Sept. 11	112	4	–	–	12	1	–	–	60	2	228	9	1,996	79	96	4	24	1	2,528
Oct. 2‡	5	1	1	–	1	–	1	–	18	3	49	8	478	81	36	6	3	1	592

* Numbers in 4 hauls. † Numbers in 2 hauls. ‡ Numbers in 1 haul.

TABLE II.

Number of Calanus Above and Below 10 Metres in the Divided Haul.

	Below 10 metres.									Above 10 metres.									
Date.	Eggs.	Npl.	I.	II.	III.	IV.	V.	♀	♂	Eggs.	Npl.	I.	II.	III.	IV.	V.	♀	♂	Total.
March 27	–	1	–	1	–	–	–	–	–	1	16	13	4	3	–	1	–	–	40
April 4	–	2	1	3	8	3	13	1	2	4	18	20	61	105	31	18	1	–	291
,, 10	3	3	1	4	4	8	16	3	3	114	7	7	13	24	40	15	1	–	266
,, 17	36	8	5	3	4	8	32	5	22	480	17	45	111	128	97	63	6	15	1,085
,, 24*	224	13	1	1	1	37	164	63	46	27	2	4	26	64	88	85	8	39	893
May 1	64	19	14	21	18	84	612	197	93	–	–	–	11	71	170	140	12	17	1,543
,, 8*	79	24	–	1	1	2	33	5	3	7	1	5	19	43	65	80	21	27	416
,, 15*	19	8	–	–	1	1	11	2	6	1	–	–	6	16	4	13	8	5	101
,, 22*	81	17	–	–	–	–	25	2	18	2,915	220	1	1	–	7	4	12	5	3,308
,, 29	241	102	–	1	–	–	86	22	27	407	82	2	1	3	2	11	5	3	995
June 5*	37	97	2	1	1	1	32	1	3	4	198	18	1	–	–	–	–	–	396
,, 12	250	103	6	2	4	4	43	1	9	31	63	73	43	31	8	1	–	–	672
,, 19*	36	19	–	3	3	5	50	4	–	4	7	38	73	37	18	–	1	–	298
,, 26*	25	8	1	3	2	3	48	11	8	203	12	–	–	1	–	1	–	–	326
July 3*	22	2	3	10	18	43	529	101	103	577	15	–	–	–	–	1	–	1	1,425
,, 10*	262	309	32	43	45	80	261	221	48	277	50	1	–	–	–	–	1	–	1,630
,, 17	317	274	162	241	177	63	337	221	57	38	2	1	–	–	–	–	–	–	1,890
,, 24	935	104	88	209	254	101	301	57	19	931	2	1	–	1	2	5	–	1	3,011
,, 31	35	90	100	85	140	167	218	132	12	42	7	3	1	2	–	–	–	–	1,034
August 7	65	45	4	26	22	80	152	38	4	23	24	2	–	–	–	3	–	–	488
,, 14	13	2	–	2	1	3	103	3	2	10	2	–	–	–	–	3	–	–	144
,, 21	8	2	1	22	16	13	202	8	6	3	1	2	1	–	–	2	–	–	287

* This haul excluded from Table I.

TABLE III.

Median Lengths of Calanus in 1933.

	Males.		Females.		Stage V.		Stage IV.		Stage III.		Stage II.		Stage I.	
Date.	No. measured.	Median length.	No. measured.	Median length.	No. measured.	Median length.	No. measured.	Median length.	No. measured.	Median length.	No. measured.	Median length.	No. measured.	Median length.
17.1.33	20	2·53	58	2·56	212	2·10	—	—	—	—	—	—	—	—
23.1.33	26	2·44	55	2·56	161	2·08	—	—	—	—	—	—	—	—
30.1.33	149	2·34	98	2·41	99	2·05	—	—	—	—	—	—	—	—
6.2.33	79	2·40	593	2·40	76	2·08	—	—	—	—	—	—	—	—
13.2.33	38	2·34	184	2·41	41	2·00	—	—	—	—	—	—	—	—
20.2.33	12	2·36	217	2·45	—	—	—	—	—	—	—	—	—	—
27.2.33	—	—	25	2·50	—	—	—	—	—	—	—	—	—	—
7.3.33	—	—	71	2·40	—	—	—	—	—	—	—	—	—	—
13.3.33	—	—	27	2·36	—	—	—	—	—	—	—	—	—	—
20.3.33	—	—	86	2·48	—	—	—	—	—	—	28	1·03	22	0·74
27.3.33	—	—	68	2·41	—	—	15	1·76	23	1·43	13	1·06	29	0·73
4.4.33	72	2·44	100	2·58	105	2·30	116	1·87	113	1·48	106	1·09	87	0·76
10.4.33	175	2·50	224	2·70	146	2·40	140	1·93	111	1·51	91	1·07	44	0·73
17.4.33	101	2·58	137	2·79	197	2·49	102	1·98	123	1·50	113	1·06	106	0·74
24.4.33	152	2·61	151	2·82	174	2·49	96	1·95	81	1·46	52	1·03	87	0·71
1.5.33	78	2·62	148	2·80	195	2·48	93	1·89	125	1·42	74	1·03	26	0·69
8.5.33	85	2·60	118	2·78	165	2·45	105	1·85	68	1·38	41	0·98	—	—
15.5.33	101	2·62	144	2·74	160	2·51	74	1·75	75	1·33	33	0·96	—	—
22.5.33	168	2·61	149	2·71	189	2·51	103	1·76	31	1·36	—	—	—	—
29.5.33	141	2·63	139	2·65	141	2·49	24	1·79	—	—	—	—	—	—
5.6.33	82	2·67	39	2·66	253	2·50	25	1·81	48	1·42	63	0·99	120	0·66
12.6.33	186	2·64	169	2·66	146	2·42	45	1·74	71	1·33	68	0·94	104	0·64
19.6.33	178	2·61	186	2·65	182	2·44	101	1·73	119	1·28	113	0·90	105	0·63
26.6.33	138	2·54	139	2·58	150	2·35	107	1·71	58	1·33	21	0·95	30	0·66
3.7.33	116	2·57	184	2·51	185	2·40	118	1·74	102	1·29	70	0·95	84	0·68
10.7.33	95	2·52	196	2·45	251	2·35	162	1·75	76	1·34	58	0·97	62	0·68
17.7.33	100	2·43	207	2·46	232	2·33	77	1·76	111	1·28	133	0·94	125	0·63
24.7.33	139	2·41	107	2·41	295	2·33	97	1·68	119	1·25	106	0·91	140	0·64
31.7.33	118	2·43	131	2·42	211	2·34	163	1·59	136	1·23	84	0·91	101	0·64
7.8.33	59	2·47	97	2·41	290	2·22	106	1·58	78	1·23	72	0·90	82	0·64
14.8.33	40	2·39	33	2·35	233	2·33	83	1·65	—	—	—	—	—	—
21.8.33	19	2·46	47	2·30	194	2·35	71	1·67	54	1·26	89	0·94	22	0·67
28.8.33	—	—	14	2·36	240	2·30	78	1·62	50	1·24	61	0·93	28	0·63
11.9.33	19	2·35	104	2·23	247	2·25	202	1·61	46	1·24	—	—	—	—
2.10.33	—	—	34	2·27	235	2·17	46	1·68	17	1·28	—	—	—	—

TABLE IV.

NUMBER OF ORGANISMS IN 20 C.C. OF SEA WATER.

Date, 1933.	Depth in m.	All Diatoms.	Skeletonema.	Thalassiosira.	Leptocylindrus.	Rhizosolenia.	Chaetoceros.	Pennate Diatoms.	Other Diatoms.	Dinoflagellates.	Silicoflagellates.	Coccolithophores*	Unidentified flagellates.*	Ciliates.	Other organisms.	T. in °C.
23·1	0	165	125	10	—	—	24	4	2	2	3	—	61	2	1	—
23·1	30	33	9	6	—	—	—	14	4	1	—	—	1	—	1	—
30·1	0	707	673	11	—	—	—	23	—	4	3	—	210	—	—	4·50
30·1	30	25	5	5	—	—	—	26	6	6	—	—	6	—	1	8·70
6·2	0	LOST														7·63
6·2	30	22	6	11	—	—	—	11	2	7	—	—	10	—	—	8·20
13·2	0	102	66	16	—	—	—	14	6	2	—	—	8	—	—	7·80
13·2	30	36	15	5	—	—	2	13	1	7	—	—	5	—	—	8·04
20·2	0	876	809	20	—	—	8	36	3	20	—	—	260	1	—	5·80
20·2	30	36	8	8	—	—	—	20	—	2	—	—	4	1	1	7·95
27·2	0	245	142	58	—	—	3	42	—	6	—	—	26	1	1	6·32
27·2	30	334	239	35	—	—	—	58	2	5	—	—	7	1	—	6·81
7·3	0	490	365	56	—	—	7	60	2	7	—	—	51	1	1	6·32
7·3	30	355	204	80	—	—	1	70	—	1	—	—	4	—	—	6·37
13·3	0	2,048	1,794	219	—	—	23	12	—	23	—	—	5,200	9	—	6·83
13·3	30	139	89	16	—	—	—	34	—	3	—	—	39	—	—	6·82
20·3	0	37,200†	34,405	2,460	—	—	25	310	—	30	—	—	12,500	2	14	6·82
20·3	30	201	155	10	—	—	—	36	—	1	—	—	20	—	—	7·03
27·3	0	166,000†	123,800	41,450	—	—	375	375	—	29	8	90	5,300	2	9	7·02
27·3	30	822	732	67	—	—	8	15	—	—	—	—	10	1	—	7·00
4·4	0	111,000†	107,100	3,900	—	—	—	—	—	3	2	—	1,260	—	6	7·27
4·4	30	11,165	10,850	240	—	—	8	67	—	1	3	—	—	—	—	6·87
10·4	0	15,228	14,700	189	—	—	66	273	—	54	2	—	3,600	3	—	8·35
10·4	30	7,466	7,300	160	—	—	—	6	—	2	4	—	17	1	1	6·92
17·4	0	5,487	5,300	10	—	9	74	82	12	61	1	30	3,500	9	1	8·07
17·4	30	2,548	2,370	156	—	—	3	8	12	5	8	—	25	3	1	7·01
24·4	0	7	2	—	—	—	—	5	—	15	1	—	48,000	—	13	8·18
24·4	30	155	142	12	—	—	—	1	—	5	1	—	500	1	—	6·97
1·5	0	26	22	—	—	—	4	—	—	33	—	—	58,000	—	—	9·01

1·5	30	249	213	34	—	—	—	2	—	7	—	—	600	—	—	7·02
8·5	0	5	—	—	—	—	—	5	—	31	—	—	63,000	—	—	10·32
8·5	30	98	85	13	—	—	—	—	—	1	1	—	800	4	—	7·47
15·5	0	17	8	1	—	—	—	8	—	8	2	—	32,000	—	—	8·79
15·5	30	56	27	26	—	—	—	2	1	2	1	—	330	—	—	7·10
22·5	0§	85,000†	74,440	10,420	—	—	—	140	—	144	4	—	11,000	4	202	13·15
22·5	30	64	49	12	—	—	2	1	—	2	—	—	700	2	—	7·22
29·5	0	65	37	8	20	—	—	—	—	72	—	30	5,000	—	2	11·45
29·5	30	64,000†	60,660	3,215	—	—	—	125	—	8	133	—	3,000	6	—	7·20
5·6	0	19	15	1	—	—	3	—	—	91	—	—	6,000	1	9	14·51
5·6	30	2,220	1,915	292	—	—	—	13	—	4	6	—	2,000	2	1	7·53
12·6	0	2	—	2	—	—	—	—	—	50	—	—	8,000	—	2	12·90
12·6	30	96	83	9	—	—	—	3	1	9	7	—	1,000	—	2	7·71
19·6	0	26	22	2	—	—	—	2	—	31	—	100	44,000	—	1	11·10
19·6	30	59	32	26	—	—	—	1	—	6	4	100	900	—	1	8·51
26·6	0	104	2	—	96	—	3	3	—	151	1	1,400	34,600	1	2	14·04
26·6	30															7·90
3·7	0	2,167	1,761	173	29	1	16	187	—	20	1	150	4,000	—	—	10·93
3·7	30	64	45	17	—	—	—	2	—	5	1	—	600	3	1	7·78
10·7	0	19,571	45	43	19,200†	8	176	95	4	209	—	500	7,600	1	10	14·06
10·7	30	48,000†	42,780	1,370	385	—	1,240	2,225	—	1	6	300	5,700	4	—	8·63
17·7	0	107	7	11	2	1	53	33	—	73	72	600	12,400	4	1	13·90
17·7	30	555	296	153	6	—	11	89	—	6	2	30	600	—	—	8·42
24·7	0	40	4	—	17	2	8	9	—	64	—	100	6,000	3	—	16·40
24·7	30	181	77	80	—	—	6	18	—	12	1	30	700	1	—	8·90
31·7	0	3,288	3	14	35	39	3,100	95	2	385	1	500	12,500	1	1	14·80
31·7	30	122	63	34	—	—	16	9	—	15	4	—	1,000	—	—	9·57
7·8	0	536	—	1	11	3	477	43	1	58	1	500	8,500	1	—	15·71
7·8	30	49	15	15	3	—	7	9	—	16	—	—	1,000	1	—	10·51
14·8	0	9,200†	—	250	1,864	48	6,800	224	14	1,007	—	400	6,600	14	8	14·53
14·8	30	143	49	10	11	2	33	37	1	20	—	30	1,000	—	1	10·35
21·8	0	6,634	—	1	5,840	92	910	147	4	26	3	1,200	4,000	—	1	13·78
21·8	30	403	27	60	65	26	144	81	—	46	—	100	1,000	1	1	12·22
28·8	0	7,992	—	5	283	87	7,600	25	2	107	—	300	9,000	1	2	14·71
28·8	30	655	12	14	62	5	499	62	1	41	2	30	1,000	—	—	12·98
11·9	0§	1,467	13	—	296	30	1,100	25	3	59	—	—	1,000	3	5	15·12
11·9	30§	69	15	2	4	3	24	15	—	8	—	—	200	—	—	10·70

* In the surface samples from March 13th onwards and in the 30m. samples from April 24th onwards, these were counted under a higher magnification on a fraction of a ruled slide.

† Calculated from partial counts on ruled slides.

§ Sample preserved in 5% formalin.

TABLE V.

	Male Calanus.				Female Calanus.				Stage V Calanus.					Females ‖ Spermatophores and condition of ovaries.				Chemical composition of hauls.		
Date.	Weight of 100 in mg.	Median length in mm.	Protein %	Fat %	Weight of 100 in mg.	Median length in mm.	Protein %	Fat %	Weight of 100 in mg.	Median length in mm.	Protein %	Fat %	% carrying spermatophores.	Early %	Medium %	Mature %	Spent %	Calculated dry weight per haul in mg.	Calculated fat per haul in mg.	Calculated protein per haul in mg.
17.1.33	20·8	2·44	—	20	15·2	2·42	35	27	15·6	2·14	33	27	8·6					9·7	2·6	3·5
			—	28	15·7	2·48	—	—		2·10	39	—								
23.1.33	20·3	2·40	—	—	17·3	2·49	—	—	15·9	2·17	—	—	5·5					8·5	2·2	3·1
30.1.33	16·7	2·29	40	25	12·3	2·32	43	—	11·6	2·04	29	27	13·3					3·8	1·0	1·1
	16·5	2·34	—	—						2·04	—	22								
6.2.33	17·9	2·36	—	27	13·3	2·34	52	24	12·3	2·09	—	34	1·3					6·5	1·7	2·9
					12·6	2·36		22												
13.2.33*	13·6	2·33	—	—	12·8	2·34	—	24	13·1	2·11	—	—	3·3					3·3	0·9	2·4
20.2.33†	13·8	2·34	—	—	15·6	2·32	40	19	16·7	2·25	—	—	0					1·5	0·3	0·6
							—	20												
27.2.33	—	—	—	—	—	—	—	—	—	—	—	—	0					0·3	0·0	0·1
7.3.33‡	12·8	2·33	—	—	13·8	2·29	72	22	13·8	2·12	—	—	0					1·1	0·2	0·7
					13·1	2·31	—	23												
13.3.33	—	—	—	—	—	—	—	—	—	—	—	—	0					0·2	0·0	0·1
20.3.33§	—	—	—	—	15·6	2·32	60	17	14·3	2·15	—	—	0					0·3	0·0	0·2
27.3.33	14·2	2·27	—	—	15·2	2·35	69	21	12·0	2·13	—	30	0					0·6	0·1	0·2
							—	22												
4.4.33	18·4	2·36	—	29	16·8	2·55	55	20	16·5	2·22	31	32	13·0	11	41	36	0	7·1	2·3	2·5
					15·3	2·53	—	—	15·0	2·25	35	31								
10.4.33	22·7	2·45	50	36	22·8	2·67	39	22	23·6	2·36	31	32	15·6	4	37	57	1	17·0	5·3	5·8
	20·8	2·46	42	34	23·6	2·67	39	22	22·4	2·34	33	30								
17.4.33	25·9	2·48	—	31	27·1	2·73	47	26	29·9	2·41	28	33	18·2	0	42	55	3	106·0	35·5	36·8
	26·5	2·50	—	31	26·9	2·73	43	—	28·0	2·40	38	36								
24.4.33	29·0	2·56	33	33	27·7	2·75	36	27	37·5	2·45	37	39	9·9	11	47	42	0	545·8	185·2	192·7
	27·9	2·57	—	32	28·0	2·76	45	30	36·1	2·44	33	31								
1.5.33	23·0	2·53	42	28	24·2	2·72	—	24	22·8	2·38	45	26	2·0	5	29	66	0	250·3	64·5	100·9
	23·1	2·54	—	27	26·7	2·71	—	27	23·7	2·39	35	25								
8.5.33	29·1	2·56	28	30	23·3	2·65	61	24	30·1	2·41	33	37	4·2	3	40	52	3	188·6	64·5	67·2
									28·6	2·43	—	—								
	29·4	2·55	31	—	23·7	2·66	—	25	30·9	2·44	31	36								
									30·0	2·45	—	—								

15.5.33	26·9	2·55	42	26	20·8	2·64	62	20	35·1	2·48	44	27	14·3	10	35	54	1	135·5	35·2	57·9
		2·55	42	25	23·1	2·68	58	20	36·6	2·46	38	26								
22.5.33	26·2	2·52	42	24	19·6	2·59	65	19	27·7	2·36	37	30	12·1	0	12	88	0	109·7	30·4	45·3
	25·9	2·51	—	28	19·9	2·56	—	20	26·4	2·37	—	—								
29.5.33	28·7	2·58	31	28	23·8	2·61	52	19	35·0	2·44	48	26	20·2	1	17	82	0	75·7	21·3	34·7
	29·5	2·58	—	25	23·8	2·57	61	20	33·8	2·41	45	35								
5.6.33	30·6	2·61	31	32	24·8	2·59	52	24	35·0	2·44	32	33	17·1	4	16	79	1	41·9	13·4	14·1
	29·3	2·60	34	32	25·2	2·62	58	20	34·1	2·43	—	33								
12.6.33	32·7	2·60	36	30	26·3	2·59	62	30	35·3	2·42	33	36	1·8	6	8	82	3	42·8	16·1	15·7
	33·4	2·62	—	40	25·6	2·60	—	29	35·0	2·39	36	42								
19.6.33	32·3	2·61	33	—	25·3	2·59	54	20	34·2	2·40	37	31	3·1	5	9	84	2	32·9	9·9	13·6
					23·5	2·56	56	18	35·3	2·39	45	31								
26.6.33	29·6	2·53	42	26	21·1	2·53	61	30	33·9	2·39	34	39	13·6	10	25	64	0	73·9	25·8	28·2
		2·51	35	35	20·3	2·50	—	26	33·2	2·35	36	34								
3.7.33	31·5	2·55	35	30	20·7	2·50	60	26	32·7	2·39	37	40	17·4	44	21	31	2	454·9	167·0	171·9
	30·3	2·53	34	31	20·8	2·50	54	29	34·8	2·38	34	38								
10.7.33	27·6	2·53	42	35	22·5	2·43	62	23	34·2	2·40	38	35	6·6	6	11	82	0	220·9	71·0	92·4
	26·2	2·49	40	35	22·2	2·46	—	23	32·8	2·38	31	36								
17.7.33	23·1	2·38	—	38	18·6	2·40	50	26	29·2	2·30	38	40	4·5	16	23	57	2	159·8	57·1	67·2
					17·5	2·37	—	24	30·5	2·33	43	37								
24.7.33	21·6	2·37	51	27	16·1	2·38	67	18	32·1	2·37	46	36	8·0	14	24	62	0	211·9	68·9	95·5
	21·6	2·36	—	32	17·2	2·43	76	21	31·3	2·34	38	33								
31.7.33	22·2	2·41	41	30	19·1	2·42	61	19	29·8	2·38	37	42	1·5	1	9	90	0	215·3	81·7	88·7
					17·8	2·46	65	20		2·37	—	42								
7.8.33	22·8	2·41	52	31	15·5	2·36	81	20	30·0	2·37	46	39	4·1	10	13	72	3	112·1	41·2	53·5
	23·7	2·43	54	31	15·2	2·40	64	20	29·7	2·35	45	38								
14.8.33	21·9	2·40	41	30	16·4	2·39	73	23	27·7	2·32	32	35	3·2	12	3	79	5	90·4	30·2	31·3
	22·9	2·41	43	32	15·9	2·37	78	22	26·9	2·33	36	32								
21.8.33	19·8	2·37	47	29	14·5	2·28	—	19	27·8	2·34	44	36	8·5	13	8	73	5	86·8	32·0	37·5
	19·4	2·36	50	28	16·5	2·36	—	18	26·9	2·32	41	39								
28.8.33	18·5	2·30	49	30	13·5	2·26	70	25	23·6	2·26	35	36	0	13	16	65	6	71·9	27·5	27·7
					13·5	2·26	67	23		2·23	41	38								
11.9.33	16·3	2·30	—	—	13·4	2·29	65	26	24·4	2·36	37	38	1·8	—	—	—	—	109·9	41·4	40·3
					13·0	2·32	—	—	25·7	2·35	35	39								
2.10.33	—	—	—	—	—	—	—	—	21·6	2·19	—	—	8·3	—	—	—	—	118·2	44·3	43·9
									23·0	2·23	—	—								

* Weight determined on 23 V.
† Weight determined on 42♂ and 21 V.
‡ Weight determined on 25♂ and 26 V.
§ Weight determined on 21 V.
} In all other cases more than 50 were used and usually 100.
‖ Abnormal Calanus are not included in the table.

Notes on the Swimming Methods and Habits of Certain Crustacean Larvæ.

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With 7 Figures in the Text.

CONTENTS.

INTRODUCTION.

UNTIL recently most work on larval Decapoda and Euphausiacea had been concerned with the elucidation of the life-histories of various species; latterly, since our knowledge of some of the commoner species has become more complete, other work has been undertaken. For example, Russell and others have clearly demonstrated the existence of diurnal migrations which these larvæ make in the sea, and we now know the extent of the migrations of various species. Other workers have experimented in the laboratory to find the cause or causes of the migrations. Little attention, however, seems to have been paid to the methods by which the migrations are accomplished; such remarks as have been made on the swimming powers and habits of these larvæ are to be found in works mainly devoted to other aspects of the problem. An attempt has been made to bring together some of these remarks and to supplement them with fresh observations on some of the more easily obtainable larvæ.

It must be made clear from the outset that plankton problems are not the only ones connected with the swimming habits of crustacean larvæ. The young crustacean being a free-living larva well adapted to its environment it follows that as swimming is the most important function at this stage of the life-history many of the morphological peculiarities of the larvæ are correlated with it. It has, therefore, been thought advisable to inquire into the closeness of the relationship between the swimming habits and the larval structure. Such a consideration appears to throw a certain amount of light on the functional significance of the abrupt changes of form met with during the life-histories of certain species.

It must be admitted that these two problems, one entirely physiological, the other bearing on points of Morphology and Phylogeny, are not necessarily closely related; but as the observations here recorded appear to merit discussion from both points of view it is convenient to bring these somewhat dissimilar subjects together rather than to deal with them separately.

I have to record my best thanks to the director of the Marine Station, Millport, for the facilities placed at my disposal during my visits to the station and for the regular supplies of plankton received at Glasgow. Also to Dr. W. T. Calman, F.R.S., and Professor J. Graham Kerr, F.R.S., for their advice and encouragement.

Materials and Methods.

The larvæ were observed both at the Marine Station at Millport and in the laboratory at Glasgow. It was found possible to transport larvæ to Glasgow; their normal swimming activities did not appear to be upset by the laboratory conditions. Temperature seemed to be the most important environmental factor, and its careful control was necessary; it was found that the condition of larvæ which had been adversely affected by a rise in temperature during the journey from Millport often improved remarkably after some hours in a more normal thermal environment.

After various methods had been tried it was found that the best way of maintaining an even temperature was to allow a constant stream of cold tap water to flow over the outside of the vessel containing the larvæ. The various jars and tubes in which the larvæ were observed were kept cooled in the same way.

The larvæ were watched in a variety of ways, the currents caused by the actions of the appendages being traced out with suspensions of carmine and indian ink. An attempt was made to test the efficiency of the swimming methods and for this purpose a jar 60 cm. in height by 5 cm. square was used. This jar had a centimetre scale attached to one side and the larvæ were timed by means of a stop-watch when making an excursion of 10 cm. In every case the larvæ were allowed to start moving before the excursion was timed, and so they were given a " flying start."

In order to have some control over the movements of the larvæ the experiments were carried out in a darkened room and advantage was taken of the fact that the larvæ showed definite responses to the stimulus of light. The jar could be illuminated either from the top or from the bottom. It was anticipated that difficulties would arise with convection currents in the experimental jar, but they were found to be negligible. During the experiments no special precautions were taken to control the temperature. The dark-room was unheated and below ground level; its temperature varied little. The glass which was put between the light and the experimental jar was thick, and readings taken at the beginning and end of each experimental period showed that the heat generated by the light did not cause any appreciable rise in the temperature of the water in the jar.

During the experiments on orientation it was found necessary to study the behaviour of the larvæ in darkness. It was found that red light, such as is used for photographic purposes, has no apparent effect on the larvæ. They neither orientate nor swim in response to its presence. These experiments were carried out at Millport and the larvæ were observed by placing the vessel containing them in front of a window of ruby glass in the wall of the dark-room. This window gave light from an adjacent room so that control of the intensity of light falling on it was easy. In all cases the least intensity in which the orientation of the larvæ could be seen was used.

THE SWIMMING METHODS OF THE LARVÆ.

In recording the swimming methods of the larvæ it is convenient to treat of one species in some detail and then to compare and contrast others with it. The type selected is the first larva of *Munida bamffica*, which was abundant in the plankton at Millport in the early spring.

Munida bamffica, first larva.

The larvæ of this species normally progress telson foremost. Motion is brought about by the action of the thoracic exopodites, which cause a stream of water to flow along the sides of the body, over the outside of the carapace and away past the head (Fig. 1). Reversal in the direction of movement was occasionally seen to be brought about by reversal in the direction of the effective beat of the thoracic exopodites, but this was never long continued. The more normal method of reversal, such as is brought into use when the larva collides with some object, is to bring the abdomen and telson slowly under the thorax ; the body is then straightened again with a violent jerk, the result being that the animal is sent rapidly head forwards.

In addition to the current caused by the thoracic appendages there is also the respiratory current created by the second maxillæ. This latter current enters the branchial cavities from behind and, passing over the bases of the thoracic limbs, leaves the cavities behind the eyes ; the eyes deflect the current outwards (Fig. 1).

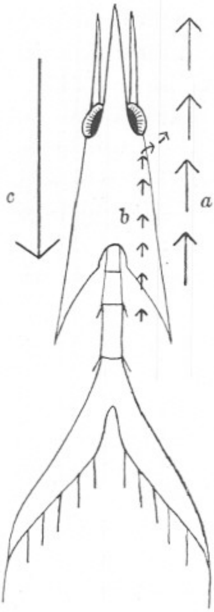

FIG. 1.—*Munida bamffica* (first larva). Diagram to show currents in water. Arrows represent: (*a*) current created by the thoracic exopodites, (*b*) respiratory current, (*c*) direction of movement.

In vertical movements swimming takes place either up or down according to the stimuli which excite the animal to make the excursion. Under experimental conditions it was found that at temperatures between 14° C. and 20° C. movement was towards the source of light. The change of direction of motion when the direction of the source of light was changed appeared almost instantaneous.

When they are not actively swimming the larvæ rest in a horizontal position, and the tendency to sink appears to be very slight. Figure 2 shows the positions of the larvæ during movement and at rest.

A study of the larva of Munida shows that (1) when swimming the body is orientated so that as little resistance as possible is offered to the water: this may be referred to as a " Stream-line effect "; (2) when resting the body is orientated so that the maximum resistance is offered to sinking; (3) that besides the normal swimming mechanism there is a well developed reversal mechanism.

Caridea.

Larvæ of Caridea were not plentiful in the material at my disposal, but two important types were observed, namely, *Pandalus* sp. and *Crangon* sp. The Pandalid larva swam towards the light telson foremost; it swam and reversed in the same manner as a Munida larva. The backward swimming habit has also been noted in the Caridea by du Cane (1839) and by Lyon (1906), who observed it in *Palæmonetes varians;* Lyon also suggested the manner in which the reversal mechanism would be found to work, but said that in this species the action was too quick to be followed by the eye.

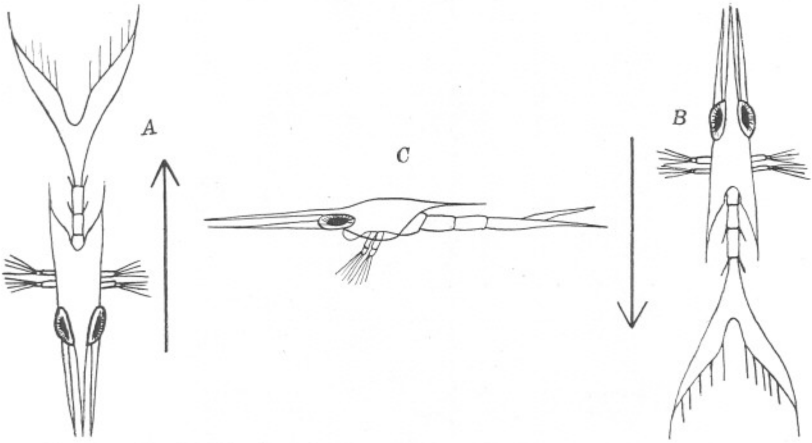

FIG. 2.—*Munida bamffica* (first larva). Diagrams to show orientation when swimming: (*A*) upwards, (*B*) downwards, (*C*) when resting.

The Crangonid larva swam head first. This is important as it shows that the habit of swimming telson foremost is not universal in the Caridea; the significance of this will be discussed later.

Williamson (1901) has also noted that the larvæ of *Crangon vulgaris* progress head first; he also records a spiral movement as do du Cane (1839) and Weldon (1889).

Astacura.

Several larvæ of *Nephrops norvegicus* were observed. In response to the stimulus of light they were found to orientate themselves with the telson and abdomen towards the light, but with the head and thorax in a plane at right angles to them, in the attitude shown in Figure 3. In this posture all the specimens moved towards the light telson first.

The swimming of the larvæ of *Homarus vulgaris* has been described by Williamson (1904), who says that they swim with the abdomen downcurved, as in Figure 4A. They swim forwards. Occasionally he saw the abdomen curved under the body, Figure 4B.

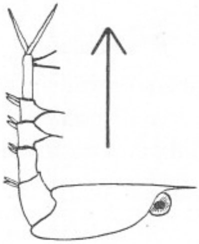

FIG. 3.—*Nephrops norvegicus* (larva). Diagram to show attitude when swimming; movement is in direction indicated by arrows.

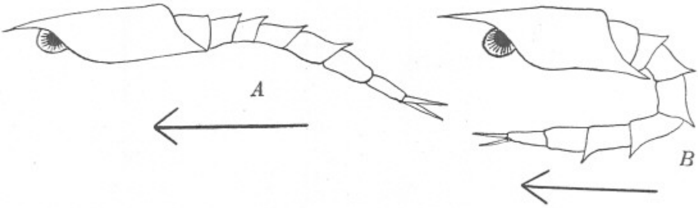

FIG. 4.—*Homarus vulgaris* (larva). Two attitudes seen when swimming. Movement takes place in the direction indicated by arrow.

Anomura.

In addition to the larvæ of *Munida bamffica*, larvæ of the following species were also observed: *Galathea strigosa* (first larva), *G. dispersa* (first larva), *Eupagurus* sp. (last larva), and *Porcellana* sp.

The swimming methods of the majority of these larvæ are essentially the same as those of Munida, but the case of Porcellana is somewhat different.

In Porcellana the larvæ normally progress head first. The long rostrum, however, tends to make them rather unwieldy creatures, and when the direction of stimulus is reversed the direction of the beat of the thoracic exopodites is reversed and the larvæ proceed backwards; they do not rapidly re-orientate themselves as do the larvæ of other Anomurous types; that this is due to the presence of the long rostrum can be shown by cutting it off. When this is done the larvæ swim in the normal manner, but if the direction of the source of light is now reversed the larvæ rapidly re-orientate themselves to it.

The method of reversal in this species is the flexure of the abdomen and telson under the body; they are drawn sharply under the thorax and the larvæ jump backwards.

Spooner (1933) has also observed the swimming habits of certain Galatheid and Porcellana larvæ, and my observations appear on the whole to tally with his account.

The swimming of Anomurous larvæ has also been observed by Thompson (1903) who recorded the backward mode of progression.

Thalassinidea.

Jaxea sp.

A few specimens of this interesting larva were observed at Millport in September, 1933. In swimming they were found to be very like the Anomurous larvæ in habit, but unlike them they were very poor swimmers. However, they orientated themselves with the head away from the light and proceeded towards it telson foremost. The peculiar form of the body, which when flexed is divided into two almost equal portions, each of which presents a similar amount of surface to the water, results in the flexure and extension of the abdomen having no pronounced effect, and the writhing movements which take place move the larva very little, but tend to displace it slightly in the direction of the telson.

Brachyura.

Zoea larvæ of several species of Brachyura were observed; they responded positively to the stimulus of light. The positions adopted when swimming, both up and down, are shown in Figure 5; in both cases the larva is seen to be orientated so that it proceeds dorsal spine foremost. The swimming actions of the thoracic exopodites were occasionally seen to be supplemented by downward jerks of the telson region, but this was rare.

In contrast with the Anomurous larvæ the Brachyurous zoeas sink rapidly when the swimming movements cease, and a larva which appears to be swimming upwards may merely be lessening its tendency to sink. This is due to there being no position of rest; these larvæ remain with the dorsal spine directed upwards, and unless the movements of the thoracic exopodites are continued the larvæ sink.

There is no really well-defined method of reversal, but in the event of a collision the telson and abdomen are violently agitated until the larva is clear of all obstruction.

The swimmimg habits of the Brachyurous zoea were studied by Weldon (1889), who came to the conclusion that the spines were of use to the larva in guiding its movements ; the validity of this assumption will be discussed later.

Although the observations recorded above relate to one stage of the life-history only, namely that in which the thoracic appendages are natatory, they will be sufficient to indicate the nature of some of the problems introduced by the study of the larvæ.

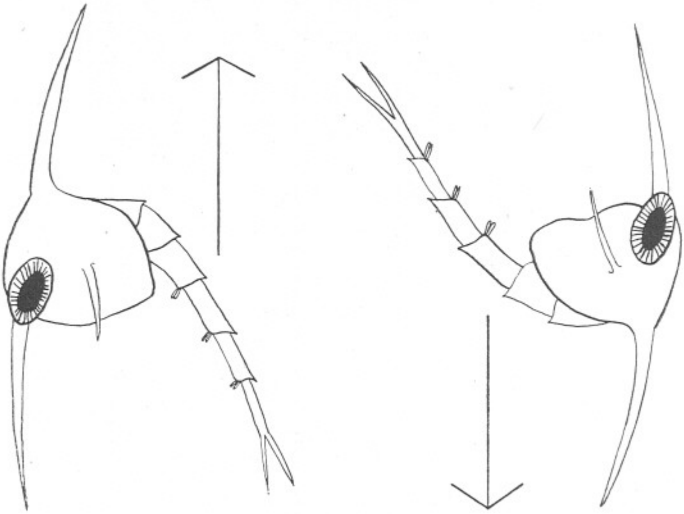

Fig. 5.—Diagram to illustrate the attitude of a Brachyurous zoea when swimming. Movement takes place in the direction indicated by arrows.

These problems may be conveniently divided into two groups :—

(1) The relation of the larva to its environment.
(2) The relation of the larva to other stages of the life-history.

The former presents physiological problems and the latter questions of morphology and phylogeny.

The Relation of the Larva to its Environment.

All larvæ have a tendency to sink. This tendency varies in (1) different species, (2) the same individual. As an example of the first it was found that at 19° C. a larva of *Porcellana* sp. when narcotised sank at the rate of 1 metre in 350 secs., while a Brachyurous zoea of the *Portunus* type, under the same conditions, sank at the rate of 1 metre in 85 secs. In the same individual the tendency to sink will vary with several physical factors, for example viscosity. It will vary also with the orientation of the larvæ to gravity.

Munida bamffica larvæ give a very good example of variation in orientation with respect to movement. Figure 2 shows that when the larva is moving the minimum resistance is offered to the water, whereas while " resting " the maximum is offered. The case of the Brachyurous larvæ is entirely different. All the specimens studied were of the type found in Portunus, that is to say that all four spines of the carapace are present and fully developed. Here there is no position of rest as in Munida, but to prevent sinking the swimming movements have to be continuous. The figure given above (1 m. in 85 secs.) for the sinking of a Brachyurous zoea is for a narcotised larva which sinks in the attitude shown in Figure 6. This attitude is never seen under normal conditions, where the dorsal spine is always directly upwards.

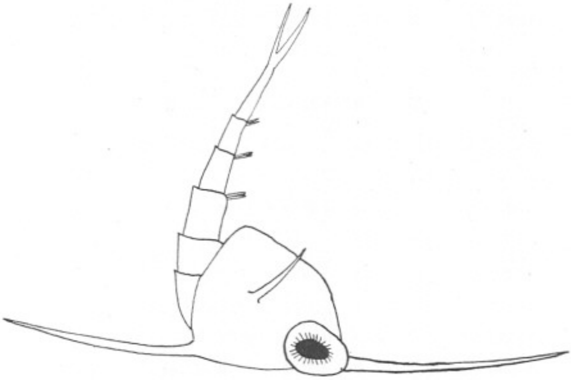

FIG. 6.—The attitude in which a narcotised Brachyurous zoea is found to sink.

This question of orientation is best discussed under the two headings of orientation to (1) Light, (2) Gravity.

(1) *Orientation to Light.*

In the case of orientation to light we are concerned with larvæ in motion. Clarke (1932), working on Daphnia, came to the conclusion that here orientation is a phenomenon with a physiological basis different from that of the other phototactic responses. In the case of Palæmonetes, Lyon (1906) remarked that the larvæ as regards the mode of orientation are negatively phototropic, while in their movements they are positively phototropic ; an idea which also indicates two distinct physiological processes. Spooner (1933) has shown that Decapod larvæ approach the source of light and not necessarily the point of greatest intensity of illumination.

This evidence suggests that certain areas of the eyes function as receptors which detect the direction of light, as appears to be the case in certain insects described by Mast (1924) and others.

Clarke (1930) pointed out that in Daphnia different responses were evoked by small and by large changes in the intensity of illumination; these latter may be considered as shock stimuli. In the observations recorded in this paper shock stimuli were used, and in this case response to the direction of light is all important, the larvæ showing no response to gravity at all; they make excursions in any direction with any side directed downwards as recorded by Weldon (1889), Thompson (1903), and by Spooner (1933).

(2) *Orientation to Gravity.*

The fact that the stimulus of light completely overcomes that of gravity does not show that the latter does not exist, as Thompson appears to imply. When the stimulus of light is removed the larvæ cease to execute forced movements and are free to carry out random movements; it is then that response to gravity is found.

Special attention has been paid to this aspect of orientation in Brachyurous zoea larvæ. In dull red light these larvæ appear to behave as if there were no light present at all. In these conditions they remain with the dorsal spine directed upwards and they carry out random movements in this attitude. The question arises as to how in the absence of light orientation is maintained. Gurney (1902) has pointed out that in the zoea stage there is no organ of balance and he suggested that the spines were in some way connected with this function. Experiments were undertaken with a view to investigating this.

It is clear from narcotising the larvæ that orientation is not a mechanical function of the body, but that it is dependent on consciousness. Amputation of the thoracic exopodites in a conscious larva also results in uncontrolled sinking, showing that orientation is also dependent on the muscular activity of these appendages.

Other functions of the spines which have been suggested are: (1) Protection; (2) Control of the direction of swimming; (3) Adaptation for resisting the tendency to sink.

These functions are not mutually exclusive, but one is probably primary, the others being secondary.

If these suggestions are examined more closely the following evidence is found.

(1) *Protection.*

Gurney (1902) found that small fish such as Gobies had difficulty in swallowing Brachyurous zoeas on account of the spines ; and I have to thank Mr. D. P. Wilson, of Plymouth, for informing me in a personal communication that he has seen Pipe-fish when feeding on a catch of mixed plankton deliberately pick out the copepods and avoid Brachyurous larvæ. When feeding the pipe-fish carefully scrutinise one organism after another and no attempt is made to get the zoeas into the mouth. While the cases are of great interest, it is difficult to suppose that small fish which exercise a choice are the chief enemies of zoeas ; for in the autumn plankton hauls many Medusæ and Ctenophores were present, and many were found to contain Decapod larvæ. Also Williamson (1904) has recorded that the larvæ of *Homarus vulgaris* eat Cancer larvæ. It would not appear, therefore, that the chief function of the spines is protective.

(2) *Direction of Swimming.*

Weldon (1889) pointed out that the spines of many Crustacean larvæ show a great tendency to develop in one straight line, parallel to the axis of the body ; he cites as examples the larvæ of Penæus and Hippolyte and the Galatheidea in general. And he said that the same result is arrived at in a slightly different way in the Brachyurous zoea. Perhaps it is not necessary to point out that this long axis of the body is in most cases the direction of movement. Weldon considered that the possession of these spines enabled the larvæ to make excursions more rapidly and in a more direct manner than larvæ which do not possess such spines. This must lead us to suppose that the spines have been developed to assist swimming movements in a definite direction. On the other hand, it must not be forgotten that if the spines were developed in connexion with some other function they would still control the direction of motion as movement in a plane at right-angles to that of the spines would be impossible for mechanical reasons.

I have to thank Dr. R. Gurney for pointing out that presumably Weldon is here referring to Claus's *Hippolyte* which has since been shewn to be *Callianassa.*

With regard to excursions in direct lines, experiments have shown that if the spines are cut off the larvæ lose none of their powers of swimming in a straight line nor are their swimming abilities in any way upset. It seems more probable that these larvæ owe their powers of direct and rapid movement to the very highly developed swimming mechanism which they possess, assisted, as Gurney's hypothesis would appear to indicate, by an efficient sensory organ functioning as does an otocyst and so helping the larva to maintain a definite orientation.

(3) *Adaptations for resisting the tendency to sink.*

In larvæ such as those of Munida, where a position of rest is taken up, there can be little doubt that the spines help to maintain the animal in a constant position in the water, but in the Brachyurous zoea no such position is known. That is to say, that the large dorsal and rostral spines are never in such a position as to aid flotation. In the case of the narcotised larva, however, these spines immediately come into the horizontal plane ; here their effectiveness as adaptations against sinking is shown by the following examples :

(1) Zoea 1.
Temp. 17·4° C.
Normal zoea.
Average sinking time for 6 journeys of 10 cm. . . . . 83·4 sec. per 1 m.
Same zoea.
Dorsal spine cut off. Average sinking time for 6 journeys of 10 cm. . . . . 66·0 sec. per 1 m.
Same zoea.
Rostral spine also cut off. Average sinking time for 6 journeys of 10 cm. . . . 64·4 sec. per 1 m.

(2) Zoea 2.
Temp. 19° C.
Normal zoea.
Average sinking time for 6 journeys of 10 cm. . . . . 130·6 sec. per 1 m.
Same zoea.
Dorsal and rostral spines cut off. Average sinking time for 6 journeys of 10 cm, . 121 sec. per 1 m.

There is, however, one period when this position seen in the narcotised larva is taken up during life, and that is during the periods of the moults when the larva has no control over its actions. Any adaptations which would lessen the tendency to sink while the moult is taking place would be an advantage, for the next stage larva would then have a lesser distance to swim up in order to regain its normal position in the plankton.

It may be pointed out that in the Megalopa stage the spines, if present, are small, and during its moult the larva must sink rapidly, so that the young crab stage automatically takes up its position at a greater depth. This point is of interest as Dr. Lebour (1928a) has pointed out that at least in British species there is only one megalopa stage.

(4) *Organs of Orientation.*

The suggestion made by Gurney (1902) that the spines in some way help the larva to orientate never appears to have had much attention devoted to it. Experiments and observations were made on living larvæ with a view to seeing if any facts could be brought to light which would strengthen or confirm Gurney's hypothesis. For the purpose of these experiments larvæ taken in the plankton were used; they were referred to the genera Portunus and Cancer. In the experiments which involved amputation of spines various control methods were devised, and it was shown that the phenomena observed were due to the injuries to the spines and not to the antennæ.

Observations on living larvæ which are not making excursions show definitely that orientation to gravity exists. The behaviour of a normal larva in dull red light has already been described; if the spines of such a larva are cut off either under an anæsthetic or not the behaviour, while remaining normal in the presence of white light, in the red light immediately becomes remarkably different. All sense of direction is lost; a larva that ceases to swim sinks in an uncontrolled manner, and larvæ which continue to swim pursue a spiral course and eventually finish with a spiral dive to the bottom of the containing vessel; once they have reached the bottom they find it very difficult to leave it again. In short, a larva which has had the spines cut off, although it behaves normally in light, in darkness cannot find its way about. The observations recorded above show that Gurney's suggestion is worthy of consideration.

How such an orientation mechanism would work is not easy to see at first glance, but the spines may probably be of assistance in magnifying differential pressure on the sides of the body. It may be noted that the spines appear to be very sensitive to touch, and if any of the four spines are touched with a needle or held with a pair of forceps, the telson is immediately bent round and scrapes the spine as if trying to remove the foreign object, in the same way that Gurney has described it cleaning the dorsal spine (1902).

In this connexion Dr. Lebour (1928b) has pointed out that the larvæ of *Ebalia tuberosa* have only rudimentary spines on the carapace and has suggested that this, together with the peculiar form of the telson, the fork of which is nearly obliterated, may be correlated with their bottom-living habit. Dr. Lebour goes on to point out that the larvæ of *Pinnotheres pisum*, another bottom-living species, show somewhat the same characters, but that the closely related *P. veterum* has all the spines of the carapace normally developed and has also a much larger telson in keeping with the fact that it is not restricted to the lower layers of the water, but is found right up to the surface.

In the absence of further evidence it is impossible to say whether the restriction of these species to the lower layers is due to their tendency to sink having no mechanical check, or whether it is due to these animals failing to find their way about during the hours of darkness.

SPEED OF SWIMMING.

Little appears to be known of the swimming capabilities of Crustacean larvæ ; Steuer (1910) records that a small Decapod larva could maintain its position against a current of water moving at the rate of 1 metre in 40 sec. The following are some average figures for specimens timed in the manner described above :—

Galathea strigosa (first larva). . .	Up at the rate of 1 m. in 50 secs.
,, ,, ,, ,, . .	Down ,, ,, 45 ,,
Galathea dispersa (first larva). . .	Up at the rate of 1 m. in 56 secs.
,, ,, ,, ,, . .	Down ,, ,, 50 ,,
Eupagurus sp. (last larva). . .	Up at the rate of 1 m. in 50 secs
,, ,, ,, ,, . .	Down ,, ,, 60 ,,

The above results were obtained at a temperature of 16° C. approx.

Pandalus sp. (late larva) at 17° C. .	Up at the rate of 1 m. in 67 secs.
,, ,, ,, ,, .	Down ,, ,, 48 ,,
Porcellana sp. at 17° C.	
When moving head first. . .	Up at the rate of 1 m. in 65 secs.
	Down ,, ,, 55 ,,
When moving telson first. . .	Up at the rate of 1 m. in 92 secs.
	Down ,, ,, 78 ,,

There are one or two remarks to be made about these figures. Firstly, they do not pretend to be very precise, but are included here as they show a rather remarkable similarity in different species and also approach the figure quoted above from Steuer. Secondly, the effect of gravity in the downward movement is not very noticeable in the smaller larvæ, such as the Anomurous forms, but in some of the larger species has a noticeable effect, for example in Pandalus. Thirdly, it will be seen that the speed of swimming in Porcellana larvæ depends on orientation.

In any attempt to apply these figures to conditions in the sea two uninvestigated factors have to be borne in mind : (1) Fatigue, we do not know how long the larvæ can keep up the speeds found in the experiments. (2) We do not know if the excursions made in the sea are really vertical and as direct as those made in response to an artificial stimulus.

If, however, the experimental conditions are in any way comparable to those found in nature, a migration of 40 metres could be carried out by a Porcellana larva, for instance, in about 40 minutes. This is well within the time given by Russell (1928), who has recorded such a migration taking place within two hours.

From the observations recorded above it is clear that the swimming activities of the larvæ are sufficient to account for the migrations which actually take place in the sea, and there is no need to invoke the aid of physical factors as do the theories of Ostwald and others. As regards the downward movement, it has been suggested that this is not due to the activities of the larvæ, but due to the injurious effect of the light inhibiting their movements so that they sink into deeper water where in the more congenial surroundings they become normally active once again. In my opinion the following facts: (1) that given a suitable stimulus the larvæ swim downwards; (2) that if the larvæ lose their power of movement they become orientated so as to afford increased resistance to the tendency to sink: show that as far as Decapod larvæ are concerned the downward movement is not a passive one, but an active one. Were the inhibition hypothesis correct, one would expect that the process of natural selection would have acted so that on loss of power of orientation the sinking to lower layers of water would have been as rapid as possible.

Finally, a practical point arises: should the vertical migrations in the sea take place at a rate in any way comparable with that found in the laboratory, the validity of conclusions as to the composition of populations as ascertained by horizontal hauls taken over any considerable length of time is brought into question. The experimental evidence leads me to suppose that marked changes in distribution may take place in such a short time as 15 minutes. This may serve to emphasise, if emphasis be needed, the importance of the time factor which has been fully discussed by Russell (1928).

THE RELATION OF THE LARVA TO THE OTHER STAGES OF THE LIFE-HISTORY.

Under this heading several points of morphological interest will be discussed. The larva may be looked upon as a free-living young stage well adapted to its mode of life; it comes between the stage passed through in the egg and the adult. During the larval stages swimming is one of the most important functions and it is not unnatural to assume that many of the structural modifications seen are connected with it. In the next few paragraphs an attempt will be made to indicate how the mode of swimming is influenced by the degree of development reached on hatching from the egg, and how, in turn, the mode of swimming influences the transition of the larva into the adult.

The nauplius is best regarded as a precociously developed head

(Graham Kerr, 1921) and it may be assumed that in an ideal larva the remaining segments of the body would develop in succession, each bearing a pair of appendages. The appendages of the nauplius do not, however, develop in their final form, but are temporarily modified to serve both swimming and feeding functions. When the later appendages appear they take over these duties, allowing the naupliar appendages to be remodelled and to assume the functions which they serve in the adult. In this way the swimming function would be passed backwards firstly to the thoracic and finally to the abdominal appendages.

It is interesting to note that this condition is nearest approached in the Penæidea where the swimming function is passed from head to thorax and then in turn to the abdomen ; but even here a modification, typical of the Eucarida, is to be noted ; this is that the segments of the hinder part of the body develop long before the appendages, and that the posterior thoracic region is compressed ; this leads on to the condition seen in other groups of the Eucarida, for example, the Caridea, where the segments of the posterior thoracic region are not differentiated until the greater part of the abdomen is developed. From the observations recorded above it would appear very likely that these modifications are due to the early need of the reversal mechanism which all these larvæ possess ; also it is for the same reason that the uropods, which form a part of the mechanism, are precociously developed in many species.

The Euphausid type of development is often quoted as being primitive, owing to the very large number of stages passed through ; but the very late appearance of the thoracic appendages would appear to point to a modification of the condition found in the Penæidea, the naupliar mode of progression being retained to a very late stage.

It should be noted that the various accounts of Euphausid larvæ are not very conclusive as to the swimming methods of these animals. From the evidence of Lebour (1925, p. 811) it would seem that the antennæ are the swimming organs until the end of the Furcilia stages is reached. It is during the Cyrtopia stages that the antennæ become differentiated into their adult constituents, and as Dr. Lebour goes on to say that the Cyrtopia merges imperceptibly into the adult one gathers that during these stages the pleopods are carrying out the function which they serve in the adult, namely, swimming. Cannon and Manton (1927), on the other hand, state (p. 247) : ". . . many larval forms, such as Euphausid larvæ, can walk on the endopodites of their thoracic limbs while the exopodites are swimming organs." They do not indicate at what stage the larvæ are observed to swim with the thoracic exopodites ; from Dr. Lebour's careful account it would not appear that this can be seen before the end of the Furcilia stages. Dr. Lebour, as is noted above, also says that the change from Cyrtopia to adult is imperceptible, so it is unlikely that any great change of function takes place here, and, as I have already said, the account given by Dr. Lebour leads me to suppose that during the Cyrtopia stages the appendages are carrying out the same functions which they serve in the adult. The functions of the appendages of the adult Euphausid have been described by Manton (1928), who says (p. 107 *et seq.*) that the pleopods are swimming organs, the thoracic exopodites being mainly concerned in producing a respiratory current. In my own limited observations all the Euphausid larvæ which I saw swam with the antennæ until the pleopods were developed.

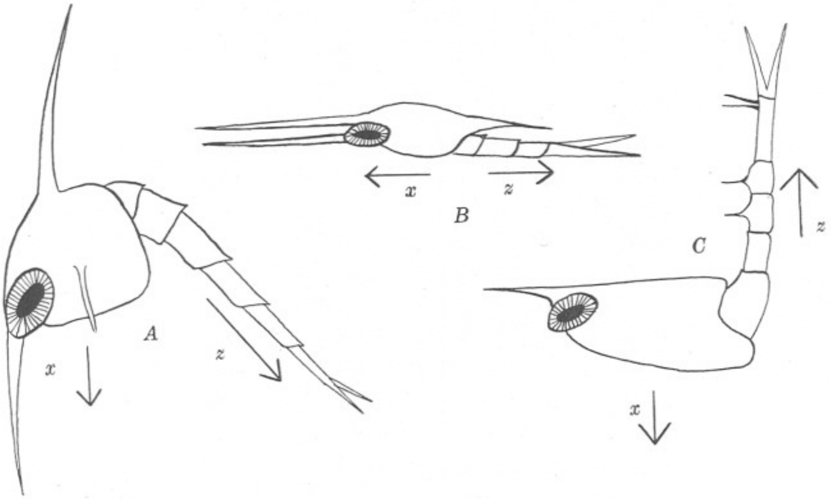

FIG. 7.—(*A*) Brachyurous zoea, (*B*) *Munida bamffica* (first larva), (*C*) *Nephrops norvegicus* larva (not to same scale). Diagram to show the direction of the effective beat of the thoracic exopodites, indicated by arrow *x*, and the direction in which the pleopods would beat if they were functional, indicated by arrow *z*.

In the Caridea although the development of the appendages is delayed, their order of appearance is from front to back, the thoracic exopodites becoming functional in sequence, except that of the fifth pereiopod which is never used for swimming. The Caridea have no naupliar stages so that no direction of movement is imposed upon the mysis stage as it would be if the antennæ were natatory as in the Penæidea. It is this absence of control which has probably resulted in the backward movement found in so many members of this and other groups. In the absence of any foreordained direction of movement the larvæ have been free to move in any direction and it is logical to assume that the backward one has been favoured, as with motion taking place in this direction the respiratory current would assist the movement and not hinder it. Not all larvæ, however, have adopted this method of progression; Crangon is an example of this: here the rotatory movement which has been recorded is probably not due to the absence of spines, as Weldon (1889) supposed, but to a relatively slow rate of movement, as compared with Portunus and Munida larvæ, caused by the antagonistic effect of the respiratory current.

The backward movement has undoubtedly contributed largely to the functional discontinuity between the mysis stage and that stage in which the pleopods first become functional. This discontinuity may also be due, in a large degree, to the postures taken up by different larvæ in which the abdomen is held in such an attitude that any action on the part of the pleopods would result in movement in a different direction to that caused by the action of the thoracic exopodites (see Figure 7).

The difference in the direction of the effective beat of the thoracic and abdominal appendages has been a dominating feature of the evolution of the larval forms of the Decapoda. As a result the natatory function has been confined to the more anterior thoracic exopodites which in such types as the Brachyurous zoea are highly specialised for this purpose.

It is disappointing that there are no records available of the swimming habits of the later larvæ of the Penæidea.* In such a species as *Penæopsis stebbingi*, the development of which has been described by Gurney (1927), it is difficult to imagine any abrupt change in swimming habits between the naupliar and mysis stages, the development of the thoracic appendages being very gradual; there is, however, a rather abrupt change to the Mastigopus stage. A form in which this latter change appears to be less marked is that of Acetes recorded by Brooks (1882). The functional significance of this discontinuity in the Penæidea is at present unknown, but occurring in this series of larvæ it is interesting as there is no apparent reason why the change from mysis to mastigopus should not be as gradual as that from nauplius to mysis. The explanation may lie in a difference of posture of thorax and abdomen such as has been described in other larvæ.

SUMMARY.

The swimming methods and habits of certain Decapod larvæ have been observed. The first larva of *Munida bamffica* was chosen for special attention. Such a study shows the importance of (1) orientation, (2) the presence of a reversal mechanism.

Observations on other types show these factors to be of great import-

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* Gurney (Ann. Mag. Nat. Hist. Ser. 9, Vol. 18, 1926, p. 26) has dealt with the swimming methods of Penæid larvæ in general terms but apart from Müller's observations there quoted we have no records of the attitudes in which these larvæ swim, especially in response to external stimuli.

ance and also show that there are a great variety of attitudes in which larvæ swim.

Points in the relation of the larvæ to their environment were next considered ; orientation is again important here, but whereas in Munida larvæ a " resting " orientation is found no such attitude is seen in Brachyurous zoeas.

Orientation to light was found to overpower completely orientation to gravity, but orientation to gravity exists, and it is argued that Gurney's hypothesis, which connects the spines of the carapace with the maintenance of equilibrium, should be examined more closely.

It is suggested that in the Brachyurous zoea the spines are of use as adaptations for lessening the tendency to sink mainly during the periods of moulting.

The speed of swimming has been considered and it is found that at temperatures of 14° C.–18° C. Anomurous larvæ can travel at the rate of 1 metre in 1 minute. This is a time well in accordance with Russell's results, obtained in the English Channel. Here fatigue is an unknown factor and it is not known if the whole migration is carried out in one stage ; if it were a migration of 40 metres such as Russell records it might take place in 40 minutes.

Reasons are given for believing that the downward migration of larvæ found at dawn is due to the activities of the animals themselves and not to physical factors or to passive sinking due to inhibition of movement resulting from an injurious effect of light.

The origin of some of the structural adaptations of the larvæ is discussed. The precocious development of the posterior region of the body is considered to be due to the early need for a reversal mechanism, provided for by the caudal fan at the end of a flexible abdomen. The importance of posture when swimming is pointed out and it is maintained that the backward movement seen in so many larvæ has helped to emphasise the metamorphosis between the last mysis stage and that in which the pleopods first become functional.

The backward movement itself is considered to be due to the absence of a naupliar stage in the life-history ; thus the mysis has no foreordained direction of movement and so in many cases swims backwards in order that the respiratory current will aid rather than hinder the speed of movement.

The swimming habits of crustacean larvæ and their bodily form are thus seen to be closely related.

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The Biology of *Balanus balanoides.* I. Growth rate and its relation to Size, Season and Tidal Level.

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With 4 Figures in the Text.

THREE workers have contributed recently to our knowledge of the growth rate of *Balanus balanoides* : Runnström (1925), and Hatton and Fischer-Piette (1932). The former kept a single patch of barnacles under observation for a year at Herdla, which is about 27 km. north-west of Bergen. By estimating at different times of year the size distribution of the spat, and of the first and second year groups, which he could differentiate by their size, colour and shape, he obtained a curve for the growth of the animal for the normal duration of its life. His investigations also cover the maturation of the gonads. And he finds that the normal course of life is for the animals to settle on the rocks in April. Towards the end of the following year the ovaries are developed, and in the spring of the third year the larvæ are liberated. Most of the adults die after this, only a possible few surviving to spawn the following spring. His measurements comprise the length only of the shells, and he says that the successive year groups may be distinguished by their degree of flattening.

Hatton and Fischer-Piette (1932) worked on the growth of individuals near St. Malo during the greater part of two years, and investigated the effects of varying degrees of shelter and tidal level on this growth rate. Their results will be referred to in greater detail later in this paper, but they may be summarised in the following two relations : the most larvæ settle, and the greatest growth takes place, at the most exposed places, and at the lowest tidal levels. They show also that growth is at a maximum from April to June-July, and practically at a standstill for the rest of the year.

METHODS.

In the present work it was felt that it would be desirable to employ a method of measurement which would allow of the calculation of the volume of the animal. This is necessary in the first place to cope with the variations of shape as between individuals, and in the second place to afford a measure which, unlike length, increases more or less in a simple ratio with age. Such a measure is more than ever necessary when, as Runnström states, the animal is continuously changing its conicity throughout life (although no such change has been detected at Port Erin). In the present paper, where the volume of the animal is referred to, this is the volume of a cone with a height equal to the height of the apex of the shell above the surface of attachment, and a basal diameter equal to the average of the length and breadth of the base. Such an assumption takes no account of the truncation of the cone, but it gives a value related sufficiently closely for our purposes to the external volume of the animal, and it is the only such value which may readily be obtained from measurements of the animal taken *in situ* on the rocks. It is hoped in a future paper, to relate this calculated volume to the true body weight of the barnacle. Where the length of the animal is given, this is the length of the base through the rostrum and carina, as in the two works referred to above.

The locality chosen was a vertical face of rock, facing south-west, in a long cleft in the rocks running from low to high-water in the Dub Reef in Port Erin Bay. The position is fairly exposed, with few fucoids growing on the rocks. Three patches of barnacles were selected on this surface, one near the bottom of the barnacles zone (B. 1), one higher up (B. 2), and a third (B. 3) at the extreme top of their range. By inspection these patches seemed quite typical for this region. Their levels, at the mid-height of the patches, are as follows :†

B. 1. —0·75 feet O.D. or about mid-tide level.
B. 2. +2·74 feet O.D.
B. 3. +4·58 feet O.D., or about high water of neap tides.

Full scale photographs allowed of the identification of individuals, about a hundred of which were kept under observation on each patch for a whole year. At intervals of from one to two months each individual was measured (length, breadth and height), and as soon as the new spat were large enough for measurements in the field, a series of these also was included. A note was made also of all individuals which died, and whose shells were either empty or missing.

As the newly settled spat were too small for measurement *in situ*, a number of these were distinguished by a ring marked round them on the rock, and a series of them was brought in from time to time for accurate measurement in the laboratory. When the barnacles are small, it is possible to detach them from the rocks without damage. Two sets of these small barnacles were collected, the first group " O " representing typical animals which had settled about the end of April, while the second

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† Levels determined by Mr. J. R. Bruce. The tidal range at Port Erin is about ± 4 feet for average neap tides, and ± 8 feet for average spring tides.

group " Q " represent spat which settled later in the year, and whose growth was apparently retarded at first by the summer heat. Finally the length of about eight hundred barnacles in each of the groups B. 1, B. 2 and B. 3 was measured in June 1932, and from these a size-distribution diagram was obtained for each group for the date in question.

TREATMENT OF RESULTS.

The individual measurements for each patch, about five thousand in all, are too numerous to reproduce here, but their analysis is given in Tables I, II and III. For each patch of barnacles there is a series of readings from which the volumes can be calculated as described above, for each of about a hundred individuals, and taken at five to seven times in the year. Each of these periods has been dealt with separately, and in it the individuals have been grouped according to their size at the commencement of the period, the limits of each group having been so chosen as to include an adequate sample. The limits of experimental error in the initial measurements are of the order of about $\pm 10\%$. This is reduced in the grouping together of a number of animals, but since the groups vary in size, no final error can be given which would be universally applicable. In each of the groups, as shown in the tables, the stated volumes and volume increments are the means of all the individuals comprised in the group. From the increase in volume in each group the *growth rate* has been calculated, this being defined as the average percentage increase in volume per ten days.

RELATION OF GROWTH RATE TO SIZE.

The figures show very marked differences in the growth rates of the barnacles, both at different sizes and at different times of the year, as well as at different levels. Comparison of the last two factors is rendered difficult by the very much greater growth rates of the smaller individuals. In Figure 1 (and Table IV), seasonal variation has been eliminated, by plotting the year's mean growth rate against size and shows the difference of growth rate with size, as well as the fact that the barnacles are growing faster at successively higher levels.

SEASONAL VARIATION IN GROWTH RATE.

The seasonal variation in growth rate may be seen from the figures in the last columns of Tables I, II and III by interpolating values to allow of the comparison of animals of the same size. The simplest condition, found in the smaller animals of all the patches, is that of an animal having a high growth rate for a short period in the spring or summer, followed by a period of slower growth throughout the winter. The time of maximum growth rate varies on the different patches, and with different sizes of barnacles, but sufficient information is not yet available to allow of an interpretation of these differences. It is to be hoped that they may become clearer when more is known about the seasonal changes in the soft parts of the barnacle. In the larger individuals of B. 1 and B. 3, there is, in addition to the summer growth period, a second period of increased growth rate in the winter, which in the largest members of B. 3 considerably surpasses the summer rate. The fact that such a winter period is not shown in B. 2 may possibly be due to the overwide spacing of the winter readings.

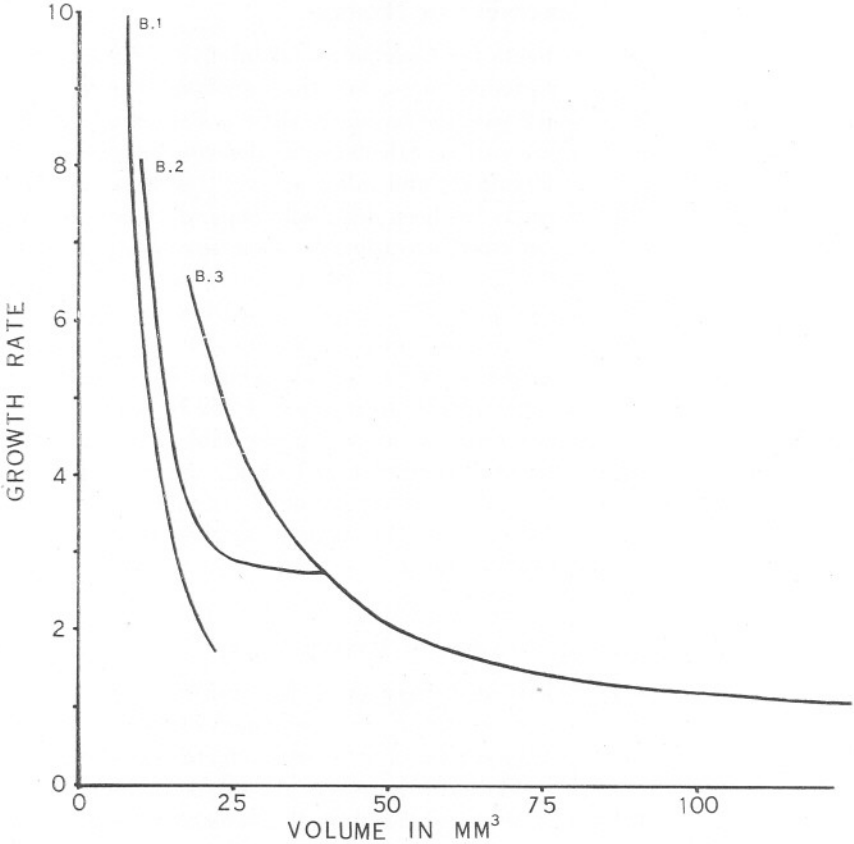

FIG. 1.—Relation of mean yearly growth rate to size. The rate is greatest in the smallest individuals, and in those at the highest level (B. 3).

THE GROWTH OF THE NEWLY-SETTLED SPAT.

All the data discussed up to this point, concern barnacles which were sufficiently large to be measured *in situ* on the rocks. It is necessary to consider here the growth curves obtained for the spat of the " O " and " Q " groups, samples of which were periodically brought into the laboratory for measurement. The measurements of these are given in Table V, and the results are shown graphically in Figure 2.

On April 25th, 1931, large numbers of Cypris larvæ commenced to settle on the rocks, and a first sample of metamorphosed individuals was collected on April 30th. The individuals marked at this time comprise the " O " group, and represent the typical members of the community. Later in the year a number of very small individuals were noticed, whose size suggested that they were newly settled. On October 5th these had a volume of 1·75 cu. mm. as compared with an average volume for the " O ' group of 12 cu. mm. A number of these smal individuals were ringed, and they comprise the " Q " group. The suggestion that these were newly settled spat was however disproved by a photograph of the rock surface taken on July 22nd in which some of the " Q " group were seen to be already present. It would appear, therefore, that these " Q " barnacles settled later than the " O " ones, and were not able to get through their early period of rapid growth before the heat of the summer.

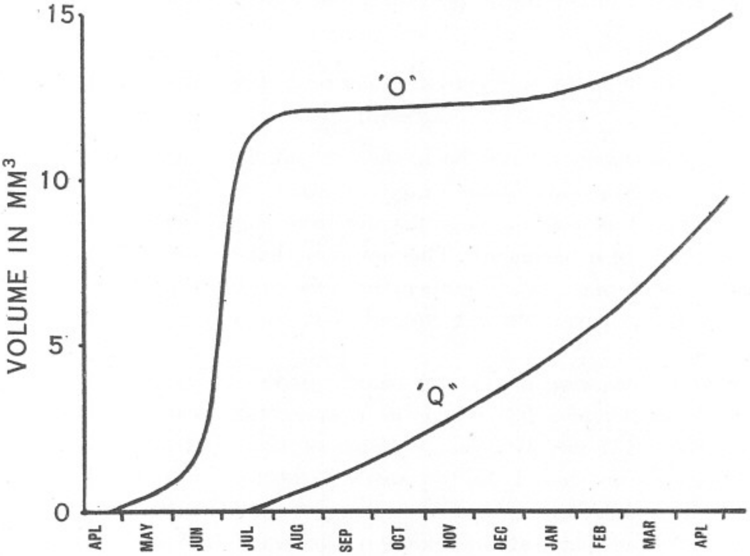

FIG. 2.—Growth of young individuals during their first year. The " O " group are typical, and the " Q " group late-settled specimens.

Figure 2 shows the retarding effect of the summer hot period on the barnacles of both groups. By the beginning of the following year, the " Q " group have made good progress, and are catching up with the " O " group, so that in May their respective volumes are 9·6 and 14·9 cu. mm. One point which emerges from the comparison of these two groups is that the wide differences of size found in first-year barnacles is not maintained in the second year, thus justifying the choosing of a definite size as representing the typical barnacle of any age, as is done below. As the barnacles of the " O " and " Q " groups were not taken from the exact level of any of the three patches, their results have not been utilised in the calculation of the initial portion of the curves shown in Figure 3.

THE GROWTH OF A TYPICAL BARNACLE THROUGH SUCCESSIVE YEARS.

The measurements have been carried out for one year only, but, since they cover the whole range of sizes of individuals found in the locality, it is possible to construct from them a curve representing the whole life of a barnacle. This assumes that the year of observation was a typical one. The temperature observations in Port Erin Bay throughout the period do not suggest that the year 1931–32 was very abnormal.

The first measurement, *in situ* on the rocks, of the young barnacles was made in August 1931 when the average first-year members of the groups B. 1, B. 2 and B. 3 had volumes of 4·66, 8·84 and 6·38 cu. mm. These figures are based on too small a number of individuals to be accurately representative, but they suggest that the greatest growth of young spat takes place at the middle of the zone (B. 2), and then successively less well at the top of the zone (B. 3) and at the bottom of it (B. 1).

Commencing with the above sizes, and using growth rates for each period, which were read from curves relating growth rate to initial size, the growth of a typical barnacle for each patch was calculated for a series of years. The figures so obtained are given in Tables VI, VII and VIII, and the results are shown graphically in Figure 3. The calculations have been continued in the case of B. 1 and B. 2 into their third year, and in the case of B. 3 into its fourth year. As will be shown later this represents the span of life of the majority of the individuals of B. 1 and B. 2, but a portion only of the life of many individuals of B. 3.

It will be seen from Figure 3 that, with the exception of the first year, the growth rate is greatest on B. 3 and slightly less on B. 2. The deficiency in the first year is regained by B. 3 by the beginning of the second year, and from then on members of B. 3 are always slightly larger than members of B. 2 of the same age. Throughout the whole of its life B. 1 has a much smaller growth rate than either of the other patches.

Runnström's data give a length at the end of the first year (Dec.–Jan.) of about 6·5 mm., and for a similar period in their second year of about 9·5 mm. Hatton and Fischer-Piette's figures for the same ages are between 2·5 and 3·0 mm. for the first year, and about 5·5 mm. for the second year. They do not give sufficient data to allow of the conversion of these data into volumes, but if the Port Erin figures are expressed as length, the results are as follows :—

	HERDLA.	PORT ERIN.			ST. MALO.
		B. 1	B. 2	B. 3	
Length at the end of the first year	6·5 mm.	4·7	5·3	5·2 mm.	2·5–3·0 mm.
Length at the end of the second year	9·5 mm.	6·5	7·6	8·1 mm.	5·5 mm.

Thus in all cases the values for Port Erin lie between those of Runnström and those of Hatton and Fischer-Piette. The former does not state the level in his locality, or its condition with regard to exposure. In the case of Hatton and Fischer-Piette's figures there is a considerable difference at the end of the first year in the sizes attained in sheltered and in exposed positions ; but this difference appears from their graph to have been entirely made up in the second year, although they do not mention the fact in the text.

The sequence of growth rates in these three localities is of interest since it is that of ascending latitude, the growth rate being highest in the most northerly latitudes. (St. Malo 49° N., Port Erin 54° N. and Herdla 60° N.)

Length of Life.

According to Runnström, most of the barnacles die after spawning, in their third year, only a possible few living to spawn again the following year. The data to be considered below show that, while this is true for the lowest zone (B. 1), and to a lesser extent for B. 2, the members of B. 3 may live for five or six years, and probably considerably longer.

It is a general observation on most parts of the coast which are not very exposed, that barnacles are smaller near low water, and become steadily larger towards high water : and further that at the extreme top of their range, there are found individuals much larger than are found anywhere lower down. In order to obtain an expression of these differences, between 700 and 1000 individuals were measured on each of the three patches, in June 1932. Owing to the large number of measurements required, lengths only, and not volumes were taken, but volumes were obtained by formula from the lengths, as will be explained later. It must be emphasised that the object of this set of readings was to obtain a measure of the frequency of occurrence of the larger members of the community, and not to obtain the year group sizes. Thus, owing to the large size of the groups taken, the exact position of the size group peaks is somewhat masked in Figure 4.

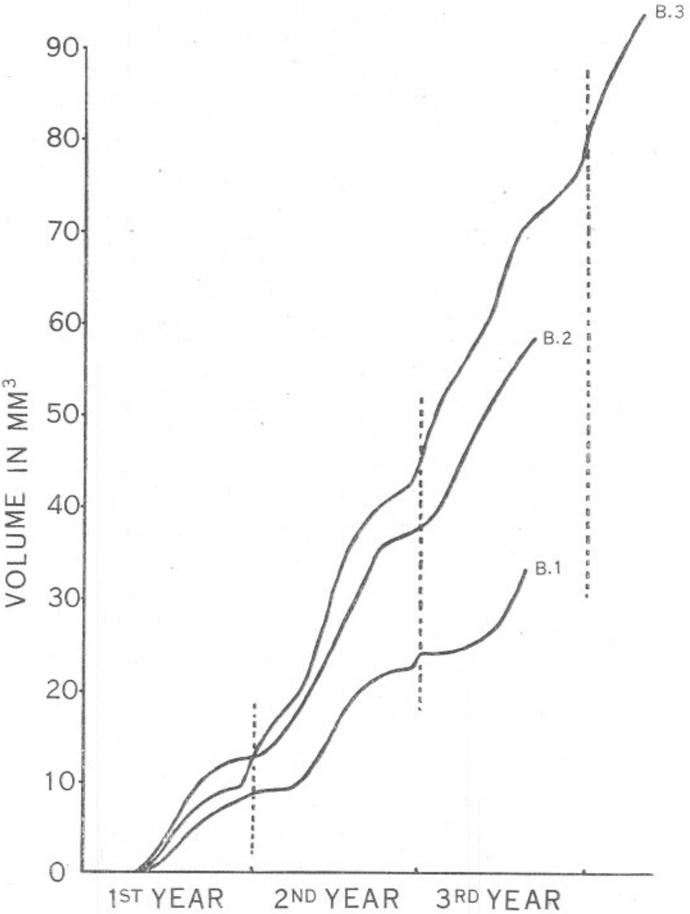

FIG. 3.—Growth throughout the life of typical individuals at the three levels. The curves for B. 1 and B. 2 represent the normal duration of life at those levels, but B. 3 individuals may live for perhaps six or more years.

The lengths were measured, as in Runnström's work, through the rostrum and carina. The percentages in each millimetre group—neglecting the spat—which were too small to be measured accurately—are given in Table IX. The spat were counted, and their numbers are entered in Table IX, but these have not been taken into account in the calculation of the percentages.

In Figure 4 these percentages have been plotted against lengths. It must be remembered, in examining this graph, that while volume is approximately a straight line function of age, length is not so. A curve has therefore been superimposed in Figure 4 relating volume to length for the barnacles in question. This has been drawn from the formula

$$\text{length} = \sqrt[3]{\frac{\text{volume}}{0{\cdot}084}}$$

which has been arrived at by taking the mean value of $\frac{\sqrt[3]{\text{volume}}}{\text{length}}$ for various sizes, in all individuals measured during the year. Runnström stated that there was a change of apical angle of the older barnacles. Our groups do not show any trace of such a change, although it has been noted on other parts of the Manx coast, especially where there is much overcrowding ; and also elsewhere in isolated specimens growing under estuarine conditions. Since in our group there is no change of shape, and the volume is a straight line function of the cube of the length, such a formula may legitimately be used to interpret the lengths of Figure 4 as volumes.

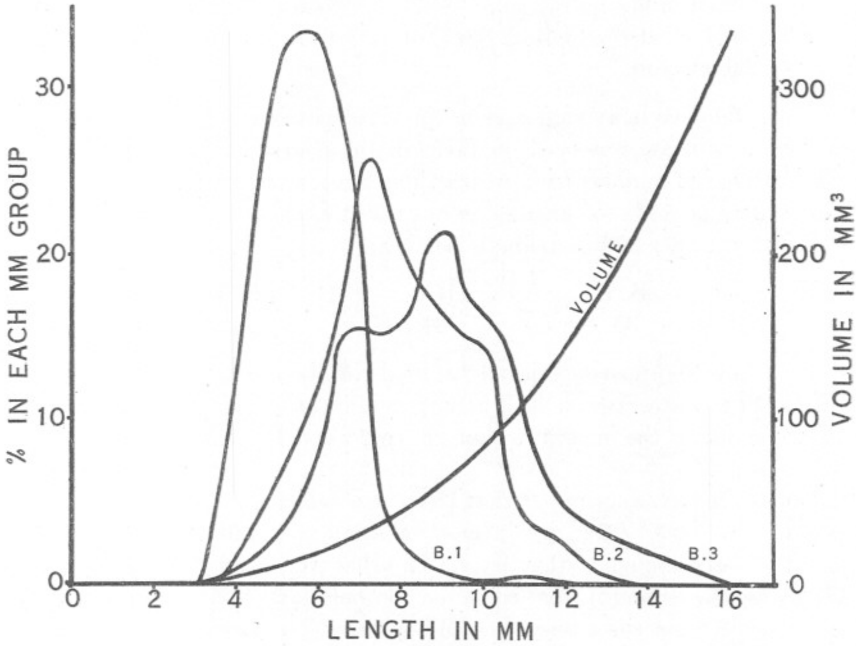

FIG. 4.—Size distribution curves for the three patches, and a curve relating to length volume.

Although not produced for this purpose, Figure 4 indicates the sizes of the various year groups on the three levels in June, and these values bear out the validity of those which have been obtained by the other methods already described. B. 1 shows a second year peak only, B. 2 a second and a doubtful fourth year peak only, and B. 3 second and third year peaks. The three curves show clearly the size differences at the three levels, especially if the lengths are translated into volumes from the curve included in the figure for that purpose. Summarising these results we get the following :—

4% of B. 1, 58% of B. 2, 72% of B. 3 have a volume greater than 50 cu. mm.

0·3% of B. 1, 18·5% of B. 2, 33·0% of B. 3 have a volume greater than 100 cu. mm.

0·0% of B. 1, 0·0% of B. 2, 6·0% of B. 3 have a volume greater than 200 cu. mm.

The difference in average age on the three patches is further borne out by the death-rate observed on them in the course of the observations. The number of animals from which these figures are drawn, is small, but their differences are too great to be the result of chance.

Death-rate per 100 individuals per year.

B. 1	B. 2	B. 3
35	21	3

The above figures concern only animals of about four months old and over. The death-rate on B. 3 is surprisingly low, and it may be noted that not one of the deaths in that group occurred among the very large specimens.

It has already been noted that there is a relatively sparse population in the top, B. 3, zone, and also that small individuals are relatively slightly less common at that level. In other words, on the top zone the young barnacles find it hard to gain a foothold, and to attain a sufficient size to withstand the adverse conditions there, but having once attained a sufficient size, they are likely to grow faster and to live longer than they would have done at a lower level where their earlier life would have been easier.

Hatton and Fischer-Piette's work shows clearly the greater numbers of young Balanus settling at lower levels, but the meaning of their mortality figures is less clear. At their most exposed locality the mortality at the end of the first year, is considerably less at low water than higher up the shore. On the other hand, in a more sheltered locality, the mortality for the first year becomes steadily greater towards low water. Unfortunately they give no figures for the mortality on the highest patch of all, at the top limit of the Balanus zone.

GENERAL.

The difference of level of the three groups of Balanus studied is not very great. It covers, however, the whole range for the shore at Port Erin. B. 1 was typical of all those barnacles growing at that and a lower level on the beach, that is to say, on this beach, down to about three feet below mean sea level. B. 2 was typical of the intermediate zone, and B. 3 of the small uppermost zone. The latter is the upper limit of their distribution, and although a few may be found slightly higher, none extend more than two feet higher, that is to say above 7·5 feet above mean sea level.

The B. 1 type of barnacles are small, and usually rather less numerous than the B. 2 type. The latter are undoubtedly the most numerous on the shore, and hence may be taken as typical. The B. 3 type, although less numerous than B. 2, is usually much larger. It almost certainly spawns many times in its life, and, being large, produces a large amount of spawn. The B. 2 type, on the other hand, usually spawns only once and then dies. (Runnström, 1925, p. 39.) It is therefore possible that the B. 3 type plays a much more significant part on the shore than its numbers would suggest. It is hoped in a later paper to extend this account to less, and more exposed localities.

I should like to express my indebtedness to Mr. J. R. Bruce for assistance in making some of the measurements, and to all members of the staff here who have assisted at various times ; also to Prof. J. H. Orton and Dr. E. J. Allen for helpful criticism of the paper.

SUMMARY.

1. The volumes of *Balanus balanoides*, at three levels of the shore, have been observed for a year.

2. The young barnacles grow very much faster than older ones.

3. The growth rate varies greatly with age, season and tidal level, but in general there is a period of maximum growth in the summer, and very little growth in the winter.

4. Growth, except during the first year, is greatest higher up the shore.

5. Young barnacles, which settle too late in the year, have their growth retarded by the summer heat, but almost catch up in size the earlier settled spat, by the beginning of the next year.

6. The growth rates found are intermediate between those recorded from Herdla (near Bergen), and those from near St. Malo.

7. Most of the lower- and middle-zone barnacles die in their third year, but those from the extreme top zone may live for five years or more.

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TABLE I.

The Growth Rates on the B. 1 Patch throughout the Year.

Volumes in cubic millimetres. Growth rate is the percentage increase in volume per ten days.

	Date.	Initial volume range.	Initial volume average.	Final volume average.	Mean volume for the period.	Growth rate.
1931	5 May	0–6	3·98	9·34	6·66	26·9
	to	6–8	7·1	13·0	10·5	16·64
	20 June	8–12	9·25	13·4	11·32	8·96
		12–	17·4	20·1	18·7	3·1
	20 June	0–8	5·4	10·43	7·91	15·0
	to	8–13	10·8	15·6	13·2	7·18
	21 Aug.	13–17	15·1	19·8	17·45	5·02
		17–	20·3	25·5	22·9	4·13
	21 Aug.	0–4	2·86	4·9	3·33	9·8
	to	4–6	5·28	8·24	6·76	7·68
	2 Nov.	6–16	10·9	14·0	12·45	3·89
		16–	21·1	23·6	22·35	1·62
	2 Nov.	0–6	4·47	5·07	4·77	3·83
	to	6–10	8·66	9·05	8·55	1·28
	7 Dec.	10–20	14·2	14·5	14·35	0·61
		20–	25·6	25·9	25·75	0·33
	7 Dec.	0–7	5·27	6·24	5·75	5·12
	to	7–10	8·85	10·13	9·49	4·03
1932	12 Jan.	10–15	12·07	13·29	12·68	2·81
		15–	21·0	22·6	21·8	2·11
	12 Jan.	0–7	4·64	4·94	4·79	1·38
	to	7–15	10·24	10·36	10·30	0·25
	9 March	15–	22·63	22·73	22·68	0·09
	9 March	0–5	3·94	5·84	4·89	8·61
	to	5–7	5·89	7·73	6·81	5·70
	3 May	7–10	8·85	10·50	9·67	4·02
		10–	12·77	14·30	13·53	2·18

TABLE II.

The Growth Rates on the B. 2 Patch throughout the Year.

Volumes in cubic millimetres.

	Date.	Initial volume range.	Initial volume average.	Final volume average.	Mean volume for the period.	Growth rate.
1931	12 Jan.	0–4	3·1	8·3	5·6	15·75
	to	4–8	5·65	12·55	9·1	11·85
	25 April	8–15	10·6	16·8	15·7	5·68
		15–25	19·4	25·4	22·4	3·0
		25–	36·6	44·3	40·35	2·20
	25 April	0–7	5·6	11·9	8·75	20·1
	to	7–10	8·5	14·0	11·25	11·5
	20 June	10–15	11·7	16·1	13·9	6·72
		15–20	17·4	22·5	19·95	5·06
		20–30	24·0	30·6	27·3	4·92
	20 June	0–12	9·6	14·2	12·9	7·75
	to	12–15	13·3	17·8	15·55	5·45
	21 Aug.	15–20	17·6	22·5	20·05	4·26
		20–	31·4	39·4	35·4	4·10
	21 Aug.	0–7	5·1	8·3	6·7	11·2
	to	7–10	8·6	11·3	9·95	5·62
	16 Oct.	10–13	11·4	14·9	13·15	5·49
		13–19	15·9	19·5	17·7	4·5
		19–30	24·4	29·6	27·0	3·81
		30–	38·9	46·2	42·55	3·34
	16 Oct.	0–10	7·12	8·57	7·84	2·27
	to	10–15	12·60	13·87	13·23	1·12
1932	14 Jan.	15–20	17·40	18·50	17·95	0·70
		20–	32·4	33·8	33·1	0·48

TABLE III.

THE GROWTH RATES ON THE B. 3 PATCH THROUGHOUT THE YEAR.

Volumes in cubic millimetres.

	Date.	Initial volume range.	Initial volume average.	Final volume average.	Mean volume for the period.	Growth rate.
1931	13 Jan.	0–6	4·2	8·8	6·5	10·4
	to	6–10	8·01	13·25	10·7	6·22
	29 April	10–30	21·9	32·0	26·95	3·91
		30–40	34·7	47·0	40·85	3·35
		40–70	57·1	68·25	62·6	1·86
		70–	129·0	142·0	135·5	0·95
	29 April	0–18	11·3	16·4	13·8	10·0
	to	18–40	22·3	29·7	26·0	7·4
	13 June	35–50	43·1	48·1	45·6	2·6
		45–55	51·0	54·0	52·5	1·74
		55–75	63·2	66·2	64·7	1·41
		75–	124·5	132·5	128·5	1·43
	13 June	0–20	15·0	26·2	20·6	11·3
	to	20–30	23·2	31·9	27·55	5·68
	18 Aug.	30–40	34·7	44·1	39·4	4·12
		40–70	53·45	63·32	57·88	2·51
		70–	147·2	154·6	150·9	0·76
	18 Aug.	0–5	4·10	5·44	4·7	5·28
	to	5–15	8·44	10·82	9·63	4·55
	19 Oct.	15–30	21·9	24·7	23·3	2·60
		30–45	38·0	41·5	39·75	1·49
		45–55	50·4	52·8	51·6	0·77
		55–65	60·6	63·6	62·1	0·80
		65–80	70·9	73·6	72·75	0·62
		80–	126·0	129·6	127·8	0·46
	19 Oct.	0–10	6·15	8·15	7·15	5·35
	to	3–15	10·35	11·72	11·03	2·27
	9 Dec.	10–50	31·8	33·8	32·8	1·0
		50–	97·1	101·5	99·3	0·74
	9 Dec.	0–10	7·09	10·07	8·58	11·65
	to	10–30	19·05	22·90	20·97	5·62
1932	14 Jan.	30–50	38·91	43·16	41·03	3·04
		50–70	58·7	63·2	60·95	2·13
		70–	94·1	100·64	97·87	1·93

TABLE IV.

RELATION OF YEAR'S MEAN GROWTH RATE TO SIZE AT THE THREE STATIONS.

Volumes in cu. mm.

B. 1		B. 2		B. 3	
Volume.	Growth rate.	Volume.	Growth rate.	Volume.	Growth rate.
7	9·95	10	8·08	17·5	6·59
10	5·94	12	6·10	20	5·85
13	3·84	15	4·32	25	3·12
16	3·25	17	3·74	35	2·04
19	2·09	20	3·27	50	1·41
22	1·70	30	2·86	75	1·19
		40	2·71	100	1·05
				125	

TABLE V.

VOLUMES (IN CU. MM.) OF YOUNG INDIVIDUALS IN THEIR FIRST YEAR.

"*O*" *Group.*	Date.	Volume.	
1931	April 25	—	Just settling on the rocks.
	April 30	0·103	
	May 14	0·329	
	June 9	1·20	
	July 1	5·57	
	July 29	12·5	
	Aug. 22	11·7	
	Sept. 15	12·6	
	Dec. 7	11·5	
1932	May 7	14·9	

"*Q*" *Group.*	Date.	Volume.	
	July 22	—	Visible in photographs.
	Oct. 5	1·75	
	Dec. 7	3·28	
	May 7	9·60	

TABLE VI.

CALCULATED GROWTH THROUGHOUT THE LIFE OF A TYPICAL MEMBER OF B. 1 PATCH, AS DEDUCED FROM CURVES DRAWN FROM TABLE I; THE INITIAL VOLUME, ON AUGUST 21, 1931, BEING 4·66 CU. MM.

	Period.	Volume at commencement of period.	Growth rate during period.
1st year	Aug. 21–Nov. 2	4·66	8·00
	Nov. 2–Dec. 7	7·38	1·68
	Dec. 7–Jan. 12	7·82	4·18
2nd year	Jan. 12–March 9	9·00	0·30
	March 9–May 1	9·13	3·58
	May 1–June 20	10·93	7·26
	June 20–Aug. 21	14·89	5·10
	Aug. 21–Nov. 2	19·60	1·80
	Nov. 2–Dec. 7	22·17	0·37
	Dec. 7–Jan. 12	22·46	2·06
3rd year	Jan. 12–March 9	24·13	0·08
	March 9–May 1	24·22	0·84
	May 1–June 20	25·34	1·53
	June 20–Aug. 21	27·28	3·99
	Aug. 21–	33·53	

TABLE VII.

CALCULATED GROWTH THROUGHOUT THE LIFE OF A TYPICAL MEMBER OF B. 2 PATCH, AS DEDUCED FROM CURVES DRAWN FROM TABLE II; THE INITIAL VOLUME, ON AUGUST 21, 1931, BEING 8·84 CU. MM.

	Period.	Volume at commencement of period.	Growth rate during period.
1st year	Aug. 21–Oct. 16	8·84	5·74
	Oct. 16–Jan. 12	11·68	1·11
2nd year	Jan. 12–April 25	12·85	4·46
	April 25–June 20	18·75	4·98
	June 20–Aug. 21	23·99	4·10
	Aug. 21–Oct. 16	30·09	3·56
	Oct. 16–Jan. 12	36·09	0·49
3rd year	Jan. 12–April 25	37·68	2·16
	April 25–June 20	46·08	4·92
	June 20	58·73	

TABLE VIII.

CALCULATED GROWTH THROUGHOUT THE LIFE OF A TYPICAL MEMBER OF B. 3 PATCH AS DEDUCED FROM CURVES DRAWN FROM TABLE III; THE INITIAL VOLUME, ON AUGUST 18, 1931, BEING 6·38 CU. MM.

	Period.	Volume at commencement of period.	Growth rate during period.
1st year	Aug. 18–Oct. 19	6·38	5·61
	Oct. 19–Dec. 9	8·59	2·63
	Dec. 9–Jan. 13	9·97	9·20
2nd year	Jan. 13–April 29	13·26	5·60
	April 29–June 13	21·13	6·60
	June 13–Aug. 18	27·40	5·35
	Aug. 18–Oct. 19	37·06	1·38
	Oct. 19–Dec. 9	40·23	0·86
	Dec. 9–Jan. 13	42·34	2·83
3rd year	Jan. 13–April 29	46·64	2·28
	April 29–June 13	57·89	1·57
	June 13–Aug. 18	61·98	2·13
	Aug. 18–Oct. 19	70·68	0·63
	Oct. 19–Dec. 9	73·44	0·76
	Dec. 9–Jan. 13	76·84	1·93
4th year	Jan. 13–April 29	82·18	1·41
	April 29–June 13	94·36	1·42
	June 13	100·40	

TABLE IX.

SIZE DISTRIBUTION (LENGTHS, IN MM.) ON THE THREE PATCHES ON JUNE 2, 1932. LENGTHS MEASURED TO THE NEAREST WHOLE MM. THE 1932 SPAT, SHOWN IN BRACKETS IN THE NUMBERS COLUMN, ARE EXCLUDED IN THE CALCULATION OF THE PERCENTAGES.

	B. 1		B. 2		B. 3	
Length.	No.	%	No.	%	No.	%
1	—	—	—	—	—	—
2	(597)	—	(559)	—	(437)	—
3	—	—	—	—	1	0·33
4	44	13·4	4	1·22	3	0·99
5	102	31·1	20	6·14	8	2·64
6	108	32·9	39	11·9	24	7·94
7	64	19·4	81	24·8	47	15·5
8	8	2·43	65	19·8	48	15·8
9	2	0·61	52	15·9	64	21·1
10	—	0·0	45	13·8	49	16·1
11	1	0·33	13	3·98	29	9·60
12	—	0·0	7	2·14	13	4·30
13	—	—	1	0·31	9	2·97
14	—	—	—	—	5	1·65
15	—	—	—	—	3	0·99
16	—	—	—	—	—	—
Total	329 +(597)		327 +(559)		303 +(437)	

A Comparison of the Biology of *Echinus esculentus* in Different Habitats.

Part I.

By

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With 5 Figures in the Text.

THE material for this study of racial differences in *Echinus esculentus* was obtained from three grounds in the neighbourhood of Port Erin, Isle of Man. The three grounds differed widely in nature, and hence the means of capture, and the ease of obtaining adequate samples was different for each ground. The first locality, designated " Breakwater," is on the lee side of a ruined breakwater in the mouth of Port Erin Bay, entirely submerged at high tides, but accessible by boat at low water. The Breakwater stands on a bottom of sand and shell, in a depth of about five fathoms. It is composed of loose concrete blocks, largely overgrown with *Balanus balanoides* and *Spirorbis borealis.* It is too exposed to support a very large Fucoid vegetation, but in the lower zones there is a very heavy growth of *Laminaria cloustoni*, *L. digitata*, and *Saccorhiza polyschides* with an undergrowth of *Gigartina stellata.* The urchins were collected with a long-handled net, and thus include some individuals which were actually exposed to the air, and others from a depth down to about one fathom at low water. In this particular locality urchins are extraordinarily abundant, and large numbers are exposed at low water of spring tides.

The second ground, the " Breast," lies about a mile off Port Erin, and in a depth of 17–20 fathoms (Fig. 1). The bottom is sand and shell, with a typical fauna (**4**, p. 36, Pl. I). Urchins were obtained from it with a small otter trawl. The third ground—" Chickens "—lies about four miles west of the Chickens rock in 37 fathoms, on a bottom of rather muddy sand mingled with boulders. The urchins are obtained from this ground in traps set by the fishermen to catch " Buckies " (*Buccinum undatum*). The urchins obtained from these creels are of small size, and it has been suggested that this is due to a selective action in the catching power of the creels. But this is negatived by the fact that similar creels, similarly baited, and set on inshore grounds, in a depth of about five fathoms, habitually take large numbers of large urchins. As only twelve creels were in use, and the supply from them was dependent on visits from fishermen, the number of urchins from this ground was limited, and the data obtained from them are in general not as full as those from the other two grounds. The present paper is concerned more particularly with the first two grounds, and it is proposed to discuss in another paper the special significance of the "Chickens" type of urchins.

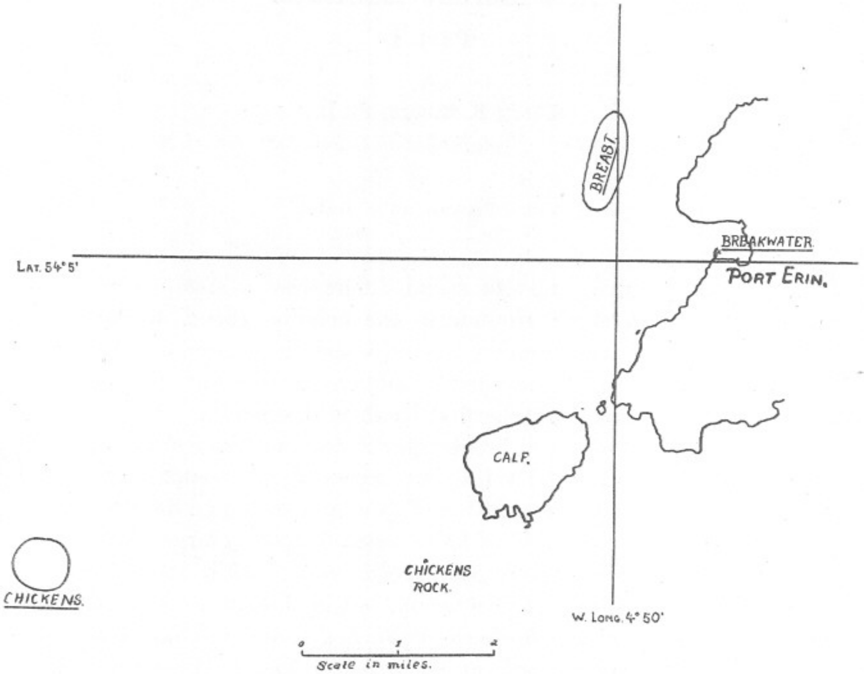

FIG. 1.—Map of the south end of the Isle of Man showing the positions of the grounds from which the three types of urchins were obtained—Breakwater (Littoral), Breast (17–20 fathoms), and Chickens (37 fathoms).

METHODS.

Wherever possible, samples of at least fifty individuals were taken, but as this was not always possible, the numbers used are in every case indicated in the tables. In a few cases, samples taken from the same ground within a few days have been grouped in order to obtain an adequate sample. With regard to the adequacy of the sample, those from the breakwater were always from exactly the same locality, and the samples are fairly regular in their constitution. Those from the Breast and Chickens are, on the other hand, liable, from the method of their collection, to come from slightly varying localities, and the resulting irregularity is apparently reflected in the less regular graphs obtained from these grounds.

The following measurements were taken, though not all of them were obtained from every specimen : *Test diameter*, taken with pointed-ended calipers between the spines. *Test height*, measured in the same way. *Test volume* (TV), obtained by immersion of the whole animal in a vessel full of sea-water, and fitted with an overflow, so that the displacement could be measured. *Gonad volume* (GV), estimated by immersing the whole gonad, after removing it from the animal, in a measuring cylinder containing a known amount of water. A series of measurements of *Shell thickness*, in conjunction with certain other factors, was made on a separate series of specimens from each ground. The measurement was made under a microscope, fitted with a micrometer eyepiece, on the ground edge of the shell, the latter having been cut at mid-height, at the suture of the inter-ambulacral plates. These shell thicknesses will be discussed in more detail in a future paper.

Ripeness was estimated by examination under a microscope of a pipette sample taken from the gonad, and smeared on a slide. The criterion of ripeness varied slightly in the two sexes. Since the male products are mostly ripe by the time they are shed into the cavity of the gonad follicle, the smear would not normally show many spermatogenesis stages, even in an unripe individual, although these would be present in the follicle wall. The presence of a considerable number of ripe and active sperm in the cavity of the follicle has been taken as the criterion of the ripeness of the male, but this does not mean that many more sperm may not be in the process of ripening. In the case of ovaries if unripe ova are present in the follicle at all, these will be found in the smear, along with any ripe ova which are present. In the case of females ripeness was recorded only when more than about 95% of the ova were actually ripe. Although this difference of criterion between the two sexes will in part account for the apparent earlier ripening of the males, it does not seem to do so entirely, and it must be remembered that the males so recorded as ripe were at least capable of yielding considerable quantities of ripe sperm.

PHYSICAL CONDITIONS ON THE GROUNDS.

A general description of the nature of the grounds has already been given. The sea temperatures for Port Erin Bay, and hence for the Breakwater specimens, are discussed later. The temperatures on the Breast are less extreme than those in the shallow waters of the Bay, and further, the intertidal specimens will, if above low water, be exposed to extremes of air temperature from which those living below low water are protected. Not much is known of other conditions on the grounds beyond the obvious fact that there is much more light on the Breakwater ground than on either of the other two. How this factor may affect the urchins is not known. The Breakwater is very much richer in food than either of the other two grounds, and examination of the urchin gut contents shows that those from the Breakwater are feeding largely on *Balanus* and algæ, both of which are very abundant in this littoral zone. Algæ appear to form a big proportion of the diet, and the specimens from the two deeper water grounds will only be able to obtain an algal diet from such weeds as may drift out to sea and settle on their grounds. The bottom on the Chickens ground is probably rather muddy, and it is known that it is bordered on the seaward side by a region of deeper water and mud bottom on which Echinus could not thrive.

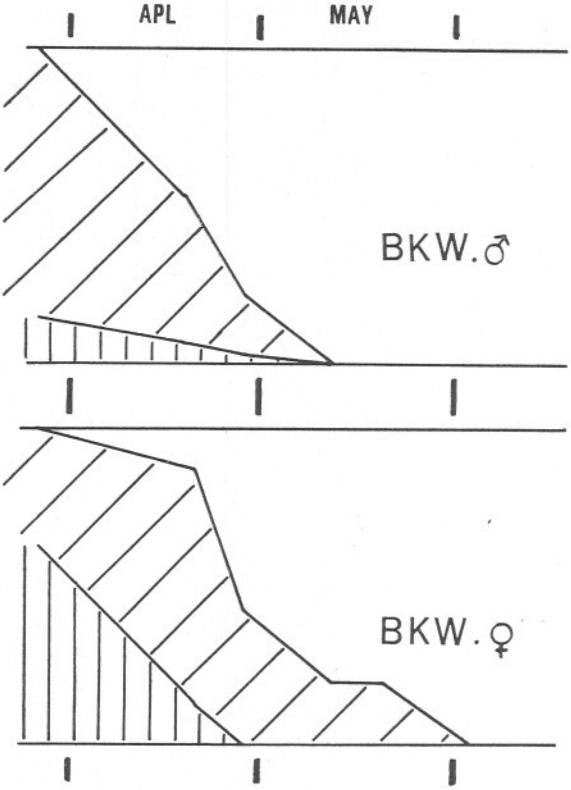

Fig. 2.—Diagram showing the relative proportions (%, vertical scale) of unripe, ripe, and spent urchins of either sex on the Breakwater in 1931. For details see Fig. 3.

RIPENING OF THE GONADS.

The available data on the condition of the gonads throughout the year are given in Tables III, IV, and V, and are also shown in Figures 2 and 3. The 1931 spawning was watched in detail on the Breakwater only, but that of 1932 was watched on all grounds. The gonad condition during the intervening period was watched on the Breakwater and Breast, but sufficient material was not available from the Chickens. It will be seen in the first place (Figs. 2 and 3) that on all grounds the males ripen before the females. The partial explanation of this has been mentioned already. On the Breakwater the males ripen during the summer, and are nearly all ripe by the autumn ; while fully ripe females do not begin to appear until February, and during the early part of the spawning time, spent females may be found alongside unripe individuals. On the Breast the males begin to ripen later, i.e. in October, and are nearly all ripe by the end of February, when the females commence to ripen. The data from the Chickens are few, but the gonad condition on that ground seems to follow a very similar course to that on the Breast.

GONAD VOLUMES.

In order to allow of the comparison of the sizes of gonads in animals of different ages, the gonad volume has been expressed in Figure 4 and Tables I and II as ten times the actual gonad volume, divided by the test volume $\left(\frac{10.GV}{TV}\right)$. The test volume has been chosen as a measure of size of animal in preference to test diameter, since the relative height may vary considerably both with increasing age, and among individuals of the same age from different grounds. At first the animals were divided into several size groups, and these considered separately, but it was found that there was no difference of relative gonad size according to the size of the animal, so all sizes were eventually grouped together, thus allowing larger samples, and more accurate results. In the same way there was found to be no difference in the time of spawning, according to the size of the individual, so in considering the time of spawning, all sizes have again been grouped together.

The great difference in size attained by the gonads on the Breakwater and on the Breast is most noticeable (Fig. 4), and is specially significant when it is remembered that the gonad is the only organ of the body in which the urchin is able to lay up a reserve of food material, and that the Breakwater affords the richest feeding-ground. That the whole of the food so stored is not required for spawning is indicated by the fact that the gonad volumes on the Breakwater do not ever fall as low as the

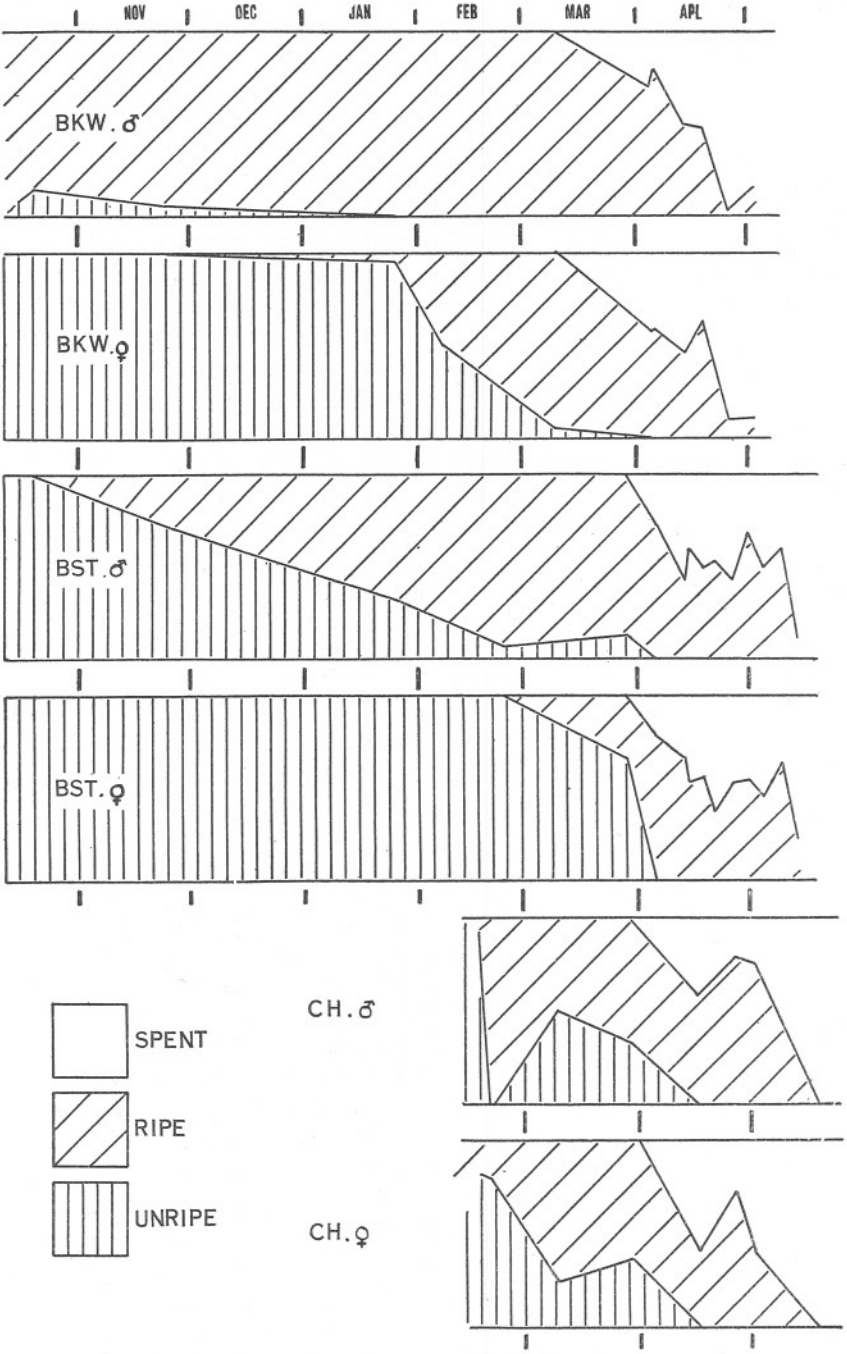

FIG. 3.—Diagram showing the relative proportions (%, vertical scale) of unripe, ripe, and spent urchins of either sex on the three grounds in 1932—Breakwater (BKW), Breast (BST), and Chickens (CH).

maximum value obtained by the gonads in the Breast. This is true not only of the population as a whole, but also of individuals. The Breakwater urchins never become spent completely, while on the Breast the spent

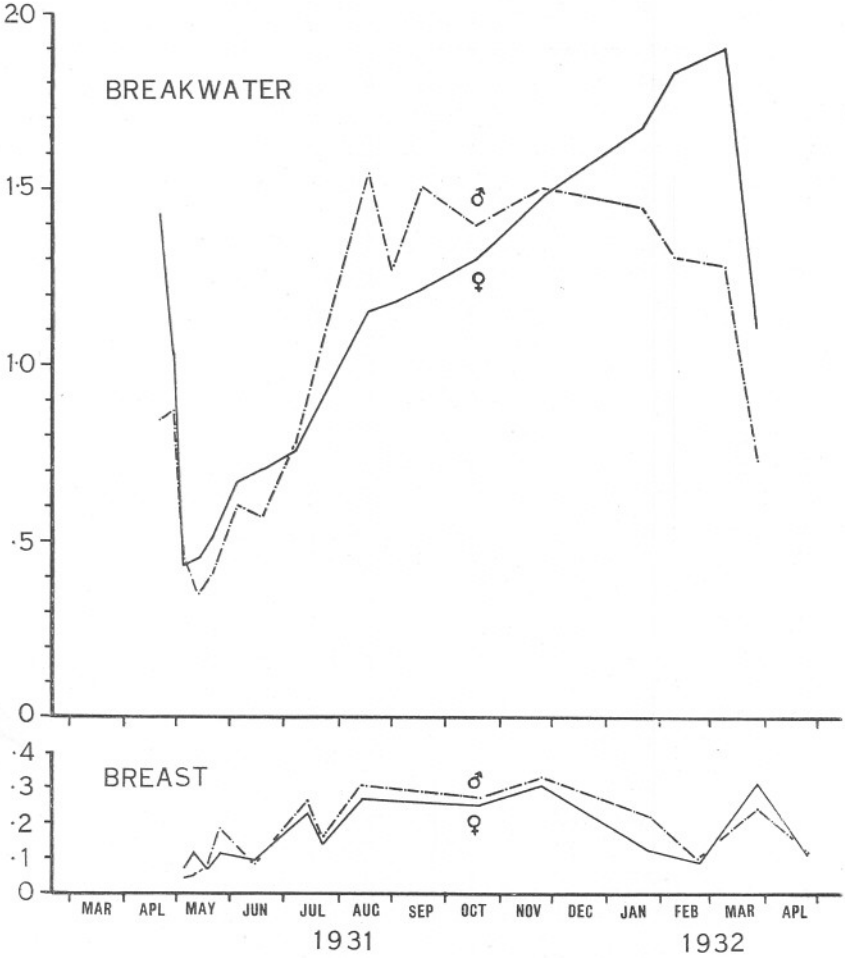

Fig. 4.—The seasonal variation in the volume of the gonads of urchins from the Breakwater and Breast grounds in 1931–32. The gonad volumes are expressed as ten times the actual gonad volume divided by the test volume of the animal.

gonad is reduced to a very small trace. At their maximum the Breast gonads attain a value of $\frac{10.GV}{TV}$ of only ca.0·4 while the values on the Breakwater rise as high as 2·0, and even higher in individuals.

On the Breakwater the males attain their maximum gonad volume in August, and then remain more or less constant until spawning sets in. The females, on the other hand, increase rather more slowly, but their gonads continue to grow in volume right up to the time when spawning commences, and by then they are considerably larger than those of the males. On the Breast both sexes seem to run a more or less similar course, reaching their maximum about August, but the variation between successive samples somewhat masks the finer details of the process. The drop in the gonad volumes in both sexes on this ground in Jan.–Feb. may be due to inequalities of sampling, but may, on the other hand, have a real significance. But since the data are insufficient to decide either way, the point need not be discussed here, although it would be most interesting if it could be investigated further.

Stott (**3**) has described the changes in the percentage of glycogen, total carbohydrate, and total fats in the gonads of urchins from the Breakwater, during maturation and over the period of spawning. In the first place he finds no significant difference in the percentages of any of these between the two sexes, and as the various percentages vary during the year, they do so more or less similarly in both sexes. The percentage of total fats does not seem to alter much throughout the year, but the percentage of total glycogen in the gonad rises very sharply after spawning (his first post-spawning measurement is in June), and then drops steadily until spawning again occurs. There is a suggestion that this glycogen is being converted into some other form of carbohydrate, at any rate immediately prior to spawning. Now he shows that the percentage of glycogen in both ova and sperm is considerably less than it is in the whole gonad from which they were obtained. This fact, together with the sudden rise in the percentage of glycogen in the gonad when the ripe genital products have been shed, suggests that the food reserves are stored in the form of glycogen in the nutritive bodies in the gonad, and are transformed into other substances as they are absorbed into the ripening genital products. Further, his data with regard to the similarity of carbohydrate and fat percentages in the two sexes, in conjunction with the evidence of different behaviour in the rate of increase of size of gonad in the male and female (Fig. 4), suggests that there must be a marked difference in the feeding behaviour between the male and female, since the former produces fresh gonad very rapidly, and then remains little changed throughout the late summer, autumn, and winter, while the female is continuously increasing throughout this period. Finally the full female has a gonad about twenty per cent bigger than that of a full male.

TIME OF SPAWNING.

The only reliable data for 1931 are for the Breakwater, and these are shown in Figure 2. The results for all grounds for 1931 are shown in Figure 3 and all are tabulated in Tables III, IV, and V. The 1932 spawning, at any rate on the Breakwater, took place between two and four weeks later than it did the preceding year, that is to say it took place in April–May in 1931 and in March–April in 1932. On the Breast and Chickens, spawning took place about a fortnight later in 1932 than on the Breakwater, and on all grounds the spawning period covered about two months. Whereas, however, the spawning of both sexes is more or less complete on both the deep water grounds, on the Breakwater relict sperm and ova are retained in considerable quantities in the gonads, and artificial fertilisations were readily made with them throughout the summer, and even as late as Christmas.

THE RELATION OF SPAWNING TO TEMPERATURE.

The later spawning of the Breakwater urchins in 1931 as compared with 1932 is associated with lower temperatures in the water of the bay in the year of later spawning (Fig. 5). The year's minimum temperature occurred in both 1931 and 1932 in the second week of March, and in both years spawning commenced within a few weeks of this date. In 1931 spawning commenced about the end of March, when the temperature in the bay was about 6·5° C., and in 1932 it commenced about the first week of March at a temperature of about 7·2° C. But, since the exact date of the commencement of spawning is difficult to determine accurately, it is preferable to compare the dates at which 50% of the community are spent. This took place in 1931 at a temperature of 7·0° C. and in 1932 at 7·8° C. No temperatures were recorded on the Breast in either of these years, but in 1933 the Breast temperatures at the spawning season were about 0·5° below the corresponding temperatures in Port Erin Bay. This would correspond with a lapse of about a fortnight before the Breast attained the temperature at which spawning set in on the Breakwater. Although this is only a rough approximation, it is in agreement with the lag of about a fortnight between the times of spawning on the Breakwater and Breast. In 1931 (Fig. 2) the urchins of both sexes ripened considerably later on the Breakwater than they did in 1932, and this also is perhaps associated with the lower temperatures in the winter of the former year.

Orton (**2**) records that urchins taken in from five to ten fathoms at Plymouth, spawned from April to June, when the temperature ranged from about 9·0° to 13·0° C. At Millport, in the Clyde, the spawning period given by Elmhirst (**1**) is from February to August, with a maximum in May. This corresponds with a temperature range there of about 7° to 13° C. with a maximum spawning at about 9·8° C. Our figures of 7° to 8° are therefore slightly lower than those for Millport, and

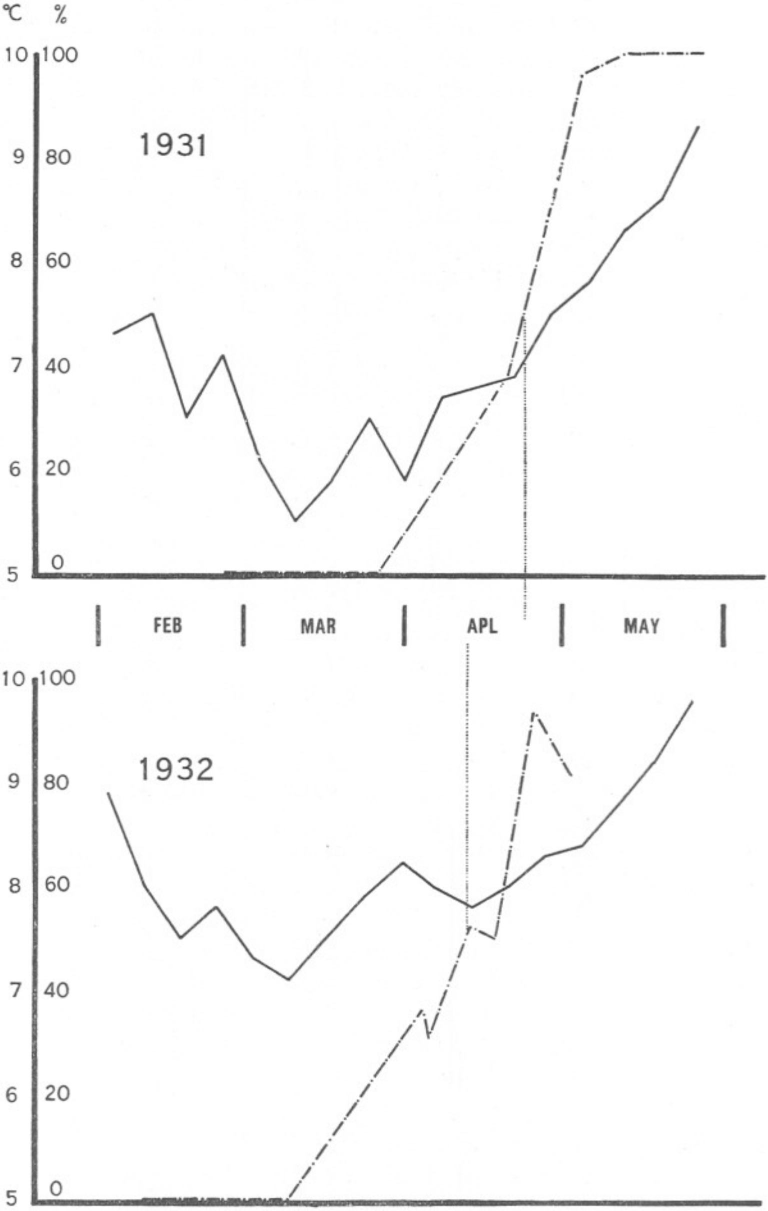

Fig. 5.—The relation of spawning (percentage of spent individuals—broken line) to temperature (whole line) on the Breakwater in 1931 and 1932. The position of 50% spawning is indicated by a vertical dotted line in each case.

definitely lower than those for Plymouth. Also the spawning time seems to be about a month earlier here than it is at either Plymouth or Millport. But in all three localities the commencement seems to follow fairly soon after the temperature first starts to rise, although the interval would seem to be least at Port Erin.

GENERAL CHARACTER OF THE URCHINS FROM THE THREE GROUNDS.

The Breakwater urchins show a greater range of colours than those from deeper water. The Breakwater ones range from violet to rusty red, the colour being present throughout a fairly thick layer in the surface of the test. The Breast and Chickens practically never show a violet colouration except in the spines, the test colour varying between pale brown and reddish.

Shape is not a good criterion since it varies greatly with age ; a young specimen of 1 cm. diameter having a value of $\frac{\text{height}}{\text{diameter}}$ of 0·52 while one of 7 cm. diameter will be considerably taller with a value of about 0·7. But this varies on the different grounds. A small sample taken in about 3½ fathoms at the Niarbyl, north of Port Erin, had a normal H/D value at 1 cm. diameter, but at 4 cm. it was 0·8. Specimens of the same size from the Breakwater were not nearly so tall. In fact these were the tallest specimens found here. There seems, further, to be a tendency for the largest specimens to flatten somewhat. The largest specimen taken by us on the Breakwater had a diameter of 12·1 cm., and an H/D of 0·63.

In shell thickness there is a regular difference between the Breakwater and the Chickens urchins at all sizes, the shell thickness for a Chickens urchin of 4 cm. diameter being 0·71 mm., while that of a Breakwater urchin of the same size is 0·96 mm. The Breast urchins are of a curious type, the young ones having a shell thickness typical of what a young Breakwater one would have were such ever found (see below), while the adults from the Breast have the typical thickness of the rarely found adult Chickens urchin. It is not intended to discuss in the present paper more than the fact that such a well defined difference does exist between the urchins from the three types of ground. Its significance will be dealt with in another paper.

Finally, the three grounds differ markedly in the size of the urchins which are found on them. On the Breakwater no very small specimens are taken, the smallest which I have seen being 2·5 cm. diameter, and even this was in 1933 when exceptionally small specimens were being taken there. Normally, urchins are hardly ever seen there with a diameter of less than about 7 cm. The same may be said of the littoral specimens obtained at the Niarbyl and in the Calf Sound, at the former of which localities urchins are abundant between tide marks on a low spring tide, but in the Sound a few only are taken. On all these grounds it is normally only large specimens which are taken. Specimens up to 10 cm. in diameter are common on the Breakwater. The largest I have seen at Port Erin measured 12·1 cm. in diameter, and came from the Breakwater, but even larger ones have been recorded there.

On the Breast, on the other hand, all the smaller sizes are very abundant, and 8 cm. diameter is about the maximum size usually attained ; a few are taken up to 9 cm., but I have not seen any as large as 10 cm.

On the Chickens ground similarly, all the smaller sizes are abundant, but here the maximum size is even smaller, few over 4 cm. diameter being taken, and none over eight. In this case it is probably a case of the migration of the larger individuals off the ground, but the discussion of this probability is postponed until more data are available.

SUMMARY OF RESULTS FOR THE BREAKWATER AND BREAST.

There are two types of ground at Port Erin, differing widely in the general environmental conditions, and each with a characteristic type of urchin on it. The difference is sufficiently well marked for the local fishermen, who collect the urchins for sale to summer visitors, to distinguish them as different types. The littoral urchins from the Breakwater are larger and thicker shelled than those from the Breast. Their gonads reach a greater maximum size, and, in fact, never fall as low even as the maximum volume for the Breast urchin gonads. This difference is probably correlated with the much greater food supply on the Breakwater, since the gonad is the one organ of the body in which the animal can store reserve food material. Spawning commences in March or April and lasts for about two months, but is slightly earlier on the Breakwater than on the Breast. Ripening also takes place considerably earlier in both sexes on the littoral ground. Spawning seems to set in at a temperature of about 7° C., and the colder winter of 1931, compared with 1932, was associated with a later ripening and spawning in the former year. Similarly it is suggested that the slightly later spawning on the Breast than on the Breakwater is correlated with the slightly later rise in the temperature of the water on the deeper water ground in the spring.

I wish to express my indebtedness to Prof. J. H. Orton who is responsible for the inception of this work on Echinus, as well as for the

examination of a number of the earlier samples : I am also indebted to Miss E. C. Herdman for obtaining some of the trawled material for me, and to Mr. J. R. Bruce for examining certain samples in my absence.

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TABLE I.

SEASONAL VARIATION IN THE GONAD VOLUME ON THE BREAKWATER.

Date.	♂		♀	
	$\frac{10\ GV^*}{TV}$	Number of specimens.	$\frac{10\ GV}{TV}$	Number of specimens
1931				
April 21	(0·84)	27	(1·43)	10
April 29	(0·87)	33	(1·03)	19
May 5	0·45	19	0·43	6
May 13	0·35	13	0·46	32
May 21	0·41	4	0·51	10
June 4	0·61	18	0·67	29
June 19	0·57	18	0·71	34
July 7	0·78	16	0·76	43
August 18	1·54	5	1·16	23
September 1	1·27	3	1·18	9
September 17	1·51	2	1·22	7
October 18	1·39	26	1·30	30
November 25	1·50	18	1·48	18
1932				
January 26	1·44	31	1·67	19
February 8	1·31	29	1·83	18
March 9	1·28	27	1·90	21
March 28	0·73	12	1·11	13

TABLE II.

SEASONAL VARIATION IN GONAD VOLUME ON THE BREAST.

Date.	♂		♀	
	$\frac{10\ GV^*}{TV}$	Number of specimens.	$\frac{10\ GV}{TV}$	Number of specimens.
1931				
April 28	(·362)	19	(·218)	17
May 5	·046	16	·072	9
May 11	·062	15	·117	10
May 18	·079	14	·073	6
May 26	·186	18	·118	28
June 16	·089	33	·099	44
July 16	·264	8	·226	12
July 22	·158	51	·143	35
August 15	·310	37	·270	45
October 20	·272	22	·263	16
November 25	·332	22	·312	36
1932				
January 26	·224	23	·125	25
February 23	·112	17	·095	7
March 28	·242	23	·316	27
April 26	·121	29	·118	20

* The gonad volume is expressed as ten times the gonad volume divided by the test volume (external).

TABLE III.

SEASONAL VARIATION IN GONAD CONDITION ON THE BREAKWATER.

	PERCENTAGES.								
Date.	Unripe.	Ripe. ♂	Spent.	Unripe.	Ripe. ♀	Spent	Numbers examined. ♂	♀	Percentage of total spent.
1931									
March 27	15·7	84·3	–	62·8	37·2	–	51	51	0
April 21	7·7	46·2	46·2	12·5	75·1	12·5	26	8	38·2
April 29	3·1	18·7	78·3	–	42·1	57·9	32	19	70·6
May 5	–	5·3	94·7	–	–	100	19	6	96·0
May 13	–	–	100	–	20	80	9	10	100
May 21	–	–	100	–	20	80	8	5	
June 4	–	–	100	–	–	100	18	29	
June 19	–	–	100	–	–	100	17	33	
July 7	–	–	100	–	–	100	16	43	
October 16	8·4	91·6	–	100	–	–	12	16	
October 20	14·3	85·7	–	100	–	–	14	12	
November 25	5·6	94·4	–	100	–	–	18	18	
1932									
January 26	–	100	–	94·7	5·3	–	30	19	
February 8	–	100	–	50	50	–	28	24	
March 9	–	100	–	4·8	95·2	–	29	21	0
April 4	–	70	30	–	57	43	30	28	36·2
April 5	–	79	21	–	58	42	28	24	30·8
April 13	–	50	50	–	46	54	8	13	52·3
April 18	–	38	62	–	63	37	26	24	50·0
April 25	–	4	97	–	10	90	33	30	93·6
May 2	–	16	84	–	11	79	18	19	81·1

TABLE IV.

SEASONAL VARIATION IN GONAD CONDITION ON THE BREAST.

	PERCENTAGES.							
Date.	Unripe.	Ripe. ♂	Spent.	Unripe.	Ripe. ♀	Spent.	Numbers examined. ♂	♀
1931								
April 28	–	–	100	–	–	100	17	19
May 5	–	–	100	–	–	100	43	39
May 10	–	–	100	–	–	100	15	10
May 26	–	–	100	–	–	100	18	27
June 16	–	–	100	–	–	100	28	32
October 20	100	–	–	100	–	–	22	16
November 27	71·5	28·5	–	100	–	–	7	18
1932								
January 26	33·3	66·6	–	100	–	–	21	26
February 24	7·2	92·8	–	100	–	–	14	7
March 28	13·6	86·4	–	66·6	33·3	–	22	27
April 5	–	73	27	–	79	21	33	28
April 13	–	43	57	–	67	33	30	20
April 14	–	60	40	–	54	46	26	25
April 18	–	50	50	–	57	43	16	21
April 21	–	54	46	–	38	62	24	26
April 26	–	42	58	–	54	46	24	33
April 30	–	69	31	–	55	45	29	27
May 4	–	50	50	–	46	54	24	24
May 9	–	60	40	–	64	36	15	31
May 13	–	8	92	–	23	77	25	26

TABLE V.

SEASONAL VARIATION IN GONAD CONDITION ON THE CHICKENS.

PERCENTAGES.

Date.	Unripe.	Ripe.	Spent.	Unripe.	Ripe.	Spent.	Numbers examined.	
		♂			♀		♂	♀
1931								
May 6	–	–	100	–	66·6	33·3	2	3
May 21	–	42·8	57·2	–	20	80	14	10
May 28	–	60	40	–	–	100	5	10
June 13	–	5	95	–	–	100	20	33
June 25	–	–	100	–	–	100	1	2
1932								
February 17	92·8	7·2	–	82·4	17·6	–	14	17
February 20	–	100	–	80	20	–	3	10
March 9	50	50	–	25	75	–	6	4
March 29	33·3	66·6	–	37·4	62·6	–	12	11
April 16	–	58·7	41·3	–	41·6	58·4	17	12
April 26	–	78·7	21·3	–	73·5	26·5	14	15
May 1	–	75	25	–	40	60	4	5
May 18	–	–	100	–	–	100	12	3

TABLE VI.

SEA TEMPERATURES IN PORT ERIN BAY.

Taken at 9 a.m., being the average temperatures for the weeks ending on the dates given.

1931.		1932.	
February 7	7·3° C.	February 6	8·9° C.
14	7·5	13	8·0
21	6·5	20	7·5
28	7·1	27	7·8
March 7	6·1	March 5	7·3
14	5·5	12	7·1
21	5·9	19	7·5
28	6·5	26	7·8
April 4	5·9	April 2	8·2
11	6·7	9	8·0
18	7·3	16	7·8
25	6·9	23	8·0
		30	8·3
May 2	7·5		
9	7·8	May 7	8·4
16	8·3	14	8·8
23	8·6	21	9·2
30	9·3	28	9·8

ECHINUS ESCULENTUS.

SUMMARY OF GONAD CONDITIONS.

1931. *BREAKWATER.*	*BREAST.*
April. Varying from half-full to full. Mostly ripe. Only about 10% unripe. A few spent.	Both sexes either spending or spent. Volumes at a minimum by the end of the month.
May. None unripe, but rather a mixed sample as to the percentage of spents. Towards the end of the month the gonad volumes are beginning to pick up a little.	Practically all spents, but some relict ova and sperm are to be found.
June. Mostly spent, and the volume definitely picking up in both sexes. Relict sperm and ova present in some quantities.	Very much as above.
July. All spent. The gonad volume is rising. Plenty of ripe sperm are still obtainable. The ovaries contain very small ova, and also, in many cases, considerable numbers of relict ova.	The gonads are picking up a little in volume. No spermatocytes could be found, but oocytes were beginning to differentiate, and there were developing ova up to 80μ in diam. in a few cases.
Aug. The gonad volumes are still increasing. The males still mostly contain some active sperm, though not usually in large quantities. The females often have some relict ova. Large quantities of small ova up to ca. 5μ and smaller numbers up to 50μ. A very few up to 95μ. No sperm morulæ recognised. Female gonads about half full. Males at about their maximum size.	Gonads of both sexes have about reached their maximum size. Ova are up to 80–90μ together with a few relicts. There were a few relict sperm, but no sperm morulæ were seen.
Sept. Very much as above. Still no sperm morulæ seen. The gonads of the males show no change in volume, but the females are still increasing.	No data.
Oct. Sperm morulæ abundant, and sperm in some individuals. Males are much the same, but some spermatocytes are to be seen. Females contain all sizes of ova up to 110μ and their volume is still increasing.	Little change in the gonads. There are ova up to 100μ.
Nov. The males contain large numbers of ripe sperm and also of sperm morulæ. The females have ova up to 145μ and some nearly ripe.	Little change. Ova up to 115μ. Males with abundant sperm morulæ. Some with ripe sperm.
Dec. No data.	No data.
1932.	
Jan. The males are nearly all full of ripe sperm, but stages of spermatogenesis are probably also present. The male gonad volumes are dropping slightly. One or two females were ripe, and a number contained up to 50% of ripe ova. The female gonad volumes were still rising.	A fair proportion of the males were ripe, many with stages of spermatogenesis. showing. Some of the females contained large ova, but none were ripe. Gonad volumes were dropping in both sexes.
Feb. Males all ripe and full, and their volume dropping slightly. Female gonad volume still rising. About 50% of the females were ripe, and the rest mostly contained some ripe ova.	The gonad volumes of both sexes had dropped considerably further. Most of the males were ripe. No females were ripe, though there were ova up to 150μ and a few ripe ova.
March. All the males, and nearly all the females were ripe, and spawning was commencing. The male gonad volume dropped slowly in the beginning of the month while the female was coming to its maximum. Later both dropped sharply.	The gonad volumes rapidly picked up again. Most of the males were ripe, and some few females. The rest of the latter were approaching ripeness.
April. Most of both sexes have spawned by the end of the month.	Spawning in progress throughout the month, and the gonad volume dropping correspondingly. Still a small proportion of unripe specimens in both sexes.
May.	Spawning practically completed by the end of the month.

Observations on the Growth of the Claspers and Cloaca in *Raia clavata* Linnaeus.

By

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With 7 Figures in the Text.

CONTENTS.

I. INTRODUCTORY.

IN the course of work on the life-history and biology of the Raiidæ in the English Channel, and especially of *R. clavata,* the most important species commercially (**4**, p. 9 *et seq.*), it has been found necessary to attempt to disentangle the migrations of sexually mature fishes from those of juvenile individuals by means of marking experiments. In both sexes sufficiently small individuals could with safety be written down as juveniles and the largest of both sexes as adults. There remained, however, a considerable but ill-defined range of sizes (different in the two sexes) within which might be found fishes of all stages—juveniles, adolescents and adults.

In dealing with male fishes this difficulty was overcome by noting the size and condition of the claspers. In the female, however, the writer was not aware of a corresponding—or any other—external feature from which could be deduced with reasonable accuracy *in a live fish* her state of sexual development. The present investigation was undertaken, therefore, in order to discover whether or not such a feature existed. Attention soon became directed to the greatly accelerated relative growth rate in the cloaca of adolescent fishes and the relatively much greater length of this organ in mature than in juvenile individuals.

During this adolescent period of greatly accelerated growth in length, the cloaca also changes markedly in shape, becoming very much widened out, especially at its inner end (*cf.* Figs. 4 and 5). These changes in the size and shape of the cloaca are so extensive as to be easily discernible by digital examination. There is thus available in the female as well as in the male a ready means of ascertaining the sexual condition of the live fish. This method is now being applied in all further Ray-marking experiments.

The results of detailed observations on these changes in the growth of the claspers and cloaca in *R. clavata* form the substance of this paper.

II. The Claspers.

All species of Rays and Skates (Raiidæ) exhibit well-marked sexual dimorphism. Some of the secondary sexual characters, such as the presence of alar and malar spines and more pointed teeth in the male, become obvious only in sexually mature or nearly mature individuals. The presence of claspers in the male can be detected, however, at a very early stage of development. Thus, during at least the latter part of their embryonic development within the egg, and throughout the entire post-embryonic life of these fishes, the presence or absence of claspers forms a ready means of distinguishing male from female. In addition to their being the most characteristic and most easily discernible feature of the male fish, the claspers serve also, better than any other externally evident character, as an index of his state of sexual development. During the entire period of juvenile growth, before the onset of adolescence,* the claspers remain relatively small and inconspicuous, so much so that they may be entirely invisible from the dorsal side being shorter than, and hidden by, the pelvic fins. But at the onset of adolescence the claspers suddenly begin to grow very rapidly, and their tips soon extend backwards far beyond the limits of the pelvic fins.

This sudden change in the size and condition of the claspers was long ago noticed by ichthyologists. In the year 1877, for example, Malm (**3**, p. 607) stated that in a male *R. clavata* 216 mm. long the claspers were only about 3 mm. in length. In 1895 Fries (**2**, p. 1106) wrote that in a male of this species about 45 cm. long the claspers were " still quite small and short, their tips extending only a little more than half-way along the ventral fins." In a specimen 52 cm. in length he records that the circumstances were " essentially the same " except that the claspers were just a little longer in relation to the fins. But in an individual " rather more than 60 cm. long " Fries remarks that the claspers were so well developed that their tips extended back to more than half-way along the length of the tail.

In order to follow more closely these changes in the relative growth rate

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* The post-embryonic life of a Ray is very clearly divided into the usual phases: (1) the *juvenile* phase, during which the fish simply grows in size; (2) the *adolescent* phase, during which fundamental changes take place very rapidly and bring the individual to puberty; (3) the *adult* (sexually mature) phase.

of the claspers, measurements have been made on representative samples of male *R. clavata* at all sizes from recently-hatched individuals upwards to the largest obtainable. In recording the lengths of the claspers, for the sake of uniformity all measurements have been made on the left clasper. The length has been taken as the distance between the tip of the clasper and its point of emergence from the skin on the inner side (Fig. 1). This point is sometimes not well defined in adult fishes with large claspers, and exact measurements are not with them possible. A small part of the variation in recorded clasper lengths of adult fishes must be ascribed, therefore, to the action of this purely extrinsic factor as well as to the individual variations in size and body-proportions which are always found in the separate representatives of every animal (and plant) species.

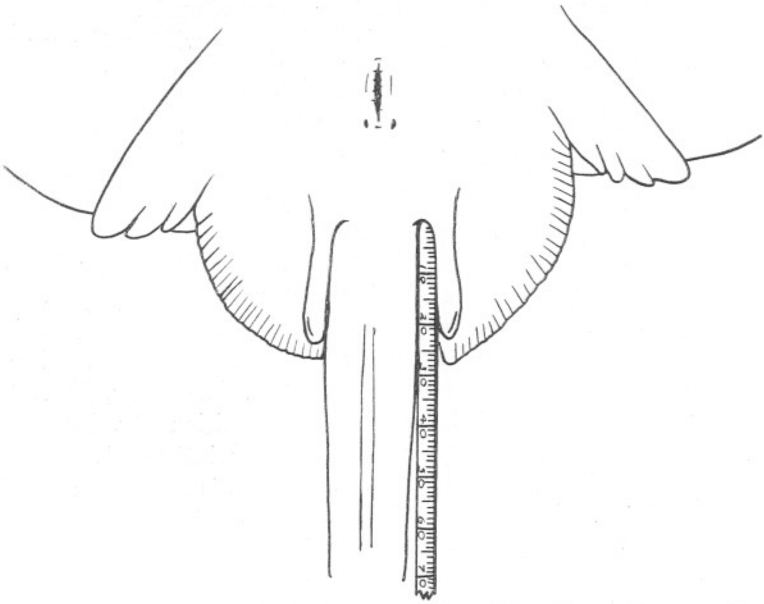

FIG. 1.—*R. clavata*—juvenile male ; 31 cm. disc width ; clasper 22 mm. × $\frac{2}{3}$. (See text.)

It is found that throughout the immature stages of development the claspers grow slowly and regularly, their length at any time during the juvenile phase showing a linear correlation with the total size of the fish, as expressed, say, by width of disc ; that is to say that points representing the length of the clasper at different times during the juvenile growth period plotted against the width of the disc fall upon a straight line. This is well shown in Figure 2. Each plotted point indicates the mean value of numerous clasper measurements in centimetre size-groups of fishes. The lengths of the vertical lines drawn through those points indicate the ranges of the measurements from which the means were drawn.*

It will be seen that for fishes up to and including the 43-cm. size-group the mean values lie very closely along the straight line *ab*, the correlation equation for which is

$$Y = 0{\cdot}993\ X - 5{\cdot}596$$

where Y = length of clasper (in mm.), and X = width of disc (in cm.). In succeeding size-groups the ranges of clasper length measurements show progressive extension in an upward direction and the mean values rise rapidly above the line *ab*. This means that in some fishes the claspers are now exhibiting a greatly accelerated relative growth rate.

In size-groups 50 cm. to 54 cm. (inclusive) disc widths, the ranges of clasper lengths reach and retain maximum values, these organs now having attained the fully adult size in some fishes while in others they still remain in the juvenile condition. Examination of Figure 2 clearly shows that the onset of the change in relative growth rate of the claspers, with which are correlated all the other phenomena of adolescence, does not always take place in all fishes at the same size. In some this change takes place when they have attained a disc width of round about 44 cm.; in others it is delayed until a much larger size is reached.

In Figure 3 these results, for the larger fishes, are shown graphically in a different manner which brings out this point more fully. Here the length of the clasper in individual fishes of 5-cm. size-groups, from 36 cm. in width of disc upwards, is indicated by the position of a dot. In the smallest size-group represented—36–40 cm. disc widths—all the claspers are still short and the range of recorded lengths is small. In the size-group next above—41–45 cm. disc widths—most of the fishes still have short claspers, but a few have entered the adolescent phase and are showing increased relative growth rate of this organ. In the size-group next higher again this process has proceeded still farther and one individual has actually become fully mature.

The size-group 51–55 cm. disc widths is of particular interest. Here the clasper length measurements show two distinct modes—one at the lower end of the range, produced by fishes which are still in the juvenile phase, and one at the upper end of the range, produced by fully adult individuals.† The approximately symmetrical bi-modal curve produced by the clasper length measurements of this group confirms the conclusions to be deduced from analyses of the complete data presented in Figures 2 and 3. These are:—

(1) that, in the English Channel area, in any sample of male *R. clavata*

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* Mean values for those size-groups which include adolescents and later stages are without significance and are not shown.

† Shortest clasper found in a fully mature male—176 mm. (*vide* dotted line, Figs. 2 and 3).

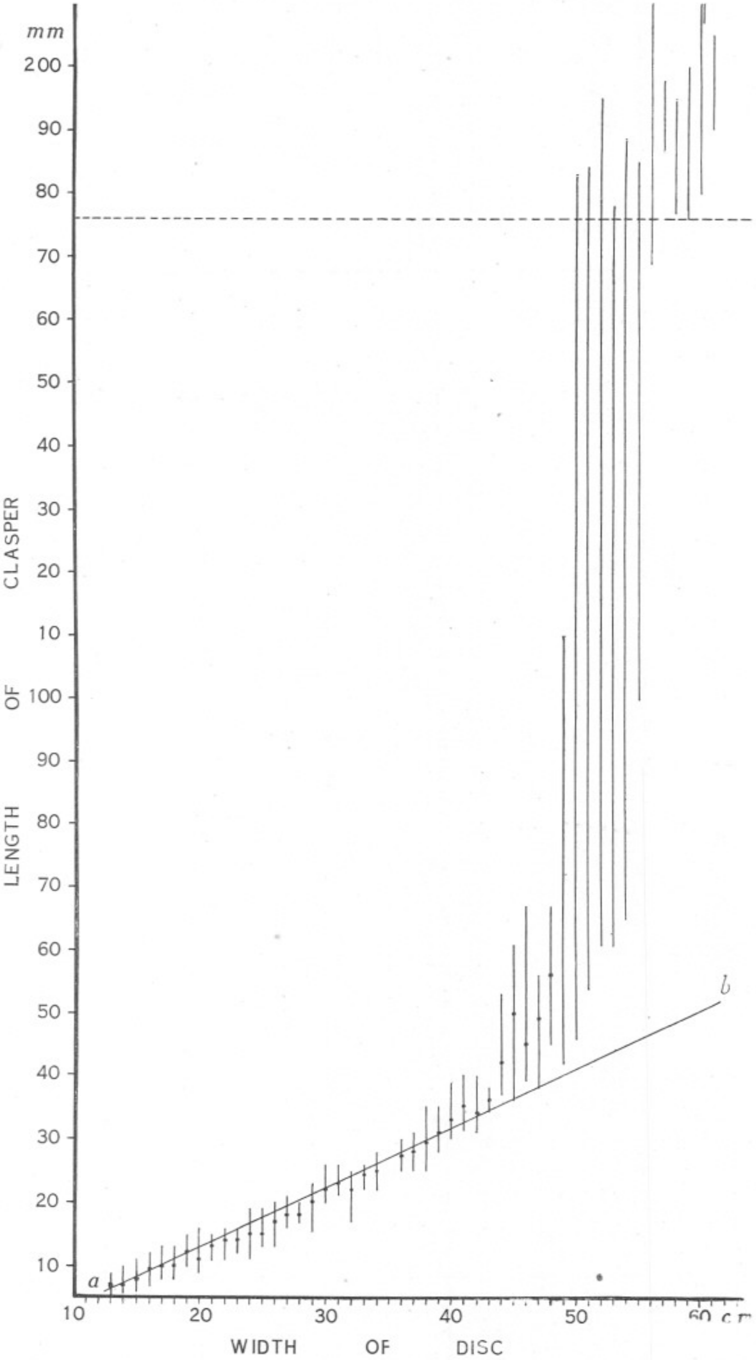

FIG. 2.—*R. clavata*—clasper length plotted against disc width in centimetre size-groups. (For explanation see text p. 889.)

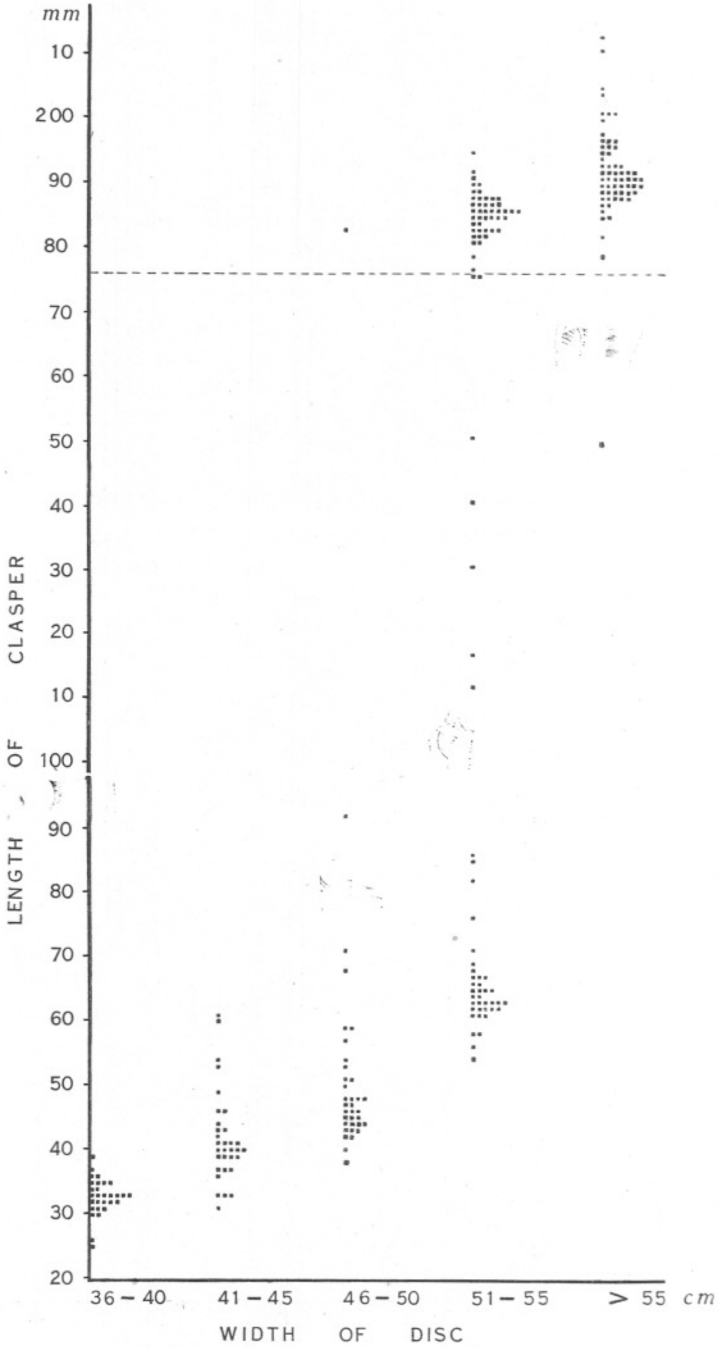

FIG. 3.—*R. clavata*—clasper length plotted against disc width in 5 cm. size-groups. (For explanation see text p. 890.)

in which no fish exceeds about 50 cm. disc width, the great majority of the individuals will be immature juveniles. This will hold true whether the sample be restricted to any arbitrary size-group of small range or consists of fishes at all sizes up to 50 cm. (about) disc width. Over most of this range samples of restricted size-groups will consist of 100 per cent juveniles, but samples at or near its extreme upper limit will contain a certain proportion of individuals at more advanced stages.

(2) that, similarly, in any sample which includes no fishes of less than approximately 56 cm. disc width, the majority of the individuals will be mature adults.

(3) that, in any representative sample of male fish of size-group 51–55 cm. (inclusive) disc widths, juveniles and adults will tend to be equally represented, while adolescents at all intermediate stages will also be found.

III. THE CLOACA.

The cloaca of the female Ray exhibits growth phenomena very similar to those found in the claspers of the male, and cloacal measurements have been made on individuals at all stages of growth. The distance from the anterior edge of the cloacal opening to the anterior end of the cloaca (in the middle line) when in normal extension, has been used as the measure of cloacal length. This measurement is made by opening the abdominal cavity and placing the tip of one finger of the left hand against the anterior end of the cloaca as it lies in position. At the same time a not too sharply pointed rod, graduated in millimetres, is inserted into the cloacal aperture and pushed forward until it presses against the left-hand finger. The length of the cloaca is then read off where the anterior edge of the cloacal external opening crosses the rod (Figs. 4 and 5).

Throughout the juvenile phase the cloaca grows only slowly and, like the clasper of the male, preserves a linear correlation between its length and the body dimensions of the whole fish. In Figure 6 the cloaca lengths in fishes of centimetre size-groups are plotted against disc widths. For fishes up to and including the 59-cm. size-group the mean values lie very closely along the straight line *ab* whose correlation equation is

$$Y = 0{\cdot}574\,X - 2{\cdot}175$$

where Y=length of cloaca (in mm.), and X=width of disc (in cm.). In fishes over this size the cloaca shows greatly accelerated relative growth rate in many individuals and the range of cloacal length measurements increases enormously, reaching and retaining maximum values in fishes of about 67–76 cm. (inclusive) disc widths.

In Figure 7 the length of the cloaca in individual fishes of 5-cm. size-groups, from 36-cm. disc width upwards, is plotted. In this figure the cloacal length measurements produce an approximately symmetrical bi-modal curve in the size-group 66–70 cm. disc widths. From perusal of Figures 6 and 7, therefore, the following conclusions can be drawn concerning the females of *R. clavata* in the English Channel area :—

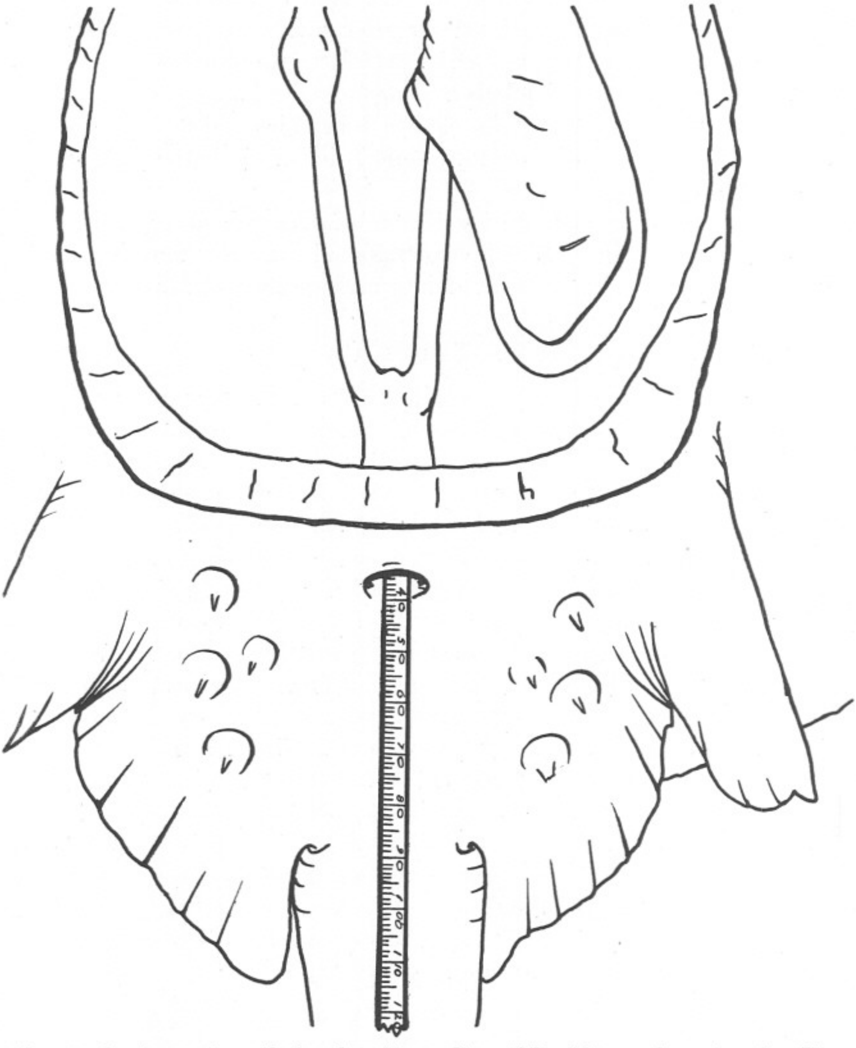

FIG. 4.—*R. clavata*—juvenile female ; 65 cm. disc width ; 36 mm. cloaca length. Dissected to show cloaca. Note immature left ovary (left *in situ*), and small shell gland. $\times \frac{2}{3}$. (For further explanation see text pp. 887 and 893.)

(1) that in any sample of female fishes of this species in which no individual exceeds about 65 cm. in width of disc the great majority will be immature juveniles. This will hold true whether the sample be restricted to any arbitrary size-group of small range or consists of fishes

at all sizes up to the 65 cm. (maximum) disc width. Over most of this range samples of restricted size-groups will consist of 100 per cent juveniles, but samples at or near its extreme upper limit will contain a certain proportion of individuals at more advanced stages.

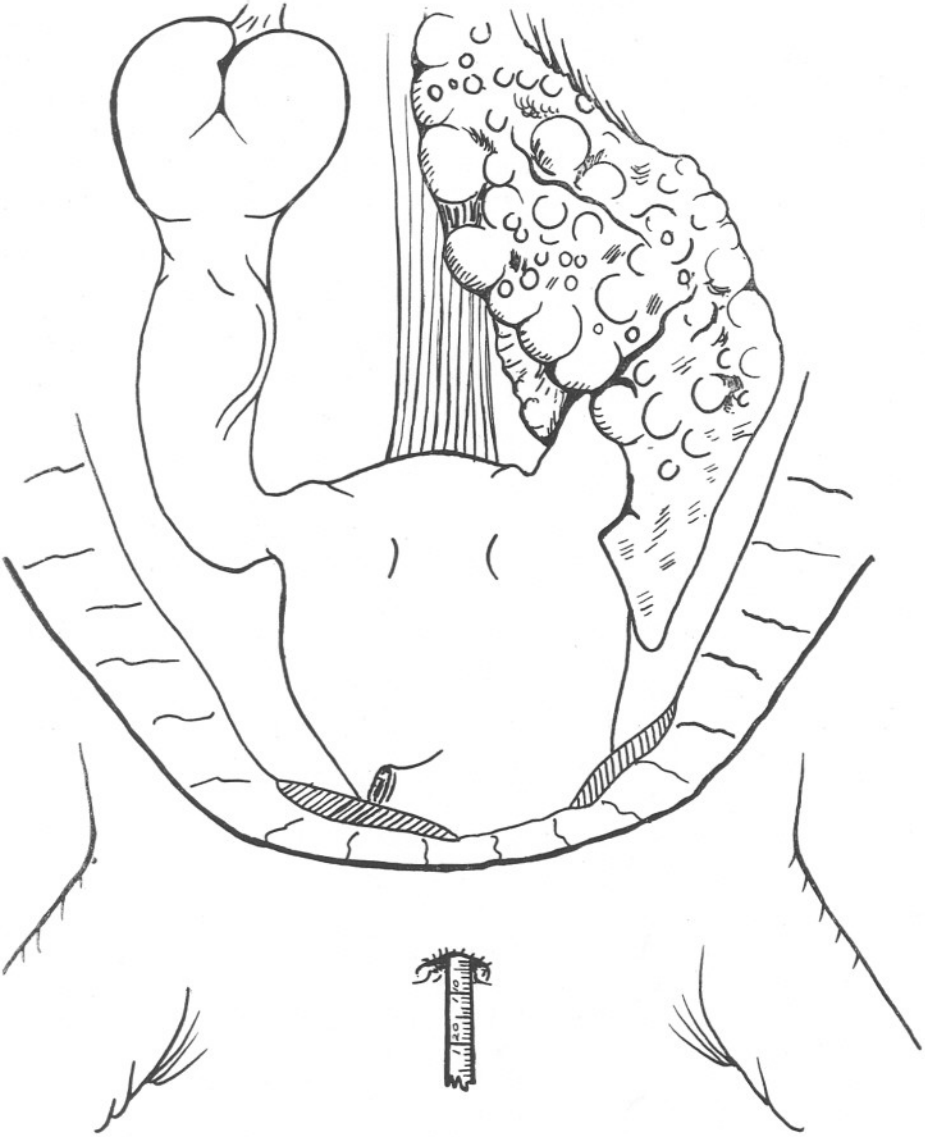

FIG. 5.—*R. clavata*—mature female; 72 cm. disc width; 102 mm. cloaca length. Dissected to show cloaca. Note also developing eggs in ovary and large shell gland. $\times \frac{2}{3}$. (For further explanation see pp. 887 and 893.)

(2) that, similarly, in any sample which includes no fishes of less than approximately 70 cm. disc width, the majority—but not all—of the individuals will be mature adults.*

(3) that in any representative sample of females of size-groups 66–70 cm. (inclusive) disc widths, juveniles and adults will tend to be equally represented, while adolescents at all intermediate stages will also be found.

In the course of this work, the possibility that, after all one season's eggs have been deposited, the cloaca may return to its virgin condition has not been overlooked. But the fact that the range of cloacal length measurements in all fishes of 76 cm. and upwards in width of disc is relatively small, grouped around a mean value of about 100 mm.—a figure far removed from that which would be expected in virgin females of those sizes—suggests very strongly that this does not happen. This conclusion is further supported by these additional observations. On Newlyn (Cornwall) fishmarket, in September, 1932, the plan was adopted of trying to find a fish of 76 cm. disc width or over with a small cloaca of say 50 mm. length or less. Though many hundreds of fishes were examined, including a large number with fully spent ovaries, the shortest cloaca length

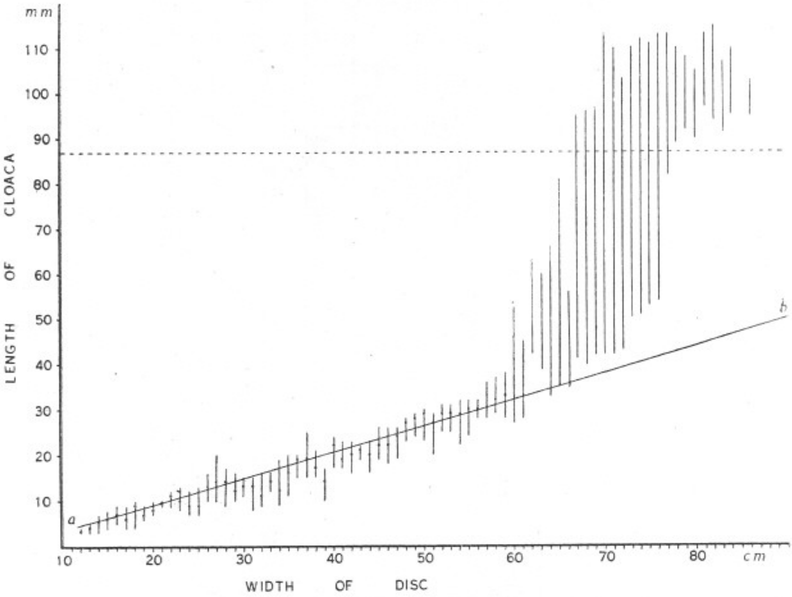

FIG. 6.—*R. clavata*—cloaca length plotted against disc width in centimetre size-groups. (For explanation see text p. 893.)

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* Shortest cloaca length recorded in a fully mature fish—87 mm. (*vide* dotted line, Figs. 6 and 7).

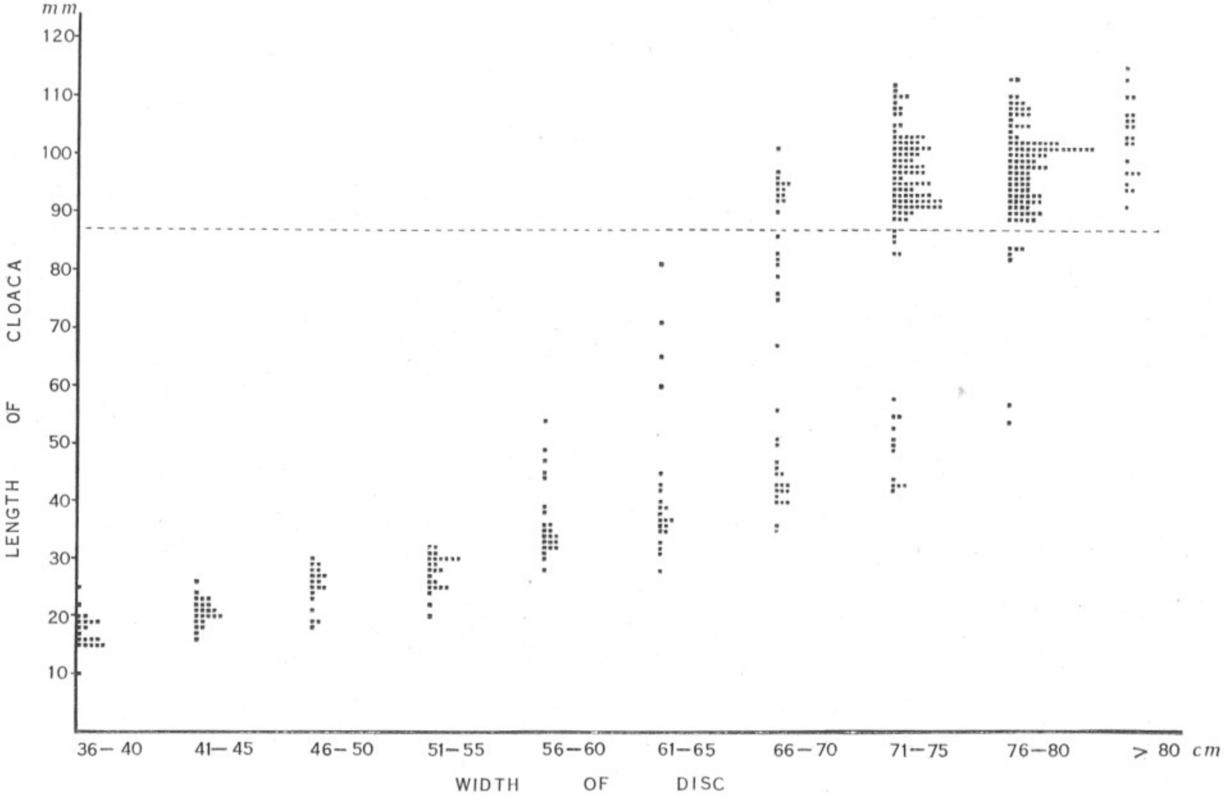

FIG. 7.—*R. clavata*—cloaca length plotted against disc width in 5 cm. size-groups. (For explanation see text p. 893.)

recorded was 87 mm. This was in a gravid female of 76 cm. disc width and containing in each uterus an egg ready for deposition.

IV. PRACTICAL APPLICATIONS.

A. It will be seen from Figure 2 that the 44-cm. (centimetre) size-group of male fishes contains the smallest individuals which show unmistakable acceleration in the relative growth rate of the claspers, thus indicating that they have entered the adolescent phase. The 50-cm. (centimetre) size-group contains the smallest fishes which have become fully mature.

It may with safety be assumed that the first (smallest) fishes to enter the adolescent phase will be also the first (smallest) fishes to reach puberty. It would thus appear that in the males of this species, the adolescent phase occupies roughly the time required to grow round about 6 cm. in width of disc.

Now the results (unpublished data) of the marking experiments so far carried out (*vide* p. 1) indicate that the adolescent males of *R. Clavata* grow at the rate of from about 3 cm. to 5 cm. disc width in the course of one annual growing period. The experiments are being continued and full details will be published in a subsequent paper. But sufficient data have already been collected to suggest that the above figures are reasonably reliable. If this be so, it would appear that in the males of this species the adolescent phase normally occupies rather more than one and not more than two growing periods. From this it may reasonably be concluded that these fishes enter the adolescent phase during one growing period and reach puberty during the growing period of the following year, the time occupied by the changes extending over part or all of the two periods.

In the females (Fig. 6) the difference in size between the smallest fishes to enter the adolescent phase and the smallest to reach puberty appears to be most frequently about 7 cm. disc width. Although females grow rather more rapidly at this stage than males, this difference in size represents in them too the growth increment of more than one and not more than two growing periods. The period of adolescence would appear, therefore, to be the same in both sexes.

B. It has been recorded in a previous paper (**5**, p. 617) that, on certain fishing grounds near Plymouth, there is in the spring months of every year, a congregation of large and fully mature Thornback Rays. At the same time that these adult fishes are being landed by fishing boats using fixed nets, other landings are being made by vessels using long lines or “ boulters ” on different grounds in the vicinity. A marked feature of the fishes caught on these lines at this time is that they frequently contain a high proportion of adolescent individuals. As with the adults from the nets (**5**, p. 617), so also with these adolescents, a landing will often consist almost entirely of one sex, either male or female. From consideration of the data set forth above it seems likely that these adolescent fishes, typical of " boulter " landings in the spring, entered the adolescent phase during the growing period of the previous year and that the majority, at any rate, of the year-class to which they belong will reach puberty during the growing period immediately following—i.e. later on in the same year. By the ensuing spring these young adults will have joined the shoals of mature fish which will populate the fixed-net fishing grounds at that time.

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A Comparative Study of *Metridium senile* (L.) var. *dianthus* (Ellis) and a Dwarf Variety of this Species occurring in the River Mersey, with a discussion on the Systematic Position of the Genus Metridium.

By

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Liverpool University.

With 5 Figures in the Text.

CONTENTS.

INTRODUCTION.

The anemone at present under consideration resembles *M. senile* (L.) var. *dianthus* (Ellis) in many respects but shows certain differences. It was for a time provisionally regarded as *M. senile,* but the body wall is thinner than in this species, sexual maturity is attained at a very small size and the disc is rarely distinctly lobed. The subsequent discovery of an abundance of penicilli in the acontia led one to think that the Dingle anemone was perhaps a Sagartia and not a Metridium. Living specimens were then sent to Professor Stephenson who identified them as one of the small local atypical forms of *M. senile* which occur in the intertidal regions of many parts of the British coasts. It is not known whether all these forms are simply varieties or whether on further investigation some of them might be justly ranked as species. The present research was undertaken with a view to solving this problem in the case of the Dingle anemone.

All sizes and all colour varieties of *M. senile* were obtained either from Plymouth or Port Erin for comparison with the Dingle form. Observations have been made on the external features and the stinging cells of specimens from these three localities along with an investigation of the anatomy of the Dingle form.

THE DINGLE ANEMONE.

HABITAT.

The anemone occurs on the river side of the revetment to the north of the oil jetty, Dingle, River Mersey (**1**, Fig. 1). Many individuals are attached to a mooring chain and other large colonies occur on the adjacent rocks. Only at extreme low water can one be sure of collecting specimens, since average tides fail to expose them.

The revetment is a low bank which lies parallel and close to the shore. It consists of large loose stones, rough with barnacles and covered with a thick deposit of fine mud. The water here is brackish and particularly foul because of the abundance of silt, the presence of an oil jetty, and a sewer in the vicinity. Often, when collecting, the water was seen to be covered with a film of oil. The average salinity of the river at Dingle is recorded by Fraser (unpublished records, 1931) as $13^{\circ}/_{\circ\circ}$ at Low Water and $20^{\circ}/_{\circ\circ}$ at High Water and the pH as about 7·9.

Large colonies of the more typical *M. senile* are found about three miles down the river on a wooden jetty situated at the north end of the Princes Landing Stage. Here, Fraser gives the average salinity as somewhat higher than at Dingle (23–$28^{\circ}/_{\circ\circ}$ in summer and 21–$27^{\circ}/_{\circ\circ}$ in winter), but the pH value as about the same. These latter colonies are not specially dealt with in this paper.

COLOUR VARIETIES, SIZE, AND HABITS.

There are four colour varieties of the Dingle anemone, salmon pink, white, olive-brown, and grey; the latter two are rare. All the individuals are small; the base of the largest one collected measured only 2·5 × 3·5 cm. and the diameter of the expanded disc rarely exceeded 2·5 cm.

Reproduction occurs by basal laceration and by the deposition of ova. Both these methods are recorded for *M. senile* (**2** and **3**), and its closely allied American forms (**4**). Laceration takes place in the ordinary way by tearing. Figure 1 shows a Dingle specimen with buds produced by this method in the laboratory between 17.9.32 and 22.12.32. It was given frequent changes of sea-water and fed with portions of Mytilus which were

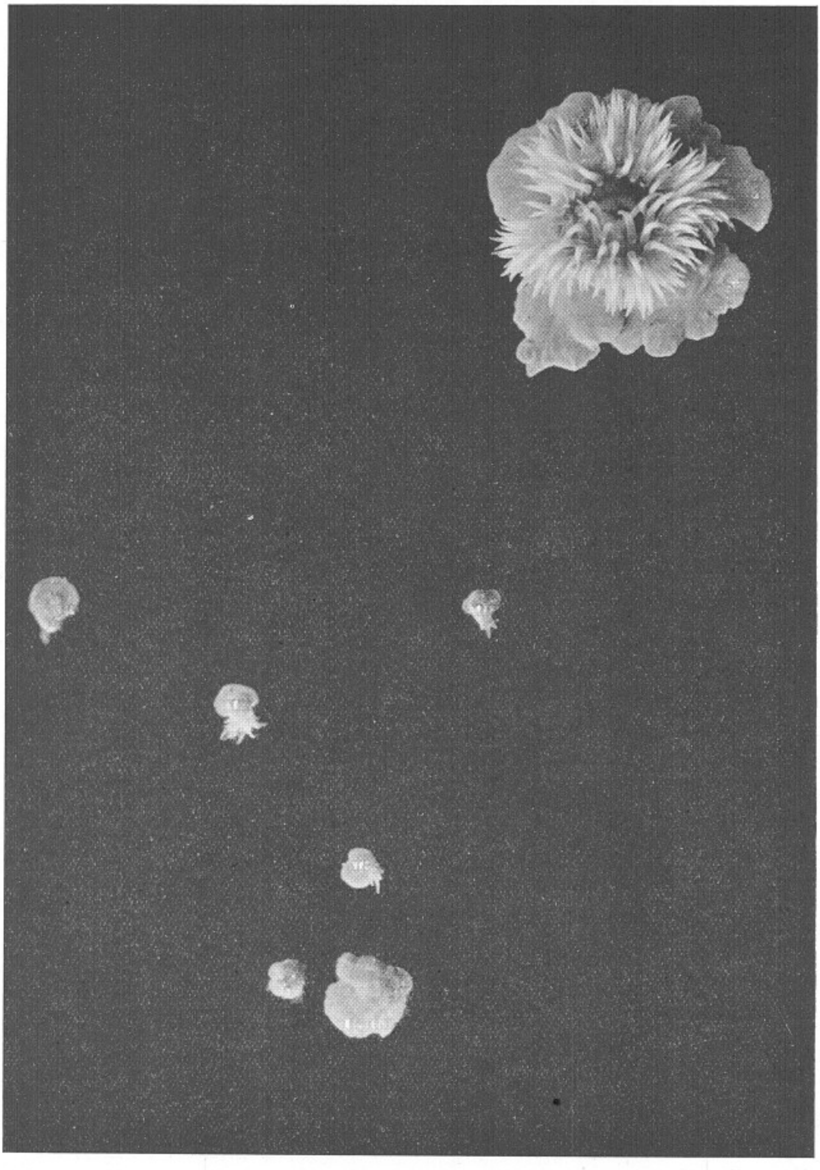

FIG. 1.—A Dingle anemone with buds produced by basal laceration. × 2. Photograph by P. Bond.

ingested, and with Nitzschia culture. Two individuals kept in captivity by Professor Orton from 5.6.30 to 5.11.30 together produced 34 buds. In this case the adults were not fed, but they were kept clean and the water was changed frequently. They were perfectly healthy.

Laceration appears to be of frequent occurrence in the Dingle anemones in their natural habitat; they often have a very irregular and sometimes torn basal outline. It has been shown in Sagartia and other anemones that the roughness and smoothness of the substratum has little or no effect on the rate of reproduction by this method (**2**). The observations of Torrey (**5**) on *M. fimbriatum* Verrill, suggest that one might possibly attribute the frequency of this process to the uncongenial habitat at Dingle. He concluded from his experiments that the mode of reproduction may be influenced by the environment. Only on one occasion did he observe basal laceration in the natural habitat, all other examples occurred in anemones which had been kept for several months in aquaria where the conditions were not so favourable. Wider observations may however show that lacerations are commoner in the field than is here suggested.

Basal buds have been seen in the Dingle anemones; they are also recorded in *M. senile* (**3**) and *M. fimbriatum* (**5**). They are probably incompletely lacerated portions of the base which have already developed tentacles, since true budding is of doubtful occurrence among the Actiniaria (**2**). No œsophageal buds such as are described in *M. fimbriatum* have been seen in the Dingle form.

Sexually mature individuals may be found in June, but the duration of the breeding season is unknown. The few available records of the spawning of *M. senile* give its breeding season from March to September although they also suggest a variation in the period according to the locality. The Millport specimens breed from March to June (**6**), whereas the Plymouth records (**7**) are from August to September. Two spawning females of the Dingle anemone were observed by Professor Orton in June, 1932. The eggs ranged from 110–130μ in diameter. Their size differs somewhat from the measurements of the eggs of *M. marginatum* (**8**) and *M. senile* (**9**), but the few observations on the eggs of the latter indicate a considerable amount of variation in their size. Gemmill (**9**) records an average diameter of 0·1 mm., but 105 eggs of a large brown specimen from Plymouth which spawned overnight in the laboratory at Liverpool on 11.11.32 had an average diameter of 173·6μ.

Sexual maturity at a small size is one of the most interesting features of the Dingle anemone. Observations on the smallest size at which *M. senile* var. *dianthus* is mature do not appear to have been made apart from Elmhirst's record. I am indebted to him for his information about the Millport specimens. Spawning does not take place, as far as he can recall, until the animals are approximately 2″ in height when expanded.

They are therefore at least twice as large as some of the ripe Dingle anemones.

When kept in finger bowls, the Dingle specimens frequently creep up the sides of the vessel until they are partly exposed to the air, a habit which they share with *M. senile* (**3**). Both young and adults possess the capacity of floating upside down beneath the surface film, although this position was only observed when the water in the bowls required renewal. In each case the animal crept up the side of the bowl to the water level, slowly released its hold and finally floated off. Sometimes a delicate horny, brown membrane covered the base. The base of such individuals frequently has a silvery appearance which one may possibly attribute to the enclosure of air between the membrane and the true base. This observation recalls the interesting modification met with in the floating Minyads, which have a hollow base containing a horny float from which the anemone is suspended head downwards.

A Comparison of *M. senile* (L.) var. *dianthus* (Ellis) with the Dingle Anemone.

(*a*) *The external features and anatomy.*

Anatomical investigations have been made to determine the characters of the Dingle anemone for comparison with those of *M. senile*. Only the salmon-coloured anemones were used. Dissections, and hand sections of material fixed in either formalin or Bouin's fluid and frozen in a solution of gum arabic were made to study the grosser anatomical features. Serial sections of material embedded in paraffin wax and stained in borax-carmine and picro-indigo-carmine were used to study the finer characters.

The results of these investigations and a careful comparison of the external features of the Dingle anemone with the accepted descriptions of *M. senile* (**3**, **10**, **11**, and **12**) indicate a very close resemblance between these two forms, but also certain differences. The general appearance of the Dingle anemone differs in some respects from the typical adult *M. senile ;* the column is often short, although it sometimes forms quite a tall pillar ; the base is broad, spreading, with an irregular outline as in some Sagartias and a diameter usually greater than the height of the column. The scapus wall is thinner and more translucent than in the typical form. Maybe, as has been suggested by Fraser (unpublished records, 1931), its different texture is due to the low salinity of the water at Dingle. In the number of tentacles and the frequent absence of clear disc lobes, the Dingle anemone resembles the young of *M. senile* rather than the adult. Individually, the above features may not be very significant, but together they give the living anemone quite a different facies from the type form. The same colour varieties and colour pattern are met with in both anemones. They are identical in the structure of their mesenteries and cinclides and in the form and distribution of the musculature of the tentacles, disc, and scapus. They both exhibit fluctuations in the number of their perfect mesenteries. The European *M. senile* and the American species of Metridium are often hexamerous, but specimens of the former are recorded with 6–11 pairs of perfect mesenteries and of the latter with 4–15 pairs. In thirty-three examples of the Dingle anemone their numbers were as follows :—

No. of pairs of perfect mesenteries.	11	10½	10	9	8½	8	7½, ½	7	6½	6	5½	5	4
No. of individuals	2	1	1	1	3	8	1	5	1	3	2	4	1

The sections of the specimens with five and ten pairs were incomplete, so that it is possible that they possessed more than this number.

A detailed study of the variation in the number of perfect mesenteries in the European *M. senile* does not appear to have been made, but this aspect of the American representatives of the genus has been the subject of various papers. A brief consideration of these is not irrelevant here, more especially as *M. fimbriatum* Verrill and *M. marginatum* Milne-Edwards are regarded as synonymous with the European *M. senile* (L.) var. *dianthus* (Ellis), (**5**) ; absolute agreement between them is, however, not yet certain (**17**).

Torrey (**4**), after working on *M. fimbriatum*, concluded that basal fragmentation was especially interesting as a factor affecting the variation in the number of mesenteries and siphonoglyphs. Experiments have shown that monoglyphic and diglyphic polyps can each give rise asexually to both kinds of buds and that the number of siphonoglyphs depends upon whether or not a detached fragment contains a portion of the parent directive system (**13**). In the majority of regenerating fragments, a pair of directive mesenteries is developed from the torn part of the body wall. If a portion of the parent directive system is also present, then a diglyphic polyp with two pairs of directive mesenteries is produced, if not, a monoglyphic form with one pair of directive mesenteries. Hahn and Torrey's experiments demonstrate that there is a definite, but not absolutely strict correlation between the mode of reproduction and the morphology of the polyp. It is considered that sexual reproduction more frequently gives rise to regular diglyphic individuals and laceration to irregular monoglyphic ones. It is probable, therefore, that the predominance of forms with an irregular number of mesenteries among the thirty-three specimens specially examined from Dingle may be attributed to the asexual mode of reproduction.

Perfect agreement has been demonstrated regarding the number of siphonoglyphs and the number of pairs of directive mesenteries (**4**) and (**10**). The variation in their number has not been particularly studied in the Dingle anemone, but twenty specimens which were examined proved to be monoglyphic with one pair of directives. It is interesting to note the variation in the percentages of monoglyphic and diglyphic polyps from various American localities (**13**). The different values may possibly be attributed in some measure to the environment. Unfortunately, the habitat is not described for all the localities which have been studied, but in each there is a greater percentage of the monoglyphic type. Assuming that basal fragmentation is correlated with an unfavourable environment, then one would expect a predominance of monoglyphic specimens at Dingle, since the chances of a detached fragment containing a portion of the parent directive system are fewer than it not containing a piece. It would be interesting to compare the percentages of monoglyphic and diglyphic polyps at Plymouth, Port Erin, and Liverpool.

The arrangement of the imperfect mesenteries in the genus Metridium is also very variable (**14**). In some of the Dingle anemones there were only two cycles of imperfect mesenteries with well-developed retractor muscles and mesenterial filaments : three such cycles are present in the young *M. senile* (**11**). This character is probably of little importance in comparing these anemones since it varies with the age of the individual.

Single unpaired mesenteries occur in the Dingle anemones ; a similar condition is recorded for *M. senile* (**10**) and *M. marginatum* (**14**). In all these forms one sometimes finds a union of the free edges of two adjacent mesenteries belonging to different mesentery pairs. Irregular specimens of *M. marginatum* and certain of the Dingle anemones agree in their tendency to concentrate the non-directive perfect mesenteries at one end of the actinopharynx.

The majority of the mesenterial filaments in the upper part of the column of the Dingle anemone have a typical trefoil appearance when viewed in transverse section. Their shape agrees fairly closely with the filament of *M. senile* (**11**, Fig. 20), but the lobes are frequently more distinct and the reticulate region better developed. Occasionally a 4 or 5-lobed appearance is presented. One may agree with E. M. Stephenson (**11**) that the specific value of the shape of the mesenterial filaments when viewed in transverse section is not yet fully understood, as a sufficient number of individuals of any one species has not been investigated.

The genus Metridium has in the past been defined as having the gonads on the imperfect mesenteries. Carlgren (**10**) and Professor Stephenson (letter to the author, 8.2.33) record examples in which gonads were present on some of the perfect mesenteries also, the former author stating that when there are more than six pairs of perfect mesenteries, gonads may occur on the additional ones. The Dingle anemones with an irregular number of perfect mesenteries may have gonads developed on some of them. A fertile specimen with only six pairs of perfect mesenteries was not found.

The inferences of importance which may be drawn from the above discussion of the mesenteries and their associated structures are :—

1. The number of perfect mesenteries present in the European *M. senile* and in the American species of Metridium is variable. A knowledge of the number of perfect mesenteries present in a particular individual cannot therefore be used as a reliable character for its identification.

2. Environment may influence habit, and cause changes in the morphology of the genus Metridium. Uncongenial surroundings possibly stimulate reproduction by basal laceration whereby polyps with an irregular number of perfect mesenteries and a varying number of siphonoglyphs are produced, although an irregular number of mesenteries is more frequently associated with the monoglyphic than with the diglyphic condition.

3. There is a definite, but not absolutely strict correlation between the mode of reproduction and the morphology of the individual. Egg embryos as a rule give rise to regular polyps while reproduction by basal laceration is the principal contributory factor to the production of irregular ones.

4. In the typical adult *M. senile* the perfect mesenteries are sterile and the gonads occur on the imperfect mesenteries. When more than six pairs of perfect mesenteries are present, some of them may develop gonads.

(*b*) *The Nematocysts.*

The nematocysts of the Dingle anemone are one of its most interesting features. It possesses all the characters of the Metridiidæ (**15**), but it has an abundance of both spirulæ and penicilli in its acontia, a character which, according to the latest classification (**16**), immediately removes it from this family. Special care was taken when removing the acontia to prevent them from touching any other tissues. The acontia were cut off with clean instruments as soon as they were extruded through the cinclides or mouth so that there was no possibility of contact with cut tissues. Portions were then finely teased in sea-water, mounted either unstained or stained in 1% acid fuchsin, and examined with a 1/12th objective. A pure sample of the acontia cannot however be guaranteed since sooner or later in their ordinary life they are bound to be contaminated with the nematocysts from the mesenterial filaments and the ectoderm.

The acontia of at least thirty individuals have been investigated. They all contained both types of nematocyst. The spirulæ were most abundant, but the penicilli were always plentiful and one was sure of finding them in any preparation of a fragment of an acontium. The two types are quite distinct when they are exploded. The spirulæ are identical with those described for *M. senile* (**16**, Fig. 1). The penicilli (Fig. 2) are of the bottle-brush type. The majority have a blunt tip, but I suspect that a few may have a short, fine, terminal thread. The average size, length and breadth of the spirula and penicillus capsules is given in Table I. Their size shows only minor fluctuations between anemones of approximately equal sizes.

A very careful search was then made for penicilli in the acontia of *M. senile* var. *dianthus* from Plymouth, Port Erin, and the Princes Landing Stage, Liverpool. They were found to be universally present in quite considerable numbers in all the small specimens which were examined from each of these localities (see Table I), although they were not so abundant as in the Dingle anemones. They occur in the white, grey, orange, and brown colour varieties. In large specimens they are sparse and sometimes absent. Since these results were obtained, Carlgren (**17**, 1933) has recently recorded the presence of a few penicilli in young specimens but has failed to find them in the adults.

The spirulæ and the penicilli from the acontia of the Dingle anemone have much the same range in size as in *M. senile* (see Figs. 4 and 5, pp. 911–2). The spirulæ of the former do not, however, attain such a large size as those of the latter and their modal value is lower. It is possible that this discrepancy is explained by a difference in the size of the Dingle anemones from which the cells were taken compared with those studied from the other localities, since smaller spirulæ (**16**) and smaller penicilli (see Table I) occur in the young than in the adults of the typical *M. senile.* The anemones from which the data were obtained for Figures 4 and 5 were all small, but their shape is so variable that only their approximate size can be measured. The penicilli do not show any appreciable difference in either their range in size or their modal value (see Fig. 5), which suggests that possibly some other factor is contributory to the smaller size of the spirulæ. Maybe it varies slightly in different localities, possibly with salinity and perhaps in the case of the Dingle anemone, the dwarfing of the body is reflected to some degree in the individual cells.

Three very large specimens, a brown one from Plymouth and an orange and a white one from Port Erin, all showed a relative scarcity of penicilli compared with their numbers in the small individuals. After several days' continued search only six were found in the Plymouth anemone. They were similar in size and shape to those of the scapus ectoderm but their capsules were only approximately half the length of the penicillus

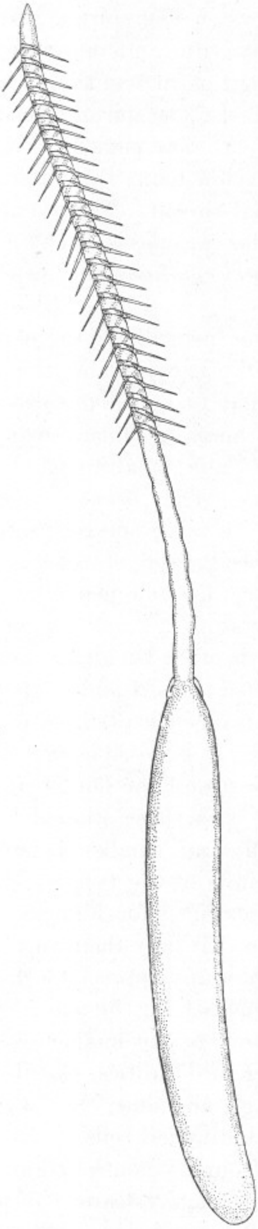

FIG. 2.—A penicillus from an acontium of a typical *M. senile* × 1800.

FIG. 3.—A penicillus from the ectoderm of a typical *M. senile* × 1600.

capsules found in the acontia of the other small individuals which had been examined. Their scarcity, together with their resemblance to those of the scapus, led one to conclude that penicilli were absent from the acontia, but that a few stray cells, probably from the ectoderm, had adhered to the acontia after or during their extrusion. Penicilli were also absent from the acontia of the white specimen from Port Erin, but a few of the usual type and size were found in the orange-coloured one (see Table I). The acontia of eight additional Plymouth specimens with a column height ranging from 3·5–6·5 cm. showed the same scarcity of penicilli.

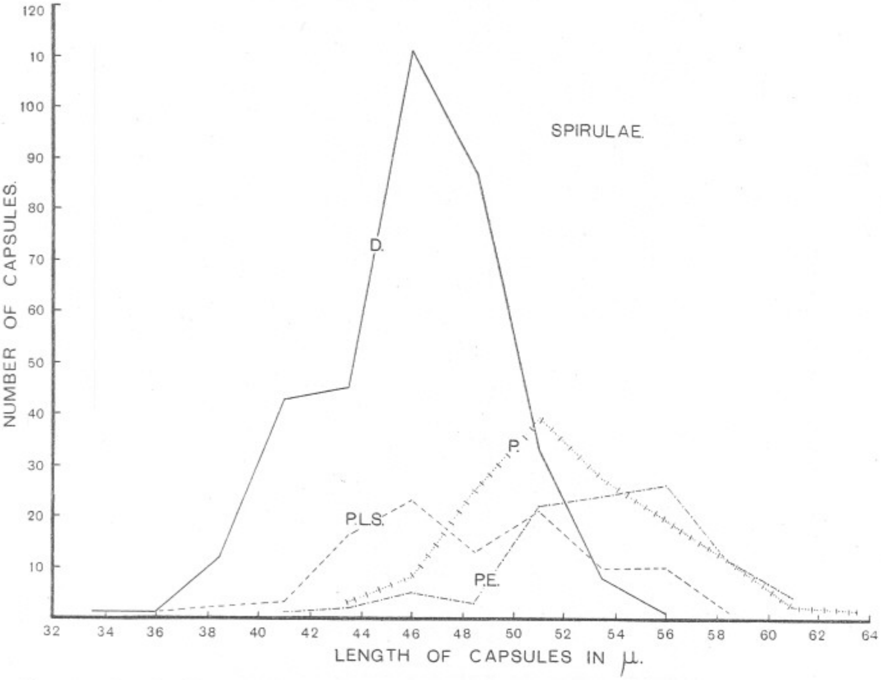

FIG. 4.—Graphs showing the variation in length of the spirula capsules, exploded and measured to the nearest 0·5μ, from the acontia of the Dingle anemone and *M. senile* from the Princes Landing Stage (Liverpool), Plymouth and Port Erin.

D.	340 cells from the Dingle specimens in Table I.
P.L.S.	100 cells from the Princes Landing Stage specimens in Table I.
P.	132 cells from the small Plymouth specimens in Table I.
P.E.	100 cells from the small Port Erin specimens in Table I.

The particular function of the penicilli is unknown and the reduction in their number in large specimens is as yet inexplicable. In some Cœlenterates (**18**), the developing nematocysts are migratory. It is possible they are so in *M. senile* and that there is a difference between their migratory powers in the young and the adults. One would expect to find wandering cells in the young rather than in the old individuals.

A comparative study of the types of cnidæ occurring in the ectoderm of the scapus has shown that these cells also are structurally similar and comparable in size in the Dingle anemone and *M. senile* (see Table I). Both spirulæ and penicilli are present. The spirula capsules are smaller than those found in the acontia. The spiral is uniform in width, limited to a short distance at the base of the thread and has three to four turns, whereas the spiral of the acontia spirulæ is much more extensive with about twenty turns and considerably expanded towards its distal end (**16**, Fig. 1). There are at least two distinct kinds of penicilli, a small one with a rather globular capsule and a distinct wisp-like terminal thread and a larger variety (Fig. 3) similar to, but smaller than those found in the acontia and with an elongated oval capsule. The latter are very much

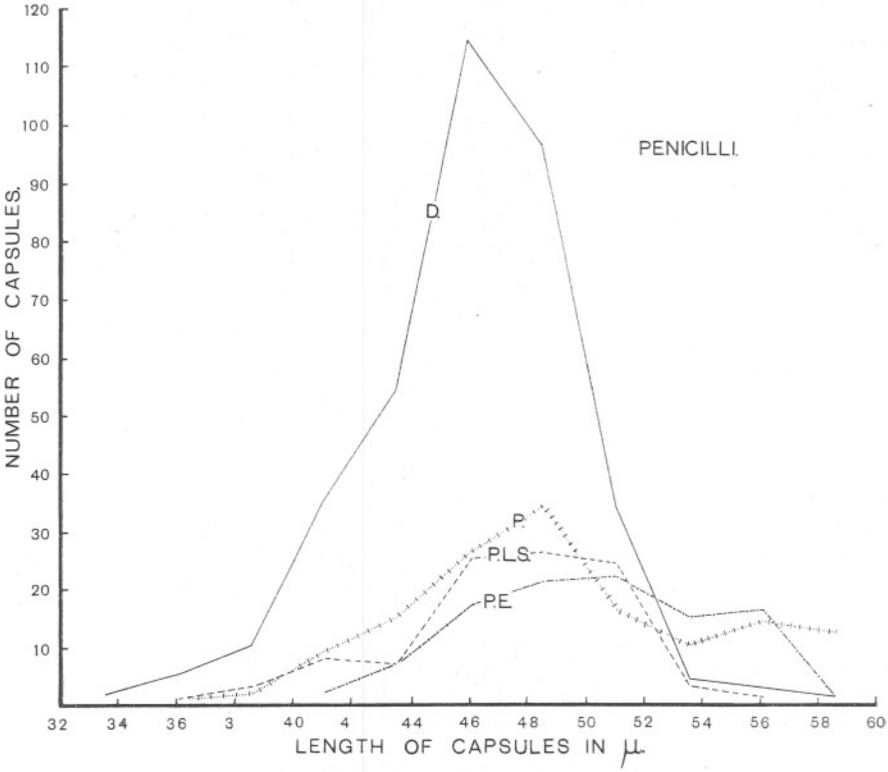

FIG. 5.—Graphs showing the variation in length of the penicillus capsules, exploded and measured to the nearest 0·5μ, from the acontia of the Dingle anemone and *M. senile* from the Princes Landing Stage (Liverpool), Plymouth and Port Erin. The cells were taken from the same anemones as gave the data for Fig. 4.

D.	354 cells from the Dingle specimens.
P.L.S.	100 cells from the Princes Landing Stage specimens.
P.	140 cells from the Plymouth specimens.
P.E.	101 cells from the Port Erin specimens.

TABLE I.

MEASUREMENTS OF THE SPIRULA (SP.) AND THE PENICILLUS CAPSULES (PEN.) OCCURRING IN THE ACONTIA AND THE SCAPUS ECTODERM OF THE DINGLE ANEMONE AND *M. senile*.

(The measurements were made on living cells exploded in sea-water and unstained except the ectoderm cells which were stained with 1% acid fuchsin.)

Locality.	No.** of specimens examined.	Approximate diameter in cm.		No. of cells measured.			Range in size of the cells in μ.	Average size of the cells in μ.
		Base	Disc					
Dingle	5	1·2	1	Ectoderm	Pen.	95	11–20·5 × 3–4·5	16·2 × 3·6
				Acontia	Sp.	100	38·5–55·5 × 3–4·5	47·9 × 3·6
				,,	Pen.	100	34·5–54 × 3·5–6	47·1 × 5
	8 (1 g.)	0·6	0·8	Acontia	Sp.	156	33–50·5 × 3–4·5	44·6 × 3·6
				,,	Pen.	160	32–51 × 3–6	44·9 × 4·9
	4	1	1	Acontia	Sp.	80	38–53·5	46·8
				,,	Pen.	80	39–58	47·1
	1		0·5	Ectoderm	Sp.	20	9·5–13 × 1·5–3·5	11·3 × 2·4
				,,	Pen.	21	13–19·5 × 3–4·5	16·3 × 3·4
	1		1	Ectoderm	Sp.	20	10–15 × 2·5–3·5	12·3 × 2·8
				,,	Pen.	20	16–20 × 3·5–4	18 × 3·7
				Ectoderm	Sp.	20*	9·5–13·5 × 2–3·5	12·5 × 2·7
				,,	Pen.	20*	13–21 × 3·5–5·5	18·8 × 4·3
Princes Landing Stage	5 (br. and p.)	1·4	1·1	Acontia	Sp.	100	35·5–59 × 3–5·5	47 × 3·8
				,,	Pen.	94	36·5–53 × 4–6·5	47·3 × 5·3
Plymouth	1† (br).		12·5	Ectoderm	Sp.	20	11–19·5 × 1·5–4	15·9 × 2·6
				,,	Pen.	21	20–27 × 2·5–4·5	24·4 × 3·4
				Acontia	Sp.	23	57–69·5 × 3–4·5	63·4 × 3·4
				,,	Pen.	0	Absent	
	1 (n.r.)		0·4	Ectoderm	Sp.	12	9–13·5 × 1·5–3	11·7 × 2·2
				,,	Pen.	16	13·5–18·5 × 3–4	16 × 3·4
				Acontia	Sp.	13	42–53 × 3–4	48 × 3·6
				,,	Pen.	21	40–48 × 4–5·5	43·4 × 4·8
	3	0·5	0·8	Ectoderm	Pen.	31	10·5–25·5 × 3–5	17·2 × 3·5
				Acontia	Sp.	60	44–59 × 3–4·5	51·3 × 3·8
				,,	Pen.	60	42–59 × 4–6	49·9 × 4·9
	4 (br. p. w. and n.r.)	0·5	0·7	Acontia	Sp.	59	45·5–64·5 × 3–5	53·6 × 3·7
				,,	Pen.	73	38–59·5 × 4–6·5	48·3 × 5
	1† (n.r.)		2·7	Ectoderm	Sp.	20	9·5–16 × 1·5–3	14·1 × 2·5
				,,	Pen.	16	16–22 × 3–4	20 × 3·4
Port Erin	5 (o. and w.)	1·4	1·4	Acontia	Sp.	100	35–62 × 2·5–4·5	53·3 × 3·5
				,,	Pen.	101	41–57·5 × 3–6·5	50·1 × 4·8
	1† (o.)		10	Acontia	Pen.	16	53–62 × 4·5–6	57·3 × 5·2

* These cells were unexploded and unstained.

† The stinging cells from these specimens are not used in Figs. 4 and 5.

** Colour pink, unless noted as :—
br. = brown, g. = grey, o. = orange, w. = white, n.r. = not recorded.

more abundant than the former; they sometimes show a terminal thread. All the measurements refer to the larger kind. Their size varies but little between different individuals of about the same size, but like the stinging cells of the acontia they are slightly larger in old specimens than in young ones.

To summarise the observations on the nematocysts one may say :—

i. the spirulæ and penicilli from the acontia and the scapus ectoderm of the Dingle anemone are identical in form and comparable in size with those found in *M. senile.*

ii. both spirulæ and penicilli are present in abundance in the acontia of typical small *M. senile* from various localities, but they are sparse and sometimes absent from large and medium-sized individuals.

iii. the acontia of the largest and the smallest specimens of the Dingle anemone contain an abundance of spirulæ and penicilli; some of the anemones were sexually mature.

The Dingle Anemone as a New Species or a Variety of *M. senile.*

The close correspondence between the habits, the methods of reproduction, the anatomy, the types and sizes of the stinging cells from the ectoderm and the acontia, as noted in the foregoing sections, gives quite sufficient evidence for regarding the Dingle anemone as *M. senile.* It nevertheless exhibits certain features which at present justify its recognition as a dwarf variety. The small size of all the individuals composing the colony and their attainment of sexual maturity while small support this suggestion. The fertile specimens also exhibit the following characters of the young of the ordinary type; the general appearance of their tentacles, the abundance of penicilli in their acontia and the absence of clear disc lobes. Much of the interest of these characters would be lost should further researches prove that the typical form is sexually mature at a smaller size than is thought at present.

Gosse (**3**) observed young specimens of Metridium between the tide-marks and suggested that with advancing age they move offshore to deeper waters. Perhaps the Dingle anemones migrate, but actual proof of this habit is difficult to ascertain. Their dwarf form is possibly associated with the separate or combined effects of the following factors; their intertidal position, the low salinity and the pollution of the water.

One small fertile specimen was sent to the Laboratory, Plymouth, where it was fed with plankton. It did not show any appreciable change in size after living there for seven months. A subject for further experiment is to determine whether the Dingle anemones are permanently dwarfed, or whether if transferred to other more favourable environments they would grow to the average size and develop all the characters of the type species.

THE SYSTEMATIC POSITION OF THE GENUS METRIDIUM.

Some of the principal changes in the systematic position of Metridium are shown below :—

Fam. SAGARTIADÆ Gosse (**3**, 1860), including the genera Actinoloba (=Metridium) Sagartia, Phellia, Adamsia, Gregoria, and Discosoma.

Fam. SAGARTIDÆ (Hertwig, 1882).

Sub. fam. Metridinæ, Carlgren (**10**, 1893), including the genera Metridium, Adamsia, Aiptasia, Stelidiactis, and Calliactis.

Fam. METRIDIIDÆ Stephenson (**15**, 1920), including the genera Metridium, Calliactis, Adamsia, Aiptasia, Aiptasiomorpha, Heteractis, and Bartholomea.

Fam. METRIDIIDÆ Stephenson (**16**, 1929), including the genera Metridium, Calliactis, Adamsia, Hormathia, Actinauge, Paraphellia, Leptoteichus, Chondrodactis, etc. (and the remaining genera included in the Metridiidæ and Chondractiniidæ **15**, 1920, with the Aiptasiids and Sagartiomorphe removed).

In 1860 it was classed with the Sagartias in the family Sagartiadæ (**3**). Many years afterwards Carlgren (**10**) placed it in his new sub-family, the Metridinæ. Stephenson (**15**) renamed the sub-family Metridinæ the Metridiidæ, and raised it to the rank of a full family on a level with the Sagartiidæ. Later, as the result of much work on the nematocysts of anemones with acontia, he revised the members and the characters of these two families (**16**, 1929), and in addition to the characters given in his earlier classification he provisionally distinguished the Sagartiidæ as forms with an abundance of spirulæ and penicilli in the acontia and the Metridiidæ as forms possessing spirulæ only. The resemblances and differences between the Sagartiidæ and the Metridiidæ (**16**) strongly suggest a reconsideration of the systematic position of the genus Metridium, as both spirulæ and penicilli have recently been found in the acontia of the young of the typical *M. senile*.

The general systematic value of the presence or absence of cinclides and the position of the gonads has already been queried (**12**). If the type of stinging cell found in the acontia is to remain a family character, then Metridium must be removed from the family Metridiidæ provided that further researches on *young* and *adult* specimens of Adamsia, Calliactis and the other genera included in the family prove the absence of penicilli from their acontia. There seem to be only two alternative positions for it, either it must once more be classed with the Sagartias in the Sagartiidæ or else it must be placed in a family by itself as recently suggested by Carlgren (**17**, 1933). There are points in favour of both these suggestions.

Since the discovery of both spirulæ and penicilli in the acontia of *M. senile* and the Dingle variety, there exists no constant difference between the Sagartiidæ and the Metridiidæ. This is the principal evidence in favour of placing Metridium with the Sagartias. Such a grouping would probably be quite satisfactory for the young individuals of *M. senile*, but the presence of a distinct collar and the possible absence of penicilli from the acontia of the adults directly oppose this classification. It is noteworthy that one of the family characters quoted in the past for the Sagartiadæ (**3**), which contained the genus Metridium, is the presence in the acontia of cnidæ with a short densely armed wire. They are obviously penicilli.

If the genus is placed in a family by itself the characters of such a family cannot be anything but indefinite because certain of the features exhibited by the young and adults are different, moreover, the form of the body, the number of perfect mesenteries and the position of the gonads are variable characters. There is, however, a more marked tendency towards the sterility of the primary mesenteries and to hexamerism in the genus Metridium than in the Sagartias.

A consideration of these characters and the above-mentioned objections to placing the genus with the Sagartiidæ, together with the further evidence of the presence of penicilli in the acontia of both *M. senile* var. *dianthus* and the Dingle variety, favours Carlgren's suggestion of restricting the Metridiidæ to the genus Metridium. The remaining genera of the present Metridiidæ may then be referred to the Chondractiniidæ (now the Hormathiidæ, **19**), as suggested by Professor Stephenson (letter to the author, 4. 4. 34). The evidence obtained from the stinging cells of the acontia and the general trend of certain characters of the genus along a path distinct from the Sagartias support these suggestions. The types of stinging cells in the acontia would not alone be a useful diagnostic character for the revised Metridiidæ, since the number of types present varies with the age of the individual. In conjunction, however, with the unique form of the spirulæ from the acontia, and the characters already described for the genus (**15**), one would have ample features on which to base a description of a family which contained the genus Metridium as its sole representative.

Unfortunately, living specimens of *M. marginatum*, Milne-Edwards, *M. fimbriatum*, Verrill, and *M. senile* var. *pallidum* (Holdsworth) have not been available for an investigation of their stinging cells, but Carlgren (**17**, 1933) has now recorded the presence of penicilli in one small

Metridium sp. and one large specimen of *M. fimbriatum.* It is highly probable therefore that all these forms would fit in with the revised Metridiidæ since the var. *pallidum* is not very different from the ordinary type and, as previously noted, certain authors regard the American species and the European *M. senile* as synonymous.

The following conclusion may be drawn from the foregoing discussion. The variation which is met with in the genus Metridium and the difficulties which present themselves in connexion with its systematic position show that the genus is transitional between the Sagartiidæ and the Metridiidæ as defined in 1929. Its affinities with the Aiptasiidæ have also been mentioned by Carlgren (**17**). Some specimens of Metridium exhibit characters which suggest a trend towards the Sagartias, but others possess features which are different from those of this family, namely, hexamerism and the sterility of the perfect mesenteries. An intensive study, nevertheless, shows that they are all referable to the one genus. The Sagartian trend of the genus is further emphasised by certain characters of the Dingle anemone. In many ways it is true to type, but in addition to the frequent occurrence of more than six pairs of perfect mesenteries, both young and adults possess an abundance of penicilli in their acontia. The latter is a feature of the Sagartias and one which at present distinguishes the adults of the Dingle form from the adults of the typical *M. senile.* The asexually produced polyps of the latter often show the Sagartian feature of more than six pairs of perfect mesenteries, some of which may bear gonads. The deviation from hexamerism is not entirely due to the mode of reproduction (see p. 906) and moreover, other anemones, e.g. Aiptasia, which reproduce by basal laceration, always give rise to daughter polyps which are diglyphic and hexamerous irrespective of the size and constitution of the original fragment (**4**). In the latter species hexamerism seems to be a stable character, whereas in Metridium the inherent tendencies to this primitive condition are not so pronounced.

The presence of acontial penicilli appears to be a constant character of the Dingle anemone and should future investigation show that irregular polyps normally arise by sexual reproduction then such a form of Metridium would be almost as near to the genus Sagartia as to the genus Metridium ; the presence of a distinct collar in the latter does, however, distinguish the two genera. A large amount of experimental work involving the rearing of egg embryos would be necessary to prove this point. Until more is known about the morphology of egg embryos the true state of affairs within the genus cannot be estimated.

SUMMARY.

1. A special study has been made of a small Metridium-like anemone found at Dingle, Liverpool, in comparison with the typical form of *Metridium senile* (L.) var. *dianthus* (Ellis).

2. Penicilli, formerly believed to be absent from the acontia of typical *M. senile*, have been discovered in abundance in the young, but rarely in the adults. In young and sexually mature specimens of the Dingle anemone they are also abundant.

3. There is close agreement between the anatomy of the Dingle form and the typical *M. senile*.

4. A considerable amount of variation occurs in the Dingle anemone, as in *M. senile* var. *dianthus* and *M. marginatum*, Milne-Edwards.

5. The resemblances and differences between the Dingle form and *M. senile* indicate that the former is a dwarf variety of the latter.

6. The discovery of an abundance of penicilli in the acontia of young typical *M. senile* and mature specimens of the Dingle variety, in conjunction with the great amount of variation in the genus Metridium, suggests that a reconsideration of the systematic position of the genus is necessary and would justify either the restriction of the family Metridiidæ to the single genus Metridium, or else the fusion of the Metridiidæ with the Sagartiidæ. The sum of the evidence appears to lie in favour of placing the genus in a family by itself.

ACKNOWLEDGEMENTS.

I am much indebted to both Professor Orton and Professor Stephenson for their kindly helpful criticism and particularly to Professor Stephenson for the manuscript of the chapter on Metridium intended for the forthcoming second volume of his monograph on the British anemones, and for his very generous help with the discussion on the systematic position. Unfortunately I have been unable to quote all his suggestions as they arrived after the paper had gone to the press.

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The Flow of Water Past the Seven Stones Lightvessel.

By

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INTRODUCTORY REMARKS—WITH BRIEF REFERENCE TO RELEVANT EXISTING INFORMATION.

THE purpose of this paper is to place on record the results of a series of current measurements carried out from the Seven Stones Lightvessel in August and September, 1933.

The observations are believed to be the first set of direct current measurements of any duration made in the area. The instrument employed was a Drift Indicator such as has long been in constant use at the Varne Lightvessel, and of which a full description is readily available in the popular pamphlet which appeared as No. 17 of the Ministry's series of " Fisheries Notices."

Details as to the duration and continuity of the observations to be dealt with can be gleaned from the table given below.

It may be recalled that what one learns from the employment of the instrument in question, is the residual current—or what Doodson has called the average constant current.

It is hoped before long to carry out from the Seven Stones Lightship, precisely similar continuous current observations to those which have been in train for more than eight years from the Varne Lightvessel, and the investigation below dealt with was in the nature of a preliminary experiment.

Thanks are due to the Trinity House for permission to make the observations from their lightship; to their District Superintendent concerned (Captain R. W. V. Plimsaul), to the officers of their steamer S.V. *Mermaid* (Messrs. J. C. McCarthy and C. E. K. Carpenter), and in particular to the Master of the lightvessel (Mr. T. Boyd) who, besides making the observations, logged the relevant wind and sea particulars.

The Seven Stones Lightship is moored at 50° 03′ N.–6° 04′ W. in 39 fathoms of water; its position therefore is about 14 miles due west of Land's End.

The observations were made (as at the Varne) at the nominal depth of six fathoms.

It would be of considerable interest fully to relate the results which we shall present below to prevailing ideas concerning the nature of the water movements in the Land's End–Scillies passage, to what is known of the circulation at large off the mouth of the Channel and the entrance to the Irish Sea, and also to the Rennell Current question.

Exigencies of space preclude more than a few brief remarks in these connections. The reader who is acquainted with the relevant literature will know that any adequate account presenting citations from the publications of Matthews, Harvey, Lumby, Gehrke, and others, would convey the impression that the most usual direction of water flow through the passage is towards the northern half of the compass.

Admiralty tidal stream observations relating to the position of the lightvessel itself, and to another position about $16\frac{1}{2}$ miles away towards S. 30° E., could be shown to imply the existence of a set towards the S.E. quadrant, but it is not at all easy to decide just what degree of reliance can be placed upon indications of overall water flow derived from vector-averaging such tidal stream data.

Examination of the records sent in to the writer when the month's observing on the Seven Stones Lightvessel was finished, revealed that there had been a flow of water towards the S.E. quadrant at the depth of six fathoms—this as the resultant for the entire period of 28 days.

In a well-known paper (**1**) setting forth the results of a hydrodynamical study of the water movements in the area here concerned, Harvey deduced the existence of a north-going difference in velocity between the surface water and the layer at 60-metres depth, amounting to $1\frac{1}{2}$ miles a day—this between Land's End and the Scillies at the end of June, 1924. He declares elsewhere, that " there can be little doubt of the existence of such a residual current superimposed on the tidal streaming, and carrying water northward into the mouth of the Bristol Channel—variable in velocity and perhaps intermittent."

Harvey's deductions from his hydrodynamical study accorded well with those earlier made by Matthews from the consideration of temperature and salinity distribution, and upon which he based his conclusions as to the circulation in the area. His (Harvey's) results do not tell us what was the overall movement of the entire water column ; his values would have to be compounded with the vectors representing the movements of the water below 60 metres before we could learn that.

Harvey's stated conclusion for the Land's End–Scillies passage was that the surface water had its own proper movement of $1\frac{1}{2}$ miles a day towards N.N.E. over the water below 60 metres—this direction of movement being declared to be suggested by the trend of the pressure contours on his chart. A glance at the latter, however, makes one suppose that " N.N.E." is a misprint for " N.N.W."

As regards the water movements in the Irish Sea at large, it is well known that there is a residual streaming towards the north, and that it has been inferred from purely physical data that the whole body of water in the Irish Sea is changed every year, and that it passes to the north between Ireland and Scotland.

When one is considering the water movements off Land's End, one's thoughts readily turn to the Rennell Current, for if a north-going flow of water across the mouth of the Channel were the most usual state of affairs, one might reasonably expect a northerly set off Land's End to be the rule. If, however, it could be shown that the direction of water flow through the Scillies–Land's End passage is most usually southerly, there would be reason to expect that the Rennell Current can be nothing more than an occasional phenomenon, and some measure of justification for supposing Krümmel to be right when he declares that "Nach alledem wäre es endlich an der Zeit, den Rennellstrom von den Karten zu tilgen."

Events *in re* currents off Land's End can hardly fail to be linked up with the water movements to the south, and the driving force of the Rennell Current merits a few words. Tait has recently found that with certain pooling-up conditions in the Moray Firth due to an unusually strong inset from seawards, an escape-current can be generated, which, trending north, can head across the ocean passage north of Scotland and cut off the usual inflow.

Since the Rennell Current is held to be born of similar effects in the Bay of Biscay, may not it too be a similarly occasional phenomenon ?

If it is, then we ought not to be unduly surprised if we find reason to suppose that there is most usually a S.E.-going flow through the Scillies–Land's End passage.

If the remarks made above, in conjunction with the results to be set out below, lead to further investigations designed to ascertain the most usual state of affairs, our chief aim in writing this paper will have been achieved.

THE RECORDS OBTAINED.

Below we tabulate the results of the 28 days' observations at the Seven Stones Lightvessel.

TIDAL STREAMS.

Our first comment on the table can well refer to the tidal streams, since comparison between our data and those available in the Admiralty Manual (**2**, page 40) besides being of interest, can be very easily made.

We find that the total mileage run per tidal period of the streams in all the directions concerned can, according to the showing of our Drift Indicator, be taken as 7·3. This value can be regarded as a representative average.

RESIDUAL CURRENTS AND WINDS AT THE SEVEN STONES LIGHTVESSEL DURING A 28-DAY PERIOD IN AUGUST–SEPTEMBER, 1933.

Serial Reference Number of the Record.	Duration of the Observation in Lunar Days.	Dates and Terminal Hours of the Observation.	Residual Current; Sea Miles per Lunar Day towards a true Direction.		Tota Mileage of To-and-fro Water Movements.	The same per Tidal Period.	Moon Phases.	Residual Wind during the time of the Observation (Based on Eight Estimates per Day made aboard) in Miles per Hour from a true Direction.		Angle in degrees between Residual Current and Residual Wind directions: "r" denotes current set to right of wind, and "l" current set to left of it.
1	1	0910 (17.8.33)–1000 (18.8.33)	6·5	S. 34° E.	12·7	6·4		14·6	S. 50° W.	96 r.
2	1	1010 (18.8.33)–1100 (19.8.33)	3·6	S. 11° E.	11·7	5·8		6·5	S. 49° W.	120 r.
3	1	1110 (19.8.33)–1200 (20.8.33)	4·9	due S.	14·8	7·4		14·0	N. 80° W.	80 r.
4	1	1210 (20.8.33)–1300 (21.8.33)	11·8	S. 21° E.	19·2	9·6	New on 21st	20·6	N. 70° W.	49 r.
5	1	1310 (21.8.33)–1400 (22.8.33)	12·4	S. 1° W.	22·7	11·4		15·2	N. 77° W.	78 r.
6	1	1410 (22.8.33)–1500 (23.8.33)	10·9	S. 2° E.	23·6	11·8		23·0	N. 68° W.	66 r.
7	1	1510 (23.8.33)–1600 (24.8.33)	9·1	due S.	20·5	10·2		6·2	N. 89° W.	89 r.
8	1	1610 (24.8.33)–1700 (25.8.33)	3·3	S. 20° W.	19·3	9·6		6·7	S. 43° E.	117 l.
9	1	1710 (25.8.33)–1800 (26.8.33)	3·7	N. 77° E.	14·6	7·3		5·7	S. 66° E.	143 r.
10	1	1810 (26.8.33)–1900 (27.8.33)	4·7	N. 32° E.	13·5	6·8		5·2	S. 24° E.	56 r.
11	1	1910 (27.8.33)–2000 (28.8.33)	2·8	N. 64° E.	13·3	6·6	First Quarter on 28th	9·4	S. 31° W.	33 r.
12	1	2010 (28.8.33)–2100 (29.8.33)	2·9	S. 79° E.	8·2	4·1		5·3	S. 70° W.	31 r.
13	3	2110 (29.8.33)–2340 (1.9.33)	2·8	N. 78° E.	29·8	5·0		6·5	N. 57° W.	45 l.
14	3	2400 (1.9.33)–0230 (5.9.33)	3·4	S. 68° E.	60·2	10·0	Full on 4th	4·5	N. 56° E.	124 l.
15	3	0240 (5.9.33)–0510 (8.9.33)	2·0	N. 4° E.	61·2	10·2		8·1	N. 77° E.	107 r.
16	3	0525 (8.9.33)–0755 (11.9.33)	1·5	N. 2° W.	32·0	5·3	Last Quarter on 11th	12·9	N. 65° E.	113 r.
17	2	0805 (11.9.33)–0945 (13.9.33)	6·4	N. 36° W.	20·9	5·2		5·8	N. 64° E.	80 r.
18	2	0955 (13.9.33)–1145 (15.9.33)	3·2	S.61° W.	11·8	3·0		4·7	N. 41° E.	20 r.
All	28	0910 (17.8.33)–1145 (15.9.33)	1·9	S. 20° E.	410·0	7·3		1·6	N. 27° W.	77 r.* 7 r.

* This average does not take account of the three "l's."

Now the Admiralty tidal stream data for the position of the Seven Stones Lightship show that the total to-and-fro streamings per tidal period amount to 10·1 miles—this being at the time of spring tides. Assuming, as seems from Warburg's manual (**3**, page 73) to be justifiable, that the average rate of the streams can be taken as three-quarters of their spring rate, we obtain the value 7·5 to compare with ours of 7·3. This degree of accordance is very satisfactory indeed.

Our Drift Indicator data show that the spring-stream speed as given in the Admiralty Manual must be exceeded on occasion, and that the neap-stream speed can be less on occasion than that inferable (5·0 miles per tidal period) from the Admiralty data.

We do not propose to set down here any further details concerning the tidal streams, save to say that the Drift Indicator records show the dominant opposing directions to be about S. by W. and N. by E.

Residual Currents : Inter-relationship Between Wind and Water Movements.

Let us next turn to consider the residual current, which is our main concern. We see that over the whole period of 28 days there was an overall set towards S. 20° E. true and of amount 1·9 miles per day. This is the quantity in which we are most interested, for, although it is an average smoothing out residual currents of varying strengths and directions, it is the quantity with which anyone making deductions from salinity distribution would unconsciously be concerned. This is so because salinity distribution would be conditioned by the integrated effects of varying sets over a considerable period.

It is seen that there was during the entire period of 28 days, a residuum of wind travelling (within a little) in the same direction as that towards which the overall transport of water at 6 fathoms depth was effected, and it is of considerable interest to note the relative magnitudes of the residual wind and water speeds concerned.

The water speed is just a little less than 5 per cent of the wind speed, and, since residual wind and residual current are here in practically the same direction, and since they refer to a period of time long enough to be significant, we can compare the result just obtained with a similar one found earlier.

The present writer in 1930 (**4**) advanced a relationship between speed of surface drift-bottle travel up-Channel and speed of wind. In that case the effective wind in an up-Channel direction was in question, and both bottle and air travel related to considerable periods of time. The corresponding relationship was :—

Bottle travel=1/18th wind travel.

The fraction 1/18th being 5·5 per cent, the two values tally very well—particularly as the lesser one has to do with a water layer so much below the surface as 6 fathoms. Statements could be quoted to the effect that in high latitudes the rate of water drift communicated is about 2 per cent of the velocity of the wind—and 4 per cent in low latitudes. Such statements would not necessarily be in conflict with our findings, for a higher percentage would be expected to apply where residual winds and residual currents representative of considerable periods of time are in question. We here regard our numerical relationship as nothing more than an empirical one good for the area concerned. It may have some potential usefulness, though we shall greatly hesitate to invest it with any real importance until further investigations have been made to see whether such a value emerges again. Such hesitancy is very understandable when it is remembered that we have been dealing with the water movements at 6 fathoms depth. Our reason for relating the two quantities : wind speed and water flow, is the realisation that the individual records evince a large measure of change on the part of the currents with the wind—which fact leads us to suppose there to be some inter-relationship. There are certain features of the entries in our table which suggest that we are far from entitled to assume that, if we repeated the observations many times for a like term, we should find that residual wind and residual current would customarily be directed so nearly in the same direction. A mere glance at the table shows that for a short period of time, residual current at 6 fathoms depth and residual wind can be at a large angle with each other.

ANGLE BETWEEN CURRENT AND WIND.

Inspection of the current and wind data relating to the individual records reveals much of interest. It is to be remarked that in fifteen records (i.e. in all but three) the current set at 6 fathoms depth was directed to the right of the wind. In the three cases (records Nos. 8, 13, and 14), where the current was directed to the left of the residual wind, there had been an abrupt change of wind.

A very interesting feature indeed is that the current was directed to the right of the wind when the latter was from any one of the four quadrants, there having been a current set to the right of the wind for :—

4 cases of wind from the S.W. quadrant.
5 cases of wind from the N.W. quadrant.
4 cases of wind from the N.E. quadrant.
2 cases of wind from the S.E. quadrant.

Much space would be needed to give an adequate analysis of the data in this connection.

Clearly from what we have seen (*in re* records No. 8, 13, and 14) there must elapse some time before, after a change of wind, the current can take up the direction which would accord with the new wind direction. The angle between wind and current at 6 fathoms depth may well be a more or less constant quantity for this area where a wind of persistent direction and long duration is concerned ; this we do not know, but in the near future shall endeavour to ascertain. Since the observations here being considered were made at a time when very changeable wind conditions were encountered (a fact in no way to be regretted since we have found what we have found about the relation of current direction to wind direction for winds from all four quarters) it results that the angles between current and wind vary greatly—from about 140 degees down to 20 degrees.

It is to this substantial variation that we must attribute the fact that the residual current and residual wind for the entire period of 28 days are directed towards the same point of the compass—within a little. The fact that the winds varied so much in strength must have meant that the current would swing into a new direction with change of wind less quickly in some cases than in others, and this would account for some measure of the variation in the value of the angle, and would add to the likelihood that it would be smoothed out of existence in the process of averaging over a " longish " period.

As it is, the residual current for the entire period of 28 days shows some small amount of " right deviation " which the compounding of such variant vectors has not entirely smoothed out.

It is to be expected that, after many months of observation on the Seven Stones Lightship, long period means would display the existence of an angle between current and wind. What the value of that angle would be we cannot presume to guess, but are surely entitled to assume that the current would set to the right of the wind.

The angle made to the right of the residual wind by the residual current at 6 fathoms depth can of course be easily worked out as an average for the 15 individual records above tabulated. The resulting mean value is about 80 degrees.

In view of the variation displayed, we may not accept this magnitude too confidently, but one thing we can do which seems promising : we can pay attention to records Nos. 3 to 7 which relate to a period of persistent strong winds from the N.W. quadrant, and can there see that the " right deviation " varies from 49 to 89 degrees.

If the value of 80 degrees were considered to be acceptably established, we should feel disposed to assume that the layer of water at 6 fathoms depth was little above that containing the centre-of-mass of the entire body of water which the wind was able to set in motion.

The prospect of evaluating the separation angle in the future is very attractive ; for the present we are interested to see that in only three out of the fifteen records showing right deviation was the angle less than the 45 degrees which needs no comment.

No further remarks are called for on this matter since it will receive detailed attention after more observations with the Drift Indicator from the Seven Stones Lightship have been made.

Generalisation from the Present Findings as to the Most Usual Direction of Water Flow through the Land's End–Scillies Passage.

It can be seen from our table that, although the overall set during the entire 28-day period was towards the S.E. quadrant, yet actually there was just as often a set towards the north of the E.-W. line as towards the south of it—14 days in each case. There was more often a set towards the east of the N.-S. line than towards the west of it—17 days against 9. In so far as our results, relating as they do to a time of dominant N.W.'ly winds, might be considered not representative of the most usual state of affairs, we should remark as follows :—

The most usual direction of wind being from the S.W. quadrant, we should, judging from what we have seen as to the relation between wind and current directions, expect the set to be most frequently directed towards the S.E. quadrant, and not (as seems to be the prevailing opinion) towards a northerly point.* We should expect a persistent set towards the quadrant between N.E. and N.W. only during months characterised by wind conditions from S.E. to N.E. respectively.

These findings and expectations would lead us to doubt the existence of the Rennell Current except as an intermittent phenomenon, that is to say, we should expect there to be a north-going set off the Channel mouth much less frequently than would entitle us to perpetuate the Rennell Current.

It seems abundantly clear that many more direct current-meter observations are needed before we can hold really definite ideas as to the most usual state of affairs concerning the currents off Land's End.

Varne Current and Drift-bottle Particulars.

During the first six days of the Seven Stones observations above dealt with, the Dover Straits current was heading strongly and boldly (i.e. with a fair amount of east in it) into the North Sea. Thereafter, up to

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* In this connection it is of real interest to recall the implications of the Admiralty tidal stream data briefly referred to above. As we now see, the S.E.—going set which they implied may well be—as Harvey (5, p. 67) supposed possible—a wind drift, but a wind drift induced by S.W.'ly winds.

September 7th, conditions of " hold-up " of the Varne current prevailed. After that the Dover Straits current was strongly reversed—this at the time when the Seven Stones current was flowing towards north and west of north.

Ten surface drift-bottles are put out each Monday from the Seven Stones Lightship. Four liberations were made during the time of the Drift Indicator observations, but as yet only one bottle (set out on September 11th) has been recovered. This was found 121 days afterwards (on January 10th, 1934) in statistical sub-rectangle UU 4g., that is on the west coast of Ireland in latitude 52° 30′ N. approximately.

Such a recovery position is very unusual, though one or two other bottles have been recovered on the west Irish coast. The bottle would have commenced its journey at the time of our record No. 17 (see Table above) and would have got a good start towards the N.W.

SUMMARY.

A brief reference to the state of opinion concerning the water movements off S.W. England is made. Then a series of Drift Indicator records relating to 28 days of observation at 6 fathoms depth from the Seven Stones Lightvessel is presented and discussed. An overall flow of water towards the S.E. quadrant and of speed approaching 2 miles per day characterised the entire period. The residual current as worked out for the individual records, displayed considerable variation in speed and direction —setting as frequently towards the northern half of the compass as towards the southern, but more frequently towards the eastern half than towards the western half. There were pronounced changes in the wind speed and direction, and it appears as though the wind can drive the water at 6 fathoms depth towards a point to the right of its own direction, no matter from which of the four quadrants it blows.

There is good reason to suppose that the angle between the 6 fathom current direction and that of the wind in this area would almost always be greater than 45 degrees. Observations occupying 21 days yielded an average value approaching 80 degrees.

During the entire period of 28 days, an overall transport of water towards the same direction (within a few degrees) as the residual wind proper to the whole period was effected at 6 fathoms depth—the speed of the water flow being about 5 per cent of that of the wind. This result accords very closely with an earlier relationship worked out between drift-bottle travel up-Channel and wind flow up-Channel. Since the most usual direction of wind is S.W.'ly, the findings regarding the angle between wind and current are held to justify the expression of opinion that the most usual direction of water flow through the Land's End–Scillies passage

will be towards the S.E. quadrant. This opinion is in conflict with deductions which have been made from the study of salinity and temperature observations.

The Rennell Current question is briefly considered.

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Replacement of Potassium by Rubidium in *Nitzschia closterium.*

By

F. A. Stanbury, M.Sc.

With 2 Figures in the Text.

Various attempts have been made to substitute certain elements for those acknowledged as essential for plant growth. Using plant material, sodium is the element usually chosen as a possible substitute for potassium, but results show that whilst sodium may be taken up in fairly considerable quantities this is only possible if small amounts of potassium be present as well. Total replacement appears to be impossible (**11**, **13**, **15**).

The failure to substitute sodium is not really surprising, for although there is considerable likeness, there are important differences between the two elements. A substance more nearly approaching potassium is the element rubidium. Rubidium can only with great difficulty be distinguished chemically from potassium. Apart from the differences of their absorption spectra—differences which are not altogether reliable when dealing with very small amounts of these elements or when in the presence of other substances (**10**)—the only means of clearly distinguishing between them appears to lie in the differences between the properties of such complex substances as their meta-stannates or the tetra-thio carbamides of their respective iodides (**10**, **5**, and **6**).

The possible substitution of rubidium was tried by Cameron (**8**) with remarkable success. He used plants of *Petroselinium sativum* grown from seeds in an artificial soil of alumina and charcoal. The alumina was stated to be free from potassium, as was the charcoal, which was obtained by the imperfect combustion of sugar, both substances having been tested spectroscopically. This artificial soil was contained in a vessel of block tin and " manured " with nutritive material containing no potassium. The seedlings were watered with a solution containing rubidium chloride. Plants producing seeds resulted from these experiments. Compared with normal control plants, the " culture " plants were not so robust, but the fact remains that a cultivated plant, in which potassium occurs in a very large proportion in the ordinary way, was grown to a state of maturity on soil free from this element. Other plants grown upon the same type of artificial medium and under identical conditions except that they were not watered with the rubidium chloride solution, very quickly died, so that it would seem that the rubidium really replaced the potassium, but as Cameron himself pointed out, it is very difficult to obtain exact results when using any of the higher plants. The seeds from which the plants were grown would contain a certain amount of potassium, and this amount, although small, might be sufficient to influence growth throughout life. In testing the ash of the matured " culture " plant Cameron reported that " minute traces " of potassium were present, and he considered that this had been derived from the seed from which the plant had been grown. To obtain really conclusive results the seeds of the " culture " plant should have been grown for a number of successive generations, for only thus would it seem possible to reduce the potassium present in the final plants to a minimum approaching elimination.

Using rubidium sulphate an attempt to replace potassium has now been made using the marine diatom *Nitzschia closterium* as the plant material. In this diatom, growth is relatively rapid, so that the products of several successive generations can be obtained in a comparatively short time. It could, therefore, be hoped to obtain by sub-culturing from normal parent stock, diatoms from which the element potassium was gradually eliminated.

The results of such experiments are presented in the following pages.

MATERIAL USED AND METHOD OF WORKING.

The stock material was that of a persistent culture of *Nitzschia closterium*, a marine diatom grown in sterilized natural sea-water to which nutritive material had been added in the form of " Miquel solution " (**17**). Artificial sea-water was made up according to the method described by Allen (**1**). All the elements of natural sea-water, excepting potassium, were present in their proper proportions. Nutrient material was added in the form of a modified " Miquel solution," the potassium salt again being omitted and substituted by one of sodium. The salts used were Kaulbaum salts, pure for analyses, or of the British Drug House—analytical quality : the water used was freshly distilled into Winchester quart bottles which had once contained strong acid, but which had been used for distilled water only for at least five years. All the ingredients were dissolved and kept in quartz vessels to prevent any possible contamination with potassium. The artificial medium gave no flame test for potassium with either the ordinary blue or with the didymium glass—a glass which transmits the blue freely whilst completely blocking the wave lengths emitted by sodium. The absence of potassium was also verified spectroscopically by a technique which was capable of detecting 2×10^{-5} mg. potassium per cubic millimetre, but failed to detect half of this amount.

This potassium-free (–K) artificial sea-water was sterilized, and 80 cubic centimetres of it were poured into a clear quartz flask and inoculated with a very small drop of Nitzschia culture containing a known number of diatoms per unit of volume. This sub-culture (A) was then covered with a quartz plate and kept sufficiently aerated, and placed in a window receiving light of a suitable intensity for diatom growth. The aeration of the sub-culture was effected by a sterilized pipette, which after sterilization had been rinsed in the sterilized potassium-free sea-water described. The counting of the diatoms was done with a hœmocytometer (**17**). In every case five counts were made and the figure recorded is the mean of five counts which were usually quite concordant.

A trace of potassium was naturally introduced with the inoculating drop. This, together with any traces of potassium present in the artificial medium, but not detectable by the spectroscopic method, was soon used up, as was indicated by the results of counting, since a point was reached where no further increase in numbers occurred. Table I. It was therefore assumed that the sub-culture A was now devoid of any available potassium. No further increase in numbers was recorded although the diatoms present appeared quite healthy, but a little smaller in size than the normal.

Using a new supply of potassium-free sea-water, a new sub-culture (B) was made from the potassium-depleted culture A. There was very little multiplication in the new sub-culture B as may be seen from Table II.

TABLE I.

TO SHOW THE GROWTH OF SUB-CULTURE A OF *NITZSCHIA CLOSTERIUM* TRANSFERRED FROM NORMAL SEA-WATER TO A POTASSIUM-FREE ARTIFICIAL MEDIUM.

Date.	No. of diatoms per unit of volume, viz. 0·1 mm^3.
12.6.32	14
15.6.32	58
19.6.32	69
26.6.32	85
3.7.32	78
8.7.32	94
13.7.32	94
13.9.32	94

The spectroscopic test showed the medium to be free from potassium, although this test is really valueless at this stage, since growth did take place in the potassium-free medium in spite of its failing to show any trace of potassium by this test. At this point the sub-culture B showed

6×10^4 diatoms per cubic centimetre of solution, and the figure remained constant for a period of several weeks.

Sub-culture B was then shaken very thoroughly to ensure equal distribution of the diatoms throughout the medium, and divided into seven equal portions, each being poured into a small quartz crucible of ten cubic centimetres capacity. To six of the divided cultures known amounts of potassium or rubidium were then added, numbers 1, 2, and 3 receiving potassium as potassium sulphate and 4, 5 and 6 receiving rubidium as rubidium sulphate. Crucible 7 was left untouched (see Table III). The crucibles were then covered with quartz glass plates and set aside in the window, and aerated and counted in the usual way. The drops taken for counting were always rejected after use. The "1a," "2a" etc. crucibles refer to a second series done later.

TABLE II.

To show the Growth of Sub-culture B of *Nitzschia closterium* transferred from the Potassium-depleted Sub-culture A, to fresh Potassium-free Artificial Medium.

Date.	No. of diatoms per unit of volume ($0{\cdot}1$ mm.^{3}).
16.9.32	New inoculation
30.9.32	3
6.10.32	5
14.10.32	6
21.10.32	6
28.10.32	6
28.11.32	6

Results.

Two series of experiments were performed. The first series during the Winter and early Spring, November 28th–March 3rd, and the second during the Autumn, September 25th–November 24th.

Previous work with *Nitzschia closterium* has shown that the growth figures at any time of the year show peculiar rising and fallings, the cause of which cannot satisfactorily be explained (**17**). The cultures at present under consideration also show these irregularities (see Tables III and IV). With the exception of the untouched cultures 7 and 7a, all show increase in growth. In the first series of experiments, the increase is fairly steady for a period of fifty-one days, and towards the end of this time the figures tend to be proportional to the amount of potassium added in cultures 1, 2, and 3. The same tendency is shown in the potassium containing cultures of the second series. The extraordinary growth of culture 2, which received 10γK per c.c. of culture solution, can only be explained on the supposition that some impurity had inadvertently been admitted whilst extracting droplets for counting. Increase in temperature and in the length of the day as the year had proceeded could not alone account for such growth (Figs. 1 and 2.)

The continued fall in numbers in culture 3, after a very short growth period, is probably due to potassium starvation, and it would seem that the limiting value of potassium-requirement is being reached—viz. 4γK per c.c. of culture. The diatoms were small and in an unhealthy condition. A similar amount of rubidium in culture 6 gave slightly better growth throughout the course of the first series of experiments, and although the diatoms were small in size they appeared quite normal and healthy in form when seen under the microscope. Culture 4 shows the poorest growth, although it contains the largest proportion of rubidium, viz. 21γRb. per c.c. of culture solution. This amount appears to be injurious for continued growth. It therefore seems that, although rubidium may be harmful in certain proportions (culture 4), in smaller

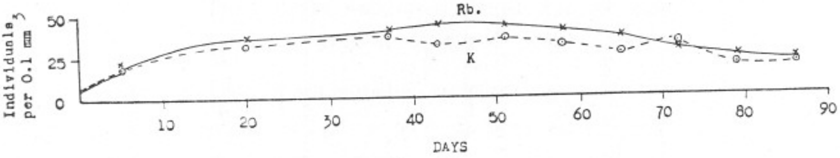

FIG. 1.

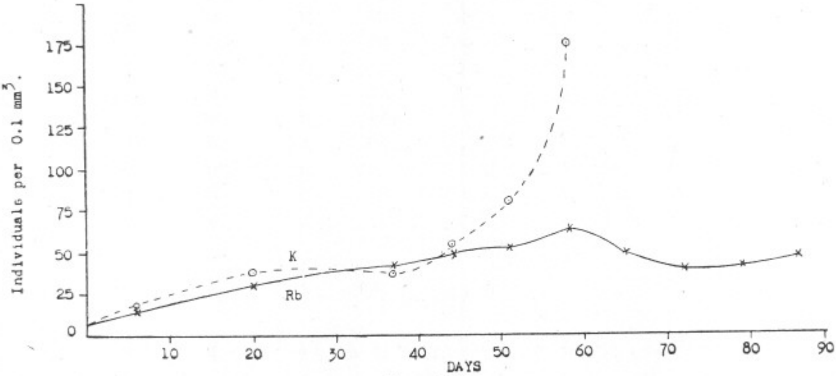

FIG. 2.

FIGS. 1 and 2.—Showing growth of *Nitzschia closterium* in artificial sea-water containing known amounts of potassium or rubidium respectively—viz. 4 micrograms of K. or Rb. in Fig. 1, and 10 micrograms of K. or Rb. in Fig. 2.*

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* In Fig. 2 the "potassium" curve shows abnormal growth after 51 days. This is probably due to some trace of impurity, possibly introduced during aeration of the cultures.

amounts (culture 6) it is quite as efficient as similar amounts of potassium, but even in that case increase is restricted to 7–11 times their original number.

TABLE III.

To show the Growth of the Sub-cultures of *Nitzschia closterium* when supplied with known Amounts of Potassium or Rubidium respectively shown as Micrograms per c.c. ($10^{-6}g=\gamma$), over a Period of 86 Days. Nov. 28th–March 3rd (1932–1933)

			Numbers of diatom per 0·1 mm.^{3} of culture.					
Culture number		7	1	2	3	4	5	6
Date.	Days.	Untreated	21 γK	10 γK	4 γK	21 γRb.	10 γRb.	4 γRb.
28.11.32	Started	6	6	6	6	6	6	6
4.12	6	6	18	20	17	12	14	17
18.12	20	6	32	37	30	36	29	34
31.12	37	6	46	37	35	41	40	37
8.1.33	44	6	102	55	30	35	48	43
15.1	51	4	162	81	33	29*	52	42
22.1	58	6	‡	175	30†	26*	64	37†
29.1	65	6		350	25	20*	50	35
5.2	72	5		420	30*	20*	39	27
19.2	79	4		500	20*	20*	42	23
3.3	86	5			22*	18*	47†	21†

TABLE IV.

Amount of Potassium and Rubidium as above. Experiment conducted over a Period of 69 Days. Sept. 25th–Nov. 24th, 1933.

1933.	Days.	7a.	1a.	2a.	3a.	4a.	5a.	6a.
25.9.33	Started.	6	6	6	6	6	6	6
6.10	11	6	18	14	13	15	12	12
13.10	18	6	32	29	23	22	32	21
20.10	25	5	60	32	27	30	54	30
27.10	32	5	100	53	39†	44	66	43†
3.11	38	4	122	63	35	50	60	39
10.11	45	3	110	53	33	43	57	36
24.11	69	3	110	50	30	40†	58†	33†

In the second series the same general tendencies in growth are shown over corresponding periods of time, the greatest difference being the better growth of the diatoms supplied with most rubidium, viz. culture 4a supplied with 21γ rubidium per c.c. of culture medium (Table V).

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* Empty frustrules numerous. Culture obviously dying off.

† Frustrules healthy, but small in size.

‡ Culture found overturned.

TABLE V.

To show the result of correlating numbers giving increase in growth and the available potassium or rubidium per diatom in gram atoms.

The Potassium-containing Cultures.

	First series.			*Second series.*		
Number of culture	1.	2.	3.	1a.	2a.	3a.
Length of time in days .	28.11.32–15.1.33 51 days.			25.9.33–10.11.33 45 days.		
Amount of potassium supplied in γ	21	10	4	21	10	4
No. of diatoms at end of period in 10^4 units . . .	161	81	33	110	53	33
Amount of potassium in 10^{-14} gram per diatom . .	1·29	1·23	1·21	1·9	1·9	1·21
10^{-16} gram atoms of potassium per diatom	3·3	3·15	3·1	4·8	4·8	3·1

TABLE VI.

The Rubidium-containing Cultures.

	First series.			*Second series.*		
Number of culture	1.	2.	3.	1a.	2a.	3a.
Length of time in days .	28.11.32–15.1.33 51 days.			25.9.33–10.11.33 45 days.		
Amount of potassium supplied in γ	21	10	4	21	10	4
No. of diatoms at end of period in 10^4 units	29	52	42	43	57	36
Amount of rubidium in 10^{-14} gram per diatom . .	7·2	1·92	0·91	4·9	1·75	0·11
10^{-16} gram atom of rubidium per diatom	8·5	2·25	1·07	5·76	2·06	1·3

Tables V and VI show the results of correlating the figures of increase in numbers, with the amounts of available potassium or rubidium present in the two series after periods of 51 days and 45 days in the first and second series respectively. During these times growth had been fairly regular and steady in the two sets of experiments.

From these figures it will be seen that the individual diatom requirement is approximately $1{\cdot}3 \times 10^{-14}$ gr. K. per unit. Using this figure it is therefore possible to estimate the amount of undetectable potassium present in the so-called potassium-free artificial medium. Reference to Table II shows that this artificial medium gives an increase of growth, reaching 6 diatoms per 0·1 mm.^{3} of culture medium. The potassium impurity must therefore approximate 0·78 micrograms per litre of solution.

It is also interesting to compare the potassium requirement of the diatom with the corresponding phosphorus need. Atkins has shown (**4**) that in fresh cultures, 1·12 mg. phosphorus as P_2O_5 will produce 1×10^9

diatoms. The phosphorus per diatom in gram atom obtained from this figure is $15 \cdot 8 \times 10^{-15}$ gram atoms as compared with $3 \cdot 3 \times 10^{-16}$ gram atoms potassium per diatom. The phosphorus-potassium ratio is therefore approximately 50.

Conclusions.

1. It is fully realised that the difficulty in detecting potassium and rubidium when present in small quantities and together with salts of sodium, is very great. The spectroscopic method used for the detection of these elements reached its limits of delicacy between 21 and 10γ potassium per c.c. in artificial sea-water.

It is calculated from the diatom growth recorded that the undetectable potassium was about 0·78 γ per litre.

2. That the growth recorded in the rubidium-containing cultures 4, 5 and 6 is not due to undetectable amounts of potassium present, as an impurity in the rubidium sulphate is fairly obvious when it is considered that the actual amounts of rubidium provided were 21, 10 and 4γ per c.c. of culture medium respectively. In view of the tested standard of purity of the chemicals used, it follows that any trace of potassium introduced, must of necessity be very small. Yet in the experiments 3 and 3a which received 4γ *potassium* per c.c. growth was no better than that of cultures 6 and 6a which received a similar amount of *rubidium.*

3. It may be concluded that when rubidium is supplied in small amounts (see cultures 6 and 6a) this element equals in efficiency similar amounts of potassium (see cultures 3 and 3a). In larger amounts, e.g. 21γ rubidium per c.c., rubidium would appear to be harmful. The diatoms in the rubidium-containing cultures seem to be limited to an increase of seven to eleven times their original number, so that even when the rubidium is not harmful the total replacement of potassium seems impossible.

4. It would seem that $3 \cdot 1 \times 10^{-16}$ gram atoms of potassium per diatom is approaching the limiting value of this element for the continued growth of *Nitzschia closterium.* For rubidium the corresponding figure is about $1 \cdot 1 – 1 \cdot 3 \times 10^{-16}$ gram atoms of rubidium per diatom.

5. Comparing the phosphorus requirement of *Nitzschia closterium* with that of its potassium need, the ratio of phosphorus-potassium is approximately 50.

I am greatly indebted to Dr. E. J. Allen for laboratory facilities and to Dr. W. R. G. Atkins for suggesting and directing the subject of the research and for his help and encouragement throughout the experiments.

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Abstracts of Memoirs.

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY.

Pinnotherion vermiforme Giard and Bonnier, an Entoniscid infecting *Pinnotheres pisum*.

By D. Atkins.

Proc. Zool. Soc., Lond., Part 2, 1933, *pp.* 319–363.

Pinnotherion vermiforme infects *Pinnotheres pisum* from the Camel Estuary, Padstow, North Cornwall.

The males are not restricted in their occurrence to the body of the female, as apparently they are in other genera of Entoniscidæ, but occur isolated in the host, as do also the cryptoniscan larvæ. Of the total Pinnotheres examined 27·69% were infected. Infection with the male parasite alone was 26·85%, with the female (sometimes with males present in addition) 0·84%. The proportion of the sexes in *P. vermiforme* was 97·67% males and 2·33% females. The presence of the adult female causes partial to almost complete atrophy of the gonad of the host. At Padstow the female parasite has been found in the female host only; the male has on two occasions been found in the male host.

The relation of the parasite to its host and the possible manner of respiratory exchange is discussed.

The female and male *P. vermiforme* are described and figured, and, so far as material allowed, the epicarid and cryptoniscan larvæ.

D. A.

The Photo-electric Measurement of the Penetration of Light of Various Wave-lengths into the Sea and the Physiological Bearing of the Results.

By W. R. G. Atkins and H. H. Poole.

Phil. Trans. Roy. Soc. B., 1933, *Vol.* 222, *pp.* 129–164.

Using a potentiometer-telephone method with sodium, potassium and thin film caesium cells, and light filters, the coefficient of absorption was found to be: for the near ultra-violet, 0·390; blue, 0·140; green, 0·155; yellow (not including red), 0·164; orange-red, 0·435; red, 0·480 and deep red, 0·567. It follows that the sub-surface illumination is reduced to 0·001 per cent at 30, 82, 74, 70, 26, 24, 20 metres, respectively. The figures given may be taken as typical of the English Channel ten miles out. For the clearest water found, twenty miles from land, the coefficient was 0·077, for blue light. Correction factors are given for certain reflection losses between air-glass and air-water surfaces and for instrumental effects. The loss at the air-water surface appears to be small in calm water, but is appreciably increased by wind.

The heating of the water below the thermocline may be attributed to the absorption of light, from yellow to violet.

The ratio of the total vertical to the diffuse vertical light, in air, increases from 2·2, for near ultra-violet, to 5·5 for deep red, as determined under a clear blue sky with sun at 52° altitude.

Data, available from the work of Marshall and Orr, for the evolution of oxygen by diatoms, yield values for the absorption coefficient chiefly between 0·15 and 0·20, corresponding to that for light from blue to yellow.

The spring increase in diatoms was not found to decrease light penetration. At a maximum the mean thickness of diatoms traversed in a 10 m. water column is only 0·25 mm. and is probably nearer one-tenth of that on an average.

The absence of red light from the deeper water may be expected to have a bearing on the colour vision of certain fish.

Hulburt's coefficients have been used to show that even in the clearest ocean water the anti-rachitic portion of the spectrum is reduced to 1 per cent of its sub-surface value at 1·1–2·2 m., according to wave-length and to 0·001 per cent at from 2·9 to 5·5 m. This has an obvious bearing on the origin of vitamin D in fish-liver oils.

W. R. G. A.

Osmotic and Ionic Regulation in the Shore Crab, *Carcinus mænas*, with notes on the Blood Concentrations of *Gammarus locusta* and *Ligia oceanica*.

By J. B. Bateman.

Journ. Exp. Biol., Vol. X, 1933, *pp.* 355–371.

Chloride and vapour pressure data for the body fluids of Carcinus living in various strengths of sea-water were obtained, Duval's observation that " osmotic " regulation is abolished in concentrated sea-water being confirmed. Then the effect of " osmotic " and " ionic " forces on the normal regulation was studied by immersing crabs in sea-water containing respectively foreign non-electrolytes and electrolytes. The substances added showed interesting specific effects, glucose in particular causing a large increase in blood chloride, but in general they supported the belief that the regulating membrane (presumably the gill) is impermeable to water. This is in agreement with other experiments which are described. Miscellaneous experiments on the effects of cyanide, pH, and temperature are given, with a discussion of the mechanism of regulation and the thermodynamic work involved.

A direct study of the body fluids demonstrated the high degree of osmotic independence of Ligia for short periods of immersion and its breakdown after longer periods. Gammarus appears to regulate in much the same way as Carcinus.

J. B. B.

The CO_2 Dissociation Curves and the Buffering of Crab's Muscle and Nerve Preparations.

By S. L. Cowan.

Journ. Exp. Biol., Vol. X, 1933, *pp.* 401–411.

Crab's muscle and nerve preparations, which had been previously soaked in aerated sea-water for an hour, were brought into equilibrium with different CO_2 nitrogen mixtures of known composition in a modified Barcroft apparatus and then the combined CO_2 was measured after acidifying the tissue. From the CO_2 dissociation curves so obtained, by means of the Henderson-Hasselbalch equation, the pH of the preparations under known CO_2 pressures was calculated.

For muscle and for nerve the relation between CO_2 pressure and cH was almost linear over the greater part of the range.

It is probable that the CO_2 binding capacities and the pH of the tissues are altered by the preliminary soaking in sea-water, and that the figures given would not hold good (for muscle and nerve) in the intact animal.

S. L. C.

The Relation between Somatic and Germ Cells in the asexually produced polyps of the Polyzoan *Alcyonidium gelatinosum*.

By G. H. Faulkner.

Annals and Magazine of Natural History, Ser. 10, *Vol. XI*, 1933, *p.* 255.

In the development of the asexually produced polyp of *Alcyonidium gelatinosum*, certain cells are very early set aside, and remain undifferentiated. They proliferate actively, and contribute to the growth of the alimentary canal; during the period of growth they form a morula-shaped mass projecting into the body cavity, attached to the cæcum of the alimentary canal adjacent to the attachment of the funiculus. In the sexual season cells persisting from this group give rise to the female sex-cells. (The origin of the male germ-cells was not traced.) These cells are inter-epithelial in position, lying between the basement membrane of the endoderm and the peritoneum. They are considered to be homologous with the neoblasts of Annelids.

G. H. F.

Recherches Sur les Hemérythrines.

By Marcel Florkin.

Arch. Int. Physiol., 1933, *Vol.* 36, *pp.* 247–328.

The haemerythrins, respiratory proteins found in the red cells in the cœlomic fluid of the Sipunculids, are typical globulins, crystallizing in the rhombohedric system. The spectrum of the haemerythrin of *Sipunculus nudus* is quite different from the spectra of all haem derivatives, and in ertain aspects more similar to the Haemocyanin (hemsbyanius) spectrum. The ratio $\frac{\text{Iron}}{\text{Oxygen}}$ is different from this ratio for the oxygenation of Haemoglobin. In conditions where Haemoglobin is transformed into Carboxy-haemoglobin, there is no combination of CO to Haemerythrin. The respiratory function of the cœlomic fluid of *Sipunculus* is analysed, and the Bohr effect shown to be absent. The different peculiarities of this cœlomic fluid show many correlations with the characters and habits of the animal considered.

M. F.

Blood Circulation of Animals possessing Chlorocruorin.

By H. Munro Fox.

Proc. Roy. Soc., Ser. B Vol. CXII, 1933, *pp.* 479–495 .

Most blood-vessels of sabellids and serpulids are rhythmically contractile, including all the blind-ending capillary vessels in crown, body wall, and coelom. In the continuous vessels the blood is circulated by peristalsis, in the capillaries there is an ebb and flow of the blood. The rhythmic contractions of the vessels are independent of the central nervous system. The simultaneity of contractions in the vessels of the separate filaments of the crown is controlled by a ganglion at the base of each half of the crown. After sabellid worms have retired into their tubes for over half an hour, the contractions of their blood-vessels cease. The contractions recommence as soon as even the tip of the crown projects beyond the end of the tube. In spite of the cessation of blood circulation, Spirographis can remain uninjured for eight hours in its tube when the latter is artificially closed. After eight hours the animal makes a new anterior lateral opening in the closed tube and re-expands its crown. When sabellids or serpulids, removed from their tubes, are put into sea-water the pH of which has been brought below 6·0 by the addition of carbon dioxide, the contractions of their blood-vessels stop. Neither water acidified with hydrochloric acid to the same pH as the water containing carbon dioxide, nor water lacking dissolved oxygen, produces this effect. The inhibition of blood-vessel contractions due to carbon dioxide is reversible when the animals are replaced in pure sea water. Carbon dioxide does not inhibit the blood-vessel contractions through a nervous reflex, it causes an internal accumulation of carbon dioxide which acts directly on the blood-vessel walls. It is probable that the cessation of blood-vessel contractions when sabellids have retired into their tubes is due to the accumulation of carbon dioxide in the water between the filaments of the crown. The threshold pH for the inhibition of blood-vessel contractions of Dasychone was determined in (*a*) sea-water containing dissolved carbon dioxide, (*b*) sea-water of abnormally high alkali reserve containing carbon dioxide, and (*c*) sea-water acidified with hydrochloric acid. From these data it was concluded that both carbon dioxide and hydrogen ions are concerned in the inhibition, but that the former is more important than the latter. Carbon dioxide also causes the reversible inhibition of contractions in the following cases: (*a*) the dorsal blood-vessel of Nereis; (*b*) the hearts of Daphnia, Artemia, Chlœon nymphs, Phallusia, chick embryos; (*c*) the contractile vesicles of Limax embryos.

H. M. F.

Einige Untersuchungen über die Eiweissverdauung bei Gastropoden.

By Sven Hörstadius.

Biologisches Zentralblatt, Vol. 53, 1933, *pp.* 645–650.

The investigation was made in Utrecht, Naples, and Plymouth, the last place thanks to a Ray Lankester Investigatorship. Several statements of phagocytosis in Gastropods have proved to be wrong. Previous investigators found ingested carmine particles in mid-gut gland cells (Helix, Planorbis). A close examination shows that, instead, granules in the cells have been stained red by carmine, that has gone into solution and thus passed into the cell by means of diffusion. Proteolytic enzymes are active in the gut, as fibrin is dissolved. Colloidal gold particles of a certain size, embedded in small pieces of fibrin, were never ingested by the cells.

Also the previous result, that chloroplasts are ingested by Aplysia cells, has proved to be based on a mistake. No phagocytosis takes place, but chlorophyll diffuses into the cells and stains granules green and brown.

On the other hand, phagocytosis was stated to occur within Pleurobranchea, by aid of the gold particle method, and within Hermæa. The latter was fed partly on Codium, partly on Bryopsis, two algæ with chloroplasts of very different size. Both kinds of chloroplasts were found in the liver cells.

S. H.

On *Ceratotrema Furcolabiata* n.g. et n.sp. and *Hemipera sharpei* n.sp. Two New Digenetic Trematodes of British Marine Fishes.

By E. Idris Jones.

Parasitology, Vol. XXV, 1933, *pp.* 248–254.

(*a*) *Ceratotrema furcolabiata* n.g. et n.sp. was found in the cœlom of *Onos mustela* at Plymouth. This is the third trematode recorded from the cœlom of fishes.

Generic Diagnosis. Length 7·3–7·8 mm. Greatest width 1·7 mm. Abdomen completely invaginated into body. Anterior sucker approximately two-thirds size of ventral sucker; average measurements 0·57 and 0·77 mm. respectively. Anterior sucker with three cushion-like projection into lumen, one anterior and two postero-lateral. Lip dorsally situated, very muscular, and strongly bifid, not overhanging the mouth. Ventral groove present. Testes two, oval, situated opposite each other immediately posterior to ventral sucker. Ovary spherical, posterior to testes. Receptaculum seminis present. Vitellaria arranged in two groups posterior to ovary; limbs of vitellaria short and thick and split up to base. Metraterm long, reaching almost to ventral sucker. Eggs green, numerous, $23\mu \times 11\mu$.

Host; *Onos mustela*, in cœlom. Types in the British Museum (Nat. Hist.). Its systematic position is indicated.

(*b*) *Hemipera sharpei* n.sp. Found under the operculum of *Cepola rubescens* at Plymouth.

Specific Diagnosis. Host; *Cepola rubescens*. Situation; under gill-cover. Large and robust. Bluntly rounded. Length, 4·77–4·85 mm. Anterior sucker, 0·372 mm. Ventral sucker, 0·744 mm. Laurer's canal present and prominent receptaculum seminis. Eggs not curved and with long filaments not intertwining. Egg measures $100\mu \times 38\mu$.

E. I. J.

Fertilisation and Egg Formation in a Digenetic Trematode, *Podocotyle atomon*.

By E. Idris Jones.

Parasitology, Vol. XXIV, 1933, *pp.* 545–547.

An account is given of the fertilisation of the ova and of subsequent egg formation in *Podocotyle atomon*. The times taken for the various processes are given.

E. I. J.

Studies on the Monogenea (Trematoda) of Plymouth. *Microbothrium caniculæ* (Johnstone, 1911).

By E. Idris Jones.

Parasitology, Vol. XXV, 1933, *pp*. 329–331.

Microbothrium caniculæ was found at Plymouth for the first time on *Scyllium canicula*. It had previously been described by Johnstone as *Paracotyle caniculæ* n.sp. in 1911. A detailed description of the morphology of the species is given and its position in the genus *Microbothrium* Olsson 1869 indicated.
E. I. J.

The Hirudinea of Plymouth. Part I.

By W. H. Leigh-Sharpe.

Parasitology, Vol. XXV, 1933, *pp*. 255–262.

This account deals with the Ichthyobdellidæ. A list is given of those hitherto found at Plymouth, and a description: of some presumably young forms found on skate: of two new species, *Branchellion borealis*, having but 31 pairs of gills, one specimen, taken by Mr. G. A. Steven on a skate; and *Janusion scorpii*, perhaps the *Platybdella scorpii* of Malm, occasionally found by the author on *Cottus scorpius*.
W. H. L.-S.

Studies on the Relation between Organism and Environment.

By J. H. Orton.

Transactions of the Liverpool Biological Society, Vol. XLVI, 1932, *pp*. 1–16.

In this short paper a summary is given of the author's experiments and observations on marine animals which demonstrate differences in the manifestation of the fundamental processes of feeding, growing, breeding, sex, and survival in different environments. It is therefore adduced that variation in the environment—and still more permanent non-lethal changes—may be expected to bring about definite changes in the organism. From the general fitness of the organism to the environment it would appear that such adaptive changes have become fixed in some manner which still remains to be demonstrated.

The author gives some hitherto unpublished observations on the characters of shells of *Patella vulgata* L.* The notably wide range of

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* The adults (i.e. with shells above about 3 cm.) were normal common limpets; many colour varieties occurred among the young individuals and traces of the coloured rays could be seen in the smaller thin-shelled low-water adults. There does not appear to be any valid reason for recognising the low-water form from this locality as the separate species, *P. intermedia* Jeffries. Typical forms of the variety (or species) *P. athletica* Bean do not occur in the locality in the habitats sampled. (See *Journ. Mar. Biol. Assoc.*, N.S., Vol. XV, p. 860.)

variation at all sizes in the relation between the mean of the length (L) and breadth (B) of the shell—and height (H)—is shown.

A close comparison of samples of limpet shells from respectively high- and low-water situations on Looe Island is made, and constant differences are demonstrated in the following relations: length and height; length and mean axis (mean axis $=\frac{L+B+H}{3}$); length and weight; approximate internal area of shell and weight at given corresponding lengths; weight and apical thickness of the shell for given lengths. The latter values are higher in all cases for high-water limpets.

The shape of a sample of shells of a given range in size is definable by the numerical value of the mean $\frac{L+B,}{2H}$ which is given for a number of samples from high- and low-water situations; the low-water samples give values constantly higher than those from high water. The high-water samples were taken from various selected situations on the south coast of England; it was found that the greater the exposure of the shells to dessication the lower was this numerical value for shell-shape. In an examination of limpet habitats extending over a large portion of the coast of Devon and Cornwall, this effect of dessication was confirmed except for a small population of limpets on an island adjacent to the Gas Works, Teignmouth Estuary, where relatively tall shells are found at about high-water neaps.

The explanation is offered that the shape of the shell in any habitat is due ultimately to habit; in situations exposed to dessication the animal must cling tightly to the substratum to maintain a moist condition of the gills, in damp situations the animal does not need to remain apposed to the substratum; these habits are known. Since increase in shell area occurs at the edge of the shell, and limpets may be assumed to grow shell while apposed to the substratum, a smaller perimeter increment of growth will be made by an apposed limpet than by one relaxed or not apposed. Hence limpets more constantly apposed to the substratum grow a higher shell than those relaxed in damp situations.

Different laws of growth are indicated for young and older individuals; first approximations are given. The studies are being continued, and other results will be communicated later.

J. H. O.

Experiments on the Suitability of some Rectifier Photo Cells for the Measurement of Daylight.

By H. H. Poole and W. R. G. Atkins.

Sci. Proc. Roy. Dublin Soc., 1933, *Vol.* 20, *pp.* 537–546.

In using rectifier cells it is necessary to know the form of the current illumination curve. The latter depends on the resistance of the external circuit, so a low resistance galvanometer should be used. A shunt was designed to reduce the galvanometer sensitivity without affecting its resistance. Temperature effects are important in some cells. The wavelength sensitivity curves of several cells were studied, that of the Bergmann selenium cell is by far the closest in form to that of the human eye. This selenium cell is also relatively the most stable.

W. R. G. A.

Reversal of the Current from a Cuprous Oxide Photo Cell in Red Light.

By H. H. Poole and W. R. G. Atkins.

Nature, 1933, *Vol.* 131, *pp.* 133 *and* 547.

The effect, observed by Auger and Lapicque, was found to exhibit a maximum at 6280 A. In the marginal region of the cell it amounted to 10·6 per cent of the maximum sensitivity of the cell for the direct current, which occurred near 5000 A. The central region gave no reversal. The explanation offered is that the normal effect is located at the front surface of the copper-oxide film, whereas the reverse effect is due to red light penetrating the film to the copper plate behind, but only where the film is thin, as at the margin. The values relate to an equal energy spectrum. At one spot in the marginal region the reverse effect was 28·5 per cent of the maximum direct current from the same region.

W. R. G. A.

BOOK NOTICE

Arachnoidiscus. An account of the genus, comprising its history, distribution, development and growth of the frustule, structure and its examination and purpose in life, and a key to and description of all known species, illustrated.

By N. E. Brown, D.Sc., A.L.S. London, W. Watson & Sons, Ltd., 1933. Price 6s. net.

Dr. Brown, who is a well-known expert with the microscope, has given us a valuable addition to our knowledge of diatoms, and his book on this one beautiful and important marine genus, both recent and fossil and of world-wide distribution, is most interesting, being a detailed study of all the species, 26 altogether. Microscopists are familiar with *Arachnoidiscus* because of its exceptionally intricate and elaborate structure with rays and meshes not unlike a spider's web, hence the name. Apparently up to the present time the nomenclature has been much confused and the species very inadequately described. This is now put right and most of the species found to have a definite distribution confined to particular areas, one species only (*A. anatus*) being widely distributed.

Perhaps the most interesting part of the work is the description of the male and female frustules, for we know so little of this side of the life of any diatom.

The photographic figures illustrating the volume are very clear and good.

M. V. L.

Marine Biological Association of the United Kingdom.

Report of the Council for 1933.

The Council and Officers.

The Council has held four meetings in London during the year at which the average attendance has been seventeen. These meetings took place in the Rooms of the Royal Society at Burlington House and the thanks of the Association are due to the President and Council of the Royal Society for the accommodation provided. A Committee of the Council, consisting of eight members, including the Chairman of Council, Prof. E. W. MacBride, F.R.S., visited and inspected the Laboratory at Plymouth on April 8th.

The Council has to record with deep regret the loss by death, since the last Annual General Meeting, of Sir William Hardy, a Vice-President of the Association, who as Chairman of the Advisory Committee of the Development Commissioners, by his interest in the work at Plymouth and his constant advice and help, had done much to make possible the progress of the Laboratory during the last ten years; of Professor G. C. Bourne, for many years a Governor of the Association representing the University of Oxford and a former Director of the Plymouth Laboratory; of Mr. Nigel O. Walker, Honorary Treasurer of the Association since 1931; and of Mr. George Evans, who had served the Association for sixteen years, from 1915 to 1931, as Honorary Treasurer.

The Plymouth Laboratory.

The Laboratory buildings and fittings have been kept in a good state of repair and the paintwork in good condition. A ladies' cloak-room has been constructed in part of the former library in the main building, and alterations have been made to the store in order to preserve the interior woodwork from the effects of damp. In connexion with extensions made by the Plymouth Corporation to the Tinside Bathing Pool below the Laboratory, the pipe lines for water from, and for compressed air to, the ejector have been in part relaid and renewed, at the expense of the Plymouth Corporation.

The Aquarium.

The Aquarium has been maintained in an attractive condition and the number of visitors has increased. A number of parties of school children, in charge of their teachers, have studied the animals in the tanks. Notable exhibits have been some Electric Rays, chiefly *Torpedo nobiliana*, but one specimen of *T. marmorata*. These Electric Rays have lived well. *Octopus vulgaris* became common during the latter part of the summer and several fine specimens have been shown in place of the usual *Eledone cirrosa* which has been scarce. Unusual captures for the district were two Sea Horses (*Hippocampus guttulatus*), one of which survived for some time, being fed daily on planktonic copepods.

The Ship and Motor-Boat.

On the 7th June last the steam-drifter " Salpa " was placed on the slips in Hawke's shipyard, Plymouth, in order to undergo Lloyd's regulation half-time survey and to have the tail shaft drawn for inspection. The old shaft—the original one—proved to be much worn and a new tail shaft had to be fitted. In the course of the hull survey some of the woodwork was found to have deteriorated somewhat rapidly since the full-time survey in the winter of 1929–30, and a considerable amount of renewal of wood was ordered by Lloyd's surveyor as a condition for the continuance of the ship's character in the Society's Register Book. The necessary repairs were carried out, and at the same time a new lavatory was fitted, the old one having been completely worn-out. The ship is now in good order and remains in Class A 1 for the remainder of the seven-year period which commenced in March 1929.

The motor-boat " Gammarus " has worked continuously throughout the year with the exception of one month in August when the 6-H.P. " Kelvin-Ricardo " engine was removed and despatched to the makers for examination and overhaul. For some time previously this engine had not worked satisfactorily and neither the local agent nor the company's engineer could ascertain the cause of the trouble. The Bergius Company offered, therefore, to carry out an exhaustive overhaul and fit new cylinders free of charge—as the old ones had shown abnormal wear. This engine is now working satisfactorily. The 3½-H.P. engine, which had given continuous service in the " Gammarus " for eleven years, has been taken out and its companion engine, which was removed and stored when the 6-H.P. engine was installed, has been put back in its place.

The Staff.

Dr. L. E. Bayliss of the Physiological Laboratory, University College, London, was appointed to succeed Dr. C. M. Yonge as Physiologist at the Plymouth Laboratory, and commenced his duties in April.

Mr. O. I. Green, after completing one year as Student-Probationer, left at the end of September to take up the study of medicine in London.

Occupation of Tables.

The following investigators have occupied tables at the Plymouth Laboratory during the year:

Dr. H. K. Adams, London (Blood of animals, especially Crustaceans).
Miss D. Atkins, London (Lamellibranch gills).
E. H. F. Baldwin, Cambridge (Bases of Cephalopod muscle).
Miss E. G. Barber, Portsmouth (Invertebrate mud fauna).
Miss F. L. Beanland, Portsmouth (Invertebrate mud fauna).
Miss A. M. Bidder, Cambridge (Digestive system of Cephalopods).
Miss M. V. Bishop, London (Yolk absorption in Purpura).
Dr. A. Brinkmann, Bergen (Laboratory Equipment and Methods).
Dr. S. C. Brooks, California (Library).
Dr. D. L. Bryce, London (Marine Rotifers).
E. Bushra, Cairo (Oceanographical Chemistry).
H. M. E. Cardwell, London (General Zoology).
Dr. and Mrs. J. ten Cate, Amsterdam (Reflexes of spinal cord of Dog-fishes).
F. A. Chrenko, London (Turbellaria).
H. O. J. Collier, Cambridge (Blood system of *Phallusia mammillata*).
S. L. Cowan, London (Chemical exchanges in Maia nerve. Action of drugs on Maia nerve).
G. I. Crawford, Cambridge (Ascidians).
Dr. A. Dannevig, Arendal, Norway (General Zoology).
J. H. Day, Liverpool and South Africa (Development of Polychæta).
R. Dennell, Manchester (Feeding mechanism of Crustacea).
Dr. M. G. Eggleton, Edinburgh (Chemistry of foot muscle of Mytilus).
Dr. P. Eggleton, Edinburgh (Isolation of Arginine phosphate).
Lt.-Commander W. I. Farquharson, Murray Expedition (Oceanography).
H. C. Gilson, Cambridge (Oceanographical Chemistry).
Dr. R. Gurney, Oxford (Plankton. Fish Parasites).
Prof. C. R. Harington, London (Inspecting raft of Civil Engineers' Institute).
Miss E. Harling, Looe (General Zoology).
T. J. Hart, "Discovery" Expedition (Plankton and Oceanography).
Prof. L. A. Harvey, Exeter (Asterina).
Dr. A. B. Hastings, London (Tunicates and Polyzoa).
Miss G. Hess, Zürich (General Zoology).
Prof. L. T. Hogben, London (Chromatophores of Mysis).
Dr. H. R. Ing, London (Action of drugs on Maia nerve).
Miss P. M. Jenkin, Cambridge, Ray Lankester Investigator (Correlation of photosynthesis of diatom cultures in the sea with photoelectric measurements of light penetration).
J. A. Kitching, London (Physiology of contractile vacuoles).
W. H. Leigh-Sharpe, London (Parasitic Copepods).
A. G. Lowndes, Marlborough (Polygraphic investigations of swimming movements of Copepods).
Dr. and Mrs. R. J. Lythgoe, London (Visual purple of fishes).
J. D. Macdonald, Aberdeen (Larvæ of Pagurids).
G. I. Mann, Plymouth (Mollusca).
A. F. Mohamed, Cairo (Oceanographical Chemistry).
Miss L. A. Morgan, Exeter (Turbellarian embryology).
Miss O. S. Mundy, Bristol (Gastric shield of Lamellibranchs).
Miss G. L. Naylor, London (Marsh Fucoids of St. John's Lake).
Dr. O. C. Neilson, Copenhagen (Preservation of nets, etc.).

G. E. Newell, London (Morphology of Melinna).
J. V. V. Nicholls, Montreal (Studies on the nerve in smooth-muscle preparations from the Ray).
Dr. E. A. T. Nicol, Edinburgh (Brackish-water fauna).
Dr. W. Nolte, Kiel (Polychæte larvæ).
Miss E. M. Oliver, London (Digestion in Gunda).
Dr. H. H. Poole, Dublin (Photo-electric measurements).
Dr. M. Ramult, Cracow (Development in Rhizocephala. Planktonic Crustaceans).
Dr. H. Rosenberg, Berlin and London (Fatigue of nerves of crabs).
Miss M. L. Rothschild, London (Parasites of Turritella).
D. Scott, London and New York (Fatigue of nerves of crabs).
H. R. Seiwell, Woods Hole, Mass. (General Zoology).
Dr. C. J. Shen, London (Life history of crabs).
F. G. W. Smith, London (Patella development).
H. G. Smith, Bristol (Chemistry of sea-water).
J. E. Smith, Manchester (Development of Cephalothrix).
S. Smith, Cambridge (Total nitrogen excretion of Carcinus).
Miss F. A. Stanbury, Plymouth (Growth of Diatoms).
F. C. Stott, Southampton (Phosphate and salinity methods).
Dr. S. Takatsuki, Tokyo (Physiology of the Oyster).
Dr. E. F. Thompson, Cambridge (Inorganic constituents of invertebrate blood. Oceanographical Chemistry).
Dr. R. Tourky, Cairo (Oceanographical Chemistry).
R. C. Vernon, Plymouth (Mollusca).
Mrs. D. P. Wilson, Plymouth (Marine algæ).
Dr. F. R. Winton, Cambridge (Excitability of foot muscle of Mytilus).
Prof. C. M. Yonge, Bristol (Crustacean chitin).
J. Z. Young, Oxford (Innervation of the viscera of fishes).

The usual Easter Vacation Course in Marine Zoology was conducted by Mr. D. P. Wilson and Mr. G. A. Steven, and was attended by forty-six students from Oxford, Cambridge, London, Edinburgh, Aberdeen, Liverpool, Sheffield, Newcastle, Birmingham, Reading, Hull, Huddersfield, Bognor Regis, and Bowden, Cheshire.

During the Summer Vacation, Professor J. H. Orton, of Liverpool University, with Miss R. Rawlinson and Mr. C. L. Smith as Demonstrators, conducted a Course in Marine Biology, which was attended by eighteen students from Cambridge, Edinburgh, Birmingham, Bristol, Bradfield, Plymouth, and Zürich, Switzerland.

Also during the Easter Vacation, Mr. J. M. Branfoot brought four students from Oundle School; Mr. B. A. Barr, two from Harrow; Mr. A. M. M. Gardiner, three from Radley College; Mr. A. H. Lewis, one from Wellington College; Mr. L. V. Turner, two from Rydal School; Mr. A. Gillespie, two from Westminster School; Mr. H. C. W. Wilson, ten from Monkton Combe; Mr. I. I. Hamilton, two from Dauntsey School, and Mr. C. B. Owen, three from Malvern College.

At Whitsuntide Mr. W. H. Leigh-Sharpe conducted a class of six students from the Chelsea Polytechnic.

The Scientific Work of the Plymouth Laboratory Staff.

The descriptions of the different investigations have again been arranged so as to indicate their bearing on the general plan of work that is being undertaken by the staff. The investigations on the physical and chemical characters of the environment are first described, then those on the vegetable and animal plankton, which form the basis of the food supply of the sea. Researches on the ecology, physiology, and genetics of the invertebrates of the sea-floor which feed on the plankton and on each other are then described. These invertebrate animals constitute the food of the bottom-living fishes and lead naturally to an account of studies on the fishes themselves and the commercial fisheries.

Physics and Chemistry of the Environment.

The productivity of the sea depends ultimately upon the amount of light available for photosynthesis. The seasonal changes in plankton are therefore dependent upon seasonal variations in light intensity and upon the clearness of the water. Certain of the zooplankton are also influenced in their movements by the illumination. For these reasons Dr. W. R. G. Atkins, in collaboration with Drs. H. H. and J. H. J. Poole of Dublin, has devoted much time in recent years to photometry. A new variety of photo-electric cell of the emission type has been studied and all types of cell available have been standardized in terms of mean noon sunlight, and also of electric arc and bulb lamp light. An improved technique has been adopted, using a potentiometer and electrometer valve null method of measuring the current.

The recording of daylight, started in 1929, has been continued, and a selection of the daily records, together with the apparatus used for submarine photometry as devised by the two Pooles, was lent to the Science Museum, London, for the Exhibition of Photo-Electric Apparatus. A study of the brightness of different parts of the sky has also been carried out.

The principal varieties of the rectifier type of photo-electric cell were also examined and a Bergman selenium cell was fitted into the submarine photometer instead of a cuprous oxide cell. There is a gain from this in stability, sensitivity and colour range. Moreover, as compared with the emission type, the limitations imposed by damp weather are removed and the closing shutter is rendered superfluous. The relation between current and illumination is, however, not rectilinear, so each rectifier cell requires to be calibrated for use in bright light. For work at sea the potentiometer amplifier null method can be used, but with a relatively low resistance.

Some measurements of submarine illumination were made in connexion with Miss P. M. Jenkin's work on diatom photosynthesis at various depths.

Hydrographic data in the mouth of the English Channel have been collected since 1921, and are now published in the Bulletin Hydrographique of the International Council. They are also worked up by Mr. H. W. Harvey. Charts of the surface salinity distribution at the mouth of the Channel are drawn for each month, utilising all available observations, and are reported upon in the Journal of this Association. The years 1931 and 1932 were remarkable for the presence of unusually high salinity water off the mouth of the Channel, patches of which moved up-channel at intervals. Salinities as high as 35·6 and 35·7 were met with on occasions, suggesting water of Mediterranean origin. The temperatures met with, on the other hand, were not extraordinary although the autumn of 1931 was marked by unusually warm water of rather low salinity.

Dr. L. H. N. Cooper has been seeking expeditious methods for determining small amounts of certain metals in sea-water. For iron, 2 : 2′-dipyridyl and Morgan and Burstall's newly discovered 2 : 2′ : 2″-tripyridyl have been found to be excellent reagents. With tripyridyl, samples containing 0, 1 and 2 mg. of iron per cubic metre can just be distinguished from one another. Ferric and organically bound iron have first to be converted to the ferrous state. A start has been made on a study of the seasonal changes in iron and also in copper in the Channel.

Delicate methods for ammonia have also been further investigated. Phenol in presence of hypochlorite gives a blue colour with ammonia, which will detect one part of nitrogen in twenty million parts of water. The reagent appears superior to the Nessler but is not quite sufficiently sensitive for work on sea-water.

The routine observations on the seasonal changes in phosphate have been continued.

Methods have been devised for the analysis of organic phosphate in sea-water and of phosphorus in plankton. In the top forty metres at Station L4 in October, when plankton was fairly abundant, the phosphate present in plankton organisms amounted to only 0·24 mg. P_2O_5 per cubic metre of water, which seemed surprising.

A tentative method for determining oxidisable organic matter in sea-water has been worked out, using solutions of dichloramine–T in acetic acid, which are reasonably stable, as an easily controllable source of chlorine, the absorption of which by the organic matter can be measured.

Measurements have again been made of the variation of excess base between the surface and bottom in the English Channel. These confirm last year's results that a very small difference exists due to a variation in calcium.

Five English and Egyptian members of the John Murray Expedition to the Indian Ocean visited the Laboratory during the Summer to familiarise themselves with chemical methods of analysis of sea-water and a good deal of time was spent by Dr. Cooper in helping them and in preparing reagents for the expedition.

Plankton.

In continuation of investigations on factors influencing the productivity of the sea—the supply of nutrient salts, hydrographic conditions and growth of diatoms—Mr. H. W. Harvey has devised a rapid method of assessing the plant pigments, and hence the phytoplankton, per cubic metre of water. A water-meter has been constructed which measures the quantity of water which has passed through a silk net while being lowered and hauled vertically through the sea. The catch is filtered on a silk disc and the yellow-green plant pigments dissolved in acetone. The resulting green solution is compared with colour standards. After various trials at Plymouth the meter was calibrated at the National Physical Laboratory for rates of water flowing through it varying between 47 and 550 litres per minute. The quantity of water which passed through and registered a unit division on the dial varied between 11·4 and 12·2 litres, sufficient constancy for practical purposes. Similar meters have now been made by London firms for the *Sir John Murray* and *Discovery II* expeditions. A closing mechanism actuated by messengers, has been evolved, which allows the gear to be fished between any two desired depths or to be hauled horizontally from a heavily weighted line.

Quantitative vertical hauls with a 200 mesh silk net have been made by Mr. Harvey at frequent intervals from the ship and motor-boat mostly between Cawsand and the Eddystone. The diatoms in an aliquot portion of the catch were examined or counted, the remainder being used to estimate the content of plant pigment.

From winter values of 15 to 190 (arbitrary) units of plant pigment per cubic metre of water, a spring maximum of some 6900 units per m^3 was observed on March 28th. During this period the growth in the more turbid in-shore waters was less than further out to sea. Between March 28th and April 4th, there was a sudden fall to winter values in the clearer water out to sea and an equally sudden increase in the quantity of zooplankton, the fæcal pellets of which, consisting largely of diatoms, were present in great numbers. This condition of little plant life and much zooplankton persisted for about a month, although there was no scarcity of light or nutrient salts. During May a growth mainly of *Rhizosolenia alata* took place, some 4800 units of pigment per m^3 being observed on May 22nd. Meanwhile the quantity of zooplankton in the catches had diminished. This crop fell away to be replaced by a crop mainly consisting of *R. stolterfothii* in June. During July, August and early September plant life was very sparse and zooplankton rich. Then, coincident with a fall in the quantity of zooplankton, an autumn crop appeared consisting mostly of *Rhizosolenia styliformis* and *Biddulphia sinensis*. From this preliminary quantitative survey it appears that, except during the winter, the quantity of phytoplankton present at any one time is largely dependent upon the quantity of zooplankton feeding upon it, and not entirely dependent upon the available nutrient salts and amount of light. Observations made by this quantitative method and a consideration of the phosphorus contents of water and phytoplankton from Dr. Cooper's analyses, suggest that from April to October the sea was a closely grazed pasture, except for short intervals in May and June.

Mr. F. S. Russell has completed the working out of his material to study the biology of Sagitta, the general results of which were outlined in the last report. These results have been published in the Journal, Vol. XVIII, No. 2. He has also completed the working up of a series of collections showing the general seasonal distribution of ring-trawl caught plankton, the information from which was printed in the last number of the Journal and is to form a basis for the study of changes in abundance of different animals from year to year. In continuation of this research Mr. Russell has examined weekly catches of plankton from the ring trawl and recorded the occurrence of various animals of interest and more especially the medusa population, and the occurrence of Sagitta. It is noteworthy that *Sagitta setosa* is still predominating in the catches over *S. elegans*, and indeed in the autumn of this year (1933) it has entirely displaced the last-named species, no *S. elegans* having been seen for several weeks.

The working up of the collections made in the summer of 1931 to study the effect of light intensity on the vertical distribution of plankton animals has now been completed. In this study collections were made from several depths simultaneously, while, either just before or after, light intensity measurements were made at different depths by Dr. Atkins. Seven series of observations were made on five days in July and August. The behaviour of *Calanus finmarchicus* adult males and females has been studied in detail. It was found that the females in July were living in the upper water layers in light intensities of 20,000-metre candles and over, but that those in August were avoiding these high intensities. This change in behaviour was coincident with a change of size of the copepods and indicated that actually there had been a change in the population being sampled and that these two populations, which differed in the size of their individuals, differed also in their behaviour towards light intensity. Measurements showed that while in July the average length of the female Calanus varied between 3·141 and 3·186 mm., in August these lengths were only 3·000 and 3·068 mm. Similar differences were shown by the adult males, which in July avoided intensities of 40,000 m.c. and over, while in August their upper limit was about 10,000 m.c. The males were consistently slightly deeper in the water than the females but appeared to show a more even distribution between their upper and lower limits.

Dr. M. V. Lebour has continued her studies of planktonic gastropods which have proved increasingly interesting. A paper on the eggs and larvæ of the Plymouth Turridæ is now ready for publication. These are very important members of the plankton, attaining a large size before metamorphosing and evidently remaining for some time as veligers. Several of them are common at Plymouth. It can be shown that the two groups, containing Mangelia on the one hand and Philbertia on the other, can be distinguished easily by the larval shell, the apex of the one being smooth and of the other elaborately sculptured, and these embryonic whorls still show on the adult. The larval animal is also different in the two groups. *Mangelia nebula*, the commonest species of the genus at Plymouth, is found to have a peculiar gauzy velum which in the later stages envelops the animal and shell like a true veil, quite unlike any form so far seen or described. The velum is ornamented with orange spots, whereas in the true Philbertias the velum is colourless. In *Philbertia gracilis* which is included in a separate sub-genus, the larva has very long velar lobes, with orange spots and a sculptured shell unlike the true Philbertias. All the other Philbertias have similarly sculptured larvæ and are very closely related. All the five British species occur at Plymouth and can be recognised by the embryonic whorls which are all of the same pattern. The larvæ of three of them have been found in the plankton and kept until metamorphosis. The eggs of *Mangelia nebula*, *Philbertia gracilis* and *P. linearis* have been obtained in plunger-jars.

Most of the Rissoidæ also occur in the plankton as veligers of a fair size and in large numbers. There is always a species of Rissoa or its allies in the plankton throughout the year, different species at different seasons. Some are even more abundant in winter than in spring and summer. By keeping the adults it has been possible to obtain the eggs of eight species, six of which have the typical sessile lens-shaped egg-capsules with a long veliger stage and two have single eggs, the larvæ emerging from the capsule in the crawling stage. One Rissoa has a planktonic egg-capsule with one egg. This has not yet been obtained from the animal itself, but gives rise to a veliger which remains long in the plankton and is one of the most important species in winter and early spring. Many of the later stages of this genus can now be distinguished.

An unusual occurrence in the September plankton near the Eddystone was three specimens on separate dates, of the last larval stage of *Dromia vulgaris*, the first record of the larva from Plymouth, although adults are occasionally found. One of them changed to a megalopa in the Laboratory. With the specimens obtained from the eggs in 1931 it has been possible to find the sequence of the larval stages. These larvæ show a complete difference from the Brachyura in almost every important point and fully justify the removal of Dromia from that group. A paper on the subject is now ready and will be published shortly by the Zoological Society.

Mr. D. P. Wilson's work on the development of *Branchiomma vesiculosum* has been continued. Sections of all stages have given interesting information, especially with regard to the metamorphosis, that from external examination only was difficult to bring into line with what is known of other species. During the summer larvæ were again reared and additional knowledge, particularly of the tube-building habits of the newly metamorphosed worms, was gained.

Audouinia tentaculata has been reared from artificially fertilised eggs to an age of three months, when the young worms were growing several of their long branchiæ and had attained most of their adult characters. The development is in the main very straightforward, the trochosphere elongating and acquiring several segments, but bristles are not formed until after metamorphosis. The prototroch disappears gradually, evidently by internal absorption.

The early stages of *Pectinaria koreni* have been obtained from an artificial fertilisation for the first time. They are extremely small, being little more than 60 μ long. Even so they possess a complicated ciliation and have already the great lateral lips characteristic of the Pectinaria larva.

Great efforts have been made to rear *Nephthys hombergi*. Good cultures of the trochospheres are easily got but they have never lived longer than a fortnight and have never formed segments.

Fauna of the Sea Floor (*Ecology, Physiology, Genetics*).

Mr. D. P. Wilson has made a preliminary examination of the micropolychæte fauna of the Eddystone Shell-gravel that has yielded some interesting unrecorded species, amongst them *Jasmineira caudata* Langerhans present in considerable numbers, and *Sphærosyllis bulbosa* Southern.

In collaboration with Mr. J. H. Day of Liverpool, Mr. Wilson has made some observations on the influence of the substratum on the metamorphosis of *Scolecolepis fuliginosa*, the development of which Mr. Day was studying. As had been shown for the Mitraria larva of *Owenia fusiformis*, the character of the bottom played an important part in inducing or delaying metamorphosis. On a muddy sand, such as the adults inhabit, ripe larvæ metamorphosed readily; on a clean sand metamorphosis was delayed for several weeks.

Dr. L. E. Bayliss has been studying the digestive enzymes of the plaice (*Pleuronectes platessa*). This fish has been shown to possess a true anatomical and physiological stomach—unlike some other teleostean fishes—which is capable of secreting a pepsin-like enzyme and the acid necessary to bring the substrate to the required hydrogen-ion concentration. Like most teleosts, the plaice possesses no distinct pancreas, and enzymes similar to those in the mammalian pancreatic juice are secreted by the mucous membrane of the intestine; a trypsin, an erepsin, a lipase, and an amylase have been identified, and alkali can be secreted in order to neutralise the acid from the stomach. There is some evidence that the trypsin is secreted more particularly in the region of the pyloric cæca; this is of interest in view of the histological identification of pancreatic tissue attached to the outer walls of the cæca. Bile, as obtained by slitting open the gall-bladder, contains a trypsin-like enzyme, which is activated by extracts of the intestinal mucous membrane; if, however, the outer surface of the gall-bladder—containing pancreatic tissue—be killed by immersion in a fixing reagent beforehand, the bile appears to be free from enzymes (*cf.* Mackay on Fundulus). The bile, also, has the normal accelerating action on the digestion of fats by the intestinal lipase.

During July, Dr. L. E. Bayliss was co-operating with Dr. and Mrs. Lythgoe on the measurement of the spectro-photometric absorption curves of the visual purple of certain marine fishes (dogfish, ray, conger, gurnard, dragonet, wrasse, plaice, pollack and mackerel). These measurements were made on a specially constructed photo-electric spectro-photometer. Unlike the land animals (frog, rat, man), all of which have an absorption maximum at a wave-length of 505 $m\mu$, and the fresh-water fishes, all of which have an absorption maximum at about 540 $m\mu$, no two of the marine fishes appear to have an absorption maximum at the same wave-length, although they all lie between 505 $m\mu$ and 540 $m\mu$. There appears to be no correlation between the position of the absorption maximum of the visual purple and the habits of the fish, the structure of its eye, or its generic relationships.

Dr. Bayliss has also collaborated with Mr. S. L. Cowan in constructing an amplifier and oscillograph in order to extend Mr. Cowan's researches on the effect of veratrine and yohimbin on the action potentials of the nerve trunks of the walking legs of the spider-crab (*Maia squinado*), the galvanometer used previously having insufficiently rapid time relations. It was found that the last two stages of the amplifier, if arranged in a paraphase-fed push-pull circuit, could be driven from the mains with only negligible distortion, so that a large high-tension battery was unnecessary. Normal nerves appear to contain two sets of fibres, in which impulses are conducted with very different velocities, the whole action potential complex lasting 1/10th to 1/20th sec. The long-continued retention of action potential previously observed as a result of poisoning the nerve with veratrine has been shown to start simultaneously with the true action potential, and to reach its maximum within $\frac{1}{2}$ sec. If single shocks are given whilst the nerve shows a considerable retention—i.e. during the earlier part of the 20 minutes necessary for its complete recovery—apparently normal action potentials can be obtained, without any further increase in the retention. During the earlier part of the retention, small rapid potential waves are observed, whose origin is unknown. A very much more rapid positive after potential which occurs as a result of poisoning with yohimbin, has been shown to occur immediately after the more rapid part of the normal action potential complex, and sometimes is masked by being superimposed on the slower portion of the normal complex. This positive after potential lasts about 1/10th sec.

A paper has been published by Mr. G. M. Spooner giving the results of various investigations, referred to in last year's Report, on the light-responses of marine plankton. It is shown that orientation in the direction of the light-rays is an all-important feature of the behaviour shown in the laboratory, so much so that it is undoubtedly of great significance under natural conditions, in so far as the animals under those circumstances respond to light. The correlation that is found between the distribution of populations in the sea and the light intensity of the surroundings is undoubtedly in a large measure the result of this kind of behaviour on the part of individuals. A start has been made on following up some of the lines of investigation suggested by the above paper; and data are being collected from various scattered sources on the effects of different light-intensities on the behaviour and physiological activities of animals.

The collection of data bearing on the question of the origin of recessive characters in *Gammarus chevreuxi* which Mrs. E. W. Sexton and Miss A. R. Clark commenced last year has been continued. For various reasons the task has proved to be more laborious than was at first anticipated, but the results which have been obtained have, in the opinion of the workers, more than justified the time spent in making the observations. The number of abnormal eyes which have occurred in breeding from new stocks collected at Chelson Meadow has been considerable, and clearly in excess of the number found previously in similar experiments during the twenty years that the work on Gammarus has been in progress. Perhaps the most interesting of these abnormal-eyed animals is one in which the eyes are of different colours, jet-black on the left side and bright red on the right. Subsequent breeding experiments with this animal have shown that it is heterozygous, although the proportions in which blacks and reds have been obtained from certain of its matings have been unexpected.

Fish and Fisheries.

In last year's Report, reference was made to the preparation by Mr. E. Ford of a comprehensive account of the different branches of herring research which he has conducted and reported on in this Journal in a series of papers entitled: "Herring Investigations at Plymouth." This account was completed and published in August, and represents an endeavour to show the essential bearing of the many seemingly distinct subjects of study upon the problems of the commercial fishery. It concludes with a consideration of the question of forecasting the yield of the fishery from information gathered in preceding years.

In continuation of past practice, Mr. Ford followed the progress of the drift-net fishery for herrings at Plymouth during the winter of 1932–33. The season proved of unusual interest, both with regard to the quality of the fish landed and the quantity caught from day to day. Large fish were greatly in evidence and it appeared that the fishable shoals had come more from westerly sources than had been the case for a number of years. Bulk catches, however, were made only during two short periods, fishing at other times being disappointingly light. Nearly one-half of the season's catch was landed during the seven days from December 12th to 18th, and a further one-sixth in the three days from January 4th to January 6th. The many fishermen, who were not fortunate enough to share in these heavy landings, had a bad season. Much significance is attached to the fact that each of these periods of good fishing followed hard upon days of strong gales, for it confirms the belief that herrings are in some way affected by the blowing of strong winds, so that fish are caught in great numbers in drift-nets which are set as soon after a gale as is practicable.

Mr. Ford has recently begun an investigation into the morphology and variation of the vertebral column in teleostean fishes. Skeletons of upwards of sixty species occurring in British waters have been prepared for examination. In addition to determining the nature and extent of variation from vertebra to vertebra in the same skeleton, from individual to individual in the same species, and from species to species, it is intended to enquire into the probable causes of the variation. First results have already raised interesting questions regarding the relation of form to function and phylogeny. They also have an important bearing upon the problem of races in fishes.

Mr. G. A. Steven has carried further his researches on the rays and skates of the western area of the English Channel, his attention having been devoted chiefly to *Raia clavata*, the most important species commercially. The post-embryonic life of a ray falls into three well-marked stages or phases: (1) the *juvenile* phase, during which the fish simply grows in size; (2) the *adolescent* phase, during which fundamental changes take place very rapidly, and bring the individual to puberty; and (3) the *adult* (sexually mature) phase. The following conclusions have been reached with regard to the growth and maturation of *Raia clavata* in the English Channel. (1) In any sample of male fish of this species in which no fish exceeds about 50 cm. in disc width the majority of individuals will be immature juveniles. This holds good whether the sample be restricted to any arbitrary size group within this range or consists of fishes at all sizes up to 50 cm. (about) maximum. In samples of small range size groups, those groups at the lower end of the range will consist of 100% juveniles, whilst those at the upper end will contain the smallest proportion of juveniles, but this will always remain *above* 50%: (2) similarly, in any sample which includes no fishes less than approximately 55 cm. in disc width, the majority of individuals will be mature adults: (3) in any sample of male fish of size groups falling between about 50 cm. and 55 cm. juveniles and adults will be approximately equally represented and adolescents at all intermediate stages will be found. In the females, which grow to a much larger maximum size than the males, these phases extend over quite different size ranges, the corresponding critical sizes being about 65 and 70 cm. respectively. From the data collected it would further appear that the onset of the changes characteristic of the adolescent period takes place during one growing period and that those changes are completed during the growing period of the following year.

The investigation into the food of Shags and Cormorants which Mr. Steven has been carrying out on behalf of the Cornwall Sea Fisheries Committee has been completed and a final report submitted to the Committee. The substance of this report was published in the Journal of this Association, Vol. XIX, No. 1. The results of the investigation have proved to be most useful and interesting. They have shown very clearly that Shags do not prey to any appreciable extent upon food fishes of any kind, but that Sand Eels and other non-marketable species form their main food. Cormorants, on the other hand, feed largely upon flatfishes and other commercial kinds. It is a grave mistake, therefore, to fail to discriminate between these two birds, more especially as the harmless Shag is fully ten times as numerous as the destructive Cormorant.

At the request of the Ministry of Agriculture and Fisheries, Mr. Steven has carried out an investigation into the complaints which are being made by fishermen along the North Cornwall coast concerning the havoc wrought by Seals amongst their several fisheries, and especially the herring fishery. They complain that the Seals haunt the herring nets and remove the herrings from them. As a result of his investigation, Mr. Steven found that Seals are very numerous on the North Cornwall coast, that the commonest species is the Great Grey Seal (*Halichœrus grypus*) and not the ordinary Brown Seal (*Phoca vitulina*), that the former haunt the nets of the herring fishermen, and that their diet includes herrings. It was quite impossible, however, with the means at disposal, to determine definitely whether the Seals which haunt the nets do so for the purpose of robbing them or simply in order to pick up the fishes which normally fall out of the meshes and are lost.

At the invitation of Colonel E. T. Peel, Mr. F. S. Russell spent in July three weeks of his summer holiday cruising in northern waters in the yacht *St. George*. This cruise, which was primarily made to study the occurrence of the Tunny, *Thunnus thynnus* L., in the North Sea was subsequently extended to cover a period of a further five weeks. The Shetlands and Faeroe Islands were visited and a large number of surface drift bottles were liberated for the Scottish Fishery Board at thirty-mile intervals across the Faeroe–Shetland channel. Water samples were also taken from different depths and collections of plankton made. Mr. Russell also assisted Mr. F. C. Fraser in the collection of specimens for the British Museum (Natural History).

In the search for Tunny many fishing vessels of different types were boarded at sea and many hours spent in watching the various kinds of gear at work and examining the catches. The Tunny were eventually located on the northern edge of the Dogger Bank and the first fish caught on August 4th, from which date onwards a number of fish were caught. It is not known whether the Tunny of the Mediterranean and those of the Atlantic are a homogeneous population or whether they can be shown to consist of two or more races. In 1931 at a joint meeting of the International Council for the Exploration of the Sea and the International Commission for the Exploration of the Mediterranean it was decided that a number of body measurements should, if possible, be made on Tunny from different areas to see whether biometric data might give any indication of constant variation between fish from different areas. This cruise afforded the opportunity of making the necessary measurements and thirty-two large fish from the North Sea were examined. Few observations have been published as yet from elsewhere and it is too early to understand the significance of the data obtained, as the results appear to be complicated by change in body proportions with growth. Samples of vertebræ were also taken from a number of fish for a study of age, and at many positions in the North Sea water samples were collected to throw light on the distribution of the Tunny in relation to the hydrographical conditions of its environment.

The weekly observations on the occurrence of young fishes in the plankton at Plymouth are being continued by Mr. Russell in connexion with his general study of the changes in the plankton from year to year.

Work of immediate financial benefit to the fishing industry has been carried out by Dr. Atkins in connexion with the preservation of nets and ropes and advice on these matters has been given to a number of firms. It has been shown, for example, that under standard conditions for rotting untreated netting lasted five months, re-treated with cutch every 2–3 months the netting lasted about two and a half years, but with cutch and a cheap form of copper dip, when re-treated every four months, the netting has lasted seven years. One firm is said to have an annual bill of £5000 for cutch. Using various copper-soap mixtures, with tar, the initial cost of preservation is higher than for cutch, but a single treatment may keep the string sound for from three to four and a half years. For ropes correspondingly good results may be expected and one copper-soap preparation has been found to penetrate rapidly. When kept under Plymouth Pier the preservatives are all relatively less efficient owing to the rapid current and wave action. In practice nets are not kept immersed, save pound-nets, but they rot while damp unless treated with preservative.

The Library.

The thanks of the Association are again due to numerous Foreign Government Departments, and to Universities and other Institutions at home and abroad for copies of books and current numbers of periodicals presented to the Library, or received in exchange for the Journal. Thanks are also due to those authors who have sent reprints of their papers, which are much appreciated. A special donation from Mr. E. T. Browne has made it possible to add a number of valuable books to the Library.

Published Memoirs.

The following papers, the outcome of work done at the Laboratory, have been published elsewhere than in the Journal of the Association:

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Okada, Yô K. *Les possibilités de la régénération de la tête chez le Polychète* Myxicola æsthetica (*Clap.*). Annot. Zool. Jap., Vol. XIII, 1932, pp. 535–550.

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Finance.

The Council have again to express their thanks to the Development Commissioners for their continued support of the Plymouth Laboratory. They are grateful also for generous grants from the Fishmongers' Company (£600), the Royal Society (£50), the British Association (£50), the Physiological Society (£30), the Ray Lankester Trustees (£20), the Universities of Cambridge (£105), Oxford (£52 10s.), London (£52 10s.), Bristol (£25), Birmingham (£15 15s.), Manchester (£10 10s.), Leeds (£10 10s.), Sheffield (£5 5s.), the Imperial College of Science and Technology (£10), and the Cornwall Sea Fisheries Committee (£25).

The Council has also to express its thanks to Mr. E. T. Browne for a special donation of £100 to be spent partly on books for the Library and partly for improvements to the store.

Vice-Presidents, Officers and Council.

The following is the list of gentlemen proposed by the Council for election for the year 1934–35 :—

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List of Annual Subscriptions

Paid during the Year, 1st April, 1933, to 31st March, 1934.

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R. R. Butler, Esq.	1	1	0
Carried forward	43	1	0

	£	s.	d.
Brought forward	43	1	0
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	£	s.	d.
Brought forward	91	7	0
Alastair Graham, Esq.	1	1	0
David H. Graham, Esq. (Balance)		6	1
Michael Graham, Esq.	1	1	0
Ronald Grant, Esq.	1	1	0
Dr. A. M. H. Gray	1	1	0
J. Gray, Esq., M.C., SC.D., F.R.S. (1928–1934)	7	7	0
Dr. H. P. Hacker	1	1	0
Wilfred Hall, Esq.	1	1	0
Ian I. Hamilton, Esq.	1	1	0
Prof. A. C. Hardy	1	1	0
Prof. C. R. Harington, F.R.S.	1	1	0
C. B. Harmsworth, Esq. (1931–1933)	3	3	0
Prof. L. A. Harvey	1	1	0
G. T. D. Henderson, Esq., D.SC.	1	1	0
C. C. Hentschel, Esq.	1	1	0
C. F. Hickling, Esq. (1932–1934)	3	3	0
Prof. Sidney J. Hickson, D.SC., F.R.S.	1	1	0
Prof. A. V. Hill, F.R.S.	1	1	0
W. T. Hillier, Esq., M.R.C.S.	1	1	0
Prof. K. Hirasaka (1932 and 1933)	2	2	0
Prof. A. D. Hobson (1931–1933)	3	3	0
Dr. E. G. Holmes	1	1	0
F. R. Horne, Esq.	1	1	0
N. H. Howes, Esq.	1	1	0
P. Hoyte, Esq.	1	1	0
Hull University College	1	1	0
O. D. Hunt, Esq.	1	1	0
Prof. J. S. Huxley	1	1	0
Independent Biological Laboratories (Tel Aviv), 1933 and 1934	2	2	0
Miss M. Jepps	1	1	0
J. J. Judge, Esq.	1	1	0
Stanley Kemp, Esq., SC.D., F.R.S.	1	1	0
Mrs. A. Redman King	1	1	0
P. Kirtisinghe, Esq.	1	1	0
J. A. Kitching, Esq.	1	1	0
Dr. G. Lapage	1	1	0
Prof. R. D. Laurie	1	1	0
A. G. Lowndes, Esq.	1	1	0
Adrian Lumley, Esq.	1	1	0
Carried forward	146	5	1

	£	s.	d.
Brought forward	146	5	1
Prof. E. W. MacBride, D.SC., F.R.S.	1	1	0
Prof. D. L. Mackinnon, D.SC. (1933 and 1934)	2	2	0
G. I. Mann, Esq.	1	1	0
B. J. Marples, Esq.	1	1	0
Sir John D. Marsden, Bart.	1	1	0
D. J. Matthews, Esq.	1	1	0
C. A. Mawson, Esq.	1	1	0
Capt. W. N. McClean	1	1	0
C. R. McKenzie, Esq.	1	1	0
Milford Haven Trawler Owners and Fish Salesmen's Association Ltd.	1	1	0
W. S. Millard, Esq.	1	1	0
Dr. G. A. Millikan	1	1	0
Sir P. Chalmers Mitchell, Kt., C.B.E., D.SC., F.R.S.	1	1	0
C. C. Morley, Esq.	1	1	0
Dr. J. Mukerji	1	1	0
National Museum of Wales, Cardiff	1	1	0
Miss G. L. Naylor	1	1	0
M. H. Neale, Esq. (1934–1935)	2	2	0
Messrs. Neale and West Ltd.	1	1	0
Dr. A. G. Nicholls	1	1	0
J. N. Nicholson, Esq.	1	1	0
J. R. Norman, Esq.	1	1	0
Dr. C. L. Oakley	1	1	0
Office Scientifique et Technique des Pêches Maritimes	1	0	0
Charles Oldham, Esq.	1	1	0
G. W. Olive, Esq.	1	1	0
Prof. J. H. Orton, D.SC. (1932–1933)	2	2	0
C. W. Parsons, Esq.	1	1	0
Messrs. Pawlyn Bros.	1	1	0
T. A. Pawlyn, Esq.	1	1	0
Messrs. Peacock & Buchan, Ltd.	1	1	0
Pease Laboratories Incorporated	1	1	0
Prof. E. Percival	1	1	0
L. E. R. Picken, Esq.	1	1	0
Plymouth Corporation (Museum Committee)	1	1	0
Plymouth Educational Authority	1	1	0
Plymouth Public Library	1	1	0
Plymouth Proprietary Library	1	1	0
Carried forward	189	5	1

	£	*s.*	*d.*
Brought forward	189	5	1
Port of Plymouth Incorporated Chamber of Commerce	1	1	0
Portsmouth Municipal College	1	1	0
W. Proctor, Esq.	1	1	0
Dr. H. E. Quick, M.B., B.S.	1	1	0
Dr. A. Ramalho	1	1	0
H. C. Regnart, Esq.	1	1	0
D. M. Reid, Esq.	1	1	0
E. A. Robbins, Esq. (1933 and 1934)	2	2	0
V. Rothschild, Esq.	1	1	0
C. H. Rudge, Esq. (1934 and 1935)	2	2	0
E. S. Russell, Esq., D.SC.	1	1	0
F. S. Russell, Esq., D.S.C., D.F.C.	1	1	0
Capt. the Hon. Lionel St. Aubyn, M.V.O.	1	1	0
The Rt. Hon. Lord St. Levan, C.B., C.V.O.	1	1	0
J. T. Saunders, Esq.	1	1	0
R. E. Savage, Esq.	1	1	0
Dr. F. F. Schacht	1	1	0
Edgar Schuster, Esq., D.SC.	1	1	0
W. L. Sclater, Esq.	1	1	0
B. Sen, Esq.	1	1	0
Lieut.-Colonel R. B. Seymour Sewell, C.I.E., I.M.S.	1	1	0
Miss Lilian Sheldon	1	1	0
C. J. Shen, Esq.	1	1	0
Prof. W. Rae Sherriffs, D.SC.	1	1	0
H. P. Sherwood, Esq.	1	1	0
B. Webster Smith, Esq. (1932, 1933 and part 1934)	2	12	6
F. G. W. Smith, Esq. (1932 and 1933)	2	2	0
Prof. E. A. Spaul	1	1	0
G. M. Spooner, Esq.	1	1	0
States Committee for Fisheries, Guernsey	1	1	0
A. C. Stephen, Esq.	1	1	3
Prof. T. A. Stephenson, D.SC.		18	6
Mrs. N. S. Steven	1	1	0
Eric J. Tabor, Esq.	1	1	0
Harold E. Tabor, Esq.	1	1	0
J. M. Tabor, Esq.	1	1	0
Prof. W. M. Tattersall, D.SC.	1	1	0
Prof. G. I. Taylor, F.R.S.	1	1	0
Sir Charles Howell Thomas, K.C.B., C.M.G.	1	1	0
Carried forward	234	16	4

	£	s.	d.
Brought forward	234	16	4
Harold Thompson, Esq., D.SC.	1	1	0
Sir Herbert F. Thompson, Bart.	1	1	0
Torquay Natural History Society	1	1	0
Phillip Ullyot, Esq.	1	1	0
R. C. Vernon, Esq.	1	1	0
H. M. Vickers, Esq.	1	1	3
Dr. A. Walton	1	1	0
Sir Nicholas E. Waterhouse, K.B.E.	1	1	0
Prof. D. M. S. Watson, F.R.S.	1	1	0
Mrs. F. J. Weldon	1	1	0
A. E. J. Went, Esq.	1	1	0
Miss K. M. White	1	1	0
P. H. F. White, Esq.	1	1	0
D. P. Wilson, Esq.	1	1	0
Mrs. D. P. Wilson, PH.D.	1	1	0
R. S. Wimpenny, Esq.	1	1	0
Ronald Winckworth, Esq., F.R.G.S.	1	1	0
V. C. Wynne-Edwards, Esq.	1	1	0
Prof. C. M. Yonge, D.SC.	1	1	0
John Z. Young, Esq.	1	1	0
Total	£255	16	7

List of Donations to the General Fund

For the Year, 1st April, 1933, to 31st March, 1934.

	£	s.	d.
D. L. Bryce, Esq.	1	1	0
G. I. Mann, Esq.		10	6
B. G. Wilson, Esq.		7	6
Total	£1	19	0

Special Donation for Improvements to the Store and for the Library

Paid during the Year, 1st April, 1933, to 31st March, 1934.

	£	s.	d.
E. T. Browne, Esq.	100	0	0
Total	£100	0	0

List of Composition Fees

Paid during the Year, 1st April, 1933, to 31st March, 1934.

	£	s.	d.
Dr. L. H. N. Cooper	15	15	0
Prof. E. J. Salisbury, D.SC., F.R.S.	15	15	0
	£31	10	0

THE MARINE BIOLOGICAL ASSOCIATION

BALANCE SHEET

	£ s. d.	£ s. d.
SUNDRY CREDITORS:		
On Open Account		87 10 8
GRANT RECEIVED IN ADVANCE		150 0 0
JEWISH SCHOLARSHIP FUND:		
First Instalment Received..	125 0 0	
Less Expenditure	33 15 10	
		91 4 2
E. T. BROWNE SPECIAL DONATION FUND:		
Donation Received	100 0 0	
Less Expenditure	74 11 10	
		25 8 2
RESERVE FOR DEPRECIATION OF BOATS AND MACHINERY:		
As at 31st March, 1933	763 3 9	
Add: Transfer from Income and Expenditure Account	269 14 2	
		1,032 17 11
SURPLUS:		
As at 31st March, 1933	5,851 16 0	
Add: Composition Fees	31 10 0	
Surplus for the year as per Income and Expenditure Account	153 18 1	
		6,037 4 1
		£7,424 5 0

(Signed) M. H. NEALE
R. A. FISHER } *Members of Council.*

TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

We report that we have examined the above Balance Sheet with the books of the
Capital expenditure on erection of Buildings on Land held on Lease from the War
Sheet is properly drawn up so as to exhibit a true and correct view of the state of the
given to us and as shown by the books of the Association.

34 *and* 35 *Bedford Street,*
Plymouth. 7*th April*, 1934.

OF THE UNITED KINGDOM.

31st MARCH, 1934.

	£ s. d.	£ s. d.
Boats and Equipment, as per Valuation as estimated by the Director at 31st March, 1931		
S.S. *Salpa*	2,000 0 0	
Motor-boat	150 0 0	
Nets, Gear and General Equipment	27 0 0	2,177 0 0
Laboratory Apparatus, Engines and Pumps:		
As per Valuation as estimated by the Director at 31st March, 1931, plus additions at cost		
As at 31st March, 1933		580 2 10
Library:		
As per Valuation as estimated by the Director at 31st March, 1931, plus additions at cost less Depreciation		
As at 31st March, 1933	2,082 1 2	
Additions during the year	518 14 0	
	2,600 15 2	
Less: Depreciation	467 11 2	2,133 4 0
Stock of Specimens, Chemicals and Journals as estimated by the Director		325 0 0
Sundry Debtors		106 11 10
Income Tax Recoverable		22 11 3
Prepayments		94 6 5
General Fund Investments at Market value as at 31st March, 1931:		
£410 14s. 8d. New Zealand 4% 1943/63	344 15 0	
£352 2s. 3d. Local Loans 3%	232 7 10	
(Market value at date £746 17s. 0d.)		577 2 10
Depreciation Fund Investments at Cost:		
£590 6s. 0d. Local Loans 3%	506 10 9	
£533 5s. 8d. Conversion Loan 3%	526 7 2	
(Market value at date £1,078 3s. 5d.)		1,032 17 11
Composition Fee Fund Investments at Cost:		
£18 8s. 6d. Local Loans 3%	15 15 0	
£63 19s. 8d. Conversion Loan 3%	63 0 0	
(Market value at date £81 0s. 6d.)		78 15 0
Cash at Bank and in Hand:		
Coutts & Co.	6 15 6	
Lloyds Bank Limited	253 13 4	
Cash in Hand	36 4 1	296 12 11
		£7,424 5 0

Association and have obtained all the information and explanations we have required.
Department is excluded. Subject to this remark we are of opinion that the Balance
Association's affairs, according to the best of our information and the explanations

(Signed) Price, Waterhouse & Co.

INCOME AND EXPENDITURE ACCOUNT

	£	s.	d.	£	s.	d.
To Salaries, including Institution's Contributions to Superannuation				6,749	7	8
,, Laboratory Wages, including National Insurance and Institution's Contribution to Superannuation ..				2,121	7	3
,, Depreciation of Library				467	11	2
,, Scientific Publications, *Less* Sales				408	13	10
,, Upkeep of Laboratories and Tank Rooms:						
Buildings and Machinery	171	16	0			
Electricity, Gas, Coal, Oil and Water	317	13	9			
Chemicals and Apparatus	348	12	4			
Rates, Taxes and Insurance	98	16	6			
Travelling	122	19	9			
Stationery, Postage, Telephone, Carriage and Sundries	303	15	5			
Specimens	109	15	10			
				1,473	9	7
,, Maintenance and Hire of Boats:						
Wages, including Diet Allowance, National Insurance and Casual Labour	1,578	16	1			
Coal, Water, Oil, Petrol, etc.	212	5	11			
Maintenance and Repairs with Nets, Gear and Apparatus	612	2	5			
Purchase of Material for Nets for Sale, excluding Labour	248	2	11			
Boat Hire and Collecting Expenses	7	9	2			
Insurance	287	0	11			
				2,945	17	5
,, Transfer to Depreciation Reserve Account ..				269	14	2
,, Balance being Surplus for the Year				153	18	1
				£14,589	19	2

YEAR ENDED 31st MARCH, 1934.

	£	s.	d.	£	s.	d.
By GRANTS :						
Ministry of Agriculture and Fisheries, Grant from Development Fund	10,949	7	2			
Fishmongers' Company	600	0	0			
British Association	50	0	0			
Royal Society	50	0	0			
Physiological Society	30	0	0			
Cornwall Sea Fisheries Committee	25	0	0			
				11,704	7	2
,, SUBSCRIPTIONS				255	16	7
,, DONATIONS				1	19	0
,, SALES :						
Specimens	1,075	9	2			
Fish (*less* expenses)	117	10	5			
Nets, Gear and Hydrographical Apparatus	325	10	7			
				1,518	10	2
,, TABLE RENT				480	11	9
,, TANK ROOM RECEIPTS				556	2	5
,, INTEREST ON INVESTMENTS (*less* Bank Charges) ..				35	17	4
,, SALE OF DR. M. V. LEBOUR'S BOOK	4	12	0			
,, SALE OF "MARINE FAUNA OF PLYMOUTH"	9	11	6			
				14	3	6
,, INCOME TAX RECOVERABLE				22	11	3
				£14,589	19	2

THE
QUARTERLY JOURNAL
OF
MICROSCOPICAL SCIENCE

EDITOR:
EDWIN S. GOODRICH, M.A., LL.D., F.R.S.

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Edited by J. GRAY

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CONTENTS

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OBJECTS

OF THE

Marine Biological Association

OF THE UNITED KINGDOM.

THE ASSOCIATION was founded at a Meeting called for the purpose in March, 1884, and held in the Rooms of the Royal Society of London.

Professor HUXLEY, at that time President of the Royal Society, took the chair, and amongst the speakers in support of the project were the Duke of ARGYLL, Sir LYON PLAYFAIR, Lord AVEBURY, Sir JOSEPH HOOKER, Dr. CARPENTER, Dr. GÜNTHER, Lord DALHOUSIE, Professor MOSELEY, Mr. ROMANES, and Sir E. RAY LANKESTER.

The Association owes its existence and its present satisfactory condition to a combination of scientific naturalists, and of gentlemen who, from philanthropic or practical reasons, are specially interested in the great sea fisheries of the United Kingdom. It is universally admitted that our knowledge of the habits and conditions of life of sea fishes is very small, and insufficient to enable either the practical fisherman or the Legislature to take measures calculated to ensure to the country the greatest return from the "harvest of the sea." Naturalists are, on the other hand, anxious to push further our knowledge of marine life and its conditions. Hence the Association has erected at Plymouth a thoroughly efficient Laboratory, where naturalists may study the history of marine animals and plants in general, and where researches on food-fishes and molluscs may be carried out with the best appliances.

The Laboratory and its fittings were completed in June, 1888, at a cost of some £12,000 and from that time until 1933 a sum of over £16,000 has been spent on additional buildings. Throughout this period investigations, practical and scientific, have been constantly pursued at Plymouth. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council; in addition, naturalists from England and from abroad have come to the Laboratory, to carry on their own independent researches, and have made valuable additions to zoological and botanical science, at the expense of a small rent for the use of a working table in the Laboratory and other appliances. The number of naturalists who can be employed by the Association in special investigations on fishery questions, and definitely retained for the purpose of carrying on those researches throughout the year, must depend on the funds subscribed by private individuals and public bodies for the purpose. The first charges on the revenue of the Association are the working of the sea-water circulation in the tanks, stocking the tanks with fish and feeding the latter, the payment of servants and fishermen, the maintenance of a research steamer and other collecting boats, and the salaries of the Resident Director and Staff. At the commencement of this number will be found the names of the gentlemen on the Staff.

The purpose of the Association is to aid at the same time both science and industry. It is national in character and constitution, and its affairs are conducted by a representative Council and an Honorary Treasurer, without any charge upon its funds, so that the whole of the subscriptions and donations received are devoted absolutely to the support of the Laboratory and the prosecution of researches by aid of its appliances.

TERMS OF MEMBERSHIP.

		£	s.	d.
Annual Members	per annum	1	1	0
Life Members	Composition Fee	15	15	0
Founders		100	0	0
Governors		500	0	0

Members of the Association have the following rights and privileges: they elect annually the Officers and Council; they receive the Journal of the Association free by post; they are admitted to view the Laboratory at Plymouth, and may introduce friends with them; they have the first claim to rent a place in the Laboratory for research, with use of tanks, boats, &c.; and have access to the books in the Library at Plymouth.

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

CONTENTS OF NEW SERIES, Vol. XIX., No. 2.

NOTICE.