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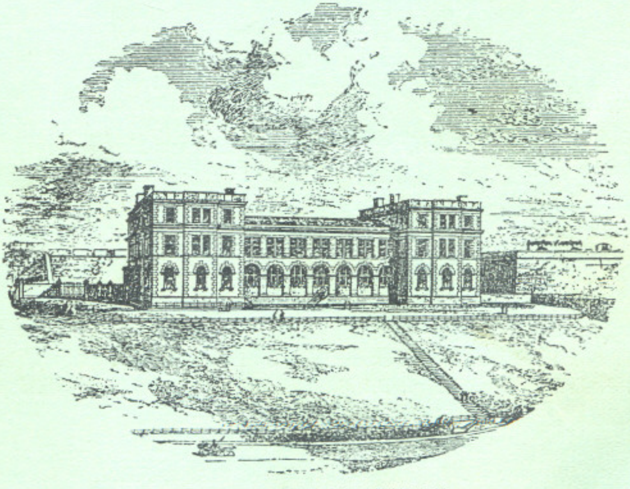

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The Nature of the Intertidal Zonation of Plants and Animals.

By

John Colman, B.A.,

From the Plymouth Laboratory and Harvard University.

With 15 Figures in the Text.

While Student-Probationer at the Plymouth Laboratory, I started a quantitative examination of the faunas associated with seaweeds, an essential preliminary to which was some knowledge of the limits of distribution of the seaweeds in relation to tidal levels. Such limits, as observed in Wembury Bay, together with those of the commoner gastropods and cirripedes, are described in this paper.

Wembury Bay is very fairly sheltered from all winds except those from between S.S.W. and S.E., the weight of sou'westerly gales being taken by the Great Mewstone (see Map, Fig. 1). Most of the bay is less than five fathoms deep at low water, and the high rocks at the seaward end of the reef protect the slightly lower middle and landward portions on which this work was done. The high, seaward rocks are in many places completely bare of algæ above the *Laminaria digitata* zone, being thickly covered instead by the barnacles *Chthamalus stellatus* and *Balanus balanoides*. That a strong southerly gale can work considerable destruction in Wembury Bay was shown on December 4th, 1929, when a belt of Laminarias was thrown up above high water mark some two hundred yards long, thirty yards wide and with a steep seaward face six feet high, all firmly pounded together, and consisting of whole plants, often with the holdfasts still attached to rocks up to twenty pounds in weight. Wembury Bay probably suffers from a minimum of pollution as the area draining into it is but sparsely inhabited, and the River Yealm brings down very little fresh water, being really an arm of the sea like Salcombe Harbour farther east.

Church Reef or Ledge, also called Blackstone Reef or Ledge, projects about a quarter of a mile into Wembury Bay, two miles east of Plymouth Sound, and is entirely covered at high water of spring tides. It was selected on the grounds of accessibility and richness of algal growth after the whole coastline had been examined from Bolt Tail to Looe.

First of all, a rock (hereafter called Central Rock or C.R.) was chosen about the middle of the reef, and from it three traverses were marked out by triangular holes cut in the rocks at intervals of about forty-five feet. Traverse A, 222·5 feet, lay towards the Coastguard lookout on Gara Head; Traverse B, 367·5 feet, towards the Great Mewstone; Traverse C, 382 feet, towards Wembury Church. In addition, Traverse D was laid out from the landward end of Traverse C for 198 feet in an easterly direction. A and B reached low water mark on the east and west sides respectively of the reef, C was almost all between high and low water neaps, and D went above the limits of marine algal vegetation. Table I gives the details of the traverses.

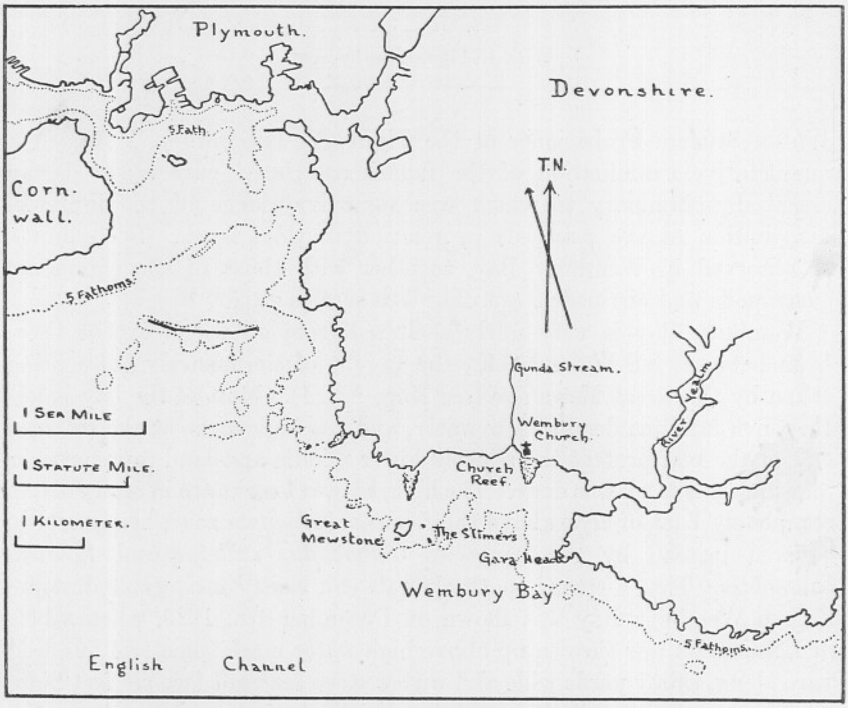

Fig. 1.—Map showing the position of Church Reef in the Plymouth District.

Their approximate positions are shown in the Map, Fig. 2, which is taken from Devonshire Sheet CXXX 6 of the 1/2500 Ordnance Survey. The position of Central Rock was obtained by a compass fix, and cannot therefore be taken as more than approximately correct.

Each traverse was examined throughout in detail with regard to the common plants and animals living on the rock, and was then levelled to the nearest hundredth of a foot, using a Casella level. This work was done by Mr. Michael Spender, to whom I am deeply grateful.

TABLE I.

Dimensions and True Bearings of Traverses.

Traverse.	A.	B.	C.	D.
True Bearing.	159°	245°	4°	94°
Central Rock to Mark I, in feet	50	43·5	65	—
C VII to D I, in feet	—	—	—	60
I to II ,,	52	44	41	61
II to III ,,	39·5	41	42	57
III to IV ,,	35	41	44	20
IV to V ,,	46	74	67	—
V to VI ,,	—	35	64	—
VI to VII ,,	—	30	59	—
VIII onwards ,,	—	59	—	—
Total ,,	222·5	367·5	382	198

The starting-point for this levelling was a bench-mark, 20·56 feet above Ordnance Datum, on the S.W. corner of the house adjoining Wembury Mill, and 2·70 feet from the ground, and all level traverses were of course checked back to the bench-mark. All the marks on the traverses and where possible all intermediate points were levelled with the foot of the staff resting on solid rock.

TABLE II.

Tidal Data for Devonport, 1930.

	Extreme Low Water Springs.	Chart Datum.	Mean Low Water Springs.	Mean Low Water Neaps.	Extreme (Highest) Low Water Neaps.	Mean Sea Level.
From Chart Datum (feet)	− 2·0	0	+0·18	+4·60	+5·60	+8·15
From Ordnance Datum (feet)	−10·42	−8·42	−8·24	−3·82	−2·82	−0·27

	Ordnance Datum.	Extreme (Lowest) High Water Neaps.	Mean High Water Neaps.	Mean High Water Springs.	Extreme High Water Springs.
From Chart Datum (feet)	+8·42	+10·60	+12·25	+15·70	+17·10
From Ordnance Datum (feet)	0	+ 2·18	+ 3·83	+ 7·28	+ 8·68

The nearest place for which accurate tidal data are available is Devonport, distant some five miles by sea, where High Water at Full Moon and Change of Moon (High Water Interval) occurs at V hours

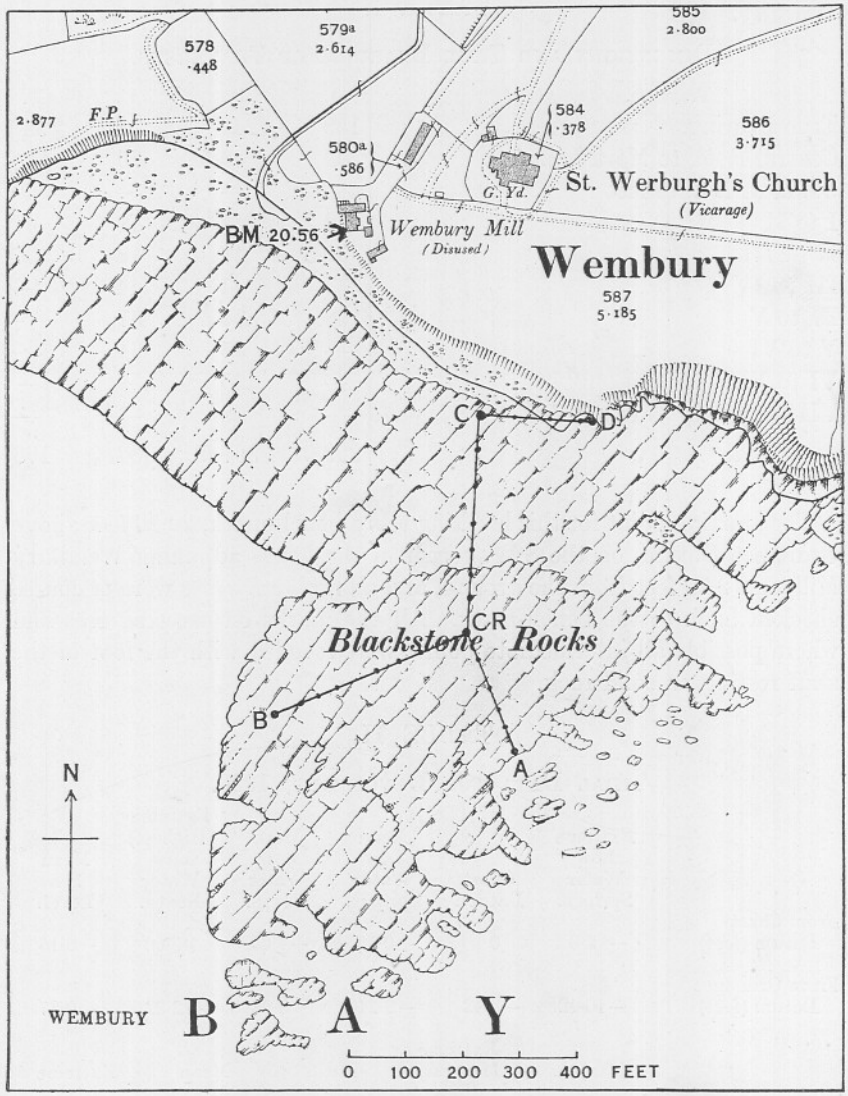

Fig. 2.—Positions of the traverses and marks on Church Reef.

37 minutes, the springs rise being 15½ feet and the neaps rise 12 feet, according to the local Admiralty Charts. Fuller tidal data are given in the Admiralty Tide Tables, Part I, and Table II of this paper is compiled

from the tide tables forecast for Devonport during the year 1930 and from Table VII on page 382 of the same volume. The datum for tide tables and charts is Low Water of Ordinary Spring Tides; Ordnance Datum is the assumed mean level of the sea at Liverpool, which is 8·42 feet above Chart Datum at Devonport.

From this table it will be seen that the extreme range of the tide at Devonport during 1930 was 19·10 feet. This did not occur on one tide, since the highest high water is not usually preceded or followed by the lowest low water, but rises of 17 or 18 feet are not uncommon at the equinoxes. The mean springs range is 15·32 feet, the mean neaps range 7·65 feet, while at some neap tides there may be as small a rise as 5 feet.

There are no accurate tidal observations for Wembury Bay, so in order to find out whether it was justifiable to use the Devonport data I wrote to the Hydrographic Department of the Admiralty, and received in answer a letter from Admiral Douglas, Hydrographer, saying: ". . . Comparison of the tides at Salcombe, the nearest place east of Devonport at which comparatively full observations have been obtained, with those at Devonport, however, shows a decrease in range of about 6%; and it is therefore probable that a very small decrease also occurs between Devonport and Wembury Bay." If this decrease is in proportion to the distance from Devonport it will not be much more than 1% at Wembury, or about 0·2 foot at springs, and of course still less at neaps. I have therefore considered the Devonport Data to be applicable in Wembury Bay. In this connection it was observed that frequently the low water level on Church Reef was a few inches above that predicted for Devonport, but on several occasions it went a few inches below. In calm weather I never noticed a discrepancy of as much as half a foot. It is also, perhaps, worth mentioning that anyone in Wembury Bay can tell the level of the sea at any time within a couple of hours of low water by observing the relative heights of the Inner and Outer Slimers, two groups of rocks east of the Great Mewstone. The Inner Slimers reach 10 feet above Chart Datum, the Outer Slimers only four. In calm weather the sea level could be estimated with confidence to the nearest foot.

Some excuse must be offered for not employing the metric system. The reason is that some of the tidal data, ordnance datum and the levelling of the traverses are, or purport to be, accurate to 1/100 foot. This is approximately 3 mm., which being more than one millimetre and less than one centimetre cannot be represented with equal accuracy on a metric scale. A conversion table is given in Table III.

The plants whose ranges were examined were only the largest and commonest on the reef, this work being originally supplementary to a quantitative estimate of their associated faunas. The animals in this paper are all common and obvious, no attempt having been made to investigate rarities.

TABLE III.

CONVERSION TABLE FOR FEET INTO METRES,

Feet.	Metres.	Feet.	Metres.
0·1	0·03	7	2·13
0·2	0·06	8	2·44
0·3	0·09	9	2·74
0·4	0·12	10	3·05
0·5	0·15	11	3·35
0·6	0·18	12	3·66
0·7	0·21	13	3·96
0·8	0·24	14	4·27
0·9	0·27	15	4·57
1	0·30	16	4·88
2	0·61	17	5·18
3	0·91	18	5·49
4	1·22	19	5·79
5	1·52	20	6·10
6	1·83		

The following plants and animals had their limits of distribution accurately worked out on Church Reef :—

ALGÆ.

FLORIDEÆ.

***Polysiphonia lanosa* (L.)=*P. fastigiata* (auct).
Chondrus crispus Stackhouse.
Gigartina stellata Stackhouse.

PHÆOPHYCEÆ.

Pelvetia canaliculata (L.).
Fucus spiralis (L.).
Fucus serratus (L.).
**Ascophyllum nodosum* (Le Jol).
Laminaria digitata (Lamouroux).

LICHENS.

Lichina pygmæa (Ag.).

MOLLUSCA.

GASTROPODA.

Littorina neritoides (L.).
Littorina saxatilis (Olivi)=*rudis* (Maton).
Littorina obtusata (L.)=*littoralis* (L.).

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* *A. nodosum* and *P. lanosa* are in this paper treated as a unit, since on the four traverses wherever *Ascophyllum* was found, there also was *Polysiphonia lanosa* growing upon it.

Littorina littorea (L.).
Osilinus lineatus (da Costa) (=*Monodonta crassa*).
Gibbula umbilicalis (da Costa).
Gibbula cineraria (L.).
Calliostoma zizyphinum (L.).
Nucella (*Purpura*) *lapillus* (L.).
Patella vulgata (L.).

CRUSTACEA.

CIRRIPEDIA.

Chthamalus stellatus (Poli).
Balanus balanoides (L.).
Balanus perforatus (Bruguière).
Verruca stroemia (O. F. Müller).

Identifications of the algæ were confirmed by Mr. Geoffrey Tandy of the British Museum (Nat. Hist.). The names are as given in Batters' (1902) Catalogue of the British Marine Algæ, with the exception of *Polysiphonia lanosa* (L.), which is more familiar as *P. fastigiata*. Tandy (1931) has shown that the latter name is indefensible.

For the identifications of the animals I am myself responsible. The names do not vary from those in the Plymouth Marine Fauna (Marine Biological Association, 1931) with the exceptions of *Littorina saxatilis* and *L. obtusata*. The necessity for these alterations is given by Dautzenburg and Fischer (1912) and by Colman (1932). I am very grateful for the help in this matter of members of the staff of the Plymouth Laboratory, in particular Messrs. G. A. Steven and J. E. Smith.

DETAILED DESCRIPTION OF TRAVERSES.

Traverse A. 222·5 feet. From Central Rock S.E. towards Gara Head. See Fig. 3.

Central Rock (C.R.), at the top of which this traverse starts, is a roughly pyramidal eminence of grit, about 10·5 feet high on the seaward side, where it is separated from the southern portion of the reef by a cleft about four feet wide whose floor is just above Mean Low Water Neaps. The upper half is largely covered with the lichen *Lichina pygmæa*, particularly on seaward or southward-facing slopes, which are exposed to the greatest amounts of both sun and surf, and the surface of the whole mass of rock is patchily covered with barnacles. Small *Patella vulgata* are fairly common as high as C.R. On Traverse A, *Lichina pygmæa* is growing thickly at C.R., 6·04 feet above Ordnance Datum (O.D.) and one foot below Mean High Water Springs, and reaches its lower limit at four places, namely 12 feet, 18 feet, 28 feet, and 38 feet from C.R., whose heights above O.D. are 0·4 feet, 0·4 feet, 0·57 feet, and 0·3 feet respectively.* (Heights are given relative to Ordnance Datum, since this level is constant throughout Great Britain. Chart Datum varies from place to place according to the amplitude of the tide.) The barnacles at C.R. belong exclusively to *Chthamalus stellatus*, which on Traverse A extends as far as 52 feet, at the foot of Central Rock, 4·44 feet below O.D. *Balanus balanoides* is also common on the lower parts of the rock, the upper limit on this traverse being at 7·5 feet, +2·5 feet. Occasional stunted plants of *Fucus spiralis* were growing between +3 feet and +5 feet, but too rarely to allow their precise limits to be determined. *Littorina saxatilis* is common on the upper parts of Central Rock, but its lower limit was not ascertained on this traverse.

After Central Rock the cleft, mentioned above, is crossed diagonally, and is paved with stones and small boulders, which are bare of algæ, excepting a little *Enteromorpha* sp. during the summer. The traverse emerges from it up a cliff 2 feet high and overhanging 1 foot, on which are *Balanus perforatus* in fair numbers and *Nucella lapillus*, between —4·45 feet and —2·36 feet.

From here onwards the traverse, while undulating, gradually descends. For 15 feet the rock is bare of algæ, but supports *Nucella lapillus* and *Balanus balanoides*, with *Gibbula umbilicalis* and Patella from 68 feet to 74 feet, between —1·53 feet and —3·0 feet. From 75 feet to 83·5 feet a belt of scattered *Ascophyllum nodosum* and *Polysiphonia lanosa* is crossed. This traverse does not cross the highest Ascophyllum in the vicinity, but the lower limit is very definite at 83·5 feet, 4·05 feet below O.D. After this point *Fucus serratus* is the dominant alga, growing thickly almost everywhere. It starts at 89 feet, at —4·05 feet (though it reaches several feet higher on other traverses), and extends down with only occasional gaps to 217·5 feet, 5 feet short of A v, the end of the traverse. On April 2nd, 1931, low water was about 2·5 feet below A v, and this just corresponded with the lower limit of *Fucus serratus*, 9 feet below O.D. to the nearest half foot. *Laminaria digitata* first appears in the pool between 116 feet and 121 feet, and occurs where the rock dries out at 130 feet, 6·39 feet below O.D. The next exposed Laminaria is at 161·5 (—6.51 feet). From 177 feet onwards the rock is largely covered by *Laminaria digitata* and *Fucus serratus*, further upper limits of the former being at 176 feet (—6·50 feet), 179 feet (—6·41 feet), 200·5 feet (—6·41 feet), and 206 feet (—6·7 feet).

Chondrus crispus first appears between 110 feet and 112·5 feet, the highest point being —5·55 feet, and *Gigartina stellata* between 104 feet

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* Heights are given to the nearest hundredth of a foot if they are where a level reading was taken. Intermediate points are given to the nearest tenth of a foot.

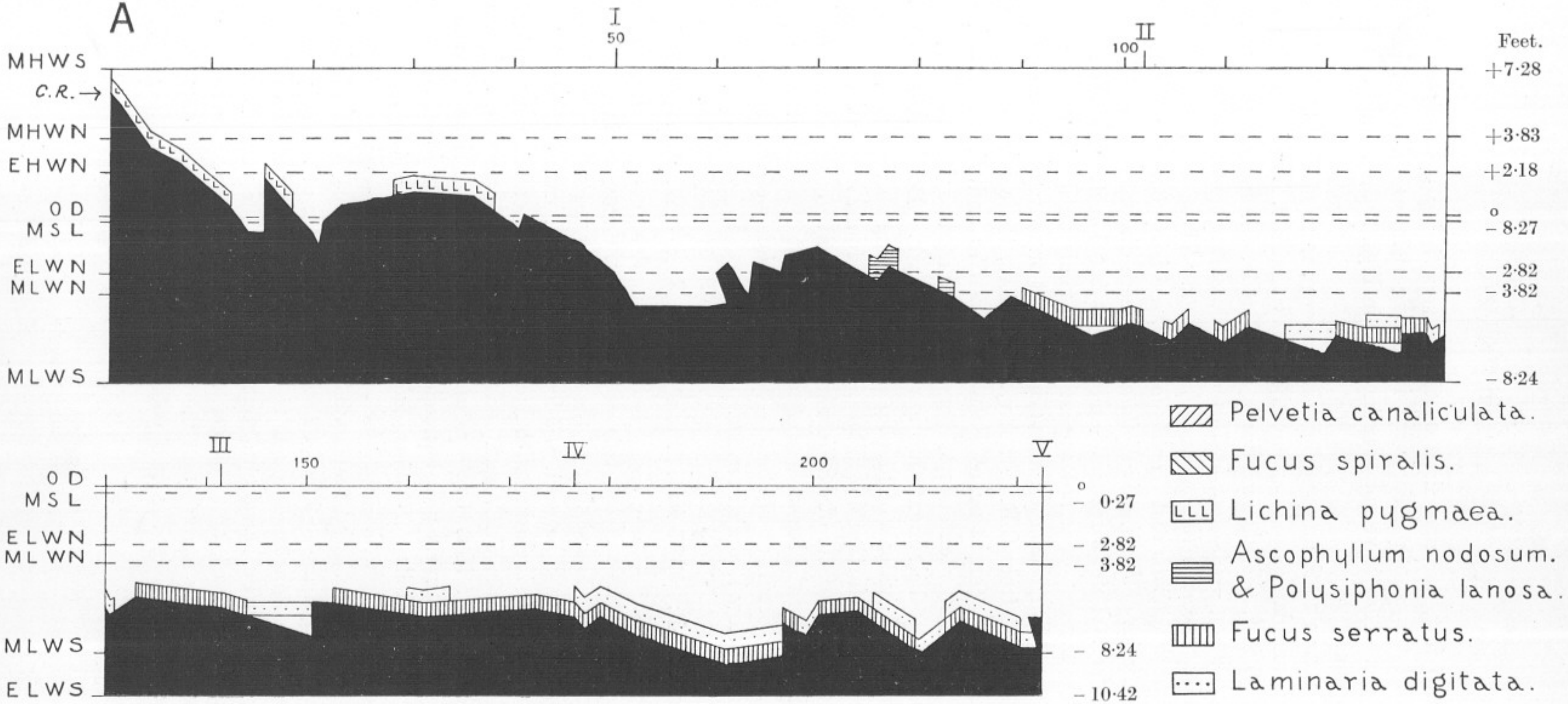

FIG. 3.—Traverse A; distribution of *Lichina pygmæa*, *Polysiphonia lanosa* and fucoid algæ. (Vertical scale twice the horizontal.)

and 107 feet, its upper limit on this traverse being –5·29 feet. Henceforward they both occur with increasing richness to the end of the traverse. They have not been included in Figs. 2, 3, 4, and 5 for fear of confusion.

To return to the animals on the traverse, from 61 feet to 75 feet the rock is undulating and supports *Balanus balanoides, Nucella lapillus,* and, from 68 feet, *Gibbula umbilicalis* and Patella, the highest point on this stretch being –1·53 feet at 70 feet. The subsequent Ascophyllum belt contains *Littorina littorea* and *L. obtusata.* These two, together with *Gibbula umbilicalis* and *Nucella lapillus,* are fairly common down to the upper limits of *Laminaria digitata,* but there die out rather suddenly at –6·5 feet. Patella reaches –6·5 feet at 200·5 feet. *Gibbula cineraria* on this traverse does not appear out of pools until this height, but is common throughout the Laminarian zone at any rate down to –8·78 feet at 191·5 feet from C.R. At A v, –6·48 feet, there is again a covering of barnacles, consisting of *Balanus balanoides* and *B. perforatus.* Of these the former extends to between one and two feet below A v and *B. perforatus* below extreme low water mark. Below A v there are occasional individuals of *Verruca strœmia* growing on the rock, becoming more common further down, but as they were found in considerable numbers on all holdfasts of *Laminaria digitata,* I have considered the upper distribution of the barnacle to coincide with that of the alga. *Calliostoma zizyphinum* occurs at 174 feet (–6·2 feet) and fairly often from that point down to below low water mark.

Traverse B. 367·5 feet. From Central Rock S.W. towards the Great Mewstone. See Fig. 4.

The first section of this traverse, down to the seaward face of Central Rock, is somewhat similar to the corresponding part of Traverse A, the cleft being crossed between 47·5 feet and 49·5 feet. Again the upper part only of the rock is clothed with *Lichina pygmæa* extending down to +0·68 feet, 16 feet from C.R., with occasional stunted *Fucus spiralis* between +3 feet and +5 feet. *Chthamalus stellatus* is abundant right down to the cleft, and is again the only barnacle in the upper region where it is accompanied by Patella ; *Balanus balanoides* appears on the slope below 40 feet at a height of +0·29 feet. *Littorina saxatilis* is very common at C.R. (+6·04 feet) and reaches 9·5 feet (+2·89 feet), while *L. obtusata* reaches as high as +0·5 feet, 22 feet from C.R. On other traverses these molluscs are sometimes found to overlap. *Gibbula umbilicalis* did not occur in the open hereabouts, but was found in the pools between 16·5 feet and 21·5 feet, and between 27 feet and 36 feet. Each pool also contained *Fucus serratus* and the second one *Laminaria digitata* as well, the water levels in the two pools being +0·77 feet and –0·62 feet respectively. These pools are both fully exposed to the sun, and only the lower one contained Laminaria. A small pool on Traverse C, however, which is higher than either of them, is sheltered from the sun and contains Laminaria. The lower part of the slope down to the cleft is covered with *Fucus serratus* and *Ascophyllum nodosum* from 44 feet to 47·5 feet (—1·27 feet to —3·16 feet), and on the cliff out of the cleft *Balanus perforatus* is fairly common (—3·16 to —1·40 feet).

From the top of this cliff until 120 feet, except in pools, the rock is more or less thickly covered with *Ascophyllum nodosum* and *Polysiphonia lanosa*, but at 120 feet they stop suddenly 3·7 feet below O.D., having reached —4·11 feet at 114 feet from C.R. This is one of the clearest zone edges on the reef, and is very obvious to anyone looking up the slope from a seaward direction. There is no grading off; the Ascophyllum is dense right down to its lower limit and is there sharply cut off. *Fucus serratus* is scattered in this portion of the Ascophyllum zone, below which it becomes the dominant alga, covering nearly all the exposed rock for the rest of the traverse, except for a section near the end, between 337 feet and 364 feet, which is below its lower limit. After the last Ascophyllum at 120 feet, the traverse slopes gently down, generally covered with *Fucus serratus* but with occasional bare patches, on which Patella are abundant at —4·2 feet, until at 183·5 feet it enters the largest rock pool on the reef, whose surface was at —6·47 feet on the day it was levelled; this was the lowest to which it sank during low water springs. The pond contains a rich growth of algæ dominated by *Laminaria digitata*, *L. saccharina* and *Fucus serratus*, and is carpeted with Corallines. At 226 feet a rock projecting from the surface is covered with *Fucus serratus* but no Laminaria.

From the end of this pond the traverse rises steeply 2 feet, and then continues gently downward, thickly covered with *Fucus serratus* except for a small bare patch on top of a rock at 278 feet (Mark VI). At 275·0 feet the traverse just touches the upper edge of the *Laminaria digitata* zone, at —6·23 feet. From 280 feet to 294·5 feet a pool is crossed, 1 foot deep, almost choked with Laminaria and carpeted with Corallines, the water level being —6·73 feet. After rising fairly steeply from this pool the traverse again undulates gently downward, still covered with *Fucus serratus*, except for another bare rock top at 308·5 feet (Mark VII). In two depressions *Laminaria digitata* appears, at 307 feet (—6·54 feet) and at 323·5 feet (—6·51 feet). From 332·5 feet the downward slope becomes steep; *Laminaria digitata* is thick from —7·01 feet down, and *Fucus serratus* dies out at —8·4 feet. Then, after 20 feet at just above extreme low water springs (I only saw this part dry out once) and reaching —10·10 feet at 359·5 feet, the traverse slopes up to its end at 367·5 feet, *Fucus serratus* reappearing at 362·5 feet at a height of —8·6 feet.

Chondrus crispus occurred from 167 feet to 169·5 feet (—5·98 feet to —5·33 feet) and was present from 243·5 feet to 263 feet except where the rocks were above —4·5 feet, and on the short slope down at 279 feet at —5·5 feet. *Gigartina stellata* appeared at 303 feet (—5·0 feet), and from there onwards both these algæ occurred intermittently to low water mark.

Littorina obtusata was abundant on all parts of the traverse above —7·5 feet which were covered by weed—it was still common in the upper foot of the Laminarian zone. *Littorina littorea* was rare on this part of the reef, as were *Gibbula umbilicalis, G. cineraria, Nucella lapillus* and *Calliostoma zizyphinum*, except that the latter was fairly common about low water mark, though never so numerous as on the eastern side of the reef. *Patella vulgata* was abundant on bare patches of rock at all levels down to —6·5 feet.

After the cleft, at 50 feet, there were no barnacles until 309 feet, just after Mark VII on top of an otherwise bare rock, where there was a small colony of *Chthamalus stellatus* at —5·22 feet. *Verruca strœmia*, as on Traverse A, was always living among the holdfasts of *Laminaria digitata*.

Traverse C. 382 feet. From Central Rock N. towards Wembury Church. See Fig. 5.

Unlike Traverses A and B, C is, except for the first few feet on Central Rock, between High and Low Water Neaps, and since it undulates considerably between these limits it gives a fairly complete picture of the state of affairs around Mean Sea Level.

Central Rock is not separated from the rest of the reef on the landward side as it is to seaward by the cleft, nor is it so steep. Except in pools it is also very bare of algæ, the only common plant being *Lichina pygmæa*. Small Patella are common on the upper portion. The traverse first of all descends in steps to the bottom of a deep pot-hole with the water level at +1·6 feet. This pot-hole contains undersized plants of *Laminaria digitata*, but, as already mentioned during the description of Traverse B, this pool is always shaded from the sun except around noon during the summer. The barnacles at the top of Central Rock were again all *Chthamalus stellatus, Balanus balanoides* appearing at 4 feet from C.R. at a height of +4·29 feet. The steep sides of the pot-hole are bare, but *Lichina pygmæa* nearly covers the rocks from C.R. to 4 feet and from 8 feet to 10 feet. *Littorina saxatilis* is common on this stretch. A shallow pool intervenes from 10 feet to 18 feet, and is almost filled with *Bifurcaria tuberculata*, after which the traverse climbs to +3·46 feet at 23 feet, being covered with Lichina, *Balanus balanoides*, Chthamalus and *Littorina saxatilis*. On the subsequent downward slope *Chthamalus stellatus* occupies the first foot, and from +2·5 feet to the bottom at a height of +0·04 feet there

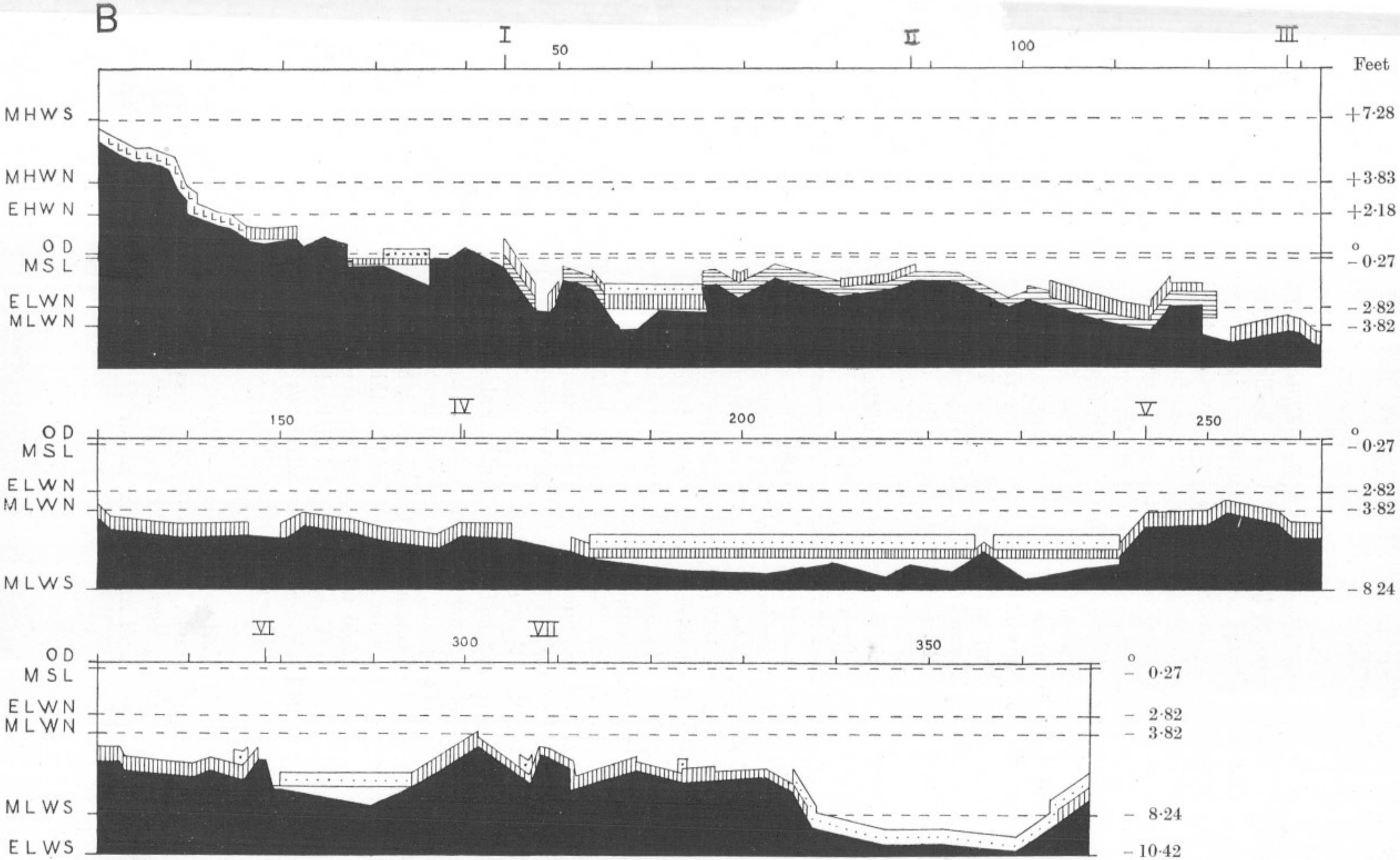

FIG. 4.—Traverse B; distribution of *Lichina pygmæa*, *Polysiphonia lanosa* and fucoid algæ. For meaning of symbols, see Fig. 3. (Vertical scale twice the horizontal.)

are *Gibbula umbilicalis* and *Nucella lapillus*, with *Littorina littorea* at the foot of the drop, 27 feet from C.R. A small pool is then crossed to 31 feet, and the landward edge is bordered by *Lichina pygmæa* above 0·04 feet. From here the traverse slopes gently upwards to 51·5 feet and is intermittently clothed with Lichina. Chthamalus is also present, and *Littorina saxatilis* reappears when the traverse reaches +1·4 feet at 41 feet. At 51·5 feet the traverse drops a foot, and on the slight rise to 60·5 feet, +2·17 feet, there are Lichina, *Nucella lapillus* and *Gibbula umbilicalis*. During the next three feet the traverse descends more than the same distance, to −1·19 feet, the drop being interrupted by a deep overhang on the floor of which were several large *Balanus perforatus*, which continued also down to the foot of the drop. The highest was at +0·88 feet. *Nucella lapillus* and *Gibbula umbilicalis* occupied the same region.

After C I, 64·5 feet, the traverse, after dropping from −1·02 feet to −1·76 feet, climbs to +1·75 feet at 76·5 feet. As far as 74·5 feet (+0·9 feet) it is partially covered with *Ascophyllum nodosum*, with a patch of *Fucus serratus* from 66·5 feet to 68·5 feet. Barnacles, mainly Chthamalus but including a few *B. balanoides*, are present from about O.D. at 72 feet, and are joined at the top of the rise by scattered *Lichina pygmæa*. The next stretch, occupied by *Gibbula umbilicalis*, *Nucella lapillus*, Chthamalus, *Balanus balanoides*, Patella and scattered Lichina, is nearly level as far as 96 feet at +1·88 feet, and is followed by a three-foot drop into a bare pot-hole, the landward side of which is rather more than a foot high. A few feet of bare rock and sparse Ascophyllum are then succeeded by an almost uninterrupted sheet of dense Ascophyllum and Polysiphonia from 108 feet to 255·5 feet, the most uniform stretch of vegetation on the reef. *Littorina obtusata* is common throughout, and *L. littorea* fairly numerous after 155 feet. At 151 feet there is a steep drop from +0·48 feet to −2·04 feet, covered with *Fucus serratus*, and with Patella and *F. vesiculosus* at the bottom. The latter alga, though growing abundantly in many places around Plymouth, such as Sutton Harbour and the Tamar and Yealm estuaries, and on restricted areas in Wembury Bay, is nowhere widespread or common on Church Reef, and is therefore not included among the common algæ dealt with in this paper. This distribution is perhaps correlated with degree of exposure, though it should be mentioned that on the south coast of Finland (where the salinity is about 4°/₀₀ and the tides are very small) *Fucus vesiculosus* grows abundantly among the breakers and attains a length of two or three metres (Segerstråle, 1928).

From 151·5 feet to 155·5 feet (−2·04 feet to −1·99 feet) there are bare stones and shingle, occupied by *Littorina littorea*, *Gibbula umbilicalis*, *G. cineraria* and *Nucella lapillus*, but the next twenty feet are covered with a thick growth of Ascophyllum with a little *Fucus serratus* at 173 feet

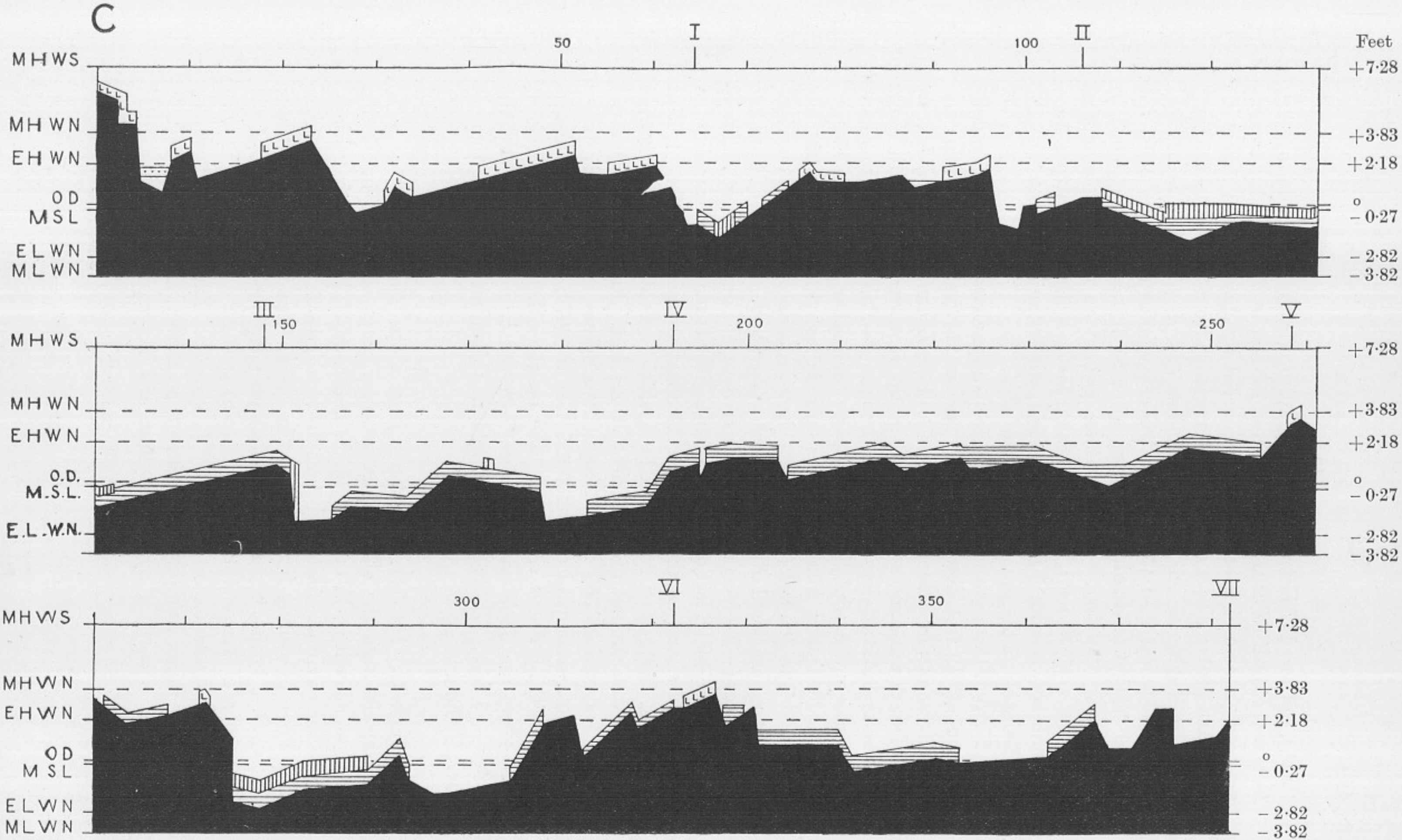

FIG. 5.—Traverse C; distribution of *Lichina pygmæa*, *Polysiphonia lanosa* and fucoid algæ. For meaning of symbols, see Fig. 3. (Vertical scale twice the horizontal.)

(O.D.), until at 177 feet there is again a drop (from −0·46 feet to −2·13 feet) covered with *Fucus serratus*. From 185 feet to 255·5 feet the traverse gradually rises and is continuously covered by Ascophyllum except for two small pools; *Fucus serratus* is also present from 212 feet to 223 feet,* attaining heights of +1·39 feet at 215 feet and of +1·40 feet at 223 feet. From 255·5 feet (+1·43 feet) the traverse climbs as far as 259·5 feet (+3·51 feet), Chthamalus appearing at +2·3 feet and being joined by Lichina at +2·9 feet. Lichina is also present on the next summit at 272·5 feet (+3·19 feet), the intervening lower section supporting Ascophyllum between 262·5 feet and 268 feet, where the rock is below +2·49 feet, hereabouts the upper limit of this alga.

At 272·5 feet comes another of the steep drops characteristic of Traverse C, from +3·19 feet down to −2·25 feet at 275 feet. Chthamalus and *Balanus balanoides* extend down to +2·5 feet, *Laurencia pinnatifida* from +1·0 feet downwards, and the rocks at the foot are covered with *Fucus serratus* and *Ascophyllum nodosum*. I found no *Balanus perforatus* here. *F. serratus* and Ascophyllum accompany each other as far as 289·5 feet, but the subsequent hump supports only Ascophyllum. From 294 feet (−1·11 feet) to 305 feet (−1·15 feet) there are stones and rocks on which are growing scattered *Fucus vesiculosus* (see above, p. 448). From 305 to 308·5 feet (+2·0 feet) there is Ascophyllum, the next few feet, followed by a drop to +0·08 feet at 312·5 feet, being bare save for Chthamalus and *B. balanoides*, and on the next rise Ascophyllum reaches +2·88 feet at 322·5 feet, being then succeeded by Lichina, accompanied by *Littorina saxatilis*, to a summit of +3·61 feet at 327 feet. From here to the end of the traverse at 382 feet, Ascophyllum occurs intermittently below +2·78 feet, accompanied from 362·5 feet to 367·5 feet (+0·15 feet to +2·25 feet) by *Fucus vesiculosus*, and on the otherwise bare rock at C VII there are *Chthamalus stellatus*, *Littorina littorea*, and *L. saxatilis* above + 3 feet. *L. obtusata* is abundant throughout wherever there is Ascophyllum.

Traverse D. 198 feet. Eastwards from C VII. See Fig. 6.

This, although the shortest, is in many ways the most interesting traverse, since it is the only one of the four to reach High Water Springs, where the environmental conditions for algal growth are far more severe than those prevailing further down the shore. The rock at C VII where the traverse begins is capped, as has been mentioned at the end of the description of Traverse C, by *Chthamalus stellatus* accompanied by *Littorina littorea* and above +3 feet by *L. saxatilis*. The traverse descends, except for minor humps, to +0·69 feet, at 25 feet, and from 6·5 feet to 17 feet it is covered by Ascophyllum and Polysiphonia, with a little

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* Not shown in Fig. 5.

Fucus vesiculosus from 6·5 feet to 10 feet at about +1·5 feet. *Littorina obtusata* and *Gibbula umbilicalis* are both common here, as is *Osilinus lineatus*, which was found on none of the other traverses, and is apparently confined to the north-eastern part of the reef where it is quite common within its narrow range. From 17 feet to 25 feet the floor is stony, and after storms is frequently covered a foot or so deep with torn-off algæ and various jetsam. From 25 feet (+0·69 feet) to 51·5 feet (+3·40) there is continuous growth of Ascophyllum, not very thick, with some bare rock showing. At 25 feet there is *Balanus balanoides* growing on the rock, and also *Littorina littorea, L. obtusata*, and *Gibbula umbilicalis*, after which the traverse climbs to +2·44 feet at 27·5 feet, where the same animals are present with the addition of *Littorina saxatilis*, whose lower limit on bare rock hereabouts just overlaps the upper limit of *L. littoralis* amongst Ascophyllum, which remains damp even after six hours' exposure to the sun on a hot June day. At 33 feet the traverse reaches +3·24 feet, and there is a small patch of *Fucus spiralis*. At 51·5 feet (+3·40 feet) Ascophyllum abruptly gives way to *Fucus spiralis*, of which there is an almost pure stand as far as 92·5 feet (+5·28 feet) where it, as abruptly, is replaced by *Pelvetia canaliculata*, of which there was previously a patch at 81·5 feet (+4·91 feet). At 96 feet (+5·2 feet), the traverse is just at the lower edge of the Pelvetia zone, and again at 105·5 feet (+5·28 feet) on the side of a ditch, after which the traverse continues its gentle upward slope to 121 feet (+6·93 feet), still covered by Pelvetia and with *Littorina saxatilis* common. At 124 feet the level has fallen to +2·95 feet, and on this drop Pelvetia extends down to +5·79 feet, *Fucus spiralis* from that point down to +3·85 feet, *Littorina saxatilis* down to +5·5 feet and *L. obtusata* up to +4·5 feet, the two gastropods failing to overlap here as they did at 27·5 feet. On the subsequent hump, *Fucus spiralis* extends from +3·5 feet to +5·45 feet with Pelvetia covering the summit which reaches +5·80 feet at 129 feet, and the further side supports *Fucus spiralis* from +5·4 feet down to the bottom at +3·19 feet, 130·5 feet from C VII.

The traverse rises again slightly to 140 feet (*Fucus spiralis*) but then descends steadily to −0·08 feet at 172 feet, patches of Ascophyllum occurring below +3·27 feet. Up the next steep climb to +3·81 feet at 178 feet Ascophyllum reaches +3·17 feet, and reappears in the next depression at 180·5 feet at a height of +3·2 feet, accompanied by Patella. The traverse then rises to the end, *Fucus spiralis* occurring between +3·50 feet and +5·6 feet, with *Littorina littorea* up to +4·3 feet, and Pelvetia from +5·6 feet up to +7·49 feet. Above this is the thickest growth of *Chthamalus stellatus*, reaching +9·6 feet hereabouts (the line of the actual traverse ended at +8·34 feet). *Littorina neritoides* is now common for the first time, and its upper limit, surprisingly sharp, was

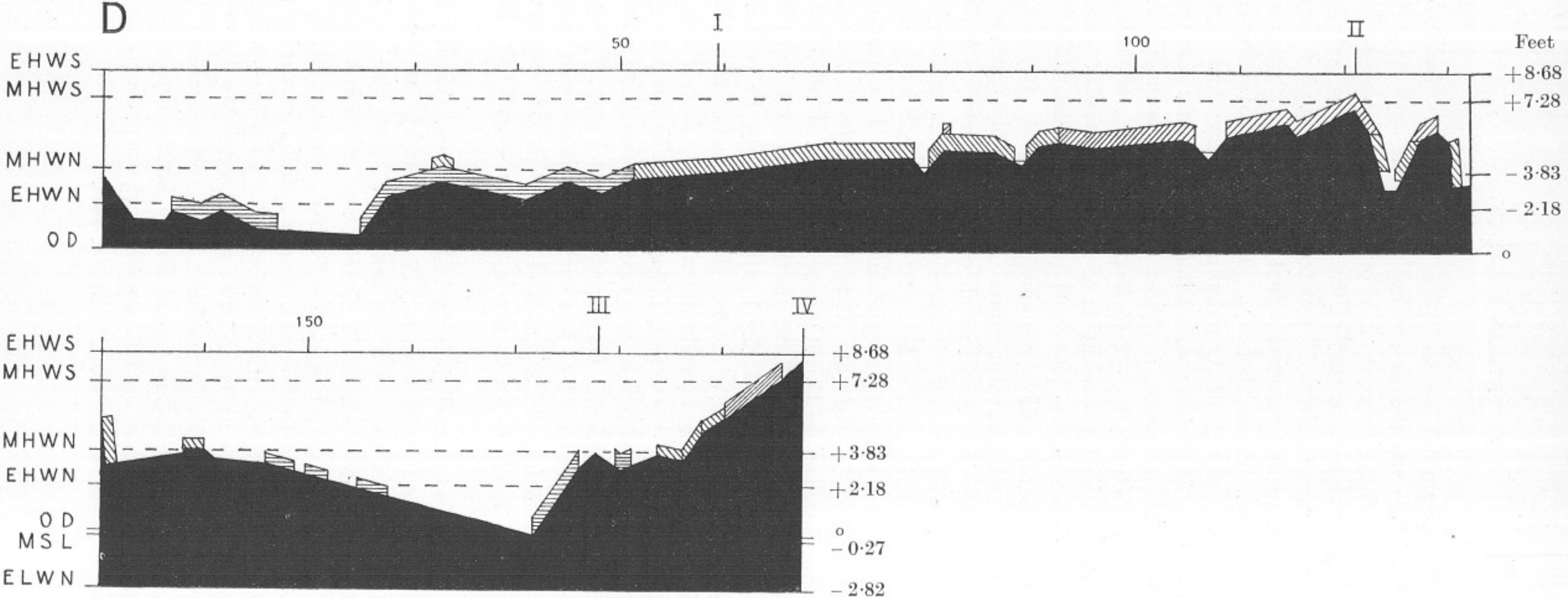

Fig. 6.—Traverse D; distribution of *Polysiphonia lanosa* and fucoid algæ. For meaning of symbols, see Fig. 3. (Vertical scale twice the horizontal.)

levelled at +14·93 feet. Its lower limit is somewhat uncertain. It was abundant down to +9·2 feet, about 1·5 above Pelvetia, and seemed to stop there, but after a prolonged search two specimens were found at the bottom of the Pelvetia zone at +5·6 feet. None could be found in the intermediate region. *Littorina saxatilis* is common to its upper limit, again quite sharp, at +14 feet, and extends without any break right through both the Pelvetia and the *Fucus spiralis* zones.

These descriptions of the traverses are summarised in Tables IV and V and in Figs. 3, 4, 5 and 6.

Splash Zone.

In an attempt to correlate tidal data with the distribution of species on the shore, it must always be borne in mind that the "splash zone" formed by the breaking waves raises the tide marks above their level predicted in the tide tables, or recorded by a tide gauge (most types of which ignore wave action). The height of the splash zone is obviously of great importance, but it is seemingly impossible to estimate with any exactness, varying as it does with the weather, with the amount of general exposure of the rocks to the surf, and with the detailed shape of the rocks. I think that two feet would be a conservative average estimate of the splash zone over a long period on Church Reef. Orton (1929) takes the same figure in considering the vertical range of *Patella vulgata*. During the winter, continued storms will keep the height of the splash zone at five feet or more, whereas during the summer there may be periods of several days when there is only the smallest sea running, or, rarely, none at all with a light off-shore breeze. It may be pointed out that a breaking sea will wet the splash zone almost at once, whereas it would take some minutes for even the superficial water to dry or drain off. It would therefore seem that for small animals, at any rate, and to a large extent for plants, the splash zone is almost as wet as the sea itself (since it is rewetted every few seconds) and is also at the same temperature as the sea, and that the tidal level at any time is that reached by the surf, and not that of the real sea-level at that time.

Exposure Related to Level on the Shore.

First of all the relation must be examined between the vertical level on the shore and the amount of exposure or immersion ; then the positions of the upper and lower limits of species can be compared with the data so obtained.

If height on the shore is plotted against hours of exposure, one of two curves will result. When plotted for one tide a simple curve is obtained (Fig. 7 A and B ; Table VI, columns *a* and *b*) ; the same is true at

TABLE IV.

PLANTS: UPPER (U.) AND LOWER (L.) LIMITS ABOVE (+) OR BELOW (—) ORDNANCE DATUM, IN FEET.
L.W.M.=LOW WATER MARK.

Traverse.	Pelvetia canaliculata.		Fucus spiralis.		Lichina pygmæa.		Ascophyllum and Polysiphonia.		Fucus serratus.		Laminaria digitata.		Chondrus crispus.		Gigartina stellata.	
	U.	L.	U.	L.	U.	L.	U.	L.	U.	L.	U.	L.	U.	L.	U.	L.
A.					↑ +6·04	+0·4 +0·4 +0·57 +0·3		−4·05		−9·0	−6·39 −6·51 −6·50 −6·41 −6·41 −6·7	L.W.M. ↓	−5·55	L.W.M. ↓	−5·29	L.W.M. ↓
B.					↑ +6·04	+0·68		−3·7 −4·11		−8·4 −8·6	−6·23 −6·54 −6·51 −7·01	L.W.M. ↓	−5·33 −4·5 −5·5	L.W.M. ↓	−5·0	L.W.M. ↓
C.					↑ +6·04	+0·04	+2·49 +2·88 +2·78		+1·39 +1·40							
D.	+7·49	+4·91 +5·28 +5·2 +5·28 +5·79 +5·45 +5·6	+5·28 +5·79 +5·45 +5·4 +5·6	+3·24 +3·40 +3·85 +3·5 +3·19 +3·5			+3·40 +3·27 +3·17 +3·2									
Extremes	+7·49	+4·91	+5·79	+3·19	↑ +6·04	+0·04	+3·40	−4·11	+1·40	−8·6	−6·23	L.W.M. ↓	−4·5	L.W.M. ↓	−5·0	L.W.M. ↓
Means	+7·49	+5·36	+5·5	+3·47	↑ +6·04	+0·4	+3·03	−3·95	+1·40	−8·7	−6·52	L.W.M. ↓	−5·22	L.W.M. ↓	−5·15	L.W.M. ↓

TABLE V.

ANIMALS: UPPER (U.) AND LOWER (L.) LIMITS ABOVE (+) OR BELOW (—) ORDNANCE DATUM, IN FEET. L.W.M.=LOW WATER MARK.

	Littorina neritoides.		Littorina saxatilis.		Littorina obtusata.		Littorina littorea.		Osilinus lineatus.		Gibbula umbilicalis.		Gibbula cineraria.	
Traverse.	U	L.	U.	L.	U.	L.	U.	L.	U.	L.	U.	L.	U.	L.
A.			↑ +6·04			−6·5		−6·5				−6·5	−6·5	
B.			↑ +6·04	+2·89		−7·5		−7·0				−8·0	−3·2	−8·6
C.			↑ +6·04	+1·4 +3	+2·88						+2·5 +2·17		−2	
D.	+14·93	+9·2 +5·6	+14	+2·44 +5·5	+2·5 +4·7		+4·3		+3·4	+1·5	+2·44			
Extremes.	+14·93	+5·6	+14	+1·4	+4·7	−7·5	+4·3	−7·0	+3·4	+1·5	+2·5	−8·0	−2	−8·6
Means.	+14·93	+7·4	+14	+3·05	+3·36	−7·0	+4·3	−6·75	+3·4	+1·5	+2·37	−7·25	−3·9	−8·6

	Calliostoma zizyphinum.		Nucella lapillus.		Patella vulgata.		Chthamalus stellatus.		Balanus balanoides.		Balanus perforatus.		Verruca strœmia,	
Traverse.	U.	L.	U.	L.	U.	L.	U.	L.	U.	L.	U.	L.	U.	L.
A.	−6·2	L.W.M. ↓		−6·5	↑ +6·04	−6·5	↑ +6·04	−4·44	+2·5	−8	−2·36	L.W.M. ↓	−6·32	L.W.M. ↓
B.	−7·0	L.W.M. ↑		−7·0	↑ +6·04	−6·5	↑ +6·04	−5·22			−1·40	L.W.M. ↓	−6·23	L.W.M. ↓
C.			+2·5 +2·17		↑ +6·04		↑ +6·04		+4·29		+0·88			
D.							+9·6							
Extremes.	−6·2	L.W.M. ↓	+2·5	−7·0	↑ +6·04	−6·5	+9·6	−5·22	+4·29	−8	+0·88	L.W.M. ↓	−6·23	L.W.M. ↓
Means.	−6·6	L.W.M. ↓	+2·33	−6·75	↑ +6·04	−6·5	+9·6	−4·83	+3·4	−8	−0·96	L.W.M. ↓	−6·27	L.W.M. ↓

TABLE VI.

EXPOSURE AT DIFFERENT LEVELS OVER VARIOUS TIDAL PERIODS; EXPRESSED IN HOURS, EXCEPT IN COLUMN *k* WHICH IS IN PERCENTAGES.

Height above Chart Datum in Feet.	March 16th. Springs. 12·27 hrs. Fig. 7A.	March 24th. Neaps. 12·85 hrs. Fig. 7B.	March 14th–18th. Springs. 120 hrs. Fig. 8A.	March 19th–23rd. Intermediate. 120 hrs. Fig. 8B.	March 21st–26th. Neaps. 120 hrs. Fig. 8C.	Jan. 14th–29th. Midwinter. 380 hrs. Fig. 9.	March 14th–29th. Vernal Equinox. 380 hrs. Fig. 9.	June 11th–26th. Midsummer. 380 hrs. Fig. 9.	Sept. 22nd–Oct. 7th. Autumnal Equinox. 380 hrs. Fig. 9.	A.D. 1930 8,760 hrs. Hours. Fig. 10.	A.D. 1930 8,760 hrs. % Exposure. Fig. 13.		March 14th–29th. 380 hrs. Continuously Dry or Wet. Fig. 11.
	a	b	c	d	e	f	g	h	i	j	k		l
17	12·27	12·85	120	120	120	380	380	380	380	8760	100	Dry	380
16	11·4	12·85	117·4	120	120	366·8	376·6	380	370·2	8612	98·3		324
15	9·6	12·85	98·6	118·6	120	347·6	356·8	380	349·6	8271	94·4		260
14	8·8	12·85	87·6	116	120	324·8	339·7	370·8	328·0	7850	89·6		210
13	8·0	12·85	80·4	108	120	296·4	317·6	339·4	303·6	7241	82·7		160
12	7·6	12·85	76·0	98·8	114·6	255·4	289·8	294·6	277·2	6445	73·6		98
11	7·2	11·6	72·2	87·2	98·0	225·4	259·4	249·4	249·5	5678	64·8		22
10	7·0	8·4	68·2	76·6	79·6	207·6	227·8	225·0	222·2	5100	58·2		
9	6·8	7·2	64·8	68·6	69·0	189·0	209·0	209·4	203·6	4688	53·5		
8	6·6	6·4	61·5	63·8	61·8	179·6	195·4	197·2	188·4	4399	50·2		
7	6·4	5·6	59·0	57·6	54·0	167·0	180·0	181·4	177·4	4085	46·6		
6	6·2	3·0	56·2	47·8	36·6	147·2	153·6	165·0	155·2	3600	41·1		
5	6·0	0	53·6	35·2	12·8	117·8	123·8	137·8	123·0	2915	33·3	Wet	84
4	5·6	0	50·0	23·8	2·0	79·4	98·4	97·2	98·6	2182	24·9		124
3	5·4	0	44·8	16·8	0	56·0	79·4	60·8	75·0	1595	18·4		148
2	4·8	0	40·2	10·2	0	35·0	60·0	32·2	51·0	1057	12·1		186
+1	4·2	0	34·8	4·0	0	16·0	41·2	2·6	32·6	556·3	6·3		236
CD	3·2	0	26·0	0	0	0	26·3	0	19·6	261·1	3·0		285
−1	2·0	0	7·0	0	0	0	7	0	2·4	53·5	0·6		338
−2	0	0	0	0	0	0	0	0	0	0	0		380

Springs over several tides taken together, as long as the amplitude of the tide is not altering (Fig. 8 A; Table VI, col. *c*). Over a complete tidal period of a fortnight a more complex curve appears. In Fig. 9 the four curves represent the exposure at various heights during four fortnights

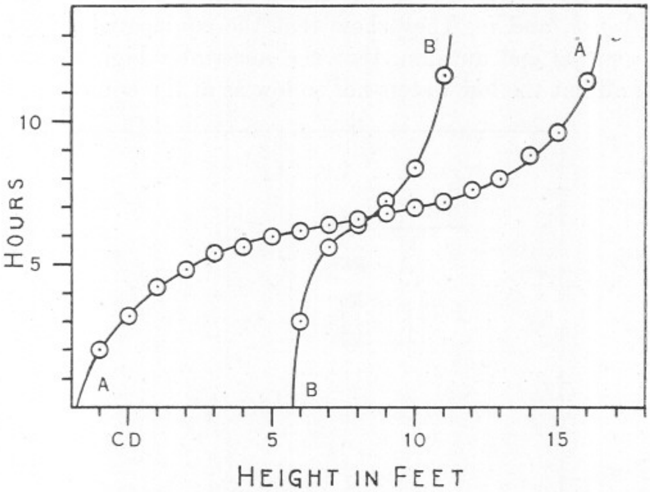

FIG. 7.—Amount of exposure at different heights during one tide. A, March 16th, 1930, springs. B, March 24th, 1930, neaps. (See Table VI, columns *a* and *b*.)

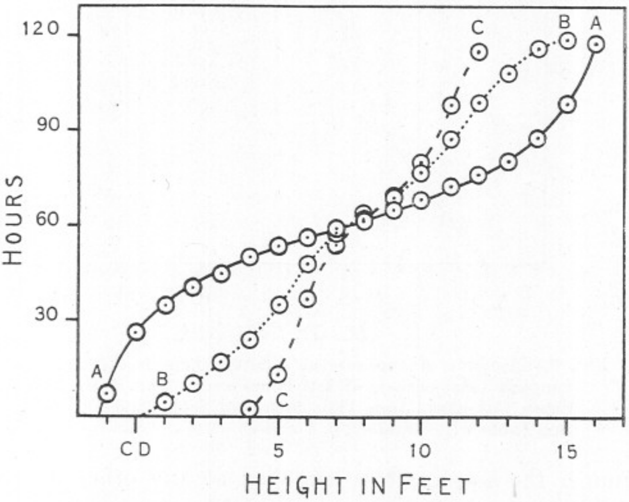

FIG. 8.—Amount of exposure at different heights during 120 hours. A, March 14th–18th, springs. B, March 19th–23rd, intermediate. C, March 21st–26th, neaps. (See Table VI, columns *c*, *d* and *e*.)

in 1930; (1) January 14th–29th (Midwinter), (2) March 14th–29th (Vernal Equinox), (3) June 11th–26th (Midsummer), (4) September 22nd–October 7th (Autumnal Equinox). These figures are given in Table VI, columns *f*, *g*, *h*, and *i*. They show that the equinoctial tides are very similar in spring and autumn, that the midwinter high waters are the highest of all but the low waters not so low as at the equinoxes, and that at midsummer the amplitude is less than at any other set of springs, high waters being lower and low waters higher.

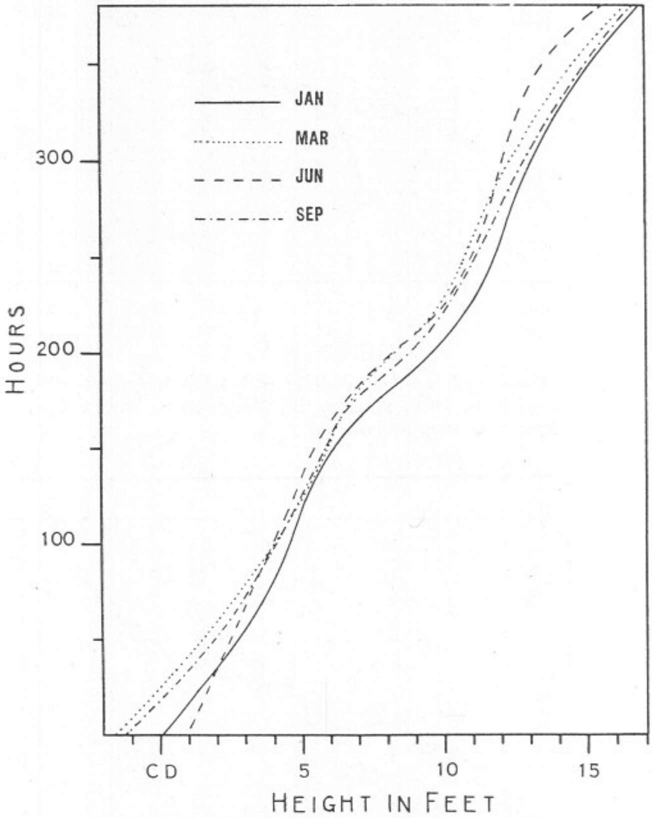

FIG. 9.—Amount of exposure at different heights during four complete tidal periods of 380 hours each: Jan. 14th–29th, March 14th–29th, June 11th–26th, and Sept. 22nd–Oct. 7th. (See Table VI, columns *f*, *g*, *h* and *i*.)

The same compound curve is obtained over any other period, longer or shorter, as long as the tidal amplitude varies (Fig. 8 B and C; Table VI, cols. *d* and *e*).

Fig. 10 (Table VI, column *j*) represents approximately the exposure at different heights during the year. It is obtained by taking the sum of the four curves in Fig. 9 and multiplying by the requisite number of hours. The same curve is shown in Fig. 13, where the time is divided into 100 units (Table VI, col. *k*).

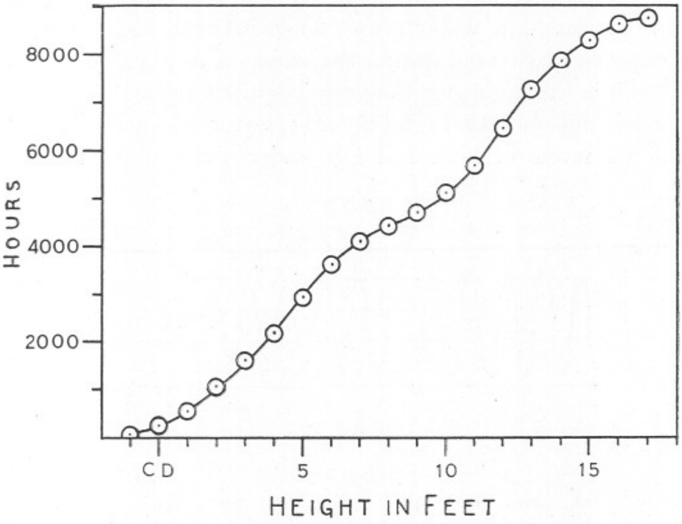

FIG. 10.—Amount of exposure at different heights during 1930. (See Table VI, column *j*.)

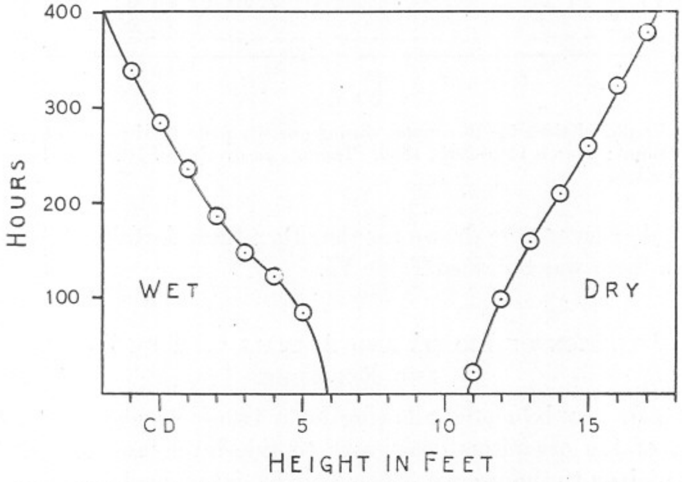

FIG. 11.—Length of time during which different levels are continuously dry or continuously wet. (See Table VI, Column *l*.)

This compound curve is built up of (1) the semidiurnal tide curve and (2) the curves, having a wave-length of a fortnight, formed by the heights of high and low waters as they vary between one set of springs and the next (see Fig. 12). These curves are also shown in another way in Fig. 11 (Table V, col. *l*), which represents the length of time during which any given level may be continuously dry or wet during one fortnight (Vernal Equinoxes). The two curves limit areas extending above extreme high and below extreme low water neaps, since between these two levels no place is exposed or covered during the whole of any one tide.

Fig. 12 shows the tides over the vernal equinox from March 14th–29th, 1930. This is not an actual tidal record; in the absence of a tide gauge the predicted levels of high and low water were joined in free-hand.

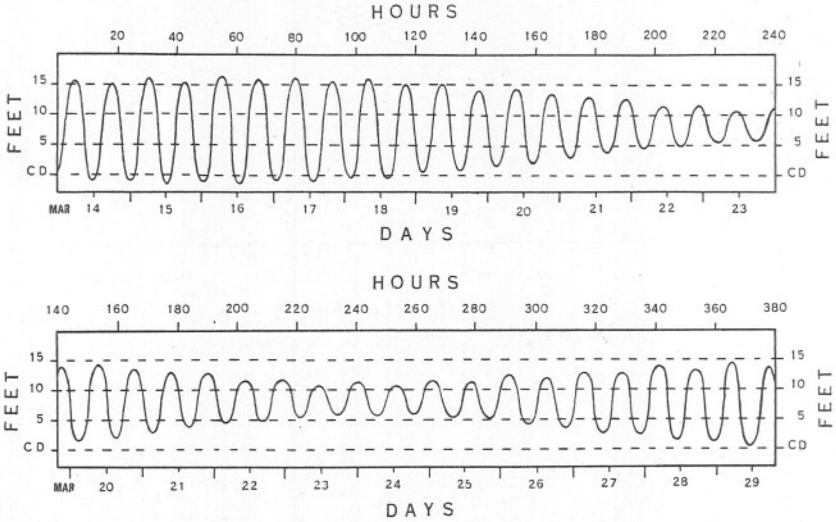

Fig. 12.—Predicted tides for Devonport during one complete tidal period of a fortnight (380 hours): March 14th–29th, 1930. There is an overlap of 100 hours between the two sections.

Similar tide curves were drawn for the other three fortnights mentioned and from them was obtained Table VI.

Relation of Plants and Animals to Tide Levels and Exposure.

A list can now be made, allowing for a two-foot splash zone, of the relations of the organisms dealt with to tide levels and to amount of exposure (given to the nearest 5%). This list is summed up in Fig. 13.

Pelvetia canaliculata: from half-way between Mean High Water Springs and Neaps down to just above Extreme (Lowest) High Water Neaps; from 90% to 70% Exposure.

Fucus spiralis: from Mean High Water Neaps down to a foot below Extreme (Lowest) High Water Neaps; from 80% to 60% Exposure.

Lichina pygmæa : from above Mean High Water Neaps down to just above Extreme (Highest) Low Water Neaps; from 85% to 45% Exposure.

Ascophyllum nodosum and *Polysiphonia lanosa :* from just below Extreme (Lowest) High Water Neaps down to half-way between Mean Low Water Neaps and Springs; from 55% to 15% Exposure. From Table IV it will be seen that the upper limits on Traverse C were on an average half a foot lower than those on Traverse D. This is unexpected, since that part of Traverse D where Ascophyllum is growing is more protected than that of Traverse C; as a rule, the greater the amount of surf the higher the upper limits of any belt, owing to the increased splash zone.

Fucus serratus : from Mean Sea Level to Extreme Low Water Springs; from 50% to 0% Exposure.

Laminaria digitata : from Mean Low Water Springs down to below all tide marks; from 5% Exposure to complete immersion.

Chondrus crispus : from half-way between Mean Low Water Neaps and Springs down to below all tide marks; from 10% Exposure to complete immersion.

Gigartina stellata : from above Mean Low Water Springs (just below *Chondrus crispus*) down to below all tide marks; from 10% Exposure to complete immersion.

Littorina neritoides : from four feet above Extreme High Water Springs down to Mean High Water Springs, with two specimens at Mean High Water Neaps; from 100% to 95%, with two specimens at 75% Exposure.

Littorina saxatilis : from three feet above Extreme High Water Springs down to Mean Sea Level; from 100% to 50% Exposure.

Littorina obtusata : from Extreme (Lowest) High Water Neaps down to just above Extreme Low Water Springs; from 65% to less than 5% Exposure.

Littorina littorea : from Extreme (Lowest) High Water Neaps down to half-way between Mean and Extreme Low Water Springs (just above *L. obtusata*); from 65% to less than 5% Exposure.

Osilinus lineatus : from just below Extreme (Lowest) High Water Neaps down to Mean Sea Level; from 60% to 50% Exposure.

Gibbula umbilicalis : from a foot above Mean Sea Level down to just above Extreme Low Water Springs; from 55% to less than 5% Exposure.

Gibbula cineraria : from Mean Low Water Neaps down to Extreme Low Water Springs; from 30% to about 0% Exposure.

Calliostoma zizyphinum : from Mean Low Water Springs down to below all tide marks; from 10% Exposure to complete immersion.

Nucella lapillus : from a foot above Mean Sea Level down to half-way

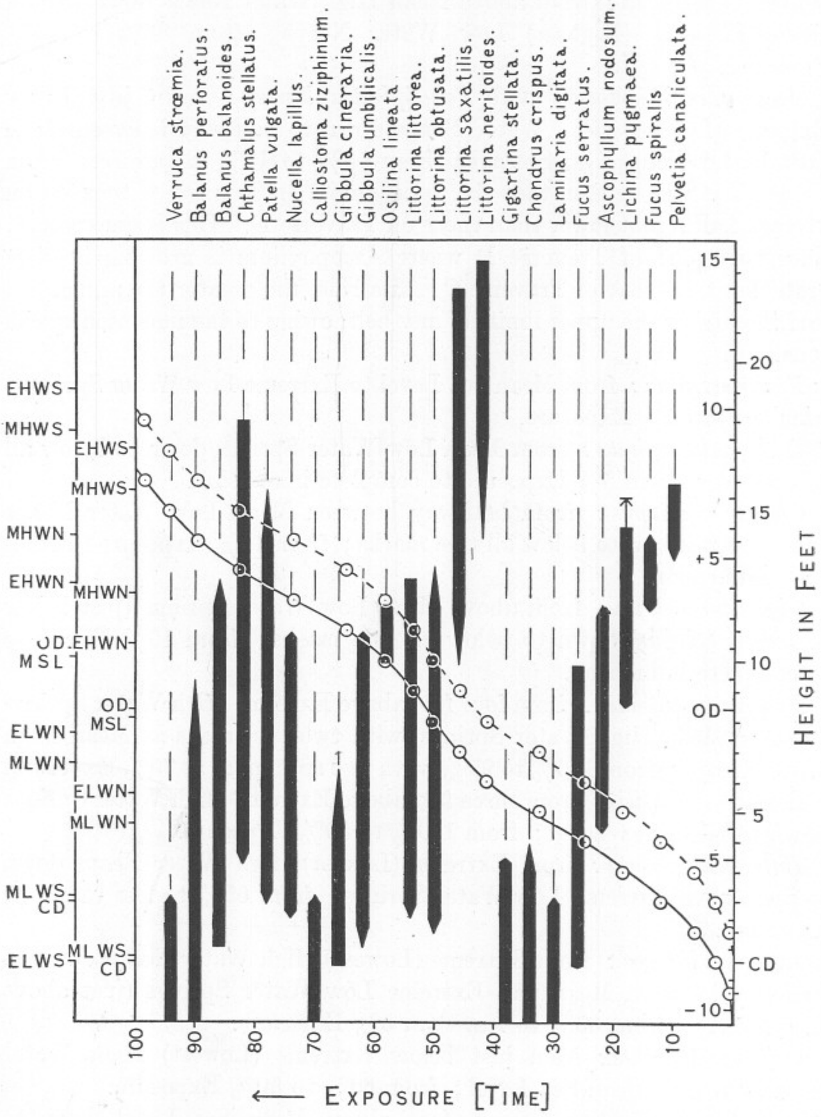

FIG. 13.—The limits of distribution of twenty-two species on the shore. Of the two columns of tide levels (EHWS to ELWS) the extreme left-hand one is two feet higher than the predicted levels, allowing for the splash zone.

The solid curve shows the percentage exposure at different heights (see Table VI, Column *k*). The broken curve is the same raised two feet throughout, allowing for the splash zone.

Two scales are shown on the right, in feet relative to Chart Datum and Ordnance Datum.

between Mean and Extreme Low Water Springs; from 55% to 10% Exposure.

Patella vulgata: from above Mean High Water Neaps down to Mean Low Water Springs; from 90% to 5% Exposure.

Chthamalus stellatus: from just above Mean High Water Springs down to above Mean Low Water Springs; from about 100% to 10% Exposure.

Balanus balanoides: from Extreme (Lowest) High Water Neaps down to just above Extreme Low Water Springs; from 60% to less than 5% Exposure.

Balanus perforatus: from between Mean Sea Level and Extreme (Highest) Low Water Neaps down to below all tide marks; from 45% Exposure to complete immersion.

Verruca strœmia: from Mean Low Water Springs down to below all tide marks; from 5% Exposure to complete immersion.

This list is summed up in Fig. 13, which shows the vertical range of each species, and the curve formed by plotting exposure against height, as in Fig. 11 and Table VI, col. *k*.

THE RELATION OF LEVELS ON THE SHORE TO THE DISTRIBUTION OF ANIMALS AND PLANTS.

The ranges of intertidal species vary widely between 2 feet (*Osilinus lineatus*, *Fucus spiralis*, *Pelvetia canaliculata*) and 14 feet (*Patella vulgata*, *Chthamalus stellatus*), and there seems to be no *a priori* reason why any particular levels should be more, or less, favourable to these species, if one allows for a wide range of adaptation and specialisation among them. Nevertheless, there are certain relationships between the height on the shore and the number of species that have either their upper or their lower limits there. If the numbers of upper and of lower limits are plotted against height on the shore, two very similar curves result; each has a sharp maximum low down on the shore, a spread-out maximum higher up the shore, and an intervening minimum. These curves are smoothed curves, obtained by taking the numbers of species whose limits are between −2 and +1 feet, −1 and +2 feet, 0 and +3 feet, and so on (Table VII and Fig. 14). These heights are relative to chart datum.

For the upper limits of species, the maximum furthest down the shore is at +2 to 5 feet, the minimum at 5 to 8 feet, while the maximum at higher levels extends from 9 to 16 feet. These heights, allowing for a two-foot splash zone, correspond to between Low Water Neaps and Springs to Mean Low Water Neaps, and from Mean Sea Level to Mean High Water Springs respectively. The highest peak on the curve corresponds to Extreme (Lowest) High Water Neaps.

In the case of the lower limits of species, the maximum furthest down the shore occurs at −1 to +2 feet, or about Extreme Low Water Springs, the minimum at 5 to 8 feet, which coincides with the minimum of upper limits at Mean Low Water Neaps, and the high-level maximum from 8 to 11 feet, or about Mean Sea Level.

TABLE VII.

NUMBER OF SPECIES, AND LIMITS OF SPECIES, IN RELATION TO TIDE LEVELS. TOTAL NUMBER OF SPECIES, 22.

Feet above or below. Chart Datum.	Lower Limits.	Upper Limits.	Total Limits.	Total Species.	Difference between Total Species and Total Limits.	Tide Levels, allowing for 2′ splash zone.
18 to 21				2	2	E.H.W.S.
17 to 20		1	1	3	2	
16 to 19		1	1	3	2	M.H.W.S.
15 to 18		3	3	6	3	
14 to 17	1	4	5	7	2	
13 to 16	2	5	7	8	1	M.H.W.N.
12 to 15	2	4	6	10	4	
11 to 14	2	5	7	11	4	E.H.W.N.
10 to 13	1	6	7	12	5	
9 to 12	4	5	9	14	5	
8 to 11	3	4	7	13	6	M.S.L.
7 to 10	3	2	5	13	8	
6 to 9	1	1	2	12	10	E.L.W.N.
5 to 8	0	1	1	11	10	M.L.W.N.
4 to 7	1	1	2	12	10	
3 to 6	2	2	4	14	10	
2 to 5	2	5	7	16	9	
1 to 4	4	5	9	15	6	
0 to +3	6	3	9	14	5	M.L.W.S.
−1 to +2	8		8	14	6	E.L.W.S.
−2 to +1	5		5	11	6	

If a curve is made in the same way for the total numbers of species occurring at various heights, there are again two maxima and one minimum (Fig. 14). The low-level maximum coincides with that of upper limits at between Low Water Neaps and Low Water Springs; the minimum coincides with the other two minima at Mean Low Water Neaps, and the high-level maximum with that of lower limits at about Mean Sea Level.

At first sight, the relative scarcity of species at the level of Mean Low Water Neaps might seem to show that this situation was distinctly unfavourable to intertidal animals and plants. Of the species, however, that build up the maxima of the curve for Total Species, several have their limits just at the heights corresponding to these maxima, as shown by the other curves in Fig. 14.

If now a curve is made, plotting against height the difference in number between the total number of species and the total number of upper and lower limits, a maximum is obtained around Mean Low Water Neaps (Fig. 15). In other words, there are more species in the groups examined flourishing at Mean Low Water Neaps than at any other level on the shore; Mean Low Water Neaps is nearer the optimum of more of these intertidal species than is any other level.

The low-level maximum on the curve for lower limits shows that many intertidal species can live as far down as the zone between Mean and Extreme Low Water Springs, without being able to survive altogether beyond the influence of tides. Such are *Fucus serratus*, *Littorina littorea*, *L. obtusata*, *Gibbula umbilicalis*, *G. cineraria*, *Nucella lapillus*, *Patella vulgata*, and *Balanus balanoides*.

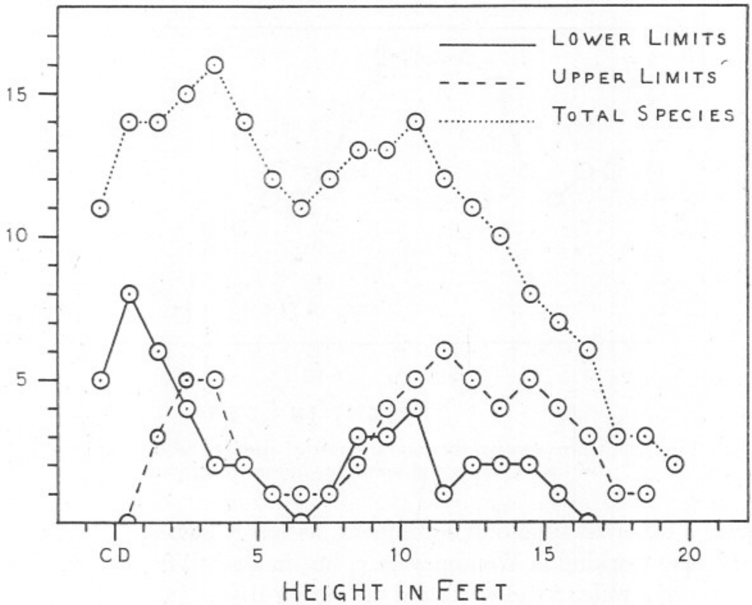

FIG. 14.—Number of species, and of upper and lower limits, at different heights.

From the low-level maximum on the curve for upper limits, it appears that several species whose range is largely below the lowest tide-mark can extend nearly as high as Mean Low Water Neaps, but usually no higher. These include *Laminaria digitata*, *Chondrus crispus*, *Gigartina stellata*, *Calliostoma zizyphinum*, and *Verruca strœmia*. *Balanus perforatus* is exceptional in nearly reaching Mean Sea Level.

The vagueness of the upper maxima in Fig. 14 seems to reflect the increasing strenuousness of the conditions for fundamentally marine creatures as high water mark is approached; in the case of the brown algæ, only by increased specialisation can they survive as they live higher, and this specialisation, of whatever nature, restricts their ranges, which decrease steadily from *Fucus serratus* through Ascophyllum and *F. spiralis* to *Pelvetia canaliculata* (Fig. 13).

One of the more critical levels is about Extreme (Lowest) High Water Neaps, where the upper limits of four animals on Church Reef are found, namely of *Balanus balanoides, Osilinus lineatus, Littorina littorea* and *L. obtusata*. This level, High Water Neaps, may also be very important in quite a different type of environment, as was shown by Pantin (1931). He was also working in Wembury Bay, but in a small fresh-water stream a quarter of a mile to the westward of Church Reef. In this stream there are large numbers of the triclad *Procerodes* (*Gunda*) *ulvæ* and the "archi-annelid" *Protodrilus flavocapitatus*, but Pantin found that they are confined between the levels of High and Low Water Neaps. Above High Water Neaps there is a "desert region" in this stream, until a fresh-water flora and fauna are encountered at High Water Springs. High Water Neaps, then, is a critical level in the very different environments of exposed rock and the bed of a fresh-water stream; but whereas on Church Reef Low Water Neaps is the optimum level for many intertidal organisms, in the stream it is the lower limit for species living in somewhat peculiar estuarine conditions. This contrast emphasises the manifold ecological importance of neap tides.

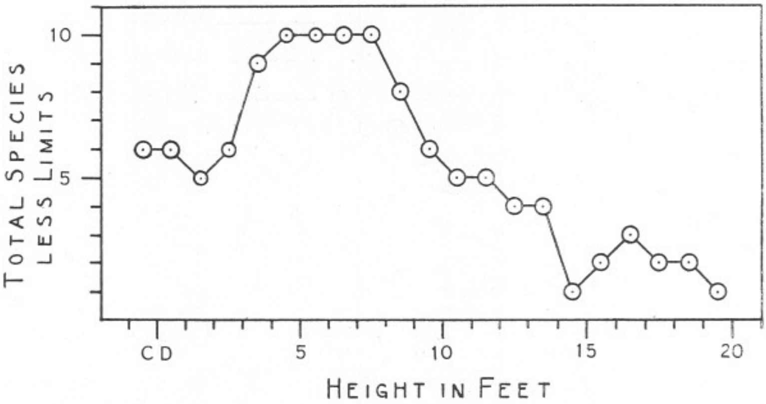

FIG. 15.—Difference between the total number of species and the total number of limits, upper and lower, at different heights.

There are, then, three levels on the shore on Church Reef which appear to be more critical than others, in the case of our 22 species.

1. Between Mean and Extreme Low Water Springs; the lower limit of several intertidal species; less than 5% Exposure.

2. Between Mean Low Water Neaps and Springs; the upper limit of several submarine species; about 20% exposure.

3. Extreme High Water Neaps; the upper limit of several intertidal species; about 60% exposure.

The least critical level is Mean Low Water Neaps, with about 40% exposure.

These statements are applicable to Algæ and Barnacles considered over a long time, since they do not move about. Gastropods complicate the issue by moving, and as this survey was done largely at Springs it cannot be stated with certainty that these animals occupy the same positions at Neaps as at Springs. However, the only gastropods which are found above the level of High Water Neaps are *Patella vulgata*, *Littorina saxatilis*, and *L. neritoides*. None of the others climb above High Water Neaps during Spring tides, and during Neaps the three gastropods mentioned can be found staying still, and not reached by the tide for several days at a time. Long period data would therefore seem to be as applicable to gastropods as to the sedentary barnacles and plants, at any rate in the upper tidal region.

To my mind the most extraordinary habitats on the shore are those of *Littorina saxatilis* and *L. neritoides*. Both of them extend up the rocks several feet above High Water Mark, where for weeks during a calm summer their sole source of moisture is dew, rain if any, and perhaps the dampness caused by salt on the rocks. They congregate not only in cracks and crannies where it is damp, but also in hollows which are quite dry and bare and also directly face the sun. It is possible that this search for hollows and cracks is more an avoidance of the mechanical force of the wind than of the desiccation caused by it (teleologically speaking). This is suggested by the fact that they are always very loosely attached to the rock, so that one can easily blow them off. Fränkel (1927), who worked on the tropistic reactions of *Littorina neritoides* at Naples, where they live between three and eight metres above the sea, found that they are (*a*) negatively geotropic, (*b*) negatively phototropic when above a horizontal substratum, but (*c*) positively phototropic when hanging from a horizontal ceiling. The resultant of these reactions would make the animals congregate round the entrances to fissures and in hollows, where, in fact, they they are found in nature. The evidence of Herdman (1890) shows that *L. saxatilis*, on exposed rock, may stay in the same place, apparently without moving at all, for a month or more. Finally, there is the question of their upper limits. Each is abundant as high as its upper limit and is there sharply cut off, but *L. neritoides* reaches a foot higher than *L. saxatilis*. What conditions in the environment can, at this height above the tides, be varying sufficiently steadily or rapidly to determine such sudden limits of these species, and at separate heights ?

Another problem, at present quite unexplained, is that of the sharpness of the boundaries of certain zones, notably those of Ascophyllum—*Fucus spiralis*, and *Fucus spiralis*—Pelvetia. These boundaries vary in height slightly from place to place, but are always remarkably distinct, one alga failing to penetrate the territory of the other alga in the pair. Since each is growing thickly down or up to the boundary, this sudden stop on the part of each would appear to be due not so much to general environmental conditions as to some noxious influence on the part of one or other alga, or of both. These sharp boundaries occurred only on the upper parts of the shore.

GENERAL DISCUSSION.

The distributions described above have, of course, been well known in a rough way for many years, but previous accounts have generally been of a more general nature, and have frequently omitted any discussion of such important levels as High and Low Waters of Neap Tides. Owing to lack of uniformity in the nomenclature of different levels on the shore, it is often difficult to make any close comparison between zonation as given in accounts from different regions, and it is therefore urged that tidal levels be given, as well as full tidal data, rather than heights only, since the amplitude of the tide is of minor or even negligible importance in deciding the character of the coastal flora and fauna and their zonation. The most striking zonation I have seen is on Loggerhead Key in the Dry Tortugas, Florida, where the extreme tidal range is less than four feet.

The zonation of algæ on Church Reef appears to be very similar in general to that at Bembridge, Isle of Wight (Baker, 1909), and that of Clare Island on the west coast of Ireland (Cotton, 1912). *Lichina pygmœa*, however, extends at Clare Island from the Pelvetia zone to about Low Water Neaps, although the Springs rise is much the same as at Plymouth, i.e. about 16 feet. At Wembury Bay and in the Plymouth district generally *Lichina pygmœa* never extends lower than Mean Sea Level, some three and a half feet above Low Water Neaps (Naylor, 1930).* Otherwise the distribution of such algæ as are mentioned from all three areas is very similar on the sheltered shore of Bembridge, on the moderately protected Church Reef and on the fully exposed Clare Island Coast. These algæ include *Fucus spiralis, Ascophyllum nodosum, Fucus serratus* and *Laminaria digitata*. (Baker dealt only with brown Algæ.)

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* Relative to predicted tides ; the splash zone at Clare Island is almost certainly greater than on Church Reef, which makes the difference in lower limit all the more remarkable.

On the North American Atlantic Coast the distribution of algæ on the shore has been studied at several places, notably Mt. Desert Island, Maine (Johnson and Skutch, 1928 (a) and (b)), and Cold Spring Harbour, Long Island (Johnson and York, 1915). Direct comparison of these places with Church Reef is difficult, since the authors of both papers fail to consider the importance of High and Low Water Neaps, giving all their data in feet above or below assumed Mean Low Water Mark, which can itself be interpreted either as Mean Low Water Springs or as the average of all low waters at a given place. In a rough way it can be seen that species common to the two sides of the Atlantic, e.g. *Ascophyllum nodosum*, *Polysiphonia lanosa*, *Fucus vesiculosus*, *Fucus spiralis* and *Chondrus crispus* have much the same distribution wherever they occur, but with one notable exception. In Cold Spring Harbour Ascophyllum is confined between about High and Low Water Neaps (7·5 feet to 1·5 feet above " Mean Low Water "), but on the rocky beaches of Long Island Sound, from which Cold Spring Harbour is an inlet, Ascophyllum grows down to 1·5 feet below " Mean Low Water," and perhaps even further. This would appear to be at least as low as Low Water Springs, and is interesting in view of the sharpness of the lower limit, at predicted Low Water Neaps, of Ascophyllum on Church Reef.

Two generalisations on the zonation of algæ are worth quoting. Baker, as a result of her experimental work on the brown algæ at Bembridge, concludes : " (1) The species of seaweeds growing high up on the shore have a power of resisting desiccation which is not possessed by those growing lower down, and this power decreases regularly in those species growing towards the lower levels. (2) The seaweeds which can best resist desiccation grow most slowly, and those that grow most quickly are the least tolerant of desiccation." Johnson and Skutch (1928 b) say : " The vertical range of a species is a measure of its tolerance of loss of water, toward its upper limit, and of loss of light, toward its lower limit."

With regard to the barnacles and the molluscs other than the four species of Littorina, I have been able to find no accurate measurements of their upper and lower limits in other places, such work as the Clare Island Survey being too general for comparison with that on Church Reef. Huntsman (1918) mentions that *Balanus balanoides* extends to below Low Water Mark at Cheticamp, Nova Scotia.

In the case of Littorina, however, there are papers by Herdman (1890), Huntsman (1918), Tattersall (1920), Gowanloch and Hayes (1926), and Hayes (1929) which contain some rather conflicting information.

Herdman, at Puffin Island, Anglesey, worked on *Littorina saxatilis* collected from well above High Water Mark. He found that in sea-water they died after thirty-six and before seventy-two hours ; in fresh water they died after four to eight days ; if kept dry they remained stationary, but alive and well, for two months at least. Specimens marked in their natural habitat above High Water Mark were observed continuously for three days and three nights, during which time they failed to move. They were still in exactly the same positions after intervals of a fortnight and of a month.

Gowanloch and Hayes (1926) worked at St. Andrews, New Brunswick, on the ecology of *Littorina saxatilis* (=*L. rudis*), *L. littorea*, and *L. obtusata*. The latter animal they call *L. palliata* (Say), but I have shown elsewhere that *L. palliata* and *L. littoralis* are synonymous with *L. obtusata* (L.) (Colman, 1932).

Gowanloch and Hayes give the ranges of the three molluscs as follows :

	Lower Limit.	*Upper Limit.*	*Optimum Level.*
L. saxatilis.	Mid Low Tide.	Mid High Tide.	Low Mid Tide.
L. littorea.	Low Low Tide.	Mid Mid Tide.	Low Tide.
L. obtusata.	High Low Tide.	High Mid Tide.	Low Mid Tide.

For purposes of comparison with the Church Reef data I venture to transcribe these as follows :

	Lower Limit.	*Upper Limit.*	*Optimum Level.*
L. saxatilis.	Above Low Water Springs.	Below High Water Springs.	Above Low Water Neaps.
L. littorea.	Low Water Springs.	Mean Sea Level.	Above Low Water Springs.
L. obtusata.	Low Water Neaps.	Below High Water Neaps.	Above Low Water Neaps.

Littorina saxatilis and *L. obtusata* are indigenous, but *L. littorea* was not introduced into Nova Scotia from Europe until shortly before 1857, but it is now abundant on the shores of New England and the Maritime Provinces of Canada (Gray, 1879 ; Sumner, Osburn and Cole, 1913).

It will be seen from the foregoing tables that at St. Andrews, New Brunswick, *L. littorea* and *L. obtusata* occupy very similar positions to those in which they are found on Church Reef. *L. saxatilis*, however, lives in a very different zone : above Low Water Springs up to below High Water Springs, instead of from Extreme (Lowest) High Water Neaps to more than five feet above Extreme High Water Springs (predicted levels). I have, however, seen *L. saxatilis* above the reach of the tide at Little Nahant, Massachusetts.

Huntsman (1918), like Gowanloch and Hayes, describes *L. littorea* as extending downwards no further than Low Water Springs, at St. Andrews, but he says that at Cheticamp, Nova Scotia, on the St. Lawrence side of Cape Breton Island, this gastropod can be dredged from all depths down to twenty fathoms.

Around Woods Hole, Mass., *Littorina littorea* shells have been dredged from numerous positions (Sumner, Osburn and Cole, 1913), to which they had in many cases been carried by hermit-crabs. In two places living specimens were caught by the dredge, but it is probable that they had got away from the intertidal region by accident. One of these two stations was at the mouth of Hadley Harbour. Near here the tide runs each way at any speed up to five knots, and there are numbers of isolated rocks supporting many *L. littorea* and exposed to the full force of the stream. It is therefore not surprising to find numbers of this mollusc on the surrounding sea-floor, where they may have sunk after being torn away from alga or rock. The other station is towards the head of Buzzards' Bay, where masses of eel-grass are commonly floating. These masses as a rule carry *Littorina littorea* along with them, and when the eel-grass dies and disrupts, the mollusc must fall to the bottom where it may be dredged. It should be mentioned that *L. littorea*, though an intertidal animal, can withstand complete immersion for more than fifty days (Hayes, 1929).

The experimental work of Gowanloch and Hayes (1926) and Hayes (1929) may be summarised here, since their results are of importance in connection with upkeep of intertidal zonations.

If Littorinæ are collected from various levels on the shore, those collected higher up show :

(*a*) Greater negative geotropism.

(*b*) Greater, and commoner, positive phototropism.

(*c*) Less, and rarer, negative phototropism. (Some individuals show positive phototropism, some negative, and some neither.)

Prolonged desiccation leads to a marked decrease in negative geotropism, while prolonged immersion induces increased negative geotropism. The combined effect of these reactions is to make it difficult for each species to get away from its normal habitat, and in fact it was found that if *L. littorea* are moved from one place to another within the range of the species, they tend to migrate back to the level from which they were taken.

Finally, Tattersall (1920) has briefly described the zonation of *Littorinæ* in the south-west of Ireland, where the four species are distributed most densely at the following levels : *L. littorea* among Laminaria and *Fucus serratus ; L. obtusata* among *Fucus vesiculosus* and *Ascophyllum nodosum ; L. saxatilis* among *Pelvetia canaliculata* and *Fucus platycarpus* (?=*spiralis*) ; *L. neritoides* between High Water Springs and High Water Neaps. From this scheme Church Reef differs in that the zones of *L. littorea* and *L. obtusata* are indistinguishable so far as vertical distribution is concerned, and that not only are the richest zones of *L. saxatilis* and *L. neritoides* concurrent over much of their extent, but they both reach some distance above Extreme High Water Mark. It appears to me that until numerous accurate determinations of levels of zones are made, with analysis of local factors such as time of day of low water springs and amount of insolation, each locality must be treated on its merits. Nevertheless, the state of affairs in South-western Ireland as described by Tattersall has been taken as generally applicable for British waters by text-books such as *The Biology of the Sea Shore*, Flattely and Walton (1922), and *Animal Ecology*, Pearse (1926). A further difference between these two localities appears to concern the hatching of *L. obtusata*, which lays its egg masses on fucoid seaweeds. Tattersall found that they hatched as late veligers, when reared in the laboratory, and had a short planktonic phase. I kept several egg masses in finger-bowls (i.e. out of a tidal environment) and the velum was always absorbed two or three days before hatching; several individuals were watched while emerging, and in every case they crawled out and never swam. All that can be said from these observations is that under roughly similar laboratory conditions there was a distinct and important difference in the hatching stages of *L. obtusata* from South-western Ireland and from Church Reef.

Two separate problems are presented by the zonation of barnacles and algæ on the one hand, and by that of free-living animals such as gastropods on the other.

In the first case, spores of algæ and larvæ of barnacles are free in the sea, and are apparently away from any influence that could affect their subsequent zonation when settled between tide marks.

The assumption is made, then, that the larvæ and spores, given a suitable substratum, settle in a manner entirely at random in respect of tide levels. The further assumption is made that a barnacle or an alga, once settled, never moves again. Before settling finally, however, the Cypris-like larva of a barnacle can crawl with its antennæ; Darwin (1851, p. 15) considers this only a minor function, and it is certainly not the only method of locomotion as is creeping among newly settled Gastropod larvæ. That the settling of a barnacle larva must in some cases be practically instantaneous, and final, and not a matter of "deliberation" or "choice," is shown by those individuals of *Chthamalus stellatus* which are found above the predicted level of Extreme High Water Springs. These barnacles can only have settled in rough weather, when the seas were raising the splash zone. Firm settling must have taken place in an interval of time not longer than that between one wave and the next, or else the larvæ would have been washed off again. A further consideration arising out of the fact that larvæ can settle in rough weather is that during such weather the water is so powerfully stirred that larvæ outside the breaker zone must settle wherever and whenever they are thrown against their substratum, their powers of swimming being quite unable to cope with strong water currents. When away from violent water movements, however, barnacle larvæ may be very deliberate about settling, as described by Visscher (1928, 1928a). He observed the settling of *Balanus improvisus* and *Balanus amphitrite* and found that the cyprid larvæ spent some time exploring the substratum after first alighting on it, taking sometimes as long as an hour and crawling as far as 12 mm. before finally settling and metamorphosing.

Zonation in the algæ and barnacles, then, is the result of a hit-or-miss method. If a spore or larva settles within the environment which will suit it as an adult, it may survive. If it settles outside this range, it will sooner or later die without maturing.

In the case of the Gastropods, the adults have considerable crawling powers, and Gowanloch and Hayes (1926) have shown that under the influence of tropisms they may use these powers to remain in, or regain, their accustomed level on the shore, thus preserving their orderly zonation between tide marks.

When the larvæ are considered, however, some complications arise. Let us take the case of the Littorinæ. *L. saxatilis* and *L. neritoides* are both viviparous, and the young are born in the zone which they are to inhabit, and from birth they are perhaps influenced by the same tropisms as their parents; circumstantial evidence for this suggestion lies in the fact that all sizes of *L. saxatilis* and *L. neritoides* can be found together, the same being true of *L. obtusata*. The latter is oviparous, but at Plymouth the young emerge in the crawling stage (the eggs having been laid on seaweeds in the *L. obtusata* zone) and therefore come under the same category as those of *L. saxatilis* and *L. neritoides*.

L. littorea, however, lays eggs which are planktonic, and hatch out as planktonic larvæ. The distribution of these when settling is therefore in all probability as much a matter of chance as with the larvæ of barnacles or the spores of algæ. The settled *L. littorea*, however, do not remain fixed—they merely exchange swimming for crawling as a method of locomotion. There is, then, a possibility that even after settling the larvæ have some time to wander about in search of a suitable environment, guided perhaps by tropisms, before being killed by adverse circumstances, the inevitable fate of a barnacle larva settling in the wrong place.

To sum up, a barnacle larva or an algal spore, when it settles, is fixed for good, and its position is a matter of chance. If it is within the range of the rest of its species, it may survive. If not, it will die. An adult gastropod, though able to move, is nevertheless forced by tropisms to remain within its normal range. The young of viviparous species are born in the same zone as their parents, and perhaps come under the same tropistic influences from birth. Some gastropods have planktonic larvæ, and these settle on the hit-or-miss method. When they settle they do not fix themselves, and may, perhaps, even if they miss their right zone, gain it by crawling instead of dying in the wrong one.

It is hoped that this paper may help to analyse the nature and maintenance of intertidal zones. Still almost untouched, however, lies the far more fundamental problem of the origin and evolution of such zones, and it should be again emphasized that only the largest and commonest plants and animals are dealt with, and that any conclusions reached are applicable with certainty only to them.

I am grateful for the advice and encouragement of Dr. E. J. Allen while the field work was being done, and during the writing of the paper to Professor Parker and Professor Bigelow of Harvard University.

SUMMARY.

1. Church Reef, in Wembury Bay, near Plymouth, was selected for a survey of common intertidal plants and animals.

2. Four traverses were accurately levelled relative to Ordnance Datum, and their floras and faunas examined.

3. The relation between predicted tide levels and probable actual levels is discussed, and the importance of the " splash zone " is stressed.

4. As an outcome of 2 and 3, it appears that on Church Reef the most critical levels on the shore, for the species examined, are : (*a*) between Mean and Extreme Low Water Springs ; (*b*) between Mean Low Water Neaps and Springs ; (*c*) at Extreme (Lowest) High Water Neaps. The least critical level is Mean Low Water Neaps.

5. Two special problems are presented by the upper limits of *Littorina saxatilis* and *L. neritoides,* and by the frontiers between Ascophyllum and *Fucus spiralis* and between *F. spiralis* and Pelvetia, where the algæ do not overlap.

6. The work of previous authors is discussed for comparison with the present paper.

7. An important difference is suggested between the nature of the zonation of sedentary animals and plants on the one hand, and that of animals capable of locomotion on the other hand.

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The British Species of Trivia: *T. arctica* and *T. monacha.*

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With one Plate.

THE two forms of Trivia which are recorded from Plymouth (Marine Biological Association, 1931) have hitherto been regarded as one species (*Trivia europea*), but recent researches (Peile, 1925; Pelseneer, 1932) have shown them to be distinct. Peile calls the two species *Trivia monacha* (Da Costa), with the spotted shell, and *Trivia arctica* (Montagu), with the unspotted shell. Pelseneer calls them respectively *Cypræa* (*Trivia*) *europæa* L. and *Cypræa* (*Trivia*) *arctica* Montagu. A closer investigation at Plymouth fully bears out the conclusion of the above-mentioned workers that there are two species and the fact, brought forward for the first time in the present paper, that the larvæ are also distinct makes the determination doubly sure.

Winckworth (1932) in his latest list of British marine mollusca retains the two as one species, *Trivia monacha* (Da Costa), distinguishing them as *Trivia monacha monacha* (Da Costa) and *Trivia monacha arctica* (Montagu). In view of these recent researches they must be regarded however as two distinct species, and we here follow Peile in calling them *Trivia monacha* (Da Costa) and *Trivia arctica* (Montagu). The name *Trivia europæa,* unfortunately, must be allowed to lapse. The two forms were recognised by Linnaeus who called them *Cypræa europæa* and *C. anglica,* but it is agreed by most systematists that these terms were only given in a geographical sense and cannot be accepted as names.

In Plymouth a smaller, lighter coloured form from deeper water has been distinguished from a coastal form which is darker, more brightly coloured, and usually larger. This difference does not altogether differentiate the two species. The smaller, lighter form from deeper water is certainly *Trivia arctica,* but the coastal animals belong both to this species and to *Trivia monacha.* The two may be separated immediately by the shells, *Trivia monacha* having brown spots on the dorsal surface, always arranged in the same way, one anterior, one posterior, and two in the centre situated obliquely one on each side of the central line and merging into one, *Trivia arctica* having no spots, or, very rarely, the merest trace of brown; generally speaking the spots being totally absent. In *Trivia monacha* they are only absent in the young forms, being formed, as Pelseneer (1932) has shown, when the transverse ribs are acquired.

The colouring of the animal of *Trivia arctica* from between tide-marks and dredged in shallow water (the Sound) may be very like that of *Trivia monacha* with dark spots and stripes, and they are usually larger than those from deeper water. *Trivia monacha* is never found in the deeper water although it may be dredged occasionally from the Sound and just outside. In the young animals before the shell is thickened the body is often very light-coloured.

The usual habitat of *Trivia monacha*, often with *Trivia arctica*, at Plymouth is under rocks and rock ledges among compound ascidians (Botryllus, Botrylloides, and Diplosoma) between tide-marks and at extreme low tide. The specimens of *T. arctica* from deeper water are dredged with ascidians and bryozoa.

The natural food of both species appears to be compound ascidians for both species devour these animals in captivity, especially *Diplosoma listerianum* (Milne Edwards) var. *gelatinosum* (Milne Edwards) which is common growing on the glass sides of the Laboratory tanks and which if detached and placed in the plunger-jars will grow there comfortably. They will also eat Botryllus, Botrylloides, and Trididemnum. Pelseneer (1926) finds that on the Brittany coast they eat *Polyclinum luteum.* Vayssière (1923) found in the stomachs of Trivia (called by him *Trivia europæa* and probably a mixture of both species) from the Gulf of Marseilles the debris of algæ mixed with foraminifera and other microscopic animalcules, but from the way they devour the compound ascidians it seems that this is the more natural food, the smaller organisms probably being taken in accidentally. The compound ascidians from the shallow water are often much darker than those from the deeper water, which fact may account for the persistent difference in the colour of *Trivia arctica* from shallow and deep water.

An interesting point in the colouring of *Trivia arctica* is that the mantle shows brown spots, more or less distinct, in the position in which they are present on the shell of *Trivia monacha* although in *Trivia arctica* there are no spots on the shell.

The general account of *Trivia europæa* by Vayssière (*op. cit.*), giving *Trivia arctica* as a synonym, embraces both species, but those he specially dissected and figured are from fairly deep water (50–80 m.) in the Gulf of Marseilles and are certainly *Trivia arctica,* having the characteristic unspotted shell, distinctive radulæ and penis of that species. Both species thus occur in the Mediterranean.

The two species are evidently closely related, but *Trivia arctica* has a more northerly distribution than *Trivia monacha.* The breeding season fits in with this fact. At Plymouth *Trivia arctica* breeds through the autumn and winter, dwindling in late spring, whilst *Trivia monacha* begins to breed in spring when *Trivia arctica* leaves off, and continues through the summer, the larva very rarely being seen in autumn.

Trivia arctica is the only species in Scandinavia extending through Britain to the Mediterranean. *Trivia monacha* begins in Britain and is common in the Mediterranean and along the western coast of France. It is difficult to quote records with certainty as the two species have been mixed together and regarded as one for so long. Pelseneer (1926, 1932) found both species together on the Brittany coast.

The species may be distinguished in the animal by the radula, the shape of the penis and by the larvæ. Of these characters the shape of the penis is perhaps the most important. The female opening corresponds in size and cross fertilisation between the species is impossible. Pelseneer (1926) first discovered this character in the two species from the Brittany coast and emphasises it in his second paper (1932). He finds that *Trivia arctica* possesses a large and flat penis, somewhat leaf-like, and in *Trivia monacha* it is filiform and cylindrical.* These differences I can confirm from the Plymouth specimens.

Peile (*op. cit.*) described the difference in the radulæ, this being confirmed by Pelseneer (1932), and I have found the difference absolutely constant. In *Trivia arctica* there are small denticles on the admedian teeth, in *Trivia monacha* there are none. Peile also found the number of rows of teeth was different in the two species, *Trivia arctica* having less than *Trivia monacha.* He also mentions an observation made by Mr. Wintle that " in the unspotted form the riblets pass quite evenly across the shell, those of the spotted form are less uniform, frequently bifurcate and sometimes anastomose." On looking into these two last-mentioned characters I have found that the number of rows of teeth is extremely variable and that the riblets very often anastomose in *T. arctica* as well as in *T. monacha.* These characters are therefore not reliable.

The mantle of Trivia is provided with a number of papillæ. These are more numerous in the young of both species, but in the adult there are many more of them in *Trivia arctica.* The number varies, but sometimes this species appears to be bristling with them like a hedge-hog.

Pelseneer (1926) first discovered the eggs of *Trivia europæa* (undifferentiated) embedded in the compound ascidian *Polyclinum luteum* on the Brittany coast, and hatched some of them out. He also describes and figures the eggs and newly hatched larvæ. As these were found in the

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* By some slip these characters are reversed in Pelseneer's first paper. The filiform penis being attributed to *Trivia arctica* and the flat one to *Trivia monacha.* This is righted in the second paper.

PLATE 1.

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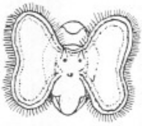

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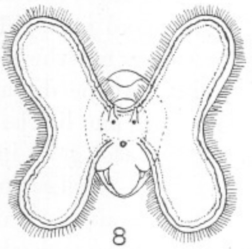

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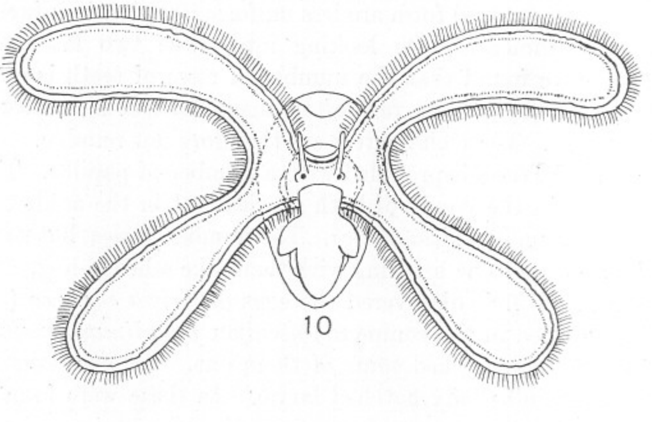

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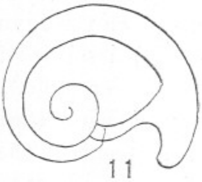

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summer they are almost certainly the eggs of *Trivia monacha*. In June, 1931, I succeeded in obtaining some eggs from *Trivia monacha* laid in compound ascidians (Botryllus and Diplosoma) in a plunger-jar, and hatched some of them out, obtaining similar larvæ and later stages from the plankton, the later stages being kept until they metamorphosed. In the same year I published a paper on the eggs and larvæ of *Trivia europœa* (Lebour, 1931a), regarding both forms as one. It is now certain, however, that the description applied to *Trivia monacha*, the only exceptions being probably the autumn and winter records of the larvæ which are almost certainly *Trivia arctica*, for it is now found that *Trivia monacha* breeds almost exclusively in late spring and summer.

The eggs of *Trivia arctica* have not been found, the adults kept in the Laboratory refusing to lay although given every facility and provided with various ascidians. It is to be expected, however, that the eggs will be very like those of *Trivia monacha*. In autumn and winter to late spring, *very* rarely in early summer, a larva was seen in the plankton which, although in the very young stages was exactly the shape of that belonging to *Trivia monacha*, differed constantly in the colouring of the animal, the intestines being yellowish with only a very little darkish pigment at the sides of the stomach (Plate 1, Figs. 1–9). In *Trivia monacha* the animal is consistently dark, from the stomach and intestine being almost black, the digestive gland also being very dark. In all stages this difference is conspicuous. At first the animal is much the same in form in both species, the accessory shell and the true shell being exactly similar (Plate 1, Figs. 1–7), but as the larva grows a distinct difference is seen in the velum. At first the lobes of the velum are oval (Plate 1, Fig. 6) and then slightly indented at the sides (Plate 1, Fig. 8). Soon, however, the indentation becomes larger in *Trivia arctica* (whilst it remains only slight until the last in *Trivia monacha*) and finally in the late larvæ the four lobes are long, much longer than the shell (Plate 1, Fig. 10). In both species the velum

EXPLANATION OF PLATE 1.

Trivia arctica from plankton.
(All drawn to the same scale.)

FIG. 1.—Very young larva, 0·40 mm. across.
FIGS. 2–4.—Slightly older larvæ, 0·48–0·60 mm. across.
FIG. 5.—Larva 0·64 mm. across.
FIG. 6.—The same, with velum expanded.
FIG. 7.—Older larva, 0·96 mm. across.
FIG. 8.—The same, with velum expanded.
FIG. 9.—Larva ready to metamorphose, 1·60 mm. across.
FIG. 10.—The same, with velum expanded.
FIG. 11.—Late larval shell, without animal.

is bordered by a fine line of dark brown. The shell is rather larger in *Trivia arctica* when metamorphosis takes place and may be 1·6 mm. across (Plate 1, Figs. 9–11), usually 1·25 mm. in *Trivia europæa*. When swimming the difference in the colouring of these late larvæ can be seen with the naked eye.

These late larvæ of *Trivia arctica* from the plankton were placed in a plunger-jar with Nitzschia and they soon metamorphosed just in the same way as is described for *Trivia monacha* (Lebour, *op. cit.*, 1931a, as *T. europæa*), the mantle growing round the accessory shell. Diplosoma was growing on the glass slides of the jar and the little metamorphosed animals began to eat this and very soon grew up. The colouring of these adolescent animals was in all cases yellowish with minute blackish purple spots, never orange or bright yellow as is often the case in *Trivia monacha*, and the spots not congregated in definite masses as in that species until much later. Later, when the stripes on the mantle begin to appear (as is described by Pelseneer (1932) for *Trivia monacha*), the spots are grouped dorsally more or less distinctly into three masses, one anterior, one posterior, and two in the centre merging into one, these masses corresponding to the positions of the spots in *Trivia monacha*. Minute dark spots are also scattered round the base of the siphon and irregularly on the body and also on the papillæ which are usually tipped with pale yellow. There are also sometimes pale yellow flecks on the siphon and tentacles. In three months the elongated shell was well formed although still thin. In four or five months the ridges were beginning to form preceded by the dark lines in the mantle. In five or six months the adult form was reached. The whole process of thickening takes place exactly as Pelseneer describes it in *Trivia monacha* (1932). At five months the distinctive denticles show on the admedians of the radula. There are now (September 1932) in the plunger-jar six fully-grown specimens of *Trivia arctica* reared from the late larvæ from the plankton. At six months these were fully grown and measured from 8 to 9 mm. in length. These vary in age from 6 to 8 months. All have a yellowish foot and mantle with fine dark spots as described above, pale yellowish spots on the tentacles, siphon, and papillæ, and many papillæ on the mantle. They have been reared on Diplosoma which they still continue to eat. Pelseneer (1932) gives the length of adult *Trivia monacha* as from 8·35 to 15·4 mm., these being the two extremes. Usually not less than 10 mm. Vayssière gives 6 to 12 mm. for the Marseilles specimens (almost certainly *Trivia arctica*). In Plymouth the deeper-water *Trivia arctica* measure usually from 8 to 10 mm. in length when adult, those from the coastal waters being larger, up to about 12 mm., *Trivia monacha* from the same locality being about 10 to 13 mm.

The larvæ of *Trivia monacha* were not so successfully reared although they metamorphosed in captivity. Those which grew beyond the round form had a bright orange mantle and the dark spots more apparent, but specimens of the same size from the Sound were sometimes lighter in colour although having the same arrangement of dark spots congregated in masses as is figured by Pelseneer (1932) and by myself (1931a). At a length of 3·5 mm. these are quite distinct and characteristic, and it is perfectly easy to distinguish the adolescent form before the thickening of the lip and the formation of the spots on the shell (in *Trivia monacha*).

Both species are common at Plymouth, sometimes at low tide they may be found together in equal numbers, sometimes only one species in one place. For instance, at Whitsand Bay in July, Mr. William Searle collected from the rocks at low tide 28 specimens of *Trivia monacha* but no *Trivia arctica*. In Wembury Bay, Rum Bay, and Drake's Island both species may be collected in fair numbers. In the Sound adult species of both may be dredged, but *Trivia monacha* is only very rarely dredged outside, whilst *Trivia arctica* is common in small numbers from the Mewstone and Eddystone grounds and even sometimes farther out. In the plankton the larvæ of *Trivia arctica* occur commonly in autumn, winter, and early spring, the early larva chiefly in autumn and winter, the late larva in spring until about the end of May, both inside and outside the Sound. From May all through the summer, dwindling in October and practically absent from November to April, the larvæ of *Trivia monacha* are common, chiefly from inside or just outside the Sound, only very occasionally farther out.

The two species are thus distinguishable both in the larval stages and in the adult by colour, *Trivia monacha* always having more pigment which extends to the shell. The adults may be separated by the following characters :—

Trivia monacha.	*Trivia arctica.*
More southerly distribution. Breeding season late spring and summer.	More northerly distribution. Breeding season autumn, winter, and early spring.
Shell spotted, usually larger than *T. arctica.*	Shell unspotted, usually smaller, but sometimes on the coast as large as *T. monacha.*
Mantle dark, foot orange or bright yellow, lighter in young forms.	Mantle light in deeper water, darker between tide-marks, foot light yellow or light orange.
Mantle with few papillæ.	Mantle with many papillæ.
Radula without denticles on the admedian teeth.	Radula with denticles on the admedian teeth.
Penis cylindrical and thin.	Penis leaf-like and broad.

Trivia monacha.	*Trivia arctica.*
Larva with very dark stomach and intestine.	Larva with light stomach and intestine.
Late larva with two-lobed velum only slightly indented at sides. Metamorphosing at about 1·25 mm.	Late larva with four-lobed velum, very long lobes. Metamorphosing at about 1·44 mm.

It is interesting to find again two closely related species of one genus having distinct larvæ corresponding to the distribution, as is the case with the two species of Nassarius, *N. reticulatus* and *N. incrassatus* (see Lebour, 1931b). In both cases the two species may live together between tidemarks but one may be found also in deeper water. In the case of the deeper-water species, the larva has very long lobes to the velum corresponding to its wider distribution and indicating one which can live longer in a planktonic state. Here we have the shore-living *Trivia monacha* and *Nassarius reticulatus* having the velum with two lobes only slightly indented and although they can live a long time in the plankton it is probable that *Trivia arctica* and *Nassarius incrassatus*, which are able to live in deeper water, with the long velar lobes are stronger and are adapted to being carried further.

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The Larval Stages of *Erato voluta* (Montagu).

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Naturalist at the Plymouth Laboratory.

With Plates 1–2.

Nothing is known of the life-history of *Erato voluta* (Montagu)=*Erato lævis* (Donovan) and in the following note the larvæ are described for the first time. Erato being very closely related to Trivia, it was to be expected that the larvæ would be somewhat similar, but, although there is here, as in Trivia, an Echinospira larva, the details of its life-history are quite different and the accessory shell when fully developed differs much from that of Trivia.

The eggs of *Erato voluta* have not yet been distinguished certainly although some gelatinous egg capsules laid in between the lobes of Botrylloides, but not embedded in it like Trivia, taken with Erato from outside waters, may belong to this mollusc.

Erato voluta, although not common, occurs fairly frequently singly or two or three at a time on gravel grounds from about 15 to 30 fathoms; occasionally at greater depths. It is not known on what it was feeding when taken with the dredge, but presumably its natural food, like Trivia, is compound ascidians, for it will eat largely of Diplosoma scraped from the tanks and has been kept alive for months in plunger-jars with this ascidian and also Botryllus and Botrylloides for food. It has however never deposited its eggs in captivity.

An Echinospira larva, rather like Trivia when young but differing from it in certain particulars and very different when older, is found fairly commonly in the plankton, usually singly or two or three at a time in spring and summer. It was the late larva of this form which was thought to be a Velutina and figured as "probably Velutina" in a paper on *Trivia europea* (Lebour, 1931, Plate IV, Fig. 2). The true Velutina larva I have now discovered and the present larva is proved to belong to Erato as it has been kept in a plunger-jar until it metamorphosed.

The youngest stage seen measures 0·64 mm. across the accessory (Echinospira) shell, the true shell inside measuring 0·32 mm. across (Plate 1, Fig. 1). At a first glance it looks like a very young Trivia, but seen more exactly it shows several differences. The accessory shell is

PLATE 1.


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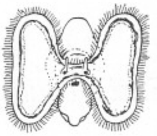
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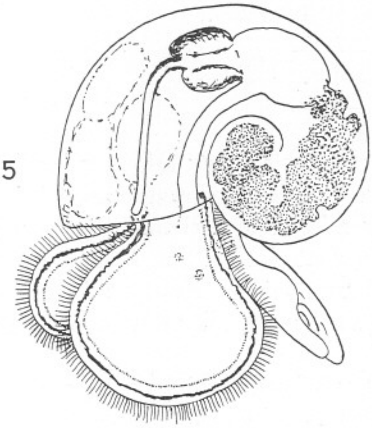
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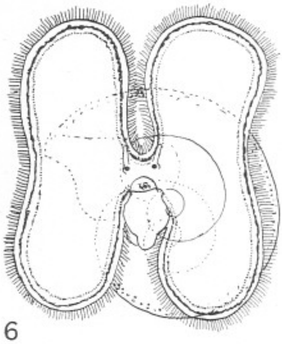
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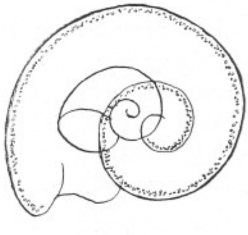
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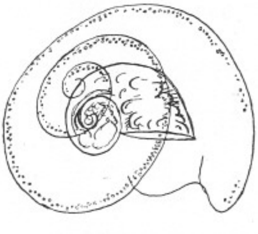
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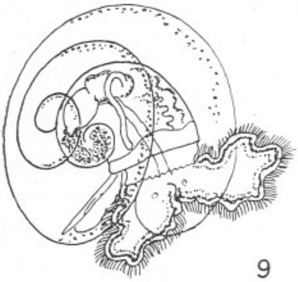
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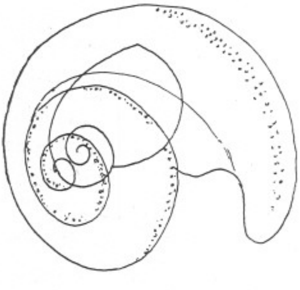
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keeled at the periphery and on each side of the keel is a border of small clear dots looking like beads, two to four in a row (Plate 1, Fig. 4). The accessory shell is helicoid and, unlike Trivia, the coils do not coincide with the true shell at any time, although in these very young stages this is difficult to see. There are lines of growth on the body whorl, the inner whorls being very clear and transparent. The true shell consisting at this stage of about one and a half whorls is also very clear and transparent and lies somewhat excentrically to the accessory shell, the aperture being round. At first the animal is almost colourless or very pale yellow, but when the accessory shell is 0·80 mm. across, the true shell being 0·40 mm. across, there is a little dark pigment on the stomach and the beginning of the intestine which persists in the later stages. The eyes, short tentacles, and otocysts are well developed and there is a broad foot, tending to be three-lobed, somewhat pointed at the end and bearing an operculum. The velum which has a narrow brown border consisting of two larger lobes, very slightly indented at the side as the animal grows, has the usual bordering of cilia leading to the mouth (Plate 1, Fig. 2). These early stages are found from April to November both in the inside and outside plankton, usually outside, and they are commonest from May to August, rare in early spring and autumn. The later stages have a very conspicuous helicoid accessory shell, still with marginal bead-like dots, but these gradually become fainter and even obliterated in some specimens. Sometimes in the older forms none are apparent. The true shell lies quite excentrically in the accessory shell with the same structure as in the early stages, the lobes of the velum, now very large, slightly indented at the sides. Sometimes, but not usually, there are a few dark spots on the velum, irregularly placed, as well as the brown border. When the accessory shell measures about 1·9 mm. across it has three and a half to four whorls, the last projecting at the aperture in a rounded process (Plate 1, Figs. 7–9).

EXPLANATION OF PLATE 1.

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

Erato voluta.

PLATE 1 (Fig. 5 Scale B, the rest Scale A).

FIG. 1.—Very young larva from plankton, 0·64 mm. across accessory shell.

FIG. 2.—Slightly older larva from plankton, 0·80 mm. across.

FIG. 3.—The same, side view with velum retracted.

FIG. 4.—The same, showing keel.

FIG. 5.—True shell of same (accessory shell omitted) showing alimentary canal.

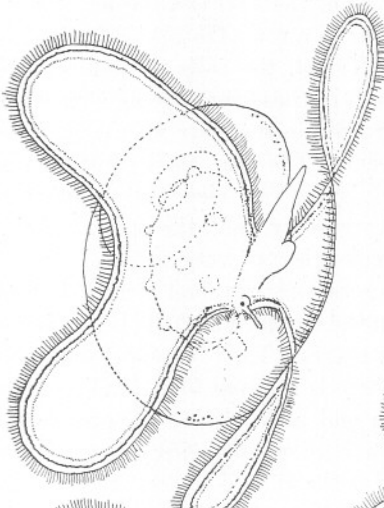
FIG. 6.—Larva from plankton, 1·90 mm. across accessory shell.

FIG. 7.—Slightly older larval shell, showing accessory shell and true shell without animal.

FIGS. 8–9.—Older larvæ from plankton.

FIG. 10.—Larval shell plankton, 2 mm. across, showing elongation of true shell.

PLATE 2.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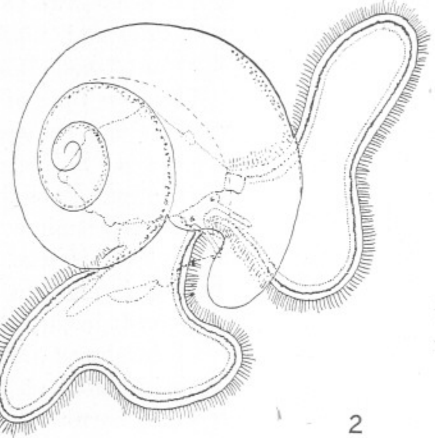
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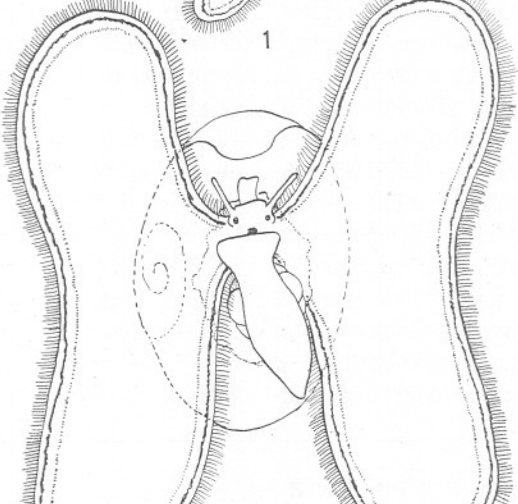
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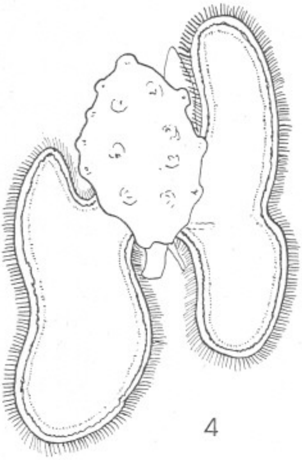
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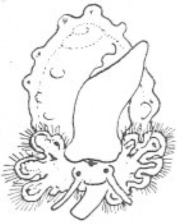
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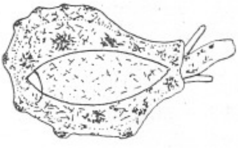
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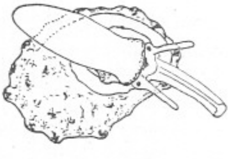
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The true shell with about two and a half whorls has a very large velum, the lobes reaching well beyond the accessory lobes, the foot three-lobed, the operculum conspicuous. It is now very nearly ready to metamorphose, and the mantle forms a thick border round the aperture of the true shell which soon begins to elongate, a partial metamorphosis taking place, the accessory shell being at its largest, about 2 mm. across and retained for some time longer. The mantle entirely surrounds the shell and is provided with conspicuous papillæ with brown and yellow pigment. No part of the true shell is left uncovered. The body whorl of the shell has elongated considerably and is not unlike a young Trivia. The siphon projects from the front end from under a fold in the mantle, the foot is still three-lobed, and is still provided with an operculum. The velum is still large, measuring about 2 mm. across (Plate 1, Fig. 10 ; Plate 2, Figs. 1–3).

This partially metamorphosed larva swims for some time longer whilst retaining the accessory shell (Plate 2, Figs. 1–3). A late larva from the outside plankton, placed in a plunger-jar with Nitzschia for food on July 8th, 1932, metamorphosed in this way on July 17th still retaining the velum, operculum and accessory shell. The last it retained until August 2nd, when it was swimming about without it ; the velum was still large but the operculum gone. A peculiar feature in the metamorphosis is that the accessory shell is shed entire and was picked up floating in the plunger-jar quite perfect. Thus Erato differs in this essential feature from Trivia in which the mantle encloses the accessory shell which is presumably eventually absorbed, and from Lamellaria which simply shrivels up, being so fragile and thin that it can no longer keep its shape. The larva after shedding the accessory shell measured 1·25 mm. in length, the shell being 1·04 mm. long (Plate 2, Fig. 4). The foot is elongated and has lost the lateral lobes which supported the operculum. The tentacles are fairly long, the siphon well developed, the eyes conspicuous, and the velum only slightly smaller, but still forming an effective swimming organ. Here again is a distinct difference from Trivia and Lamellaria in which the velum disappears at metamorphosis. The mantle has dark brown and yellow pigment especially on the numerous papillæ which

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EXPLANATION OF PLATE 2.

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

Erato voluta.

PLATE 2 (Scale A).

FIGS. 1–3.—Larvæ from plankton kept for some weeks in a plunger-jar showing metamorphosed animal still in the accessory shell, 2 mm. across.

FIG. 4.—Larva having lost the accessory shell.

FIG. 5.—The same with velum dwindling.

FIGS. 6–7.—The same completely metamorphosed, 1·25 mm. long.

stand out from it in a conspicuous manner. A few days later the velum is dwindling and although still able to swim the larva spends much time at the bottom of the jar (Plate 2, Fig. 5). The velum remained for three weeks more. On August 24th it had disappeared, but the animal had not grown. Even early in September it was still the same size, but had altered considerably (Plate 2, Figs. 6–7), the siphon being very long, the colour much darker having a network of brown pigment on the papillæ and mantle both outside and on the lines inside the shell, and there is a very large muscular proboscis capable of protrusion for a long way. There is now a separation of the sides of the mantle leaving the shell exposed dorsally as in the adult. The animal is now like the adult except for the thickening of the shell and the colouring which is at present mainly brown with very little yellow and no red has as yet appeared, the adult animal being spotted with red on the foot and siphon. A difference from Trivia is seen in the siphon which comes from below the dorsal mantle so that there is a fold between them, whereas in Trivia it is continuous with the dorsal mantle.

Small pieces of Diplosoma had been placed in the plunger-jar and although the young Erato was not seen to eat it must almost certainly have eaten this as it was well and healthy.

Although the adult *Erato voluta* is very like Trivia in the animal, the form of the shell distinguishes it at once, the spire being exposed and the shell smooth. The elucidation of its larval history fully justifies their separation into distinct genera. The life-history is peculiar and the larvæ behave in a totally different way from those of Trivia—indeed, from those of any known molluscan larvæ.

On August 11th two individuals were pairing in a plunger-jar. This was provided with a piece of a hard bryozoon on which grew some small masses of Botrylloides from deep water, but no eggs were laid.

LITERATURE.

Lebour, M. V. 1931. The Eggs and Larvæ of *Trivia europea*. Journ. Mar. Biol. Assoc., N.S., Vol. XVIII, No. 3, pp. 819–830.

The Life-Histories of *Cerithiopsis tubercularis* (Montagu), *C. barleei* Jeffreys and *Triphora perversa* (L.).

By

Marie V. Lebour, D.Sc.,
Naturalist at the Plymouth Laboratory.

With Plates 1–2.

The life-histories of the two species of Cerithiopsis are described here for the first time, that of *Triphora perversa* is partly known already. All three species are common in Plymouth and their larvæ are very common in the plankton in spring and summer. Pelseneer (1926) has described the eggs and newly-hatched larvæ of *Triphora perversa* from the Brittany coast and Fischer (1884) has noted that it has a very long free-swimming life, still being a veliger with up to 7 or 8 whorls. The eggs of *Cerithiopsis barleei* have now been found at Plymouth and the larvæ reared as far as a stage just before settling down, the late stages from the plankton being reared to the crawling stage in plunger-jar. The eggs of *Cerithiopsis tubercularis* have not yet been seen, but the larvæ are common in the plankton and the late larvæ have also been reared in a plunger-jar until the crawling stage.

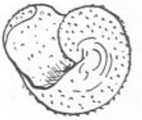
The larvæ of all the three are small and have the velum bilobed and colourless with rounded lobes, and they have one character in common which is the marked process from the outer lip which projects between the outer marginal lobes of the velum. This process is less marked in Triphora, but is peculiarly large in both of the Cerithiopsis species, especially *Cerithiopsis tubercularis*. The larval shells of both *Triphora perversa* and *Cerithiopsis barleei* are finely sculptured with beautiful patterns for several whorls so that they are easy to recognise, but the larval shell of *Cerithiopsis tubercularis* is smooth. All of these species retain the larval shell as the apex and do not lose it, as is the case with some turreted shells, thus making the larvæ easy to recognise.

TRIPHORA PERVERSA (L.).

(Plate 1, Figs. 1–7.)

Fairly common both in the Sound and outside ; occasionally in deeper water. Those from inshore are usually found in crevices of rock, on bryozoa

PLATE 1.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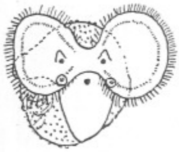
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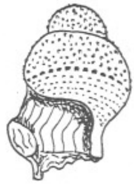
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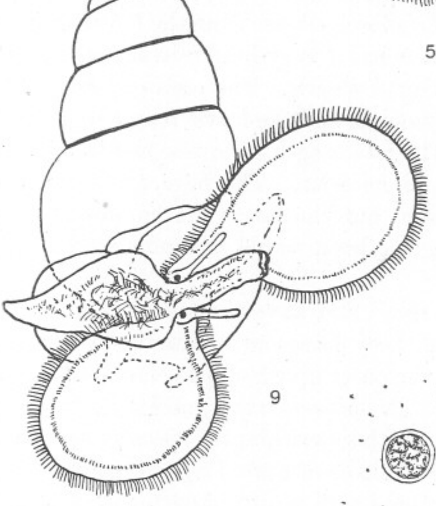
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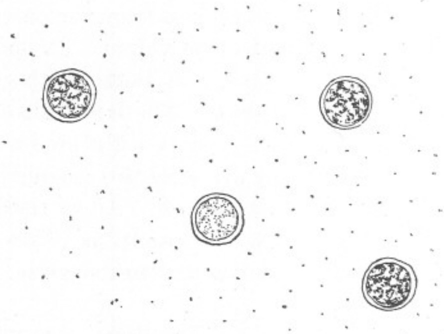
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or in sponges and are inconspicuous and easily passed over. The larvæ are common in spring and summer, especially summer, both inside and outside the Sound. Even as far out as Station E1, fourteen miles from Plymouth, they are abundant. All stages from the newly hatched larvæ to those with six or seven whorls are found in the plankton, but the eggs have not yet been obtained at Plymouth although adults have been kept for months in plunger-jars. They apparently feed on debris which has accumulated in the jars for no special food was given to them. Pelseneer (1926) found the eggs laid on old shells at Roscoff and describes these and the newly hatched larvæ and figures the latter. They are laid in gelatinous capsules and the larvæ hatching from them are tiny sinistral molluscs with one whorl. He does not mention any sculpture on the shell, but those from Plymouth, obviously only a day or two old, were sculptured with fine dots. *Triphora perversa* is truly sinistral in both animal and shell, and therefore easily recognisable in all stages.

The early larvæ obtained from the plankton (Plate 1, Figs. 1–3) measure 0·16 mm. across the shell which is covered with raised dots except at the base where there are spiral striæ, the outer lip being slightly produced and incurved. The colour of the shell is brown, and it is rather thick and not very transparent. The animal is pale yellowish white, the velum quite colourless. There is a short foot, the eyes, short tentacles and otocysts conspicuous. The velum which has two almost round lobes measures 0·18 mm. across and has the usual cilia bordering the groove to the mouth (Plate 1, Fig. 1). This young larva is very like that of *Cerithiopsis barleei*,

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EXPLANATION OF PLATE 1.

(Scale B is six times the scale of A, Scale C, twice the scale of A.)

(Figs. 1–4, 6, 8, 9 Scale B, Fig. 5 Scale C, Figs. 7, 10–11, 13 Scale A, Fig. 12 on a smaller scale.)

Figs. 1–7. *Triphora perversa.*

FIG. 1.—Early larva, shell 0·16 mm. across, from plankton.
FIGS. 2–3.—Shells of same.
FIG. 4.—Shell slightly older, 0·24 mm. long, from plankton.
FIG. 5.—Older larva from plankton, shell 0·64 mm. long.
FIG. 6.—Apex of shell of same.
FIG. 7.—Apex of adult shell.

Figs. 8–11. *Cerithiopsis tubercularis.*

FIG. 8.—Young shell from plankton, 0·24 mm. long.
FIG. 9.—Older larvæ from plankton, shell 0·48 mm. long.
FIG. 10.—Shell of older larva from plankton, ready to metamorphose, 0·64 mm. long.
FIG. 11.—Apex of adult shell.

Figs. 12–13. *Cerithiopsis barleei.*

FIG. 12.—Egg nests laid in *Ficulina ficus.*
FIG. 13.—Apex of adult shell.

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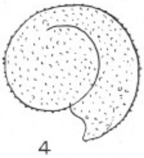

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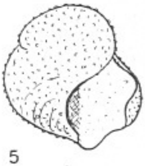

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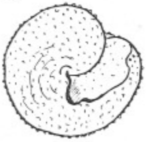

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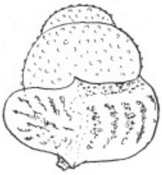

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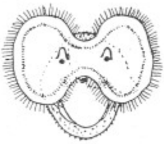

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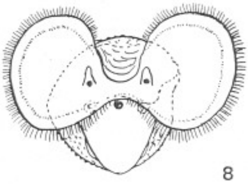

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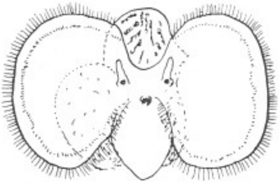

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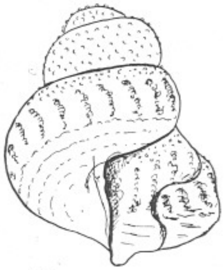

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except that it is sinistral in both animal and shell. The shape, colour and sculpture are very similar and show that the two species are obviously closely related. Indeed, they are much more like one another than are the larvæ of the two Cerithiopsis species, *Cerithiopsis barleei* and *Cerithiopsis tubercularis*.

With two whorls the shell measures 0·2 mm. long (Plate 1, Fig. 4), the upper whorl and a half dotted with raised spots, the second half of the last whorl striated with oblique wavy longitudinal striæ, the outer lip being produced in a conspicuous process. Later stages have the whorls with similar striæ, with dots at the sutures, the tentacles growing longer and the velum larger. When the shell measures 0·64 mm. long there are six to seven whorls, the first one and a half dotted, the next five striated with a slight keel at the periphery, altering at the seventh whorl into the adult tuberculated sculpture (Plate 1, Figs. 4–6). The last part of the seventh whorl and the eighth are beginning to be tuberculate on each side of the keel. At this stage the animal is ready to crawl and will soon lose the velum. Some of the larvæ with seven whorls lost the velum in the plunger-jars, others in the plankton still had the velum with seven and a half whorls. The late larvæ have an almost colourless animal with a colourless velum, the lobes nearly round and each nearly as long as the shell. One lobe is usually smaller than the other. The foot is pointed behind, slightly produced in front and the tentacles are long (Plate 1, Fig. 5). Up to now the larva is a planktonic feeder, but when it crawls it apparently eats detritus or algæ as the older stages live very happily in the plunger-jars feeding on the bottom or sides of the glass where there is a slight deposit or algal growth. This long larval life must last for some months, but no exact data are available. Early stages are found in late May and throughout the summer and early autumn, late stages in summer and autumn. Vayssière (1931) has recently figured from the Mediterranean a larva, gastropod shell which he names *Sinusigera dautzenbergi*. This is almost certainly a late larval stage of *Triphora perversa*.

EXPLANATION OF PLATE 2.

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

Cerithiopsis barleei.

(Figs. 1–15 Scale B, Fig. 16 Scale A.)

FIGS. 1–3.—Newly hatched larva from egg, shell 0·14 mm. across.
FIGS. 4–6.—Shells of slightly older larvæ reared in plunger-jar.
FIGS. 7–13.—Older larvæ reared in plunger-jar.
FIG. 14.—Older larva, shell 0·2 mm. long, reared in plunger-jar.
FIG. 15.—Shell 0·32 mm. long, reared in plunger-jar.
FIG. 16.—Late larva, ready to metamorphose, from plankton, shell 0·64 mm. long.

Cerithiopsis tubercularis (Montagu).

(Plate 1, Figs. 8–11.)

This mollusc is common both inside and outside the Sound, usually on or in sponges. Even as far out as Station E1 the larvæ are common as well as being very frequently found in the shallower waters. It is probable that its eggs are laid on or in the sponges, but it is difficult to keep these sponges alive in the plunger-jars, and this fact probably accounts for the eggs never having been found although the adults were kept for months in the plunger-jars and lived quite happily without the sponges, probably feeding on debris or small algæ.

It is already well known that the apex of this shell is smooth and consists of about four and a half whorls before the tubercles of the adult shell are formed. This smooth part, which is a transparent horn colour, sticks out prominently from the adult shell being more cylindrical and of more even width than the remaining whorls (Plate 1, Fig. 11). It is this part which constitutes the larval shell. The youngest larvæ seen consisted of two to two and a half whorls, the outer lip having an enormous plate-like outgrowth which bends over the aperture, the lobes of the velum protruding at each side when the animal is swimming (Plate 1, Fig. 8). This outgrowth is marked by concentric layers of growth with dots in between for rather more than a semicircle, the sculpture being obliterated as growth proceeds leaving the larval shell smooth except for this labial outgrowth. With two and a half whorls the length of the shell is 0·24 mm. with three and a half whorls it is about 0·28 mm. long, whilst when approaching the end of its larval life with four to four and a half whorls it measures up to 0·64 mm. in length (Plate 1, Figs. 9–10). Just before metamorphosis the last half-whorl has the typical tubercles of the adult. There is a dark line at the suture of all the larval whorls and on the columella and the aperture there is also dark brown, the base being carinated and the outer lip at the last larval stages having lost the large process on the outer lip although the velum is still present. The animal is pale yellowish white with a colourless velum. The foot which is mottled with grey on the sole and pointed posteriorly is flexible in front forming a long process which can be moved about under the head region. The tentacles are long and the eyes conspicuous, the velum with two rounded lobes, one usually larger than the other (Plate 1, Fig. 9). The larvæ at 0·64 mm. began to crawl in the plunger-jars and soon lost the velum. Here again there must be a long larval life although probably not so long as that of Triphora.

CERITHIOPSIS BARLEEI JEFFREYS.

(Plate 1, Figs. 12–13 ; Plate 2.)

This mollusc is common, living in *Ficulina ficus*. It is usually in those from outside the Sound where they are found, although it is sometimes seen in those from inside and the larvæ occur both outside and inside in late spring and summer, even as far as Station E1, where all three of these species described may occur in numbers together.

Early in May, 1932, a mass of Ficulina containing a hermit crab was obtained from outside, and crawling on it was an adult *Cerithiopsis barleei*. This was placed in a plunger-jar and a few days afterwards small round patches were noticed in the sponge. These were about 1·5 mm. across, placed at intervals of about 5 mm. or more apart, pinkish white or brownish purple. On closer investigation it was seen that each mass was a nest of eggs embedded in the sponge, the top hardly raised from the sponge surface (Plate 1, Fig. 12). Inside each nest were many eggs, the undeveloped eggs pinkish, the later stages brown ; some of them nearly ready to hatch with a fully formed horny shell and bilobed velum with rounded lobes. There were 13 of these egg-masses at first, each containing about 200 eggs. Later on more were laid, about 20 altogether, laid by the one mollusc. The eggs began to hatch out on May 23rd and continued to do so for some days. On inspection it was seen that the shell was exactly like the tip of the adult, and as it grew it was easy to see that it was the young of *Cerithiopsis barleei* which has a very characteristic apex (Plate 1, Fig. 13). The sculpture is very like that of *Triphora perversa*, the top two whorls dotted with raised spots, the third and fourth striated with undulating striæ, the fifth tuberculated with the sculpture of the adult shell. One would expect therefore to find the larval shell with four to four and a half whorls to be planktonic which proves to be the case, the latest larvæ being found in the plankton at this stage and almost immediately losing the velum and crawling. Those hatched from the egg lived until they had nearly four whorls, feeding on Nitzschia in the plunger-jars.

The newly hatched larva has a slightly produced horn-coloured shell about 0·14 mm. across and consisting of one and a quarter whorls (Plate 2. Figs. 1–3). The surface is covered with raised dots except at the base where it is striated. The outer lip is slightly drawn out. The colourless velum measures 0·16 mm. across, having round lobes with the usual ciliary structure, the rest of the animal is a pale yellowish, almost colourless, the eyes and otocysts conspicuous, the tentacles rudimentary, the foot rounded. The larva grows quickly and soon a large process grows from the outer lip similar to that in *Cerithiopsis tubercularis*. In this character the two species are much alike. A two-days' old larva has a shell measuring 0·16 mm. across with one and a half whorls. One slightly older has the outer lip drawn out and the process long with striated markings, the velum being about 0·24 mm. across (Plate 2, Figs. 4–10). The shell has now the beginning of a third whorl which has the undulating striæ on the upper part. The tentacles are now longer and the velum large (Plate 2, Figs. 10–14). The process from the outer lip grows very large, about as long as half the shell diameter, and the shell increases to three to three and a half whorls with a length of 0·32 mm. They were reared in a plunger-jar as far as this stage (Plate 2, Fig. 15) and were about four weeks old. Similar stages were found in the plankton and all the younger stages ; also older forms which were kept until they crawled. The latest larval stages with four and a half whorls measured 0·64 mm. long. The foot has an elongated and mobile front like that of *Cerithiopsis tubercularis*, the tentacles are long and the velum large. The larva now loses the velum and crawls.

In July and August several more adults were found laying eggs in Ficulina and continued to lay them in the plunger-jar.

One sees that in all these species the larval life is somewhat similar, although distinct differences are seen and all are easily distinguishable. The length of larval life varies, being longest in *Triphora perversa*. The shell may be sculptured or unsculptured, and this is apparently not a generic distinction as of the two species of Cerithiopsis, one is sculptured, the other smooth in its larval shell. A character common to all is the great production of the outer lip into a plate-like process—largest of all in *Cerithiopsis tubercularis*, large in *Cerithiopsis barleei*, less pronounced in *Triphora perversa*. They all agree in the form of the animal, pointed foot with flexible front, fairly long tentacles, and a simple colourless bilobed velum with rounded lobes.

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The Eggs and Larvæ of *Turritella communis* Lamarck and *Aporrhais pes-pelicani* (L.).

By

Marie V. Lebour, D.Sc.,
Naturalist at the Plymouth Laboratory.

With Plates 1–2.

Nothing is known of the eggs and larvæ of *Turritella communis* and, except for the young shells which have already metamorphosed, those of *Aporrhais pes-pelicani* are also unknown. The following descriptions are therefore new, both molluscs having been kept in plunger-jars until they laid their eggs.

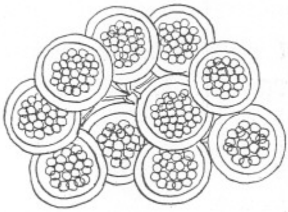
Turritella communis Lamarck.

(Plate 1.)

Turritella communis is dredged alive in abundance in certain localities round Plymouth on muddy and sandy gravel, 15–30 fathoms or, rarely in over 40 fathoms (see *Plymouth Marine Fauna*, 1931, Marine Biological Association). Many were kept alive in plunger-jars, but, although they lived for a long time, feeding on detritus accumulating on the glass sides, no eggs were obtained for several months. At last, in May, some eggs were deposited in one of the jars, and after that several lots were laid up to August. Occasionally detached egg capsules were found in the plankton. Ripe sperm and nearly ripe eggs were found in November and February in a few individuals. I am indebted to Miss M. Rothschild and Mr. Idris Jones for records of much ripe sperm and ripe eggs in April, and very few in September. Apparently April to July is the natural breeding season as after June most of the eggs were shed.

Three egg-masses were found in a plunger-jar, 12.5.32. Each of these was a large cluster of capsules measuring from 6 to 10 mm. across of a pinkish brown colour, sometimes rather yellowish when seen in a mass, the opaque eggs showing through the transparent capsules as small pink dots. The clusters have a peculiar lumpy appearance unlike the usual mollusc eggs. The capsules are held together by stalks, each capsule being roundish, oval and thick-walled, measuring about 0·64 mm. to 1·12 mm. across, those of the smaller diameter being the younger, the wall stretches as the eggs develop and becomes much thinner walled (Plate 1,

PLATE 1.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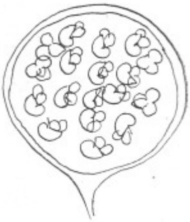
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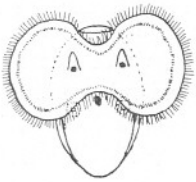
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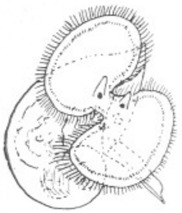
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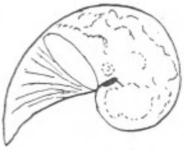
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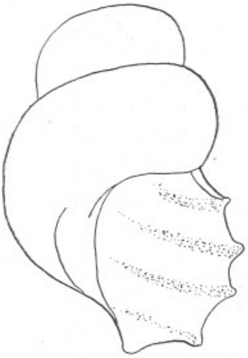
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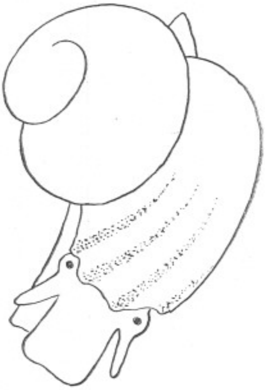
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Figs. 1–3). Each egg when newly laid measures about 0·10 mm. across and they lie at first closely packed together in the centre of the capsule with a space between them and the capsule wall, afterwards as they develop they are scattered about fairly far away from one another. There are from about 6 to 20 eggs or even more in each capsule and some hundreds of capsules in each egg-mass.

The eggs take about a week or ten days to hatch, but they are moving in the capsules with a well-formed velum a few days before this. Normally all the eggs develop and none of them devours its neighbour. The newly hatched larva is colourless, the shell consisting of one whorl, transparent and without sculpture, the shell measuring about 0·16 mm. across. The outer lip is hardly drawn out into a tooth, the eyes and otocysts are conspicuous, the tentacles short and blunt, the velum about 0·18 mm. across and perfectly colourless with the usual cilia bordering a groove to the mouth (Plate 1, Figs. 4–5). The larva has no special characteristics and resembles many other gastropod veligers, the simple outer lip being hardly in-curved indicating a short larval life as probably the velum will not be large. As the second whorl grows the blunt characteristic apex is in evidence. These larvæ only grew very little, the shell reaching a breadth of 0·18 mm., and then they died (Plate 1, Figs. 6–7). It seems evident that they stay only for a short time swimming in the plankton and the shape of the velum probably does not change. No later larvæ were found in the plankton except one from the Mewstone Grounds which had already lost the velum, 4.7.32, although it only measured 0·48 mm. in length (Plate 1, Figs. 8–9). The shell had two and a half whorls with a large apex—very large for the size of the shell—and sculptureless except for the last part of the second whorl which begins to have spiral ridges sculptured with fine dots. This is the beginning of the adult sculpture. The larva would thus begin to crawl with only about two to two and a quarter whorls, and would probably be very young, two or three weeks at the most. This crawling stage had an oblong proboscis, the tentacles

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EXPLANATION OF PLATE 1.

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

Turritella communis.

(Figs. 2, 3–10 Scale A, Figs. 4–9 Scale B, Fig. 1 on a smaller scale.)

FIG. 1.—Part of cluster of egg-capsules laid in plunger-jar.
FIG. 2.—Newly laid capsule, 0·64 mm. across.
FIG. 3.—Older capsule, 1·2 mm. across.
FIG. 4–5.—Newly hatched larva from egg, 0·16 mm. across.
FIG. 6–7.—Larva 4 days old, 0·18 mm. across.
FIG. 8–9.—Turritella from plankton, having lost the velum, shell 0·48 mm. long.
FIG. 10.—Apex of half-grown Turritella.

PLATE 2.


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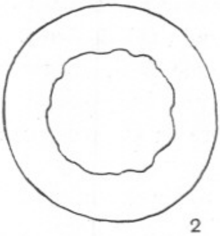
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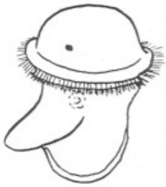
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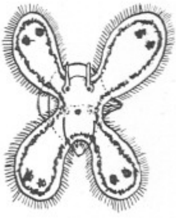
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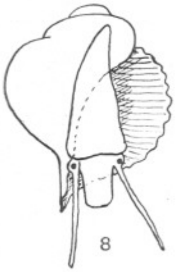
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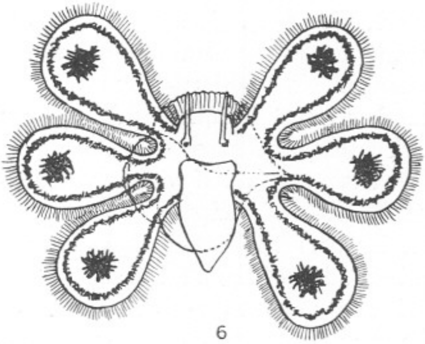
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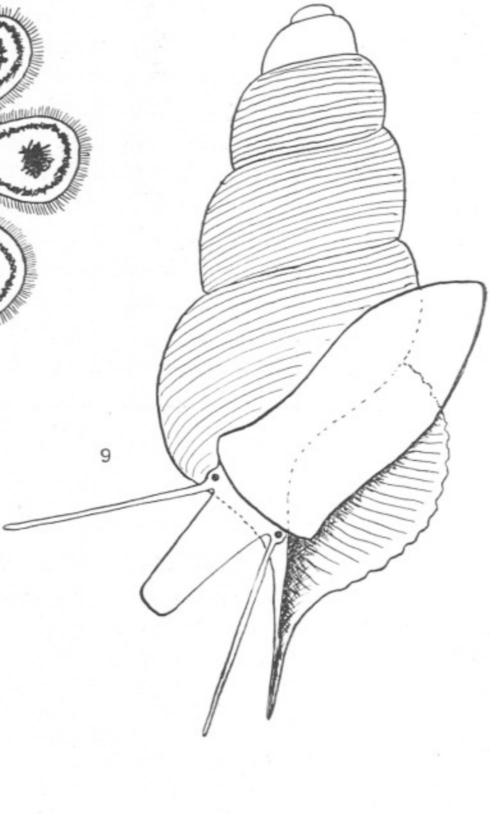
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rather shorter than the proboscis, a short foot with a very contractile anterior portion. The body is pale yellowish, the shell a very pale brownish horn-colour. This tiny shell exactly corresponds with the apex of the older Turritella when that is intact (Plate 1, Fig. 10). Usually this tip is broken off in the adult shell. Except for the shorter tentacles and proboscis the young animal is very like the adult.

APORRHAIS PES-PELICANI (L.).

(Plate 2.)

The young shells of *Aporrhais pes-pelicani* are known and have been described. Jeffreys (1867) gives an account of them, but apparently they have never been figured. The remainder of the life-history (eggs and free-swimming larvæ) is entirely unknown.

During the last few years whilst trying to unravel the problems of planktonic gastropod larvæ I have kept many molluscs that they might lay their eggs. Amongst these were several specimens of *Aporrhais pes-pelicani*. It is not uncommon in the Plymouth waters, occurring occasionally both inside and outside the Sound, usually on muddy gravel in 5 to 35 fathoms. Six specimens, two of which were without the outer expanded lip and therefore young, were collected from Jennycliff Bay in the Sound and placed in a plunger-jar, January and March, 1932. Two of them were covered with growing red algæ. No food was given them, but apparently they found enough detritus to serve them as nourishment for they all flourished. Aporrhais is a detritus feeder, picking up with its long proboscis any small food from the sides and bottom of the plunger-jar.

On March 31st amongst the debris at the bottom of the jar consisting of

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EXPLANATION OF PLATE 2.

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

Aporrhais pes-pelicani.

(Figs. 1, 5–9 Scale A, Figs. 2–4 Scale B, Fig. 10 on a smaller scale.)

FIGS. 1, 2.—Eggs 0·25 mm. across laid in plunger-jar.

FIGS. 3–4.—Larvæ hatched from same, 0·24 mm. across.

FIG. 5.—Young larva from plankton (probably belonging to Aporrhais, 0·56 mm. across shell).

FIG. 6.—Late larva from plankton, shell 1·25 mm. long.

FIG. 7.—Late larva nearly ready to metamorphose, from plankton, shell 1·5 mm. long.

FIG. 8.—The same, metamorphosed in plunger-jar.

FIG. 9.—The same, a month old, shell 5 mm. long.

FIG. 10.—The same, 6·5 mm. long.

fine sand grains and mud, several eggs were found and these continued to be laid for some weeks. The eggs were transferred to a fresh plunger-jar with Nitzschia, but although a few of them hatched out they did not live longer than a few days.

This is, I believe, the first time that the eggs of Aporrhais have been seen.

The eggs are unexpectedly small and laid singly, or two or three together, adhering to the sand and debris. The egg is spherical and measures about 0·24 mm. across (Plate 2, Figs. 1–2) with a thick tough coat, transparent and yellowish, with a good deal of fine dirt usually accumulated on its surface. The developing embryos inside measure about 0·12 mm. across when spherical, but develop rapidly and soon become elongated. It was not possible to be sure of the length of time taken between laying and hatching as the eggs were all at different stages of development when found, probably a fortnight or so. From the egg came a very backwardly developed free-swimming larva, about 0·17 mm. long, 0·16 mm. at its widest near the velum. The larva is perfectly transparent and colourless with a short bilobed ciliated velum by means of which it moves, a large rounded protuberance in front, eyes without tentacles, otoliths, mouth and a short foot not reaching to the apex of the body. The shell itself is not yet formed. One or two long hairs project from the apex. These very backward larvæ soon died, none of them eating anything.

There is a gap in the life-history during the early larval life from the time of the formation of the shell to the late larval stages. The shelled early larva must have a fairly large shell, transparent and unsculptured. The velum changes from a bilobed to a six-lobed structure and must gradually acquire a brown spot at the end of each lobe. One larva was found in the plankton (Plate 2, Fig. 5) with a four-lobed velum, each lobe with two spots at the end, which probably was an Aporrhais, but as it did not live it was not possible to be certain of its identity. The shell of this larva was similar to the early portion of the late larva known to be Aporrhais. It is only when the velum is six-lobed that the larva is certainly identified. This occurs sparingly in the plankton in spring (May), both inside and outside the Sound. It is a very conspicuous and beautiful veliger (Plate 2, Fig. 6) with a shell of about three whorls, measuring 1·12 mm. in length and about 1·0 mm. in breadth. The upper whorls are clear and transparent without any sculpture, but the last half of the body whorl near the outer lip is distinctly striated transversely. There is no central process in the outer lip at this stage and the posterior end is pointed forming a very narrow siphon. The shell is a very pale yellowish horn colour. The animal is striking, having a smallish foot with a little brown pigment, pointed behind and produced into two blunt lobes in front covering the mouth which is also coloured brown, eyes at the base of long thin tentacles and between them the front produced in a broad lobe which will become the proboscis. The most conspicuous feature, however, is the velum which is large with six lobes, the whole stretch reaching for about 2·8 mm. The lobes have a narrow brown border, and at the end of each is a large brownish black spot. The whole has the usual outer border of longish cilia and a shorter border below, the two forming a groove to the mouth. As usual the shell is below the outstretched velum when swimming. This veliger, not very unlike that of the late larvæ of *Nassarius incrassatus* when the velum is retracted, can be distinguished by the broader apex and pointed siphon ; when the velum is expanded the six lobes distinguish it at once.

Four of these late veligers were placed in a plunger-jar provided with Nitzschia. One of them, put in on May 11th, settled down almost at once and lost the velum, the shell in a day or two measuring 1·5 mm. long. The foot had elongated slightly and lost the pigment, the tentacles were much longer and an oblong proboscis formed. This little shell was crawling about quite happily on the sides of the plunger-jar eating the debris very thinly accumulated on them. On May 31st it had grown to a length of 5 mm. and was quite definitely a young Aporrhais. The proboscis was long and slightly tinged with red, the tentacles very long and waving. The shell has now five whorls, four of which form the somewhat cylindrical apex, the last being bulbous and coming out distinctly from the rest. The three last whorls are spirally striated and the pointed siphon is much longer. The siphon of the animal, which is very small, does not show at all. The shell now looks very like a Fusus or a Trophonopsis (Plate 1, Fig. 9). It grows very quickly, in two days having added another millimetre to its length. The little mollusc of 6 mm. crawls on the sides of the plunger-jar and can be seen to be eating the small masses of debris which cling to the glass in exactly the same way as the parents eat. At about 6·5 mm., at about a month since its metamorphosis, the shell begins to have dark brown bands, one below the suture between the penultimate whorl and the body whorl and one round the periphery of the body whorl, the last being slightly keeled and having a faint indication of longitudinal ribs. As it gets older the shell is more distinctly coloured, but now its growth is much slower and for a second month it hardly grows half a millimetre although feeding well and moving about happily in the plunger-jar. It is still alive (August, 1932).

The other late larvæ died, but one collected a few days later metamorphosed in another plunger-jar but did not reach such a large size before it died. After May no larvæ were seen in the plankton. The spring months, especially April and early May, evidently being the time for them.

A comparison with an Aporrhais, full-grown except for the outer lip, shows the top whorls to correspond exactly with the young one reared in the plunger-jar. Usually these top whorls are lost later and a shelly stopping covers the breakage.

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The Eggs and Larvæ of *Philbertia gracilis* (Montagu).

By

Marie V. Lebour, D.Sc.,
Naturalist at the Plymouth Laboratory.

With Plate 1.

THE genus Philbertia, belonging to the family Turridæ, is well known to have the larval shell beautifully sculptured and, as it is retained as the apex of the adult shell instead of being knocked off or concealed as is the case with many gastropods, it is easy to identify as belonging to this group, the veligers also reaching a large size and being conspicuous in the plankton.

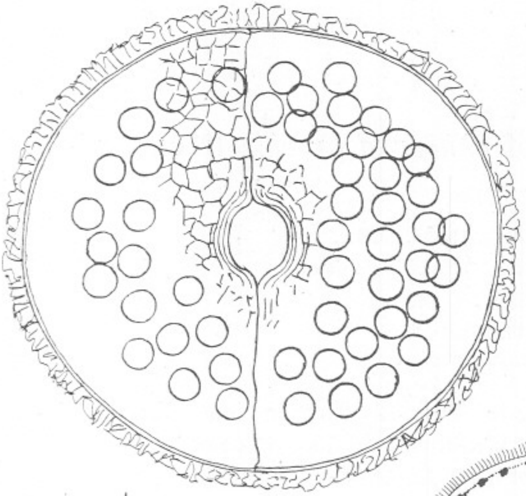
Philbertia (*Comarmondia*) *gracilis* is fairly common in the Plymouth waters from 20–35 fathoms, usually in muddy ground, sometimes living with Turritella. Crawshay found one living from 40–42 fathoms S.W. of the Eddystone (see *Plymouth Marine Fauna,* 1931, Marine Biological Association). Its larvæ are quite common in small numbers in the plankton from inside and outside the Sound, usually outside, in spring and summer, the greatest number in the summer. It is one of the largest of the planktonic larval molluscs, reaching a length of 1·76 mm. or even more, and must stay for a long time in the plankton.

Jeffreys (1867) describes the apical whorls of this species (as *Defrancia gracilis*), although his description does not agree exactly with the Plymouth specimen, as he says that the top whorls are reticulated whereas they are really dotted and striated.

In the summer of 1931 two adult shells were placed in a plunger-jar where they lived quite comfortably, eating the deposits on the sides and bottom. In March of the following year seven capsules were laid on the side of the glass. Later, in April, another specimen was placed in the same jar which also laid several capsules of eggs. The eggs have not been seen before, and they and the larvæ are described here for the first time.

The capsules are very characteristic (Plate 1, Figs. 1–2), thick walled but fairly transparent, measuring 3·4 mm. across, the height about one-fifth of the diameter. The lower surface, attached to the glass, is flat, the upper raised portion reticulated with an irregular mesh raised into spiny processes. At the top is an oval depression covered by a much thinner skin through which the larvæ emerge. Each capsule contains about

PLATE 1.



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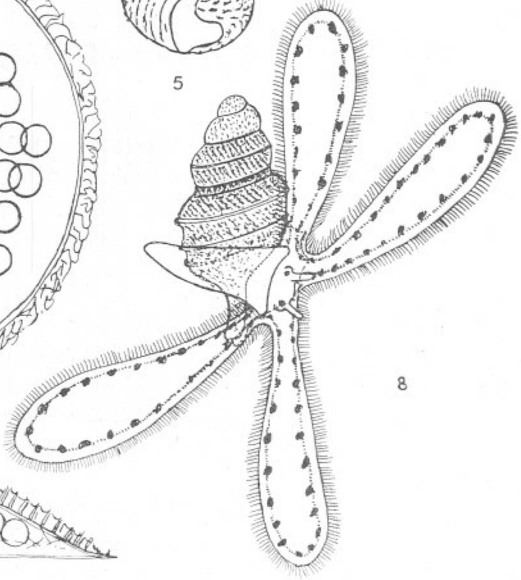

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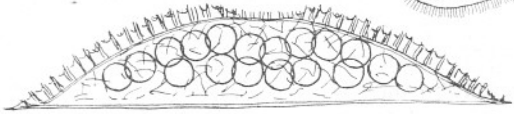

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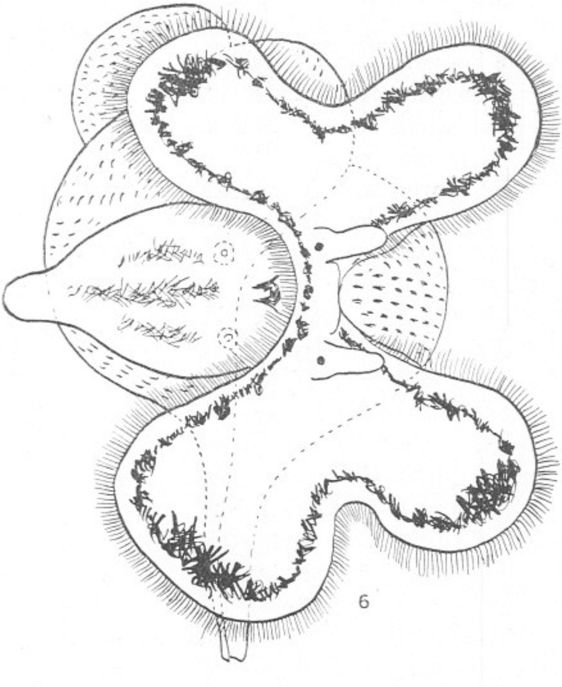

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50 eggs, each egg measuring about 0·16 mm. across. The eggs take a long time to develop and many are devoured by the others, about six to twelve larvæ remaining to grow into veligers. The earliest eggs (17.3.32) did not develop into veligers for several weeks (Plate 1, Fig. 3), and when they were ready to hatch (29.4.32) they did not live. An unusual feature of these veligers is that the velum is provided with conspicuous brown pigment some time before the larva emerges from the capsule. The veligers are moving about for many days inside. This was the case in all those in the plunger-jars. No egg capsules were seen under natural conditions. The velum is slightly bilobed and attain a large size before hatching.

The shell of the newly hatched larva from the egg measures about 0·24 mm. across with a brown horn-coloured shell, sculptured with irregular dots and flecks (Plate 1, Figs. 4–5). The mouth is drawn out slightly to form the beginning of a canal and the outer lip drawn out and inflected to form a supporting central tooth with a hollow each side for support of the velum. The velum extends for some way beyond the shell, measuring about 0·60 mm. across, each lobe being indented in the centre so that there is an indication of four lobes, and there is a large amount of brown pigment forming a border and masses of dark brown at the corners. The cilia surround the velum in the usual manner, the upper and lower rows on ridges forming a groove to the mouth. In front of the eyes there is a broad lobe, the tentacles are short and otocysts conspicuous. The short foot is rounded and slightly drawn out behind and the operculum large. The mouth shows in front of the foot. Young similar to this can be found in the plankton, usually in early summer and late spring, and stages up to the late veligers ready to metamorphose in summer and early autumn.

The canal grows quickly and shells with only two to two and a half whorls have a very long one (Plate 1, Figs. 6–7). At this stage the shell

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EXPLANATION OF PLATE 1.

Philbertia (Comarmondia) gracilis.

(Scale B is six times the scale of A. Figs. 1–4, 7–9 Scale A, Figs. 5, 6 Scale B.)

FIG. 1.—Egg capsule seen from above, laid on glass of plunger-jar, 3·4 mm. across.

FIG. 2.—The same, side view.

FIG. 3.—Larva from inside the capsule, nearly ready to hatch.

FIG. 4.—Newly hatched larva.

FIG. 5.—Shell of newly hatched larva from plankton.

FIG. 6.—Young larva, rather older, from plankton, shell 0·80 mm. long.

FIG. 7.—Shell of same.

FIG. 8.—Larva nearly ready to metamorphose from plankton.

FIG. 9.—Larva metamorphosed in plunger-jar, 1·76 mm. long.

measures about 0·80 mm. long, the velum having a brownish tinge, the sides still more indented and the brown border more conspicuous but not yet broken up into definite spots. The tentacles are longer and the foot more drawn out with grey pigment on the sole. The shell is still flecked, but with a definite pattern on the second whorl. Later larvæ show a gradual lengthening of the velar lobes and large orange and brown spots are scattered irregularly along the border, the velum itself being brown, the rest of the animal yellowish. The third and fourth whorls of the shell are keeled and sculptured with conspicuous oblique striations (Plate 1, Fig. 8). The canal is now not so long compared with the shell and contains the siphon which in the latest stages is dotted with bright pink as it is in the adult. When the shell measures about 1·76 mm. in length and the velar lobes are very long, projecting well beyond the shell, the veliger is at its largest and will soon metamorphose. The sculpture of the shell is very characteristic, the apex dotted and flecked for about one and a half whorls, the next whorl keeled with oblique irregular striæ formed of dots above and below the keel, the last whorl with three keels with oblique dots and striæ. Below the suture is a row of regular dots and the two last whorls. The velar lobes are very long and narrow, bordered with regular dark brown and orange spots at intervals ; the foot is somewhat pointed behind and drawn out anteriorly at the sides covering the mouth ; the tentacles are rather short. The animal can now either swim or crawl, and very soon loses the velum. Late larvæ were kept in plunger-jars until the velum disappeared (Plate 1, Fig. 9).

This late larva is a beautiful little object and quite easy to see with the naked eye. When swimming the shell is below, the velum above with the long lobes outstretched or sometimes curving over the shell. It is one of the larvæ most often seen in the summer plankton at Plymouth and must stay for a long time as a veliger.

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The Larval Stages of *Notomastus latericeus* Sars.

By

Douglas P. Wilson, M.Sc.,
Assistant Naturalist at the Plymouth Laboratory.

With one Plate.

CONTENTS.

INTRODUCTION.

Of no species of Notomastus has the development yet been described, so that a brief account of the general appearance of the larvæ of a member of this genus is not without interest and should be of value to plankton workers. For the closely allied genus Capitella we are indebted to Eisig (**2**) for an exhaustive treatise on the embryology of *C. capitata*. It seems likely that in its main histological details the development of Notomastus will follow closely that of Capitella ; indeed the few external differences that are here shown to exist are of quite minor importance.

METHOD.

Notomastus latericeus is a common inhabitant of the soft mud banks of the Salcombe estuary, especially in the upper region near the Salstone. There the adults were collected, sometimes by myself and sometimes for me by Mr. William Searle. The worms were usually found coiled in a spiral burrow and were placed with as little disturbance as possible in jars of mud for conveyance to Plymouth. During the journey they invariably broke themselves up into many pieces, which however remained alive for a few hours. They were dealt with at once on arrival at the Laboratory, mature-looking pieces being washed free from mud and slit with needles in small dishes of filtered outside sea-water. Eggs were transferred to finger-bowls, fertilised, and washed free from sperm.

Larvæ which swam up to the surface on the following day were pipetted off into finger-bowls or plunger-jars. All outside sea-water used was passed through a Berkefeld filter and Nitzschia (kindly supplied by Dr. Allen) was added for food. Drawings to scale were made of the living larvæ with the aid of a squared net micrometer and squared paper. On account of their extreme activity it was necessary to trap the larvæ lightly beneath a supported cover-glass. Specimens fixed in Bouin at 60° C. were mounted and used to check the drawings.

The above method of making the fertilisation is in this species probably more artificial than usual, as copulation is the general rule for Capitellids, and is said to occur in Notomastus. Capitella in addition broods its eggs until the larvæ swim away. According to Eisig (**1**, p. 286) no other genus of the family does this.

Successful fertilisations were made in April and June, 1928, and in May, 1932. In each case the larvæ were reared through the metamorphosis and for about twelve days afterwards. The times given in this paper are for the May rearing in 1932, when the Laboratory air temperatures for the first eleven days of the development (from fertilisation to metamorphosis) averaged 58·6° F. and for the succeeding eleven days 61·5° F. The temperature of the water in the plunger-jar would be approximately the same.

THE DEVELOPMENT.

The newly shed unfertilised egg is approximately 150μ in diameter and is closely invested in a relatively thick (3–4μ) membrane. There is a large and fairly conspicuous germinal vesicle, and large numbers of oily-looking yolk globules. The general colour is greyish by both transmitted and reflected light.

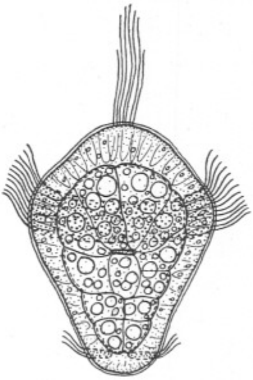
About fifteen hours after fertilisation the larvæ begin to swim by means of the prototroch and before the appearance of the telotroch and apical tuft. The cilia can be seen to pass through the egg membrane, which separated from the egg surface (possibly as a fertilisation membrane) before the first cleavage. This membrane from now on forms a cuticle round the larva. According to Eisig (**2**, pp. 44 and 98) it does not do this in Capitella but is thrown off about the third day, being replaced by a cuticle formed underneath. His evidence, however, does not seem very satisfactory and as I have not seen it thrown off in Notomastus and as appearances are all to the contrary, I believe it to persist as stated.

Twenty-four hours later the trochosphere stage, shown in Plate 1, Fig. 1, is reached. The larva is widest in the region of the prototroch, which forms a broad band of rapidly beating cilia. It is not quite a complete ring as there is a very slight dorsal gap, which however soon closes up. The telotroch is also a band of cilia, shorter than those of the prototroch, and it likewise has a gap, only ventrally. An apical tuft of about fifteen long and fairly strong cilia springs from the anterior end, directed forwards in the line of movement. The motion forwards is relatively very rapid. The endoderm forms a large central mass of big cells, the outlines of which are clearly visible. These cells are crowded with large oily yolk globules. The blastocœl is almost completely occluded. The ectoderm is thick, practically colourless and with few oil globules. Its cell boundaries are faintly visible. The stomodæal invagination is visible as a transverse slit just posterior to the prototroch in the mid-ventral line.

A few hours later additional cilia are acquired: a broad neurotroch which passes through the ventral gap in the telotroch in its course from mouth to anus; a narrow metatroch of short posteriorly directed cilia immediately behind the prototroch, a complete ring except where it is interrupted by the mouth; and three patches of short beating cilia close to the apical tuft. Of these three patches one is median and forms a semicircle tending to embrace the base of the long apical tuft dorsally; the other two are short arcs situated a little more posteriorly, one on either side. A pair of eyespots composed of a few reddish brown globules appears. Each eyespot is situated laterally just anterior to the prototroch. The larva becomes contractile, and the apical plate can be indented. It elongates and widens posteriorly, narrowing in the region of the prototroch. In this way is reached the four days' old stage shown in Plate 1, Fig. 2. The trunk is now segmented, the first segment—peristomium—being bristleless, the following three just beginning to grow a bristle from each noto- and neuropodium, the notopodial being the more advanced. The anterior extremities of these segments are indicated approximately by irregular bands of colourless but refringent ectodermal globules. A similar band is present anterior to the prototroch, while similar globules are scattered on the prostomium and the pygidium. The central greenish yellow yolk mass of numerous large globules is conspicuous. Its cell boundaries are less distinct than before. The cuticular membrane (egg or fertilisation membrane) is thinner than previously as though it had been stretched by increase in size of the contained larva. By the time the stage shown in Plate 1, Fig. 3, is reached it is only about 1μ thick. No attempt has been made to show it in Fig. 2 and subsequent drawings.

From now on the most striking feature of the larvæ is their extreme contractility. The drawings—which are little better than caricatures of extremely beautiful creatures—show as closely as could be judged the normally extended or resting condition. At extreme extension larvæ are considerably longer than this, at contraction much shorter. The stage of Fig. 3 can contract into a ball. When lightly trapped beneath a coverglass contractile activity is exhibited with great vigour.

PLATE 1.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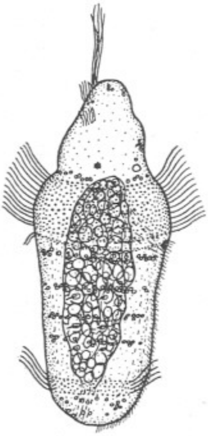
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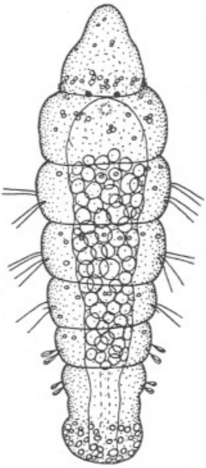
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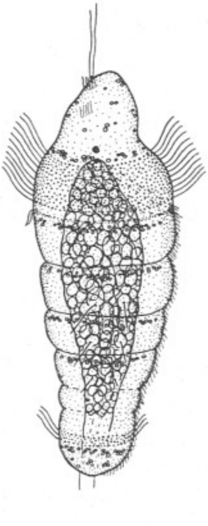
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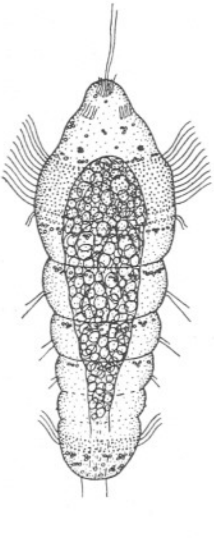
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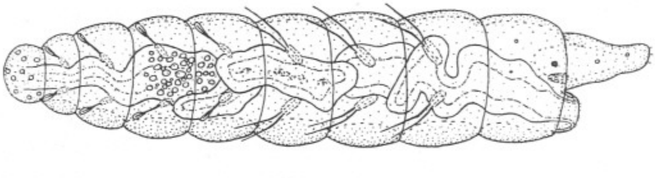
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The larva continues to elongate and the segmentation becomes more distinct (Plate 1, Figs. 3 and 4). The bristles, one dorsal and one ventral in each parapodium, are much longer. The fourth chætigerous segment is marked out and is obtaining noto- and neuropodial hooks, the former being more advanced than the latter. At this stage, six days from fertilisation, the long apical cilia are fewer in number and are probably falling off. Figs. 3 and 4 show two cilia still remaining although many larvæ otherwise similar have quite lost them. There is individual variation as to the time at which they are lost. There are two or three very fine sensory cilia near the anus; these only last a few days. The majority of the larvæ swim actively just clear of the bottom, unless stirred up away from it, and a day or so later may even rest thereon. This is in contrast to the earliest stages which crowded up to the surface. They now crawl well under a cover-glass.

Four or five days later when the larvæ are about ten days old the external cilia are lost, including the neurotroch which is the last to disappear. The disappearance of the prototroch is gradual and apparently takes place in stages, as larvæ with very narrow prototrochs are seen. Such larvæ still retain the metatroch. Whether any part of the prototroch is thrown off as Eisig (**2**, p. 81) described for Capitella, or whether it is all absorbed internally, is uncertain as no such throwing off has been seen and the matter has not been investigated in histological detail. The loss of the broad prototroch results in the prostomium directly joining on to the peristomium as a comparison of Figs. 4 and 5 will make clear.

At the time the prototroch is lost the larva has about five chætigerous segments, the first three with two bristles in each noto- and neuropodial bundle, the last two with a single dorsal and ventral-hooded hook on either

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EXPLANATION OF PLATE I.

Larvæ and juveniles of *Notomastus latericeus* Sars. Drawings 1–6 from life, ×156. Drawings 7 and 8 by camera lucida, ×1380. All measurements given below exclude apical cilia. Ages are for May rearing, 1932.

In these drawings the cilia and their distribution are of necessity illustrated very diagrammatically, and the same remark applies to the central yolk mass.

FIG. 1.—Ventral view about 40 hours after fertilisation. Actual length approx. 210μ (see page 512).

FIG. 2.—View of right side, four days old. Actual length approx. 285μ (see page 513).

FIG. 3.—View of right side, six days old. Actual length approx. 335 μ (see page 515).

FIG. 4.—Dorsal view of same stage as Fig. 3.

FIG. 5.—Dorsal view of a young worm eleven days old and recently metamorphosed. Actual length approx. 380μ (see page 516).

FIG. 6.—Lateral view of a young worm twenty-three days old. Actual length approx. 535μ (see page 516).

FIG. 7.—Outline of a bristle from a young worm.

FIG. 8.—Outline of a hook from a young worm.

side. There is, however, considerable variation as to the age and stage at which the swimming girdles are lost and a twelve-day old larva with six chætigerous segments possessed a set of cilia complete even to the apical tuft. On the other hand, in the April rearing of 1928, several larvæ seven days old and with only four chætigerous segments had lost all their cilia except the neurotroch which disappeared a little later.

A recently metamorphosed worm eleven days old is shown in Fig. 5. On either side at the junction of the prostomium with the peristomium can be seen one of the pair of nuchal organs. These had been seen while the prototroch was still present, they were just anterior to it. The eyes are deep seated and as the worm expands and contracts they move backwards and forwards relative to the anterior boundary of the peristomium. The refringent ectodermal globules form less definite bands on the segments than formerly. The pygidium is crowded with them. Yolk appears to be present in less quantity than before and is situated mainly dorsally. Cell outlines of the gut cannot be made out. The introvert is forming anteriorly, but the worm does not yet seem to be feeding. Worms at this stage crawl actively on the bottom of the plunger-jar.

Fig. 6 shows in lateral view a young worm from the bottom of a plunger-jar twelve days later, twenty-three days after fertilisation. Seven chætigerous segments are present, the first three with two winged bristles in each bundle, the last four with a single-hooded hook in each noto- and neuropodium. Outlines of a bristle and a hook are shown in Figs. 7 and 8. The pygidium has become smaller. Most of the yolk is used up, a little remaining in the gut walls rather posteriorly. Anterior to this the gut is longer than the worm at normal extension and is thrown into loops. The introvert is protrusible and has been for a few days; in the drawing it is shown partially protruded. Since it could be everted the worm has been feeding, for the gut has contained brown diatomaceous material for some days past. The creature is beautifully transparent and colourless, the septa and the muscles moving the chæta-sacs can be seen, and large corpuscles floating in the cœlomic fluid are very noticeable. The definite bands of refringent ectodermal globules have disappeared. A few short sensory cilia have appeared on the tip of the prostomium. These young worms crawl very actively under a cover-glass, and also at times on the bottom of finger-bowls, but in the latter they often remain in one place for a considerable period.

I have not been able to rear the young worms much further than the stage just described. Probably they require mud rich in a variety of small living creatures suitable for food. It is difficult however to keep such mud in a satisfactory condition in a plunger-jar or a finger-bowl, and attempts to rear these larvæ in mud have so far failed. No doubt they could be reared easily if the right conditions were found and maintained.

COMPARATIVE.

It is in the apparent lack of highly specialised larval organs adapting it to a pelagic existence that the Notomastus larva is of interest in comparison with some other Polychætes. The absence of long provisional bristles, or a spacious blastocœl or a prototroch enlarged in diameter, such as some others possess (e.g. Sabellaria, Polydora, Owenia, Polygordius, etc.), may perhaps be correlated with what seems to be a relatively high swimming speed and an unprolonged pelagic life. But the comparison must not be pressed too far, for swimming speeds have not been measured, nor do we yet know enough about the larvæ of all groups of Polychætes to enable such generalisations to be made.

A few points in comparison with Capitella as described by Eisig (**2**) are of interest. In Notomastus there are about five chætigerous segments marked out at the time when the cilia are lost, but in Capitella there are thirteen. The age at that time is about the same, but as actual temperatures cannot be compared little meaning can be attached to this. If one can judge from some of Eisig's figures the prototroch of Capitella is not as broad a band as that of Notomastus, nor does it appear to be followed by a metatroch. Bearing these considerations in mind one can state definitely that the larva figured by McIntosh (**3**, Plate XCIII, Fig. 10), and thought by him (p. 275) to be possibly that of *Notomastus latericeus*, is not so. It has too many parapodia, too narrow a prototroch and is the wrong colour.

SUMMARY.

1. Artificial fertilisations of *Notomastus latericeus* Sars were made and the larvæ reared.

2. The two-day old trochosphere is provided with a large central mass of yolk. It has a broad prototroch, a telotroch, a neurotroch and an apical tuft. It swims rapidly.

3. Development consists in the appearance of trunk segments. The most anterior of these is the achætous peristomium. Those following acquire neuro- and notopodial chætæ.

4. At an age of about ten days the cilia are gradually lost. The larva then has about five chætigerous segments, the first three bearing bristles, the last two hooded hooks.

5. The young worms lived for some twelve days after metamorphosis and by that time had seven chætigerous segments. Only a little of the yolk still remained. The worms possessed a protrusible introvert and were feeding on diatoms.

6. The larva apart from its strong prototroch and rapidity of swimming does not exhibit any special structural adaptations to pelagic life, such as are found in some other Polychæte larvæ. In comparison with Capitella it has fewer segments when it metamorphoses.

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The Nauplii of *Notodelphys agilis* Thorell and *Doropygus porcicauda* Brady.

By

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Lecturer in Vertebrate Embryology in the Department of Zoology of the University of Edinburgh.

With 1 Figure in the Text.

INTRODUCTION.

THE Notodelphoidea are a heterogeneous collection of copepods which are found parasitic within urochordates and there is considerable doubt as to the exact systematic position which should be occupied by this group. It comprises—in the sense in which it is used by Sars (1921)—six families of excessively doubtful affinities in that there are grouped together Copepods (1) which brood their eggs (Notodelphys, Doropygus, etc.), (2) others which are possessed of elongate egg-strings (Entericola), (3) and others which deposit their eggs singly (Mycophilus). Now it appears to the present writer that such great variation in habit must argue an equally great variation in the structure of the genital organs, for the " cement gland " and " hardening gland " (see Gray, 1928) may be presumed to be absent if egg-strings are not formed. It is doubtful, therefore, whether any useful discussion on the classification of these forms can take place without a parallel and detailed investigation of the internal anatomy. There is, however, another line of approach—the study of larval forms. It is equally as a preliminary skirmish along this line of attack, and as a contribution to our knowledge of larval forms, that the present brief note is presented.

MATERIAL.

Doropygus porcicauda occurs with moderate frequency within the branchial basket of *Corella parallelograma* at Millport. The eggs contained within the brood pouch are an exceedingly dark olive-green, a colour which is retained by the nauplius. All the eggs in any pouch appear to be at the same stage of development and hatch into a first nauplius before birth. These nauplii are then forced out by an arching of the back of the parasite, and appear incapable of movement for about ten seconds, after which they swim with the usual jerky motion. Only a single specimen gave birth to nauplii while under observation.

Notodelphys agilis is much rarer and was taken only twice, in each instance from the branchial basket of *Ascidicola virginea*. In one case the nauplii had been shed only a few seconds before the host was opened up, but there were a few specimens remaining in the brood pouch and these were dissected out.

The attempt to rear these nauplii was unsuccessful.

Description.

Nauplius of Notodelphys agilis Thorell (Fig. 1A).

Body in shape a cylinder with rounded ends, dark olive-green, greatly distended with yolk globules. The labrum is exceedingly small; at the posterior end of the body there are the usual small furcal setæ.

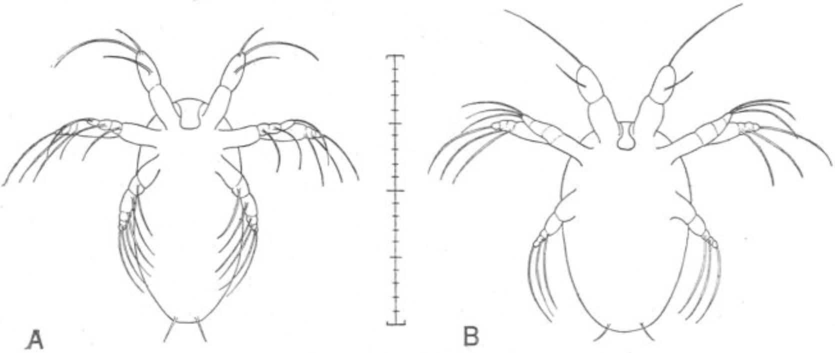

Fig. 1.—A. Nauplius of *Notodelphys agilis* Thorell. Ventral aspect.
B. Nauplius of *Doropygus porcicauda* Brady. Ventral aspect.
(The scale represents 0·2 mm. divided into 20 parts.)

Antenna I of two segments, the distal bearing one terminal and two ventral setæ, one of these latter being sub-terminal, the other arising just posterior to the middle of the segment.

Antenna II without demarcation between coxal and basal segments. Exopodite four-jointed, the proximal segment rather more than twice as long as the three terminals combined; each of the three terminals bears one long, recurved seta. Endopodite greatly reduced, of three segments, each bearing a recurved seta.

Mandible lacking the endopodite. This uniramous appendage shows six segments of which the terminal five bear long recurved setæ.

Nauplius of Doropygus porcicauda Brady (Fig. 1B).

Body egg-shaped, of a dark olive-green and greatly distended with yolk. The labrum is even smaller than in the last; the furcal setæ are widely spaced and curve outwards.

Antenna I of two segments, the distal bearing an elongate recurved terminal seta and one short medially inserted seta.

Antenna II without demarcation between coxal and basal segments. Expodite of four segments, the proximal not greatly exceeding the length of the three distals combined; each distal bears a long recurved seta. Endopodite of three segments well developed, only the last bearing three terminal setæ.

Mandible lacking the endopodite. The appendage shows five segments of which only the three distal bear each a long recurved seta.

DISCUSSION.

Both these nauplii differ sharply from all other known nauplii in the uniramous form of the mandible. The appendages are also rather more slender than is usual in the copepoda and bear considerably fewer setæ; indeed, the whole armature is greatly reduced, being obviously adapted for life under the highly specialised conditions into which the larvæ are born. The complete absence of spines from the bases of the first two appendages, coupled with the very great reduction of the labrum, render impossible the usual naupliar feeding mechanism and it seems obvious that the nauplius must depend upon its yolk reserves until a later instar.

The great reduction of the mandible is of the highest interest. The adult copepod is in both instances furnished in the adult with normal mandibles which are, however, absent from some other members of the group (e.g. Mycophilus). Yet the nauplius of this latter (Gray, 1932) is furnished with biramous mandibles! The great resemblance between the two forms shows clearly—what is in any case apparent from the adult—that the families Notodelphidæ and Doropygidæ are closely allied to each other.

The affinities of these families are rather interesting as there is, to my mind, little doubt that they are descended from a Calanoid ancestor. There is little or no resemblance, either as to habits, structure or life-history, with any Harpacticoid or Cyclopoid type. The resemblances with the Calanoid are both many and striking. The eggs of Calanus, for example, though not actually brooded, are at least accumulated in a dorsal chamber for a considerable time before laying; the eggs are, moreover, frequently of a dark olive-green colour, never observed in other groups of copepoda. The general shape of the nauplius and the actual armature of the appendages are similar in both groups and there are considerable resemblances between the adult appendages.

The writer is indebted to Mr. Richard Elmhirst, Superintendent of the Millport Marine Biological Station, for rendering possible the collection of the present material and for very considerable assistance in the identification of the hosts. The author also wishes to express his thanks to Professor J. H. Ashworth, F.R.S., for his criticism of the manuscript.

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Mycophilus rosovula n. sp., a Notodelphoid Copepod Parasitic within *B.* (*Botrylloides*) *leachii* Sav., with a Description of the Nauplius and Notes on the Habits.

By

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With 2 Figures in the Text.

INTRODUCTION.

THE notodelphoid copepods parasitic within Ascidians have been generally ignored for a long time. In May 1932 the present writer collected a considerable number at Millport Marine Biological Station, and was amazed at the frequency with which they occur. It may be that the Clyde area is especially favourable to their development, or it may be that the season was particularly good, for about thirty specimens were collected of ten species, of which at least one—the subject of the present paper—was new to science. If this abundance of forms is indeed usual, it is difficult to understand why records are not more frequent, and it would be interesting to learn how frequently these fascinating and aberrant forms are lost in the course of class dissections of their hosts.

The genus *Mycophilus* was founded by Hesse (1865) for the species *roseus*, and was subsequently included by Sars (1921) in his family Entericolidæ. It is not proposed here to enter into a discussion as to the validity of that heterogeneous group the "Notodelphoidea," nor yet to question the equally doubtful "Entericolidæ," for it is the opinion of the present writer that this cannot properly be done without a knowledge of the internal anatomy, and, above all, of the reproductive system. It is hoped to bring forward an account of the internal organisation of some of the most typical Notodelphoids at an early date.

Generic peculiarities.

The genus differs strikingly from all other known copepods in the position ot the anus, which opens in the median dorsal line between the 3rd and 4th (*M. roseus*) or 4th and 5th (*M. rosovula*) "trunk segments." The appendages are also peculiar in that they are devoid of setæ or bristles of any kind, while these parasites are again unique in their egg-laying habits (*vide infra*). The general form is worm-like (Fig. 1, B and C), the body posterior to the anus being divided into an apparently variable number of " segments," the genital aperture being at the extreme posterior end. It appears very unlikely that the anus has in reality shifted forward over a number of segments and the present author would regard the whole body posterior to the anus as a backward extension of the last segment, which has itself acquired a pseudo-segmentation from continual expansion and contraction during the egg-laying season. The four body segments anterior to the anus each bear a pair of " legs " which are in reality lateral expansions of the body wall from which they are not separated by any articulation ; each " leg " bears at its tip one (*M. rosovula*) or two (*M. roseus*) short rounded prominences, stated by Sars (*loc. cit.*) to be the " rudiments of the rami." The extreme posterior end of the body carries two small spatulate projections (AA, Fig. 1C) which may, or equally well may not, be the rudiments of the caudal rami ; the present writer proposes to continue the use of the ambiguous term " abdominal appendages," already current for the analagous structures of other parasitic copepoda.

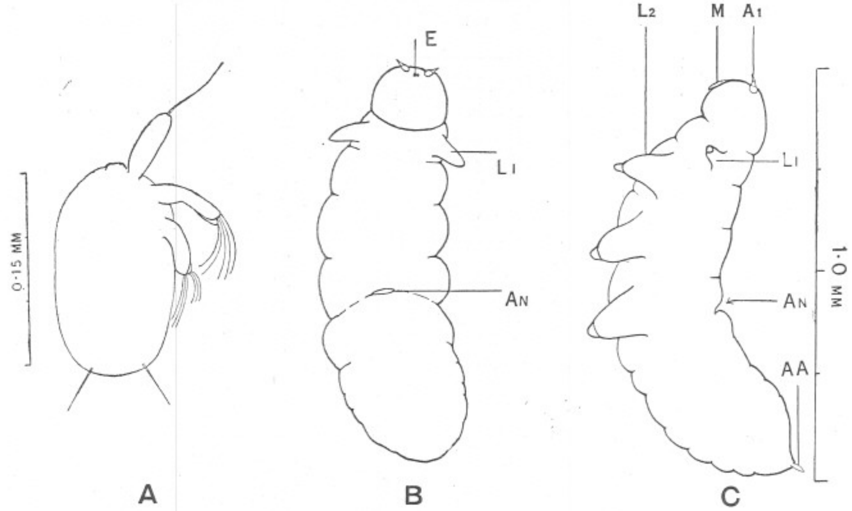

Fig. 1.—A. Nauplius of *Mycophilus rosovula*. Ventral aspect.
B. The same specimen. Dorsal aspect.
C. *Mycophilus rosovula* n. sp. ♀. Lateral aspect.
AA, abdominal appendage. An. anus. A1, first antenna. E, eye.
L1–L2, legs. M, mandible.

The head (Fig. 2) bears only four pairs of appendages of which the first two pairs are universally admitted to be the antennæ. The third pair is variably termed mandible and maxilla ; no useful decision can possibly be given on this point until the larval history is known and, since the nauplius is hatched with a perfectly normal mandible, this term will be employed in the specific description which follows. The fourth pair of head appendages will correspondingly be referred to as maxillæ. The dorsal surface of the head bears a vivid scarlet eye, rectangular in shape and divided along the middle line by a colourless bar.

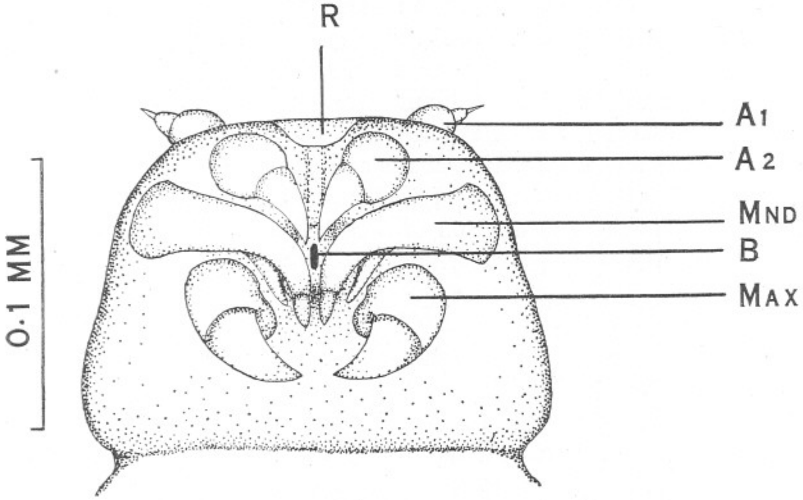

FIG. 2.—Mouth parts of *Mycophilus rosovula* ♀. Ventral aspect.
A1, A2, antennæ. B, mouth. Max, maxilla. Mnd, mandible. R, rostrum.

SPECIFIC DESCRIPTION.

Female. Body more or less recurved dorsally ; head clearly demarcated. Antenna 1 of three segments, the basal considerably expanded ; the whole conical in form, the terminal segment being greatly reduced. Antenna 2 as in *M. roseus.* Mandible inserted very close to the lateral margins of the head and bearing a larger uni-articulate palp than *M. roseus.* Maxillae as in *M. roseus* but rather stronger. First leg inserted laterally upon the body, greatly reduced and bearing a single conical projection at the tip. Second, third and fourth legs as in *M. roseus* but with only a single " terminal projection."

Body colourless and translucent ; the eggs awaiting deposition are of a dark orange-carmine and very conspicuous. Egg strings never formed.

Size of adult female 1·0 to 1·3 mm.

Male. Unknown.

This species may be distinguished instantly from *M. roseus* by the lateral placing of the reduced first legs. The present writer is unaware whether the "body" of *M. roseus* is in reality rose-red (as stated by Sars (*loc. cit.*)) or whether this appearance is due, as in the present example, to the colour of the eggs; in the former case there would here be an additional distinction between *M. roseus* and *M. rosovula*. It appears also doubtful whether the apparent difference in size between the two would remain valid were several hundred specimens to be examined.

The lateral attachment of the first legs, the widely spaced insertion of the mandibles and the position of the anus, together with certain minor differences in the appearance of the various appendages, would seem sufficient to justify the erection of a new species for which the name *rosovula* is accordingly proposed.

HABITS.

M. rosovula is found exclusively in the canals which run through the matrix of *B.* (*Botrylloides*) *leachii* Sav., through the transparent test of which the colour of the undelivered eggs can be seen with the naked eye. Very few colonies contained more than a single parasite, which was present in about 20% of those examined; no parasite was ever found in any other species of colonial ascidian, though both a B. (Botryllus) and a Leptoclinum were abundantly associated with the infected form.

The egg-laying habits are different from those of any other copepod at present known, in that the eggs are deposited singly or occasionally in patches of two or three. No cement is present, each egg being surrounded only with a thin transparent membrane. After a period, which is not less than five days (eggs already present in a colony hatched after five days' observation; eggs laid under observation failed to hatch), nauplii hatch out. The nauplius (Fig. 1 A), which has the form of a short cylinder with rounded ends and retains the rose colour of the egg, is very much larger than one would expect. The first antenna bears at its end a single, long-curved seta. The second antenna has three such setæ upon the main stem and two upon the inner ramus. The mandible is similar to the second antenna, but has three terminal setæ upon each ramus. There is a distinct, square rostrum in front and a pair of posterior setæ; the median eye is vivid scarlet and rectangular in outline.

The movements of the nauplius are much more rapid than its clumsy shape would lead one to suppose. The newly hatched larvæ soon leave the security of the canals and pass on to the top of the colony, on whose slightly rough surface their long curved setæ enable them to move with rapidity. Their motion strongly recalls that of Lepisma as they scuttle from the cover of one lump of debris to another, often vanishing into the branchial cavities of the host at the least sign of danger. They are intensely timid and will not resume motion until any unusual movement of the water has ceased ; in this they differ markedly from the harpacticoid nauplii, with many of which they share the surface of the colony. If washed off by a sudden stream of water they swim in short sharp jerks but are unable to sustain the motion for long and soon fall to the bottom where they lie motionless for a second or two before recommencing their struggles ; if they should chance to fall on to any particle of debris equal in size to, or larger than themselves, they will remain clasped to it apparently indefinitely.

No success was attained in the attempt to rear these nauplii. One hatch survived for three days without undergoing a moult. The large numbers of unidentified, and at present unidentifiable, harpacticoid larval instars which are always present on the surface of compound ascidians, rendered valueless all attempts to reconstruct a life-history by collection.

The movements of the female adult are clumsy in the extreme. Fitting tightly into the canal, she moves with slow awkward wrigglings of the body assisted by convulsive movements of the legs. One specimen observed moved 18 mm. in four hours and in this time deposited three eggs at about equal distances. Upon being dissected out from the host, the parasite immediately assumed the recurved shape seen in the drawings of the preserved specimens and continued to reproduce the motions slowly crawling. An isolated specimen was placed on the surface of a colony and managed to drag itself a distance of nearly 3 mm. before collapsing helplessly on its side. Upon being placed exactly over an inhalent aperture of the host, the parasite clawed its way inside but was found to be dead when dissected out three hours later.

It would seem, therefore, that infection of a new host must take place by a larval form and it is very difficult to account for the specific preference shown by the parasite.

I am indebted to Mr. Richard Elmhirst, Superintendent of the Millport Marine Biological Station, for the facilities he afforded me for the collection and examination of these parasites and for his invariably useful suggestions ; and to Professor J. H. Ashworth, F.R.S., for his helpfully critical examination of the manuscript.

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The Development Stages of *Oithona helgolandica* and *Oithona spinirostris,* with a Note on the Occurrence of Body Spines in Cyclopoid Nauplii.

By

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and

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With 1 Figure in the Text and Plates 1–3.

INTRODUCTION.

In recent years the development stages of Copepoda have been the subject of study by various workers. Their attention, however, has been mainly directed to fresh-water species, presumably because the material is more readily available, and it seems desirable that our knowledge of the development of marine Copepoda should be extended. The material utilised for the present work was collected on the periodic and comprehensive fishery cruises carried out by the F.R.S. *Explorer*, and we are indebted to the Fishery Board for Scotland for permission to undertake this detailed study. Since the appearance of Grobben's standard work on *Cetochilus septentrionalis* Goodsir (*Calanus finmarchicus* Gunn.), the only important publication dealing with the life-histories of marine Copepoda, so far as we have been able to ascertain, is that of Oberg, who, in *Die Metamorphose der Plankton-Copepoden der Kieler Bucht*, describes the development stages of seven common marine forms. Oberg's choice of species, which are all more or less neritic, was again obviously dictated to him by the material at his disposal, and it is hoped that our collections, which cover not only the northern part of the North Sea, but also the Faroe–Shetland Channel, and part of the Atlantic itself, will furnish material for the establishment of the life-histories of some of the more oceanic forms.

A careful checking of Oberg's drawings and tables, however, has shown that, as far as his account of *Oithona similis* (hereinafter referred to as *Oithona helgolandica,* which, as Sars points out, is the first name under which it was described) is concerned, he has missed several points in the six nauplius stages which, from the point of view of comparison with other species, may be considered of some importance. His work on this species was therefore carefully revised, and criticised where necessary before the corresponding stages of *Oithona spinirostris* were attacked. It will be seen that the differences separating the nauplii of these two species are nowhere very pronounced, and the first and second nauplius stages are to be distinguished chiefly by size and shape, together with a certain small feature to be observed in the armature of the labrum. The important part that the labrum might play in determining species must have been overlooked by Oberg, since his figures of this organ are extremely rough and inaccurate.

The development stages of *Oithona spinirostris* have not, so far as we are aware, been described hitherto.

OITHONA HELGOLANDICA CLAUS.

Syn. *Oithona similis* Claus.
,, *spinifrons* Boeck.
,, *pygmæa* ,,
,, *spinirostris* Giesbrecht (not Claus).

As Oberg has already shown, *Oithona helgolandica* retains the full number of six nauplius stages in its development, but as the armature of the appendages appears to differ somewhat from that described by him, a full description is given here.

The First Nauplius Stage. Length, ·115 mm. (Plate 1, Fig. 1).

Body egg-shaped, and considerably flattened dorso-ventrally. The furcal armature at this stage consists of a single pair of long thin bristles which tend to be directed outwards and dorsally. The ventral body spines to which reference will be made later are already visible at this stage. The labrum, well seen in a ventral view of the whole animal, is distinct in form, and retains the same appearance throughout all the six nauplius stages. It is rounded anteriorly, and three very fine forwardly directed bristles can be seen in this region on either side. Posteriorly it is produced laterally to a three-spined point on each side, the outermost spine being the largest and the innermost the smallest. On the posterior margin, on either side of the median line, is a group of four spines, of which the innermost and outermost are both fairly small, while the other two are larger, the one nearest the inside being very long and strong.

Appendage 1, *The Antennule.* (Plate 1, Fig. 1.) This appendage is three-jointed. The first joint is unarmed; the second joint bears three bristles, the third of which is very much longer than in Oberg's figure, reaching well beyond the end of the third joint. The third joint bears four bristles, two at the extreme distal end, and one, which is directed dorsally, immediately behind, while the remaining bristle is very small and thin, and is to be seen on the dorsal side of the segment, nearer the proximal end. These last two bristles do not appear in Oberg's description.

Appendage 2, *The Antenna.* (Plate 1, Fig. 1B.) The coxopodite has a sharp masticatory process with a short bristle arising at its base. The basipodite has two fine bristles and a very small accessory bristle which is not shown in Oberg's figures. The endopodite is simple, and has two inside bristles and two end bristles. The exopodite is six-jointed, the second joint being the longest. The first joint is unarmed, the second to the fifth joints have one bristle each, while the sixth joint has one lateral and one end bristle, making six bristles in all for the whole exopodite.

Appendage 3, *The Mandible.* (Plate 1, Fig. 1C.) The coxopodite bears a small sharp bristle. The basipodite has one strong short inside bristle. The endopodite is in two joints, the first of which bears two inwardly-directed strong masticatory processes, and is so short that it appears almost as a part of the basipodite. The second joint of the endopodite has two small inside bristles and two end bristles of unequal length. The exopodite is four-jointed, the first joint being the longest, and each joint is furnished with one bristle. There is no sign of the maxillæ at this stage.

The Second Nauplius Stage. Length, ·130 mm.

In appearance this stage is difficult to distinguish from the preceding stage, as the difference in size is so small as not to be readily noticed. A careful examination shows that two fine long bristles, which are the rudiments of the coming maxillæ, can be seen in the postero-ventral region, and the presence or absence of these is the best key for the separation of Stages 1 and 2. The furcal armature has undergone no change. (Plate 1, Fig. 2E.)

Except in the matter of size, the labrum in this stage is identical with that in the preceding stage.

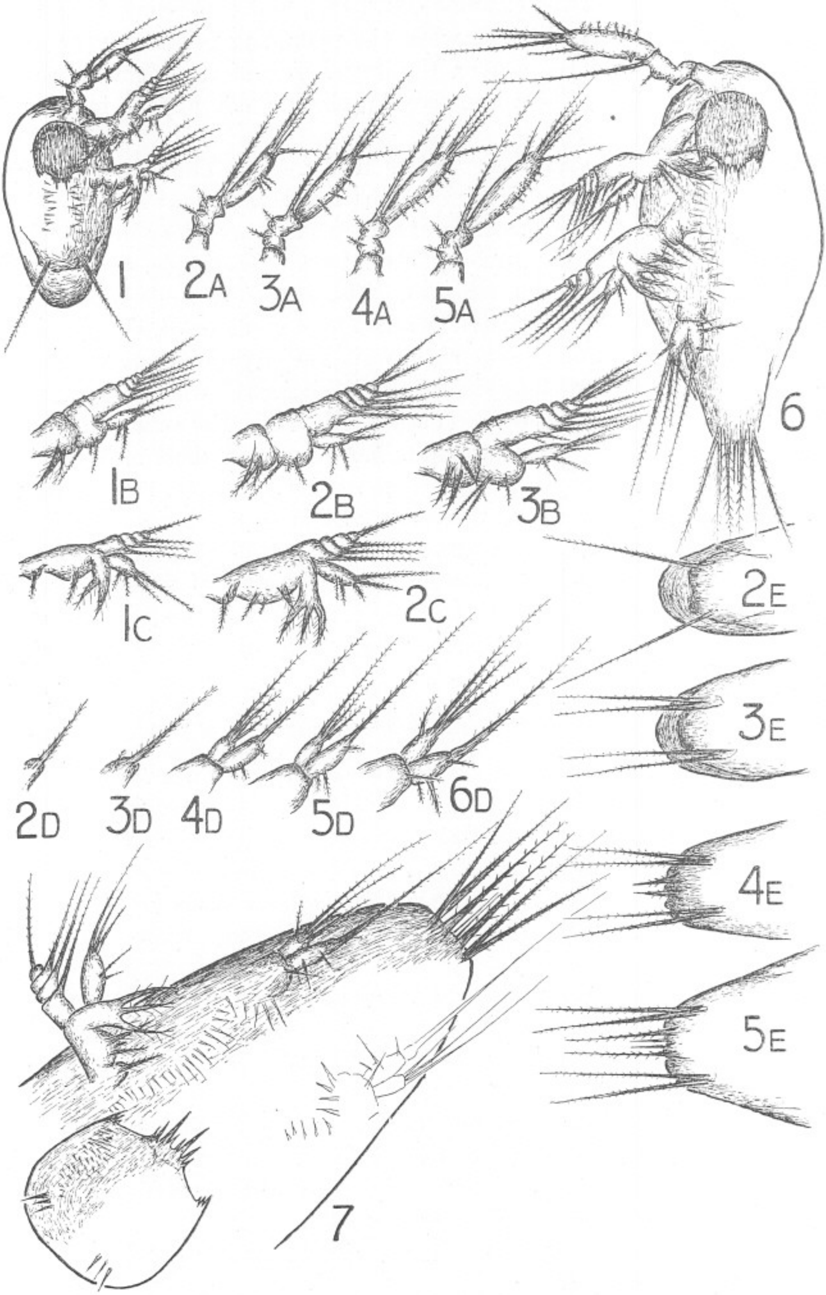
Appendage 1, *The Antennule.* (Plate 1, Fig. 2A.) Proximal and second joints exactly as in Stage I.

The distal joint has three end bristles, a dorsally directed one just behind them, and three fine dorsal bristles in the middle of the segment, making seven bristles in all for the third joint of the antennule. Here again Oberg figures only the three end bristles.

Appendage 2, *The Antenna.* (Plate 1, Fig. 2B.) Coxopodite and basipodite as in Stage I.

The endopodite has five bristles, two at the distal end and three on the inner margin. (Oberg figures three at the distal end and two on the

PLATE 1.



inner margin.) The exopodite is similar to Stage I, except that the second joint bears a small accessory bristle in addition to its single long bristle.

Appendage 3, *The Mandible.* (Plate 1, Fig. 2C.) The coxopodite as in Stage I. The basipodite has two small bristles and a third smaller bristle on the inner edge. The endopodite is two-jointed, the first joint very short, and bearing the masticatory processes, now three in number. Second joint of the endopodite with two inner and three end bristles. The exopodite is exactly as in the preceding stage.

Appendage 3, *The Maxillule.* (Plate 1, Fig. 2D.) These appear at this stage only as rudiments represented by a protuberance on each side, bearing a single long, well-developed bristle.

The Third Nauplius Stage. Length, ·140 mm.

The general shape of the body is still oval, but slightly longer in proportion to its width. The posterior end of the body does not yet protrude beyond the cephalothoracic shield. (Plate 1, Fig. 3E.)

This stage can be easily recognised by the furcal armature which is distinctive. It consists of a pair of long bristles on either side. They are of more or less equal length, and seem to have a common origin at the point where the single bristles of the preceding stage were to be seen.

The labrum is again unchanged in appearance.

Appendage I, *The Antennule.* (Plate 1, Fig. 3A.) The first and second joints are again as in Stage I. The distal joint has three end bristles and a dorsally-directed bristle just behind them as in the preceding stage, but in addition a ventral bristle is now seen on the distal end of the ventral margin of the segment, while there are four very fine dorsal bristles, making nine bristles in all on the third segment of the antennule. Oberg only figures four bristles for this segment at this stage.

EXPLANATION OF PLATE 1.

Oithona helgolandica. Nauplius Stages.

FIG. 1. First Nauplius Stage.

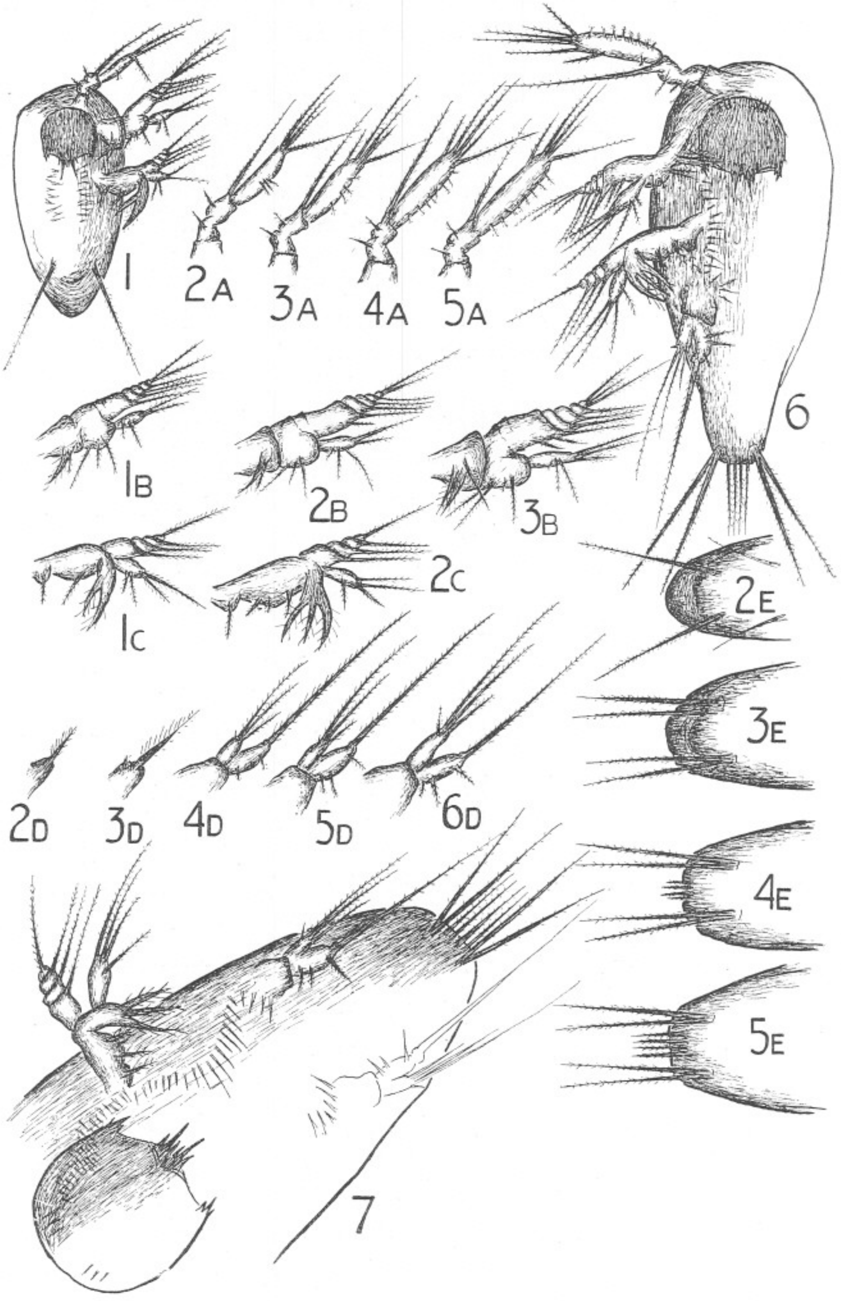
In the subsequent figs. the numbers 1–6 refer to the successive Nauplius stages, and the letters A–E to the parts figured:—

A = Antennule.
B = Antenna.
C = Mandible.
D = Maxillule.
E = Posterior part of body, ventral view.

FIG. 7. Stage 6, ventral view, showing arrangement of body spines.

All figures drawn to the same scale at a magnification of about 600 diameters, except Fig. 7, which is somewhat larger.

PLATE 2.



Appendage 2, *The Antenna.* (Plate 1, Fig. 3B.) The coxopodite has now two strong masticatory processes of approximately equal size, and in addition a long fine bristle. The basipodite resembles that of the preceding stage except that the proximal bristle is now paired, both bristles arising in the same position.

The endopodite resembles that of the previous stage, but has now three end bristles in place of two. The exopodite is still six-jointed, but the second joint has two small accessory bristles in addition to its long bristle, making three bristles in all for the second segment, while the distal segment has now three end bristles in place of the two of the preceding stage.

Appendage 3, *The Mandible.* (Plate 1, Fig. 2C.) This appendage is in all respects the same as that of the last stage.

Appendage 4, *The Maxillule.* (Plate 1, Fig. 3D.) No great change is yet to be seen in this appendage from the previous stage, but there is a tendency for a two-lobed structure, as shown by the presence of a second small bristle close to the first, which is itself somewhat longer than in Stage II.

The Fourth Nauplius Stage. Length ·165 mm.

Considerable difference in size can now be made out, but the whole of the body is still under the cephalothoracic shield. The furcal armature consists of the paired lateral spines as in the last stage, but in addition there are to be seen two small but stout end spines, one on each side of the median line at the extreme posterior end of the body. (Plate 1, Fig. 4E.) The labrum remains the same as in Stage III.

Appendage 1, *The Antennule.* (Plate 1, Fig. 4A.) The proximal and second joints remain the same as in the previous stage, and the distal end of the last joint with its three end bristles and the dorsally directed one is also unchanged. The ventral edge shows distally the bristle which

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EXPLANATION OF PLATE 2.

Oithona spinirostris. Nauplius Stages.

Fig. 1. First Nauplius Stage.

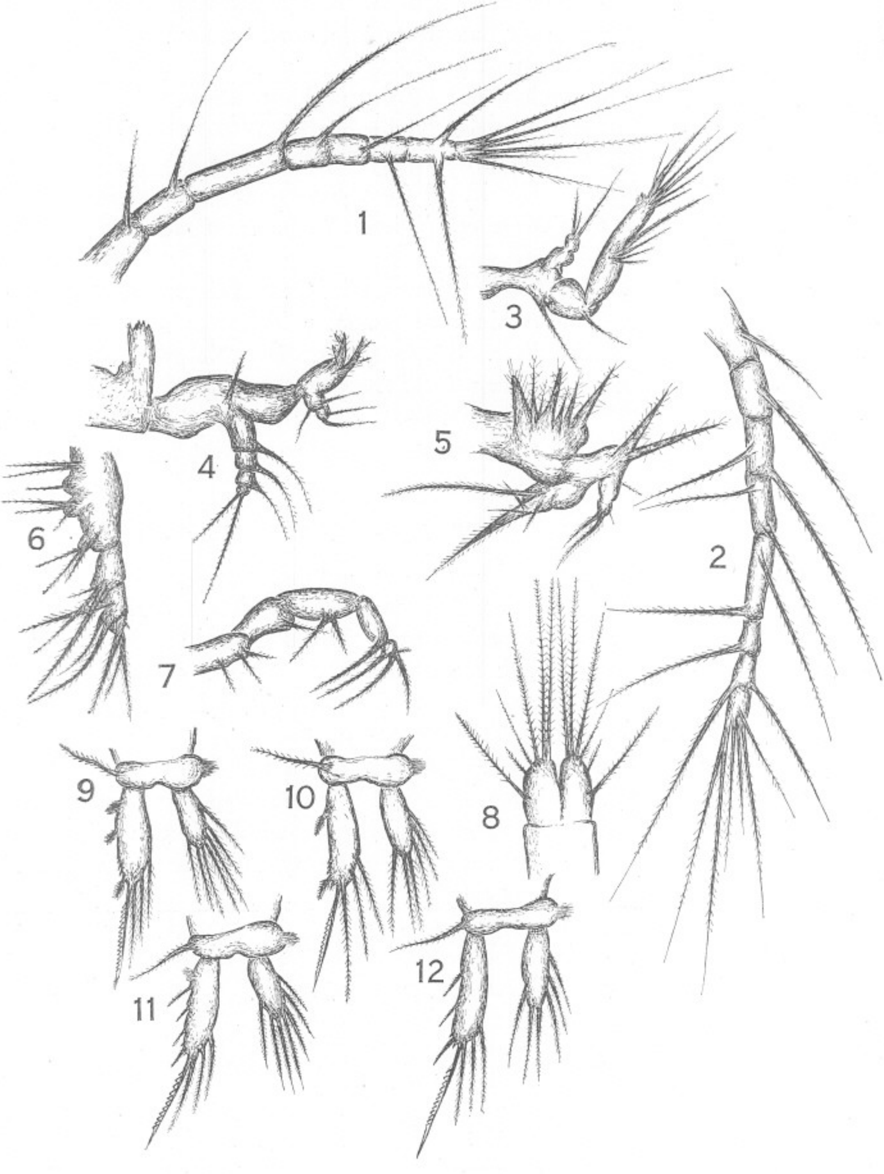
In the subsequent figs. the numbers 1–6 refer to the successive Nauplius stages, and the letters A–E to the parts figured:—

A = Antennule.
B = Antenna.
C = Mandible.
D = Maxillule.
E = Posterior part of body, ventral view.

Fig. 7. Stage 6, ventral view, showing arrangement of body spines.

Magnification slightly less than in Plate I to make the figures correspond in size.

PLATE 3.



first appeared in Stage III, but the dorsal edge of this third joint bears eight fine bristles which are not easily distinguished. This is the first stage in which Oberg figures these fine bristles, and he does not state the number seen.

Appendage 2, *The Antenna.* (Plate 1, Fig. 3B.) This appendage remains unchanged from the preceding stage in all respects.

Appendage 3, *The Mandible.* (Plate 1, Fig. 2C.) No change is to be seen from the preceding stage.

Appendage 4, *The Maxillule.* (Plate 1, Fig. 4D.) This appendage is now distinctly biramous, endopodite and exopodite being clearly separated from one another. The exopodite has three end bristles of which the outermost one is the longest. The endopodite has one very long and strong bristle and three very small inside bristles. The coxopodite and basipodite, as yet scarcely distinguishable, bear no visible armature.

The Fifth Nauplius Stage. Length ·190 mm.

In this stage the body, now becoming more markedly elongated, is seen to project beyond the end of the cephalothoracic shield. The furcal armature has been increased by a pair of very small fine end bristles which are to be seen inside the two end spines first mentioned in the last stage. These two fine bristles are placed parallel to the stronger spines, but inside them, one on each side of the median line, so that they are very close together. The two short strong spines seen in the last stage have now become much longer, and are only slightly shorter than the paired bristles at each side, which, however, are somewhat shorter than when they were first seen in Stage I. It is to be doubted if any actual reduction in their length has taken place, but they have not appreciably increased in length during the successive stages, so that in proportion to the

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EXPLANATION OF PLATE 3.

First Copepodid Stage.

FIG. 1. *Oithona helgolandica.* Antennule.
,, 2. *O. spinirostris.* ,,
,, 3. Antenna
,, 4. Mandible
,, 5. Maxillule
,, 6. Maxilla
,, 7. Maxillipede
,, 8. Furca
Both species.
,, 9 & 10. 1st and 2nd pleopods of *O. helgolandica.*
,, 11 & 12. 1st and 2nd pleopods of *O. spinirostris.*

Magnification as in Plate I.

increasing body-length they appear shorter. (Plate 1, Fig. 5E.) The labrum shows no difference from the preceding stage.

Appendage 1, *The Antennule.* (Plate 1, Fig. 5A.) Except for a very slight increase in size this appendage shows no change from the corresponding one in the previous stage.

Appendage 2, *The Antenna.* (Plate 1, Fig. 3B.) This appendage has undergone no change from that of the fourth nauplius stage.

Appendage 3, *The Mandible.* (Plate 1, Fig. 2C.) No change from that of the last two stages.

Appendage 4, *The Maxillule.* (Plate 1, Fig. 5D.) No change from the preceding stage.

The Sixth Nauplius Stage. Length ·215 mm.

The posterior end of the body now projects well beyond the cephalothoracic shield, and the whole animal is more elongated in general form, having its greatest width about the middle. The furcal armature is the same in design as that of the previous stage, but the two end spines are somewhat longer, and the two fine bristles found inwards from them are about twice as long as in the fifth stage, though still very thin and weak in appearance. The labrum which has remained the same in pattern throughout all the stages shows no difference from that of the last stage.

Appendage 1, *The Antennule.* (Plate 1, Fig. 6.) The proximal and second joints are still unchanged, but there are differences in the distal joint. A second smaller bristle is added on the ventral edge distally, just behind the first one seen in the previous three stages, and there is also a short thorn-like bristle on the ventral border of the segment near the proximal end. Neither of these two is figured by Oberg. The end bristles and the eight bristles on the dorsal edge remain the same as in the last stages.

Appendage 2, *The Antenna.* (Plate 1, Fig. 3B.) This appendage still shows no change in its appearance from that of the third nauplius stage.

Appendage 3, *The Mandible.* (Plate 1, Fig. 2C.) In appearance and armature this appendage is the same as in all the preceding stages since the second nauplius stage.

Appendage 4, *The Maxillule.* (Plate 1, Fig. 6D.) This appendage has grown in size somewhat, but presents only small differences from that of the fifth nauplius stage. A small bristle has been added to the basipodite, and a very small extra bristle can be made out on the exterior edge of the expodite; otherwise there is no visible change in the armature.

From this stage the animal moults into the first copepodid stage. This was isolated and examined carefully, the various appendages being dissected off from the trunk, and, as in the case of the nauplii, examined under the oil immersion lens to obtain the fullest detail.

The First Copepodid Stage. (Plate 3.) Length ·36–·37 mm.

As good figures of the appendages of this stage are wanting in Oberg's paper, they are shown here in some detail. Oberg has seemed more intent on the fate of the various bristles in the nauplius stage in the moult to the first copepodid than in giving a clear description of the armature of the appendages in this stage.

It must be mentioned here that the body spines which have been present in all the nauplius stages and to which reference is to be made later in this paper, disappear on the moult to the copepodid and no trace of them has been seen in this stage.

The furca, which is bifurcated from this stage onwards, has on each side three long end bristles, a shorter lateral bristle, and, between these two groups in a postero-lateral position, two small bristles of unequal length, the exterior one of which is the smaller. Both these bristles are directed postero-laterally and can be seen in dorsal or ventral view of the furca.

Appendage 1, *The Antennule.* (Plate 3, Fig. 1.) Consisting of eight segments, the third being the longest. Each of the first six bears a single bristle, that on the long third segment being longer than any of the others. The seventh joint has two large bristles, one at each side. The end joint has six bristles, five originating at the distal end, the sixth about half-way down the joint. Of these six bristles four are very long and strong, while the remaining two are about half the length of the others.

Appendage 2, *The Antenna.* (Plate 3, Fig. 3.) The exopodite in this appendage is greatly reduced, and consists only of a two-lobed rudiment, the distal lobe of which bears three bristles, one of which is very small. The basipodite is long and thin, and has one bristle at its distal end. The endopodite forms the adult antenna, and bears three sets of bristles, one bristle proximally, three small and one large bristle at the constriction in the middle of its length, and six end bristles, three of which are large and three small. Just behind the end bristles are to be seen numbers of very fine hairs on the inner margin of the segment.

Appendage 3, *The Mandible.* (Plate 3, Fig. 4.) The coxopodite exhibits a strong toothed process. The basipodite is furnished with one medium-sized bristle. The endopodite is of curious shape, having a large basal joint bearing two strong bristled spines distally and two bristles proximally on a protuberance from which the second joint of the appendage arises. This second joint also bears two bristles. The exopodite is four-jointed, joints one to three having one bristle each, while the end joint has two bristles.

Appendage 4, *The Maxillule.* (Plate 3, Fig. 5.) The coxopodite is greatly enlarged with seven masticatory spines, of which three, the two outer ones and the middle one, are particularly powerful. The endopodite bears two strong spines on an inner lobe. The exopodite is in two small portions, the proximal having one very small bristle and the distal two end bristles and a very small accessory bristle. The basipodite bears on its outer margin a large lobe, the epipodite, on the distal portion of which are to be seen two large and three very small bristles.

Appendage 5, *The Maxilla.* (Plate 3, Fig. 6.) Coxopodite with three groups of bristles, two in the first, one in the second, and three in the third. The basipodite with a lobe bearing three bristles. Endopodite of three segments, the first and second each with two very long and one smaller bristle, the third with three end bristles and one very small accessory bristle. Except for one more articulation which is not yet apparent, this appendage is the same as in the adult animal save in point of size.

Appendage 6, *The Maxillipede.* (Plate 3, Fig. 7.) The coxopodite appears divided into two parts, the first with three stout bristles, two of which are close together, and the second with one stout bristle distally. The basipodite with two stiff bristles about the middle of its length and directed inwards. The endopodite of two segments, the first with one bristle distally, the second with three long bristles and a very short bristle.

Appendage 7, *The First Pleopod.* (Plate 3, Fig. 9.) The basipodite has a long external bristle and some fine hairs on the inside. The endopodite is unsegmented and has seven bristles. The exopodite has three inside bristles, a terminal serrated spine, and two strong short spines on the outside edge. Near the most distal of these are two or three much smaller spines close together. Close to the proximal end of the exopodite on the exterior edge are to be seen some fine hairs.

Appendage 8, *The Second Pleopod.* (Plate 3, Fig. 10.) The basipodite as in the first pleopod. The endopodite is unsegmented and bears six bristles. The exopodite resembles that of the anterior pleopod, except that the fine hairs are absent at the proximal end, and there is an additional small spine between the distal short spine and the long serrated spine.

It is not deemed necessary here to describe the ensuing copepodid stages up to the adult animal. The changes which take place are for the most part of a minor nature, and in the first copepodid stage all the principal characteristics of the adult animal can be easily recognised.

OITHONA SPINIROSTRIS CLAUS.

Syn. *Oithona challengeri* Thompson.
,, *plumifera* Scott (not Baird).
,, *atlantica* Farran.

As already stated, no account of the development stages of this species has as yet been seen in the literature examined, and for this reason a comparison of the stages with those of the preceding species is of considerable interest.

Throughout the development stages of these two Cyclopoids one cannot but marvel at the similarity between the corresponding stages, especially in the case of the first two nauplius stages. In actual detail of structure regarding the appendages there is practically no difference at all to be seen, and indeed the antennule and antenna are the same throughout the nauplius stages for both the species. The chief distinguishing points are those of size, general shape, and in the older nauplii the armature of the hind end of the body, while the mandible and maxillule furnish two minor differences between the species.

The First Nauplius Stage. Length ·130 mm. (Plate 2, Fig. 1.)

Body oval in shape, but slightly more pointed posteriorly and broader anteriorly than Stage I of the preceding species. The labrum shows two small but nevertheless distinct points of difference. Its central group of strong spines on the posterior margin of the organ consists of three on each side of the median line in place of four on each side as in *O. helgolandica*. Of these three spines the middle one is by far the longest and strongest. In addition the three spines which form the postero-lateral termination of the labrum are of unequal size as in the last species but the middle one and not the outermost is the longest, while the outermost itself is small and more outwardly directed.

Appendages. (Plate 2, Figs. 1, 1B, and 1C.) In this, the first nauplius stage, all the three appendages are exactly similar to the corresponding appendages in the first stage of *O. helgolandica*.

The Second Nauplius Stage. Length ·150 mm. (Plate 2, Figs. 2A, B, C, D, and E.)

The body is similar in shape to that of the first nauplius stage but slightly more elongated, and the difference in size between the two species at this stage is more pronounced, though it is as yet insufficient to enable them to be distinguished without the aid of careful measurements.

Appendages. With the exception of the mandible the appendages of the second stage are again the same as those of the corresponding stage of the preceding species. The armature of the hind end of the body, too, is in no way different. The mandible itself, however, shows one small point of difference which from now on persists through all the remaining nauplius stages. It is seen in the endopodite, on the inner margin of which only one bristle is now to be seen, whereas in *O. helgolandica* there are two small bristles on the inner margin of the mandibular endopodite in all the stages. The first nauplius stage of *O. spinirostris* also shows these two small bristles, but, curiously enough, the second, and all later stages in this species show only one bristle in this position.

The Third Nauplius Stage. Length ·170 mm. (Plate 2, Figs. 3A and B, 2C, 3D and E.)

The difference in size from *O. helgolandica* is now becoming still more pronounced, and with a high power the two species can sometimes be separated by size alone, though there is still a very considerable overlap if they are examined in quantity.

Appendages. With the exception of the difference in the armature of the mandibular endopodite mentioned in the last stage, the appendages and armature of the hind end of the body are the same as for the former species.

The Fourth Nauplius Stage. Length ·200 mm. (Plate 2, Figs. 4A, 3B, 2C, 4D, and E.)

In this stage the animal is now distinctly larger than in the same stage of the preceding species. General body shape is not essentially different, but in *O. spinorostris* there is a tendency for the greatest breadth to lie more anteriorly than in *O. helgolandica.* The armature of the furca at this stage, too, becomes distinctive, and from this stage on the species can be isolated at once by this means. In place of the two stout short medianly placed end spines of *O. helgolandica* there are to be seen four short thinner spines occupying exactly the same position. There is no other difference in the armature.

Appendages. Again, excepting the mandible, which is the same at this stage as in the second stage, the appendages show no difference from the fourth stage of the last species.

The Fifth Nauplius Stage. Length ·230–·235 mm. (Plate 2, Figs. 5A, 3B, 2C, 5D, and E.)

The difference in size at this stage can clearly be seen. The body is distinctly broader anteriorly than in the last species. With the exception of the mandible the appendages are again identical in armature with those of *O. helgolandica*. The furcal armature is the same as in the last stage, but the spines are about double the length of those in the fourth stage, and still four in number. The long lateral bristles show no change.

The Sixth Nauplius Stage. Length ·265–·270 mm.

The size difference is now obvious.

The body shape, as shown in Plate 2, Fig. 6, is stouter anteriorly than that of *O. helgolandica*, and is correspondingly more slim posteriorly. Other than the mandible, which is again the same as in the earlier stages, the maxillule is the only appendage that differs in any way from those of the previous species. The small bristle seen on the basipodite of the maxillule in *O. helgolandica* does not appear in the present species at this stage. (Plate 2, Fig. 6D. cf. Plate 1, Fig. 6D.) The furcal armature resembles that of the fifth stage, but the four median spines are now quite long, though not much more than half the length of the lateral bristles.

This is the last of the nauplius stages, and the animal now moults into the first copepodid stage. As in the preceding species, six nauplius stages have been retained in the development, and the similarity in all the stages is certainly striking. The body spines referred to above are to be seen equally well in both the species, and no differences in the number or arrangement of them have been noticed. Though the differences in the labrum are not great between the two species, they are at least common to all the stages and seem to supply a quite sound assistance in the identification of these two Oithonas.

The First Copepodid Stage. Length ·42 mm.

Save in the matter of size, which is, of course, now the chief distinguishing feature, there is remarkably little difference between the first copepodid stages of these two species. Plate 3 shows the appendages of this stage. The pleopods and the antennule are the only appendages which show the least difference in the armature, so that in Plate 3, Figs. 3, 4, 5, 6, 7, and 8 apply equally well to both species. Fig. 2 shows the antennule of *O. spinirostris*, and can be compared with that of *O. helgolandica* in Fig. 1. The only difference is that in *O. spinirostris* there are two bristles on each of the third, fourth, and fifth joints in place of one. The end bristles are the same in both cases. In the pleopods the basipodites and the endopodites are the same in both, but the exopodites show a distinct difference. The bristles and end blades, or serrated spines, are the same in both species, but the armature of the exterior edge is characteristic. In the first pleopod of *O. spinirostris* (Plate 3, Fig. 11) there are four outer spines in place of the two in *O. helgolandica*. These spines are somewhat longer, and are not so heavily bristled as in the former case (Fig. 9). Also the small accessory spines seen between the two in this figure do not appear in *O. spinirostris* and in the expodite of the second pleopod (Fig. 12) the same state of affairs is seen except that there are in the present species three definite long spines instead of the four of the last pleopod, and in place of the two shorter spines of the preceding species.

As in the former case, it is not thought necessary to enter into the copepodid stages further here. As in *O. helgolandica*, all the characteristics of the adult can now be recognised.

MEASUREMENTS OF NAUPLII.

In order to show how a careful series of measurements could separate the species the following results of such a series have been included in this work :—

NUMBERS MEASURED.

Length mm.	Stage I.	Stage II.	Stage III.	Stage IV.	Stage V.	Stage VI.
·100	5	–	–		–	–
·105	16	–	–	–	–	–
·110	32	–	–	–	–	–
·115	52	–	–	–	–	–
·120	24	11	–	–	–	–
·125	16	16	2	–	–	–
·130	32	40	9	–	–	–
·135	20	27	22	–	–	–
·140	3	27	40	–	–	–
·145	–	12	26	–	–	–
·150	–	47	20	–	–	–
·155	–	17	7	8	–	–
·160	–	3	10	20	–	–
·165	–	–	14	34	–	–
·170	–	–	28	28	–	–
·175	–	–	16	12	–	–
·180	–	–	4	4	6	–
·185	–	–	2	–	17	–
·190	–	–	–	–	44	–
·195	–	–	–	6	28	–
·200	–	–	–	14	19	–
·205	–	–	–	48	5	8
·210	–	–	–	22	–	25
·215	–	–	–	4	–	46
·220	–	–	–	–	6	30
·225	–	–	–	–	14	11
·230	–	–	–	–	18	–
·235	–	–	–	–	26	–
·240	–	–	–	–	14	–
·245	–	–	–	–	3	–
·250	–	–	–	–	–	4
·255	–	–	–	–	–	9
·260	–	–	–	–	–	15
·265	–	–	–	–	–	16
·270	–	–	–	–	–	24
·275	–	–	–	–	–	9
·280	–	–	–	–	–	3

In measuring large numbers it was found impossible to employ sufficiently high magnification to make a detailed examination of each specimen, and the difficulty presented itself that while it was a comparatively simple matter to separate the species in Stages IV, V, and VI, in Stages I, II, and III this was not so easy, although the stages themselves could be fairly readily distinguished. For this reason a large number of specimens of each stage was measured regardless of species, and in every case two modal points appeared clearly which corresponded to the two species at the size at which each most frequently occurred. Two hundred specimens at each stage were measured, and the species were then separated out by the maxima in the table. Where there was obvious overlap between the modes the overlapping numbers were divided between the two species in proportion to the modal maxima. This was done because *O. helgolandica* was more abundant in the material than *O. spinirostris*.

This separating out of the species is shown in the following table, which shows the range of size at each stage to be considerable.

OITHONA HELGOLANDICA—NAUPLIUS STAGES.

Stage.	Range of Length (mm.).	Modal Length (mm.).	Number measured at :—(mm.).							Total No.
I.	·100–	·115	·100	·105	·110	·115	·120	·125	–	125
	·125		5	16	32	52	16	4	–	
II.	·120–	·130	·120	·125	·130	·135	·140	–	–	115
	·140		11	16	40	27	21	–	–	
III.	·125–	·140	·125	·130	·135	·140	·145	·150	·155	123
	·155		2	9	22	40	26	20	4	
IV.	·155–	·165	·155	·160	·165	·170	·175	·180	–	106
	·180		8	20	34	28	12	4	–	
V.	·180–	·190	·180	·185	·190	·195	·200	·205	–	119
	·205		6	17	44	28	19	5	–	
VI.	·205–	·215	·205	·210	·215	·220	·225	–	–	120
	·225		8	25	46	30	11	–	–	

OITHONA SPINIROSTRIS—NAUPLIUS STAGES.

Stage.	Range of Length (mm.).	Modal Length (mm.).	Number measured at :—(mm.).							Total No.
I.	·120–	·130	·120	·125	·130	·135	·140	–	–	75
	·140		8	12	32	20	3	–	–	
II.	·140–	·150	·140	·145	·150	·155	·160	–	–	85
	·160		6	12	47	17	3	–	–	
III.	·155–	·170	·155	·160	·165	·170	·175	·180	·185	77
	·185		3	10	14	28	16	4	2	
IV.	·190–	·200	·190	·195	·200	·205	·210	–	–	94
	·210		6	14	48	22	4	–	–	
V.	·220–	·235	·220	·225	·230	·235	·240	·245	–	81
	·245		6	14	18	26	14	3	–	
VI.	·250–	·270	·250	·255	·260	·265	·270	·275	·280	80
	·280		4	9	15	16	24	9	3	

From these tables the graphs shown in Text-Fig. 1, are constructed. The former of these two tables gives us Graph 1, the first part of which is not very explicit, because the early stages of *O. spinirostris* tend to coincide in size with the next later stages of *O. helgolandica.*

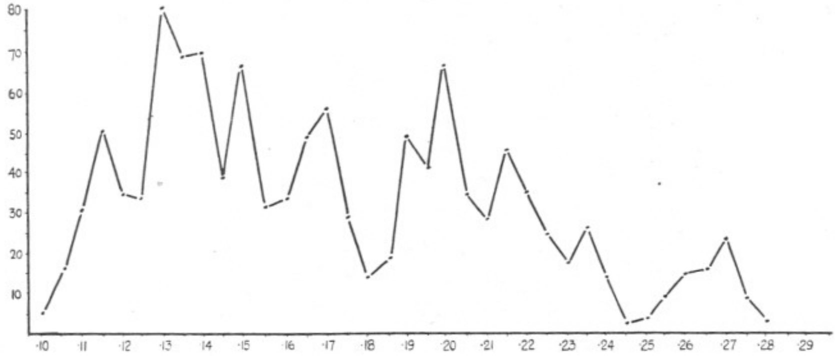
From the second table Graphs 2 and 3 are plotted, allowance having been made for overlapping of the stages in the manner already described. In this way it becomes clear that the first peaks of Graph 1 are the result of the overlapping, not of different stages of one species, or of corresponding stages of the two species, but of two or more non-corresponding stages of the two species, e.g., Stage I—*O. spinirostris* and Stage II—*O. helgolandica.* From Stage IV onward there is no appreciable overlap of the stages or species.

COPEPODID SIZES.

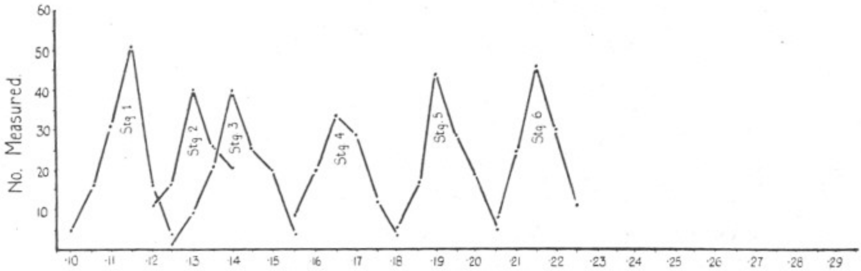
A large number of the first Copepodid stage of both species was measured, and the range of size was found to be considerable. The modal size for *O. helgolandica* was ·36 to ·37 mm., and for *O. spinirostris* ·42 mm.

THE BODY SPINES.

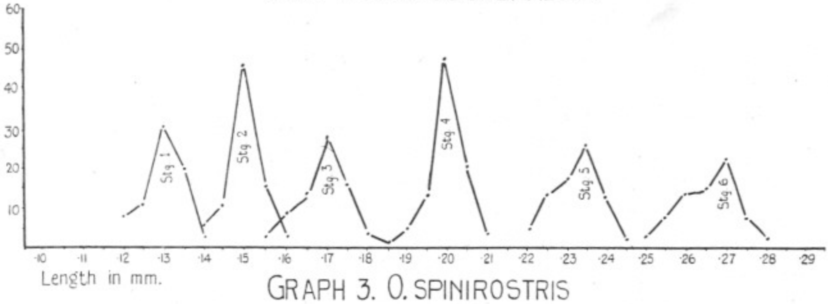
The body spines referred to above were first seen in the fifth nauplius stage of *Oithona helgolandica.* The specimen under examination was well displayed with the appendages extending straight out from the body, affording a good view of the ventral body surface. Three or four spines were observed ventro-laterally, slightly anterior to the developing maxillule, and it was indeed at first thought that they were part of the maxillary rudiment. A careful scrutiny revealed the fact that they were not attached in any way to the maxillule, but arose from the body wall itself, being directed ventrally and slightly inwards. By following them carefully a row of spines fifteen to sixteen in number and varying in size



GRAPH 1. BOTH SPECIES



GRAPH 2. O. HELGOLANDICA



GRAPH 3. O. SPINIROSTRIS

TEXT FIG. 1.

was disclosed, passing up from the region of the maxillule towards the labrum on each side of the body. They were at first to be discerned only with an oil immersion lens, and even then the fact that they were only slightly inclined to the vertical, and supported by the water in which the nauplius was mounted, made them appear for the most part only as points. As the preparation became less moist they could be seen lying inwards at an angle, but on being further depressed they became almost indistinguishable as they lay flat on the body surface.

All six nauplius stages were subsequently seen to possess these body spines. In the first nauplius stage only six or seven spines could be seen on each side, but in the last nauplius stage about twenty were visible. These spines do not arise in a straight line, but in two definite curves on each side of the body, as shown in Plates 1 and 2, Fig. 7. Although the spines are not all of equal length they vary but slightly from one to the next, their size diminishing and increasing gradually. In the later nauplius stages they are seen to extend beneath the labrum to a point where, diminishing in size, they terminate in an indefinite cluster. The closest examination of the first copepodid stage fails to reveal a trace of any such structures, so that they are to be regarded as peculiar to the nauplius alone.

A careful study of the existing literature has shown that though several workers have seen spinules and hairs on various parts of the body, and have used their presence or absence as a means of identification of species, yet there appears to be no mention of spines of anything like the size seen in this case. Their position down the sides of the body, too, is different from that shown for most of the groups of body hairs, which seem as a rule to show a transverse arrangement. Then again there appears to be no reference to any body spines in the case of marine Cyclopoida, probably because fresh material is too scanty and not easily obtained.

Since there seemed to be no exact parallel to these spines, it was decided that the investigation might be carried further with advantage. We therefore directed our attention to the study of other marine Cyclopoids in the nauplius stage in order to ascertain whether the spines were confined only to the one genus Oithona. Here the difficulty of obtaining material was encountered, inasmuch as marine Cyclopoids are by no means common even in the adult stage. However, a large marine Cyclopoid nauplius of greater dimensions than that of Oithona was found in the Firth of Forth. Its species is as yet in doubt, but it evidently belongs to one of the largest of the Cyclopoida. The chief point concerning it at present, however, is that all the specimens seen, in all stages of development, show the same arrangement of body spines as does the nauplius of the Oithonas. They were, as in the previous case, very difficult to see, but under the same mounting conditions as were used in the case of the Oithonas they appeared fairly distinctly, showing the same relative position as in that genus. In order to show that these spines were really attached to the body, and not merely seen through the cuticle, a cast of each of the species of nauplius was picked out from the material and examined under the oil immersion lens. The spines in the ventro-lateral body region were now clearly to be seen, showing that they did project from the body wall in life, and were withdrawn from their sheaths in ecdysis.

As a natural consequence of these results it occurred to us that possibly the nauplii of fresh water Cyclopoids would exhibit the same structure, although among the vast collection of literature on these species no reference to any such spines was to be found. Accordingly, after a spell of warm weather in February an expedition was made to a small fresh-water loch in the vicinity of Aberdeen, and a fine silk net was towed across it to a depth of two or three feet. On examining the resulting collection in the laboratory a number of Cyclops species was found, in varying copepodid stages, and also a few nauplii, which, from their structure, were easily identified as Cyclopoid nauplii. Some of these were carefully mounted ventral side up in a drop of water with a light coverslip placed on top. The oil immersion lens was again requisitioned for the examination. At first little could be seen owing to the rather dense character of the body of the animal, but as the preparation became less moist body spines of exactly the same type as those in the preceding species became visible, occupying the same relative positions, and directed inwards towards the middle line of the body.

Thus in three genera of Cyclopoids these spines occur in the nauplius stages, and since two, at any rate, of these genera are widely separated, one being marine, the other fresh water, it appears probable that these body spines are common to most of the nauplii of Cyclopoid Copepoda. Such a statement as this cannot be definitely made until more species have been examined, but it is in our opinion more than a possibility.

As to the meaning or function of a double row of such relatively large spines it is hard to give any accurate solution, but the probability seems to us that, from their position and distribution, they form some kind of channel leading towards the mouth, and that they assist in some way the feeding processes, or act as a guide for a feeding current. Owing to their situation an examination of the spines in a live condition is next to an impossibility. Further Cyclopoid nauplii are to be examined as soon as the material can be obtained, and the results of this extended examination will, it is hoped, be made known at a later date.

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On the Occurrence of Young Stages of Caligidæ on Pelagic Young Fish in the Plymouth Area.

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During my researches on the vertical and seasonal distribution of young fishes I soon noticed that occasionally a specimen was found to which a Caligid copepod in an early chalimus stage was attached. As every fish caught was examined under the lens while being measured, I kept a look out for these young stages of the parasites and all occurrences were recorded. The results of this examination are given in Table I which shows also the lengths in millimetres of all the fish thus parasitised found in the collections made during 1925 and 1926 (see **1**, **2**, **3** and **4**).

The most striking result is that out of the 57 species of fish which pass under our notice during the year the young Caligids appeared only on 7 species, namely *Gadus merlangus* (Whiting), *Ammodytes lanceolatus* (Sand-eel), Onos sp. (Rockling), Clupea sp. (probably Pilchard), Trigla sp. (Gurnard), *Caranx trachurus* (Horse-Mackerel), and Rhombus sp. (Turbot or Brill). Furthermore, of these 7 species the whiting and the sand-eel were the only two parasitised regularly.

In Table I it will be seen that no parasites were found on the whiting except on specimens of about 11 mm. in length and over. Now it is at about this length that the young whiting starts its association with the jellyfish Cyanea, living under and around the umbrella surface. It seems possible that this apparent preference for the early stages of Caligids to attack the young whiting may be indirectly due to this fish's habit of associating with Cyanea. It is at any rate curious that no parasites were found on such closely related Gadoids as the pollack and the poor-cod (*G. minutus*). It may be that the early stages of Caligids are responsive to a passing shadow, thus enabling them to find their future hosts. Under such circumstances they might tend to congregate under the Cyanea and thus find the small whiting sheltering there. It is interesting that of the other species of young fish recorded as having parasites, the rockling have the habit of sheltering under drift weed, and the horse-mackerel also associate with large medusæ as do the whiting. The young sand-eels might also be more liable than other fish to pick up the parasites on account of their habit of swimming in dense shoals.

Little is apparently known of the early life-history of the Caligids. Wilson (**6**) says of *Caligus rapax* that at the right seasons the chalimus stages of development may be found attached to the fins and scales of flounder and cod. I have myself seen chalimus stages fixed in large numbers to the fins of mullet (**5**), though this was admittedly under crowded circumstances. It would however be rather expected that the normal hosts for the early chalimus stages are the larger and adult fish on which the parent Caligids live. In that case the attachment of young stages on the pelagic young fish would rather be of chance occurrence, and this is upheld by the few recorded instances among the many thousands of fish that I have examined.

The chalimus stages were almost always found fixed either on the head itself or somewhere near it, and usually the former. Occasionally young fish were found with more than one parasite attached, the greatest number being five on a specimen of *G. merlangus*, 26 mm. long, on July 1st, 1925, and four on an *A. lanceolatus*, 30½ mm. long, on the same date. The number of fish infested compared with those available for attack was however on the whole low. For instance, I have counted up all the whiting of 11 mm. and over caught, and they amounted to 231 in 1925, and to 389 in 1926 ; of the former 22 were parasitised and of the latter only 13.

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TABLE I.

Occurrence of Chalimus Stages of Caligids on Young Fishes.

		Length in Millimetres of Fish carrying parasites.						
Date.	Depth in metres.	*Gadus merlangus.*	*Ammodytes lanceolatus.*	Onos sp.	Clupea sp.	Trigla sp.	*Caranx trachurus.*	Rhombus sp.
29.iv.25	12·5	–	20	–	–	–	–	–
19.v.25 L4	9·9	–	18½	–	–	–	–	–
,,	20·8	13½ : 11	12	–	–	–	–	–
,,	32·6	–	18	–	–	–	–	–
17.vi.25 (i)	29·8	19	–	–	–	–	–	–
,,		10 : 16 : 19½	–	–	–	–	–	–
18.vi.25 (iv)	26·8	30	–	–	–	–	–	–
18.vi.25 (vi)	19·4	11½	–	–	–	–	–	–
19.vi.25 (vii)	16·6	–	33	–	–	–	–	–
,,	25·8	10½	–	–	–	–	–	–
19.vi.25 (viii)	S.	23½	–	–	–	–	–	–
,,	3·6	33	33	–	–	–	–	–
,,	13·9	26 : 33 : 24½ : 26½	–	–	–	–	–	–
1.vii.25 A.	2	–	30½(4)	–	–	–	–	–
,,	19·8	26(5)	–	–	–	–	–	–
,,	23·1	12(2)	–	–	–	–	–	–
1.vii.25 L4	3·5	–	21	–	–	–	–	–
,,	21·3	16(2) : 27½(3)	–	–	–	14 : 12	–	–
,,	27·1	15	–	–	–	–	–	–
,,	36·7	–	16	–	19	–	–	–
16.vii.25	16·5	18	16½	–	–	–	–	–
,,	22·2	–	18 : 15	–	–	–	–	–
,,	32·3	–	19	–	–	–	–	–
16.vii.25 m.n.	25·8	–	18 : 15	–	–	–	–	–
29.vii.25	25·8	42	21	–	–	–	–	–
26.iv.26	20·8	21½	–	–	–	–	–	–
6.v.26	20·4	25 : 29 : 15 : 24	–	–	–	–	–	–
,,	37·1	–	–	7½	–	–	–	–
19.v.26	17·6	–	18	–	–	–	–	–
3.vi.26 (ii)	4·4	25 : 39 : 25	–	–	–	–	–	–
4.vi.26 (iv)	4	24½ : 20½	–	–	–	–	–	–
4.vi.26 (v)	10	15 : 35	–	–	–	–	–	–
4.viii.26	S.	–	–	–	–	–	–	10
,,	3·5	50	–	–	–	–	–	–
,,	9·5	–	–	–	–	–	14	–
,,	22·2	–	–	–	–	–	13	–

Note.—The small figures in brackets indicate the number of parasites present on the fish in question when more than one.

On the Biology of Sagitta. III. A Further Observation on the Growth and Breeding of *Sagitta setosa* in the Plymouth Area.

By

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

Naturalist at the Plymouth Laboratory.

With 1 Figure in the Text.

In a previous paper an account was given of the breeding and growth of *Sagitta setosa* throughout a year (**2**). The results appeared to show that the last spawning took place in October and the resulting offspring lived through November and December without maturing and that by February there were indications that a number were spawning. At the end of the following April and beginning of May a complete spawning population was formed. Owing to the large size at which these matured it was assumed (**2**, p. 148) that they had been the offspring of adults spawning in February. The true trend of events was however by no means clear as the increase in average size from January to May was very even (**2**, Plate II). There was a distinct difference at this period between *S. elegans* and *S. setosa*. In *S. elegans* a spawning population of individuals all about the same length was produced in February which apparently gave rise to a brood which had grown to a large size by April and May, and the change in size from February to May was much more abrupt than in *S. setosa* (**1**, Plate I). It was clear that while the February curve for *S. elegans* showed very little variation in size for the majority of the population caught, the population in May tended to be very widely dispersed. In *S. setosa*, on the other hand, there was a gradual narrowing down of the dispersion until a spawning population with little variation in length was produced by May.

It was felt that it might be worth while examining this period for another year for *S. setosa*, and accordingly observations were made in exactly the same way as previously from December, 1931, to May, 1932.

The results are given in Figure 1 where the curves show the percentage length-distribution of samples of *S. setosa* taken in oblique hauls of the ring-trawl on the dates given. On these curves are superimposed the stages of development of the Sagitta as explained in Plate I of **1**. This

FIG. 1.—The percentage size distribution of *Sagitta setosa* caught in the ring-trawl on the days given. The black, cross-hatched, and shaded areas represent the various stages of development. For further explanation, see **1**, Plate I.

figure shows, as in the previous results (**2**, Plate II), the gradual closing up of the length-distribution of the population until apparently a spawning population was formed in May. It appears, however, on this occasion that there was a much smaller proportion of ripe individuals in February and that these tended to disappear in March, there being a comparative absence of the individuals above 11 to 12 mm. in length which appeared in the previous year. From an examination of Figure 1 it is open to question whether the May spawning population may not be formed of a mixture of the offspring of the October spawners which have lived right through the winter and not matured until May, and of the offspring of the February spawners which have grown quickly to a large size by May. It seems natural that any offspring produced in February must have grown to form the May adults as there is no indication of any small unripe individuals in May. On the other hand, the ripening in February may have been premature and the spawning a failure.

It seems that the method adopted here is inadequate to clear this point up and that similar observations should be supplemented by finer tow-nettings to search for eggs and very young stages in February and March.

The confirmation given by the general trend of the curves that the complete spawning population is not formed until May is however striking and as such constitutes a distinct difference from the trend of events during the same period of the year for *S. elegans*. It is felt that it is unnecessary to print the tables of measurements here as in the previous reports (**1** and **2**) since Figure 1 gives all the necessary data. The actual numbers caught since the last date given in the previous publications are inserted in Table I.

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2. —— On the Biology of Sagitta. II. The Breeding and Growth of *Sagitta setosa* J. Müller in the Plymouth Area, 1930–31, with a Comparison with that of *S. elegans* Verrill. *Ibid.*, Vol. XVIII, No. 1, pp. 147–160, 1932.

TABLE I.

Total numbers of *S. elegans* and *S. setosa* in half-hour Oblique Ring-trawl Collections.

1931.	*S. elegans.*	*S. setosa.*	1932.	*S. elegans.*	*S. setosa.*
Sept. 17th	420	28,530	Jan. 19th	124	43
,, 24th	200	12,560	,, 26th	300	415
Oct. 1st	20	4,880	Feb. 3rd	195	260
,, 8th	+	2,520	,, 10th	128	505
,, 15th	–	8,780	,, 17th	90	535
,, 22nd	20	9,300	Mar. 9th	–	1,550
,, 29th	20	8,040	,, 16th	15	2,810
Nov. 25th	20	2,340	,, 23rd	–	119
Dec. 4th	15	180	,, 30th	5	248
,, 9th	50	730	April 5th	–	700
,, 16th	320	1,760	,, 14th	–	11
,, 22nd	60	1,090	,, 20th	–	9
,, 30th	10	665	,, 28th	3	13
1932.			May 4th	–	11
Jan. 7th	60	530	,, 11th	–	284
,, 12th	250	410	,, 19th	90	599

On the Biology of Sagitta. IV. Observations on the Natural History of *Sagitta elegans* Verrill and *Sagitta setosa* J. Müller in the Plymouth Area.

By

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With 3 Figures in the Text.

VERY little is known of the habits and life-cycles of any of our plankton animals throughout the year. In this report an attempt is made to piece together the results of studies of different aspects of the natural history of *Sagitta elegans* Verrill and *Sagitta setosa* J. Müller in the offshore waters near Plymouth, to see how far we can get towards making a complete picture of the two species.

I have already published three reports attempting to give an idea of the growth and breeding of Sagitta throughout the year (**9**, **10**, and **11**), and an account of its changes in vertical distribution from day to night (**8**). In the present paper I shall give results of observations on the vertical distribution of the two species in the daytime, together with data on their relative abundance during the seasons, and review these results and those on breeding and growth as a whole. The paper is accordingly divided into three parts: 1, on the vertical distribution; 2, on the seasonal abundance; and 3, the whole picture as far as indications show at the moment.

THE VERTICAL DISTRIBUTION OF *S. ELEGANS* AND *S. SETOSA*.

Collections were made in 1926, during the period from April to September inclusive, with the 2-metre stramin ring-trawl. Some of the results of these collections have already been published, namely, on the young fishes (**7**) and on the copepod, *Calanus finmarchicus* (**6**). The full details of collecting have been given in the first of these publications (**7**), so that it will be sufficient here to give only the actual results of the collections. These are shown in Table I and in the diagrams of the vertical distribution in Figure 1. In this figure are given the percentage vertical distribution in the daytime at different times of the year for *S. elegans* (above) and *S. setosa* (below). The actual distributions on the days in question can be seen at a glance from the figure. It is, however, necessary

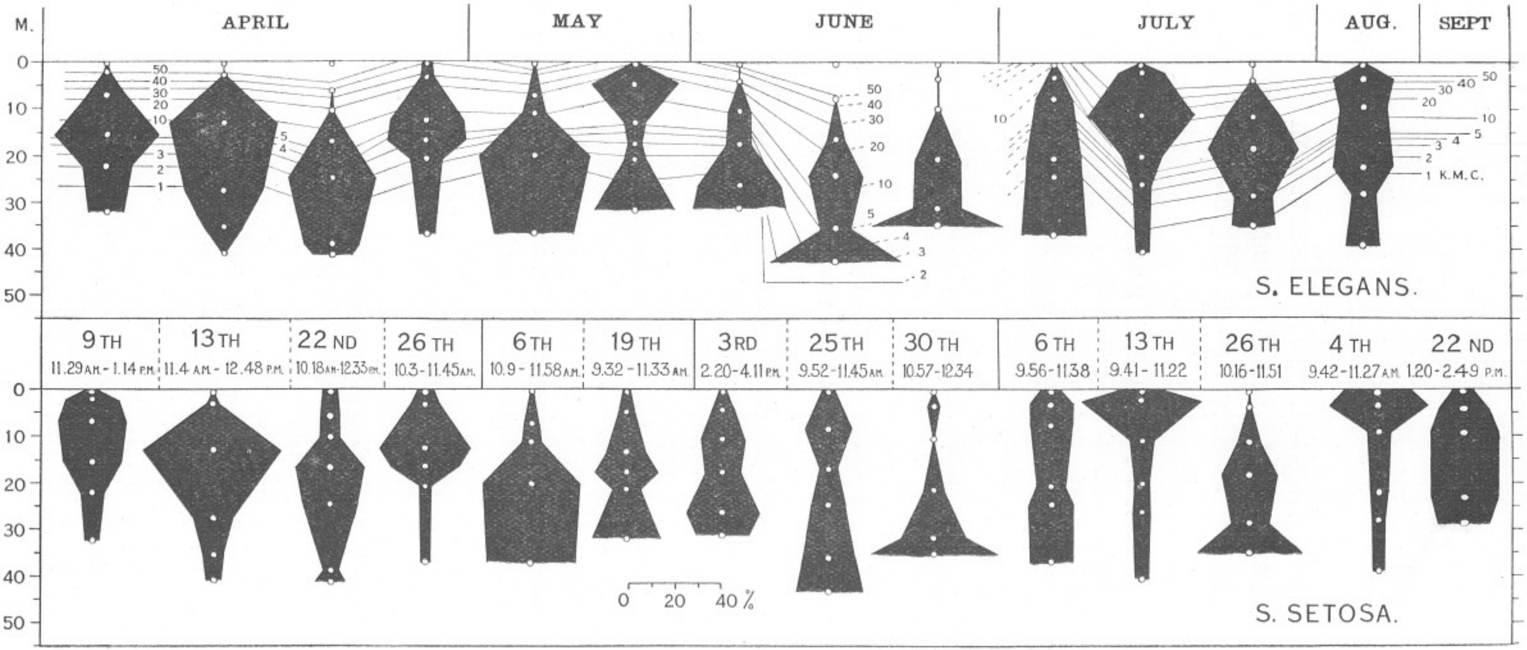

FIG. 1.—The percentage vertical distribution of *Sagitta elegans* and of *S. setosa* in the daytime on the dates given in 1926. The white spots and black circles indicate the average depths at which the hauls were made. The times given are Greenwich Mean Time and denote the time at which the first haul in a series was begun and at which the last haul was finished. In the upper half are superimposed the curves of equal light intensities in kilo metre-candles based on transparency measurements with the Secchi disc at the time of collecting and estimated air illuminations (see text). On June 30th there was no transparency measurement.

to point out that this distribution relates only to a population such as is sampled by the stramin material of which the ring-trawl is made. On the whole, therefore, the majority of the early stages, probably from about 7 or 8 mm. in length and less, will be missing.* It must also be realised that these diagrams show the distributions of the populations thus sampled *as a whole ;* it has already been shown by others and myself (**8**) that there is a tendency for the younger animals to be nearer the surface than the older. It is probable though that on account of the selective capacity of the stramin net our data deal mostly with the larger individuals so that we have a fairly true idea of the behaviour of the average-sized full-grown individuals ; the very small and very large will also usually be too few in number to make any very marked difference in the precentage figures.

At the time the collections were taken observations were made on the weather and sky conditions, and also on the transparency of the water by means of a Secchi disc. These observations are published in the complete log given on pages 668 to 670 of a previous report (**7**). An attempt has here been made to translate these observations into the rather more definite terms of light intensity. For the past two years Dr. W. R. G. Atkins has kept a continuous light intensity recorder in action with the recording photo-electric cell on the roof of the Plymouth laboratory (**3**). From studying the curves of intensity thus obtained he has gained a fund of knowledge on the strengths of light to be found at different times of the year under varying weather and sky conditions. On the basis of my observations at the time of collecting he has very kindly given me the approximate light intensities to be expected under the various weather and sky conditions. As each series of collections took about two hours it is necessary to decide on a time on which to base the light intensity approximations, and the times taken are those about midway through the collecting periods.

I give on page 562 the figures for light intensity† given me by Dr. Atkins, the times on which they were based, and also the depths at which the Secchi disc disappeared on the days in question.

From the readings obtained by means of the Secchi disc I have calculated coefficients of absorption for the days in question using the formula $\mu = \frac{1{\cdot}7}{\mathrm{D.}}$ given by Poole and Atkins (**2**, p. 310). It must be realised that this formula is approximate only, being the average of a number of rather widely varying readings as Poole and Atkins' table shows (**2**, p. 310).

Using the coefficients of absorption thus obtained and allowing for a

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* I have confirmed that this is so by comparison with silk net catches at about the same time.

† Based on carbon arc carbonisation.

reflection loss of 15% (Poole and Atkins, **2**, p. 309), I have calculated what the light intensity might have been beneath the sea's surface using the figures for air illumination given below. From these results I have inserted in Figure 1, on the diagrams for *S. elegans*, the lines of equal intensities for 50, 40, 30, 20, 10, 5, 4, 3, 2, and 1 k.m.c. (On June 30th and Sept. 22nd no Secchi disc observations were made and therefore no intensities could be calculated.)

It cannot be too strongly insisted that these light intensity figures are not actual data obtained at the times of collecting, and that while the surface illuminations may reasonably be supposed to lie fairly near the truth the coefficients of absorption as given by the Secchi disc are only very approximate, the effect of a slight increase or decrease in transparency having a comparatively greater effect on the penetration of light than wide variations in surface illumination. I have, however, inserted these calculated results as they probably give a more concrete guide to the light conditions beneath the sea on the days on which collections were made than would such expressions as "cloudless" or "dull."

1926.	Time.	k.m.c.*	S.D. metres.
April 9th	12 p.m.	85	10–12
13th	11.40 a.m.	85	10–12
,, 22nd	11 a.m.	115	10–11
,, 26th	10.45 a.m.	50	11·5–13
May 6th	10.45 a.m.	82	9·5–9
,, 19th	10.15 a.m.	40	11–13
June 3rd	3 p.m.	70	10
,, 25th	10.30 a.m.	100	19·5–20·5
,, 30th	11.30 a.m.	115	—
July 6th	10.30 a.m.	26	14
,, 13th	10.30 a.m.	122	13
,, 26th	10.50 a.m.	115	12
Aug. 4th	10.20 a.m.	106	9
Sept. 22nd	2 p.m.	50	—

* 1 kilo metre-candle=1000 m.c.

With this understanding, then, we can examine the diagrams in Figure 1. We notice that from April to June there is a distinct tendency for the *Sagitta elegans* to move deeper in the water; that while in April they are mostly concentrated around about 15–25 metres, in June they are mostly well below the 20-metre level, and indeed judging from the low numbers caught (see Table I) it seems probable that the majority may have been lying considerably deeper than the lowest level sampled. At the same time there are differences to be noticed from day to day, slight rises or falls in the depths at which the animals are most abundant. It is interesting to note that these differences appear to be definitely correlated with the strength of the light, rising and falling in agreement with the lines of equal intensities.

Bearing in mind the limitations of our method also it is interesting to see that during this period the Sagitta have certainly avoided the high-light intensities from about 20 k.m.c. upwards. There is also an indication that in May and June the regions of maximum abundance lie even below 5 k.m.c., this perhaps being an indication that with advancing age the Sagitta become more sensitive to light. The only exception to this is on May 19th when a small secondary region of maximum abundance appears at 5 metres; examination of the Sagitta has, however, shown that this maximum was composed entirely of very small individuals and all the larger animals were deep down ; the numbers caught on this day also were extremely low.

When now we examine the diagrams for July, August, and September the indications are quite materially different. We find on the three bright days, July 13th and 26th and August 4th, a great number of Sagitta up above the ten-metre level where they must have experienced light intensities of over 20 k.m.c., many living in 30, 40, and even 50 k.m.c.* These are intensities which the Sagitta very definitely seemed to avoid earlier in the year. It is also interesting to note that on July 6th, when the weather was very dull and cloudy and these high-light intensities were not even to be found on the surface itself, the Sagitta were much more evenly distributed from the upper layers downwards, and showed no definite massing at any depth as they did on other days. They were, however, absent at the surface itself.

An examination of the diagrams for *S. setosa* shows exactly the same type of results. In this species, however, the animals are almost consistently a little higher in the water than *S. elegans*. In a previous report on the distribution of *S. setosa* at dusk (**8**, p. 396) it was stated that " on the whole there is a tendency for all stages to be slightly higher in the water than the corresponding stages of *S. elegans* at the same time : whether this difference is shown also in the daytime we cannot say until further observations have been made." This suggestion then would appear now to be confirmed.

We notice also the same rising towards the surface in July and August, and the tendency towards an even distribution from the surface downwards on July 6th, and also on September 22nd, another dull day, but on this day hardly any *S. elegans* were caught. It seems almost as though at

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* This does not hold so well on July 26th, but the conditions may not have been correctly estimated.

this time of year the lower limit of light intensity above which the Sagitta are perhaps stimulated to move upwards towards an optimum is very high, and that below this limit they become indifferent to light, a phenomenon that would only have appeared after dusk intensities earlier in the year. It is interesting that the copepod *Anomalocera patersoni* shows a parallel behaviour. This is an animal which on bright sunny days crowds right near the surface, and it also shows a tendency to become more evenly distributed from the surface downwards on dull days (see **4**, p. 585 and Fig. 7). One wonders whether after such dull days Sagitta would migrate at all at night.

If we compare the results for Sagitta given in Figure 1 with those in a previous publication (**4**, p. 577 and Fig. 5) recording similar observations made in 1925 we find a general confirmation. On that occasion the correct identification of the Sagitta had not been made and the two species were grouped together as *S. bipunctata*. The diagrams given in Figure 5 of **4** appear, however, to be so like those for *S. elegans* in 1926 given in Figure 1 here that it is probable that they refer to this species. The 1925 results also show the sudden rise of Sagitta into the upper layers during July and August, and the avoidance of the actual surface itself which is more characteristic of *S. elegans* than of *S. setosa*.

This appearance of Sagitta in the upper well-illuminated layers in July and August, and perhaps September, is very striking. I have already shown that the copepod *Calanus finmarchicus* shows the same behaviour (**6**). A similar change in vertical distribution was also shown by *Tomopteris helgolandica* in 1925 (**4**, p. 578 ; Fig. 5, and pp. 575–576) although they did not seem to rise so near the surface. The post-larval young of teleostean fish also showed a similar type of change, the young of summer spawning species tending on the whole to live nearer the surface than those of spring spawning species (**7**, p. 646).

That animals belonging to such widely different groups should all show this same type of change in behaviour at this period of the year is very remarkable and it must surely indicate a phenomenon of rather fundamental importance, and may have some significance in the relation of vitamin content (**12**).

THE SEASONAL ABUNDANCE OF *S. ELEGANS* AND *S. SETOSA*.

Since February, 1930, regular collections, usually at weekly intervals, have been made with the 2-metre stramin ring-trawl at a position 2 miles east of the Eddystone. These were oblique hauls of half an hour's duration (see **7**, p. 640). The numbers of *S. elegans* and *S. setosa* in these catches have been recorded and for most dates are already published in Tables in **9**, **10**, and **11**. The results of any collections not yet published are given in Table II at the end of this paper. The numbers of Sagitta caught in each haul during the period February, 1930, to September, 1932, are shown graphically in Figure 2 in which the curve for *S. elegans* is the unbroken line and that for *S. setosa* is the broken line. In the lower half of this same figure (Fig. 2) are given the percentage proportions of the two species in each catch (*S. elegans*, black ; *S. setosa*, white). It can be seen at once from these percentage figures that during the period examined there has been a change over in the composition of the catches from almost pure *S. elegans* in 1930 to almost pure *S. setosa* in 1932. A similar preponderance of one species over the other in different years has also been shown by Meek (**1**) for the North Sea.

As regards the actual abundance there appears to be a regular periodicity in the curves. That for *S. elegans* shows two periods of maximum abundance both in 1930 and in 1931, namely, in February and in July, August and September in 1930, and in March and in August-September in 1931. After this date its numbers died down too low to show significant changes, though they are slightly indicated in January and in August in 1932.

The curve for *S. setosa* also appears to show two periods of maximum abundance both in 1931 and in 1932, namely April and a period starting in August and lasting until November in 1931, and in March and in August to November again in 1932 (see Table II, p. 573). In 1930 *S. setosa* was not sufficiently abundant to give significant results.

With our knowledge of the breeding periods of Sagitta one would assume that the increase in numbers shown by both species in these oblique haul collections was due to an increase in stock following the successive summer spawnings. This stock of *S. elegans* appears to die down in September after the last spawning for the year, while the stock of *S. setosa* appears to die down in November after the last spawning of the year, which for this species occurs in October. During the winter months their numbers are very low. From further observations it appears, however, that this impression may be false. From July, 1927, until May, 1928, collections were made with a stramin plankton net fishing immediately above the bottom (**5** and **7**, p. 647). These collections were made at three positions offshore, usually at weekly intervals, and each haul was of half an hour's duration. The numbers of Sagitta taken in these collections are given in Table III, in which also are given the average catch per week and these averages multiplied by 8·5 (**7**, p. 647) to make them comparable with those of a two-metre stramin net.

Examination of Table III shows that there is no indication whatever of the great diminution of numbers of Sagitta shown by the oblique hauls in the winter months in Figure 2.

It is unfortunate that oblique haul collections are not available for the same twelve months as those in which the bottom-net catches were made.

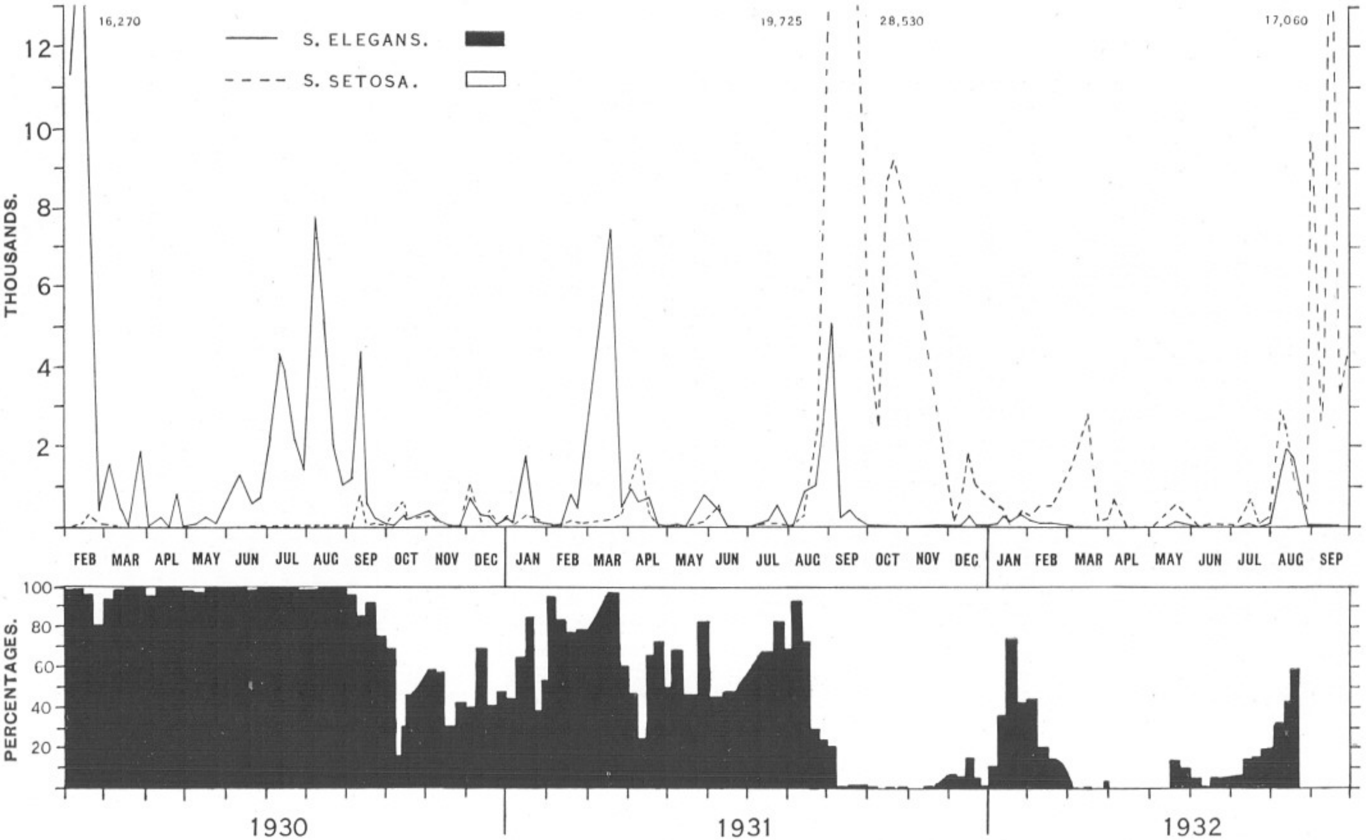

FIG. 2.—Above, curves showing the actual abundance of *S. elegans* (——) and *S. setosa* (– – – –) in half-hour oblique hauls with the 2-metre ring-trawl made usually at weekly intervals during the years 1930, 1931, and 1932. (The numbers are in thousands.) Below, the percentage composition of the Sagitta populations during the same period; *S. elegans*, black; *S. setosa*, white.

N.B. As shown in the text on page 565 the picture of actual seasonal abundance produced by the upper curves may be fallacious, in that at certain periods of the year the Sagitta may be below the lowest layer sampled by the net.

But in view of the consistency of the results shown by the oblique hauls it seems permissible to assume that in the twelve months in 1927–1928 if oblique hauls had been available the same dying down in numbers would have been shown during the winter months as in other years. This would indicate that the decrease in numbers does not represent an actual dying off of the Sagitta, but is due to a descent of the animals to the bottom layers, either very close to the bottom itself or at any rate below the deepest level reached by the oblique hauls. I have indirect confirmatory evidence that this may be so in that in the bottom-net catches the copepod, *Calanus finmarchicus*, did show a genuine diminution in numbers in the winter months as it does in the oblique hauls. If Sagitta too dies down it should also have shown a diminution in the bottom catches as did Calanus, but as we have said this was not so.

There is furthermore evidence that most small catches of Sagitta occurred in the bottom net during the months May to October ; and it is significant that in July, August, and September, at any rate, the Sagitta are high in the water. Possibly also *S. setosa* may be high in the water in October as it is spawning during that month—the bottom-net catches for October were almost all *S. setosa*, showing that it predominated over *S. elegans* at that period. One cannot help feeling that simultaneous oblique and bottom hauls would show that generally when the numbers of Sagitta were low in one net they would be high in the other and *vice versa*. There is, however, a possibility that there may be a genuine diminution in numbers in May and June as both the oblique hauls and the bottom hauls show low numbers in these months ; but the number of observations made with the bottom net in these months is insufficient to draw definite conclusions, and I have already shown that on a very bright day in June the Sagitta may be driven right to the bottom and only appear in larger numbers in hauls in the upper water layers at night (**8**, p. 404). In the daytime the oblique hauls would fish for the majority of the time in the upper unpopulated layers and would consequently give small catches.

A complete analysis of the two species in the bottom-net catches was not made as the results would not have warranted the labour, seeing that oblique haul catches were not available at the same time. But an examination of occasional catches showed that while in the period June, 1927, to February, 1928, *S. setosa* predominated completely, after that date *S. elegans* and *S. setosa* were present in about equal proportions.

The results so far obtained emphasize that in a study of the seasonal distribution of Sagitta it is essential that all water layers be sampled from the very bottom to the surface if we are not to be misled in our conclusions. I have already shown this to be so for adult *Tomopteris helgolandica* (**4**, p. 576).

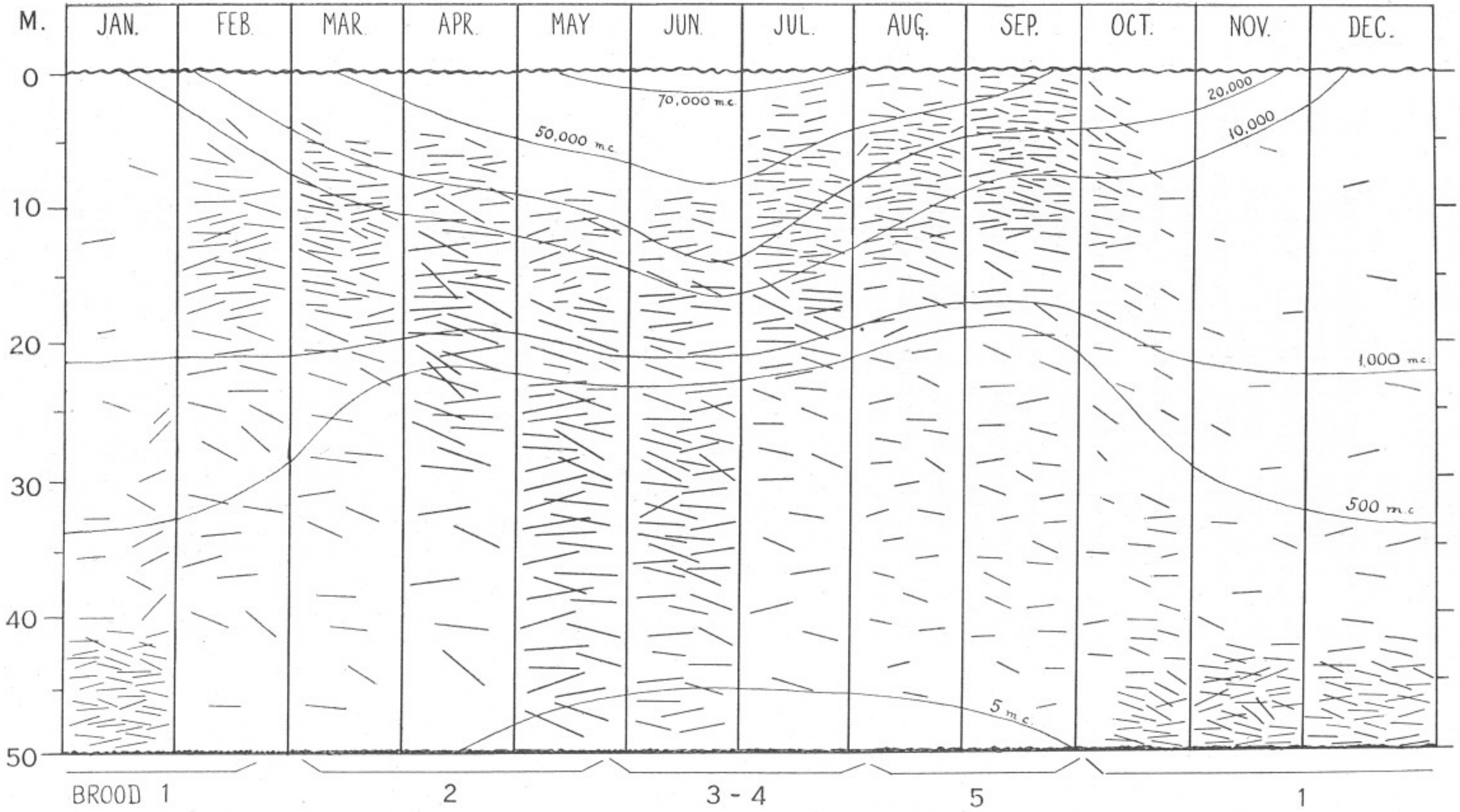

FIG. 3.—Hypothetical picture of vertical distribution of *S. elegans* throughout the year at midday on a bright day. The Sagitta are drawn to scale (half natural) to indicate the successive changes in the sizes of the adults of the different broods. Curves of equal intensities of light in metre candles that might be expected at midday on cloudless days at different times of the year are inserted based on the work of Atkins and Poole (2).

THE NATURAL HISTORY OF SAGITTA IN OFFSHORE WATERS OFF PLYMOUTH.

When we review the results of the previous observations on Sagitta we feel that we can begin to assemble a partial picture of their life-stories and habits.

Sagitta is an animal which passes through several generations in the year, possibly 5 or 6 according to the species. During November to January there is no breeding. The adults of the different broods grow to different sizes, the adults appearing in April and May being the largest on the average. During the spring months the Sagitta are living in the upper water layers in the daytime, appearing to dwell around a depth at which a light intensity of a little below 20 k.m.c. will be found. At the same time the larger individuals tend to seek lower intensities and thus go deeper in the water which is consonant with the increased sensitivity with advancing age. At this period of the year (April and May) on dull days the Sagitta will be nearer the surface than on fine days. The brood succeeding in June appears to show a similar habit and on very bright days may retire almost to the bottom itself. But the new broods appearing in July and August show a marked difference, not avoiding on bright days those depths in the upper water layers where intensities of 20 k.m.c. and over may be found. At this time of year if the day is dull they appear to be indifferent to the light and may be found in equal numbers at almost any depth. The offspring of the last spawning brood in September in *S. elegans* and October in *S. setosa* perhaps (if the bottom net results be rightly construed) leave the upper layers and keep near the bottom until the following February, when they are mature and ready to spawn, at which time they appear to rise in the water again, as is indicated by the sudden increase in numbers of *S. elegans* in the oblique hauls in February. Throughout the year, at any rate in the summer months, the vertical distribution of Sagitta changes daily when night comes on, the animals either migrating right to the surface at dusk or exhibiting other types of distribution ending in an even distribution at night according to their position in the water on the previous day.

This is the general indication that appears to come out of these researches and I have expressed this idea graphically in Figure 3 for *S. elegans*. In this figure the Sagitta are drawn to scale (half natural size) to show the difference in size of the adults at different times of the year. I have also inserted the curves of equal intensities of light that might be expected about midday on cloudless days (based on Poole and Atkins, **2**). Of special interest is the brightening of the deeper layers in the winter owing to the increasing transparency of the water perhaps due to the scarcity of plankton animals at that time. (For an idea of the approximate strengths of light see **8**, p. 400 and Fig. 5.) It must be realised that this figure is very hypothetical as it cannot be said yet that any of our results are sufficiently definite to supply the whole picture, especially during the period November to March inclusive; but I have given it in this form to clarify our ideas on the subject so that we may see the whole problem at a glance, and in order that others may be stimulated to make a completer survey of this and other plankton animals.

SUMMARY.

1. Observations are given on the vertical distribution of *Sagitta elegans* and *S. setosa* in the daytime.

2. An account is given of the seasonal abundance of both species of Sagitta throughout the year as shown by collections made with oblique hauls with the 2-metre stramin ring-trawl and hauls with a bottom plankton net.

3. An attempt is made to piece together as much as possible of the life-stories and habits of Sagitta in offshore waters off Plymouth on the basis of these and previous observations.

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TABLE I.

Average Depths of each Haul (*D*) in Metres and Numbers of *S. elegans* (*El.*) and *S. setosa* (*Se.*) in each Catch with the 2-Metre Stramin Ring-trawl, 1926.

April 9th			April 13th (i)			April 13th (ii)			April 22nd			April 26th		
D.	El.	Se.	*D.*	El.	Se.	*D.*	El.	Se.	*D.*	El.	Se.	*D.*	El.	Se.
S.	—	3,075	*S.*	—	3	*S.*	—	115	*S.*	1	118	*S.*	9	40
2	266	13,044	*2·8*	4	202	*5·8*	37	888	*5·9*	3	131	*3·2*	19	51
7	1,695	17,135	*13*	275	2,030	*13·8*	116	1,334	*10·4*	5	140	*12·6*	83	167
15·5	4,650	14,710	*27·6*	200	570	*21·6*	304	646	*16·9*	46	464	*16·7*	86	124
22·4	2,137	6,083	*35·4*	102	323	*40·1*	41	509	*24·6*	97	363	*20·8*	36	24
32·4	1,503	3,507	*41*	12	218				*39*	61	109	*37·1*	23	19
									41·3	44	206			

May 6th			May 19th			June 3rd			June 25th			June 30th		
D.	El.	Se.	*D.*	El.	Se.	*D.*	El.	Se.	*D.*	El.	Se.	*D.*	El.	Se.
S.	1	4	*S.*	—	2	*S.*	40	13	*S.*	—	50	*S.*	—	20
7·3	16	16	*4·6*	31	4	*4·3*	92	49	*8·2*	—	200	*3·5*	22	258
11·2	25	17	*13·4*	8	9	*10·8*	1,028	92	*16·9*	33	77	*10·4*	17	20
20·4	118	79	*17·6*	6	15	*18*	1,117	83	*24·6*	96	144	*21·4*	326	354
37·1	84	72	*21·1*	8	7	*26·6*	3,784	167	*36*	54	216	*31·6*	355	1,125
			32	29	16	*31·5*	4,090	120	*43·1*	228	278	*35·2*	955	2,125

July 6th			July 13th			July 26th			Aug. 4th			Sept. 22nd		
D.	El.	Se.	*D.*	El.	Se.	*D.*	El.	Se.	*D.*	El.	Se.	*D.*	El.	Se.
S.	—	350	*S.*	14	666	*S.*	—	100	{ *S* (*i*)	—	6,550	*S.*	—	770
3·3	76	764	*2·3*	166	1,904	*3·9*	22	408	{ *S* (*ii*)	—	5,200	*4·4*	—	2,460
7·9	173	787	*11·2*	385	385	*11·5*	442	1,568	*3·5*	1,618	7,902	*9·6*	34	3,326
20·9	250	530	*20·1*	144	256	*18·5*	727	3,553	*9·5*	1,278	1,502	*23·5*	—	2,840
24·7	265	795	*26·4*	72	288	*28·7*	321	2,599	*22·2*	1,633	1,447	*28·7*	25	2,465
37·2	302	778	*40·7*	52	208	*35·1*	347	6,593	*28·2*	672	1,008			
									39·4	970	970			

TABLE II.

NUMBERS OF SAGITTA TAKEN IN HALF-HOUR OBLIQUE HAULS OF THE 2-METRE STRAMIN RING-TRAWL.

		S. elegans.	*S. setosa.*
1930			
February	4th	11,360	—
,,	12th	16,270	130
,,	19th	10,411	389
,,	26th	452	110
March	5th	1,517	93
,,	12th	455	5
,,	18th	8	—
,,	27th	1,860	—
April	2nd	24	1
,,	11th	240	—
,,	16th	21	—
,,	24th	860	—
,,	29th	39	1
May	7th	77	2
1931			
September	17th	420	28,530
,,	24th	200	12,560
October	1st	20	4,880
,,	8th	—	2,520
,,	15th	—	8,780
,,	22nd	20	9,300
,,	29th	20	8,040
November	25th	2,340	20
December	4th	15	180
,,	9th	50	730
,,	16th	320	1,760
,,	22nd	60	1,090
,,	30th	10	665
1932			
January	7th	60	530
,,	12th	250	410
,,	19th	124	43
,,	26th	300	415
February	3rd	195	260
1932			
February	10th	128	505
,,	17th	90	535
March	9th	—	1,550
,,	16th	15	2,810
,,	23rd	—	119
,,	30th	5	248
April	5th	—	700
,,	14th	—	11
,,	20th	—	9
,,	28th	3	1
May	4th	—	11
,,	11th	—	284
,,	19th	90	599
,,	25th	45	425
June	1st	13	240
,,	8th	—	3
,,	17th	6	117
July	5th	6	86
,,	14th	120	700
,,	21st	8	44
,,	27th	100	420
August	5th	1,460	2,900
,,	10th	1,920	2,460
,,	17th	1,680	1,160
,,	26th	1	470
September	1st	21	9,660
,,	7th	—	2,600
,,	14th	40	17,060
,,	21st	80	3,360
,,	29th	1	4,210
October	4th	10	910
,,	11th	—	1,320
,,	19th	280	8,280
,,	26th	—	5,780
November	14th	210	2,760
,,	22nd	26	379

TABLE III.

CATCHES OF SAGITTA IN HAULS WITH BOTTOM STRAMIN NET.

	Duration of Haul.	A.	*Rame Mud.*	L4.	Average per 30 min.	*Av.× 8·5*
2.6.27	10 min.	11			18	*153*
,,	20 min.	9				
,,	30 min.		1			
,,	,,		24			
29.6.27	,,	3,535	8,330		5,384	*45,764*
,,	,,	2,010	7,660			
8.7.27	,,	225	170	175	203	*1,725*
,,	10 min.		81			
15.7.27	30 min.	220	30	230	160	*1,360*
5.8.27	,,			190	190	*1,615*
12.8.27	,,	4,940	365	820	2,042	*17,357*
19.8.27	,,	1,980	1,640	3,620	2,413	*20,511*
25.8.27	,,	630	275	340	415	*3,528*
31.8.27	,,	2,070	1,140*	1,530*	2,470	*20,995*
6.9.27	,,	1,480	1,360	1,120	1,320	*11,220*
15.9.27	,,	67	80	260	136	*1,156*
20.9.27	,,	840	730	1,881	1,150	*9,775*
30.9.17	,,	40	505	264	270	*2,295*
4.10.27	,,	185	240	165	197	*1,585*
13.10.27	,,	115	810	210	378	*3,213*
18.10.27	,,	1,170	360	350	627	*5,330*
25.10.27	,,	350	2,270	735	1,118	*9,503*
1.11.27	,,	5,180	10,720	10,780	8,893	*75,591*
6.12.27	,,	1,580	1,950	2,720	2,083	*17,706*
15.12.27	,,	670	280	1,040	663	*5,616*
21.12.27	,,	260	840	630	577	*4,905*
3.1.28	,,	4,900	5,180		5,040	*42,840*
11.1.28	,,	1,780	1,820	4,060	2,553	*21,701*
17.1.28	,,	2,980	2,580	5,880	3,813	*32,411*
26.1.28	,,	630	580	820	677	*5,755*
3.2.28	,,	1,130	2,280	1,540	1,650	*14,025*
10.2.28	,,	5,160	670	630	2,153	*18,301*
14.2.28	,,	950	80	970	667	*5,670*
24.2.28	,,	2,160	260	1,600	1,340	*11,390*
29.2.28	,,	670	830	1,950	1,150	*9,775*
8.3.28	,,	790	420	1,220	810	*6,885*
23.3.28	,,	170	770	420	453	*3,851*
30.3.28	,,	6,860	1,680	390	2,977	*25,305*
12.4.28	,,	380			380	*3,230*
18.4.28	,,	1,490	1,960	1,090	1,513	*12,861*
23.4.28	,,	520			520	*4,420*
24.4.28	,,		1,740	3,020	2,380	*20,230*
30.4.28	,,	640	720	660	673	*5,721*
11.5.28	,,	340	180	180	233	*1,981*

* 15 min.

Vertical Distribution in *Calanus finmarchicus.*

By

A. C. Gardiner, M.A.

With 9 Figures in the Text.

Introduction.

In 1925 Hardy (1925) published a preliminary account of a " Plankton Indicator " designed to assist those engaged in fishing for Herring and Mackerel by means of drift-nets. Recently Professor Hardy has produced an improved model, smaller than the original and differing from it in that it is fitted with a diving plane and is towed from above. A full description of this instrument will shortly appear.

It is outside the scope of this paper to discuss the value of the new machine as an " indicator," in which connexion Professor Hardy has authorised me to state that he has made further experiments. In the present instance I have been concerned solely with the instrument as a means of determining the vertical distribution of one species of the zooplankton, *Calanus finmarchicus*. The results which I obtained with the instrument have convinced me that it provides a satisfactory method not only of studying vertical distribution but also of diurnal migration.

I should like to take this opportunity of tendering my thanks to Mr. Michael Graham who was responsible for much of the sea work on which this account is based.

Objects of the Experiments.

The main objects were to obtain a general idea of the distribution of the macroplankton (especially *Calanus finmarchicus*) in that area off Shields in which the spring herring fishery is centred. (See Savage, 1931, p. 17.) In addition, the extent to which the vertical distribution of this species may be expected to vary from place to place, or from day to day, was to be examined.

Five days, May 21st to 26th, 1931, were spent in the area during which five sets of observations, comprising in all some 165 collections, were obtained. The course followed on the cruise, and the position of the stations are shown in Figure 1.

The collections made on May 24th were enumerated at sea and for that reason have not been included.

Description of Methods.

Although the instruments are fitted with diving planes these were found to be too small under the conditions of use, and depths of more than 10 fathoms could not be attained. On this account the three instruments were made fast to one main warp, to the bottom end of which was attached a "kite." It is not proposed to give the actual calibrations of the apparatus, since the original kite has now been replaced by the more efficient "submarine sentry" (see Wharton and Field, 1920, pp. 406–408).

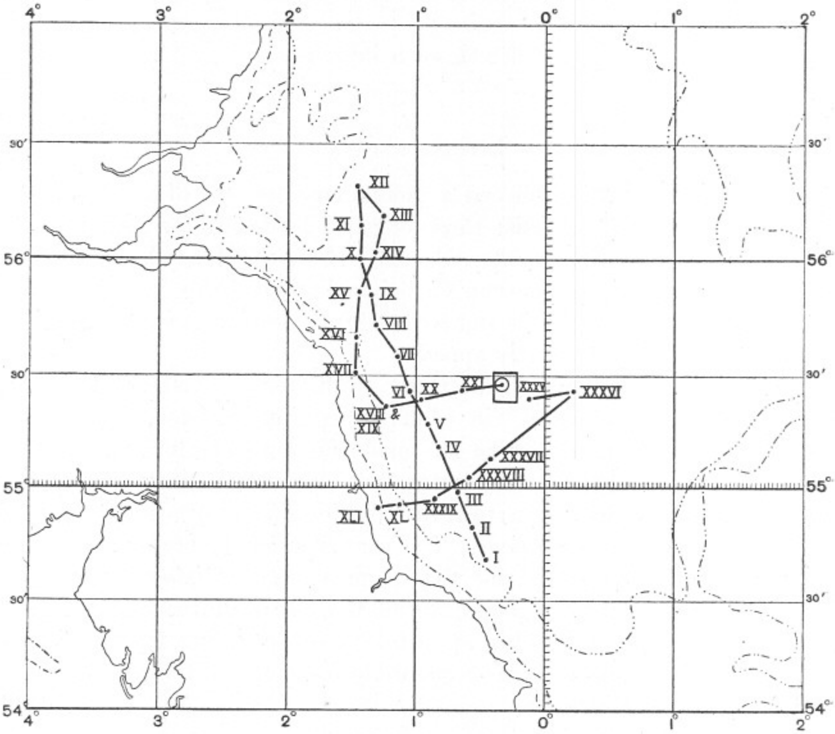

Fig. 1.—Position of Stations.

1st Day. Stations 1–9.
2nd Day. Stations 10–18.
3rd Day. Stations 19–24.
4th Day. Stations 25–34.
5th Day. Stations 35–41.

⊙ indicates Stations 22a–g.
☐ indicates Stations 23–34.

The approximate depth at which each of the three instruments fished was estimated beforehand by measuring the angle taken up by the wire as successive lengths, each of 10 fathoms, were run out. On the assumption that this angle remains constant for each length, no matter whether the particular stretch is near the surface or at a greater depth, it is a simple matter to draw the curve of the whole length, and so be able to gauge the depth at any point when the total length out is known.

The estimated depths were checked against readings of a "Kelvin Tube" attached to the kite. The greatest depth reached was 37½ fathoms which was sufficient for the greater part of the area visited. Each haul was of 20 minutes duration, which at the speed of towing meant that the hauls were about 1 mile in length. As a rule the vessel steamed for 9 miles between stations, on the completion of which distance the apparatus was lowered and towed at slow speed for 1 mile. The speed of towing was controlled by counting engine revolutions. Except at certain stations mentioned in Appendix A, p. 597, all hauls were made in daylight between the hours of 0600 and 1800 G.M.T. (Sunrise and sunset are approximately 0356 and 1958 at this period of the year.)

The silk discs used in the instrument for retaining the catch were of No. 30 silk, having, when new, 30 threads to the inch. This silk shrinks only slightly after use, and the average size of the opening in old silk is 0·7×0·7 mm.

Criticism of the Method.

The idea of fishing a number of nets at different levels on the same wire is, of course, by no means new. So far as I am aware, however, this is the first occasion on which use has been made of a number of these "Hardy" instruments to obtain collections of plankton which it is desired to treat quantitatively. On this account it will be necessary to discuss the advantages of the method and to lay stress upon possible sources of error.

Perhaps the chief advantage of the method is that it enables different levels to be sampled at one and the same time.

In the present experiment three instruments were used simultaneously at near the surface, mid-water and near the bottom, but there is no practical reason why four or more could not be used. On this account, then, the method has much to recommend it since in those cases where either a series of horizontal hauls or vertical "stage catches"* are made there must inevitably be a considerable interval of time between the first and last collections of a series. Russell (VI, 1928, p. 81), for instance, in his studies on the vertical distribution of marine macroplankton, found that the time taken to sample the six different depths comprising his first series was nearly two hours. As he points out, there is "sufficient time for the vertical distribution of the plankton to become considerably altered." There is, too, risk of the population changing (Russell, I, 1925,

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* i.e. The hauling of a vertical net up through selected distances of an entire water column.

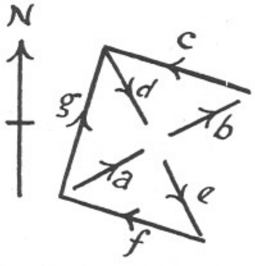
p. 777), due either to the time interval or to the fact that the samples are taken from a number of different bodies of water. The observations given by Gardiner (1931, pp. 451–452) demonstrate clearly how great this risk is.

The chief sources of error in the present experiments are due to the bottom and mid-water samplers being hauled to the surface unclosed. In the first place, of course, since both continue fishing right up to the surface the resulting samples will contain a certain proportion of individuals from the upper levels. The error will be greatest when the organisms are abundant in the upper waters and scarce in the lower layers. In the second place, the mid-water and bottom hauls are actually longer both in point of distance and time than the corresponding surface haul. These two sources of error apply no less to the use of the ring-trawl, and the question is discussed by Russell (V, 1927, pp. 558–561).

In his case the length of the haul was only 10 minutes, so that the addition of 2½ minutes (the time taken to raise the net from the deepest layer sampled to the surface) is a matter needing consideration. In the present case the length of haul was 20 minutes, so that, although the time taken to get the lowest sampler to the surface was about 2 minutes, the magnitude of the error is only half as great.

I have no means of arriving at the significance of these errors, but I have little doubt from the following that it is not great.

In series 22a to 22g, for instance, hauls were made in the manner shown in the accompanying text-figure. The traverses c, f, and g were longer than were a, b, d, and e, the former taking 28 minutes to complete, the latter 20 minutes. The whole area sampled was approximately 2 square miles. One would not expect marked differences in density of population in so small an area, nor in the course of the 3½ hours taken to complete the collections would one expect any considerable change in the vertical distribution to have taken place.



If, now, the catches in the longer hauls c, f, and g, were all bigger than those in the four remaining shorter hauls, a, b, d, and e, there would be reason to suppose that towing the bottom sampler for two minutes more than the surface one, as was done each time in the routine collections, would probably have resulted in the catches at the bottom being too big by a relatively constant amount. It is clear from the following table that the longer hauls are not the bigger.

Haul.	a	b	**c**	d	e	**f**	**g**
No. of Calanus (all three depths)	362	217	**351**	490	213	**143**	**184**

Any differences due to increased length of tow, which there might have been, have been masked by irregularities in the horizontal distribution, and I am fairly confident that this will usually be so.

The chief disadvantage of an instrument of the type used probably lies in the small size of the mouth, the diameter of which is only 3·8 centimetres, and the number of individuals captured even in a twenty-minute haul may be very small. Also it is impossible to rid oneself of the impression that a considerable proportion of the larger and more active animals will escape capture. Against this there is abundant evidence that the instrument does capture decapod and fish larvæ, since specimens of the latter up to 20 millimetres* long have been taken.

There is also the feeling that with so small an instrument the chances of obtaining a misleading picture are enormously increased should the animals be irregularly distributed, or worse still, should they be in "swarms."

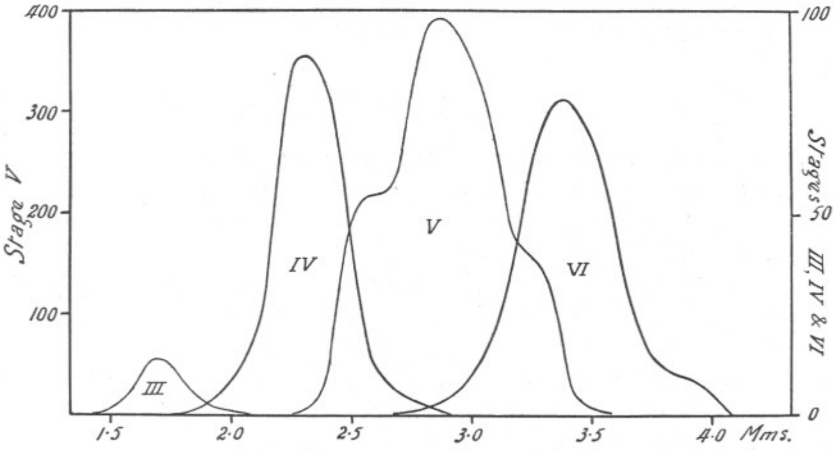


FIG. 2.—Length-frequency distribution of Calanus in Stages III–VI.

All things considered, however, I am of the opinion that the advantages outweigh the disadvantages. It would undoubtedly be better to sample more than three levels, and this presents no difficulties. It is possible, too, that a more representative catch would result from a sampler of the same type with a larger mouth.

MATERIAL.

In working out the collections, the different developmental stages of Calanus were recognised and enumerated separately. The nomenclature adopted is that given by Lebour (1916). In addition, the length of all

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* This was a lemon sole.

specimens in Stage V was determined, as well as that of a sufficient number in Stages IV and VI to give reliable modal lengths.

So large a mesh as the No. 30 silk used allows practically all the smaller species, such as *Temora longicornis* and *Pseudocalanus elongatus*, as well as the bulk of the younger *Calanus finmarchicus* to escape. It retains, however, almost all individuals of Calanus in Stage IV and, of course, the older specimens. The actual sizes retained by the mesh are shown in Figure 2, where the length-frequency distribution of Stages III–VI is given.

The population sampled by the gear during the period covered by the experiment comprised 19% in Stage VI, 49% in Stage V, and 32% in Stages IV and III. The numbers in Stage III were extremely small, and throughout the present paper have been included with those of Stage IV. As will be seen later, the percentage composition of the population in respect to age classes varied considerably from day to day.

VERTICAL DISTRIBUTION.

Full data are given in Tables IV–VII, pp. 603–606. An attempt has been made to present them graphically in Figures 3–6. In these figures the areas of the circles are proportional to the total number of individuals taken at each level. Each circle will be seen to be subdivided into, usually, three sectors, the areas of which are proportional to the numbers of individuals in Stages VI (♂+♀), V, and IV and III, respectively. These sectors are differently shaded, black representing Stage VI, cross-hatching Stage V and unshaded representing Stages IV and III. (As pointed out above, the number in Stage III retained by the mesh was very small.) The calculated depth at which each collection was made can be read off from the scale of depths on the left-hand side of the figures. Soundings at each station have been indicated by the curved line at the base of the figures. (This does not, of course, represent the actual depth contours, the vertical scale being enormously exaggerated at the expense of the horizontal.) Where the number of individuals in any collection was less than 2, the observation has been recorded as a small black circle. Reference to Figure 1 will give the distances between individual stations. Save on the third day (May 23rd), Figure 5, when seven hauls were made in quick succession (Stations 22a–g, see p. 578), stations were usually about 10 miles apart. It is important not to lose sight of this since the differences in vertical distribution, which are so immediately apparent, may result equally from the collections having been made at considerable distances from one another with, it might be, differences in thermal stratification, as from changes in the amount of light.

In addition to this graphical mode of expression, the data have been

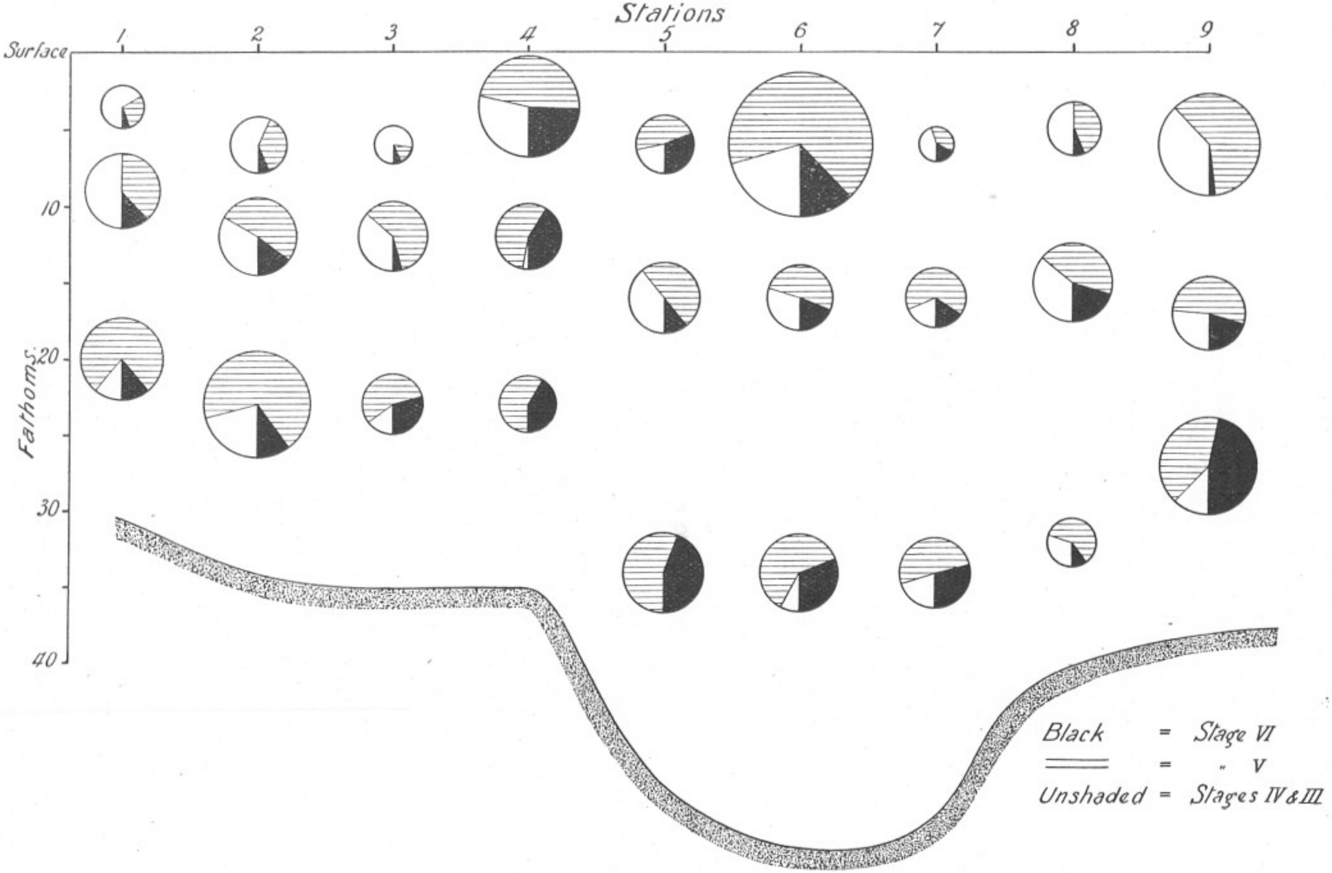

Fig. 3.—Vertical distribution of Calanus at Stations 1 to 9 (1st Day, May 21st).

summarised in Figure 7. The method adopted was to calculate the "centre of gravity" of distribution of each age class at each station. For instance, suppose the distribution to be as follows :—10 individuals at 5 fathoms, 20 at 15 fathoms, and 50 at 30 fathoms, we should then probably be entitled to say, even from three collections, that the individuals favoured the deeper water, and to determine the mean depth at which the main mass of the individuals occurred. In the case quoted this would be at about 23 fathoms. The limitations of the method, however, must be clearly understood, particularly in those cases where the numbers of individuals occurring in the surface, mid-water, and bottom collections do not show such good continuity. In other words, should large numbers of individuals be found in both surface and bottom collections whilst the mid-water one was small, the "centre of gravity," as calculated, would lie at a depth roughly half-way between the surface and bottom where, clearly, the results indicate that the greatest concentration has not occurred.

For the primary purpose for which it is proposed to use the data, namely, the study of changes in vertical distribution of the species from place to place, or day to day, the detailed diagrams, Figures 3–6, will undoubtedly provide a more accurate picture. For the secondary purpose of determining the relative abundance of individuals of different age occurring at the depths sampled at each station, the determination of the "centre of gravity," Figure 7, greatly facilitates the interpretation of the results and is almost certainly sound. Here, clearly, we are not concerned so much to find the actual depth at which the majority of the individuals lived, as to see in the samples, no matter at what particular depth they were collected, whether one age class lived above or below another.

Day 1, *May* 21*st*. Stations 1 to 9. Figure 3. Table IV.

This series of stations was worked on a line roughly parallel to the coast, extending from off Whitby to off Berwick. The day was one of bright sunshine, with a light E.N.E. breeze, force 1 on the Beaufort Scale.

The composition of the population sampled was as follows :—

Age Class.	Number.	Percentage.
VI	279	19·4%
V	792	55·2%
IV+III	364	25·4%
Total	1435	100·0

Considering, in the first place, all four age classes together, there is very little consistency in the vertical distribution of the species on this day. At Stations 1 and 2 the biggest catches were in the bottom collections. At

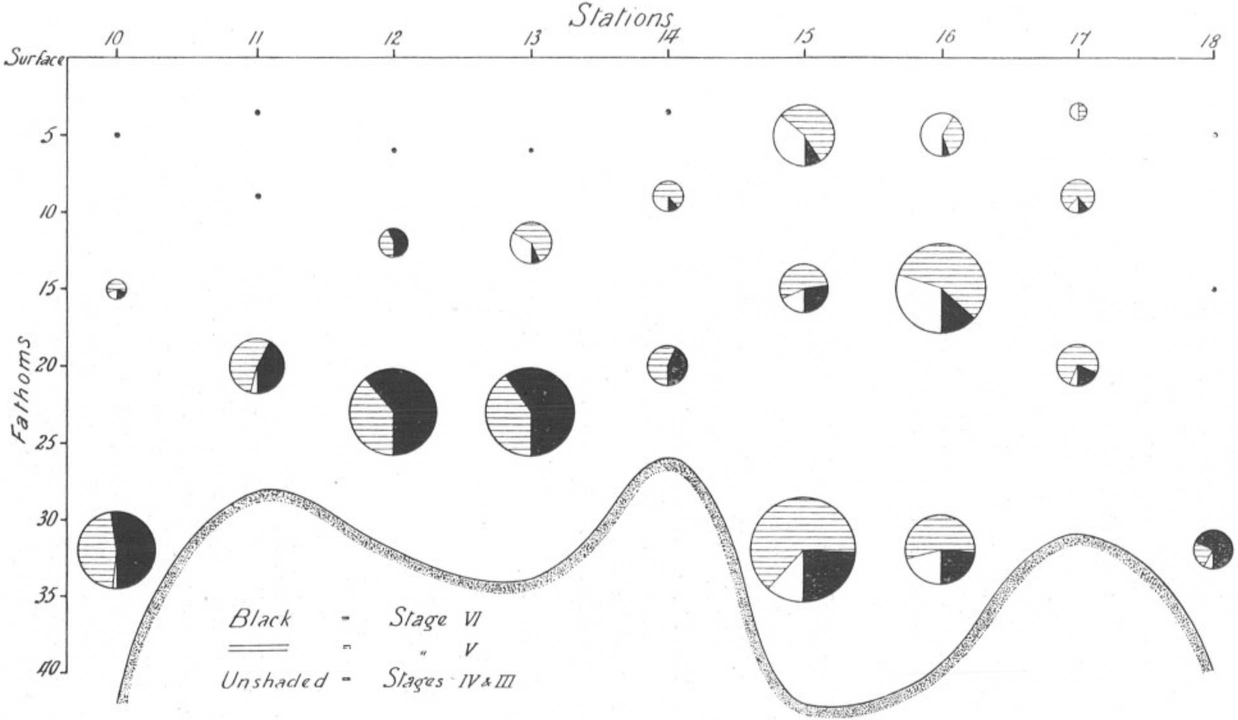

FIG. 4.—Vertical distribution of Calanus at Stations 10–18 (2nd Day, May 22nd).

Stations 4 and 6, however, surface catches greatly exceeded those at the other two depths. Stations 5, 7, and 8, on the other hand, yielded only very small surface catches, whilst at Station 9 the numbers in surface and bottom hauls were approximately equal.

As far as the behaviour of the individual age classes is concerned, inspection of Figures 3 and 7 shows that, on the whole, Stages IV and III were most abundant in the upper waters. Stage VI, on the other hand, seemed to find its optimum conditions below 10 fathoms, for in only two cases, Stations 4 and 6, did the surface collections yield the biggest catches. The " centres of gravity " of distribution of Stage V lie usually between those of Stage VI and Stages IV+III. On the whole Stage V seems to find its optimum nearer that of Stage VI than that of the younger individuals.

Day 2, *May* 22*nd*. Stations 10 to 18. Figure 4. Table V.

Leaving Station 9, of the previous evening, a line of stations was run in a northerly direction as far as 56° 19′ N. Here the ship was turned and a southerly line run, crossing the northern line between Stations 9 and 10. The line ended off Coquet Island. The day was one of heavy cloud with some rain. Wind was mainly E.N.E. and stronger, force 2–3 on the Beaufort Scale.

The composition of the population sampled was as follows :—

Age Class.	Number.	Percentage.
VI	206	33·8%
V	319	52·4%
IV+III	84	13·8%
Total	609	100·0

This day differed from the preceding one not only in that the total number of individuals captured was less than half, but also in that the percentage of adults had increased from 19% to 34%, almost entirely at the expense of the younger individuals, Stages IV+III. The vertical distribution of the species as a whole, too, differed very markedly from that of the preceding day. In only one case, Station 15, did the number of individuals taken in the surface catches exceed 30, while on two occasions none was taken, and on four only a single specimen occurred. Similarly, with one exception (Station 16) the mid-water collections were well below the average.

At the first five Stations (10–14) and at the last two (17 and 18), young individuals (Stages IV+III) were virtually absent. At the two remaining

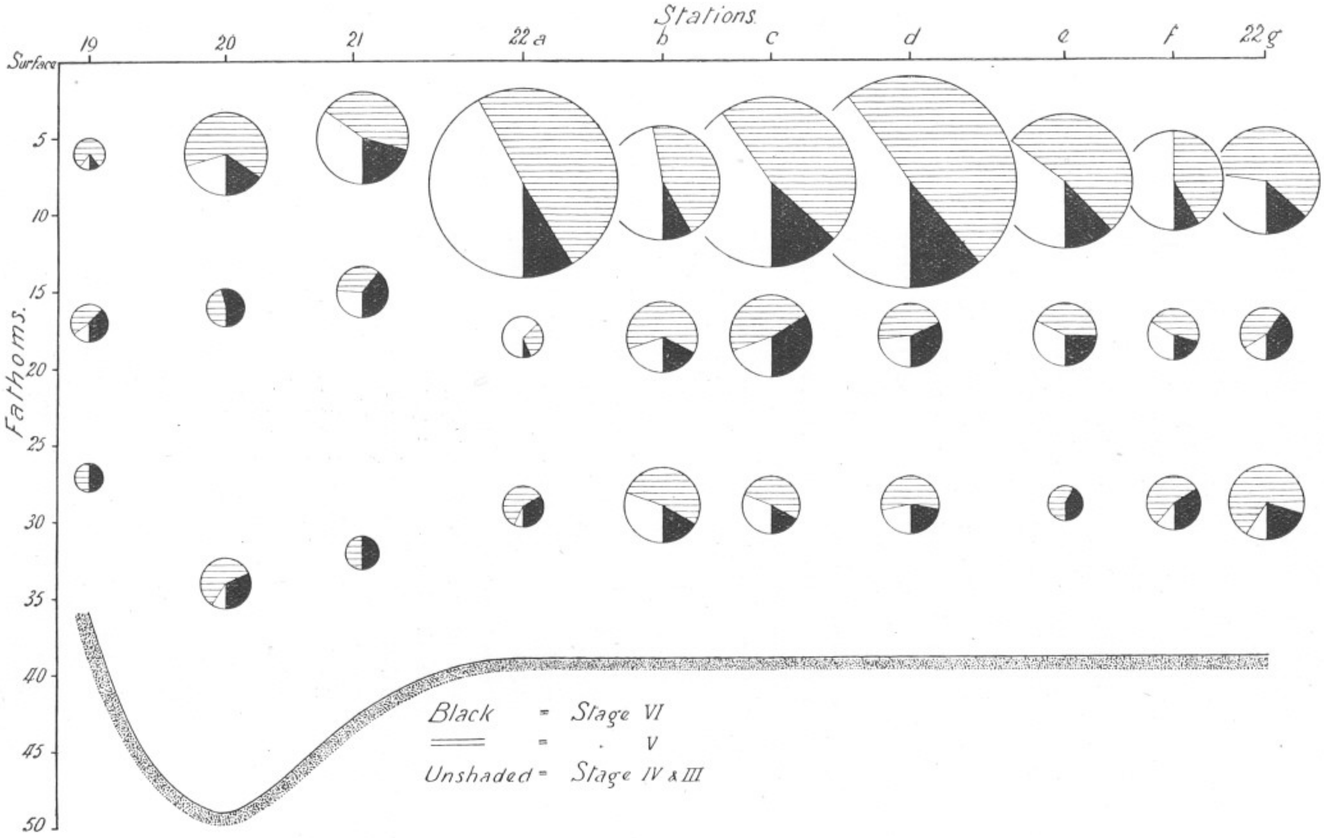

FIG. 5.—Vertical distribution of Calanus at Stations 19–22g (3rd Day, May 23rd).

Stations, 15 and 16, small numbers occurred in the collections at all three depths. The older individuals (Stages V and VI) showed a decided preference for the lower levels. As before, the " centres of gravity " of Stage V were slightly above those of Stage VI.

This day differed so markedly from the preceding one, and indeed from the two following, that it would be unwise to draw any hard-and-fast conclusions from these isolated observations. It is impossible, however, to ignore the inference that the absence of individuals in Stages IV and III has been very largely responsible for the small surface catches. Why, at the same time, adults and those individuals in Stage V have not occurred in the upper levels where there is abundant evidence from the other days that they may be present in large numbers, it is impossible to say. Conditions of illumination on this day were such that, a priori, one would have expected the surface catches to have been the biggest. It is possible, of course, that a quite superficial haul might have resulted in large catches, although the evidence from Stations 14 and 17, at which the surface hauls were taken at a depth of about 3½ fathoms below the surface, would seem to suggest that this was unlikely.

It is a disturbing thought, that in the course of quite a few miles it is possible to pass to an area where the composition of the population could show such marked differences.

Day 3, *May* 23rd. Stations 19 to 22g. Figure 5. Table VI.

Fog near the coast prevented the southerly line being continued, and a line of three stations was run in an easterly direction, after which a series of 7 Stations (22a–22g) were worked in the manner described on page 578. All seven of these stations were completed within a period of 3½ hours and represent an attempt to obtain a measure of the uniformity of horizontal distribution. The day was one of light cloud and fine haze, but with frequent sunny periods. Wind was S.E. and light, force 2 on the Beaufort Scale.

The composition of the population sampled was as follows :—

Age Class.	Number.	Percentage.
VI	345	15·7%
V	1097	49·9%
IV+III	758	34·4%
Total	2200	100·0

The vertical distribution on this day was on the whole remarkably consistent. At all save the first station the surface collections greatly exceeded those from the other levels.

In the case of all age classes, the numbers occurring in the surface hauls were the largest. The figures are as follows :—

Number of	Surface Hauls.	Mid-water + Bottom Hauls.
Stage VI	191	154
,, V	807	290
,, IV+III	643	115

In this respect this day contrasts sharply not only with the preceding one, but also with the first day, where it will be recalled the biggest numbers of Stage VI, with only two exceptions, did not occur in the surface collections. Despite this, the several age classes can be distinguished in respect of their depth preferences, where these are determined by means of the "centre of gravity." Reference to Figure 7 shows that, in every case, the mean depth at which the main mass of adults (Stage VI) occurred was the lowest, and that of Stages IV+III usually well above. The "centres of gravity" of individuals in Stage V lie about midway between those of the two other classes.

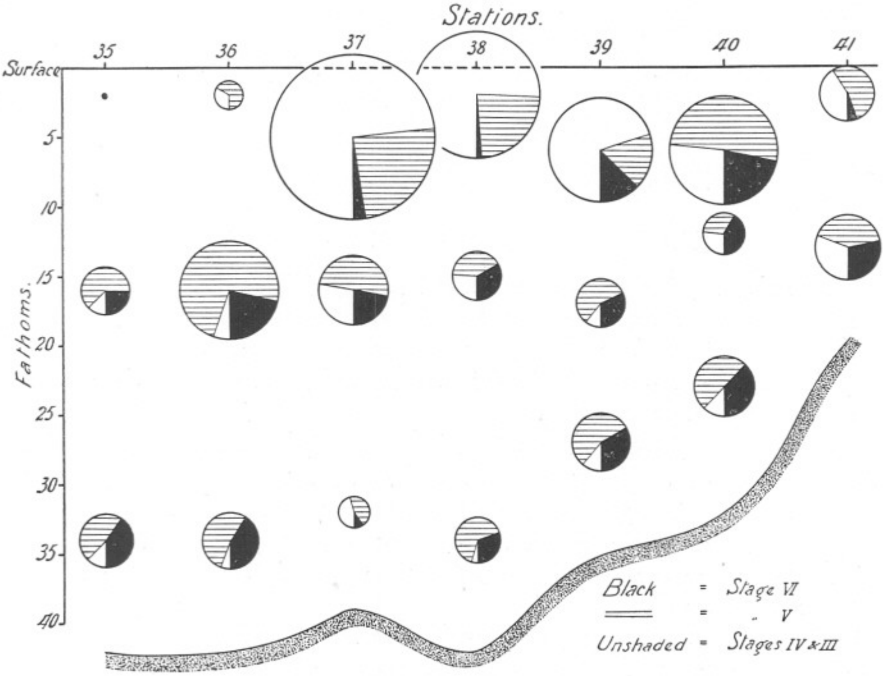

FIG. 6.—Vertical distribution of Calanus at Stations 35–41 (5th Day, May 25th).

It is interesting to note that in this area the percentage of Stages IV+III was more than double that in the area covered on the preceding day. The total number of individuals in all classes was the highest recorded on this voyage.

Day 5, *May 25th.* Stations 35 to 41. Figure 6. Table VII.

This line of stations was run in a roughly diagonal direction from the S.E. corner of the N.E. bank to the coast off the River Tyne. The day was one of frequent sunny periods. Stations 38 and 40 were worked in bright sunlight, whilst at Station 39 the sun was obscured by cloud. Wind was variable from a S.E. or S.W. direction, force 2–3 on the Beaufort Scale.

The composition of the population sampled was as follows :—

Age Class.	Number.	Percentage.
VI	201	15·9%
V	498	39·4%
IV+III	564	44·7%
Total	1263	100·0

Ignoring for the moment the last station, which was taken in quite shallow water near the coast, and considering the preceding four, one sees a type of vertical distribution very similar to that given by Stations 22a–g (Day 3). The first two stations, however, 35 and 36, gave only very few specimens in the surface hauls.

At Stations 37, 38, and 39, young individuals (Stages IV+III) are both relatively and absolutely very numerous, and on the whole this age class shows once more a decided preference for the upper levels. The " centres of gravity " of Stages V and VI are, with two exceptions, in accordance with what we have been led to expect from a study of the results of the other three days.

A more detailed study of Figure 7 reveals a very high degree of consistency in the behaviour of the youngest class of individuals (Stages IV+III). On no occasion was the " centre of gravity " of distribution found to lie below that of Stage VI, and on only one occasion was it lower than that of Stage V, namely at Station 11.

The " centre of gravity " of Stage V was usually found to be intermediate between that of Stages VI and Stages IV+III. There were five exceptions to this (i.e. 14%), viz. at Stations 1, 2, 8, 39, and 41. It would seem, then, that towards the end of May the different stages show decided depth preferences, those in Stages IV+III living, usually, well above the two older classes, and Stage V living at a depth intermediate between Stages IV and VI.

THE RELATIONSHIP BETWEEN LENGTH AND VERTICAL DISTRIBUTION.

The preceding pages may be summarised very briefly as follows: On the whole, individuals in Stages IV+III favoured the surface waters. Those in Stages V and VI showed no such preference, being sometimes more numerous in the surface collections, but at other stations occurring in greatest numbers at either of the other two levels. However, the mean depth (the "centre of gravity") at which the main mass of individuals

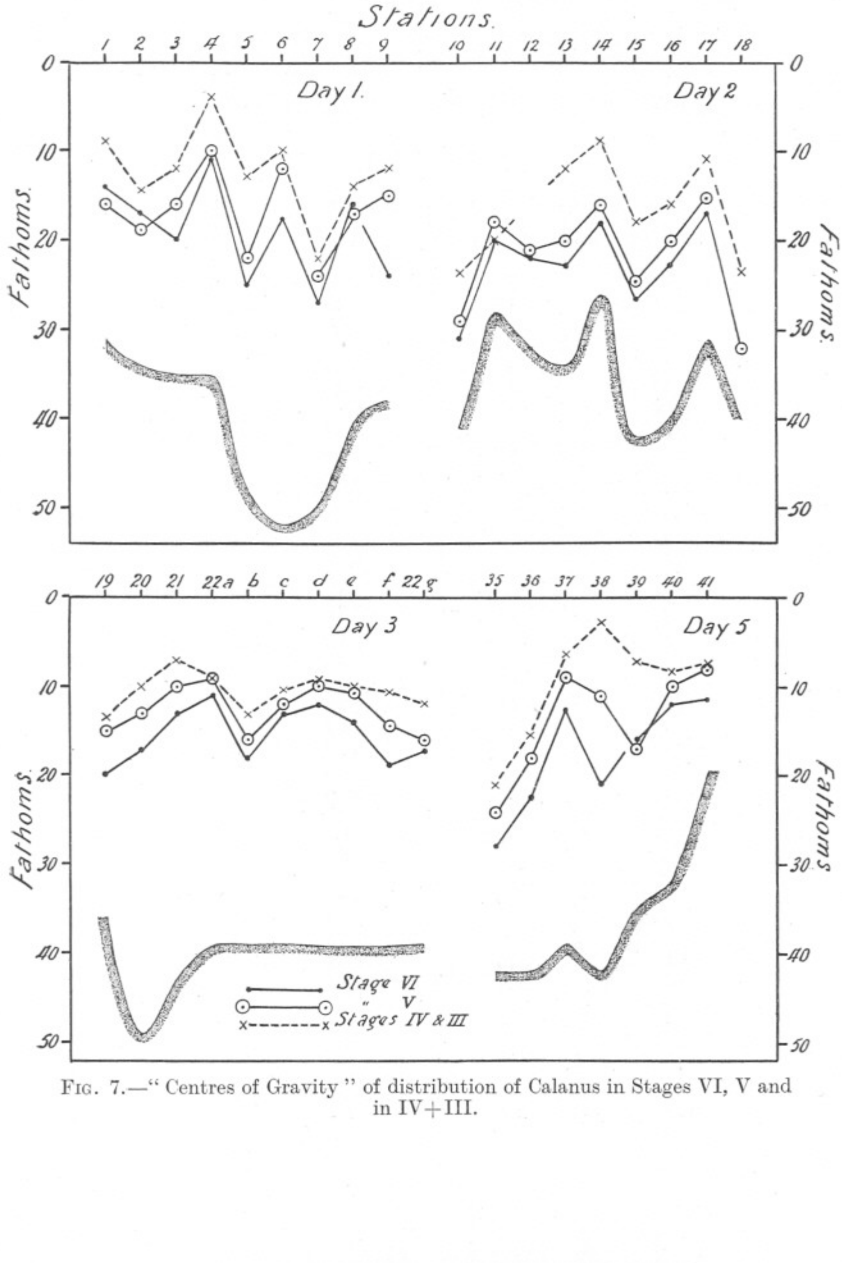

FIG. 7.—"Centres of Gravity" of distribution of Calanus in Stages VI, V and in IV+III.

in the age classes recognised occurred, showed that the three classes exhibited a fairly clearly defined depth preference.

As the material was sorted, the impression was gained that the individuals in Stage V were larger in size in the bottom than in the surface collections. It seemed, too, as if specimens of this age group in the mid-water samples occupied an intermediate position as regards length. The same thing was noticed in the adults. In their case, however, the numbers were never very large and it was thought better to restrict a detailed examination to Stage V.

In all, 1443 Calanus in this Stage were measured, 483 from the surface collections, 409 from mid-water, and 551 from the bottom collections. There was, of course, no selection. These measurements are set out in Table I.

TABLE I.

MEAN LENGTHS (IN MM.) OF CALANUS IN STAGE V IN SURFACE, MID-WATER, AND BOTTOM COLLECTIONS.

Station.	Surface. mm.	Mid-water. mm.	Bottom. mm.
1	2·67	—	3·00
2	2·87	2·85	2·96
3	2·37	2·91	3·04
4	2·96	2·92	3·11
5	2·92	2·81	3·16
6	2·77	2·82	2·88
7	2·52	2·65	2·78
8	2·51	2·76	2·77
9	2·55	2·67	2·80
10	—	2·53	2·96
11	—	—	2·92
12	—	3·03	3·12
13	—	2·89	3·11
14	—	2·71	2·79
15	2·73	2·80	2·77
16	2·51	2·83	2·84
17	—	2·60	2·97
18	—	—	3·07
19	2·85	2·83	2·69
20	2·87	2·87	3·06
21	2·85	2·78	2·99
22a	2·96	2·83	3·06
b	2·77	2·88	3·03
c	2·81	2·97	2·86
d	2·86	2·91	3·05
e	2·81	2·91	2·81
f	2·78	2·90	2·96
g	2·89	2·86	3·01
35	—	2·85	2·94
36	2·82	2·70	2·88
37	2·79	2·92	2·84
38	2·91	2·81	3·02
39	2·67	2·78	2·93
40	2·85	2·85	2·84
41	2·74	—	2·93
General Average (mm.)	2·76	2·82	2·94
Number measured	*483*	*409*	*551*

The mean lengths of individuals in the surface, mid-water, and bottom collections were found to be 2·76, 2·82, and 2·94 millimetres respectively. Taken by itself this is not, perhaps, very impressive since the differences in mean length are so small, especially when it is recalled that the length of the class as a whole ranged from under 2·5 mm. to 3·5 mm. (*vide* Figure 2). It must be remembered, however, that the figures quoted above are mean lengths. In addition to this it will be seen in Table I that the mean lengths of individuals in surface hauls are less than those of the corresponding bottom hauls in twenty-four cases out of twenty-seven in which this comparison is possible. A definitely ascending order of mean length from surface, through mid-water to bottom is shown in ten cases.

Further work is needed to show whether the latter condition is generally to be expected. At the moment it is perhaps nothing more than an interesting possibility.

DISCUSSION.

It has been shown that the depth at which Calanus of different ages may be found from day to day is subject, particularly in the older individuals, to considerable variation. The youngest classes studied (Stages IV and III) have undoubtedly tended to find their daytime optimum above 10 fathoms. The exceptions to this have been but few. The adults (Stage VI), on the other hand, have shown far less consistency, and from a study of their behaviour extending over four days in May, it has not been possible to determine the optimum level. Stage V would seem to have behaved in a manner more closely allied to that of the adults than to that of the younger classes. (*Vide infra* where some of Russell's data are examined.)

It is not possible to say how far the differences in vertical distribution from day to day were due to the prevailing meteorological conditions, and how far to the fact that the collections were made over a wide area. Russell's hypothesis of optimum illumination (Russell, 1927, p. 247, *et seq.*) would have led one to expect that on the cloudy day the older individuals, at any rate, should have been nearer to the surface. It would seem, however, that in the present case the reverse has occurred. Russell himself (Russell, VII, 1928, p. 447) says that " the rise towards the surface was evident on sunny days as well as dull, indicating that the suggestion that dull weather and low light intensity was its cause in 1925 " (*vide* Russell, IV, 1926, p. 427) " may possibly have been incorrect."

One must bear in mind the possibility that the position at which the majority of individuals occurred in the early hours of the day and again towards evening, where this differs from that at the other hours of the same day, may have been influenced by diurnal migrations. The first station of each day was made shortly after 6 a.m. and with sunrise at 4 a.m.

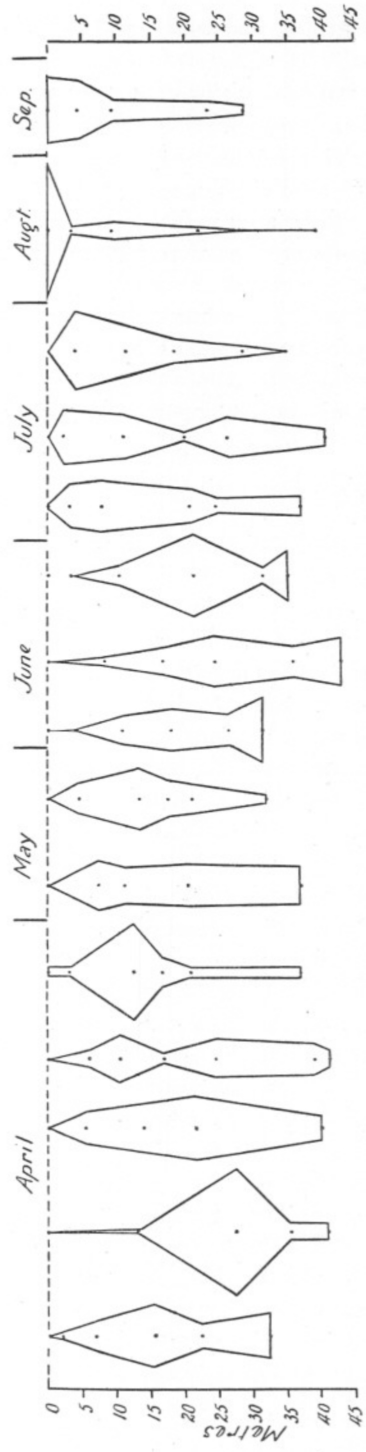

FIG. 8.—Vertical distribution of Stage V, Calanus, from Russell, VII, Table VII, p. 454 (see text).

it is possible that, at this time, the animals might not yet have finished moving either up or down from the position adopted during the hours of darkness. The results of a single night's observations on the diurnal migrations of individuals of different age are given in Appendix A and should be studied in this connexion.

As regards the position taken up by day by specimens of different age in one and the same series of surface, mid-water and bottom collections, it would appear that the "centre of gravity" of distribution of Stages IV + III, of Stage V, and of Stage VI is, with few exceptions, in the order in which the Stages are here written down. The data from which this has been derived are shown graphically in Figure 7.

Finally, there is the suggestion on pp. 590–591 that for Stage V, the only one so far examined in this connexion, the greater the length of the individual the lower down in the water it will be found.

This study of the behaviour of Calanus of different age has shown once more (*vide* Farran, 1911, p. 84; Southern and Gardiner, 1926, p. 323, and 1932; Russell, 1927, p. 239; Russell, X, 1931, p. 394; Worthington, 1931, p. 406; etc.) the importance of the ontogenetical state of the individual in relation to its vertical distribution. Russell, who has made such a close study of the vertical distribution of Calanus has restricted himself almost entirely to the use of the ring-trawl, the bag of which is made of stramin with 16 threads to the inch. The population sampled by this large mesh is composed mainly of fully grown specimens, and Russell's findings are thus almost entirely restricted to adults. On occasions, however, this net has captured individuals in Stage V in considerable quantity (*vide* Russell, VII, 1928, p. 446), but as he says, *loc. cit.*, he has " not attempted to express diagrammatically their vertical distribution " since it is obvious that " the stramin ring-trawl cannot be regarded as an efficient instrument for the capture of these last copepodid stages . . ."

With this I find myself in only partial agreement. Admittedly selection by the net will have restricted the population sampled, but if this be realised, the data are perhaps all the more valuable since, by reason of net-selection, they relate to a class of individuals more uniform in size than mine. Figure 8, which represents diagrammatically the vertical distribution of, presumably, only the larger specimens in Stage V, has been drawn up from the data given by Russell (VII, 1928, Table VII, p. 454). The depths at which the collections were made were taken from the same paper, Table I, p. 449. If this figure be compared with Russell's Figure 1, p. 430, it will be seen that the vertical distribution of Stage V in Figure 8 is more akin to that of the females than to that of the males. The males, it will be remembered, live lower down than the females, *vide* Russell, *loc. cit.*, p. 447. It would not appear, however, that in his findings, as in mine, the optimum level in Stage V is above that of the adults. To what extent, if indeed at all, this is due to the fact that my observations on Russell's data refer only to the behaviour of the larger Stage V individuals owing to the selective action of the big mesh, it is impossible to say.

The study of the daytime vertical distribution of Calanus at different seasons of the year enabled Russell (VII, p. 446) to state " that there is a gradual descent of the region of maximum abundance from about 10 metres in April to 20 metres in June, with a definite rise towards the surface in July, August, and September. (This rise is already apparent *early* in July.) A seasonal variation in the median length of all classes of individuals measured was observed by the same worker who noted (*loc. cit.*, p. 447) " a brood of small adults occurring in July, August, and September, as opposed to a brood of large adults which dominated in the spring." If Russell's measurements for Stage V (Table V, p. 453) are plotted, the curve obtained resembles that of the males and females given on p. 442, Figure 6B, in that this class, too, shows a decrease in median length after the beginning of June. From a consideration of the data, Russell makes the suggestion that the broods are physiologically different, the small type preferring a higher light intensity than the large type. My results would certainly seem to lend support to such a view. Not only do the adults live lower down than the younger classes, but also in Stage V the mean length of individuals is greatest in the bottom hauls. In this connexion, however, it must be clearly understood that I do not believe that individuals of length n millimetres will find their optimum at m fathoms, whilst those of $(n+n')$ millimetres will be found at $(m+m')$ fathoms, where m and $(m+m')$ are relatively constant for the particular season of the year. I think it to be nearer the truth to suppose that if for some reasons at present not understood, the bulk of the individuals of those classes so far investigated, be found at a certain depth, then the main mass of the largest specimens will be deeper and that of the smaller individuals will be at a lesser depth.

The causes which prompt the animals to mass at any particular level on a given day are, in my opinion, not yet determined, and I cannot help but think that Russell himself would agree with this (Russell, VII, 1928, p. 447, item 2 of the Summary). Light intensity alone would certainly not seem to be the full explanation. Moreover, the rise towards the surface in July, August, and September, when the smaller broods predominate, would seem to be referable to at least two factors, size *and* diminishing light intensity, but which is the more potent it is not yet possible to say.

It must be remembered that my data, with one exception (*vide* p. 596), refer to observations extending over a considerable area. Russell's, on the other hand, deal with observations in the same area, but, for the most part, are derived from not more than one observation on any one day (excluding, of course, those experiments on diurnal migration). Moreover, the interval of time separating Russell's consecutive observations, was usually one of several days, and frequently much more. In any further work of this kind I should attempt to repeat my observations much in the manner described here, but with the important difference that I should deal as far as possible with the same body of water.

In conclusion, it would appear that there are likely to be considerable differences in the depth at which the older individuals may be found from day to day. Furthermore, it is not possible, from the intensity of illumination, to predict the level at which the concentration will occur. It follows from this that should attempts be made to relate the abundance of herring with, *inter alia*, that of Calanus, the greatest caution will have to be exercised in the interpretation of results, especially if only one sampler is employed.

APPENDIX A.

Diurnal Migration in *Calanus finmarchicus*.

The diurnal migrations of *Calanus finmarchicus* in the waters off Plymouth have been studied in detail by Russell (1925, p. 793; VI, 1928, p. 89). This worker used the stramin ring-trawl, the meshes of which retain only the larger individuals, and it is probably safe to assume that his findings are based to a large extent on the behaviour of adults. It will be recalled that he believes the course of the migration to be as follows: (1927, p. 237) " . . . there is a movement towards the surface as the light fails, but at night when the lowest intensity has faded away and the directional stimulus is removed, the animals become free to go where they will and become evenly distributed from top to bottom. As the light increases the following day those near the surface mass around the optimum intensity as soon as it arrives and follow it downwards, ever increasing their numbers by recruits from deeper layers who gradually come into the sphere of influence of the light or have been prevented from reaching the optimum on account of slow movement." In a more recent paper (XI, 1931, pp. 768–771), where the behaviour of a considerable number of planktonic animals is compared in different years, Russell makes the following statements: "After careful study of the available data it is evident that whatever be the physical and chemical conditions of the environment that control the behaviour of the animals and provide the necessary stimuli, there are two factors inherent in the animals themselves which are largely responsible for the types of distribution shown by any species during the night, namely:—

1. The depth at which the animal has been living during the previous daylight.
2. The speed at which the animal is capable of swimming upwards."

On p. 770 Russell, having recorded that "more of the deep-living animals reached the layers up to the surface in the nights in June, 1925, than they did on either of the nights in July, 1924, or June, 1926," goes on to say that "it seems possible that owing to the scarcity of plankton animals on the nights in 1925 their passage upwards was less impeded by obstructing animals. The presence of other animals in large numbers must in itself cause modification of the behaviour to be expected of an animal in perfectly uninhabited water." Such a condition, however, can rarely be encountered. He concludes with these words: "Both avoiding reactions and feeding reactions must tend to divert an animal from its pure responses to physical and chemical environmental stimuli."

It is by no means clear what is intended by these observations, and to me it seems that one is entitled to re-write Russell's concluding sentence thus : Pure responses to physical and chemical stimuli must tend to divert an animal from its (normal) avoiding and feeding reactions. At the same time I wish to make it quite clear that none of my own work has provided tangible proof that my conception of the motive forces behind these migrations is the more correct.

Recently Savage (1931, pp. 24 and 33) published an account of the diurnal migrations of this species based on collections in the North Sea. His results, particularly in the months of August and September, show only a modified agreement with Russell's. During the midnight period, for instance, the migrations were quite at variance with the hypothetical picture suggested by Russell. The daytime results, however, confirm the observation that during the late summer the animals live higher in the water than in the spring. It must be remembered, however, that Savage used the International closing net of No. 60 silk, and that his material would, on account of the smaller mesh, be very different from Russell's.

Evidence is accumulating that the study of the diurnal migrations of a population, all of one species but mixed in respect of age classes, will be unlikely to give clear-cut results, for the reason that individuals of different age do not behave in the same way. As far as *Calanus finmarchicus* is concerned the data on this point are far from complete, but there are definite indications that it will be necessary to differentiate between the behaviour of young and old individuals.

In the present paper I have attempted to show that, by day, individuals in Stage IV (and III) tend to live nearer the surface than do the adults. I have also produced evidence that even in one age class (Stage V) the larger individuals may be found to live nearer the bottom than the smaller ones. Owing to a variety of causes it was not possible on the Cruise under discussion to make an exhaustive study of the behaviour of Calanus during the hours of darkness. For this reason I have relegated to an Appendix such data as I was able to collect.

It will be recalled that on the third day, May 23rd, a small area centred on the position 55°28′ N., 0°20′ W., was studied in some detail, seven series of hauls being taken between the hours of 1118 and 1435. It was found that, on the whole, the vertical distribution, as well as the total numbers occurring in successive hauls, remained fairly constant. It was accordingly decided to remain in the area and to make further observations during the ensuing hours of darkness.

The same methods of collection were employed (see p. 577) and a further five series of simultaneous hauls at 8, 18, and 28 fathoms were taken at 1905, before sunset ; 2100, after sunset ; at 0145, during darkness ; and at 0310 and 0508, about one hour before and after sunrise. The hauls were made as far as could be judged in the same body of water. In the subsequent examination the individuals were separated into the same age classes as before, viz. Stages IV+III, V, and VI (males and females).

The data are given in Table II below.

TABLE II.

Numbers of Calanus in Stage VI, V, and in Stages IV+III, taken in Surface, Mid-water, and Bottom Collections, and Percentage of total Number occurring at each Level.

Station	22(a)			22(g)			22(h)			22(j)			
Time, G.M.T.	1118			1435			1905			2100			
S=Surface M=Mid-water B=Bottom	S.	M.	B.	S.	M.	B.	S.	M.	B.	S.*	S.	M.	B.
Stage VI													
Number	29	1	5	14	10	11	–	8	7	1	3	6	14
Percentage	83%	3%	14%	40%	29%	31%	–	53%	47%	4%	12%	25%	58%
Stage V													
Number	162	5	9	62	11	39	12	28	30	3	16	20	12
Percentage	92%	3%	5%	55%	10%	35%	17%	40%	43%	6%	31%	39%	24%
Stages IV+III													
Number	140	10	1	28	4	5	11	9	6	6	12	4	1
Percentage	93%	6%	1%	75%	11%	14%	42%	35%	23%	26%	52%	17%	4%

Station	22(k)			22(l)			22(m)		
Time, G.M.T.	0145			0310			0508		
	S.	M.	B.	S.	M.	B.	S.	M.	B.
Stage VI									
Number	0	6	10	6	14	13	6	9	16
Percentage	–	37%	63%	18%	42%	39%	19%	29%	52%
Stage V									
Number	4	19	23	48	44	9	38	14	37
Percentage	9%	41%	50%	47%	44%	9%	43%	16%	41%
Stages IV+III									
Number	6	9	2	66	15	4	58	10	18
Percentage	35%	53%	12%	77%	18%	5%	67%	12%	21%

The hauls studied include two of the daytime series (Nos. 22a and 22g), taken at 1118 and 1435 respectively. During the course of the seven daytime hauls, Stations 22a–g, the numbers of individuals in all classes remained fairly high, the averages being: Stage VI, 40; Stage V, 139; and Stages IV+III, 101. By 1435 (Station 22g) the numbers had declined to 35, 112, and 37 respectively. Four and a half hours later, at 1900, before sunset, the numbers had dropped still further to 15, 70, and 26. Being able to sample only three levels, it was impossible to tell whether this was due to the ship being in an area where there were fewer Calanus, or whether the individuals had migrated to some different level. When after sunset, at 2100, the numbers in all classes had dropped still

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* Additional haul at 2 metres.

further, an additional haul about 2 fathoms below the surface was taken. (It was not considered wise to attempt a deeper sample than that at 28 fathoms.) Numbers continued low until the collection made before sunrise (Station 221 at 0310) when there was a very definite increase especially in the case of the younger classes. Numerical fluctuations during the course of a period of 24 hours' observations are by no means uncommon.

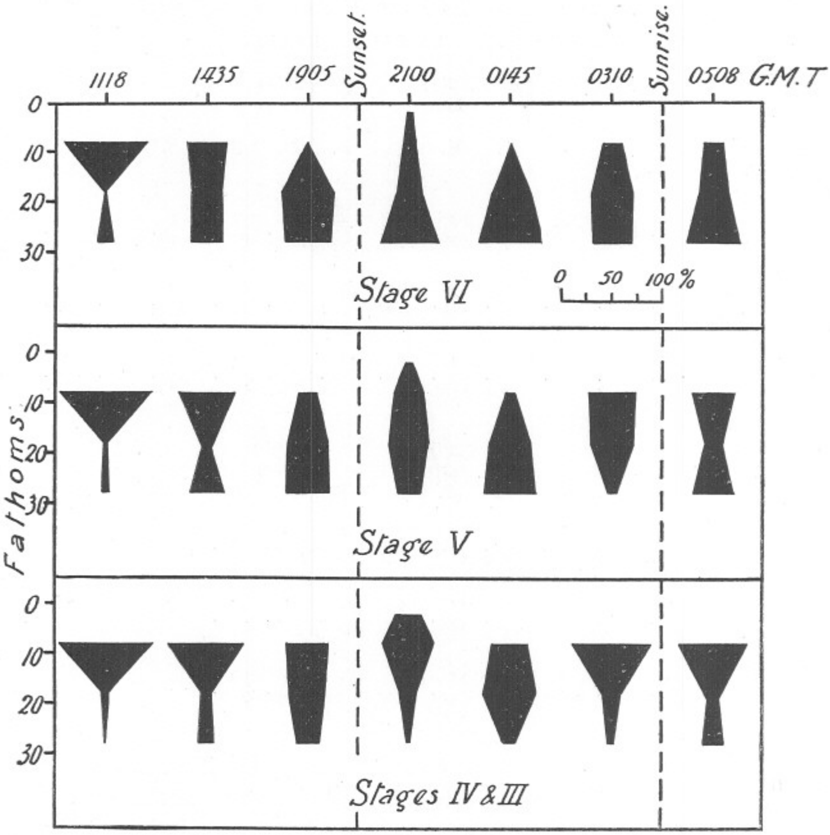

Fig. 9.—Diurnal migration in *Calanus finmarchicus*.

So far as I am aware, however, the catches during the hours of darkness have usually been the bigger. Russell, for instance, gets the following results for Calanus (1925, p. 793 ; IV, 1926, p. 433) :—

Daylight (p.m.).	Dusk.	Dark.	Dawn.	Daylight (a.m.).	
2580	8014	9156	2641	2330	July, 1924.
5920	3650	9780	1986	1407	June, 1925.
	3504	8610	2470	4876	

In an earlier paper (Gardiner, 1931, p. 464) when some data were examined in this connexion, from a population of Calanus sampled with the International net of No. 60 silk, the average number in 15 hauls made during the daytime was 112, whilst the average number in 18 hauls made in the hours of darkness was 107.

The diurnal migrations of these three classes, in so far as they can be determined from samples at only three levels, are shown graphically in Figure 9. The diagrams have been constructed by computing what percentage of the total number occurred in each of the three collections. In one case (Station 22j) as already mentioned, an additional sample was taken as near the surface as possible.

So far as the data go, it would seem that adults and Stage V behave much in the same way. These two classes are seen to have moved progressively downwards from 1118, when they were obviously concentrated at a depth of 8 fathoms, until 0145, when the greatest numbers were found at a depth of 28 fathoms. The two subsequent Stations showed an upward migration, which was more rapid in the case of individuals in Stage V. It is interesting to record that in neither class are the catches in the quite superficial water large, showing that if the decline in numbers referred to above was due to the animals' migrations, the direction would probably have been downward.

As far as the younger individuals, Stages IV+III, are concerned, the behaviour differed from that of the older classes in that the catches at the 8-fathom level were, with one exception, the biggest. These individuals, too, would not seem to have sunk to the deeper water during the hours of darkness as have the older specimens.

It would probably not be justifiable to contrast these data with those of Russell, from which, of course, they do differ. Neither are a single night's observations sufficient upon which to base general conclusions as to the probable course of the migrations of a species.

APPENDIX B.

The Rate of Sinking of *Calanus finmarchicus*.

By A. C. Gardiner, with the assistance of J. A. Robertson.

Introduction.

The fact that these observations on the sinking rate of different sized specimens of Calanus have been appended to an account of the vertical distribution of the same species, may be taken to indicate that we believe there to be a direct connexion between the two subjects. In other words, it may be assumed that we think that since a small specimen sinks more slowly than a larger one it is not surprising to find the smaller individuals living, on the whole, nearest to the surface. Some such idea did occur to us, but the knowledge that adults may also be abundant in the surface layers is evidence that the greater difficulty which a larger specimen *may* experience in maintaining itself at any given level is only one factor, and probably not a vital one.

At the same time we wish to give it as our opinion that in specimens of different sizes the relationship between the muscular energy and the tendency to sink is one of which sight must not be lost.

The measurements in Table VIII, p. 606, are those of the time, in seconds, taken by anæsthetised specimens of *Calanus finmarchicus* to sink through a column of sea-water of salinity 35·01‰, 250 millimetres in height, maintained at a temperature of 18·5° C. The experiments were carried out upon the animals within 3–5 days of their capture, and in the intervening time they were kept in two large aquaria aerated by means of a " plunger " mechanism.

The methods were as follows : A few specimens were transferred to a smaller glass bowl, from which they could easily be removed by means of a net to a second bowl containing a solution of 2·5 grams of Urethane in 100 c.c. of sea-water. As a rule the animals were kept in the solution for a period of five to ten minutes. Experience showed that this produced anæsthesia of about 1–2 minutes' duration. In those cases where the animal revived too soon, it was immediately re-anæsthetised and a second test made. In any case of doubt that the specimen had been killed it was transferred to a third bowl and carefully observed. Although owing to unavoidable delays some few specimens had really considerable periods in the anæsthetising solution, none was killed. As soon as the animal was deemed to be anæsthetised it was rinsed in sea-water and thence transferred to the test cylinder by means of a wide-mouthed pipette, the end of which was bent at right angles. In this way each animal was introduced into the cylinder with no initial downward velocity. The time taken to sink through the measured distance was read to the nearest tenth of a second from a stop-watch. On reaching the bottom of the cylinder the animal was removed and immediately killed and preserved in 2% formaldehyde. Subsequently the length of each was determined as well as the developmental stage or sex. The test cylinder was an ordinary 1000 m.l. measuring cylinder standing in a bell-jar in which water was circulating. The temperature was read every time an observation was made.

Notes were made on the position in which the antennæ were held during test. In the majority of cases these were fully extended, the animals sinking vertically, tail first, with the longitudinal axis of the body at only a very slight angle to the vertical. This is the position in which unanæsthetised specimens also were observed to sink. Where the antennæ were partially or completely folded to the sides the animals sank head first, with the longitudinal axis at an angle of about 30° to the vertical and frequently with the ventral surface uppermost. No unanæsthetised specimen was at any time observed in such a position. It was anticipated that there would be marked differences in the times taken in sinking by specimens of nearly the same size, according to whether the antennæ were folded or not. Such, however, was not found to be the case.

Experimental Results.

The time that each specimen took to sink through the measured distance of 250 mm., the length of the specimen in millimetres, measured from the head to the end of the caudal furcæ (caudal setæ not included)

TABLE III.

Average Time, in Seconds, required for Anæsthetised *Calanus finmarchicus* of Different Lengths (in mm.) to Sink through a Column of Water 250 mm. long.

Length (mm.).	Mean time (seconds).
2·1	181·3
2·2	135·0
2·3	110·6
2·4	118·7
2·6	114·9
2·7	99·9
2·8	106·8
2·9	120·8
3·0	74·3
3·1	70·4
3·2	70·3
3·3	58·4
3·4	58·9
3·5	60·0
3·6	57·9
3·7	43·8
3·9	43·9 (1 only)
4·0	31·0 (1 only)

and the developmental stage are given in Table VIII. The observations have been arranged in groups, in ascending order of size of the specimens. These results have been summarised in Table III, which shows that on the whole the time taken to sink through a fixed distance varies inversely as the length of the individual.

The correlation between sinking time and length, expressed as the coefficient of correlation, worked out at $r = -0{\cdot}63$, which may be taken as fairly satisfactory.

Variations in temperature were small. 89% of the observations lay within an interval of 0·3° C., of which the mean temperature, 18·55° C., was the mid-point. Thus, alterations in the viscosity of the water, due to temperature changes, which would be considerable for large fluctuations in temperature, may be ignored.

SUMMARY AND DISCUSSION.

One hundred and twenty-one specimens of *Calanus finmarchicus* were anæsthetised in a dilute solution of Urethane (2·5 grms. in 100 c.c. of sea-water) and the time taken by each to sink through a measured distance determined. The length of each specimen, in millimetres, was noted, and the relationship between sinking time and length of the individual was determined. The coefficient of correlation, r, was found to be $-0{\cdot}63$.

Apstein (1910, p. 23), working with preserved material, found that the time taken by adult Calanus was less than that taken by young. He does not give actual length measurements. Eyden (1923, p. 53) showed that for anæsthetised specimens of *Daphnia pulex*, the average rate of fall was approximately twice as great in specimens of length 2·5–3·0 mm. as in smaller ones, whose length varied from 1·5–2·0 mm.

The position in which specimens sank was conditioned by the manner in which the antennæ were held. It was found, however, that this had not as great an influence on the sinking rate as might have been expected.

Of the 121 specimens examined, 21 were in Stage IV, 41 in Stage V; 59 were adult, of which 54 were females and only 5 were males.

TABLE IV.

NUMBERS OF CALANUS IN STAGE VI, V, AND IN STAGES IV+III, TAKEN IN SURFACE, MID-WATER, AND BOTTOM COLLECTIONS. MAY 21ST.

Station	1			2			3			4			5		
Time, G.M.T.	0620			0805			0935			1105			1230		
Depth in fathoms	31			34			35			35			48		
S=Surface M=Mid-water B=Bottom	S.	M.	B.	S.	M.	B.	S.	M.	B.	S.	M.	B.	S.	M.	B.
Total Calanus	19	50	64	30	54	110	13	47	34	98	39	29	32	46	61
Stage VI															
Male	–	2	5	1	6	7	1	–	7	15	10	8	5	2	16
Female	1	4	2	1	2	4	–	2	3	9	6	4	5	3	11
Total	1	6	7	2	8	11	1	2	10	24	16	12	10	5	27
Stage V	5	19	50	11	28	76	2	28	19	46	22	17	15	23	34
Stages IV+111	12	25	7	17	18	23	10	17	5	28	1	–	7	18	–

Station	6			7			8			9					
Time, G.M.T.	1427			1602			1730			1855					
Depth in fathoms	52			50			40			38			Totals.		
	S.	M.	B.	S.	M.	B.	S.	M.	B.	S.	M.	B.	S.	M.	B.
Total Calanus	189	37	54	11	32	45	28	58	20	97	49	90	517	412	507
Stage VI															
Male	16	5	10	2	3	11	–	5	2	–	7	29	40	40	95
Female	7	2	7	–	2	2	2	7	–	2	3	13	27	31	46
Total	23	7	17	2	5	13	2	12	2	2	10	42	67	71	141
Stage V	127	19	33	4	21	23	12	25	12	58	26	37	280	211	301
Stages IV+III	39	11	4	5	6	9	14	21	6	37	13	11	169	130	65

TABLE V.

NUMBERS OF CALANUS IN STAGE VI, V, AND IN STAGES IV+III, TAKEN IN SURFACE, MID-WATER, AND BOTTOM COLLECTIONS. MAY 22ND.

Station	10			11			12			13			14		
Time, G.M.T.	0612			0733			0915			1051			1222		
Depth in fathoms	41			28			32			34			26		
S=Surface M=Mid-water B=Bottom	S.	M.	B.	S.	M.	B.	S.	M.	B.	S.	M.	B.	S.	M.	B.
Total Calanus	1	5	54	1	2	26	1	7	70	1	15	72	–	8	14
Stage VI															
Male	–	1	19	–	–	6	–	1	22	–	–	21	–	1	3
Female	–	–	9	–	–	5	–	3	21	–	1	22	–	–	3
Total	–	1	28	–	–	11	–	4	43	–	1	43	–	1	6
Stage V	1	3	25	1	2	14	1	3	27	1	9	29	–	5	8
Stages IV+III	–	1	1	–	–	1	–	–	–	–	5	–	–	2	–

Station	15			16			17			18					
Time, G.M.T.	1350			1517			1643			1819					
Depth in fathoms	42			39½			31			40			Totals.		
	S.	M.	B.	S.	M.	B.	S.	M.	B.	S.	M.	B.	S.	M.	B.
Total Calanus	33	22	103	17	73	43	2	9	16	–	1	13	56	142	411
Stage VI															
Male	1	1	11	1	7	7	–	1	1	–	–	3	2	12	93
Female	2	5	14	–	3	3	–	–	2	–	–	6	2	12	85
Total	3	6	25	1	10	10	–	1	3	–	–	9	4	24	178
Stage V	18	12	66	6	41	24	1	7	12	–	–	3	29	82	208
Stages IV+III	12	4	12	10	22	9	1	1	1	–	1	1	23	36	25

TABLE VI.

NUMBERS OF CALANUS IN STAGE VI, V, AND IN STAGES IV+III, TAKEN IN SURFACE, MID-WATER, AND BOTTOM COLLECTIONS. MAY 23RD.

Station		19			20			21			22(a)			22(b)	
Time, G.M.T.		0640			0825			0957			1118			1150	
Depth in fahoms		36			49			42½			39			39	
S=Surface M=Mid-water B=Bottom	S.	M.	B.	S.	M.	B.	S.	M.	B.	S.	M.	B.	S.	M.	B.
Total Calanus	9	13	8	64	13	22	77	23	10	331	16	15	120	45	53
Stage VI															
Male	–	1	3	3	2	5	10	8	5	18	1	3	8	7	6
Female	1	4	1	7	5	2	6	1	–	11	–	2	2	1	3
Total	1	5	4	10	7	7	16	9	5	29	1	5	10	8	9
Stage V	7	6	4	41	6	13	34	8	5	162	5	9	53	28	28
Stages IV+III	1	2	–	13	–	2	27	6	–	140	10	1	57	9	16

Station		22(c)			22(d)			22(e)			22(f)			22(g)				
Time, G.M.T.		1220			1255			1325			1400			1435			Totals.	
Depth in fathoms		39			39			39			39			38				
	S.	M.	B.	S.	M.	B.	S.	M.	B.	S.	M.	B.	S.	M.	B.	S.	M.	B.
Total Calanus	260	62	29	420	38	32	164	37	12	92	24	27	104	25	55	1641	296	263
Stage VI																		
Male	12	8	3	12	9	3	12	6	5	6	4	4	6	10	9	87	56	46
Female	23	13	2	36	3	4	8	3	–	2	1	5	8	–	2	104	31	21
Total	35	21	5	48	12	7	20	9	5	8	5	9	14	10	11	191	87	67
Stage V	120	29	15	204	17	18	86	16	7	38	11	15	62	11	39	807	137	153
Stages IV+III	105	12	9	168	9	7	58	12	–	46	8	3	28	4	5	643	72	43

TABLE VII.

NUMBERS OF CALANUS IN STAGE VI, V, AND IN STAGES IV+III, TAKEN IN SURFACE, MID-WATER, AND BOTTOM COLLECTIONS. MAY 25TH.

Station.	35			36			37			38		
Time, G.M.T.	0628			0812			1216			1403		
Depth in fathoms	42			42			39			42		
S=Surface M=Mid-water B=Bottom	S.	M.	B.	S.	M.	B.	S.	M.	B.	S.	M.	B.
Total Calanus	3	24	32	9	112	34	300	54	11	174	27	23
Stage VI												
Male	–	6	7	–	2	8	4	2	1	–	5	4
Female	–	–	6	–	22	6	4	10	–	2	4	3
Total	–	6	13	–	24	14	8	12	1	2	9	7
Stage V	1	15	15	6	82	18	72	27	5	40	11	15
Stages IV+III	2	3	4	3	6	2	220	15	5	132	7	1

Station	39			40			41					
Time, G.M.T.	1629			1821			1927					
Depth in fathoms	35			32			19½					
										Totals.		
	S.	M.	B.	S.	M.	B.	S.	M.	B.	S.	M.	B.
Total Calanus	117	28	36	138	19	42	34		46	775	264	224
Stage VI												
Male	10	4	9	19	5	9	–	No observation.	7	33	24	45
Female	5	5	3	11	3	7	2		6	24	44	31
Total	15	9	12	30	8	16	2		13	57	68	76
Stage V	20	16	20	71	6	21	18		19	228	157	113
Stages IV+III	82	3	4	37	5	5	14		14	490	39	35

TABLE VIII.

TIME (IN SECONDS) TAKEN BY CALANUS TO SINK THROUGH 250 MM. OF WATER.

(The observations have been arranged in order of length.)

Length. mm.	Stage.	Time. Secs.	Remarks.
2·1	IV	238·8	Antennæ fully extended.
	IV	205·3	,, ,, ,,
	IV	99·9	,, ,, ,,
2·2	IV	123·7	,, folded.
	IV	153·3	,, fully extended.
	IV	191·3	,, ,, ,,
	IV	78·9	,, folded.
	IV	127·8	,, ,,
2·3	IV	48·0	,, fully extended.
	IV	72·0	,, ,, ,,
	IV	89·0	,, ,, ,,
	IV	121·3	,, ,, ,,
	IV	135·9	,, ,, ,,
	IV	147·7	,, ,, ,,
	IV	187·6	,, ,, ,,
	IV	83·0	,, folded.

TABLE VIII—*continued.*

Length. mm.	Stage.	Time. Secs.	Remarks.
2·4	IV	150·6	Antennæ folded.
	IV	99·3	,, ,,
	IV	93·4	,, ,,
	IV	94·6	,, ,,
	IV	155·5	,, fully extended.
2·6	V	106·7	,, ¾ folded.
	V	123·1	,, folded.
2·7	V	96·1	,, fully extended.
	V	78·1	,, folded.
	V	75·0	,, fully extended.
	V	122·1	,, ,, ,,
	V	98·3	,, ,, ,,
	V	189·1	,, ,, ,,
	V	72·1	,, ,, ,,
	V	63·7	,, ,, ,,
2·8	V	123·5	,, ,, ,,
	V	120·1	,, folded.
	♀	62·7	,, fully extended.
	V	75·4	,, ,, ,,
	V	110·8	,, folded.
	V	124 8	,, fully extended.
	V	73·3	,, ,, ,,
	V	163·4	,, ,, ,,
2·9	V	72·5	,, folded.
	V	103·9	,, fully extended.
	V	176·4	,, ¾ folded.
	V	132·4	,, fully extended.
	V	68·7	,, folded.
	V	170·7	,, fully extended.
3·0	V	53·3	,, folded.
	V	38·6	,, ,,
	♀	64·1	,, ,,
	♂	56·1	,, ,,
	V	84·2	,, ,,
	V	75·7	,, fully extended.
	V	61·0	,, folded.
	V	117·9	,, ,,
	V	84·6	,, ,,
	V	112·2	,, ,,
	V	73·6	,, fully extended.
3·1	♀	57·6	,, ,, ,,
	V	69·9	,, folded.
	♂	52·5	,, ,,
	♀	83·9	,, fully extended.
	V	39·1	,, folded.
	♀	65·8	,, fully extended.
	V	75·0	,, ,, ,,
	V	70·7	,, folded.
	V	170·0	,, ,,
	♀	58·5	,, fully extended.
3·2	♀	57·8	,, ,, ,,
	♀	60·9	,, ,, ,,
	♀	55·4	,, folded.
	♂	39·5	,, ,,

TABLE VIII—*continued*.

Length. mm.	Stage.	Time. Secs.	Remarks.
3·2	V	130·4	Antennæ fully extended.
	♀	82·7	,, ,, ,,
	♀	67·9	,, ,, ,,
	♀	55·5	,, folded.
	♀	71·5	,, fully extended
	♀	59·7	,, ,, ,,
	♀	47·3	,, folded.
	V	59·7	,, ,,
	♀	71·4	,, fully extended.
	♀	55·0*	,, ,, ,,
	V	110·8	,, ,, ,,
	♀	88·6	,, ,, ,,
	♀	53·2	,, folded.
	V	98·4	,, fully extended
3·3	♀	58·6	,, ,, ,,
	♀	98·2	,, ,, ,,
	♀	68·6	,, ,, ,,
	♀	50·3	,, folded.
	♂	42·2	,, ,,
	♀	45·3	,, ,,
	♀	48·5	,, ,,
	♀	62·0	,, ¾ extended.
	♀	38·3	,, folded.
	♀	63·8	,, fully extended.
	♀	58·3	,, ,, ,,
	♀	62·9	,, ,, ,,
	♀	53·5	,, ,, ,,
	♀	67·3	,, ,, ,,
3·4	♀	54·4	,, ,, ,,
	♀	58·5	,, ,, ,,
	♀	54·5	,, ,, ,,
	♀	70·0	,, folded.
	♀	57·1	,, fully extended.
3·5	♀	114·2	,, ,, ,,
	♀	31·9	,, folded.
	♀	63·3	,, fully extended.
	♂	56·4	,, ¾ folded.
	♀	46·0	,, fully extended.
	♀	58·7	,, folded.
	♀	49·4	,, ,,
3·6	♀	86·2	,, ,,
	♀	46·0	,, fully extended.
	♀	45·3	,, ,, ,,
	♀	65·7	,, ,, ,,
	♀	54·7	,, ,, ,,
	♀	49·3	,, ,, ,,
3·7	♀	49·1	,, ,, ,,
	♀	36·9	,, folded.
	♀	45·4	,, fully extended.
3·9	♀	43·9	,, folded.
4·0	♀	31·0	,, ,,

* Mean of six runs.

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Rays and Skates of Devon and Cornwall. III. The Proportions of the Sexes in Nature and in Commercial Landings, and their Significance to the Fishery.

By

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With 1 Figure in the Text.

INTRODUCTION.

THE belief for long was held by early investigators that among most if not among all Elasmobranch fishes the number of females in the stocks exceeded that of the males. As long ago as 1884 Day (**4**, p. 345) remarked concerning the Thornback Ray, *Raia clavata*, " It has been said that the number of females is in excess of that of the males." Haacke (**9**, p. 246), writing in 1885, says of the Sharks and Rays which he had observed in South Australian waters, " Bei den südaustralischen Haien und Rochen, auf deren Fang ich zu wiederholten Malen ausgezogen bin und von denen mir auch nicht selten Exemplare für das Adelaider Museum zugeschickt wurden, habe ich die Wahrnehmung gemacht, dass Männchen verhältnismässig sehr selten gefangen werden. Ob diese Wahrnehmung auch anderswo gemacht worden ist, weiss ich nicht, jedoch ist es nicht unwahrscheinlich ; in der mir zu Gebote stehenden Litteratur finde ich nichts darüber. Die seltenheit der geschlechtsreifen Männchen, soweit sie sich wenigstens durch die Fangresultate dokumentiert, gilt für sämtliche Species der ziemlich artenreichen südaustralischen Selachierfauna."

In the year 1890 Fulton (**7**, p. 350) made the surprisingly definite statement that " among skates and rays females are in excess ; the ratio being 175 females to 100 males. The observations were mainly made on the thornback ray (*Raia clavata*), but also on the starry ray (*Raia radiata*) and grey skate (*Raia batis*). The females specially preponderate in the latter species." By 1903, however, Fulton had acquired additional data which seem to have caused him to be less certain of the exact numerical ratio of the sexes among these fishes, for in that year, after recording separately his data for each species, he wrote more guardedly as follows : " It will be observed that in no case do the males exceed the females in number, and that with the exception of the shagreen ray,* where the

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* Only 8 specimens were examined—4 males and 4 females.

numbers are probably too small to indicate the real proportion, the females are in excess. The amount of excess, however, varies. There is almost equality in the case of the common skate,* while with the thornback, the starry ray, and the sandy ray—although here the figures are small—the excess of females is very considerable."

Lamont (**11**, p. 78) records the proportions of the sexes among Rays and Skates received for dissection at the Zoology Department of Edinburgh University during the four academic years 1921–25. She points out that, so far as she could ascertain, only one source of error might possibly have affected her counts in such a way as to cause them to give an inaccurate picture of the true state of affairs in nature : i.e. that in very immature male specimens the claspers are so small as to be very easily hidden by the pelvic fins, and hence, if they were overlooked, some males might have been recorded as females. It is but little likely, however, that a careful worker would fail to observe the claspers in even the most immature specimens likely to be met with in the dissecting-room.

The numbers† dealt with are small and it seems unnecessary to reproduce them here. It is enough to point out that Lamont found the combined totals for all five species (*R. clavata*, *R. radiata*, *R. fullonica*, *R. circularis*, *R. batis*) which passed through her hands to " show a slight excess of males over females, but this excess was not maintained by each species when considered separately. The excess of males was most marked in *batis*, and was also considerable in *circularis*, but in *clavata* and *fullonica* the condition was reversed and there was a still greater disparity in numbers in favour of the female sex." The results for *R. radiata*, this author points out, call for special remark " because in the last year the occurrence of a great excess of females entirely upset the ratios established for that species during the previous three years." Lamont finally came to the conclusion that while her data " undoubtedly indicate that in the early stages of *batis* males are most numerous, they also appear to provide some justification for the conclusion that in the early stages of *radiata* the opposite is the case and females predominate." She was unable, however, to correlate the great preponderance of females during 1924–25 with any unusual degree of immaturity in the fish of that species dealt with throughout the session. Not only so ; the records obtained for *R. radiata* in that year caused her to modify her " opinion formed at the end of the third year to the effect that in adult *radiata* males come to outnumber the females."

Craigie (**3**, p. 492), from data preserved in the files of the Atlantic Biological Station, St. Andrews, N.B., Canada, found that among four species of Raia represented in the records, all showed a predominance

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* Common Skate=Grey Skate already referred to above. Compare the two statements.

† A total of 757 males and 727 females distributed among 5 species.

of females, the percentage of males ranging from 45% in *R. erinacea*, the Tobacco-box Skate, to 35% in *R. lævis*, the Barn-door Skate. This author then proceeds to point out that an abnormal sex ratio having been found in any fish (a 50/50 ratio being considered normal) it is then necessary to find out the cause. This, however—apart from tabulating some highly theoretical possibilities such as differential fertilisation, differential mortality of gametes, differential mortality of zygotes, the conversion of an X- into a Y-chromosome or *vice versa*, etc., he does not himself make any endeavour to do but "attempts merely to make a general survey of available data in order to find out in what cases among Canadian marine fishes there is a problem of abnormal sex-ratio awaiting study."

The above is a brief résumé of all the previous work which the present writer has been able to find on the proportions of the sexes in certain of the Raiidæ. It will serve to show that although there is some evidence which seems to suggest that as a general rule females tend to outnumber the males, such evidence is by no means conclusive, and that there remains yet much to be learned.

Ford (**5**, p. 483), however, in the course of researches on the life-history of the Spur Dogfish (*Acanthias vulgaris*) found that his data concerning the proportions of the sexes in that Elasmobranch also showed a decided preponderance of females in a total of 3022 fish from 13 samples drawn from commercial landings caught over a period of seven months, there being 1947 females and 975 males. At the same time he found that, among large numbers of embryos obtained *ex utero*, males and females were represented in approximately equal numbers, and therefore presumably would have been born in equal numbers, for the embryos in which the sex could be determined must have been all at such a stage of development that differential mortality would be but little likely to supervene before birth.

Now although a differential mortality of gametes or of zygotes is known to occur in some animals and operates to produce an excess of one sex or of the other, that explanation, in view of Ford's results, obviously does not apply to the Spur Dogfish. A differential survival of the young is a factor which might operate after birth to produce an unbalanced sex ratio. Apart from the fact that there is no evidence to suggest that such a factor is operative, it need not seriously be considered because a much more satisfactory explanation has already been put forward. It has been shown by Ford (**5**, p. 484) and confirmed by Hickling (**10**, p. 537) that there is a very definite segregation of these fish according to age and state of sexual development. The latter author has further shown that normally the males are present in shallower water than the females of the same size and that therefore, owing to the strict segregation of both sexes by size and the smaller size attained by the males, in deeper water females predominate. These large females are mostly pregnant and migrate from deep to shallow water to bear their young. "It is therefore," says Hickling, "hardly possible to speak of the sex ratio among dogfishes as if that were a constant; it will clearly vary with depth and also, almost certainly, with season." It is obvious, too, that such differences of habit exhibited by the male and female fish will render them liable in different degree to capture. As the males, though produced in numbers equal to those of the females, are taken less frequently and in smaller numbers than the latter, it is evident that the habits of the females render them the more accessible and/or vulnerable to the usual fishing implements.

The observations of Haacke (*op. cit.*) in Australian waters point to exactly the same conclusion with regard to the Elasmobranch species observed by him in that region. Of the shark, *Mustelus antarcticus*, though females were common, he had never seen a male specimen. Yet when 22 embryos which he was able to obtain were examined they yielded no less than 13 males. Similarly, nearly every adult specimen of *Trygonorhina fasciata* which Haacke encountered was a female. Nevertheless, out of 26 embryos which he examined 15 were males. Of *Rhinobates vincentianus*, a somewhat rare fish, this author had seen but 6 adults, of which only one was a male. But he was able to obtain from 2 of the 5 females which came into his possession 30 embryos—from the one 5 males and 12 females and from the other 10 males and 3 females.

"Es wird interessant sein," continues Haacke, "noch weitere und genauere auf unseren Gegenstand bezügliche, statistische Angaben auch für andere Arten zu sammeln und womöglich die Ursachen der scheinbaren oder wirklichen Minderzahl der geschlechtsreifen Selachiermännchen aufzuklären. Ob die erwachsenen Männchen nicht so leicht an die Angel gehen wie die Weibchen, oder ob viele davon von anderen Männchen ihrer Art im 'Kampf um die Ehe' getötet werden, oder ob endlich junge Männchen einer grösseren Sterblichkeit ausgesetzt sind, vermag ich nicht zu sagen." The most probable explanation almost certainly is that there is some sort of segregation of the sexes amongst the adult fish and that the shoals of males and females exhibit such differences of habit and/or distribution that the former are very much less exposed to capture than the latter.

RESULTS OF PLYMOUTH INVESTIGATIONS.

In order to glean some further information on the vexed question of the proportions of the sexes in the British Raiidæ the writer, in the course of his work among these fishes, recorded whenever possible the numbers of the sexes in the samples examined by him. These samples have been drawn from commercial landings by steam, motor, and sailing trawlers by long liners, and by small vessels fishing with set nets, in addition to landings by the Marine Biological Association's research steamer *Salpa*.

In Table III (p. 620) are recorded the numbers of the sexes observed in samples of the seven species most commonly taken in smaller or larger numbers in the English Channel and for which the data are therefore most adequate. Both the actual numbers and the percentages of the sexes have been recorded separately for each sample, irrespective of mode of capture. Two records opposite one date mean that the samples examined on that day were drawn from two separate landings by different vessels. In order to facilitate interpretation an additional column is inserted in which an excess of males in a catch is indicated by an M and excess of females by an F, while the symbol = indicates that the sexes were equally represented. It will at once be seen on referring to this table that females are considerably in excess of the males both in actual numbers and in the number of samples in which they predominate. This applies to all the seven species. But further examination of the figures for individual samples reveals that there is absolutely no constancy in the proportions of the sexes in the different catches of any species. The proportions vary within wide limits. If reference now be made to Table II, which records the landings* from a very specialised local fishery, or to Figure 1 in which the results are graphically represented, this variation will be found there to vary from 100% females to 100% males. It should here be noted that all these landings came from exactly the same very restricted fishing ground (*vide* **12**, p. 6), and were taken with exactly the same fishing gear.

It is practically impossible to determine the proportions of the sexes among our British Rays at or shortly before birth in order to find out how they compare with the conditions found in commercial catches of the adults. All the species are oviparous, and it has not yet been found possible to collect Ray eggs in any number after they have been deposited in the sea so that the developing embryos may be examined for sex. But very recently-hatched individuals of *R. clavata* from about 9 cm. upwards in width of disc have been taken not infrequently by the *Salpa* in her trawl. Of 91 such young individuals of 12·5 cm. and under in width of disc, which have been obtained and their sex recorded, 47 were males and 44 were females. Similar observations on reasonably large numbers of equally young specimens of other species† have not been possible. But interesting and strongly confirmatory data‡ were obtained by observing the proportions of the sexes in 20 out of 21 hauls made by a Plymouth steam trawler during a week's fishing at the mouth of the English Channel

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* These figures are not included in Table III.

† Thirty-seven *R. montagui* under 15 cm. in width of disc yielded 17 males and 20 females.

‡ I am indebted to Mr. F. G. Walton Smith, B.Sc., for having collected these data.

TABLE I.

Proportions of the Sexes in Separate Trawl Hauls* taken by a Steam Trawler during one fishing trip.

K = fish kept for sale. D = fish discarded as too small.

Date (August, 1932)			19				20		21				22				23	24		
Locality.			Bishop Light bearing E. × S. 30 miles.				Bishop Light bearing E. 50 miles.		Bishop Light bearing E. × S. 30 miles.				Longships Light bearing S.E. × E. 90 miles.				Longships Light bearing S.E. × E. 90 miles.	Wolf Light bearing N. 20 miles.		Totals for each Species.
Duration of Haul (hours)			3½	3½	3½	3½	3	4	3½	3½	3½	3½	3	4	4	4	4	4		
Serial No. of Haul			1	2	3	4	5	6	9	10	11	12	13	15	16	18	20	21		
R. clavata	K	♂♂	–	–	–	1	–	–	–	–	–	–	2	1	4	2	9	5	24
		♀♀	1	–	–	–	1	–	1	–	–	–	–	2	2	1	27	5	40
	D	♂♂	–	1	–	–	1	2	–	–	–	1	–	–	–	–	9	1	15
		♀♀	–	1	–	–	3	–	–	–	–	1	–	–	–	–	6	1	12
R. montagui	K	♂♂	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	4
		♀♀	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	5	9
	D	♂♂	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	2
		♀♀	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	2
R. brachyura	K	♂♂	–	3	–	–	–	2	–	–	–	–	–	4	–	–	17	17	43
		♀♀	–	–	–	–	–	–	–	–	1	–	2	7	–	–	25	18	53
	D	♂♂	–	–	–	–	–	1	–	–	–	–	–	–	6	–	4	5	16
		♀♀	–	3	–	–	–	–	–	–	1	–	–	–	2	–	3	2	11
R. nævus	K	♂♂	–	1	–	–	–	–	–	–	–	1	–	1	20	–	10	12	45
		♀♀	–	–	–	–	–	–	–	–	–	–	–	–	6	–	7	9	22
	D	♂♂	–	–	–	–	–	–	–	–	–	–	–	–	2	–	3	–	5
		♀♀	–	–	–	–	–	–	–	–	–	–	–	–	1	–	4	–	5
R. circularis	K	♂♂	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		♀♀	1	–	1	1	–	–	3	–	–	1	–	–	1	–	–	–	8
	D	♂♂	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		♀♀	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
R. fullonica	K	♂♂	3	6	–	4	2	3	12	3	–	11	1	–	–	1	5	2	53
		♀♀	3	3	–	3	1	2	5	3	5	7	2	–	8	2	9	2	55
	D	♂♂	1	1	–	2	–	1	2	–	–	2	–	–	–	–	1	–	10
		♀♀	1	–	–	3	–	–	1	–	–	1	–	–	–	–	1	–	7
R. batis	K	♂♂	1	–	2	1	–	–	–	2	–	–	2	3	6	6	–	–	23
		♀♀	–	1	1	–	–	–	–	–	1	–	–	1	9	4	–	–	17
	D	♂♂	–	1	1	1	–	1	–	1	1	1	1	1	–	2	–	–	11
		♀♀	1	1	1	1	–	–	2	–	–	–	–	–	1	1	–	2	10
R. oxyrhynchus	K	♂♂	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
		♀♀	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	2
	D	♂♂	–	–	–	–	–	1	–	–	–	1	–	–	–	–	–	1	3
		♀♀	–	–	1	–	–	–	1	–	–	–	–	–	1	–	–	–	3

* Haul 8 contained no Rays.
Hauls 7, 14, 19 contained no fish. Trawl torn.
Haul 17 was not recorded.
Haul 3 contained 1 male *R. undulata*—the only specimen taken.

in August, 1932. The data obtained from those fish which were kept for sale and from those which were discarded as being too small to be marketable have been noted separately. All Rays exceeding about 25 cm. in width of disc and Skates of about 35 cm. and over were retained.* The results are summarised in Table I, to which reference should now be made. It will be seen that although in 5 out of the 8 species taken females predominate among the larger retained fish, in not a single instance is this true of the totals for the rejected "smalls." It seems clear, therefore, that in *R. clavata* at any rate, as in *Squalus acanthias*, *Mustelus antarcticus*, *Trygonorhina fasciata*, and *Rhinobates vincentianus*—that is to say, in all the Elasmobranchs in which the embryos or very young fish have been examined for sex—the young are born with the sexes approximately equally represented.† This applies also, almost certainly, to several, if not to all the other Ray species, and possibly to all the Elasmobranchs.

If, then, male and female Rays are born in equal numbers the question arises is there any factor, such as the segregation and shoaling habits found in the Spur Dogfish, which may reasonably be expected to account for the difficulty of obtaining a true picture of the proportions of the sexes in the adults?

It has already been pointed out briefly by the present writer (**12**, p. 17) that there is ample evidence of sexual segregation among adult Rays of several species and that the same probably is true for all the Channel, if not for all Ray species. Such segregation was first brought forcibly to the writer's notice by the composition of the catches landed on Plymouth market by vessels engaged in fishing for Rays with a kind of fixed net which superficially resembles a trammel but consists of only a single wall and acts simply as a straightforward tangle net. The first of such landings was observed on February 20th, 1930.‡ It will be seen from Table II—in which the entire catches landed by the various boats are recorded separately, each landing opposite one date being the total catch of one vessel—that the earlier landings observed in 1930 consisted almost entirely of female fish. With the approach of March, however, more males appeared and in the last landing recorded there was not a single female present. In the years 1931 and 1932 the landings from the net fishery were examined from the very beginning of the season. It will be

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* These sizes are considerably smaller than usual because at the time of this trip fish were very scarce and so nothing was discarded which might add even a little to the total returns for the voyage.

† Clark (**1**, p. 595), however, in the course of investigations on the eggs and young of British Raiidæ, hatched out artificially 23 *R. clavata* of which 15 were females. This is clearly an abnormal ratio (which would probably have been corrected if larger numbers from several fish had been examined—cf. Haacke's results with Rhinobates described on p. 7), for even among the adults a 2 : 1 ratio of females to males does not hold good.

‡ There had been earlier landings but the writer, having had only just taken up the study of the Raiidæ, was until this date quite unaware of the existence of such a fishery.

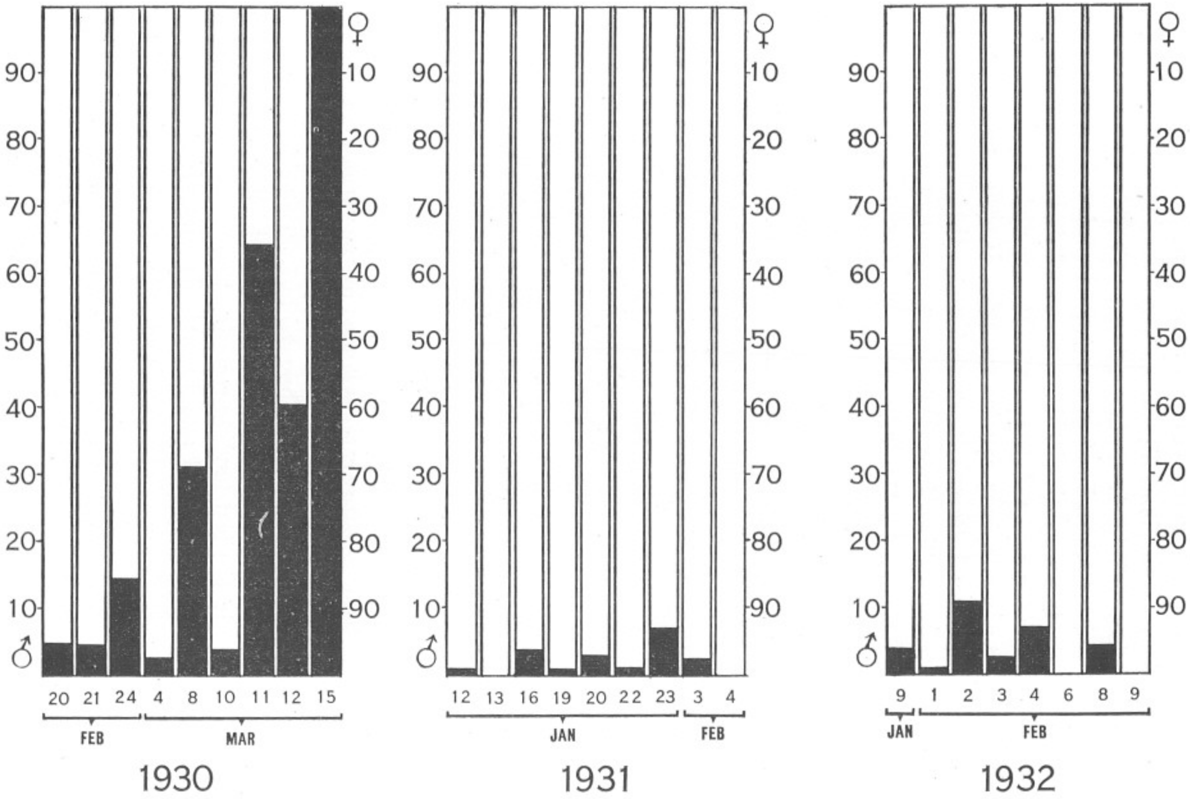

Fig. 1.—Graphical representation of composition of landings of *R. clavata* from Ray Nets in seasons 1930–31–32. Each vertical column represents the *total* landings on one day, the black component being the percentage of male fish and the white component being the percentage of female fish included therein.

TABLE II.

Composition of Landings from Ray Nets—Seasons 1930, 1931, and 1932.

(Not included in Table III, p. 620.)

Date. 1930.		Total number of Fish in Landing.	Total ♂♂	Total ♀♀	Percentage ♂♂	Percentage ♀♀
February	20	137	7	130	5	95
,,	20	65	3	62	5	95
,,	21	156	7	149	4	96
,,	21	52	3	49	6	94
,,	24	197	21	176	11	89
,,	24	36	13	23	36	64
March	4	34	1	33	3	97
,,	8	26	8	18	31	69
,,	8	38	12	26	32	68
,,	10	35	2	33	6	94
,,	10	14	0	14	0	100
,,	11	104	67	37	64	36
,,	12	69	28	41	41	59
,,	15	38	38	0	100	0
1931.						
January	12	161	2	159	1	99
,,	13	5	0	5	0	100
,,	13	14	0	14	0	100
,,	13	102	0	102	0	100
,,	16	51	2	49	4	96
,,	19	60	0	60	0	100
,,	19	72	0	72	0	100
,,	19	68	2	66	3	97
,,	20	108	3	105	3	97
,,	20	53	2	51	4	96
,,	22	64	1	63	2	98
,,	22	12	0	12	0	100
,,	23	72	9	63	12·5	87·5
,,	23	68	8	60	12	88
February	3	17	1	16	6	94
,,	3	24	0	24	0	100
,,	3	38	1	37	3	97
,,	4	5	0	5	0	100
,,	4	14	0	14	0	100
,,	4	102	0	102	0	100
1932.						
January	9	75	3	72	4	96
February	1	53	1	52	2	98
,,	1	15	0	15	0	100
,,	1	24	0	24	0	100
,,	1	3	0	3	0	100
,,	2	23	0	23	0	100
,,	2	51	8	43	16	84
,,	3	16	0	16	0	100
,,	3	8	0	8	0	100
,,	3	50	2	48	4	96
,,	4	34	4	30	12	88
,,	4	22	1	21	5	95
,,	4	14	0	14	0	100
,,	6	15	0	15	0	100
,,	8	64	8	56	12·5	87·5
,,	8	14	0	14	0	100
,,	8	11	2	9	18	82
,,	8	7	1	6	14	86
,,	9	10	0	10	0	100
,,	9	10	0	10	0	100
,,	9	12	0	12	0	100

TABLE III.

NUMBERS (WITH PERCENTAGES) OF MALES AND FEMALES OF SEVEN SPECIES OF RAIA INCLUDED IN SAMPLES FROM LANDINGS FROM THE ENGLISH CHANNEL—IRRESPECTIVE OF MODE OF CAPTURE.

Date.		R. clavata.					R. montagui.					R. brachyura.					R. nævus.					R. circularis.					R. fullonica.					R. batis.				
		Male.		Female.		Sex Predominating.	Male.		Female.		Sex Predominating.	Male.		Female.		Sex Predominating.	Male.		Female.		Sex Predominating.	Male.		Female.		Sex Predominating.	Male.		Female.		Sex Predominating.	Male.		Female.		Sex Predominating.
		No.	%	%	No.		No.	%	%	No.		No.	%	%	No.		No.	%	%	No.		No.	%	%	No.		No.	%	%	No.		No.	%	%	No.	
1930																																				
January	15	33	52	48	30	M	9	30	70	21	F	11	42	58	15	F	–	–	–	–		–	–	–	–		12	67	33	6	M	–	–	–	–	
,,	16	2	100	–	–	M	24	47	53	27	F	22	38	62	36	F	25	51	49	24	M	–	–	–	–		2	50	50	2	=	–	–	–	–	
,,	17	39	62	38	24	M	4	33	67	8	F	5	50	50	5	=	–	–	–	–		3	43	57	4	F	2	33	67	4	F	2	100	–	–	M
,,	17	10	40	60	15	F	7	47	53	8	F	–	–	–	–		1	100	–	–	M	–	–	–	–		5	42	58	7	F	1	50	50	1	=
,,	20	3	60	40	2	M	23	49	51	22	M	18	53	47	16	M	19	54	46	16	M	–	–	–	–		4	57	43	3	M	–	–	–	–	
,,	20	17	42·5	57·5	23	F	17	44	56	22	F	–	–	100	1	F	–	–	–	–		–	–	–	–		1	50	50	1	=	–	–	–		
,,	22	12	22	78	43	F	15	60	40	10	M	10	48	52	11	F	–	–	–	–		–	–	–	–		–	–	100	3	F	–	–	–	–	
,,	23	11	32	68	23	F	29	48	52	31	F	1	100	–	–	M	17	44	56	22	F	–	–	–	–		2	50	50	2	=	2	50	50	2	=
,,	24	10	45	55	12	F	8	44	56	10	F	10	32	68	21	F	–	–	–	–		–	–	–	–		1	100	–	–	M	–	–	–	–	
,,	25	10	40	60	15	F	12	43	57	16	F	–	–	–	–		11	46	54	13	F	–	–	–	–		2	25	75	6	F	–	–	100	1	F
,,	27	8	44	56	10	F	23	59	41	16	M	4	36	64	7	F	14	82	18	3	M	–	–	–	–		4	40	60	6	F	22	56	44	17	M
,,	31	20	61	39	13	M	12	39	61	19	F	–	–	100	1	F	13	30	70	31	F	–	–	–	–		4	50	50	4	=	1	50	50	1	=
February	2	23	62	38	14	M	2	12	88	14	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
,,	3	6	60	40	4	M	8	50	50	8	=	10	40	60	15	F	–	–	100	10	F	–	–	–	–		–	–	100	3	F	–	–	–	–	
,,	3	19	56	44	15	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
,,	5	33	43	57	43	F	4	44	56	5	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
,,	11	10	50	50	10	=	11	31	69	24	F	17	30	70	40	F	–	–	–	–		–	–	100	1	F	4	67	33	2	M	–	–	–	–	
,,	11	13	57	43	10	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
,,	17	13	46	54	15	F	20	42	58	28	F	15	43	57	20	F	5	31	69	11	F	4	33	67	8	F	3	33	67	6	F	–	–	–	–	
,,	17	22	61	39	14	M	13	42	58	18	F	16	42	58	22	F	6	32	68	13	F	–	–	–	–		12	50	50	12	=	3	75	25	1	M
,,	17	14	38	62	23	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
,,	27	28	37	63	47	F	3	50	50	3	=	–	–	100	1	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
March	3	17	42·5	57·5	23	F	1	33	67	2	F	–	–	–	–		1	100	–	–	M	–	–	–	–		–	–	–	–		–	–	–	–	
,,	5	10	37	63	17	F	11	44	56	14	F	22	41	59	32	F	3	37·5	62·5	5	F	3	30	70	7	F	6	60	40	4	M	–	–	–	–	
,,	7	21	60	40	14	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
,,	12	23	46	54	27	F	19	46	54	22	F	28	42	58	39	F	13	42	58	18	F	–	–	–	–		9	45	55	11	F	3	50	50	3	=
,,	16	–	–	100	207	F	–	–	–	–		3	100	–	–	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
,,	19	7	28	72	18	F	11	32	68	23	F	16	40	60	24	F	15	56	44	12	M	4	31	69	9	F	4	36	64	7	F	10	40	60	15	F
April	4	6	55	45	5	M	2	67	33	1	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
,,	10	31	53	47	28	M	1	50	50	1	=	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
,,	28	6	24	76	19	F	1	100	–	–	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
May	6	7	58	42	5	M	2	50	50	2	=	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
,,	14	25	48	52	27	F	13	39	61	20	F	1	33	67	2	F	12	29	71	30	F	–	–	–	–		3	33	67	6	F	–	–	–	–	
,,	21	14	37	63	24	F	6	37·5	62·5	10	F	20	39	61	31	F	–	–	–	–		–	–	–	–		9	35	65	17	F	1	33	67	2	F
,,	28	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		41	25	75	125	F
,,	29	10	18	82	46	F	–	–	100	2	F	–	–	–	–		2	100	–	–	M	1	14	86	6	F	4	57	43	3	M	–	–	–	–	
,,	30	24	44	56	30	F	–	–	–	–		–	–	–	–		1	100	–	–	M	1	14	86	6	F	12	29	71	29	F	–	–	–	–	
,,	31	54	39	61	85	F	4	44	56	5	F	–	–	100	2	F	8	57	43	6	M	4	25	75	12	F	19	41	59	27	F	–	–	–	–	
June	2	3	16	84	16	F	1	100	–	–	M	–	–	–	–		2	40	60	3	F	2	50	50	2	=	4	40	60	6	F	–	–	–	–	
,,	3	6	43	57	8	F	5	45	55	6	F	–	–	100	1	F	5	42	58	7	F	–	–	–	–		7	64	36	4	M	–	–	–	–	
,,	3	2	67	33	1	M	6	60	40	4	M	152	83	17	31	M	–	–	100	9	F	–	–	–	–		–	–	–	–		–	–	–	–	
,,	4	–	–	–	–		1	3	97	28	F	469	57	43	355	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
,,	14	99	40	60	147	F	7	47	53	8	F	–	–	–	–		13	28	72	33	F	6	32	68	13	F	89	47	53	102	F	–	–	–	–	

July	10	7	47	53	8	F	6	29	71	15	F	8	24	76	25	F	—	—	—	—		1	50	50	1	=	4	80	20	1	M	—	—	—	—	
,,	17	13	43	57	17	F	17	50	50	17	=	8	36	64	14	F	9	64	36	5	M	—	—	—	—		4	44	56	5	F	10	48	52	11	F
,,	21	16	44	56	20	F	16	39	61	25	F	19	43	57	25	F	9	37·5	62·5	15	F	5	36	64	9	F	4	36	64	7	F	—	—	—	—	
August	1	26	47	53	29	F	14	54	46	12	M	3	37·5	62·5	5	F	20	51	49	19	M	4	40	60	6	F	—	—	—	—		—	—	—	—	
,,	20	15	36	64	27	F	—	—	—	—		—	—	—	—		33	35	65	62	F	2	40	60	3	F	—	—	100	3	F	2	29	71	5	F
,,	20	—	—	—	—		—	—	100	1	F	1	1	99	170	F	2	100	—	—	M	—	—	—	—		—	—	—	—		—	—	—	—	
,,	21	12	29	61	19	F	3	37·5	62·5	5	F	—	—	—	—		25	34	66	49	F	—	—	—	—		3	60	40	2	M	—	—	—	—	
,,	23	—	—	—	—		4	57	43	3	M	60	43	57	79	F	—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—	
,,	23	—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—		—	—	100	9	F	—	—	—	—	
November	7	6	43	57	8	F	15	52	48	14	M	19	38	62	31	F	—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—	
,,	10	14	42	58	19	F	4	33	67	8	F	5	33	67	10	F	—	—	—	—		1	3	67	2	F	4	57	43	3	M	1	50	50	1	=
,,	18	31	42	58	42	F	23	40	60	34	F	32	46	54	38	F	14	58	42	10	M	5	33	67	10	F	6	40	60	9	F	2	50	50	2	=
,,	24	17	39	61	27	F	6	37·5	62·5	16	F	11	48	52	12	F	—	—	—	—		—	—	—	—		9	82	18	2	M	2	33	67	4	F
,,	28	18	39	61	28	F	11	58	42	8	M	—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—	
December	8	24	50	50	24	=	19	59	41	13	M	2	29	71	5	F	15	44	56	19	F	—	—	—	—		4	44	56	5	F	—	—	—	—	
,,	11	16	43	57	21	F	22	52	48	20	M	—	—	100	2	F	18	50	50	18	=	—	—	—	—		6	50	50	6	=	—	—	—	—	
,,	16	22	71	21	9	M	2	33	67	4	F	5	36	64	9	F	—	—	100	4	F	—	—	—	—		—	—	—	—		—	—	—	—	
,,	22	—	—	100	2	F	1	17	83	5	F	13	43	57	17	F	—	—	—	—		—	—	—	—		7	64	36	4	M	—	—	—	—	
1931.																																				
January	8	—	—	100	4	F	22	51	49	21	M	—	—	—	—		11	37	63	19	F	—	—	100	1	F	—	—	—	—		—	—	—	—	
,,	16	27	37·5	62·5	45	F	2	25	75	6	F	—	—	—	—		—	—	—	—		—	—	—	—		—	—	100	6	F	1	50	50	1	=
,,	17	14	48	52	15	F	10	53	47	9	M	1	13	67	2	F	—	—	100	1	F	—	—	—	—		10	62·5	37·5	6	M	—	—	—	—	
,,	23	1	33	67	2	F	23	55	45	19	M	26	39	61	40	F	33	59	41	23	M	—	—	—	—		1	20	80	4	F	—	—	100	2	F
February	3	7	17	83	35	F	14	52	48	13	M	31	60	40	21	M	—	—	—	—		—	—	—	—		4	27	73	11	F	—	—	100	4	F
,,	5	21	40	60	32	F	26	51	49	25	M	—	—	100	1	F	—	—	—	—		—	—	—	—		1	50	50	1	=	—	—	—	—	
,,	9	25	43	57	33	F	30	49	51	31	F	—	—	—	—		22	61	39	14	M	—	—	—	—		—	—	—	—		—	—	—	—	
,,	13	11	44	56	14	F	3	27	73	8	F	—	—	—	—		—	—	—	—		—	—	—	—		5	42	58	7	F	12	44	56	15	F
,,	16	1	25	75	3	F	14	34	66	27	F	11	44	56	14	F	12	33	67	24	F	—	—	—	—		4	31	69	9	F	1	33	67	2	F
,,	21	21	47	53	24	F	29	43	57	39	F	1	100	—	—	M	29	66	24	15	M	—	—	—	—		3	60	40	2	M	—	—	—	—	
,,	24	28	65	35	15	M	7	24	76	22	F	23	50	50	23	=	—	—	—	—		—	—	—	—		5	38	62	8	F	—	—	—	—	
,,	26	12	40	60	18	F	11	61	39	7	M	—	—	—	—		17	40	60	26	F	—	—	—	—		—	—	100	3	F	1	50	50	1	=
March	3	14	47	53	16	F	5	36	64	9	F	—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—	
,,	3	—	—	—	—		17	50	50	17	=	—	—	—	—		16	46	54	19	F	5	29	71	12	F	12	80	20	3	M	2	50	50	2	=
,,	5	18	53	47	16	M	24	56	44	19	M	14	31	69	31	F	—	—	—	—		4	50	50	4	=	6	60	40	4	M	5	28	72	13	F
,,	9	2	40	60	3	F	13	41	59	19	F	15	39	61	23	F	7	24	76	22	F	—	—	—	—		—	—	—	—		2	33	67	4	F
April	25	16	43	57	21	F	16	46	54	19	F	22	54	46	19	M	—	—	—	—		7	44	56	9	F	6	55	45	5	M	—	—	—	—	
,,	29	16	39	61	25	F	10	48	52	11	F	26	39	61	41	F	—	—	—	—		—	—	—	—		—	—	—	—		8	31	69	18	F
May	4	18	55	45	15	M	4	14	86	25	F	12	32	68	26	F	—	—	—	—		12	52	48	11	M	—	—	—	—		1	33	67	2	F
,,	11	20	43	57	26	F	27	45	55	33	F	19	40	60	28	F	—	—	—	—		—	—	—	—		14	70	30	6	M	1	33	67	2	F
,,	12	14	54	46	12	M	3	50	50	3	=	1	25	75	3	F	—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—	
,,	22	21	47	53	24	F	8	26	74	23	F	14	40	60	21	F	—	—	—	—		—	—	—	—		3	37·5	62·5	5	F	2	33	67	4	F
,,	26	21	42	58	29	F	15	48	52	16	F	3	100	—	—	M	19	47·5	52·5	21	F	—	—	—	—		5	83	17	1	M	—	—	—	—	
June	1	11	37	63	19	F	2	40	60	3	F	—	—	—	—		1	100	—	—	M	—	—	—	—		9	69	31	4	M	—	—	—	—	
,,	4	29	45	55	36	F	29	48	52	31	F	2	100	—	—	M	35	49	51	36	F	—	—	—	—		3	33	67	6	F	3	33	67	6	F
,,	4	6	40	60	9	F	11	50	50	11	=	—	—	—	—		—	—	—	—		—	—	—	—		6	29	71	15	F	2	40	60	3	F
,,	8	5	42	58	7	F	10	62·5	37·5	6	M	11	34	66	21	F	19	49	51	20	F	—	—	—	—		15	47	53	17	F	—	—	—	—	
,,	10	27	44	56	34	F	29	41	59	41	F	—	—	—	—		3	30	70	7	F	—	—	—	—		12	52	48	11	M	1	33	67	2	F
,,	15	20	48	52	22	F	19	46	54	22	F	18	51	49	17	M	—	—	—	—		—	—	—	—		7	39	61	11	F	—	—	100	1	F
,,	16	22	48	52	24	F	26	50	50	26	=	—	—	100	1	F	31	47	53	35	F	—	—	—	—		10	48	52	11	F	5	50	50	5	=
,,	23	29	63	37	17	M	15	79	21	4	M	23	38	62	37	F	—	—	—	—		—	—	—	—		3	43	57	4	F	3	43	57	4	F
July	3	17	49	51	18	F	9	50	50	9	=	15	65	35	8	M	—	—	—	—		—	—	—	—		4	57	43	3	M	—	—	100	1	F
,,	3	16	67	33	8	M	—	—	100	1	F	—	—	—	—		8	62	38	5	M	—	—	—	—		4	50	50	4	=	—	—	—	—	
,,	13	13	48	52	14	F	18	47	53	20	F	27	47	53	31	F	—	—	—	—		3	50	50	3	=	3	43	57	4	F	—	—	—	—	
,,	14	17	57	43	13	M	8	62	38	5	M	1	100	—	—	M	—	—	100	9	F	—	—	—	—		—	—	—	—		—	—	—	—	
,,	29	26	15	85	149	F	—	—	—	—		—	—	—	—		12	63	37	7	M	—	—	100	1	F	17	52	48	16	M	—	—	100	1	F
October	10	22	51	49	21	M	1	50	50	1	=	7	70	30	3	M	—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—	
,,	28	14	45	55	17	F	4	50	50	4	=	—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—	
November	2	—	—	100	3	F	2	50	50	2	=	2	67	33	1	M	—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—	
,,	27	5	23	77	17	F	—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—	
December	2	4	40	60	6	F	—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—	
,,	15	6	32	68	13	F	2	50	50	2	=	—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—	
,,	23	11	61	39	7	M	4	57	43	3	M	—	—	100	2	F	—	—				—	—				—	—				—	—	—	—	

seen from the table that few males were present in any landing and that not infrequently an entire catch would consist wholly of female fish. This is not explainable by any selective action of the nets as these were the same at the beginning as at the end of the season in 1930. Nor does it appear to be true that the males are not caught because they exhibit some difference (or absence) of movement. When present they are taken quite as successfully as the females.

There is no doubt, therefore, that on this particular fishing ground, during the first three or four months of the year, the Ray population may consist entirely or almost entirely of one sex of a single species. The composition of this population may change rapidly and completely during the brief season of the net fishery, which is simply the time during which fully adult fish are present on the ground in large numbers. The main population consists first, and for the greater part of the season, of mature females with, in some seasons at least, mature males appearing later and for a shorter time towards the end of the season.* Finally, for the greater part of the year, only a residuum of immature individuals of both sexes is present, the adult fish having migrated elsewhere.

Having discovered such very definite segregation of the sexes of *R. clavata* on the Plymouth net fishing ground, coupled with a definite migratory movement of greater or less extent, the question now arises as to whether or not this is an isolated phenomenon or whether there is evidence of similar segregations and migrations elsewhere and for other species. For the purpose of obtaining true samples of fish stocks fixed nets possess a unique superiority over other fishing implements such as trawls and long-lines in that their fishing action is restricted to one very small patch of ground. Unfortunately the writer is not aware of the existence of any other ray-net fishery such as that carried on from Plymouth at any other point on the coast, at any rate within his range of investigation. Nevertheless, a considerable though less complete body of evidence is available from catches obtained by other methods of fishing.

On the night of Saturday–Sunday, March 15th–16th, 1930, between the hours of 7 p.m. and 2 a.m., a steam trawler fishing in shallow water off the Cornish coast caught 210 large Rays, 207 of them being *R. clavata*, every one of which was a female. Obviously this vessel had fallen upon a shoal of female fish similar to that fished by the nets on the Plymouth grounds. It is not to be expected, however, that such a pure landing will occur in trawl or line fishing except at very rare intervals, because even one haul of a trawl or a fleet of lines once shot samples a large area of the sea floor ; and every landing is the product not of one but of many hauls

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* Unfortunately, owing to the onset of unfavourable weather conditions, this fishery was brought to a premature close in both 1931 and 1932, so that it is not known whether or not the males appeared towards the end of the season in those years.

of the trawl or a fleet of lines several if not many times shot. That the landings from both trawlers and liners should, in spite of this, not infrequently consist largely and sometimes almost entirely of one sex of a single species points clearly to the occurrence of sexual segregation among species other than *R. clavata* and on grounds other than that fished by the Plymouth nets. Some of the most striking of such landings recorded by the present writer are enumerated below.

On June 3rd, 1930, a small inshore trawler fishing near Newlyn, Cornwall, brought ashore 205 Rays. Of these no less than 183 were *R. brachyura*, all immature, and containing 152 males. Nine *R. nævus* were included in this catch, every one a female. On the following day a small liner fishing on or near the same ground landed 853 Rays, 824 of which were immature specimens of *R. brachyura*. In this catch, however, males and females were present in more nearly equal numbers, there being 469 males and 355 females. *R. montagui* was the only other species included in the catch. Of these 29 individuals, all were adult fish and consisted of 28 females with only a single male included among them. In August of the same year this liner was still fishing on the same ground, but the *R. brachyura* which she was then landing were all mature fish which must have migrated there (*vide* **12**, p. 23). On August 20th this vessel landed 171 adult Rays of this species of which only one was a male. Three days later another but smaller catch was landed in which adult males and females were almost equally represented, there being 60 of the former and 79 of the latter sex. After this date the writer had to leave Newlyn, otherwise it would have been interesting to have noted whether or not the males eventually exceeded the females in number or even completely " replaced " them as happened in the case of *R. clavata* on the Plymouth net grounds in the spring of the year.

There was another interesting landing on August 23rd. A liner which had been fishing in deep water caught only 9 Rays on its full fleet of lines which had been shot once. All these were *R. fullonica* and all adult females.

On July 29th, 1931, a liner from the same port landed 175 *R. clavata* in addition to small numbers of other species. Of these Thornback Rays 149 were adult females ; the 26 males were mostly immature. On May 31st, 1932, a liner's catch was observed to contain 19 *R. marginata*, all females over 100 cm. in width of disc, and all containing ripening ova. On June 2nd another landing contained 39 *R. batis* of which 37 were mature or nearly mature males and 2 were immature females.

In no instance was any information available as to how the fish were distributed on the lines. In the hope that an interesting catch similar to one of those mentioned might be taken in his presence the writer went to sea in a liner and recorded the species and sex of every Ray which came up in the order in which it appeared (*vide* **12**, p. 28). Unfortunately only a very " ordinary " catch rewarded his efforts ; 192 *R. clavata* were taken the majority of which were immature and the two sexes were more or less indiscriminately intermingled all along the line. There was a slight excess of females. The catch of *R. nævus*, the only other species taken in any numbers, was more interesting ; 142 specimens were taken, 104 of which were males, most of them fully adult. The females, of which only an occasional specimen occurred here and there at wide intervals, were found on examination to be mainly immature, only 7 out of the total 38 containing ripe or ripening ova.

Other species were represented by only a very few scattered individuals.

It seems clear, however, from the main body of the evidence brought together in this paper, that the so-called abnormal sex-ratio found among the commercial landings of Rays and Skates is due not to any differential production of males and females at birth, or to a differential mortality after birth, but to differential catches of the sexes owing to segregation of the larger fish into unisexual shoals for at least part of the year. The females, particularly when in a gravid or spawning condition, form more compact schools than do the males, and therefore tend to be captured in greater numbers.

This fact is of much more than theoretical interest ; it has a direct practical bearing on the commercial fishery for these species, which have now become of primary and growing importance as national food fishes. It is well known that for the maintenance of any animal stock the female is, from the numerical point of view, the more important sex. Since, therefore, the females of the Raiidæ as a general rule are captured in considerably greater numbers than the males, it follows that the greatest drain of the fishery upon the fish stock falls upon its most vulnerable part. These Elasmobranch fishes will therefore be much more rapidly and more severely affected by intense fishing in any particular area—such as the English Channel—than species in which there is not an excess of females caught by ordinary fishing methods. Such an effect will tend to be greatly minimised in the case of strongly migratory species—such as the Spur Dogfish, for instance. The stock of such fishes on any particular fishing ground will be exposed to capture only for so long as it remains in that region. Not only so, its numbers will always tend to be sustained or replenished by immigrants from other localities where fishing is less intense or non-existent. It may be highly significant, therefore, that from being a very flourishing concern, the English Channel fishery for Spur Dogfish has, in the course of the last five years, shrunken to almost negligible proportions* owing to the

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* The Ministry of Agriculture and Fisheries returns of landings from the English Channel during this period are : 1928, 54,206 cwt. ; 1929, 28,920 cwt. ; 1930, 27,188 cwt. ; 1931, 16,049 cwt. ; 1932, figures not yet available.

scarcity of these fish—*and that in spite of their being a pelagic and migratory species.*

On the other hand, the adverse effect of intensive fishing will be correspondingly increased in the case of species—such as the Raiidæ—whose migrations appear to be very restricted or even quite local in character. Moreover, these very same factors which by their action will assist the commercial forces of depletion will be equally potent in retarding recovery once a decline has been brought about in the stocks.

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Some Records of Parasitic Worms from Marine Fishes at Plymouth.

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Records of parasitic worms from British marine fishes are still rather scanty. A good deal of attention has been paid to the subject of the Trematodes by Nicoll, whose valuable list (1915) is indispensable to anyone working in this field. Nicoll is himself responsible for the records of the majority of the 49 species of Trematodes given in the second edition (1931) of the "Plymouth Marine Fauna." The only work done on the Cestodes of fishes at Plymouth appears to have been that of Woodland (1927, a and b), as a result of which 14 species have been placed on record. Very few data are available as to the Nematodes, and none as to the Acanthocephala, of the Plymouth fauna.

During the latter part of May, 1932, the senior author spent some ten days at the Plymouth Laboratory of the Marine Biological Association, collecting parasitic worms from fishes. Over 100 fish were dissected, including representatives of about 40 species. No attempt was made to collect every parasite, including larval forms, but attention was paid almost exclusively to the adult forms living in the alimentary canal or on the gills and external surfaces. The parasites found were simply preserved at once, and were not determined until after the author's return to London.

The hosts were almost all named by Mr. G. A. Steven, of the Laboratory staff, to whom grateful acknowledgment is due for his kind and unfailing help. Mr. Steven suggested that it might be of some interest to record the sizes of the fish found to be infested with parasites. This had not been done during the first day of collecting, but was done regularly thereafter. For all species except skates the measurement given is the length from snout to tip of tail, to the nearest 5 mm. In the case of skates Mr. Steven's usual practice was followed of measuring across the "wings" from tip to tip.

The names here used for the hosts are those used in the " Plymouth Marine Fauna " (second edition, 1931).

The junior author has, at various times, also visited the Laboratory at Plymouth and collected Trematodes from fishes. His identifications are principally from living specimens. In order to avoid the duplication of records, it has been thought desirable to include them all in one list. Both authors, of course, frequently collected the same species from the same hosts, and where this occurred the records given in the subjoined list, unless otherwise indicated, are the senior author's.

The joint list contains 12 species of Trematodes, 4 of Cestodes, 11 of Nematodes, and 2 of Acanthocephala which have not hitherto been included in the " Plymouth Marine Fauna." These are indicated by an asterisk (*). Hosts which are believed to be new for the species in question are indicated by a dagger (†), while a double dagger (‡) indicates that the record is the junior author's.

Some of the Nematodes, unfortunately, could not be specifically determined owing to the absence of male specimens or to the incompleteness of the material. The occurrence of the little-known form Ascarophis is of particular interest, and a paper on this Nematode will appear elsewhere. *Echinorhynchus leidyi* has hitherto been recorded only from " lake trout " in the Great Lakes region of North America. The determination of the specimens from the rockling is therefore open to question, though they appear to agree very closely with the description of *E. leidyi.*

As regards the nomenclature of the parasites recorded, current usage has generally been followed. Two nomenclatural changes have, however, been introduced among the Trematodes, and these call for some explanation.

(1) We have treated the genus *Paracotyle* Johnstone, 1911, as synonymous with *Microbothrium* Olsson, 1869, because *P. caniculæ,* the genotype of Paracotyle, appears to be almost certainly congeneric with *M. apiculatum,* the genotype of Microbothrium. A paper on this form by the junior author will appear elsewhere.

(2) We have substituted the genus *Mazocraes* Hermann, 1782, for *Octobothrium* F. S. Leuckart, 1827. It appears to be generally admitted that its genotype, *Mazocraes alosæ* Hermann, is identical with *Octobothrium lanceolatum* Leuckart, the genotype of Octobothrium. Hence the name Octobothrium must fall into the synonymy of Mazocraes, and there is no justification for retaining the better-known name Octobothrium and treating Mazocraes as a synonym, as has been done by some recent authors.

The junior author has found certain Trematodes which are believed to represent new species. These are not included in the present list, and will be described elsewhere.

It is a pleasure to acknowledge the kind attention and help which we received at the hands of the Director and staff of the Plymouth Laboratory, and the interest which they took in our work.

LIST OF SPECIES COLLECTED.

TREMATODA.

Order MONOGENEA.

Fam. **Capsalidæ** (=Tristomatidæ).

ENTOBDELLA SOLEÆ (v. Ben. and Hesse, 1864). Skin of *Solea vulgaris*.

Fam. **Udonellidæ.**

*UDONELLA CALIGORUM Johnston, 1835. Numerous young specimens attached to a Caligus ♀ (determined by Dr. I. Gordon as probably *C. rapax* M. Edw., 1840) found free in plankton, January 12th, 1932, by Mr. F. S. Russell.

Fam. **Monocotylidæ.**

CALICOTYLE KROYERI Diesing, 1850. Cloaca of *Raja maculata*.

*MICROBOTHRIUM [PARACOTYLE] CANICULÆ (Johnstone, 1911). Skin, on dorsal surface, of ‡*Scyllium canicula*.

ACANTHOCOTYLE SP. Skin of *Raja clavata* and ‡*R. maculata*.

Fam. **Polystomatidæ.**

*ONCHOCOTYLE APPENDICULATA (Kuhn, 1829). Gills of *Raja clavata* (26 cm. across), *R. blanda* (41 cm.), †‡*R. oxyrhynchus*, ‡*R. batis* and ‡*Scyllium canicula*.

Fam. **Octocotylidæ.**

*MAZOCRAES ALOSÆ Hermann, 1782 (=*Octobothrium lanceolatum* Leuckart, 1827). Gills of ‡*Clupea finta*.

*MAZOCRAES HARENGI (v. Ben. and Hesse, 1864). Gills of †‡*Clupea alosa*.

MAZOCRAES SCOMBRI (Kuhn, 1829). Gills of *Scomber scombrus*.

*DACTYCOTYLE DENTICULATA (Olsson, 1876). Gills of †‡*Merluccius merluccius*.

DACTYCOTYLE MERLANGI (Kuhn, 1829). Gills of ‡*Gadus merlangus*.

*GASTROCOTYLE TRACHURI v. Ben. and Hesse, 1864. Gills of ‡*Caranx trachurus*.

AXINE BELONES Abildgaard, 1794. Gills of §*Belone acus* (abundant in several specimens).

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§ Collected by Miss M. Rothschild.

Order DIGENEA.

Fam. **Bucephalidæ.**

BUCEPHALOPSIS GRACILESCENS (Rud., 1819). Stomach and intestine of *Lophius piscatorius* (in each of 3 specimens); 2 specimens in stomach of †*Conger vulgaris* (about 3 ft.), possibly accidental.

RHIPIDOCOTYLE MINIMA (Wagener, 1852). Intestine of *Trigla hirundo* (24 cm.) and *T. cuculus* (24 cm.).

PROSORHYNCHUS ACULEATUS Odhner, 1904. Stomach, intestine and rectum of *Conger vulgaris*.

PROSORHYNCHUS CRUCIBULUM (Rud., 1819). Intestine of *Conger vulgaris;* one immature specimen (?) in intestine of *Lophius piscatorius* (47 cm.).

Fam. **Fellodistomidæ** (=Steringophoridæ).

*STERINGOPHORUS FURCIGER (Olsson, 1868). Immature specimens in stomach and intestine of *Pleuronectes limanda* (18·5 and 19 cm.).

STERINGOTREMA CLUTHENSE (Nicoll, 1909). Immature specimens in intestine of *Pleuronectes microcephalus* (21·5 cm.) and *P. limanda* (18·5 cm.).

STERINGOTREMA DIVERGENS (Rud., 1809). Stomach and intestine of *Blennius ocellaris*, each of three specimens (12–14 cm.).

Fam. **Zoogonidæ.**

*ZOOGONUS? RUBELLUS (Olsson, 1868). Immature specimens in intestine of †*Pleuronectes limanda* (16 cm.) and †*Labrus mixtus* (27 cm.).

ZOOGONOIDES VIVIPARUS (Olsson, 1868). Rectum of ‡*Callionymus lyra* and ‡*Pleuronectes microcephalus;* immature specimens in rectum of *Pleuronectes platessa* (36·5 cm.).

Fam. **Allocreadiidæ.**

PODOCOTYLE ATOMON (Rud., 1802). Intestine of *Cottus bubalis*.

PODOCOTYLE REFLEXA (Creplin, 1825). Intestine of *Spinachia vulgaris*, each of 4 specimens (12·5–16 cm.); intestine of †‡*Onos tricirratus*.

PODOCOTYLE SYNGNATHI Nicoll, 1913. One specimen in intestine of *Entelurus æquoreus* (44 cm.).

LEBOURIA VARIA Nicoll, 1910. Intestine of *Callionymus lyra*, †*Labrus mixtus* (two out of four specimens, ♂ 27 cm., ♀ 21 cm.) and †‡*Labrus bergylta*.

*HELICOMETRA FASCIATA (Rud., 1819). Intestine of ‡*Crenilabrus melops*.

TABLE II.

COMPOSITION OF LANDINGS FROM RAY NETS—SEASONS 1930, 1931, AND 1932.

(Not included in Table III, p. 620.)

Date.	Total number of Fish in Landing.	Total ♂♂	Total ♀♀	Percentage ♂♂	Percentage ♀♀
1930.					
February 20	137	7	130	5	95
,, 20	65	3	62	5	95
,, 21	156	7	149	4	96
,, 21	52	3	49	6	94
,, 24	197	21	176	11	89
,, 24	36	13	23	36	64
March 4	34	1	33	3	97
,, 8	26	8	18	31	69
,, 8	38	12	26	32	68
,, 10	35	2	33	6	94
,, 10	14	0	14	0	100
,, 11	104	67	37	64	36
,, 12	69	28	41	41	59
,, 15	38	38	0	100	0
1931.					
January 12	161	2	159	1	99
,, 13	5	0	5	0	100
,, 13	14	0	14	0	100
,, 13	102	0	102	0	100
,, 16	51	2	49	4	96
,, 19	60	0	60	0	100
,, 19	72	0	72	0	100
,, 19	68	2	66	3	97
,, 20	108	3	105	3	97
,, 20	53	2	51	4	96
,, 22	64	1	63	2	98
,, 22	12	0	12	0	100
,, 23	72	9	63	12·5	87·5
,, 23	68	8	60	12	88
February 3	17	1	16	6	94
,, 3	24	0	24	0	100
,, 3	38	1	37	3	97
,, 4	5	0	5	0	100
,, 4	14	0	14	0	100
,, 4	102	0	102	0	100
1932.					
January 9	75	3	72	4	96
February 1	53	1	52	2	98
,, 1	15	0	15	0	100
,, 1	24	0	24	0	100
,, 1	3	0	3	0	100
,, 2	23	0	23	0	100
,, 2	51	8	43	16	84
,, 3	16	0	16	0	100
,, 3	8	0	8	0	100
,, 3	50	2	48	4	96
,, 4	34	4	30	12	88
,, 4	22	1	21	5	95
,, 4	14	0	14	0	100
,, 6	15	0	15	0	100
,, 8	64	8	56	12·5	87·5
,, 8	14	0	14	0	100
,, 8	11	2	9	18	82
,, 8	7	1	6	14	86
,, 9	10	0	10	0	100
,, 9	10	0	10	0	100
,, 9	12	0	12	0	100

TABLE III.

NUMBERS (WITH PERCENTAGES) OF MALES AND FEMALES OF SEVEN SPECIES OF RAIA INCLUDED IN SAMPLES FROM LANDINGS FROM THE ENGLISH CHANNEL—IRRESPECTIVE OF MODE OF CAPTURE.

Date.		R. clavata.					R. montagui.					R. brachyura.					R. nævus.					R. circularis.					R. fullonica.					R. batis.				
		Male. No.	Male. %	Female. %	Female. No.	Sex Predominating.	Male. No.	Male. %	Female. %	Female. No.	Sex Predominating.	Male. No.	Male. %	Female. %	Female. No.	Sex Predominating.	Male. No.	Male. %	Female. %	Female. No.	Sex Predominating.	Male. No.	Male. %	Female. %	Female. No.	Sex Predominating.	Male. No.	Male. %	Female. %	Female. No.	Sex Predominating.	Male. No.	Male. %	Female. %	Female. No.	Sex Predominating.
1930																																				
January	15	33	52	48	30	M	9	30	70	21	F	11	42	58	15	F	–	–	–	–		–	–	–	–		12	67	33	6	M	–	–	–	–	
,,	16	2	100	–	–	M	24	47	53	27	F	22	38	62	36	F	25	51	49	24	M	–	–	–	–		2	50	50	2	=	–	–	–	–	
,,	17	39	62	38	24	M	4	33	67	8	F	5	50	50	5	=	–	–	–	–		3	43	57	4	F	2	33	67	4	F	2	100	–	–	M
,,	17	10	40	60	15	F	7	47	53	8	F	–	–	–	–		1	100	–	–	M	–	–	–	–		5	42	58	7	F	1	50	50	1	=
,,	20	3	60	40	2	M	23	49	51	22	M	18	53	47	16	M	19	54	46	16	M	–	–	–	–		4	57	43	3	M	–	–	–	–	
,,	20	17	42·5	57·5	23	F	17	44	56	22	F	–	–	100	1	F	–	–	–	–		–	–	–	–		1	50	50	1	=	–	–	–		
,,	22	12	22	78	43	F	15	60	40	10	M	10	48	52	11	F	–	–	–	–		–	–	–	–		–	–	100	3	F	–	–	–	–	
,,	23	11	32	68	23	F	29	48	52	31	F	1	100	–	–	M	17	44	56	22	F	–	–	–	–		2	50	50	2	=	2	50	50	2	=
,,	24	10	45	55	12	F	8	44	56	10	F	10	32	68	21	F	–	–	–	–		–	–	–	–		1	100	–	–	M	–	–	–	–	
,,	25	10	40	60	15	F	12	43	57	16	F	–	–	–	–		11	46	54	13	F	–	–	–	–		2	25	75	6	F	–	–	100	1	F
,,	27	8	44	56	10	F	23	59	41	16	M	4	36	64	7	F	14	82	18	3	M	–	–	–	–		4	40	60	6	F	22	56	44	17	M
,,	31	20	61	39	13	M	12	39	61	19	F	–	–	100	1	F	13	30	70	31	F	–	–	–	–		4	50	50	4	=	1	50	50	1	=
February	2	23	62	38	14	M	2	12	88	14	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
,,	3	6	60	40	4	M	8	50	50	8	=	10	40	60	15	F	–	–	100	10	F	–	–	–	–		–	–	100	3	F	–	–	–	–	
,,	3	19	56	44	15	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
,,	5	33	43	57	43	F	4	44	56	5	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
,,	11	10	50	50	10	=	11	31	69	24	F	17	30	70	40	F	–	–	–	–		–	–	100	1	F	4	67	33	2	M	–	–	–	–	
,,	11	13	57	43	10	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
,,	17	13	46	54	15	F	20	42	58	28	F	15	43	57	20	F	5	31	69	11	F	4	33	67	8	F	3	33	67	6	F	–	–	–	–	
,,	17	22	61	39	14	M	13	42	58	18	F	16	42	58	22	F	6	32	68	13	F	–	–	–	–		12	50	50	12	=	3	75	25	1	M
,,	17	14	38	62	23	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
,,	27	28	37	63	47	F	3	50	50	3	=	–	–	100	1	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
March	3	17	42·5	57·5	23	F	1	33	67	2	F	–	–	–	–		1	100	–	–	M	–	–	–	–		–	–	–	–		–	–	–	–	
,,	5	10	37	63	17	F	11	44	56	14	F	22	41	59	32	F	3	37·5	62·5	5	F	3	30	70	7	F	6	60	40	4	M	–	–	–	–	
,,	7	21	60	40	14	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
,,	12	23	46	54	27	F	19	46	54	22	F	28	42	58	39	F	13	42	58	18	F	–	–	–	–		9	45	55	11	F	3	50	50	3	=
,,	16	–	–	100	207	F	–	–	–	–		3	100	–	–	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
,,	19	7	28	72	18	F	11	32	68	23	F	16	40	60	24	F	15	56	44	12	M	4	31	69	9	F	4	36	64	7	F	10	40	60	15	F
April	4	6	55	45	5	M	2	67	33	1	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
,,	10	31	53	47	28	M	1	50	50	1	=	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
,,	28	6	24	76	19	F	1	100	–	–	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
May	6	7	58	42	5	M	2	50	50	2	=	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
,,	14	25	48	52	27	F	13	39	61	20	F	1	33	67	2	F	12	29	71	30	F	–	–	–	–		3	33	67	6	F	–	–	–	–	
,,	21	14	37	63	24	F	6	37·5	62·5	10	F	20	39	61	31	F	–	–	–	–		–	–	–	–		9	35	65	17	F	1	33	67	2	F
,,	28	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		41	25	75	125	F
,,	29	10	18	82	46	F	–	–	100	2	F	–	–	–	–		2	100	–	–	M	1	14	86	6	F	4	57	43	3	M	–	–	–	–	
,,	30	24	44	56	30	F	–	–	–	–		–	–	–	–		1	100	–	–	M	1	14	86	6	F	12	29	71	29	F	–	–	–	–	
,,	31	54	39	61	85	F	4	44	56	5	F	–	–	100	2	F	8	57	43	6	M	4	25	75	12	F	19	41	59	27	F	–	–	–	–	
June	2	3	16	84	16	F	1	100	–	–	M	–	–	–	–		2	40	60	3	F	2	50	50	2	=	4	40	60	6	F	–	–	–	–	
,,	3	6	43	57	8	F	5	45	55	6	F	–	–	100	1	F	5	42	58	7	F	–	–	–	–		7	64	36	4	M	–	–	–	–	
,,	3	2	67	33	1	M	6	60	40	4	M	152	83	17	31	M	–	–	100	9	F	–	–	–	–		–	–	–	–		–	–	–	–	
,,	4	–	–	–	–		1	3	97	28	F	469	57	43	355	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
,,	14	99	40	60	147	F	7	47	53	8	F	–	–	–	–		13	28	72	33	F	6	32	68	13	F	89	47	53	102	F	–	–	–	–	

July	**10**	**7**	**47**	**53**	**8**	**F**	**6**	**29**	**71**	**15**	**F**	**8**	**24**	**76**	**25**	**F**	–	–	–	–		**1**	**60**	**60**	**1**	**=**	**4**	**80**	**20**	**1**	**M**	–	–	–	–	
..	17	13	43	57	17	F	17	50	50	17	=	8	36	64	14	F	9	64	36	5	M	–	–	–	–		4	44	56	5	F	10	48	52	11	F
..	21	16	44	56	20	F	16	39	61	25	F	19	43	57	25	F	9	37·5	62·5	15	F	5	36	64	9	F	4	36	64	7	F	–	–	–	–	
August	1	26	47	53	29	F	14	54	46	12	M	3	37·5	62·5	5	F	20	51	49	19	M	4	40	60	6	F	–	–	–	–		–	–	–	–	
..	20	15	36	64	27	F	–	–	–	–		–	–	–	–		33	35	65	62	F	2	40	60	3	F	–	–	100	3	F	2	29	71	5	F
..	20	–	–	–	–		–	–	100	1	F	1	1	99	170	F	2	100	–	–	M	–	–	–	–		–	–	–	–		–	–	–	–	
..	21	12	29	61	19	F	3	37·5	62·5	5	F	–	–	–	–		25	34	66	49	F	–	–	–	–		3	60	40	2	M	–	–	–	–	
..	23	–	–	–	–		4	57	43	3	M	60	43	57	79	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	23	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	100	9	F	–	–	–	–	
November	7	6	43	57	8	F	15	52	48	14	M	19	38	62	31	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	10	14	42	58	19	F	4	33	67	8	F	5	33	67	10	F	–	–	–	–		1	3	67	2	F	4	57	43	3	M	1	50	50	1	=
..	18	31	42	58	42	F	23	40	60	34	F	32	46	54	38	F	14	58	42	10	M	5	33	67	10	F	6	40	60	9	F	2	50	50	2	=
..	24	17	39	61	27	F	6	37·5	62·5	10	F	11	48	52	12	F	–	–	–	–		–	–	–	–		9	82	18	2	M	2	33	67	4	F
..	28	18	39	61	28	F	11	58	42	8	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
December	8	24	50	50	24	=	19	59	41	13	M	2	29	71	5	F	15	44	56	19	F	–	–	–	–		4	44	56	5	F	–	–	–	–	
..	11	16	43	57	21	F	22	52	48	20	M	–	–	100	2	F	18	50	50	18	=	–	–	–	–		6	50	50	6	=	–	–	–	–	
..	16	22	71	21	9	M	2	33	67	4	F	5	36	64	9	F	–	–	100	4	F	–	–	–	–		–	–	–	–		–	–	–	–	
..	22	–	–	100	2	F	1	17	83	5	F	13	43	57	17	F	–	–	–	–		–	–	–	–		7	64	36	4	M	–	–	–	–	
1931.																																				
January	8	–	–	100	4	F	22	51	49	21	M	–	–	–	–		11	37	63	19	F	–	–	100	1	F	–	–	–	–		–	–	–	–	
..	16	27	37·5	62·5	45	F	2	25	75	6	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	100	6	F	1	50	50	1	=
..	17	14	48	52	15	F	10	53	47	9	M	1	13	67	2	F	–	–	100	1	F	–	–	–	–		10	62·5	37·5	6	M	–	–	–	–	
..	23	1	33	67	2	F	23	55	45	19	M	26	39	61	40	F	33	59	41	23	M	–	–	–	–		1	20	80	4	F	–	–	100	2	F
February	3	7	17	83	35	F	14	52	48	13	M	31	60	40	21	M	–	–	–	–		–	–	–	–		4	27	73	11	F	–	–	100	4	F
..	5	21	40	60	32	F	26	51	49	25	M	–	–	100	1	F	–	–	–	–		–	–	–	–		1	50	50	1	=	–	–	–	–	
..	9	25	43	57	33	F	30	49	51	31	F	–	–	–	–		22	61	39	14	M	–	–	–	–		–	–	–	–		–	–	–	–	
..	13	11	44	56	14	F	3	27	73	8	F	–	–	–	–		–	–	–	–		–	–	–	–		5	42	58	7	F	12	44	56	15	F
..	16	1	25	75	3	F	14	34	66	27	F	11	44	56	14	F	12	33	67	24	F	–	–	–	–		4	31	69	9	F	1	33	67	2	F
..	21	21	47	53	24	F	29	43	57	39	F	1	100	–	–	M	29	66	24	15	M	–	–	–	–		3	60	40	2	M	–	–	–	–	
..	24	28	65	35	15	M	7	24	76	22	F	23	50	50	23	=	–	–	–	–		–	–	–	–		5	38	62	8	F	–	–	–	–	
..	26	12	40	60	18	F	11	61	39	7	M	–	–	–	–		17	40	60	26	F	–	–	–	–		–	–	100	3	F	1	50	50	1	=
March	3	14	47	53	16	F	5	36	64	9	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	3	–	–	–	–		17	50	50	17	=	–	–	–	–		16	46	54	19	F	5	29	71	12	F	12	80	20	3	M	2	50	50	2	=
..	5	18	53	47	16	M	24	56	44	19	M	14	31	69	31	F	–	–	–	–		4	50	50	4	=	6	60	40	4	M	5	28	72	13	F
..	9	2	40	60	3	F	13	41	59	19	F	15	39	61	23	F	7	24	76	22	F	–	–	–	–		–	–	–	–		2	33	67	4	F
April	25	16	43	57	21	F	16	46	54	19	F	22	54	46	19	M	–	–	–	–		7	44	56	9	F	6	55	45	5	M	–	–	–	–	
..	29	16	39	61	25	F	10	48	52	11	F	26	39	61	41	F	–	–	–	–		–	–	–	–		–	–	–	–		8	31	69	18	F
May	4	18	55	45	15	M	4	14	86	25	F	12	32	68	26	F	–	–	–	–		12	52	48	11	M	–	–	–	–		1	33	67	2	F
..	11	20	43	57	26	F	27	45	55	33	F	19	40	60	28	F	–	–	–	–		–	–	–	–		14	70	30	6	M	1	33	67	2	F
..	12	14	54	46	12	M	3	50	50	3	=	1	25	75	3	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	22	21	47	53	24	F	8	26	74	23	F	14	40	60	21	F	–	–	–	–		–	–	–	–		3	37·5	62·5	5	F	2	33	67	4	F
..	26	21	42	58	29	F	15	48	52	16	F	3	100	–	–	M	19	47·5	52·5	21	F	–	–	–	–		5	83	17	1	M	–	–	–	–	
June	1	11	37	63	19	F	2	40	60	3	F	–	–	–	–		1	100	–	–	M	–	–	–	–		9	69	31	4	M	–	–	–	–	
..	4	29	45	55	36	F	29	48	52	31	F	2	100	–	–	M	35	49	51	36	F	–	–	–	–		3	33	67	6	F	3	33	67	6	F
..	4	6	40	60	9	F	11	50	50	11	=	–	–	–	–		–	–	–	–		–	–	–	–		6	29	71	15	F	2	40	60	3	F
..	8	5	42	58	7	F	10	62·5	37·5	6	M	11	34	66	21	F	19	49	51	20	F	–	–	–	–		15	47	53	17	F	–	–	–	–	
..	10	27	44	56	34	F	29	41	59	41	F	–	–	–	–		3	30	70	7	F	–	–	–	–		12	52	48	11	M	1	33	67	2	F
..	15	20	48	52	22	F	19	46	54	22	F	18	51	49	17	M	–	–	–	–		–	–	–	–		7	39	61	11	F	–	–	100	1	F
..	16	22	48	52	24	F	26	50	50	26	=	–	–	100	1	F	31	47	53	35	F	–	–	–	–		10	48	52	11	F	5	50	50	5	=
..	23	29	63	37	17	M	15	79	21	4	M	23	38	62	37	F	–	–	–	–		–	–	–	–		3	43	57	4	F	3	43	57	4	F
July	3	17	49	51	18	F	9	50	50	9	=	15	65	35	8	M	–	–	–	–		–	–	–	–		4	57	43	3	M	–	–	100	1	F
..	3	16	67	33	8	M	–	–	100	1	F	–	–	–	–		8	62	38	5	M	–	–	–	–		4	50	50	4	=	–	–	–	–	
..	13	13	48	52	14	F	18	47	53	20	F	27	47	53	31	F	–	–	–	–		3	50	50	3	=	3	43	57	4	F	–	–	–	–	
..	14	17	57	43	13	M	8	62	38	5	M	1	100	–	–	M	–	–	100	9	F	–	–	–	–		–	–	–	–		–	–	–	–	
..	29	26	15	85	149	F	–	–	–	–		–	–	–	–		12	63	37	7	M	–	–	100	1	F	17	52	48	16	M	–	–	100	1	F
October	10	22	51	49	21	M	1	50	50	1	=	7	70	30	3	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	28	14	45	55	17	F	4	50	50	4	=	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
November	2	–	–	100	3	F	2	50	50	2	=	2	67	33	1	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	27	5	23	77	17	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
December	2	4	40	60	6	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	15	6	32	68	13	F	2	50	50	2	=	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	23	11	61	39	7	M	4	57	43	3	M	–	–	100	2	F	–	–				–	–				–	–				–	–	–	–	

seen from the table that few males were present in any landing and that not infrequently an entire catch would consist wholly of female fish. This is not explainable by any selective action of the nets as these were the same at the beginning as at the end of the season in 1930. Nor does it appear to be true that the males are not caught because they exhibit some difference (or absence) of movement. When present they are taken quite as successfully as the females.

There is no doubt, therefore, that on this particular fishing ground, during the first three or four months of the year, the Ray population may consist entirely or almost entirely of one sex of a single species. The composition of this population may change rapidly and completely during the brief season of the net fishery, which is simply the time during which fully adult fish are present on the ground in large numbers. The main population consists first, and for the greater part of the season, of mature females with, in some seasons at least, mature males appearing later and for a shorter time towards the end of the season.* Finally, for the greater part of the year, only a residuum of immature individuals of both sexes is present, the adult fish having migrated elsewhere.

Having discovered such very definite segregation of the sexes of *R. clavata* on the Plymouth net fishing ground, coupled with a definite migratory movement of greater or less extent, the question now arises as to whether or not this is an isolated phenomenon or whether there is evidence of similar segregations and migrations elsewhere and for other species. For the purpose of obtaining true samples of fish stocks fixed nets possess a unique superiority over other fishing implements such as trawls and long-lines in that their fishing action is restricted to one very small patch of ground. Unfortunately the writer is not aware of the existence of any other ray-net fishery such as that carried on from Plymouth at any other point on the coast, at any rate within his range of investigation. Nevertheless, a considerable though less complete body of evidence is available from catches obtained by other methods of fishing.

On the night of Saturday–Sunday, March 15th–16th, 1930, between the hours of 7 p.m. and 2 a.m., a steam trawler fishing in shallow water off the Cornish coast caught 210 large Rays, 207 of them being *R. clavata*, every one of which was a female. Obviously this vessel had fallen upon a shoal of female fish similar to that fished by the nets on the Plymouth grounds. It is not to be expected, however, that such a pure landing will occur in trawl or line fishing except at very rare intervals, because even one haul of a trawl or a fleet of lines once shot samples a large area of the sea floor ; and every landing is the product not of one but of many hauls

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* Unfortunately, owing to the onset of unfavourable weather conditions, this fishery was brought to a premature close in both 1931 and 1932, so that it is not known whether or not the males appeared towards the end of the season in those years.

of the trawl or a fleet of lines several if not many times shot. That the landings from both trawlers and liners should, in spite of this, not infrequently consist largely and sometimes almost entirely of one sex of a single species points clearly to the occurrence of sexual segregation among species other than *R. clavata* and on grounds other than that fished by the Plymouth nets. Some of the most striking of such landings recorded by the present writer are enumerated below.

On June 3rd, 1930, a small inshore trawler fishing near Newlyn, Cornwall, brought ashore 205 Rays. Of these no less than 183 were *R. brachyura*, all immature, and containing 152 males. Nine *R. nævus* were included in this catch, every one a female. On the following day a small liner fishing on or near the same ground landed 853 Rays, 824 of which were immature specimens of *R. brachyura*. In this catch, however, males and females were present in more nearly equal numbers, there being 469 males and 355 females. *R. montagui* was the only other species included in the catch. Of these 29 individuals, all were adult fish and consisted of 28 females with only a single male included among them. In August of the same year this liner was still fishing on the same ground, but the *R. brachyura* which she was then landing were all mature fish which must have migrated there (*vide* **12**, p. 23). On August 20th this vessel landed 171 adult Rays of this species of which only one was a male. Three days later another but smaller catch was landed in which adult males and females were almost equally represented, there being 60 of the former and 79 of the latter sex. After this date the writer had to leave Newlyn, otherwise it would have been interesting to have noted whether or not the males eventually exceeded the females in number or even completely " replaced " them as happened in the case of *R. clavata* on the Plymouth net grounds in the spring of the year.

There was another interesting landing on August 23rd. A liner which had been fishing in deep water caught only 9 Rays on its full fleet of lines which had been shot once. All these were *R. fullonica* and all adult females.

On July 29th, 1931, a liner from the same port landed 175 *R. clavata* in addition to small numbers of other species. Of these Thornback Rays 149 were adult females ; the 26 males were mostly immature. On May 31st, 1932, a liner's catch was observed to contain 19 *R. marginata*, all females over 100 cm. in width of disc, and all containing ripening ova. On June 2nd another landing contained 39 *R. batis* of which 37 were mature or nearly mature males and 2 were immature females.

In no instance was any information available as to how the fish were distributed on the lines. In the hope that an interesting catch similar to one of those mentioned might be taken in his presence the writer went to sea in a liner and recorded the species and sex of every Ray which came up in the order in which it appeared (*vide* **12**, p. 28). Unfortunately only a very " ordinary " catch rewarded his efforts ; 192 *R. clavata* were taken the majority of which were immature and the two sexes were more or less indiscriminately intermingled all along the line. There was a slight excess of females. The catch of *R. nævus*, the only other species taken in any numbers, was more interesting ; 142 specimens were taken, 104 of which were males, most of them fully adult. The females, of which only an occasional specimen occurred here and there at wide intervals, were found on examination to be mainly immature, only 7 out of the total 38 containing ripe or ripening ova.

Other species were represented by only a very few scattered individuals.

It seems clear, however, from the main body of the evidence brought together in this paper, that the so-called abnormal sex-ratio found among the commercial landings of Rays and Skates is due not to any differential production of males and females at birth, or to a differential mortality after birth, but to differential catches of the sexes owing to segregation of the larger fish into unisexual shoals for at least part of the year. The females, particularly when in a gravid or spawning condition, form more compact schools than do the males, and therefore tend to be captured in greater numbers.

This fact is of much more than theoretical interest ; it has a direct practical bearing on the commercial fishery for these species, which have now become of primary and growing importance as national food fishes. It is well known that for the maintenance of any animal stock the female is, from the numerical point of view, the more important sex. Since, therefore, the females of the Raiidæ as a general rule are captured in considerably greater numbers than the males, it follows that the greatest drain of the fishery upon the fish stock falls upon its most vulnerable part. These Elasmobranch fishes will therefore be much more rapidly and more severely affected by intense fishing in any particular area—such as the English Channel—than species in which there is not an excess of females caught by ordinary fishing methods. Such an effect will tend to be greatly minimised in the case of strongly migratory species—such as the Spur Dogfish, for instance. The stock of such fishes on any particular fishing ground will be exposed to capture only for so long as it remains in that region. Not only so, its numbers will always tend to be sustained or replenished by immigrants from other localities where fishing is less intense or non-existent. It may be highly significant, therefore, that from being a very flourishing concern, the English Channel fishery for Spur Dogfish has, in the course of the last five years, shrunken to almost negligible proportions* owing to the

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* The Ministry of Agriculture and Fisheries returns of landings from the English Channel during this period are : 1928, 54,206 cwt. ; 1929, 28,920 cwt. ; 1930, 27,188 cwt. ; 1931, 16,049 cwt. ; 1932, figures not yet available.

scarcity of these fish—*and that in spite of their being a pelagic and migratory species.*

On the other hand, the adverse effect of intensive fishing will be correspondingly increased in the case of species—such as the Raiidæ—whose migrations appear to be very restricted or even quite local in character. Moreover, these very same factors which by their action will assist the commercial forces of depletion will be equally potent in retarding recovery once a decline has been brought about in the stocks.

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Some Records of Parasitic Worms from Marine Fishes at Plymouth.

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RECORDS of parasitic worms from British marine fishes are still rather scanty. A good deal of attention has been paid to the subject of the Trematodes by Nicoll, whose valuable list (1915) is indispensable to anyone working in this field. Nicoll is himself responsible for the records of the majority of the 49 species of Trematodes given in the second edition (1931) of the "Plymouth Marine Fauna." The only work done on the Cestodes of fishes at Plymouth appears to have been that of Woodland (1927, a and b), as a result of which 14 species have been placed on record. Very few data are available as to the Nematodes, and none as to the Acanthocephala, of the Plymouth fauna.

During the latter part of May, 1932, the senior author spent some ten days at the Plymouth Laboratory of the Marine Biological Association, collecting parasitic worms from fishes. Over 100 fish were dissected, including representatives of about 40 species. No attempt was made to collect every parasite, including larval forms, but attention was paid almost exclusively to the adult forms living in the alimentary canal or on the gills and external surfaces. The parasites found were simply preserved at once, and were not determined until after the author's return to London.

The hosts were almost all named by Mr. G. A. Steven, of the Laboratory staff, to whom grateful acknowledgment is due for his kind and unfailing help. Mr. Steven suggested that it might be of some interest to record the sizes of the fish found to be infested with parasites. This had not been done during the first day of collecting, but was done regularly thereafter. For all species except skates the measurement given is the length from snout to tip of tail, to the nearest 5 mm. In the case of skates Mr. Steven's usual practice was followed of measuring across the "wings" from tip to tip.

The names here used for the hosts are those used in the " Plymouth Marine Fauna " (second edition, 1931).

The junior author has, at various times, also visited the Laboratory at Plymouth and collected Trematodes from fishes. His identifications are principally from living specimens. In order to avoid the duplication of records, it has been thought desirable to include them all in one list. Both authors, of course, frequently collected the same species from the same hosts, and where this occurred the records given in the subjoined list, unless otherwise indicated, are the senior author's.

The joint list contains 12 species of Trematodes, 4 of Cestodes, 11 of Nematodes, and 2 of Acanthocephala which have not hitherto been included in the " Plymouth Marine Fauna." These are indicated by an asterisk (*). Hosts which are believed to be new for the species in question are indicated by a dagger (†), while a double dagger (‡) indicates that the record is the junior author's.

Some of the Nematodes, unfortunately, could not be specifically determined owing to the absence of male specimens or to the incompleteness of the material. The occurrence of the little-known form Ascarophis is of particular interest, and a paper on this Nematode will appear elsewhere. *Echinorhynchus leidyi* has hitherto been recorded only from " lake trout " in the Great Lakes region of North America. The determination of the specimens from the rockling is therefore open to question, though they appear to agree very closely with the description of *E. leidyi.*

As regards the nomenclature of the parasites recorded, current usage has generally been followed. Two nomenclatural changes have, however, been introduced among the Trematodes, and these call for some explanation.

(1) We have treated the genus *Paracotyle* Johnstone, 1911, as synonymous with *Microbothrium* Olsson, 1869, because *P. caniculæ,* the genotype of Paracotyle, appears to be almost certainly congeneric with *M. apiculatum,* the genotype of Microbothrium. A paper on this form by the junior author will appear elsewhere.

(2) We have substituted the genus *Mazocraes* Hermann, 1782, for *Octobothrium* F. S. Leuckart, 1827. It appears to be generally admitted that its genotype, *Mazocraes alosæ* Hermann, is identical with *Octobothrium lanceolatum* Leuckart, the genotype of Octobothrium. Hence the name Octobothrium must fall into the synonymy of Mazocraes, and there is no justification for retaining the better-known name Octobothrium and treating Mazocraes as a synonym, as has been done by some recent authors.

The junior author has found certain Trematodes which are believed to represent new species. These are not included in the present list, and will be described elsewhere.

It is a pleasure to acknowledge the kind attention and help which we received at the hands of the Director and staff of the Plymouth Laboratory, and the interest which they took in our work.

LIST OF SPECIES COLLECTED.

TREMATODA.

Order MONOGENEA.

Fam. **Capsalidæ** (=Tristomatidæ).

ENTOBDELLA SOLEÆ (v. Ben. and Hesse, 1864). Skin of *Solea vulgaris*.

Fam. **Udonellidæ.**

*UDONELLA CALIGORUM Johnston, 1835. Numerous young specimens attached to a Caligus ♀ (determined by Dr. I. Gordon as probably *C. rapax* M. Edw., 1840) found free in plankton, January 12th, 1932, by Mr. F. S. Russell.

Fam. **Monocotylidæ.**

CALICOTYLE KROYERI Diesing, 1850. Cloaca of *Raja maculata*.

*MICROBOTHRIUM [PARACOTYLE] CANICULÆ (Johnstone, 1911). Skin, on dorsal surface, of ‡*Scyllium canicula*.

ACANTHOCOTYLE SP. Skin of *Raja clavata* and ‡*R. maculata*.

Fam. **Polystomatidæ.**

*ONCHOCOTYLE APPENDICULATA (Kuhn, 1829). Gills of *Raja clavata* (26 cm. across), *R. blanda* (41 cm.), †‡*R. oxyrhynchus*, ‡*R. batis* and ‡*Scyllium canicula*.

Fam. **Octocotylidæ.**

*MAZOCRAES ALOSÆ Hermann, 1782 (=*Octobothrium lanceolatum* Leuckart, 1827). Gills of ‡*Clupea finta*.

*MAZOCRAES HARENGI (v. Ben. and Hesse, 1864). Gills of †‡*Clupea alosa*.

MAZOCRAES SCOMBRI (Kuhn, 1829). Gills of *Scomber scombrus*.

*DACTYCOTYLE DENTICULATA (Olsson, 1876). Gills of †‡*Merluccius merluccius*.

DACTYCOTYLE MERLANGI (Kuhn, 1829). Gills of ‡*Gadus merlangus*.

*GASTROCOTYLE TRACHURI v. Ben. and Hesse, 1864. Gills of ‡*Caranx trachurus*.

AXINE BELONES Abildgaard, 1794. Gills of §*Belone acus* (abundant in several specimens).

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§ Collected by Miss M. Rothschild.

Order DIGENEA.

Fam. **Bucephalidæ.**

BUCEPHALOPSIS GRACILESCENS (Rud., 1819). Stomach and intestine of *Lophius piscatorius* (in each of 3 specimens); 2 specimens in stomach of †*Conger vulgaris* (about 3 ft.), possibly accidental.

RHIPIDOCOTYLE MINIMA (Wagener, 1852). Intestine of *Trigla hirundo* (24 cm.) and *T. cuculus* (24 cm.).

PROSORHYNCHUS ACULEATUS Odhner, 1904. Stomach, intestine and rectum of *Conger vulgaris.*

PROSORHYNCHUS CRUCIBULUM (Rud., 1819). Intestine of *Conger vulgaris;* one immature specimen (?) in intestine of *Lophius piscatorius* (47 cm.).

Fam. **Fellodistomidæ** (=Steringophoridæ).

*STERINGOPHORUS FURCIGER (Olsson, 1868). Immature specimens in stomach and intestine of *Pleuronectes limanda* (18·5 and 19 cm.).

STERINGOTREMA CLUTHENSE (Nicoll, 1909). Immature specimens in intestine of *Pleuronectes microcephalus* (21·5 cm.) and *P. limanda* (18·5 cm.).

STERINGOTREMA DIVERGENS (Rud., 1809). Stomach and intestine of *Blennius ocellaris,* each of three specimens (12–14 cm.).

Fam. **Zoogonidæ.**

*ZOOGONUS? RUBELLUS (Olsson, 1868). Immature specimens in intestine of †*Pleuronectes limanda* (16 cm.) and †*Labrus mixtus* (27 cm.).

ZOOGONOIDES VIVIPARUS (Olsson, 1868). Rectum of ‡*Callionymus lyra* and ‡*Pleuronectes microcephalus;* immature specimens in rectum of *Pleuronectes platessa* (36·5 cm.).

Fam. **Allocreadiidæ.**

PODOCOTYLE ATOMON (Rud., 1802). Intestine of *Cottus bubalis.*

PODOCOTYLE REFLEXA (Creplin, 1825). Intestine of *Spinachia vulgaris,* each of 4 specimens (12·5–16 cm.); intestine of †‡*Onos tricirratus.*

PODOCOTYLE SYNGNATHI Nicoll, 1913. One specimen in intestine of *Entelurus æquoreus* (44 cm.).

LEBOURIA VARIA Nicoll, 1910. Intestine of *Callionymus lyra,* †*Labrus mixtus* (two out of four specimens, ♂ 27 cm., ♀ 21 cm.) and †‡*Labrus bergylta.*

*HELICOMETRA FASCIATA (Rud., 1819). Intestine of ‡*Crenilabrus melops.*

HELICOMETRA PULCHELLA (Rud., 1819). Intestine of †*Trigla lineata* (26 cm.), †‡*T. hirundo* and *Serranus cabrilla* (18 cm.); stomach of ‡*Trigla cuculus*.

Fam. **Azygiidæ.**

PTYCHOGONIMUS MEGASTOMUS (Rud., 1819). Stomach of ‡*Mustelus vulgaris*.

Fam. **Hemiuridæ.**

HEMIURUS COMMUNIS Odhner, 1905. Stomach of *Molva vulgaris* (57 cm.); *Lophius piscatorius* (two out of three specimens); *Gadus merlangus* (25 cm.); *Trigla lineata* (26 cm.); †*Conger vulgaris* (about 3 ft.); ‡*Cottus scorpius*. Usually only one specimen found in each fish, but twelve in *C. scorpius*.

LECITHOCHIRIUM RUFOVIRIDE (Rud., 1819). Stomach of *Conger vulgaris* (each of three specimens); stomach of ‡*Lophius piscatorius*.

*LECITHOCHIRIUM GRAVIDUM Looss, 1907. Stomach of *Conger vulgaris* (each of three specimens).

LECITHASTER GIBBOSUS (Rud., 1802). Intestine of †*Cepola rubescens* (two out of four specimens, 54 and 55 cm.); one immature specimen (?) in intestine of *Scophthalmus norvegicus* (9·5 cm.).

DEROGENES VARICUS (Müller, 1784). Stomach of *Gadus merlangus* (25 cm.), *Merluccius merluccius* (27·5 cm.), *Trigla hirundo* (29·5 cm.); †‡*Trigla cuculus;* stomach and intestine of *Lophius piscatorius* (about 2 ft.); mouth of ‡*Cottus bubalis*.

HEMIPERA OVOCAUDATA Nicoll, 1913. Mouth of †‡*Onos mustela* and †‡*O. tricirratus*.

SYNAPTOBOTHRIUM CAUDIPORUM (Rud., 1819). Stomach of †‡*Rhombus lævis;* stomach of †‡*Conger vulgaris*. One specimen (?) in stomach of *Trigla hirundo* (24 cm.).

*STERRHURUS FUSIFORMIS (Lühe, 1901). Stomach of ‡*Conger vulgaris;* stomach of †‡*Lophius piscatorius*.

LECITHOCLADIUM EXCISUM (Rud., 1819). Stomach of ‡*Scomber scombrus* (four in each of two specimens).

CESTODA.

Order BOTHRIOCEPHALIDEA.

Fam. **Bothriocephalidæ.**

*BOTHRIOCEPHALUS SCORPII (Müller, 1776), (=*bipunctatus* Zed.). Intestine of †*Scophthalmus norvegicus* (9·5 cm.), †*Arnoglossus laterna* (each of two specimens, 12 and 14 cm.), *Cottus bubalis* (attached to pyloric cæca); a fragment in stomach of *Merluccius merluccius* (28 cm.), probably accidental.

Order TETRARHYNCHIDEA.

Fam. **Tentaculariidæ** (=Tetrarhynchidæ).

*GRILLOTIA [TETRARHYNCHUS] ERINACEUS (v. Ben., 1858). Spiral valve of *Raja clavata*.

Order TÆNIIDEA.

Fam. **Onchobothriidæ.**

ACANTHOBOTHRIUM CORONATUM (Rud., 1819). Four immature specimens in spiral valve of *Scyllium catulus* (46 cm.).

CALLIOBOTHRIUM VERTICILLATUM (Rud., 1819). Intestine of ‡*Mustelus vulgaris*.

Fam. **Phyllobothriidæ.**

*PHYLLOBOTHRIUM THRIDAX v. Ben., 1850. Spiral valve of *Raja clavata* and *R. blanda* (41 cm. across).

*ANTHOBOTHRIUM AURICULATUM (Rud., 1819) of Johnstone, 1906. One specimen in spiral valve of *Raja blanda* (41 cm. across).

(?) ECHENEIBOTHRIUM TUMIDULUM (Rud., 1819), (=*E. variabile* v. Ben.). Spiral valve of *Raja clavata* (one in each of two out of five specimens).

NEMATODA.

Order ASCAROIDEA.

Fam. **Ascaridæ.**

*CONTRACÆCUM CLAVATUM (Rud., 1809). Intestine of *Conger vulgaris* (about 3 ft.); stomach of *Gadus merlangus* (27 cm., 33·5 cm.); stomach of *Merluccius merluccius* (27·5 cm.)—immature specimens also in stomach and intestine of two other examples (17·5 and 28 cm.); stomach and intestine of *Lophius piscatorius* (about 2 ft. and 47 cm.); stomach of *Cottus bubalis;* stomach of *Zeus faber* (three out of four specimens, 15·5–27·5 cm.); intestine of *Capros aper* (6 cm.); intestine [and gill-chamber] of *Mullus surmuletus* (22·5 cm.).

*CONTRACÆCUM RIGIDUM (Rud., 1809). In tumours in stomach of *Lophius piscatorius* (two out of three specimens, one 47 cm.).

Order FILARIOIDEA.

Fam. **Philometridæ** (=Dracunculidæ).

*PHILOMETRA sp. Females found twice in intestine of *Trigla cuculus* (22 and 15 cm.).

Fam. **Spiruridæ.**

*PROLEPTUS OBTUSUS Duj., 1845. Stomach and anterior portion of intestine of *Scyllium canicula* and *S. catulus* (every specimen examined).

*PROLEPTUS ? ROBUSTUS (v. Ben., 1871). Stomach of *Raja clavata* (three out of five specimens, 26, 28, and 40 cm. across).

Fam. **Cucullanidæ.**

*CUCULLANUS HETEROCHROUS Rud., 1802. Intestine and rectum of *Pleuronectes platessa* (two out of three specimens, 26 and 27·5 cm.); intestine of *Solea vulgaris* (one out of three specimens, 39·5 cm.).

*CUCULLANUS HIANS (Duj., 1845). Intestine of *Conger vulgaris* (each of three specimens); one specimen in intestine of *Lophius piscatorius* (47 cm.).

*CUCULLANUS sp. Intestine of ‡*Mullus surmuletus.*

Fam. Incert.

*ASCAROPHIS ? MORRHUÆ v. Beneden, 1871. Two female specimens in stomach of †*Trigla lineata* (26 cm.).

Order TRICHINELLOIDEA.

Fam. **Trichinellidæ.**

*CAPILLARIA sp. One female specimen in spiral valve of *Scyllium catulus* (46 cm.).

*CAPILLARIA sp. Two immature females in rectum of *Pleuronectes platessa* (26 cm.).

ACANTHOCEPHALA.

Fam. **Echinorhynchidæ.**

*ECHINORHYNCHUS GADI Zoega, in Müller, 1776. One specimen in intestine of †*Spinachia vulgaris* (one out of four specimens).

*ECHINORHYNCHUS ? LEIDYI Van Cleave, 1924. A pair of specimens in intestine of †*Onos mustela.*

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On the Occurrence of Pelagic Tunicates (Thaliacea) in the Waters of the English Channel off Plymouth.

By

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It is only occasionally that pelagic tunicates of the genera Doliolum and Salpa are recorded in numbers in the waters off Plymouth. In view of their possible use as indicators of the presence of Atlantic water (see Bowman, 1923; and Schmidt, 1909, p. 159), it is of value that their occurrence should be put on record. Regular weekly catches of plankton have been made since 1930 with half-hour oblique hauls with the two-metre stramin ring-trawl. During this period species of both genera have appeared in such numbers that it has seemed desirable to make a careful examination of the species occurring.

Previous Records.

Doliolids.

Doliolum* was found in considerable numbers in tow-nettings at Plymouth in August and the beginning of September, 1893, soon becoming scarce (Garstang, 1894, p. 222; Browne, 1896, p. 171). In 1895 Doliolum was exceedingly abundant at the beginning of September and there was a gradual decrease towards the end of the month (Browne, 1896, p. 171). In September, 1897, Doliolum was not found (Browne, 1898, p. 191). The only other record in the Plymouth Marine Fauna (1931) is of several specimens of *D. nationalis* taken in November, 1904.

Salps.

Large shoals of *Salpa democratica* visited the Sound from the middle of June to the end of the first week in July, 1893 (Garstang, 1894, p. 222, *Thalia democratica-mucronata*). In September, 1893 and 1897, none were taken and in September, 1895, a few on the 9th only (Browne, 1896, p. 171; 1898, p. 191).

Salpa fusiformis was taken in the region of the Eddystone in August, 1901, and July and September, 1925 (Plymouth Marine Fauna, 1931).

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* Specimens of *D. nationalis* recorded as *D. tritonis*, see Fowler, 1898, p. 593.

It was also present in large numbers in the Sound in September, 1917, but no collections were available from offshore waters.

Salpa zonaria was taken in numbers by Professor J. H. Orton when on a cruise in s.s. *Oithona* in September, 1914, off Falmouth Bay. We are indebted to Professor Orton for allowing us to examine these specimens.

RECENT OBSERVATIONS.

In Table I are given records of the numbers of tunicates taken in the weekly oblique hauls in 1931 and 1932. Throughout the whole of 1930 none were seen, and in Table I only those months in which specimens were seen are included.

TABLE I.

NUMBERS OF DOLIOLIDS AND SALPS IN HALF-HOUR OBLIQUE HAULS WITH THE 2-METRE STRAMIN RING-TRAWL.

1931	*Doliolum.*	*S. mucronata.*	*S. fusiformis.*
Sept. 10th	–	3 solitary 2 aggregate	–
,, 24th	21	–	–
Oct. 1st	60	20 aggregate	–
,, 8th	798	–	–
,, 15th	1513	–	–
,, 22nd	515	–	–
,, 29th*	1412	–	–
1932			
Aug. 26th	–	–	18 aggregate.
Sept. 1st	–	–	47 aggregate. 14 solitary.
,, 7th	–	–	103 aggregate. 4 solitary.
,, 14th	32	–	696 aggregate. 6 solitary.
,, 21st	199	–	311 aggregate. 199 solitary.
,, 29th	213	–	116 aggregate.
Oct. 4th	164	–	1330 aggregate. 120 solitary.
,, 11th	1722	–	–
,, 19th	3450	–	1 aggregate.
,, 26th	2357	–	–
Nov. 14th	331	–	–

* The next haul was on November 25th, when none were seen.

The Table shows that the autumn of 1931 was notable for the appearance of Doliolids and a few *S. mucronata;* and that 1932 is notable for the occurrence of Doliolids and also of *Salpa fusiformis* which has appeared in numbers greater than in living memory of any member of the Plymouth Laboratory staff, except perhaps for the year 1917 when it invaded the Sound and Hamoaze. Examinations were also made of ring-trawl catches during the following periods, but no Doliolids or Salps seen—May to July, 1924; April to August, 1925; April to September, 1926; April to December, 1927; January to April, 1928; April to October, 1929. (For dates of collections, see Russell, 1930, p. 714.)

Two species of Doliolum were taken in large numbers in 1931, namely *D. nationalis* and *D. gegenbauri.* In 1932, however, it is to be noted that only *D. nationalis* was seen. Table II shows the composition of samples of some of the catches.

TABLE II.

COMPOSITION OF SAMPLES OF DOLIOLUM CAUGHT ON THE DATES GIVEN.

		8.10.31.	15.10.31.	22.10.31.	29.10.31.
D. nationalis	(phorozooids)	84	103	7	51
	(gonozooids)	5	–	–	–
D. gegenbauri	(phorozooids)	17	17	4	24
	(gonozooids)	21	40	12	76
D. sp.	(old blastozooids)	64	15	11	49
D. ? nationalis	(blastozooids)	–	–	–	1

	14.9.32.	21.9.32.	26.9.32.	29.9.32.	11.10.32.	19.10.32.	26.10.32
D. nationalis (phorozooids)	13	83	311	72	646	303	388

THE SPECIES OF THALIACEA OCCURRING IN THE ENGLISH CHANNEL OFF PLYMOUTH.

(1) *Salpa fusiformis* Cuvier, 1804, p. 382, Pl. LXVIII, Fig. 10.

The specimens of *S. fusiformis* obtained in 1932 have the smooth test of the typical form. The relationship of this form to *S. fusiformis aspera* (Cham.) (=*S. echinata* Herdman, see Ihle, 1912, p. 40) is still debatable. Ritter (1905, p. 69) maintained that the characters of *aspera* appeared in older specimens. Apstein (1906, p. 268) regarded it as the cold water form. Examination of the material in the British Museum has given no conclusive evidence.

(2) *Salpa democratica* Forskål, 1775, p. 113.

(3) *Salpa zonaria* (Pall.). *Holothurium zonarium* Pallas, 1774, p. 26. Pl. I, fig. 17 A, B, C. Only recorded off Falmouth Bay.

(4) *Doliolum nationalis* Borgert, 1893, p. 406, text-fig.

(5) *Doliolum gegenbauri* Ulianin, 1884, p. 134, Pl. VII, fig. 5.

No member of the group of species to which *D. gegenbauri* belongs had previously been recorded at Plymouth, for Garstang's record of *D. tritonis* was based on material of *D. nationalis* (see above). *D. gegenbauri* and *D. tritonis* are very closely allied and may yet prove to be synonymous. The gonozooids are distinguished by the stigmata, which end ventrally at the 5th muscle band in *D. gegenbauri* and in *D. tritonis* extend a little further forward to end between the 4th and 5th bands. Except in a few badly crushed specimens, where the position of the stigmata could not be made out at all, the Plymouth material was all clearly of the *gegenbauri* type.

6) Blastozooids of Doliolum.

The blastozooids obtained in 1931 are nearly all too old for identification. One, however, has the stigmata and gut complete, though the stigmata are a little crushed so that their exact shape cannot be determined. It agrees closely with the blastozooid of *D. denticulatum** (Grobben, 1882, Pl. I, figs. 3–5 ; for synonymy see Neumann, 1906, p. 222), no difference being apparent except that the endostyle extends a little further back, reaching the 5th muscle band. *D. denticulatum* does not occur at Plymouth, but its nearest ally, *D. nationalis*, together with *D. gegenbauri*, was in the haul in which this one blastozooid was taken. Fowler (1905, p. 93) had exactly similar blastozooids, some of which are in the British Museum (Nat. Hist.). He attributed them very tentatively to *D. tritonis*, recognising *D. nationalis* as the only alternative. Ritter (1905, p. 86) has shown reasons for connecting a different blastozooid with *D. tritonis*. In it the intestine is short and slightly twisted, the anus presumably being further forward than in Fowler's blastozooid, in which the intestine is straight and reaches the 8th band. The otocyst is in the third intermuscular space in both, but in Ritter's is nearer the 3rd, in Fowler's nearer the 4th band. Despite the fact that *D. gegenbauri* is the classical material for the study of the life-history of Doliolum, there appears to be no precise information about the characters of the intestine

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* Ritter (1905, p. 93) gives no reasons for his conclusion that this blastozooid belongs, not to *D. denticulatum*, but to some unknown gonozooid. The name *D. ehrenbergii* Ulianin belongs to a gonozooid (which may not exist) with the stigmata reaching the first muscle band. Ritter's use of the name for his blastozooid would only be justified if he had proved that it developed from a gonozooid of that type. His references to *gegenbauri* in this paragraph must be read as *ehrenbergii*.

of the blastozooid, except that the anus lies between the 7th and 8th bands (Neumann, 1906, p. 219). There is thus some reason for distinguishing Fowler's blastozooid with its straight intestine and anus under the 8th band from both *D. tritonis* and *D. gegenbauri*, whether they are synonymous or not, and for concluding that it belongs to *D. nationalis*.

DISTRIBUTION.

All the five species of Thaliacea recorded above are widely distributed in the warmer seas of the world. The Salps are all found in the Atlantic, Indian, and Pacific Oceans. Apstein (1906, pp. 261–277) states that *S. democratica* is the commonest Salp in warm water, and that it is carried northwards in the Gulf Stream; that *S. fusiformis* is one of the most frequent Salps, above all at home in warm water but occurring in higher latitudes; and that *S. zonaria* is found above all in the warm parts of the oceans but is carried north in the Gulf Stream. Of all the warm-water species of Salps, these three especially appear to be able to withstand a considerable lowering of temperature, being carried north into temperatures of 10° C. in waters north of Scotland.

Neumann (1913, p. 230–231) states that *D. nationalis* and *D. gegenbauri* occur in the Atlantic and Indian Oceans and in the Mediterranean. They however appear to be more confined to the warm water than do the above species of Salps.

It is hoped that when future records are available it will be possible to indicate to what extent the presence of these tunicates in English Channel waters may be due either to movement of Atlantic water or to high temperatures allowing successful reproduction and survival in the area.

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Syllidian Miscellany.

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With 6 Figures in the Text.

I. *AUTOLYTUS ROSEUS* CLAPARÈDE WITH SPECIAL REFERENCE TO ITS HEAD APPENDAGES.

THIS Autolytus has been known only in the form of Sacconereis, i.e. as the female stolon of an unknown Syllid. It was discovered in 1864 by a French zoologist, E. Claparède, at Port-Vendres (Pyrénées Orientales). According to the original figures and description it is an ordinary female individual in its general appearance, carrying a large egg-sac on the ventral side. The latter is " étranglé en 8 " and turkish blue, the colour being due to the contained eggs. The body consists of about 60 segments, the dorsal surface of which is transversely banded by pigment of rose colour. Modification of the segments for swimming commences at the 9th setigerous segment and stops at the 21st. The following 40 segments (about) are not modified like the 8 in the first region just behind the head. The most striking character, by which the present stolon is distinguished from any other Sacconereis, is the presence of a pair of extra appendages in front of the head in addition to the median and lateral tentacles. Claparède states that the presence of these appendages, " qui n'ont été signalés chez aucune autre Sacconereide," is by no means very astonishing, since there are two such ones in Polybostricus. Claparède clearly predicted their homology to the frontal lobes of the bifid antenna-like appendages in the male head. A. Malaquin (1893) actually explained the bifid condition of the frontal appendages of the male as due to their origin in the fusion of the lateral tentacles and the palpi.

Since its first discovery, there has been no second record of the peculiar Sacconereis in question. Fortunately, during my stay at Plymouth, a female stolon, which is closely allied or even identical to *Autolytus roseus*, was captured at a place two miles east of the Eddystone Lighthouse with a ring-trawl, September 17th, 1928. I am greatly indebted to Mr. F. S. Russell of the Plymouth Laboratory for bringing it to my notice.

Since it was found among other planktonic organisms preserved in

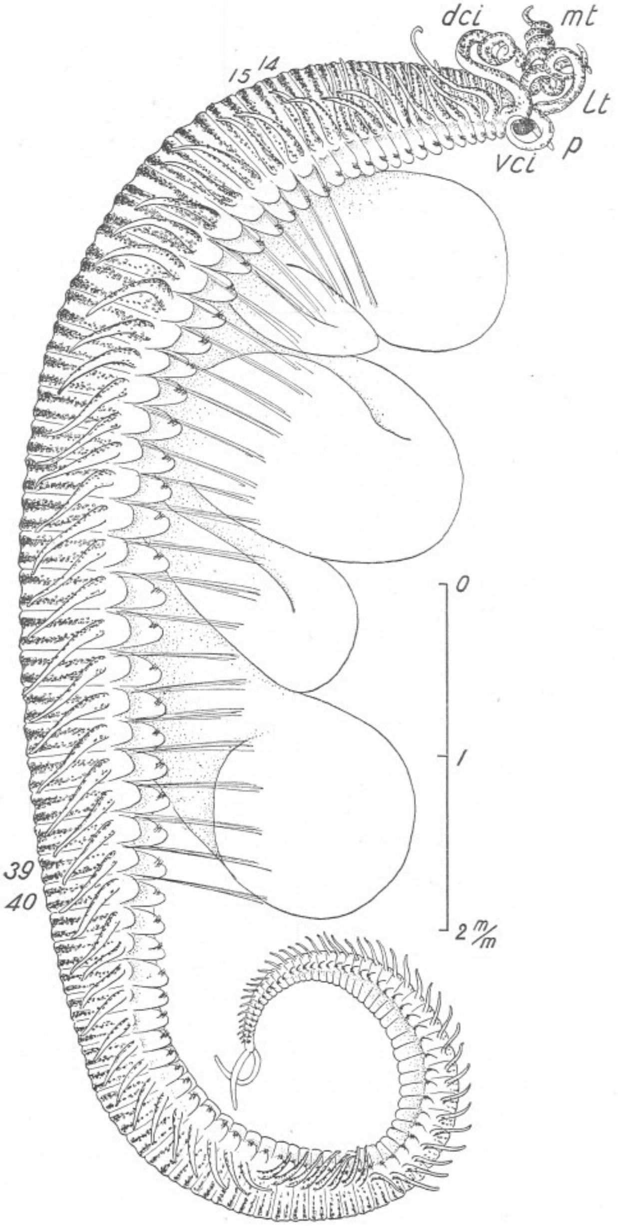

FIG. 1.—*Autolytus roseus ?* from Plymouth district.

5% formalin, its colour in the living condition is not exactly known, although a red hue is still abundantly retained; the colour is due to numerous microscopic patches of red pigment disposed in two transverse bands on the dorsal surface of each segment and its dorsal cirri. On the head the appendages are strongly contracted, coiled in spirals and massed up almost together. Their condition naturally makes the small appendages in question very difficult to examine. At any rate, I shall first sketch out the general appearance of the specimen here (Fig. 1).

As the figure shows, the Sacconereis closely resembles *Autolytus roseus* of Claparède, except in the number of unmodified segments in the first region. Here we count 14 segments as opposed to 8 in that case, and this difference deserves a little consideration before proceeding to the main problem of the present enquiry.

With regard to the sexual metamorphosis of the segments for swimming, the stolons of the Autolytinæ among Syllids may be divided into two categories, the first including those stolons of short length and possessing a smaller number of segments. In these forms the body is generally made up of the anteriorly unmodified and the posteriorly modified segments. The stolons of the second category consist of three regions having modified segments between the anterior and posterior unmodified ones. To the first category belong the stolons of *Myrianida* (Milne-Edwards) and *Autolytus* (Grube), and to the second those of *Proceræa* (Ehlers), *Procerastea* (Langerhans) and *Virchowia* (Langerhans). In the stolons of the first category the anterior unmodified region consists of only two (female) or three (male) segments, but in those of the second category there are, as a rule, 6 segments in this region, whether in the male or the female. The sexual individuals of *Proceræa* (*Autolytus*) *longeferiens* (Saint-Joseph) described under the title of *Autolytus alexandri* by Malmgren are, however, excepted from the general rule, since the first region of this Sacconereis contains 14 unmodified segments (see Okada, 1929, Fig. 30). In *Autolytus roseus*, as mentioned above, 8 segments are assigned to the first region. Therefore, if the original count be not mistaken, we have another exception to the general constitution of the Autolytan stolons of the second category. Now in connection with this number of unmodified segments in the first region the question arises whether it is truly specific to this stolon or whether it is rather due to a chance variation in the only specimen observed. Since the material at my disposal is also single, the problem cannot be settled by the method of simple comparison. Therefore turning to the other side, I examined a large number of stolons of different species, so far as I have been able to capture them by towing, and finally found some stolons of Procerastea having 3 segments in the first unmodified region instead of the usual 6. Hence, a hypomeric variation is possible at least in the case of Procerastea. On the other hand, no single instance of hypermeric variation was detected during the whole of my examination. Generalising from this result I may conclude that 8 unmodified segments in the first region of *Autolytus roseus* would be due to a hypomeric change of the original 14 segments.

I continued my examination of other Sacconereis belonging to the second category, hoping to find some other forms possessing a pair of problematical appendages in front of the head, and at length found them in female individuals of *Procerœa picta* Ehlers and of *Procerœa aurantiaca* Claparède. A pair of small appendages does exist in the head besides the median and lateral tentacles of the prostomium and the tentacular cirri of the peristomium. The general constitution of the head of the first species is sketched out in Figure 2.

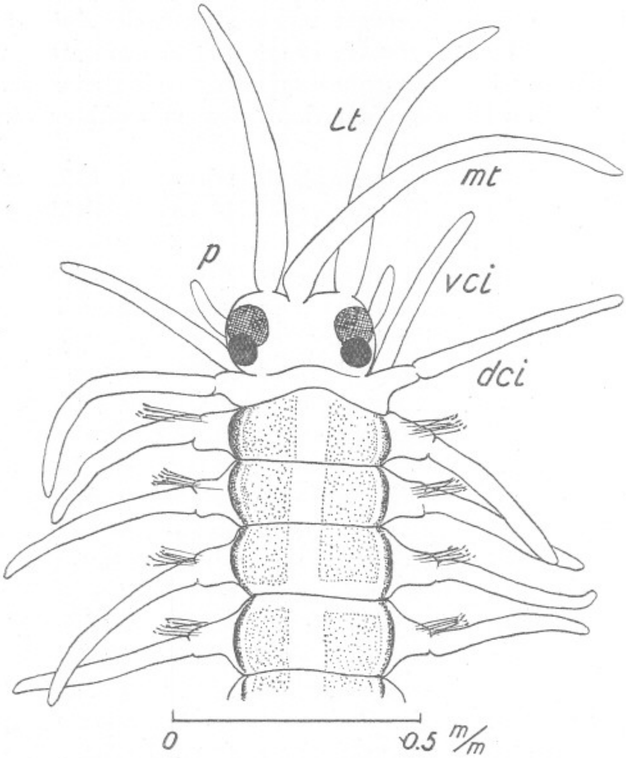

FIG. 2.—Anterior part of female individual of *Procerœa picta*.

The appendages in question are, however, not exactly in front but slightly posterior to the anterior end of the head, and placed on each side beneath the position of the dorsal eyes. They are, of course, not the lateral tentacles, since the latter, which are highly developed, are found anterior to them at each frontal edge of the head. Also they do not represent the ventral cirri of the peristomial segment, since there is a pair of cirri, dorsally long and ventrally short, on each side of the posterior boundary of the head. I do not hesitate therefore in comparing this pair of short appendages with the problematical frontal ones of *Autolytus roseus* and to say that they are homologous with the palpi of the asexual animal.* Hence the constitution of the head of *Autolytus roseus* described by Claparède is probably not due to a teratological formation, while the absence of the appendages in the head of other stolons closely allied to it shown in the figures of previous authors is probably incorrect.

II. Appearance of *Autolytus cornutus* A. Agassiz in Europe.

My second visit to the Plymouth Laboratory was in June, 1929. This time I obtained a tiny Syllid abundantly on Laminaria covered by Obelia always in close association with *Autolytus edwarsi* Saint-Joseph. It differs, however, from the latter not only in size but distinctly also in colour, which is rather pale green, and in the fact that the dorsal surface of the segments is fringed with more or less dark pigment. It produces a single stolon, either male or female, and does not carry a chain of stolons, the posterior segments separating from the anterior with a new formation of the head always on the anterior boundary of the 14th setigerous segment (Fig. 3).

The female individual consists of three distinct regions, the first containing 6 unmodified segments, the second 12 modified, and the third again 8–13 unmodified ones.

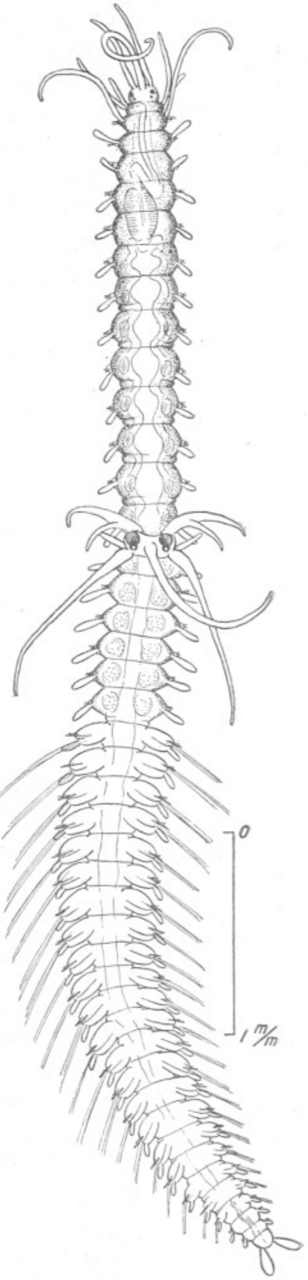

FIG. 3.—*Autolytus cornutus* from Plymouth district.

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* In the Autolytinæ the palpi are generally reduced in size and fused into a lip-like structure in front of the mouth opening.

This constitution would make the stolon belong to the type of Proceræa or the second category of my classification. The male individual, however, has only two regions. The anterior unmodified region is made up of 6 segments as in the other sex, while in the following region of the body all the segments except the anal one are metamorphosed for swimming. According to my classification, stolons having more than 6 segments in the first region must belong to the second category, although the Polybostricus of the present species represents the type of the first category.

In connection with the number of segments in the first unmodified region, A. Agassiz (1862, p. 394) has mentioned that "the number of rings which are not provided with long setæ, and have short dorsal cirri, are five, instead of six as in the female." But judging from the subsequent statement that "the spermatozoa (Pl. XI, Fig. 8, o) are found on the sides of these six rings only, and extend also into the cirri, but never into the posterior rings, as is the case with the eggs of the female," Agassiz seems to have mistakenly counted the most anterior segment as being in the head, since the spermatozoa are only produced in the original segments, i.e. from the 14th to the 20th setigerous segment of the asexual stage, and never in the new head.

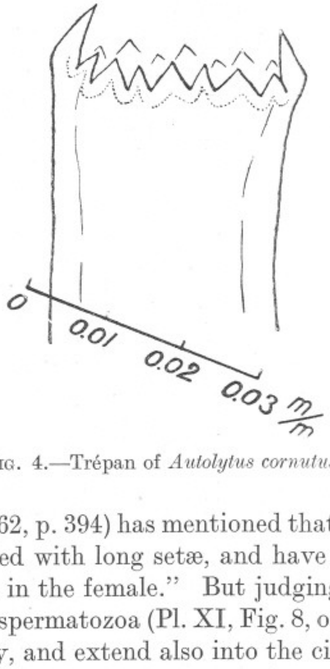

FIG. 4.—Trépan of *Autolytus cornutus*.

Agassiz did not give the dentation of the pharynx, so it may be rather risky to identify the present species with the American only by its external resemblance. Nevertheless, the following two reasons would make this identification not improbable: first, the species was not found before during my stay from June, 1927, to April of the next year, in spite of its being so common in the summer of 1929. Secondly, this district of

England is the first port of Europe touched by steamers coming from America. It is possible that its appearance in Plymouth Sound was due to its being carried by a steamer from its native country. Of course, it is probably not simply carried by adhering to the bottom of a ship, but the latter would first be covered by some hydroids including Obelia, to which the Syllid attaches itself secondarily.

III. *PROCERÆA PICTA* EHLERS AND *STEPHANOSYLLIS SCAPULARIS* CLAPARÈDE.

This Syllid described by E. Ehlers (1864, p. 587) under the title of "Proceræa picta" is most easily distinguished from other forms of the same type of animal by its characteristic pigmentation. The dorsal surface is covered with a deep deposit of black or dark brown pigment, with the exception of a mid-dorsal longitudinal line, which is free of pigment and hence appears white, and a series of transverse bands free of pigment and hence also appearing white. The white bands are especially well marked after the 7th setigerous segment, developing between the following segments: 7 & 8, 9 & 10, 11 & 12, 13 & 14, 19 & 20, 22 & 23, 26 & 27, 30 & 31, 34 & 35, 42 & 43, 45 & 46, 48 & 49, 52 & 53, 56 & 57, 60 & 61, 64 & 65, 68 & 69, 72 & 73; they become gradually obscure towards the caudal extremity. The pigmentation is further complicated on each segment. By the white line in the middle, the coloured area is divided into left and right halves, which are further subdivided into several narrow bands. This part of the centre is fringed by a longitudinal stripe of especially deep pigment. The latter is restricted to narrow limits on each side of the segments but stretches continuously from just behind the head to the tail end, without being interrupted by the transverse white bands mentioned above. Anteriorly at the level of the 3rd setigerous segment the peripheral fringes of deep pigment come from each side to the middle and meet together between a pair of nuchal organs, which are also deeply pigmented. Sometimes, especially in large individuals, the pigmentation in front of the 14th setigerous segment is more or less different from that of the posterior part of the body, the former part being always much more intense than the latter. This fact is easily understood when the method of stolonisation of this Syllid is considered; those segments posterior to the critical position are separated at each time of stolonisation and the missing part is replaced by new segments.

P. Langerhans (1879, p. 578) state that "bei jungeren Individuen ist die Färbung einfacher, nur die beiden braunen Längsstreifen sind zu erkennen. Das bestimmt mich zwei junge Thiere von 1 cm. und 50 Segmenten, die ich in Funchal am Strande gefangen habe, hierher zu stellen. Sie hatte nur zwei dunkelbraune dorsale Längsstreifen, die sich über das ganze Thier bis zum Analsegment erstreckten. Aber sie stimmten sonst ganz mit der picta überein. Namentlich hatte der Pharynx wie bei dieser 20 Zähne, 10 grössere abwechselnd mit 10 kleineren. Analcirren kurz." Unfortunately this statement cannot be applied to all small individuals of the so-called " Autolytus pictus " in the Plymouth district. There are plenty of specimens which measure even less than 1 cm. and consist of less than 60 segments, yet showing the special pattern of pigmentation detailed above, while on the other hand there are also nearly as many specimens whose pigmentation is indeed " einfach," without the transverse white bands. These worms are, however, by no means always smaller than those of the other type. On the contrary, they are sometimes as big as the largest worms of the other type, and have even been observed in the act of producing the stolon. It is almost certain, therefore, that we are dealing here with two different species or varieties at least and not two developmental stages of one and the same species. Ehlers (1864, p. 257) has mentioned the existence of some variations among his " Proceræa picta " : " Ein dritte Form ist diejenige, wo die gleichmässig gelb gefärbte Rückenfläche an den Kanten von einem braunen Längsstreifen eingefasst wird, wobei die Stirnfühler und Cirren des zweiten Segmentes braun, die das ersten und dritten Segmenten nur an der Spitze braun, sonst weiss waren." Such pigmentation may be well applicable to " Stephanosyllis scapularis " described by Claparède in the same year from Port-Vendres (Pyrénées Orientales).

The stolon of the so-called *Autolytus pictus* was first shown by Saint-Joseph (1886, Figs. 102–105). It represents the male individual of the type " picta," while as to the other sex Saint-Joseph states, " Je ne vois jamais de Sacconereis se détacher ; je constate seulement que la tête en est semblable à celle figurée par moi pour la Sacconereis de *l'Autolytus ornatus*." In his monograph on " The British Annelids " McIntosh (1908, Pl. XLVII, Fig. 1) has figured a young Polybostricus of the same type. Now it might be asked whether this banded type of the Autolytus in question is not the male producing animal, and the other non-banded simply pigmented type the female producing one. Actually among Mrs. E. W. Sexton's sketches of the Plymouth Polychætes (unpublished and preserved in the Laboratory) there is a Sacconereis certainly belonging to the latter type. This consists of 28 setigerous segments in addition to the head and tail ones, differentiated into 6 unmodified, 13 modified, and 9 unmodified. However, there is also a female stolon of the banded type in the same collection of sketches. Therefore, sexual dimorphism cannot be applied here to explain the colour differences of the Autolytus in question. At any rate, to settle the problem definitely I cultivated the banded and non-banded animals separately to see what kind of stolons come out. As a result each type was found to produce both male and female stolons independently, and those stolons well preserve their original pattern of pigmentation even after being separated from the anterior part.

Stolonisation, either in the banded or in the non-banded type, takes place quite easily even when the animals are confined in a finger-bowl filled with sea-water during the warmer season from June to August, while the stolons are most abundant in the plankton from April to June. A quite astonishing fact is that after September, in spite of its being still quite warm in Plymouth, the animals cultivated *in vitro* never produce any more stolons, although some of them are full of green eggs or milky-white spermatozoa. Apparently stolonisation in nature also stops after the summer season, just as in culture experiments. At about the same time we find no more stolons in the plankton, although there are still plenty of asexual individuals among the dredgings. Among the latter there are also specimens whose body segments are filled with sexual products. Claparède (*l.c.*, p. 108) observed in his " Stephanosyllis scapularis " the eggs contained up to the 10th setigerous segment, without, however, any sign of stolonisation. Langerhans (*l.c.*, p. 579) has also mentioned a similar case of sexual maturity in *Proceræa aurantiaca :* " Ich habe nur einmal bei dem grössten meiner Exemplare im December vom 16 Segment an Ei gefunden, ohne Anzeigen einer Knospenbildung." Since such specimens are obtained mostly in the winter season, it may be supposed that the stolonisation of Proceræa and its allied species would depend upon the temperature of the sea-water. However, examining Mrs. Sexton's drawings of Plymouth Polychætes again I find an example of *Autolytus prolifer*, which is full of ripe eggs and yet without any indication of forming a stolon. It was captured, according to a note attached, at Millbay pit on July 1st, 1914. In July the sea-water at Plymouth is by no means cold. As has been mentioned already, stolonisation in both *Proceræa picta* and *scapularis* stops nearly at the same time, about the end of August, while sexual individuals are quite abundant in the plankton in April. The temperature of the sea-water at Plymouth in September is never lower than in April, so that stolonisation of these Autolytids at least could not be simply due to the temperature of the external medium, but must be inherent and due to some other factors.

The regeneration of *Proceræa picta* is most interesting to study. As I have already shown in a former publication (1929, p. 560) if we cut the anterior segments, the posterior piece almost invariably regenerates the head up to about the level of the 42nd setigerous segment. But the regenerative power is not the same throughout the body. From the head to the end of the 5th setigerous segment the number of new segments almost always corresponds to that of the missing ones. Behind this level the number of regenerated segments is more or less smaller than the original number, the maximum number being still, however, the same as the missing. Posterior to this level but up to the end of the 7th segment, the same maximum regeneration cannot as a rule exceed 4 setigerous segments in addition to the head ; and this 6-segmental recovery holds to the end of the 13th segment. Between the 14th and the 42nd setigerous segment, the regeneration is quite isopotential, only the head plus one setigerous segment being produced before sexual maturity, and only the head part in the sexually matured animal. Moreover, beyond the level of the 13th setigerous segment there is absolutely no stomodeal invagination in regenerated segments, and the cut end of the intestine opens directly to the exterior as a mouth. However, as I have mentioned before, "this interesting result that there is so distinctly regional difference in regeneration, cannot be extended and applied to the body of other Syllids, even within the bounds of the same genus." So far as my experiments are concerned only *Proceræa scapularis* presents the same regional difference in regeneration according to the point at which the cut is made.

Fragmentation is not a characteristic phenomenon in these species of Autolytids, but it has been well investigated in them. There are two methods of provoking artificial fragmentation, viz. dilution of sea-water with fresh or distilled water (Allen's dilution method) and employing a solution of KCl. As has been explained, the fragmentation due to KCl solution depends upon a muscular action, while the same phenomenon in diluted sea-water is due to the osmotic changes in the intestine. According to my former experiment almost no effect is produced by dilution until the degree of 60% (not 6% as printed in the former publication, Okada, 1929, p. 586) of distilled water in sea-water is reached. Proceræa can live quite normally in such a medium. Nevertheless, if we cut or injure any part of the body with the exception of the extreme anterior or posterior portion, fragmentation takes place even in such a low degree of dilution. In *Proceræa picta* two consecutive united groups of segments at each white band separate first on the dorsal surface, a transverse crack appearing in the middle of the white band. *Proceræa scapularis* has no transverse bands, but fragmentation of segments takes place exactly in the same manner as in the preceding case. The external and internal changes of the segments, which are observed in this case of fragmentation, have been described in the former paper. They are also illustrated here by the three microphotographs in Figure 5.

It was stated that " the swollen intestine is generally coloured brown, while in its normal condition it is almost without colour or at the most pale yellow." This change of colour in the intestine is found to be closely related to the change in the chemical nature of the granules contained in the intestinal cells. The granules in the normal specimens are slightly stained by eosin or other acid dyes, but not at all by Heidenhain's iron hæmatoxylin, while the same granules in the fragmenting or fragmented specimens are highly stainable by the last-mentioned stain.

The structure of the pharynx, especially the dentation, is the most important clue for the identification of these Syllids. Ehlers (*l.c.*, p. 260) mentions that "am vorderen Eingange ist der Rand dieser Cuticula so eingeschnitten, dass etwa 10 kleine Zähne, welche schräg nach vorn und gegen die centrale Längsaxe convergiren, die Eingangsöffnung umgeben und verkleinern." Claparède (1868, p. 221) states that "la cuticule de la trompe s'épaissit en avant pour former un cercle d'une dizaine de dents un peu crochues." Langerhans (*l.c.*, p. 577) describes the "trépan" a

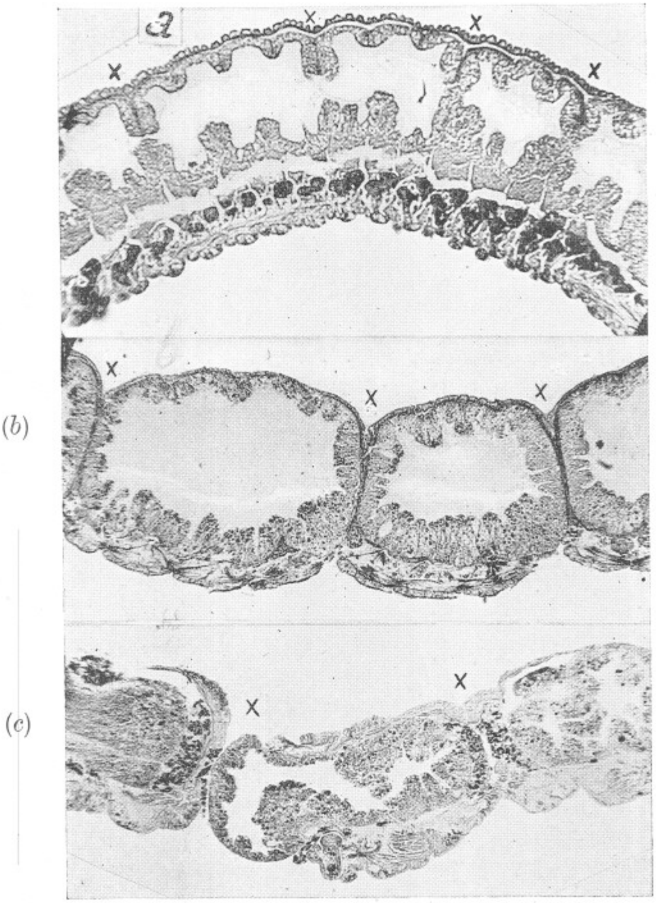

FIG. 5.—(*a*) Longitudinal section of *Proceræa picta*; (*b*) same of fragmenting, and (*c*) fragmented specimens, x indicating positions of macrosepta.

little more precisely: "Pharynx mit 20 Zähne, 10 grössere, 10 kleine Zähne." This number of 20 of two kinds of larger and smaller teeth disposed alternately is also given by Saint-Joseph (1886, Fig. 101, also P. Fauvel, 1923, p. 316, Fig. 121b). However, it is doubtful whether these authors really counted all the teeth carefully or whether they counted only one side of the trépan and doubled the number. There are just 5 larger and 5 smaller teeth on one side of each trépan when we count them without moving the screw of the microscope. But if we count all the teeth with a little more patience, we find the number is 18 instead of 20; 9 larger teeth are disposed alternately with 9 smaller teeth forming a circle (Fig. 6). In *Proceræa picta* the difference in size between the larger and smaller teeth is great. They are, however, of the same size and shape among those of the same category. On the other hand, the smaller teeth are much developed in *Proceræa scapularis*, and the difference in size between them and the larger teeth is accordingly reduced. Moreover, in the latter species the larger teeth are not uniformly shaped, some being broader than others, while the latter are more sharply pointed and longer than the former. Although this character is not very constant, yet it

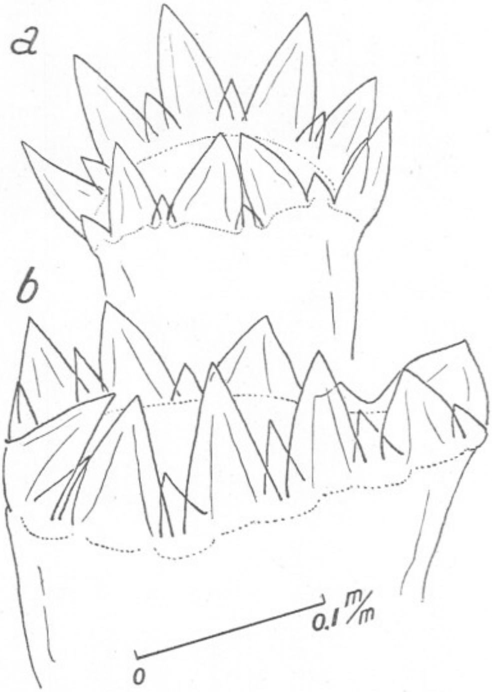

FIG. 6.—Trépan of *Proceræa picta* (*a*), and *scapularis* (*b*).

is never found in the trépan of *Proceræa picta*. It cannot be considered teratological, since the structure is met with in too many cases. On account of the different dentation, as well as the difference in the colour pattern, I propose to revive the name *Proceræa scupularis* to be applied to the so-called " Autolytus pictus " with non-banded simple pigmentation and purple tentacles and cirri.

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Remarks on the Reversible Asymmetry in the Opercula of the Polychæte Hydroides.

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With 5 Figures in the Text.

THE members of the family Serpulidæ are the most highly differentiated and most truly tubicolous Polychætes. They are not large as a rule, and live in a calcareous tube or in a spirally wound shell, which they build outside the body. For this manner of living one of the gill filaments, either right or left or rarely both of them, develop into a sort of plug, the operculum, that closes the opening of the tube when the animal retreats into it. C. Zeleny first showed in *Hydroides dianthus* (1901) and in other allied species of Polychætes (1905), that if the operculum is cut off, the small rudiment on the opposite side begins to grow, and in the course of a few weeks becomes as large as the one removed and acts as a functional organ, while from the stump of the original operculum a new small rudiment develops. An animal with a right-handed operculum is thus easily transformed into one with a left-handed one, and this can be brought back to the original right-handed form.

When the small rudimentary operculum is removed, the large functional one remains unchanged. However, if both the functional and the rudimentary opercula are taken off at the same time, the original rudimentary one may sometimes be the first to regenerate and after several days is distinctly larger than the one regenerated on the opposite side ; compensatory regulation takes place here also. That the presence of a functional organ holds its mate in check is evident. The nature of this influence is a matter for investigation.

Compensatory regulation takes place also in the asymmetrical development of the claws of the Crustacean Alpheus (H. Przibram, 1901). E. B. Wilson (1903) found that after removal of the large chela, if the nerve of the rudimentary small one be cut at the base, " the reversal in some cases at least does not take place, or is incomplete."

One of Zeleny's experiments in which the Polychæte was cut in the thoracic region, with the resulting production of double functional opercula, is especially interesting in connection with the explanation that the nervous system controls the reversal of asymmetry. The failure to establish the original asymmetry is here suggested to be due to the absence or to the undeveloped state of the cerebral ganglia while opercula are forming.

In *Hydroides norvegica* of the Plymouth district with which I have experimented, the opercula regenerated from a transverse cut of the thoracic region are rather rarely symmetrical, while in the majority of cases one rudiment is, from the first, always larger or develops more quickly than that of the opposite side, and it alone gives rise to a functional organ. I have got only a few specimens of double opercula out of each 50 cuts, three times repeated, while specimens with two fully developed opercula on the right and the left side can be easily obtained, as will be shown later, when the growing tip of the rudimentary operculum is injured after removal of the functional one (see Fig. 3). The asymmetrical development of the opercula seems, therefore, to be more deeply impressed in the organisation of *Hydroides norvegica* than we have learned from Zeleny's experiments on *Hydroides dianthus* and other allied species, but this condition of asymmetry is very unstable, and is easily reversible by an external influence ; there is only a tendency in the Polychæta for the opercula to show right-handed development. The origin of the asymmetry is due to the growth difference between two sides in the same kind of organ. Actually most of my specimens, from which a part of the thoracic segments had been removed, produced first two almost symmetrical rudiments of opercula, but one of them, generally that of the right side, grew more quickly than that of the other side, and it alone, as mentioned above, gave rise to a functional organ, possibly suppressing the development of its mate.

Zeleny also cut the anterior part of the Polychæte in question longitudinally into approximately equally right and left halves and then took off one side. A few of them are said to have showed clear structures which corresponded very well with young regenerating branchial circlets, but none lived long enough to allow of a full development of the new organs.

According to my own experience, one side of the anterior segments including the head can be cut off (obliquely, of course) almost without impeding the regenerative power of the animal. In such an operation, if the brain is left attached to the side bearing the rudimentary operculum, the latter grows and becomes a functional organ as in the case where the functional operculum only is removed ; the growth of the rudimentary operculum takes place even before any other organ is regenerated from the cut surface. On the other hand, if the brain is taken off with the functional operculum, growth does not occur in the rudimentary organ. Nevertheless, growth of the latter does take place as soon as the missing half of the head segment is regenerated.

As a result of his study on the "Scherenumkehr" of the decapod Crustacea, H. Przibram (1907) definitely questions whether this phenomenon of compensatory regulation is dependent on a nervous reflex set in motion by the stimulation of damaged nerves in the functional organ. According to him the nervous stimulus here plays only a secondary role, its influence being at most "Wachstumhemmung" in the developing organs.

It has already been mentioned that the presence of a functional organ in Hydroides holds the development of its mate in check. When the functional operculum is removed growth is, therefore, induced in the rudimentary one, while removal of the latter has no apparent effect on the former. When both are operated on at the same time, there will be found in some cases a reversal of asymmetry, but in other cases two functional opercula are developed, one on each side.

Since removal of the rudimentary operculum has no specific influence either on the opposite functional organ or on its own regeneration, Zeleny considers that the differences of level of the cut have no influence upon the character of the result. The condition is, however, different in the functional operculum. According to his experimental facts the most distal and the most proximal cuts agree in giving rise to a reversal of the original asymmetry, while cuts in the intermediate levels give rise in a majority of the cases to two functional opercula. Zeleny attributes this difference in the results to differences in the regeneratory development of the old functional operculum. And as to what factor or factors hold it in the rudimentary condition in some cases, while in others it is allowed to develop into a full-sized functional organ, he suggests, first, the influence of the position of the cut upon the initial stages of regeneration, and, second, the possibility of a retarding influence emanating from the new functional organ which is formed on the opposite side from the originally rudimentary one. Zeleny states that the most distal cuts do not affect the embryonic tissue at the base of the functional operculum as quickly as do the more proximal cuts, while the cuts too near the base directly injure the tissue in question, and for either reason the tissue will have had only a small start when the opposite rudimentary organ has already a considerable size. After cuts at the intermediate levels the regenerated bud on the old functional side shows greater development than after the most distal or proximal cuts, and assuming the uniform development of the bud of the rudimentary side in all cases, it has attained a considerable size at the time when the latter begins to grow. "Therefore, in the first cases, the result of simultaneous operation on both opercula is a reversal of the original condition, while in the second, it is the production of two functional opercula."

Zeleny considers the tissue forming the base of the functional operculum in the region below the breaking joint to be embryonic. In *Hydroides norvegica* the connective tissue of the corresponding region is, however, not observed to be particularly different from that of the other parts. The cells of the ectodermal layer are, indeed, taller and visibly more crowded together than elsewhere, but the nuclei have a similar size and the cytoplasm shows the same appearance as in other parts (see Fig. 1, *rb*, *lb*). With only such a simple fact as the crowding of the cells in the ectoderm, it is rather difficult to say that the basal part of the functional operculum, as Zeleny claims, is embryonic. On the other hand, the rudimentary operculum is everywhere distinctly embryonic, the cells being plump and having large nuclei, and being deeply stainable with dyes. It is somewhat club-shaped and when later it develops into a structure of two cups, it is first constricted at the level of the distal third of its length, and this distal part is further subdivided into two with accompanying growth ; thus from the basal section arises the shaft, and from the middle and the distal section the lower and the upper cup of the functional operculum respectively.

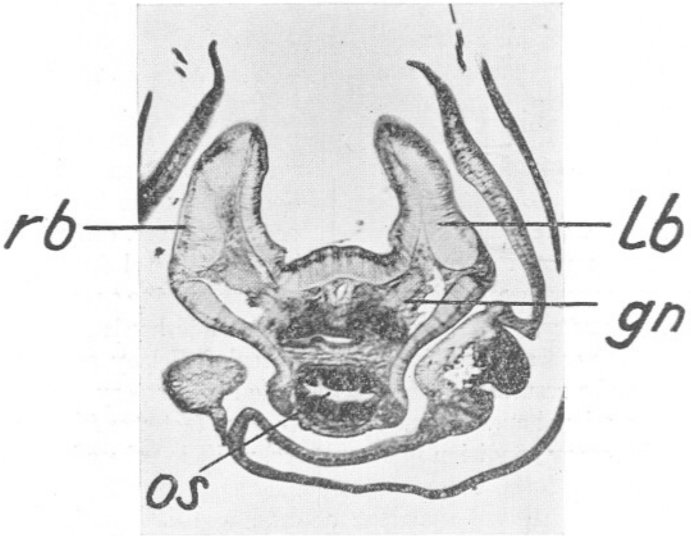

FIG. 1.—Transverse section through head of *Hydroides norvegica*, *rb* and *lb* indicating basal parts of right and left gills.

When the functional operculum is injured the rudimentary organ on the opposite side is ready to start development. From 20 to 30 hours after the operation the latter has already a fairly large size and shows its three sections distinctly. At this stage cutting within the limit of the distal section is followed almost invariably by regeneration of the missing part, while below this level the power of regeneration decreases towards the base, and there is almost no regeneration after cuts of the basal section. The assumption of uniform regeneration of the rudimentary operculum following cuts at different levels is, therefore, challenged. In regeneration from the basal section, the future shaft is generally imperfect. When this part of the rudimentary operculum is cut after removal of the functional one, there is sometimes no reversal of the original asymmetry, since an imperfect organ practically cannot inhibit the regenerative development of the stump of the old functional operculum, or in other cases the wounded shaft of the latter does not drop off. In this case perhaps an equilibrium can in some way be attained between the imperfect structures on each side. If, however, either one is taken off from the base, the equilibrium is broken, and a new rudiment is soon formed from its stump.

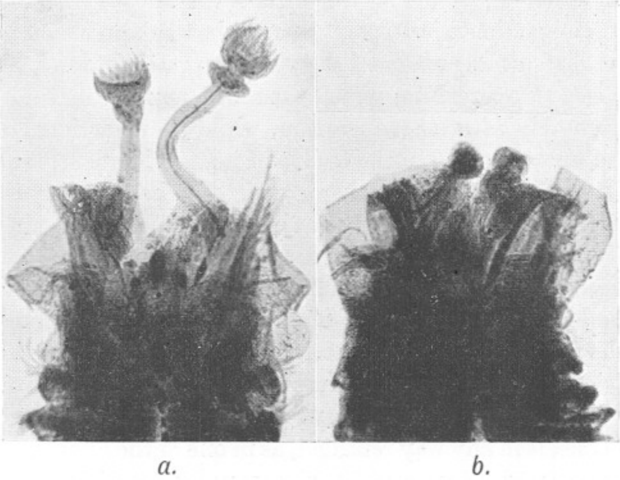

FIG. 2.—Artificial induction of symmetrical opercula, (*a*) both functional, (*b*) both rudimentary.

In a similar experiment where the rudimentary operculum was severed within the limit of the distal section, there was as a rule a reversal of asymmetry, because a prompt regeneration was still possible in the operated organ before a new rudiment makes its appearance on the opposite side. If, at the time of the operation, the functional operculum was removed from its base, two small opercula, one on each side, were formed, and in some cases both gave rise to functional organs (Fig. 2a), or in other cases both remain rudimentary (Fig. 2b). In the first case one may suppose that the new rudiment from the stump of the removed functional operculum has already advanced to a certain degree of development, while regeneration is going on in the operated rudimentary one, and thus it can continue to grow in spite of the presence of an inhibitory agent on the opposite side. On the other hand, if the inhibitory influence of each organ acts too strongly and checks the development of the other rudiment, the second case would result. In either case, whether inhibition takes place or not, its effect on the growth of an organ on the opposite side should be equal, otherwise one rudiment will develop more than the other.

The fact that the functional operculum has no regenerative capacity, while the rudimentary one has, leads us also to suppose that the former has used up something which the latter still retains for use in development. The difference in the results, after simultaneous operation on both functional and rudimentary opercula, may be explainable on an assumption, somewhat different from Zeleny's interpretation cited above, that the rudimentary operculum, which remained more embryonic, regenerated immediately after the operation, while the functional operculum which used up something in the course of its development, required time to regain this something, or in other words, to get back again to its original state of development. There must exist a difference of time in the regeneration of the opercula of the two sides, and according to the nature of the organ in question, the larger or well developed always checks the growth of the smaller or less developed. As a result of this antagonistic action only the larger gives rise to a functional organ, while the smaller on the opposite side is forced to remain rudimentary. When the growth of the originally rudimentary operculum, which is larger after the removal of the functional one, is in any way retarded, as in one of the above experiments, and shows no great difference from the growth-state of the new rudiment from the old functional operculum, specimens with two functional opercula may easily be produced, Figure 3*d* being one of such productions.

T. H. Morgan (1923 and '24) has comparatively recently investigated the problem of the asymmetrical development in the chelæ of the male fiddler crab, *Gelasimus pugnax*, in which a reversal of asymmetry does not occur. According to him, the young male crabs have two claws, one as large as the other, and both are a little larger than those of the female of the same age, and show the swollen shape of the male large claw. At some time most of the young males lose one of the claws and produce at the next moult, in place of the lost one, a small claw of the female type. This relation, once attained, becomes fixed and even in young crabs no reversal after the removal of the large claw is possible. If young male crabs with two large claws are carefully protected from injury, they usually retain both claws throughout successive moults, and develop into a symmetrical male with two large claws. On the other hand, if both claws are removed from young males, at the next moult two small female claws develop, and this condition of symmetry is also retained in the successive moult. Thus an accident determines the first asymmetry of the chelæ in male Gelasimus, and it is not due to any preformative character. The asymmetry may even be introduced in this case relatively late in development, but the relation, once attained, becomes fixed and no further reversibility is possible.

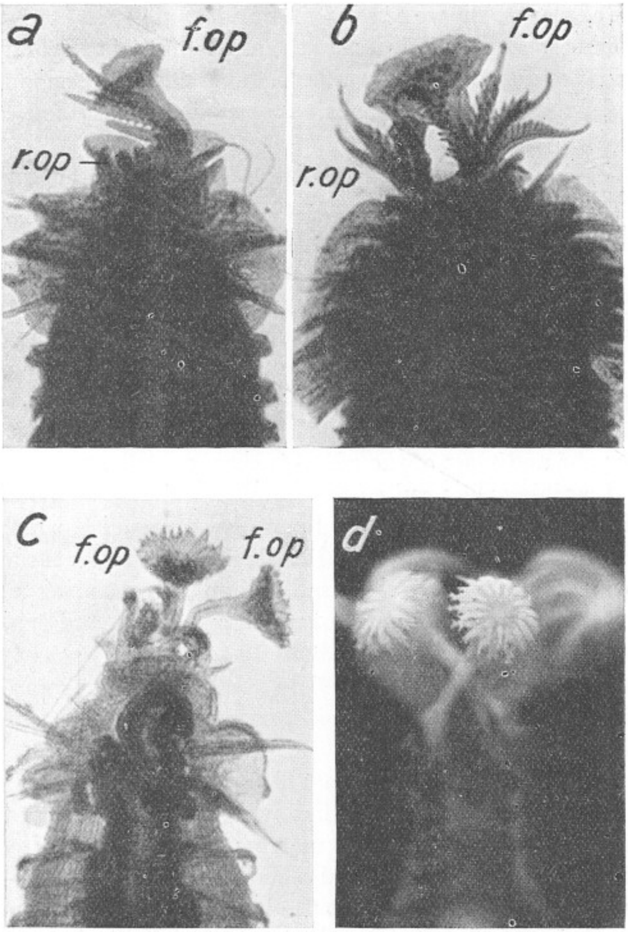

FIG. 3.—(*a*)-(*c*) Anterior regenerations from thoracic segments, (*d*) di-opercular specimen artificially produced.

As to the origin of the asymmetrical development of the opercula in Polychætes, we are much tempted to refer it also to an accidental cause, but it should not be forgotten that there is no critical period of fixation as in the case of the male fiddler crab. Without doubt an injury of the functional operculum is due to accident, and this external cause brings a reversal of asymmetry. But how does this external influence result in the growth of the rudimentary organ on the opposite side of the body ? We know many analogous phenomena in other animal structures as well as in those of plants, but we have as yet no adequate explanation of them. The only thing we can say here is that the mechanism of this compensatory regulation is not due to a nervous reflex set up in the wounded organ, since, for example, the influence depends to a certain extent upon degrees of injury.

Zeleny (1905) has already observed that a removal of the upper cup of the functional operculum does not as a rule cause a reversal of asymmetry, while an injury below this part to the main portion of the operculum or to its stalk always does. This fact makes us doubt whether there is any special localisation of the inhibitory influence in the rudimentary organ, and leads us to suppose that if such special localisation does exist, it will be found in some part of the functional operculum. It may be mentioned in passing that growth of the rudimentary operculum does not take place in an animal with a perfect functional operculum, even when it is drawn out of the tube and most of the gill filaments are cut off.

Before describing the results of my own experiments, a brief account is necessary of the structure of the functional operculum, which consists of a distal crown and a long proximal shaft. The former, or the operculum in the strict sense, is made up of basally, a cup corresponding to the operculum of Serpula, from the centre of which arises a second cup, which is larger than the lower and carries about 10 to 20 spines sharply pointed towards the ends. These spines radiate in all directions from the centre to the periphery, and each in *Hydroides norvegica* is more or less dentated (Fig. 4).

The operculum is nothing but a gill filament functionally modified. Therefore, as in the latter, immediately beneath the cuticle there lies a tall epithelium and below this a marrow-like reticulum of connective tissue, which contains a large axial blood vessel (see Fig. 4, b–d). The blood vessel coming up the shaft to the base of the lower cup and giving off ramifications to the peripheral structures of the latter, proceeds further upwards to enter the upper cup, passing through the narrow isthmus that forms the centre of the circlet of the distal spines. Thus each spine receives a direct supply of blood, which is of greenish colour in the fresh condition, and its distribution through the operculum can be easily traced in the living specimen. The distal half of the spines in the upper cup and the leaf-like processes in the lower cup have, however, no direct supply of blood.

With this preparatory knowledge of the structure of the operculum, in

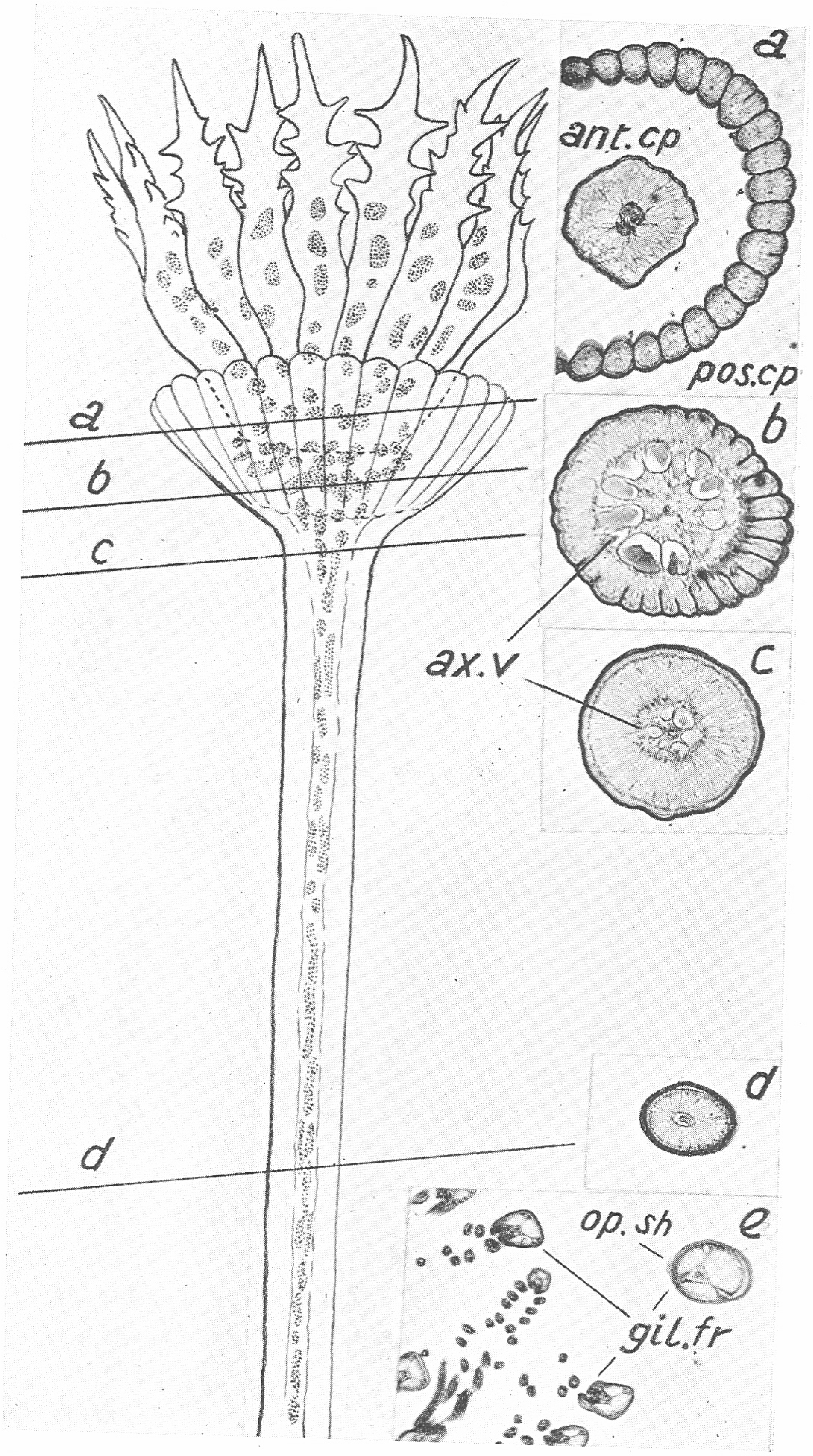

FIG. 4.—Functional operculum and its regional structural differences in transverse sections.

the first series of my experiments the entire circlet of the distal spines and a half of the proximal cup were removed, but the other half of the latter and the entire shaft remained intact. As a result compensatory growth took place in the rudimentary organ, which developed at the end of two weeks into a fully functional organ.

The inhibitory influence of the functional operculum must be found, therefore, outside the limit of the shaft, since in spite of its presence growth takes place in the rudimentary organ.

Next, one side of the distal as well as the proximal cup was cut off in varying degrees, but always more than half of each cup remained intact. In all cases, without exception, the rudimentary operculum grew as in the preceding experiment and developed into a functional organ. Here also it is evident that inhibitory influence of the functional operculum is not localised either in the proximal or in the distal cup, but it seems to depend on the presence of both or either one of the cups as a complete structure.

We may now ask whether or not the inhibition functions when one only of two cups, either the upper or the lower, is perfect, or whether it requires the presence of both of them. To answer this question I removed the distal circlet of spines carefully, while retaining the proximal cup intact. In that case the rudimentary operculum on the opposite side grew more slowly, compared with those of the preceding experiments, but it developed into a functional operculum in the end. The same result was obtained when one side of the proximal cup was operated on, while the circlet of distal spines remained intact. Hence we are forced to conclude that the presence of both complete cups is necessary to check the development of the rudimentary operculum.

But it was sometimes found that an imperfect removal of the spines in the distal cup or the leaf-like processes in the proximal cup did not cause a reversal of asymmetry. After repeated experiments it was found that cutting off the spines of the distal cup or taking off the leaf-like processes of the proximal cup, even all of them, but outside the limit of the direct supply of blood, had no effect, while an injury of either cup deep enough to cause an outflow of blood, induced almost invariably a growth of the rudimentary organ. Therefore, it is not necessary to take off any part of the functional operculum, but is sufficient to make a deep cut to the inner part. From these experiments it may be said that the inhibitory influence of the functional operculum depends upon the intactness of its internal constitution. Those peripheral parts such as the spines of the distal cup or the leaf-like processes of the proximal cup can be taken off, without any effect on the present phenomenon of a reversible asymmetry. Here it should be added that such a simple injury as puncturing with a fine needle, however deeply it may go, has no effect. But when the inner structure of the operculum is destroyed by some injury to such an extent that a greenish fluid, namely the blood, flows out, growth ensues in the rudimentary operculum.

Since cutting off the peripheral structures or a simple puncturing of the functional operculum has no effect, while deeper injuries accompanied by an outflow of blood have such an effect, we may well suppose that the phenomenon in question might be due to a circulatory disturbance. It cannot however be due to loss of blood, since on cutting off all the gill filaments or other parts of the body except the functional operculum, with greater loss of blood, there was no case in which growth took place in the rudimentary organ. It seems more plausible, therefore, to suppose a production of some substance in the wounded part of the functional operculum, and that this substance either stimulates the rudimentary organ to development or destroys the inhibitory influence of its own side, with secondarily resulting growth of the other side.

Therefore, the next step in the experiments was first to ligature the functional operculum at a given position of the shaft with a fine baby's hair and then to injure it in the more distal part, in order to see whether or not ligation stops a circulation of such a presumptive substance. The result of this experiment was entirely contrary to what was expected, and in all specimens without exception the small rudimentary operculum developed into a functional organ in due course. In the control experiment, in which the shaft of the operculum was simply ligated without subsequent injury of the distal part, the same degree of growth was also found in the rudimentary organ.

Ligation may indeed stop the circulation of blood and the distribution of material from the distal part of the operated operculum to the other parts of the body, but from the control experiment it is doubtful whether the same material might also be produced in the ligated part of the shaft in consequence of the strong constriction. I therefore abandoned this method of experiment, and injected the substance squeezed out of the wounded operculum into the body of another individual having an intact operculum. For this purpose I had to pull out 20 large animals from their calcareous tubes and to injure the tip of the functional operculum. The rudimentary organ on the opposite side was thus made to start growing. After well confirming the growth of the latter, the inner tissue of the severed operculum (two days after the operation) was pressed out with the back of a dissection knife into a clean watch glass. The substance thus obtained from 20 animals was then ground down and passed through fine meshed silk. After making double the original volume by adding filtered clean sea-water, the preparation was injected into 10 sound individuals by means of a very fine glass pipette through the biggest thoracic vein. The operated animals lived very well, but none of them showed any sign of a reversal of the original condition of asymmetry. Moreover there was no change either in the functional or in the rudimentary operculum to the last, even after waiting more than two weeks. Thus we have only negative results for proving the production of a growth stimulating substance in the injured operculum.

On the other hand there is no significant localisation in the functional operculum of the inhibitory influence upon the growth of the rudimentary one, while the influence most evidently depends upon the presence of a complete organisation of the former or at least upon the intactness of its internal constitution. This organ of inhibition has no regenerative capacity, as has been well demonstrated by the preceding experiments. When it is cut or injured, the part remaining is thrown off sooner or later from the body, separating by a breaking joint at the base, and a new start repeats from the beginning the original development. Generally the old shaft remains attached to the body, and the rudimentary organ begins to grow. The growth takes place only when the functional operculum is injured, but never even when all gill filaments of that side are cut off. Therefore, it is not plausible that a certain substance, even admitting such a production in the wounded place, particularly stimulates the rudimentary organ to development, since the same substance would also be produced in the severed gill filaments as in the operated operculum. In the present case, however, it is quite certain that the wound has its direct effect upon the inhibitory influence of the functional operculum itself. Yet it still remains to be shown whether this action is due to the production of a certain substance in the wounded tissue of the operculum. At any rate, as soon as the inhibitory influence of the functional operculum is destroyed, the rudimentary organ starts to grow and in the absence of the former controls the whole system, restricting the development of the new rudiment from the stump of the old functional operculum to its own former state ; a reversal of asymmetry is thus induced.

When the body of Hydroides is cut into two in the thoracic region, in some cases a specimen with two symmetrical opercula is produced, but in most cases one operculum is bigger than the other. Since, however, either the right or the left is able to develop into the functional organ, the inhibitory influence would act at first in both alike, unless a threshold value is assumed. Then it is only a question of chance which one gets the start of the other. (In *Hydroides norvegica* it is as a rule the right-hand one that grows more quickly than the other.) When this chance is missed either both rudiments develop into two functional organs, one as large as the other, or both remain rudimentary. I. Irosa (1921) has described a specimen of *Hydroides pectinata* (*H. norvegica* according to P. Fauvel, 1927, p. 359) with two symmetrical opercula under the name of *Hydroides pectinata* var. *bioperculata* (*l.c.*, p. 50, Tav. 4, Fig. 8). I think this is a case of double opercular formation in nature instead of one in the ordinary case.

As a rule the anterior regeneration of Hydroides is only possible from the thoracic segments and not from the abdominal ones; the power of anterior regeneration is, therefore, quite limited in this Polychæte. Moreover there is generally no recovery of the missing setigerous segments, only the head being regenerated. According to Zeleny (1905), the most posterior region showing regeneration of branchial and opercular structures (in *Hydroides uncinata*) is an anterior cut surface, located between the next to the last (6th) and the last (7th) thoracic segments. In a cut posterior to this limit the anterior cut surface heals over, but no regeneration takes place.

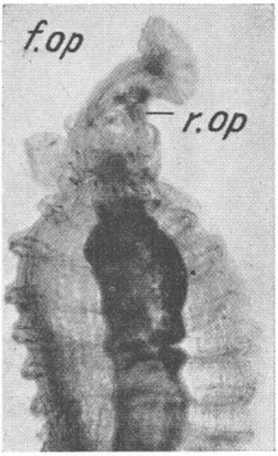

FIG. 5.—Anterior regeneration from abdominal segment.

Contrary to this general rule, I have got a specimen in which a head is regenerated from one of the abdominal segments. Figure 5 is a photographic reproduction of this specimen. As is well shown by the figure, there are no specialised thoracic segments, while the head is formed directly in front of the abdominal segments. Since there is no recovery of the setigerous segments in this Polychæte, there is little difficulty in concluding that regeneration can take place from one of the abdominal segments. Actually I found this specimen in a lot, in which the experimental animals were divided into two by a transverse section at the anterior part of the abdominal region. Besides this peculiarity of the exceptional regeneration, the most important thing which should not be overlooked, is that its two opercula are not symmetrical in development, the right-handed (left side in the figure) being far larger than the left. That in *Hydroides* *norvegica* the opercula show an asymmetrical development from the beginning, is here again confirmed. This tendency to asymmetry, according to Zeleny's observation (*l.c.*, p. 41), was already distinct in the larval stage, when the opercula first differentiate. Therefore, it may be said that Hydroides opercula have a sort of labile asymmetry from the beginning of their development. However, there is no critical stage when it is invariably fixed. It is easily reversed to another type of asymmetry or is altered to the symmetrical condition by an external influence. In this respect the nature of the asymmetry seems to be quite different from that of the male fiddler crab, in which the asymmetry of the chelæ is said to be derived from the symmetrical condition relatively late in development, and the relation, once attained, becomes fixed and there is no more reversal of the asymmetry.

SUMMARY.

(1) The asymmetrical development in Hydroides opercula is due to the growth difference between two sides in the same kind of organs. The presence of a functional organ holds its mate in check. Therefore, taking off the functional operculum results in the development of the rudimentary side.

(2) This phenomenon of compensatory regulation cannot be considered to be brought about by a nervous reflex set in motion by the stimulation of damaged nerves in the operated operculum, since, for example, the inhibitory influence to a certain extent depends on the degrees of injury.

(3) It is also not proved to be due to the production of a certain chemical substance which stimulates the rudimentary organ to grow, while the wound itself affects directly the inhibitory action of the functional operculum.

(4) The inhibitory influence is only localized in the operculum and not outside of it. Therefore, cutting off the gill filaments or other parts of the body does not bring a reversal of asymmetry.

(5) Within the limit of the operculum there is no special centre of the inhibitory influence, which depends on the intactness of the internal constitution of the organ. Those peripheral parts outside the limit of direct blood supply can be cut off, without the resulting reversal of asymmetry. A simple puncturing with a fine needle also has no effect. But greater injury accompanied by an outflow of blood always starts the rudimentary organ developing.

(6) The functional operculum has no regenerative capacity, while the rudimentary one still has. The injured operculum is thrown off sooner or later from the body, and a new start repeats from the beginning the original development. By accelerating this regenerative development of the old functional organ, or properly controlling the growth of the rudimentary organ on the opposite side, a symmetrical animal with two large opercula can easily be derived. On the other hand, if both rudiments antagonistically check each other's development, a symmetrical animal with two small rudimentary opercula is produced.

(7) Since, however, either the right or the left or even both rudiments can be made to develop into a functional organ, the inhibitory influence must act at first on both alike, unless a threshold value is assumed. In the present species of Polychæte it is as a rule the right-handed one that grows more quickly than the other.

(8) With regard to the nature of the asymmetry in Hydroides it seems to be quite different from that in the male Gelasimus in which the asymmetry of the chelæ is said to be derived from the symmetrical condition relatively late in development, and the relation, once attained, becomes fixed.

(9) In *Hydroides norvegica* at least, the opercula show a tendency to right-handed growth from the beginning of their development, but this condition of asymmetry is very unstable and is easily reversible by an external influence even in the adult state, i.e. there is no critical stage at which it is irreversibly determined.

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The Effect of Cyanides on the Gill Colour of Fish.

By

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INTRODUCTION.

IN the course of an investigation into the causes of death of migrating salmon and sea trout smolts in the estuary of the River Tees, it was found, by chemical methods, that the main toxic constituent of the Estuary waters was cyanide, and that this was almost entirely responsible for the mortality.* During the survey attempts were made to determine the nature of the toxic substances concerned from the appearance of dead or dying smolts picked up in the Estuary.

In the spring of 1930 some thousands of dead smolts found on the estuary banks were examined, the fish being opened, and the macroscopic appearance of the organs noted. Their condition varied so widely, partly owing to the fact that the smolts could not always be collected immediately after their death, that no evidence of the nature of the lethal factor was obtained.

It was observed that, in cases where fish were poisoned in the Laboratory by exposure to solutions of cyanides, the gills became considerably brighter in colour than those of normal fish. This brightening is due to the arterial condition of the blood caused by the inhibition by cyanide of the action of the oxidase responsible for the transference of oxygen from the blood to the tissues. The change in colour in the gills of yearling rainbow trout (*Salmo irideus* Gibb.) brought about by cyanide poisoning was measured quantitatively by matching the gill colour of normal and dying fish against a graded colour chart. The method of preparation and calibration of this chart are described on page 675. The chart consisted of a series of eight colours ranging from bright red (Colour No. 2) to dark crimson (Colour No. 16): intermediate colours could be judged, giving a series of fifteen shades in all.

EXPERIMENTAL.

The principal conditions which may adversely affect fish-life in the Tees Estuary are the presence of cyanides (which are of preponderating importance), sewage, "tar acids" and possibly naphthalene, and a

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* Southgate, B. A., Pentelow, F. T. K., and Bassindale, R. *Biochem. J.*, XXVI, No. 2, pp. 273–284, 1932.

deficiency of dissolved oxygen. Experiments were carried out in which the changes in the gill colour of rainbow trout, and later of sea trout smolts (*Salmo trutta* L.), brought about by these factors were observed.

TABLE I.

THE CHANGE OF GILL COLOUR OF RAINBOW TROUT IN A SOLUTION OF KCN EQUIVALENT TO 0·017 GM. (CN) PER 100 LITRES.

	Colour No. 5	6	7	8	9	10	Average Gill Colour No.
No. of fish before poisoning				2	11	3	9
No. of fish after poisoning*	3	6	7				6
No. of fish on recovery			3	7	4	1	8
No. of fish 1 hr. after recovery		2	4	5	3	1	8

* 1 died.

TABLE II.

CHANGE OF GILL COLOUR OF FISH DURING POISONING. AN INCREASE IN THE GILL COLOUR NO. INDICATES A DARKENING OF COLOUR.

Experimental solution.	Rainbow Trout. Average Gill Colours. No. of fish used.	Before poisoning (1).	After poisoning (2).	Difference (2) minus (1).	Sea Trout Smolts. Average Gill Colours. No. of fish used.	Before poisoning (1).	After poisoning (2).	Difference (2) minus (1).
KCN.								
0·017 gm. (CN) per 100 litres	16	9	6	−3				
0·020 gm. (CN) per 100 litres					4	10	8	−2
1·00 gm. (CN) per 100 litres	13	9½	6½	−3				
p-Cresol.								
0·7 gm. per 100 litres	13	8	11½	+3½				
0·8 gm. per 100 litres					3	10	13½	+3½
1·0 gm. per 100 litres	13	7	10	+3				
Coke oven effluent containing 0·094% tar acids and no cyanide.								
1% solution containing 0·94 gm. tar acids per 100 litres	14	9	12½	+3½				
Naphthalene.								
¼-saturated solution	8	10½	13½	+3				
Fresh crude sewage.								
50%	25	8½	8½	0				
Oxygen deficiency	4	10	14	+4				

In a typical experiment, the gill colours of about twelve normal fish were determined, after which they were exposed to an experimental solution. When at least half the fish had turned over on their side, they were removed, their gill colours were again observed, and they were allowed to recover in fresh water, further observations being made during the period of recovery. The results of a typical experiment are shown in Table I.

The whole of the results obtained are summarised in Table II.

Only in the case of cyanide was there any brightening of the gill colour, a marked darkening occurring during the other two types of poisoning most likely to be met with in the Estuary, that is by oxygen deficiency or by "tar acids" (represented in one of the series of experiments by p-cresol).

Since cyanides, which cause a brightening of gill colour, and tar acids, which cause a darkening, are both constituents of certain industrial effluents, and are found together in the waters of the Estuary of the Tees, some experiments were carried out to determine whether the brightening of the one was neutralised by the darkening due to the other (Table III).

TABLE III.

Change in Gill Colour of Fish in Mixtures of Poisons. An Increase in the Gill Colour No. Indicates a Darkening of Gill Colour.

	Rainbow Trout. Average Gill Colours.				Sea Trout. Average Gill Colours.			
Experimental solution.	No. of fish used.	Before poisoning (1).	After poisoning (2).	Difference (2) minus (1).	No. of fish used.	Before poisoning (1).	After poisoning (2).	Difference (2) minus (1).
(1) *KCN.* 0·015 gm. (CN) per 100 litres *p-Cresol.* 0·3 gm. p-cresol per 100 litres					3	12	8½	−3½
(2) *KCN.* 0·024 gm. (CN) per 100 litres *p-Cresol.* 0·43 gm. p-cresol per 100 litres	12	8½	7½	−1	3	11	8	−3
(3) *Coke oven effluent.* 2% solution Solution contains 0·014 gm. (CN) per 100 litres 0·013 gm. Tar Acids per 100 litres.	14	9	7½	−1½				

In the Tees Estuary the concentration of (CN) found by analysis does not usually exceed 0·02 gm. per 100 litres and that of tar acids 0·05 gm. per 100 litres. Even when the concentration of tar acid is twenty times that of (CN), as in Experiment 1 of Table III, the brightening due to the cyanide is well marked. In Experiment 2, the concentrations of p-cresol and KCN used were of equal toxicity to rainbow trout. The industrial wastes discharged into the Tees Estuary consist mainly of two types of coke oven effluent. The change in gill colour brought about by one type, which owes its toxicity to tar acids, is recorded in Table II, and that due to the other type, the main toxic constituent of which is cyanide, is recorded in Table III. In neither of these cases did any other substance interfere with the characteristic gill colour change of the main toxic constituent. The data for sea trout smolts are not so complete as those for rainbow trout owing to the difficulty of keeping the smolts, but since the reaction of the two species to the solutions in which they were tested is similar, it is reasonable to suppose that it would also be similar for other substances.

THE GILL COLOUR OF SALMON AND SEA TROUT SMOLTS FOUND DYING IN THE TEES ESTUARY.

During the annual seaward migration of smolts in 1931, numbers of smolts of both sea trout and salmon (*Salmo salar* L.) were picked up in a dying condition in the Estuary, and their gill colours were compared with the colours of the standard chart. Only fish which were obviously alive and which were taken from the water were used. Some smolts were allowed to recover in freshwater tanks, after which the gill colours of the normal fish were recorded. The results obtained are given in Table IV.

TABLE IV.

THE GILL COLOUR OF SALMON AND SEA TROUT SMOLTS DYING IN THE TEES ESTUARY.

	Salmon smolts.		Sea Trout smolts.	
	Normal.	Dying.	Normal.	Dying.
No. of smolts from which gill colour records were taken	40	66	76	131
Average gill colour	12·5	8·5	11·7	7·1

The gill colour of the dying fish was, in both cases, brighter than that of the normal fish, the average difference being 4·0 units in the case of salmon and 4·6 in the case of sea trout smolts. These results indicated that the smolts were dying from cyanide poisoning, a conclusion which was borne out by chemical observations.

The Gill Colour Scale.

Eight colours were prepared by mixing three solutions of coloured inks (Winsor and Newton's Mandarin Waterproof) in various proportions. Details of the colour mixtures used are given below :—

Solution A. Scarlet ink, 3 vols. Distilled water, 1 vol.
Solution B. Ultramarine ink, 1·7 vols. Vermilion, 20 vols. Scarlet, 20 vols.
Solution C. Ultramarine ink, 3 vols. Brown, 2 vols. Distilled water, 4 vols.

TABLE V.

Colour No.	Solution A. vols.	Solution B. vols.	Solution C. vols.
2	8	1	0
4	6	3	0
6	4	5	0
8	3	6	½
10	1	8	2
12	0	9	4
14	0	9	6
16	0	9	9

Strips of Whatman's No. 1 filter paper were soaked in these solutions, excess ink being immediately removed with blotting-paper. The colours referred to in Table V are those of the rough side of the filter paper. An analysis of the colours of the standard chart, made with a Lovibond Tintometer, modified for use with reflected light, is given in Table VI.

TABLE VI.

Gill Colour Scale No.	Lovibond Tintometer Units. Red.	Yellow.	Blue.
2	15·8	1·5	0
4	15·3	1·5	0
6	14·2	1·9	0
8	12·8	1·9	0·3
10	11·0	2·5	1·3
12	9·5	2·5	2·6
14	8·9	2·8	3·4
16	6·0	2·8	4·0

SUMMARY.

1. The changes brought about in the colour of the gills of rainbow trout and sea trout smolts by various poisons are described.

2. Cyanide causes a marked brightening, whilst phenolic substances, dissolved oxygen deficiency and naphthalene bring about a darkening of the gill colour. Fresh, untreated sewage has no effect.

3. The gill colour of smolts dying in the Tees Estuary was brighter than normal, indicating cyanide poisoning. This conclusion was confirmed by chemical methods.

The work described in this paper was carried out as part of the programme of the Water Pollution Research Board of the Department of Scientific and Industrial Research and is published by permission of the Department. We are indebted to Mr. N. Strafford, of the British Dyestuffs Corporation, Ltd., for calibration of the standard colour chart by the Lovibond Tintometer.

Chemical Constituents of Biological Importance in the English Channel, November, 1930, to January, 1932. Part I. Phosphate, silicate, nitrate, nitrite, ammonia.

By

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Assistant Chemist at the Plymouth Laboratory.

With 15 Figures in the Text.

CONTENTS.

I. INTRODUCTION.

In studying the fertility of the sea and its suitability for the production of the microscopic plant life which forms the ultimate foodstuff of other life in the sea, it is desirable to accumulate an unbroken series of data on the inorganic nutrient salts over a period of years. Both phosphate and nitrate are essential for growth and reproduction of phytoplankton and, when possible, data for the two are desirable since each may bring out factors not shown by the other. The actual quantity determined represents at any one time a balance between salt abstracted by living organisms and that regenerated by the decay of dead material, and the balance may be struck differently for the two salts at different times of year. Regeneration of phosphate is apparently a simple liberation from proteid material, whereas the nitrogen has to be returned through a multi-stage cycle, so that regeneration of nitrate is felt later than that of phosphate.

Much work remains to be done on minor constituents of sea-water other than phosphate and nitrate before we can arrive at a satisfactory picture of the changes taking place. Further, it is not enough to investigate such substances singly on isolated occasions since the essential interrelations may then be missed. For this reason simultaneous analyses have also been made for silicate, nitrite, ammonia, oxygen, hydrogen ion concentration, and excess base. Temperature and salinity data are also available.

Attention has been concentrated on the International Hydrographic Station, E1, 22 miles S. 37° W. from Plymouth, which is far enough from land to be but slightly affected by land drainage. Apart from the tidal flow of water up and down Channel there is, so far as can at present be seen, a small residual current, but generally speaking the character of the water remains fairly constant. Any marked change due to an influx of ocean water as in the autumn of 1921 (Harvey, 1923), or of fresh water from the land as in July, 1931 (this paper), is commonly indicated by unusual temperatures or salinities.

Station L4, 8 miles S. 37° W. from Plymouth, has been worked for surface and bottom samples in order to obtain comparative information on the effect of proximity to shore and of land drainage. Ammonia and nitrite have been determined at all the L series of stations which stretch from Plymouth Sound to E1 in order to determine their behaviour in inshore water. The results obtained are presented graphically. Photographic copies of the numerical data are available at the Plymouth Laboratory.

The positions of the Stations are as follows :—

		Miles from Laboratory.
L1	Mallard Buoy under Laboratory, Plymouth Sound	$\frac{1}{4}$
L2	West end of Plymouth Breakwater	2
L3	On course S. 37° W. from Plymouth	5
L4	,, ,, ,, ,,	8
L5	,, ,, ,, ,, (Eddystone)	12
L6	,, ,, ,, ,,	17
E1	,, ,, ,, ,,	22
Midway Stn.	,, ,, ,, ,,	39
E2	,, ,, ,, ,, (Mid-Channel)	56
E3	,, ,, ,, ,, (7 miles N.W. of Ushant)	107

Cruises were made on :—

1930, August 12th (P_2O_5 and SiO_2 only), September 10th (P_2O_5), October 9th (E2 ; P_2O_5 and SiO_2), November 11th (complete series), December 4th.

1931, January 13th, February 4th (E3), February 19th, March 23rd, April 7th, April 22nd (E2), May 18th, July 10th, August 26th (E2), September 8th, September 25th, October 20th, November 30th (E2), December 31st.

1932, January 28th.

Complete series of analyses were not made on February 4th and December 31st, 1931, and January 28th, 1932.

II. TEMPERATURE, SALINITY, AND WEATHER CONDITIONS.

The distribution of salinity and temperature will be discussed by Harvey in his work on the Hydrography of the English Channel. Numerical records are available in the Rapport Atlantique, 1930 and 1931 (Rapp. et procès-verbaux du Cons. Int.). The most interesting occurrence was the low salinity of the water above the thermocline at E1 in July due to river water spreading over the surface following the heavy rainfall over South-Western England during June and early July, 1931. The temperature changes are shown as profiles in Fig. 1 (E1) and Fig. 7 (E2).

Sunshine much in excess of normal occurred in January, 1931. February was also a sunny month (Table I). This favoured the early onset of diatom growth on the north side of the Channel. From March right on to the end of the " summer ", sunshine was much below normal. This sunless weather was accompanied by overcast skies and windy and rainy weather gener-

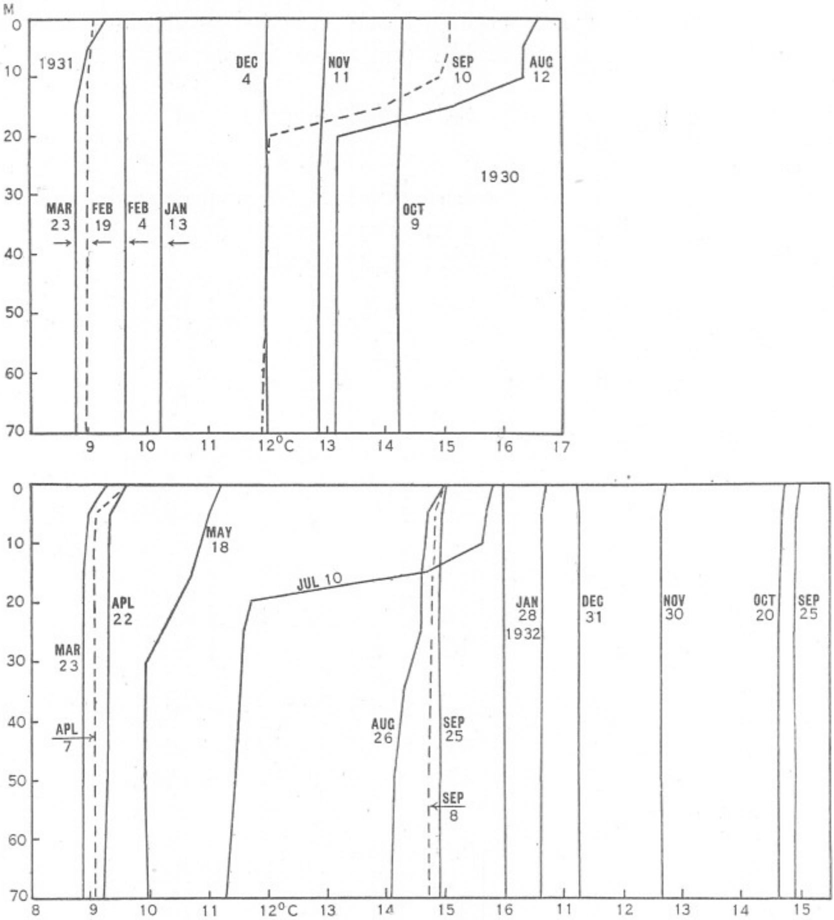

FIG. 1.—Temperature profiles at Station E1, August, 1930, to January, 1932. The first panel shows the records from August 12th, 1930, until the winter minimum on March 23rd, 1931. The second illustrates the period from March 23rd until the maximum on September 25th, 1931. The last shows the autumn isothermal cooling. The late formation and early breakdown of the thermocline in 1931 are clearly shown.

ally. In consequence the thermocline was late in forming, allowing the bottom stores of nutrient salts to be very completely used up, and as a result of the severe August gales it broke up exceptionally early. On August 26th it was found to have been completely obliterated at E1, there being an almost uniform gradient from surface to bottom. At E2 a thermocline was found, but at the unusual depth of 45 metres. After the 26th, the gales returned and completed the work of vertical mixing by September 8th.

TABLE I.

Hours of Sunshine Per Day.

1931.	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.
Normal*	1·67	2·63	3·96	5·53	6·58	6·79	6·39	6·04	4·96
Plymouth (Mt. Batten)	2·77	2·61	3·66	4·05	5·28	5·82	4·77	5·08	4·22
Channel Islands†	1·92	2·54	3·87	5·58	6·56	8·86	7·63	5·38	4·84?

III. PHOSPHATE.

Atkins (1923 (1) *et seq.*) has published data for phosphate from March, 1923, to April, 1929, with a gap from March to October, 1927. The series, resumed by the writer in August, 1930, was continued to January, 1932, when work was stopped owing to illness.

Station E1.

The seasonal variation in phosphate with depth at E1 is shown in Figs. 2 and 8. During August, 1930, there was little change in the water column, but onwards from the end of September steady regeneration led to the winter maximum being reached in December when surface and bottom were markedly richer than the middle layers. A similar distribution is apparent in the profiles for January and February and favours the view that regeneration was largely a surface and bottom phenomenon. Such a distribution in winter was found in the earlier work of Atkins (1930 (2), Table 3 and p. 850, § 4), which thus receives yet further confirmation.

Surface depletion was very marked during late December, 1930, or early January, 1931. This was not entirely due to mixing in of the enriched surface layer since the whole column showed a similar though somewhat smaller decrease which seems to point to a small mid-winter outburst. Similar mid-winter outbursts occurred in mid-December, 1925, and late December, 1926 (Atkins, 1930, p. 829). During the latter half of January the phosphate-content of the surface increased slightly although the column as a whole showed a slight decrease during a period of the year

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* Normal number of hours of bright sunshine per day for South Wales and South Western England. The normals for the Channel Islands are considerably greater.

† Mean of Jersey and Guernsey.

when the maximum is often reached. Since the average daily sunshine for January was 2·75 hours—50% above the normal for the month and the highest recorded since phosphate determinations were begun here in

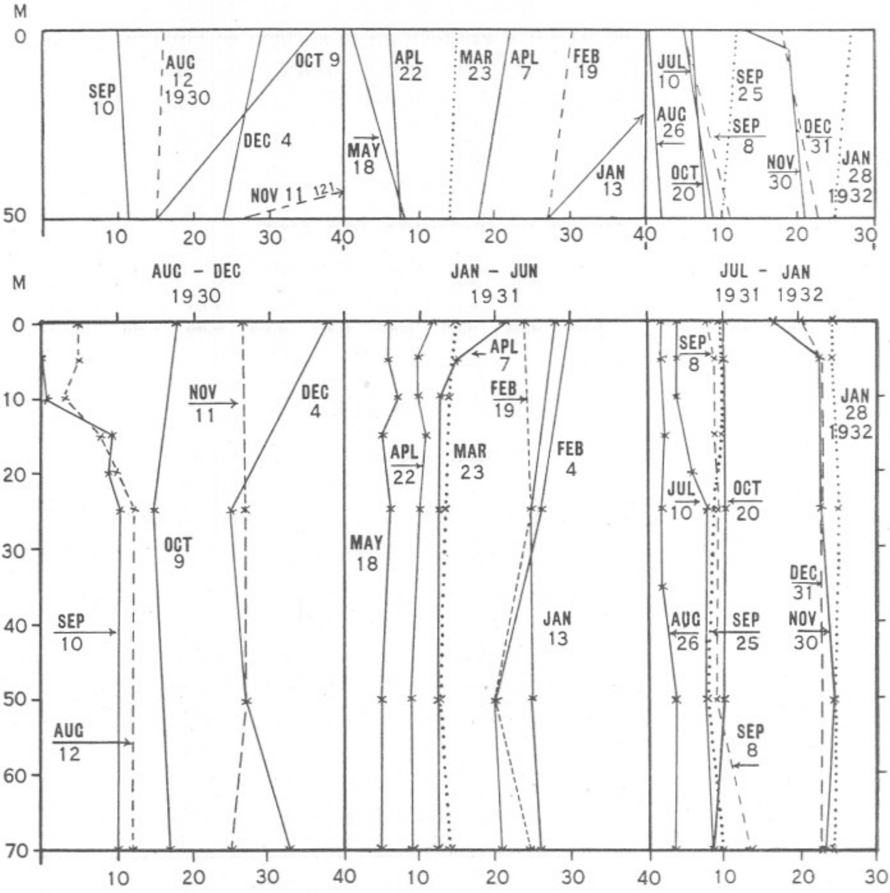

Fig. 2.—Profiles showing variation of phosphate with depth August, 1930, to January, 1932, as mg. P_2O_5 per m³. The depth scale for L4 (top) is half that for E1 (bottom). The spring consumption by diatoms commencing in March, 1931, and regeneration in the autumn of 1930 and late autumn of 1931 are clearly shown. The static condition existing between September 8th and October 20th, 1931, is noteworthy, as is also the very low value shown by the whole column on August 26th, 1931 (cf. August 12th, 1930, which is " normal "), (cf. Atkins, 1930, Fig. 1, p. 824).

1923—it seems possible that regeneration was being just balanced by an incipient diatom outbreak. The excessive sunshine in January was no doubt associated with the prevalent north sector winds (cf. Atkins, 1928) and probably started an outburst which went on with increasing impetus during February.

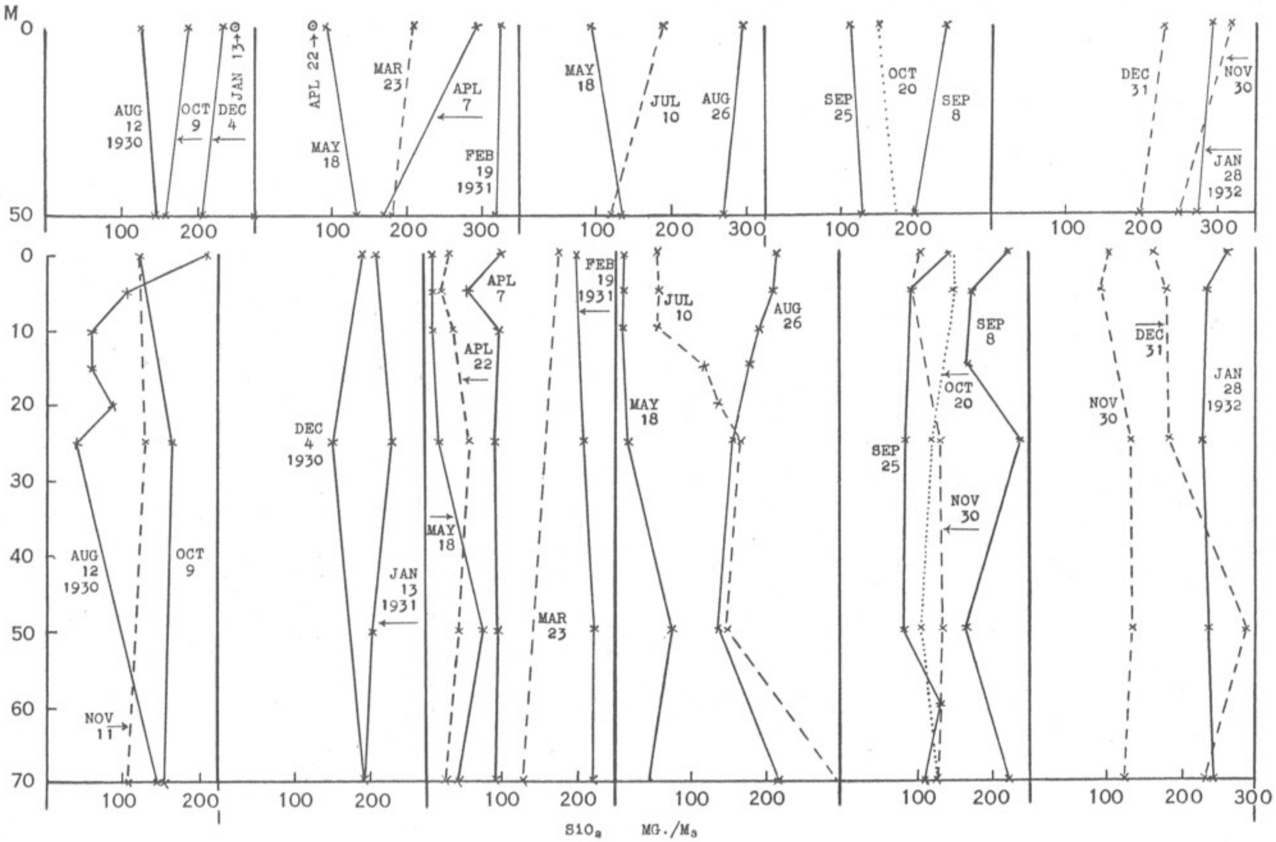

FIG. 3.—Profiles showing variation of silicate with depth at Stations L4 and E1, August, 1930, to January, 1932. The depth scale for L4 (top) is half that for E1 (bottom). The spring consumption by diatoms is clearly shown in the third E1 panel. The high values and the distribution during July to September appeared to indicate regeneration of silicate in the bottom 20 metres, followed by consumption of silicate throughout the column. All values are correct according to King and Lucas' standard.

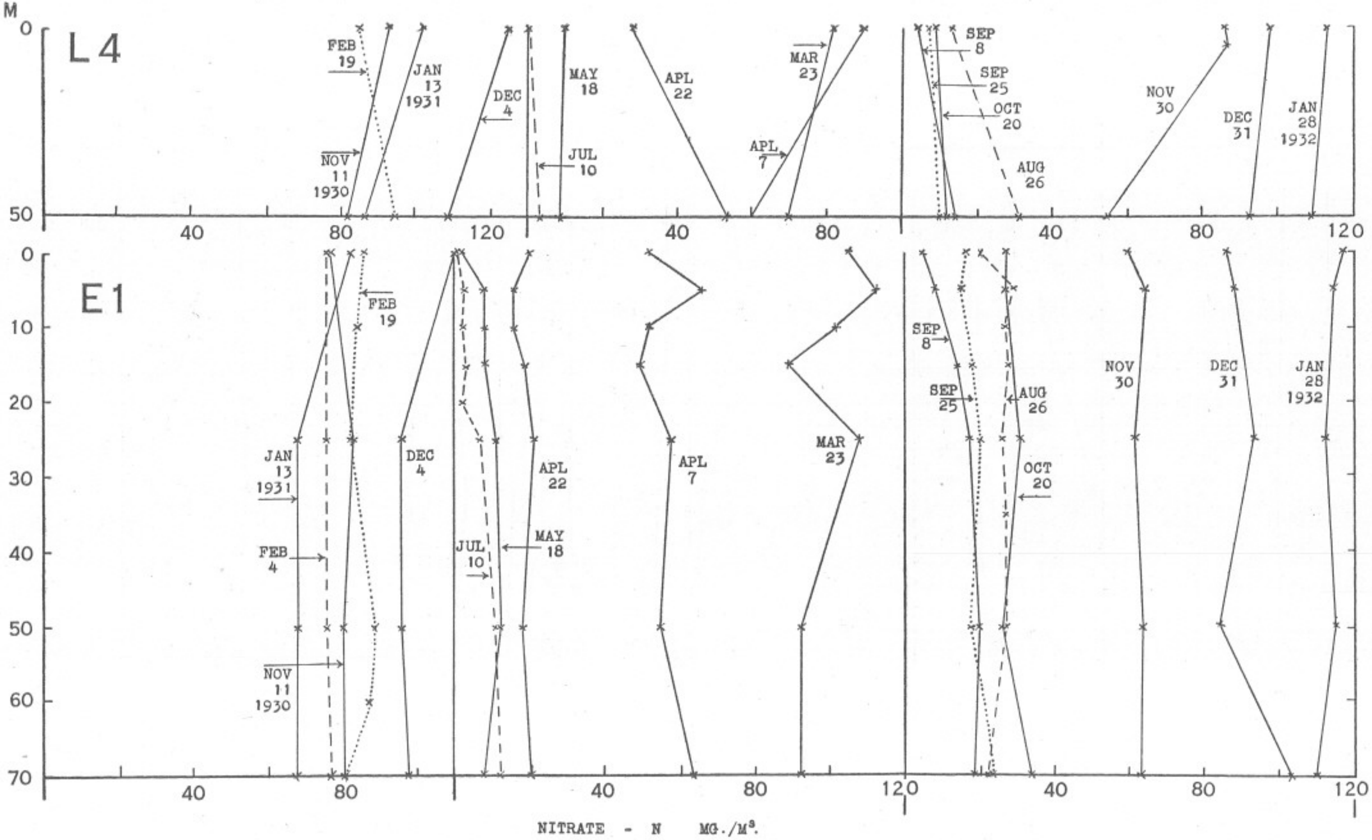

Fig. 4.—Profiles showing variation in nitrate (including nitrite) with depth November, 1930–January, 1932. The depth scale for L4 (top) is half that for E1 (bottom). Two maxima were reached on December 4th, 1930, and March 23rd, 1931. The results for December 31st, 1931, and January 28th, 1932, are approximate only.

The main outburst, however, started about the beginning of March and went on, probably, until the end of May. For the fifteen days from March 7th to March 22nd the average daily sunshine was 5·25 hours and accompanied marked decrease in phosphate. A "static" condition existed between March 23rd and April 7th, when only one hour of sunshine per day was recorded. On March 23rd Dr. Lebour reported large quantities of the diatom, *Biddulphia sinensis*, in the tow-nettings taken at E1, and still greater quantities in the medium tow-net catch on April 7th. On this date plankton generally was

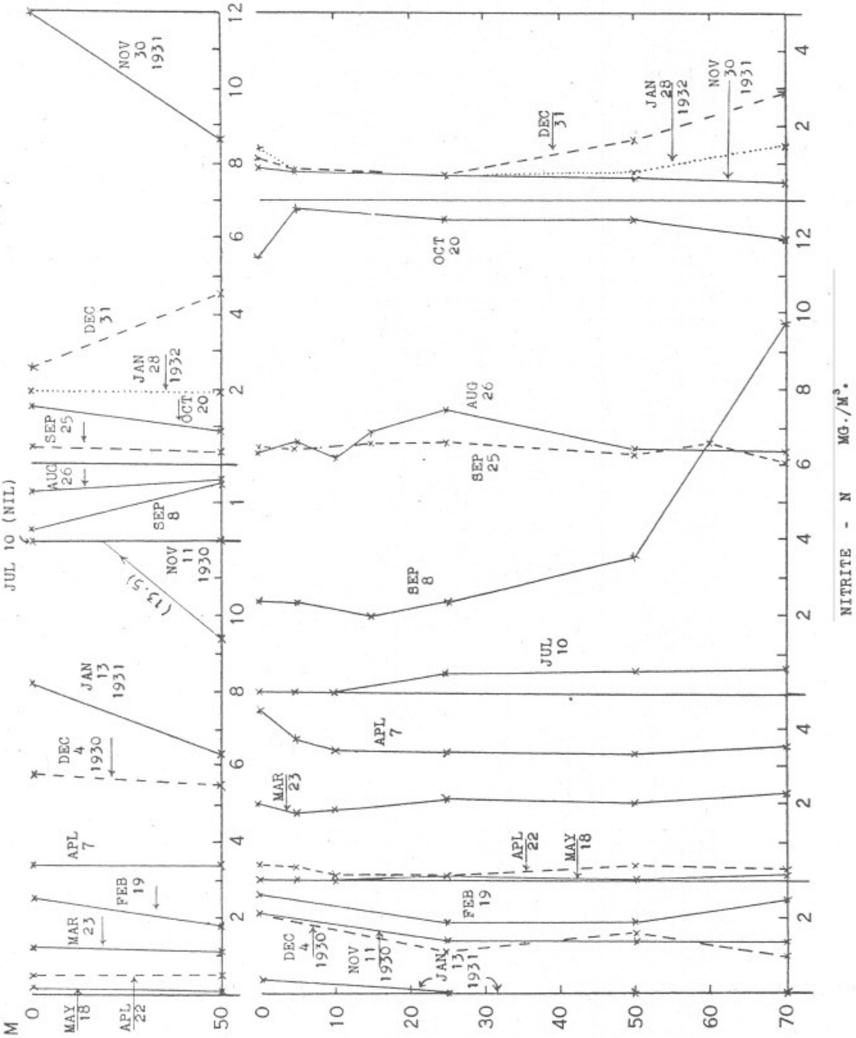

FIG. 5.—Depth profiles for nitrite, November, 1930–January, 1932. The depth scale for L4 (top) is half that for E1 (bottom).

very abundant in the E1 tow-nettings and Phæocystis in particular was very conspicuous in the sample bottles from 10 and 15 metres. With the return of bright sunshine further rapid depletion of the whole column took place. Thus 1931 was definitely an early year, and taking the changes in the water column as a whole it may be said to be the earliest year yet recorded at Plymouth, no doubt due to the exceptional amount of sunshine falling in January. It was also remarkable for the efficiency with which the bottom store was brought to the illuminated regions and utilised. The nearest approach to the conditions of 1931 was found in the spring of 1924, but even in that year the bottom phosphate was usually 5 mg. P_2O_5 per cubic metre greater. The spring of 1931 is further notable for the absence of any period when regeneration definitely exceeded consumption.

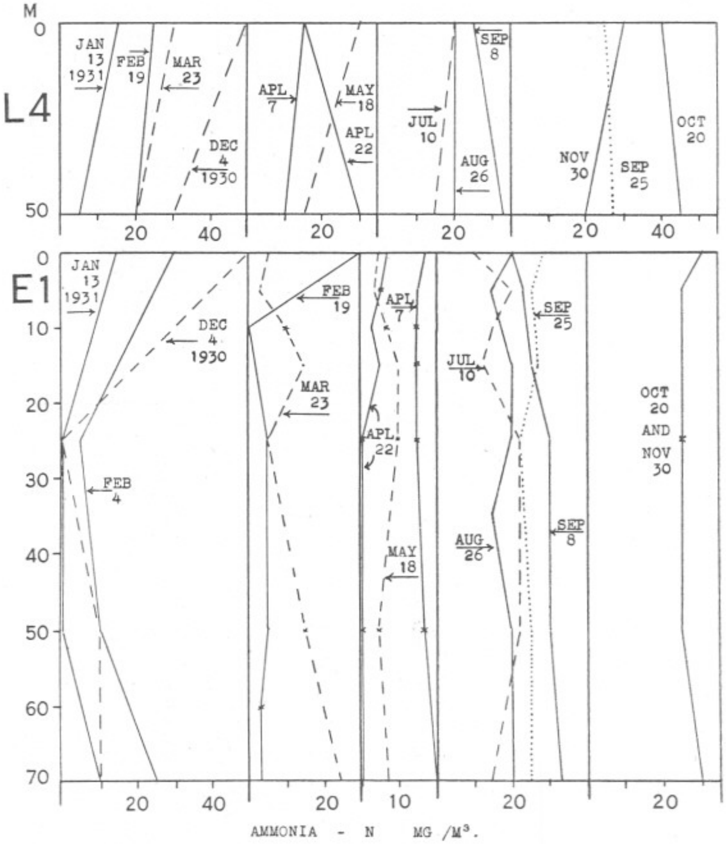

Fig. 6.—Depth profiles for ammonia, November, 1930–November, 1931. The depth scale for L4 is half that for E1.

The summer period of 1931 which may be said to begin at the end of

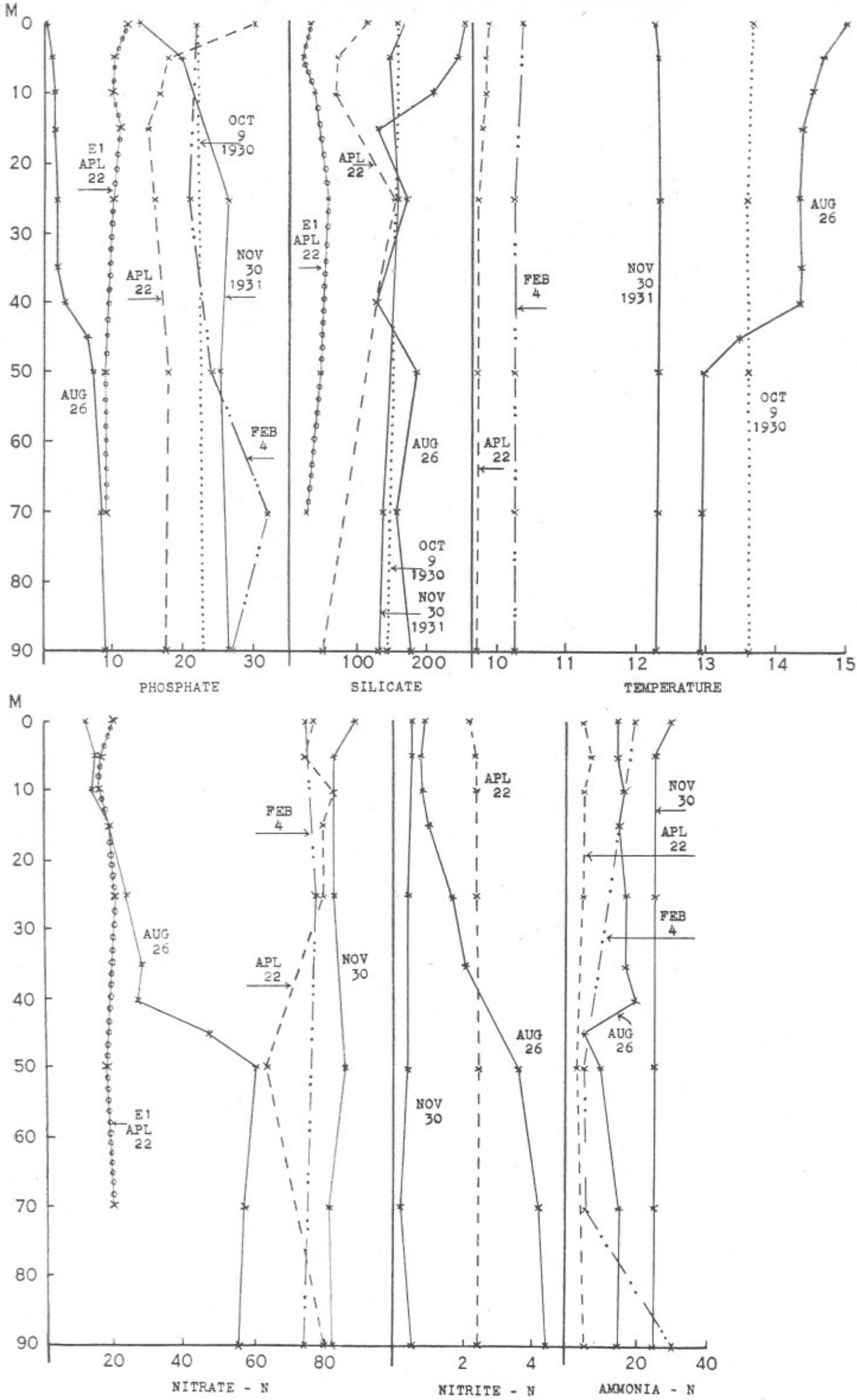

FIG. 7.—Station E2. Phosphate (P_2O_5, mg./m³.); Silicate (SiO_2, mg./m³.); Temperature (°C.); Nitrate, Nitrite, and Ammonia (each mg. Nitrogen/m³.). Curves for E1 (circles) are included for P_2O_5, SiO_2, and nitrate for April 22nd for comparison with those for E2 on this date (pecked).

May was also unique and was undoubtedly affected by the stormy and sunless weather experienced. The spring diatom outbreak had left the bottom waters very poor in phosphate (5 mg. on May 18th). A little regeneration took place at the bottom during June, but this was in no way comparable with that which has taken place in some previous years, e.g. 1925. The surface content did not fall below 5 mg. P_2O_5 per cubic metre until some time in August, but on August 26th the whole column was almost entirely depleted with 2 mg. in the surface and 4 mg. in the bottom layers. This depletion was probably facilitated by the very early breakdown of the thermocline in August (Fig. 1) due to the exceptionally stormy weather of mid-August. The average phosphate-content of the water column*—2·8 mg. P_2O_5—was by far the lowest yet recorded. The next lowest figures are 5·1 mg. on August 31st, 1925, 6·9 mg. on July 8th, 1925, and 7·7 mg. on July 10th, 1923. Indeed, average contents less than 9 mg. are comparatively rare, and are usually isolated occurrences in the course of a summer. In 1931, by contrast, the average value remained continuously at or below 7 mg. from May 18th to August 26th. But it should be pointed out that owing to a combination of circumstances, principally bad weather, only one cruise—that on July 10th—was made between these dates, so that a period of regeneration might have occurred and not have been observed. In 1925 there were periods of regeneration when the phosphate content of the bottom water rose to over 20 mg. P_2O_5 per cubic metre. In none of the five former summers for which data are available has any comparable period of low bottom phosphate been found. Comparison with Atkins' papers is informative.

Between August 26th and September 8th, marked regeneration set in, particularly at the bottom, and the average content of the water column increased from 2·8 mg. to 10·6 mg. P_2O_5 per cubic metre. In September and October a state of balance existed, consumption of phosphate just equalling regeneration. Absence of sunlight does not explain the regeneration found in the first week of September as Table II shows (compare also Section V).

TABLE II.

RELATION BETWEEN CHANGES IN PHOSPHATE AND NITRATE AND SUNSHINE IN THE EARLY AUTUMN OF 1931.

1931.	Average Daily Sunshine in Hours.	Change in Average Phosphate Content per 7 days, mg. P_2O_5 per m^3.	Change in Average Content of Nitrate (and Nitrite) per 7 days, mg. N per m^3.
26/8 to 7/9	4·6	+4·2	−5·3
8/9 to 24/9	4·9	−0·6	+1·1
25/9 to 19/10	2·7	+0·25	+3·0

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* For the method of arriving at this quantity see p. 722.

There must therefore have been some other factor, probably nitrate, hindering the re-utilisation of the phosphate as it was returned into circulation. As soon, however, as sufficient nitrate became available, phosphate was utilised as quickly as it was re-formed, and a state of balance was set up which persisted even with the reduced October sunshine (see p. 701). During November consumption became unimportant and regeneration proceeded apace. During the next two months covering the period in which the maximum is usually reached, there was little further change in the water column, although the surface content of phosphate increased, becoming uniform with the rest of the column. If the figures for January 28th, 1932 (24·7 mg.), really represent the winter maximum, this is the lowest on record. The previous lowest was on December 4th, 1930, with 29·1 mg. of P_2O_5 per cubic metre.

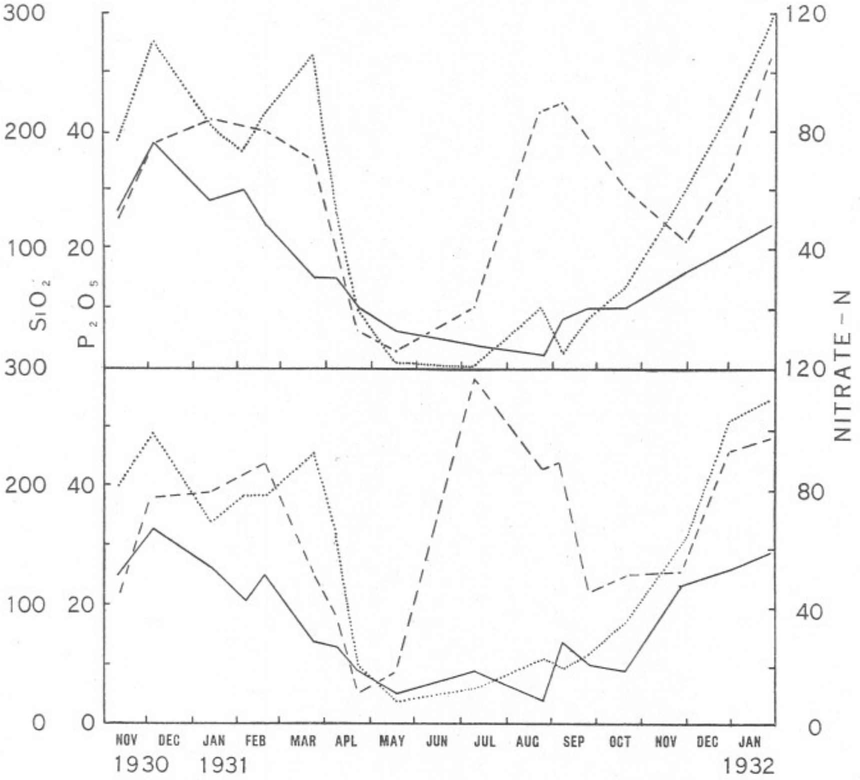

FIG. 8.—Phosphate, silicate and nitrate at Station E1 during 1931. Phosphate as P_2O_5 (full line), silicate as SiO_2 (pecked), nitrate (which includes nitrite) as N (dotted), in each case mg. per m³. The lower portion depicts the changes at the bottom, the upper those at the surface, except that for phosphate, 5 m. values are plotted for April 7th and 22nd.

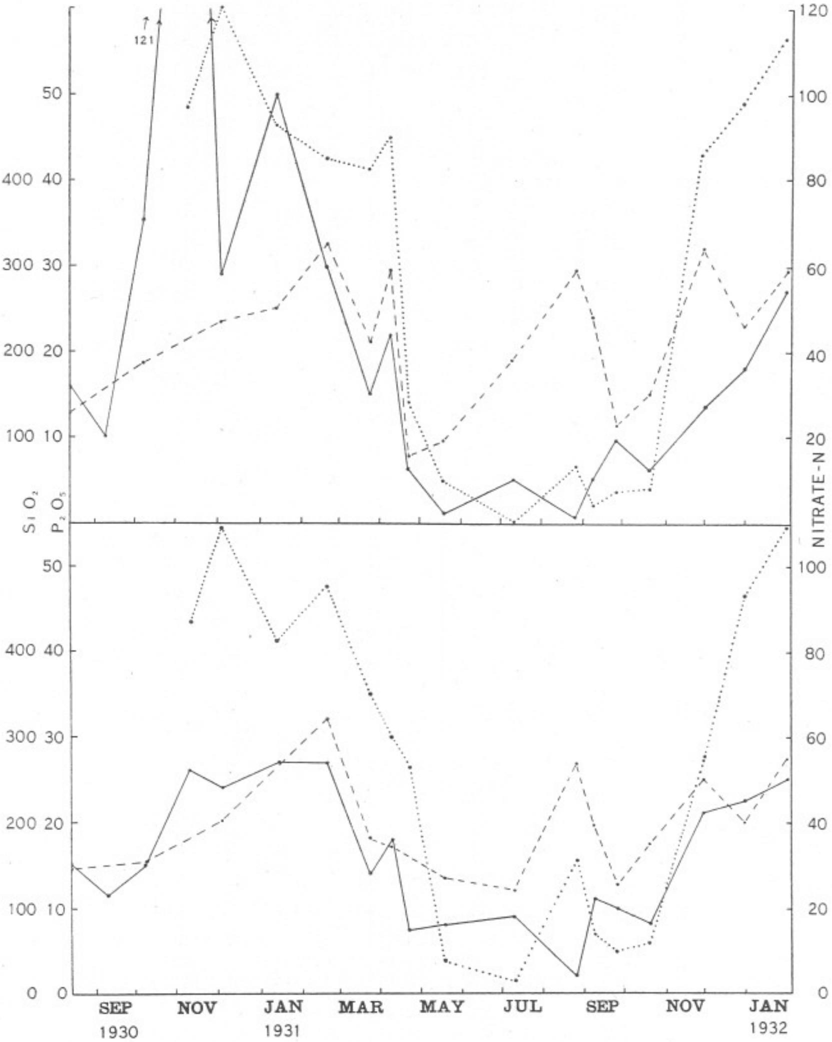

FIG. 9.—Seasonal variation at surface (upper half) and bottom (lower half) at Station L4 of phosphate (full line), silicate (pecked line), and nitrate (+nitrite) (dotted line), as P_2O_5, SiO_2, and N, mg./m³. August 12th, 1930, to January 28th, 1932.

STATION L4.

The picture of events here presents some points of difference from that at E1 (cf. Figs. 2 and 9). On November 11th, 1930, and January 13th, 1931, figures were obtained for the surface greatly in excess of those for the bottom and probably represent decomposition of organic matter occurring on the surface, an effect not extending to any depth. The bottom figures are therefore a more reliable guide to the true general behaviour of phosphate and point to the winter maximum being around 27 mg. P_2O_5 per cubic metre in January, compared with 29 mg. at E1 in early December. The start of the spring outburst cannot be fixed with certainty, but probably occurred in the middle of February. Marked regeneration took place in the sunless period between March 23rd and April 7th when E1 showed little change. From then on until October events followed much the same course as at E1, but subsequently regeneration at L4 proceeded rather the more slowly until the end of the year.

STATIONS E2 AND E3.

In October, 1930, when regeneration at the L surface stations was proceeding rapidly, conditions at E2 (Fig. 7) were found to be very similar to those at E1 with 22 mg. P_2O_5 per cubic metre throughout the water column. The lower surface figures at E2 on the cruise of February 4th–5th, 1931, indicated that an outburst of diatom growth had begun there, but not at E3 which showed uniform distribution throughout the column. On April 22nd an interesting picture is presented. At L4 and E1 the phosphate was distributed uniformly from 5 metres to the bottom with 10 mg. P_2O_5 per cubic metre or less. At E2, however, about 17 mg. remained distributed throughout the column and very marked regeneration was proceeding at the surface. Nitrate was also much greater at E2 than at E1 (p. 703), so that the early start in consumption by diatoms made at E2 in February was evidently not maintained.

Visual examination of the sample bottles drawn on April 22nd and the rate of clearing in the horizontal comparison tubes during the course of the silicate analyses, also showed plankton to be much less abundant at E2 than at E1.

The distinctive behaviour of Stations E1 and E2 is a regular event (cf. Table III). In five out of six years the outbreak has started earlier at E2 than at E1. Yet in April–May phosphate was usually decidedly higher at E2 than at E1 and in no year was it definitely lower. Nitrate is not a reliable guide to crop production in the early spring, but the data available for 1926 and 1931 show the same relation. The outbreak therefore tends to start earlier at E2 in mid-Channel than at E1, but for some reason the early start is not maintained. By the middle of May E1 has shown much the greater production.

TABLE III.

PHOSPHATE CONTENT OF THE WATER FOUND ON THE FIRST AND SECOND CRUISES OF THE YEAR TO E2 AND E3.

Average values over six years (1924, '25, '26, '27, '28, '31). The year 1929 is excluded since the cruises were six weeks or more earlier than in the other years. Actual number of observations in parenthesis. P_2O_5, mg./m^3.

	Period Feb. 4–March 11.					Period April 22–May 21.				
	E1	Midway	E2	Midway	E3	E1	Midway	E2	Midway	E3
0 metres	29(6)	22(4)	16(6)	12(3)	20(6)	6(5)	7(3)	15(5)	17(3)	17(4)
5 metres	31(4)	–	25(4)	–	28(3)	9(5)	–	14(4)	–	25(2)
Average content of water column	30(6)	–	26(6)	–	26(6)	12(5)	–	17(5)	–	25(4)

The surface at E2 in late August, 1931, was almost completely exhausted of phosphate although greater reserves remained in the bottom waters at E2 than at E1. This no doubt is connected with the persistence of a thermocline at E2 after the August gales, although very deep at 45 metres (cf. Figs. 1 and 7). On November 30th regeneration had reached a similar stage to that at E1. Surface values at L4, E1, Midway Station, and E2 were all 5·5–7 mg. P_2O_5/m^3 lower than those at 5 metres, pointing to a very late continuance of diatom growth in the surface layers right across the Channel.

DIFFERENTIAL METHOD OF REPRESENTING INTENSITY OF PLANKTON OUTBURSTS IN TERMS OF CHANGE IN PHOSPHATE.

Atkins (1930, Figs. 4, 5, and 6) suggested graphical methods of following the intensity of utilisation of phosphate. By the method of Fig. 10, both total consumption and rate of consumption between two cruises may be shown simultaneously as explained in the legend. The effect of the time elapsing between the cruises may thus be eliminated. In 1928 frequent cruises were made in connection with the work on illumination, whereas in 1926 they were about a month apart. The spring of 1926 was characterised by periods of excessive consumption with intervening periods of marked regeneration, quite different from the spring of 1931 when regeneration never exceeded consumption. The period of phosphate regeneration in the first week of September, 1931, is shown to have been very marked.

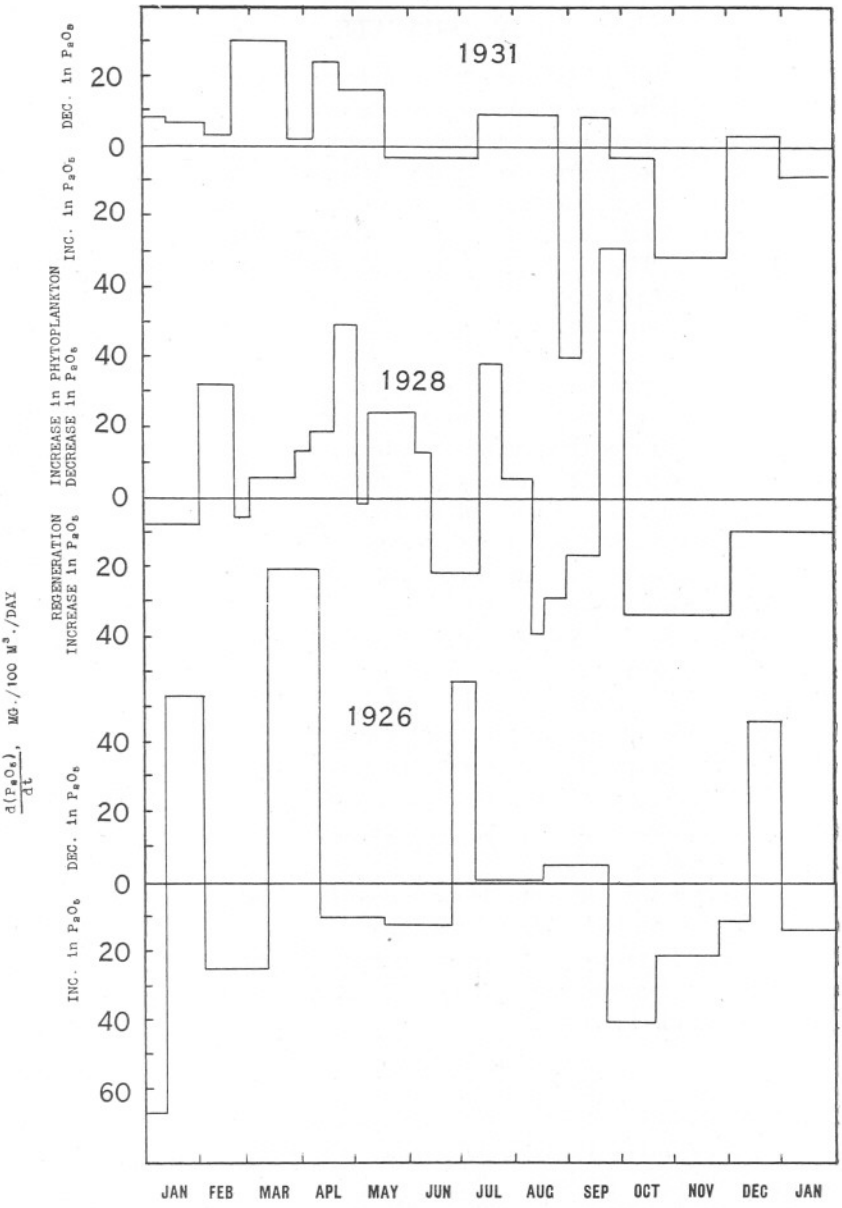

FIG. 10.—The production of phytoplankton at Station E1 may be deduced from the areas above the zero line. These really show the decrease in average phosphate concentration of the water column between two successive cruises. The height of the horizontal boundary line is a measure of the intensity of the outburst and is measured as $\frac{\delta(P_2O_5)}{\delta t}$, i.e. rate of change of phosphate in mg. P_2O_5 per 100 cubic metres per day. From data by Atkins (1928, 1930; see 1930, Figs. 4 and 5), and this paper.

IV. SILICATE.

Silicate was first determined in the waters of the English Channel by the present colorimetric method by Atkins (1923 (2)). Since then determinations have been made at intervals although less frequently and in less detail than for phosphate (Atkins, 1926 (1), 1928, 1930 (2)). In the more recent years surface and bottom determinations only were made. Since August, 1930, depth series as for phosphate have been taken in waxed bottles. The results (Figs. 3 and 8) show striking differences from the behaviour of phosphate.

Station E1.

Fig. 3 shows that the vertical distribution of silicate is by no means uniform even when the water column is isothermal. The progressive decrease during the spring period of diatom growth is also clearly shown, but between March 23rd and April 7th, when sunlight and phosphate both point to a halt in plankton production, silicate (and also nitrate) showed a very marked fall, the reason for which is not very clear. On May 18th the surface contained less than 15 mg. SiO_2 per cubic metre, the minimum which can be detected by the method with any degree of certainty (see Section XI, Methods), so that the water was quite likely completely exhausted of silicate.

The very different state of affairs on July 10th is also shown by Fig. 3. The remarkable dilution of the surface with fresh water was probably related to the heavy rainfall over South-West England during June and early July, leading to river water flowing out over the surface. Part of this seems to have mixed across the thermocline diluting somewhat the bottom water also.

Solution of bottom siliceous deposits seems to give the only reasonable explanation of the high values for silicate at the bottom, although land drainage may have been a contributory factor. The greater content of silicate in the bottom waters persisted in lessening degree until mid-October as Table IV shows.

TABLE IV.

Illustrating the much greater Silicate Content of Bottom Water compared with that of Water 20 metres off the Bottom in Summer and Autumn.

		1930	1931				
		12/8	10/7	26/8	8/9	25/9	20/10
SiO_2 mg./m^3	50 m.	38*	148	136	165	83	105
	Bottom (68–71 m.)	145	291	213	221	111	125
	Difference	+107	+143	+77	+56	+28	+20
ΔT, °C.		−0·07*	−0·18	−0·05	−0·02	0·00	0·00

* 25 m. No analysis for 50 m.

There is no direct correlation with the dilution with river water which was primarily a surface phenomenon.

The difference in temperature in the bottom 20 metres on July 10th was only 0·18°, and after August 26th it practically vanished, so that there was little hindrance to vertical mixing. A similar distribution was also present in August, 1930. Such great differences in the silicate content of the water within 20 metres from the bottom seem very strong evidence in favour of purely chemical re-solution of the siliceous bottom deposits. It is, of course, possible that this re-solution goes on the whole year round, but that it is most evident in late summer owing to the stability of the layers under the thermocline.

Regarding the water column as a whole, silicate is seen to suffer a very unequal distribution in the late summer and early autumn (Fig. 3). Although the average values for the column on July 10th, August 26th, and September 8th (154, 168, 154 mg. SiO_2/m^3. respectively) were similar, the distributions were quite different. A great increase took place at the surface during August, 1931, and at 25 metres between August 26th and September 8th. These increases are much greater than the experimental error and indicate that re-solution of silicate may occur not only at the bottom but on a lesser scale at the surface and in the middle layers as well. More detailed data are required to establish the point, but these erratic results are probably correlated with the position in the water of the dying and dead diatoms. If these are especially copious around, say, 25 metres, re-solution will occur most rapidly there and a silicate maximum will be observed.

The large decrease in the middle of September, during a period when the balance of consumption and regeneration of phosphate and nitrate remained undisturbed and sunlight was adequate for photosynthesis, suggests an autumn diatom outburst. The distinctive behaviour of the three salts is a little mystifying. An explanation probably requires detailed knowledge of the plankton species propagating at the time. Nevertheless, a steady state for phosphate in the autumn may indicate a diatom outbreak as clearly as a definite decrease in the spring, owing to the more extensive simultaneous regeneration of phosphate.

THE SUMMER MAXIMUM FOR SILICATE.
MECHANISM OF RE-SOLUTION OF SILICA IN THE SEA.

The seasonal change in the silicate content of surface water at E1 in different years is illustrated by Fig. 11. In each spring there has been a rapid decrease associated with the diatom outburst. The great differences in the winter maximum discussed below are clearly shown, whilst in 1924, 1925, 1930, and 1931 marked regeneration of both surface and bottom

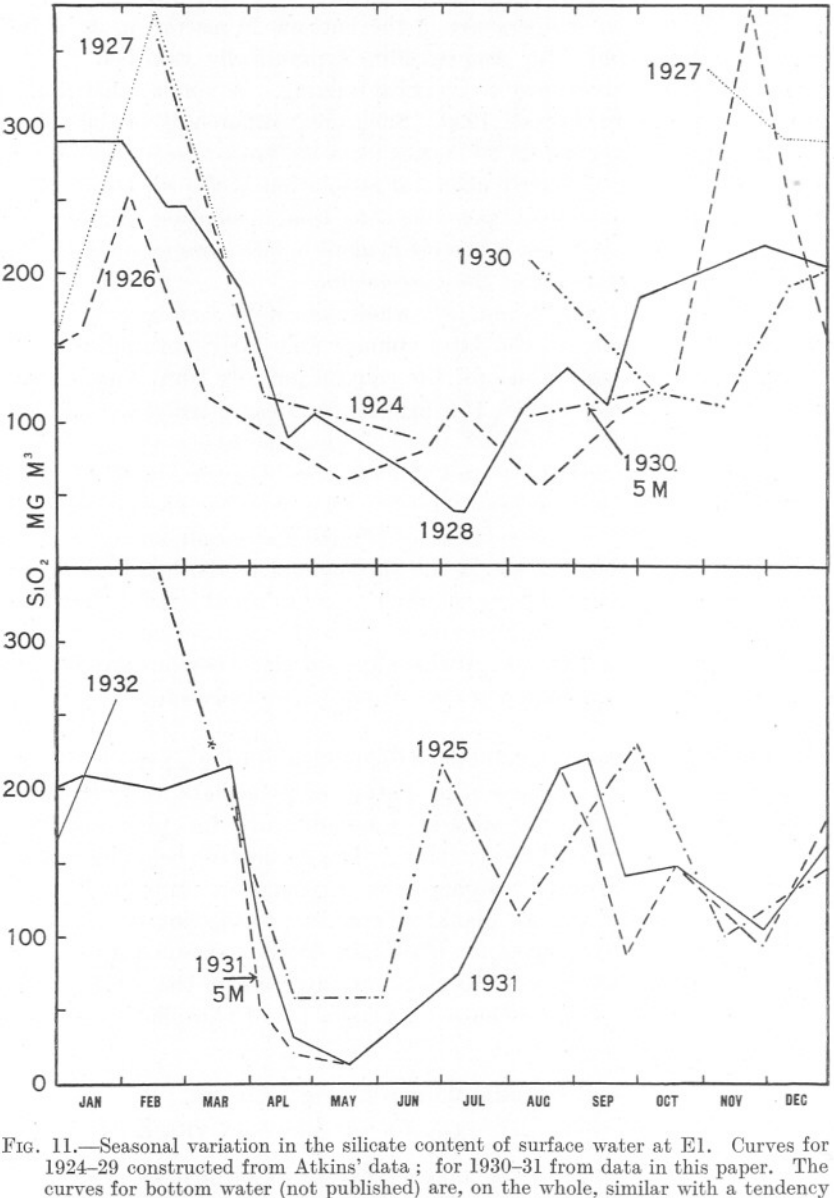

FIG. 11.—Seasonal variation in the silicate content of surface water at E1. Curves for 1924–29 constructed from Atkins' data; for 1930–31 from data in this paper. The curves for bottom water (not published) are, on the whole, similar with a tendency for greater concentration of silicate in spring and early summer than at the surface. SiO_2, mg./m^3.

silicate occurred during the summer months. In 1925, the silicate maxima were not simultaneous with the phosphate maxima observed at the bottom. However, the values for August 12th, 1930, show that comparatively high surface and bottom values may be found when the middle layers are nearly exhausted of silicate. In this case the surface and bottom values taken alone would give a quite erroneous picture of the state of the water column as a whole. Nevertheless, it can scarcely be fortuitous that very definite increases at surface and bottom have been observed in three out of the four summers for which data are available.

At first sight it seems scarcely possible that the siliceous tests of diatoms dying off after the spring outburst can be so quickly re-dissolved; yet this is the conclusion to which the above discussion leads. But inasmuch as the siliceous skeletons offer an enormously greater surface to the solvent action of the somewhat alkaline sea-water (pH about 8·2) than, say, an equal weight of sand grains, such rapid re-solution seems a sound explanation of the results. Of this Miss Stanbury's observations (1931) in this Laboratory of the rapidity with which skeletons of dead diatoms may disappear in culture experiments afford confirmation.

Such dissolution of silica may occur not only from dead diatom skeletons. Bachrach and Lefèvre (1928, 1929) have observed the complete loss of the external skeletons from a number of living plants reared on sterilised media even in the presence of silicate. The pH of their media is not discussed. The genera most susceptible to this peculiar behaviour are Nitzschia, Navicula, Fragilaria, and Licmophora. The removal of the siliceous skeleton may require weeks or only a few days. The defective diatoms appear to live and reproduce quite normally although after a few generations they become so shapeless that identification is impossible. This work points to the rapidity with which the skeletons may dissolve in sea-water and to the possible adaptability to shortage of silicate of diatoms leading an otherwise normal life in the sea. The pH of the water is almost certainly of prime importance.

There is another way in which the occurrence of diatoms appears to be a function of the amount of silicate present. For the spring of 1932 no chemical data are available, but by analogy with other years silicate may be assumed to be plentiful in March and scarce in May. On March 21st Dr. Lebour found *Coscinodiscus granii* and *Bacillaria paradoxa* (normally an inshore form) to be predominant constituents of the tow-nettings taken beyond the Eddystone, whereas on May 26th, Cerataulina were very plentiful. There is thus a direct relation with the available silicate, since the March forms are thick walled and the May diatom thin walled, requiring relatively little silica.

According to N. Peters (1932), in the South Atlantic short-horned, robust Ceratia were found in waters rich in phosphate and plankton and long-horned, fragile forms in phosphate poor water. The phenomena may be a direct function of phosphate or possibly of another nutrient salt (such as (?) silicate).

During September, with isothermal conditions prevailing, there seems to have been extensive utilisation of silicate by an autumn outburst of diatoms, although phosphate remained steady and nitrate showed only a small fall. Subsequently, until January 28th, when observations ceased, there was a steady rise to about 235 mg. SiO_2 throughout the water column.

INCREASE IN SILICATE WITH PROXIMITY TO SHORE.

Determinations of silicate at the L Stations, other than L4, were not continued after October, 1930. The results obtained till then lend support to Atkins' conclusion (1926) that silicate due to land drainage increases rapidly on approaching a river mouth (Table V).

TABLE V.

EFFECT OF RIVER WATER ON SILICATE CONTENT OF THE SEA. HIGH SILICATE IN THE SOUND IS ASSOCIATED WITH THE LOW SALINITY AT LOW TIDE.

1930	State of Tide at L1. Hours Ebb.	L1.	L2.	L3.	L4.	L5.	L6.	E1.	E2.
			Silicate SiO_2 mg./m^3						
August 12	1	290	132	176	127	155	148	210*	—
October 9	5	600	520	—	188	185	167	122	159
				Salinity ‰					
August 12	1	33·95	34·47	34·90	34·91	35·01	35·03	35·00	—
October 9	5	29·25	32·50	33·83	35·00	35·03	35·14	35·21	35·26

STATION L4.

The results at L4 (surface and bottom, 50 m., only), although decidedly higher than at E1 due to proximity to land, showed on the whole a similar trend (Figs. 3 and 9). The maximum for the winter (325 mg. SiO_2 per cubic metre) was reached on February 19th, here also at least a month later than for phosphate. The subsequent fall was followed by a rise contrasting with the simultaneous drop at E1, but concordant with the small increase in phosphate and with the deficient sunlight. The minimum for the year was found on April 22nd (77 mg. at the surface, no analysis of bottom water), so that the more inshore water was never so completely depleted as was the surface at E1 on May 18th. Here also summer

* 5 metres, 104 mg.; 10 metres, 59 mg.

regeneration took place leading to a summer maximum for the whole water column of 280 mg. per cubic metre on August 26th. From then until November 30th the results are concordant with those at E1. A secondary minimum was found at L4 only on December 31st, 1931.

STATION E2.

On October 9th, 1930, and November 30, 1931, conditions were not very different from those at E1 (Fig. 7). On April 22nd, the E2 depth series was very erratic, and on the whole considerably greater than that for E1, thus agreeing with the higher phosphate and nitrate figures which showed the spring outburst of diatoms to have been much delayed at E2. The very different values found for 25 m. and 89 m. (bottom)—154 mg. and 50 mg. SiO_2 per cubic metre—are worthy of remark although no water was available from waxed bottles for confirmatory analyses. For the interesting distribution of August 26th, the remarks made for E1 apply.

Thus the work at L4 and E2 fits in very well with the conclusions deduced for E1—that a summer silicate maximum may be expected about August and that the winter silicate maximum occurs about a month later than that for phosphate.

V. NITRATE.

Harvey's work (1926, 1928 (1)) in the English Channel had established that nitrate fluctuations followed a seasonal course similar to that of phosphate (cf. Brandt and Raben (Brandt, 1916, 1927)). Maxima were recorded in two winters and minima around midsummer approaching complete exhaustion with intervening rapid depletion during the height of the spring outburst of diatom growth. The present work in every way supports the accuracy of this picture for the Channel.

STATION E1.

Observations began on November 11th, 1930. Examination of the depth profiles (Fig. 4 and also Fig. 13) shows that a first maximum was reached on December 4, but onwards until mid-January a decrease correlating with the decrease in phosphate was found. Regeneration of nitrate then proceeded apace, and a second maximum was reached on March 23rd when phosphate and silicate were well on the downward slope (cf. Fig. 8).

That plankton was present in quantity on this date was further indicated since the nitrate analyses were possible only after the samples had first been centrifuged (Cooper, 1932). *Thus nitrate continued to increase when the diatom outburst was well under way.*

The course of events between March 23rd and April 7th is not at all clear. Sunshine averaged only one hour per day, phosphate remained almost unchanged, yet the average content of nitrate-nitrogen throughout the water column fell by 40 mg. per cubic metre (41% fall) and silicate by 60 mg. SiO_2 (40% fall). There was little change in salinity or temperature so that no important water movements can have occurred.

A progressive fall in nitrate followed. On May 18th and July 10th, the surface was almost entirely depleted. There followed a gain in the whole water column in the rest of July and August of 14 mg. of nitrate-nitrogen per cubic metre after allowing for nitrite which also increased. During the same period phosphate decreased in the whole column to give a record low figure for phosphate.

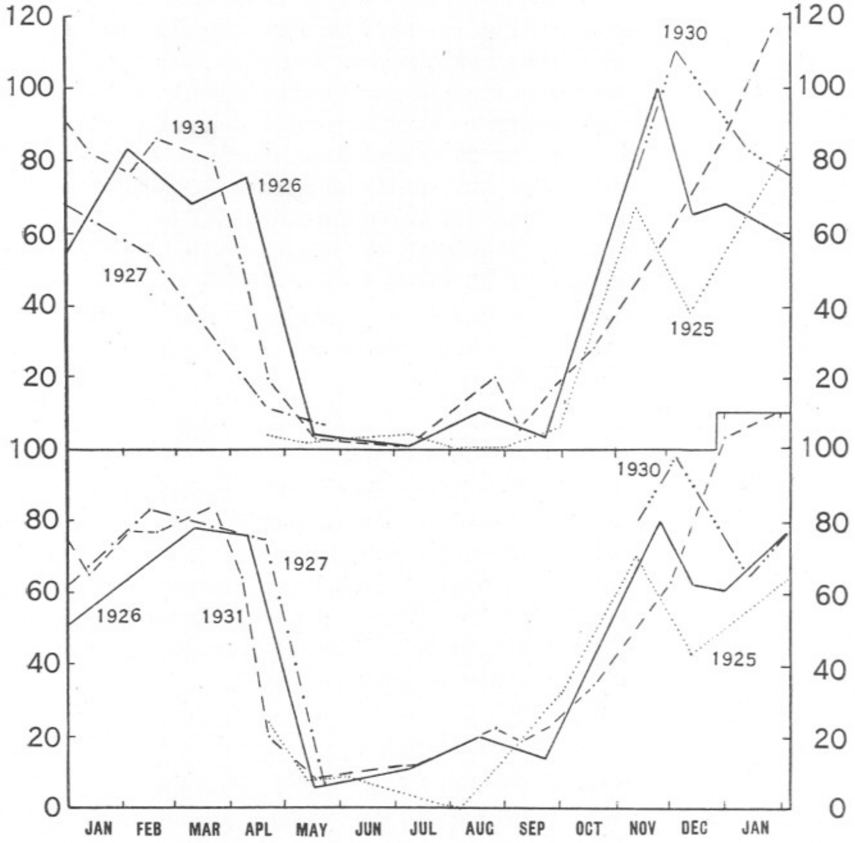

FIG. 12.—Comparison of the seasonal changes of nitrate (including nitrite) in 1930–31 with former years (Harvey). Upper portion, surface; lower portion, bottom; mg. N/m³.

In the first week in September, nitrate and phosphate again moved in opposite directions. The fall in nitrate fits in with that in mean silicate

(14 mg. SiO_2) and the plentiful sunlight (4·6 hours per day). It would seem that excessive regeneration of phosphate was masking its consumption by phytoplankton and that nitrate, since its return follows a long chain of chemical or bacterial reactions, is a more certain criterion of autumnal outbursts particularly if allowance can be made for nitrite (cf. Table II).

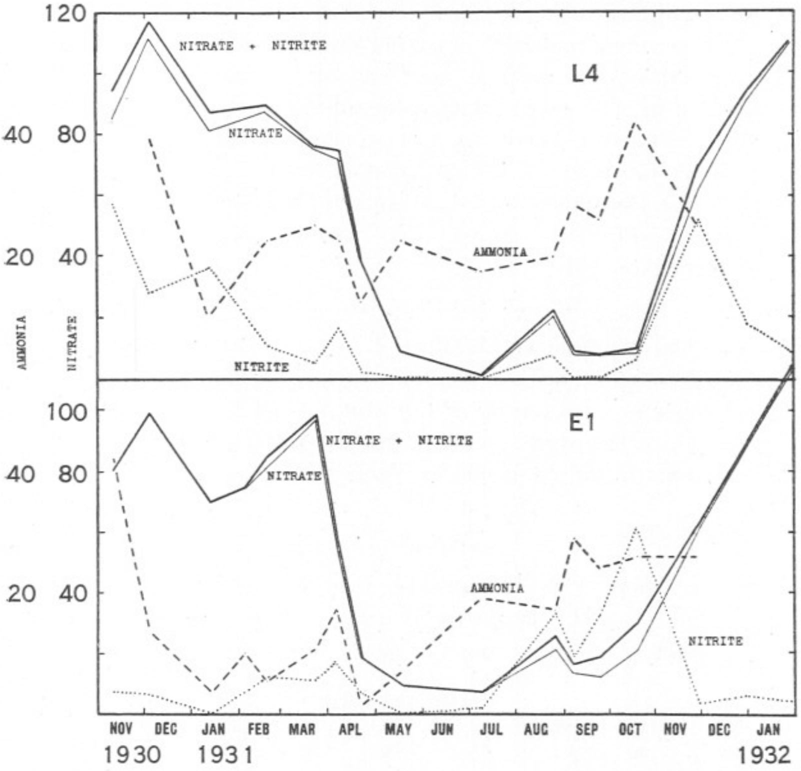

FIG. 13.—Seasonal changes in nitrogen compounds at Stations L4 and E1 between November, 1930, and January, 1932. Averages for the whole water column, all in mg. nitrogen/m³. The scales for nitrate, ammonia, and nitrite are in the ratio 1 : 2 : 5. The thin line representing nitrate shows the effect of subtracting nitrite (× factor 0·8., see Cooper, 1932) from the results obtained with the reduced strychnine reagent (thick line) which also determines nitrite.

As with phosphate, down-grade processes did not finally get the upper hand till about the end of October.

In Fig. 12 the seasonal changes in nitrate at E1, surface and bottom, are compared with the corresponding results for previous years (Harvey, 1926, 1928). The fall in nitrate in the spring of 1931 followed a very similar course to that in 1926, although probably it occurred about a fortnight earlier. Both in 1926, between April 10th and May 17th, and in

1931, between March 23rd and April 22nd, this fall in nitrate was very rapid and extended right to the bottom of the water column. Thus vertical circulation of the water must have brought the bottom store of nitrate rapidly into regions where it could be quickly utilised. The apparent utilisation of the available nitrate thus appears to be much more efficient than that of phosphate owing to the slower simultaneous regeneration of nitrate (see below).

In all three summers nitrate remained very low, but the rise in August, 1931, and subsequent drop is very similar to that in August, 1926. Regeneration in 1931 subsequently proceeded more slowly than in either of the former years ; nevertheless, at the end of January, 1932, the highest value—about 110 mg.—so far recorded at E1 was reached. Although the figures for December 31st and January 28th are only approximate, due to poor calibration curves, there can be no doubt that former maxima were exceeded.

Station L4.

The seasonal changes at L4 (Figs. 4, 9 and 13) were, on the whole, similar to those at E1 with a tendency towards higher values in winter. There was only one maximum at this station—on December 4th, 1930.

The changes in the average nitrate and phosphate contents of the water columns at L4 and E1 are shown by Table VI.

TABLE VI.

Average Content of Phosphate and Nitrate at L4 and E1 in Winter and Spring of 1930–31.

	11/11/30	4/12	13/1/31	4/2	19/2	23/3	7/4	22/4	18/5
					Nitrate, mg. N per m^3				
L4	95	118	87	—	90	76	75	40	9
E1	80·5	99	70	75	84	98·5	58	18·5	10
					Phosphate, mg. P_2O_5 per m^3				
L4	>26	26·5	ca 38	—	29	14·5	20	7	4·5
E1	24	29	26	24	23·5	13·8	13·5	9·8	5·5

There was thus no March nitrate maximum at L4 like that at E1. Further, whereas the main fall in phosphate began at the end of February or beginning of March, the related fall in nitrate was a month later at E1 and five weeks later at L4. Although at both stations in May the average nitrate content of the water column was about the same, the surface was less depleted at L4, the shallower and more inshore station, with 10 mg. of nitrate-nitrogen per cubic metre as against 2 mg. at E1. In the middle of July, by contrast, bottom nitrate was considerably higher at E1. Indeed, at L4 the very low bottom value of 3 mg. was then found.

From then until end of the year events at the two stations followed a very similar course—a marked increase in August followed by consumption in September, little change in October and very rapid regeneration in November. The highest values were reached on January 28th, 1932, when observations ceased.

STATIONS E2 AND E3.

On February 4th–5th the distribution at E1, E2, and E3 was almost identical within the limits of experimental error with 76 mg. nitrate-nitrogen throughout each water column. Signs of an early surface outbreak of phytoplankton at E2 as shown by phosphate determinations (p. 691) were thus lacking. The cruise of April 22nd revealed a strikingly different condition at E1 and E2. Whereas in the intervening twelve weeks average nitrate at E1 had fallen to 18·5 mg. nitrogen per cubic metre, the position at E2 was unchanged with 74 mg. remaining right through the water column (cf. Fig. 7). The comparable changes for phosphate were from 24 down to 9·8 mg. at E1 and from 25 to 17 mg. at E2. Silicate in April also showed lower values at E1. Quite definitely, therefore, the diatom outburst up to the middle of April as inferred from chemical data was less intense in mid-Channel at E2 than at E1 (see p. 691).

VI. COMPARATIVE BEHAVIOUR OF NUTRIENT SALTS.

SEASONAL VARIATION IN DAILY CONSUMPTION AND REGENERATION OF NUTRIENT SALTS.

The differential method of representing change in mean phosphate outlined in Section III may be applied equally well to changes in mean silicate and nitrate (Fig. 14). For the six weeks preceding January 13th consumption of phosphate and nitrate was accompanied by slight regeneration of silicate. Right up to the middle of May consumption of phosphate exceeded regeneration and the general prevalence of growth processes in the sea during the whole period is supported by the silicate analyses and by various observations on the plankton (see Section III). Yet as late as March 23rd regeneration of nitrate was paramount. Nitrate must necessarily have been consumed in quantity during this period, but its re-formation as the last process in the long nitrogen regenerative cycle must have been so pronounced as to obscure its consumption. Thus, during the first three months of the year, nitrate data alone would have given an entirely erroneous picture.

Nevertheless the fortnight immediately following March 23rd showed an absolutely different state of affairs. Net mean consumption of phosphate was trivial and there was actually an increase in phosphate at

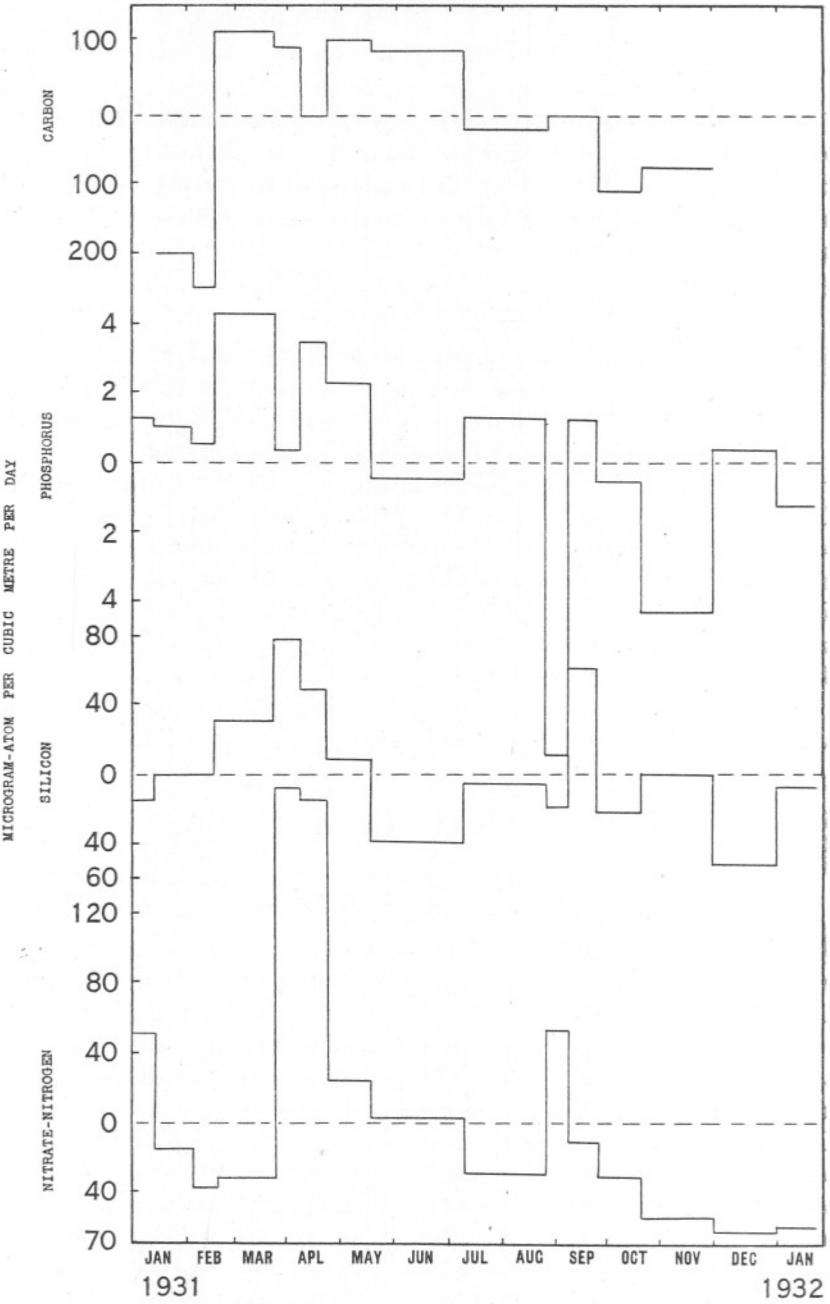

FIG. 14.—Daily consumption and regeneration of nutrient salts throughout the year. The area above or below the zero line represents total consumption or regeneration between successive cruises. The height of the horizontal represents rate of consumption or regeneration during the period, i.e. $\frac{\delta(\mathrm{Salt})}{\delta t}$, the unit of salt concentration being the microgram-atom (10^{-6} gram-atom) of P, Si, N, or C, and the unit of time being the day. The ratio of the scales is :—C : Si : N : P : : 1 : 2·5 : 2·5 : 50. Each diagram gives the atomic concentrations of P, Si, N, and C, or the molecular concentrations of H_3PO_4 (or $\frac{1}{2}$ P_2O_5), H_2SiO_3 (or SiO_2), HNO_3 (or N), and CO_2, or the ionic concentrations of PO_4''', SiO_3'', NO_3', and CO_3''. The diagrams show clearly the much greater growth requirements of N and Si than of P. The carbon diagram is discussed in Part II.

the surface, yet nitrate and silicate were used up at an enormous speed. Here phosphate seems to have been rather misleading. Subsequently until April 22nd all three salts were utilised in a fairly proportionate manner. All three show the spring outburst to be easing up by May 18th.

The early summer was a period of relative stagnation. The enormous increase in silicate at the bottom in June-August is not fully brought out owing to its peculiar distribution in the water. September provided some strange inconsistencies owing to the effect of "random" regeneration. Between August 26th and September 8th there was a short period of intense phosphate regeneration, yet nitrate showed a quite intense period of consumption. In the following fortnight the noteworthy feature was silicate consumption which went hand in hand with comparatively trivial net consumption of phosphate and with regeneration of nitrate. From October onwards the rate of return of nitrate grew steadily which seems very significant in light of its position at the end of the nitrogen return cycle and of its behaviour at the beginning of the year. Neither phosphate nor silicate showed any such regularity although downgrade processes definitely held the upper hand.

Comparison of the Magnitude and Date of Occurrence of the Winter Maxima for Phosphate, Silicate, and Nitrate.

The maximum values reached for each of the three salts varies considerably from year to year (Table VII).

TABLE VII.

Maximum values for SiO_2, P_2O_5, and Nitrate (as Nitrogen and including Nitrite) reached at Station E1 in different Winters with dates of Observation.

Each as mg. per m^3; average content of water column.

	SiO_2		P_2O_5		Nitrate—N	
	Max.	Date.	Max.	Date.	Max.	Date.
1923–24	288	15/2	37	2/1	–	–
1924–25	≧345	17/2	32	9/12	–	–
1925–26	250	3/2	40	12/1	71·5	10/4
1926–27	375	15/2	30	13/12	88	24/11
1927–28	350	4/11	34·7	31/1	–	–
1928–29	240	4/3	31	2/1	–	–
1930–31	210 (twice)	13/1 19/2	29·1	4/12	98·5 (twice)	4/12 23/3
Mean maximum	294	(7/2)	33·4	(27/12)	86	–
No. of winters investigated	7		7		3	

Why the silicate winter maximum should vary so much more from winter to winter than phosphate or nitrate is not at all clear. A large positive deviation for silicate may coincide with an equally large negative one for phosphate or *vice versa*. There is here manifestly a factor fraught with possibilities as to the suitability of the sea to particular planktonic species in any particular season. A season with high phosphate and low silicate maxima such as 1925–26 would seem to favour those species of plankton which require little silica.

The approximate date when the silicate winter maximum was reached in the English Channel is seen to be about a month later than for phosphate—February 7th compared with December 27th. The winter of 1931–32 cannot be included since observations do not extend beyond January 28th, when the highest values, viz. 235 mg. SiO_2, 24·7 mg. P_2O_5 and 115 mg. nitrate-nitrogen were found. These may have been exceeded subsequently.

In Table VIII the maxima found during the period, August, 1930, to January, 1932, for the five nutrient salts are given.

TABLE VIII.

MAXIMA FOR FIVE NUTRIENT SALTS AND TIME WHEN REACHED. IN EACH CASE MG./M^3.

	P_2O_5	SiO_2	NO_3'–N	NO_2'–N	NH_3–N
Period investigated	Aug. '30– Jan. '32.	Aug. '30– Jan. '32.	Nov. '30– Jan. '32.	Nov. '30– Jan. '32.	Nov. '30– Nov. '31.
Station					
L4	>30*	320	118	11·5	>40
	11/11/30 13/1/31	19/2/31	4/12/30	11/11/30	11/11/30 20/10/31
E1	29·1	210	115‡	12·4	40†
	4/12/30	13/1/31 19/2/31	28/1/32	20/10/31	11/11/31

The maxima for the winter of 1931–32 may not have been reached when observations ceased.

APPARENT EFFICIENCY OF UTILISATION OF PHOSPHATE AND NITRATE.

Examination of the available data for the English Channel has shown that bottom nitrate is liable to undergo much more severe and prolonged depletion during the summer than is bottom phosphate. This also applies to a lesser extent to the surface salts. The nitrate used up in the spring

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* High values at surface which cannot be used for calculating average content of the water column.

† This value may be slightly high. 30 mg. represents the upper limit which tended to be reached at seaward stations on other occasions.

‡ In 1930–31 maxima of 98·5 mg. were reached on 4/12/30 and 23/3/31.

outburst was not materially restored by regeneration in the following months owing to the long cycle of reactions required to break down nitrogen in dead organic matter to nitrate. The re-formation of inorganic phosphate being so much simpler enabled this salt to be made available for a second growth process much more quickly. These conclusions, it is true, apply more obviously to waters below the thermocline, but similar regeneration in the surface waters, if it does occur, is more likely to be obscured.

Once the spring outburst is complete, it would seem that nitrate is much more likely to prove a limiting factor hindering further growth than is phosphate and that a marked increase in phosphate at midsummer may not necessarily be followed by a second phytoplankton outbreak. Thus during this period of the year nitrate is likely to prove the more reliable guide to the subsequent economy of the sea.

VII. NITRITE.

Buch (1925, 1928) has made a detailed spectrographic study of the effect of temperature, time and salinity on colour development with the Griess-Ilosvay reagent. Orr (1926) found that in the Clyde Sea area in June, 1925, nitrite-nitrogen rarely exceeded 10 mg. per cubic metre, and was occasionally less than 1 mg. He discussed five different ways in which the nitrite content of sea-water might be changed. Atkins (1930 (1)) examined the fluctuations in nitrite in the English Channel between August, 1928, and March, 1929, and found as much as 38·9 mg. below the thermocline in August.

On the whole during 1931 nitrite was distributed uniformly throughout the water column (Figs. 5 and 13). At E1 minima were found in January, May, and July, and on the last two occasions the surface appeared to be completely exhausted. A combination of circumstances on the cruise of July 10th (see Methods, p. 722) favoured a very delicate series of analyses. At surface Stations L3 to L6 inclusive and at E1, surface, 5 and 10 metres, nitrite was shown definitely to be less than 0·02 mg. nitrogen per cubic metre or less than one part in 50,000,000,000 parts of sea-water. To the writer's knowledge this is the most complete exhaustion of a constituent of sea-water yet recorded and probably approaches the analytical limit that can be attained by purely chemical technique.

The small increase over the January null values which occurred in the spring may be attributed to oxidation of ammonia and a maximum was reached on April 7th. In the succeeding fortnight, when heavy inroads were made on the store of nitrate, nitrite suffered a marked fall which would agree with its utilisation as a source of nitrogen. During the height of the summer it remained very low. With the onset of late summer regeneration a marked increase set in, but no values comparable with the exceedingly high values found by Atkins in 1928 were determined.

The three profiles for August and September illustrate the desirability of making nitrite determinations at as close intervals as possible. If the profiles for August 26th and September 25th, showing similar vertical distributions, stood alone, they might be interpreted as showing a period of little change. Yet the intervening profile for September 8th shows a quite different, far from uniform distribution.

There is laboratory evidence (p. 712) that nitrite would not decrease by 4 mg. nitrogen per cubic metre at the surface in thirteen days unless some noteworthy influence were at work.

At Station L4 the conditions through the year were so different from those at E1 as to make it impossible to draw a general inference. In mid-winter 1930–31 and on November 30th, 1931, the nitrite content at L4 was several times that at E1. On January 13th, 1931, 7·2 mg. nitrogen per cubic metre was present in the water column at L4, whereas at E1 below 25 metres nitrite was not even detectable (i.e., less than 0·05 mg.). Yet in the early autumn of 1931 the distribution was quite reversed. Further, at this season the waters at L6 and E2 show only quite a rough relation with those at E1. This topic is further discussed below.

Owing to tidal and other water movements, precisely the same body of water cannot be sampled at a working station on every cruise. It is evident that distribution of nitrite is an exceptionally localised phenomenon in the English Channel and the state of affairs at one station may give not the slightest indication of what may be occurring only a few miles away.

Correlation between Nitrite Distribution and Hydrodynamic Conditions.

The effect of the thermocline on the distribution of nitrite may be seen by comparing Atkins' data (1930 (1)) for the late summer and autumn of 1928 with those for the corresponding period of 1931 (Table IV). In 1928 values in excess of 30 mg. nitrogen per cubic metre were found only beneath the thermocline and during its existence. After the breakdown of the thermocline at the end of September uniformity was soon approached.

In 1931, in July, the thermocline played no part since the entire water column was depleted. The temperature profile for August was in marked contrast to that of August, 1928. The stormy weather of mid-August, 1931, had destroyed the thermocline and although a temperature gradient still existed mixing of the waters must have been very considerable. As a result the high values of 1928 were not reproduced. The comparatively low results for 1931 and the uneven distribution for September 8th agree with the idea that nitrite as it comes into the upper layers may be directly assimilated by plants, and thus never become so high as when it is locked up beneath the thermocline.

The similar falling off in November in both years is striking.

THE BEHAVIOUR OF NITRITE IN THE ENGLISH CHANNEL, BARENTS SEA AND ANTARCTIC WATERS.

N. Verjbinskaya (1932), working in the Barents Sea, has found nitrite figures which show striking similarities with E1 in the English Channel. In the work in the Barents Sea a large number of stations have been sampled quarterly, whereas in the Channel one station, E1, has been worked at more frequent intervals. The inshore Channel Station, L4, does not admit of detailed comparison with either E1 or the Barents Sea owing to land influences.

In midwinter in 1929 and 1930 along the meridian 73°30′ E. from the Murmansk coast to the ice margin, and in January, 1931, at E1 in the Channel, nitrite was scarcely detectable.* In both cases nitrification was presumably at a standstill. Intense consumption of phosphate and nitrate occurred in early April at E1 and in June in the Barents Sea. On both occasions nitrite appeared in fair quantity (around 4 mg. per cubic metre). In the region of water of Atlantic origin, the nitrite content was higher and the distribution in the water column more even than in Arctic or coast waters. Subsequently at E1 with vanishing nitrate, nitrite became very low. In August in the Barents Sea nearly all the nitrite was confined within the 50–100-metre layer, where it sometimes reached 14 mg. per cubic metre. Hydrodynamical conditions were similar at E1 in 1928 and nitrite then reached 38 mg. In both cases a thermocline (E1, 25 metres ; Barents Sea, around 40–50 metres) prevented the nitrite in the enriched layers getting up to the surface.

Data for the Antarctic regions have been obtained by the *Discovery* Investigations. In the surface waters there, 6 to 8 mg. of nitrite-nitrogen per cubic metre was found in the presence of 350–500 mg. of nitrate-nitrogen over a wide area in summer. In the sub-Antarctic water, 3·5–5·5 mg. of nitrite-nitrogen accompanies about 200 mg. of nitrate-nitrogen in the surface to 100-metres layer. Thus nitrite has not yet been found anywhere in the Antarctic to reach values commonly reached in the Channel.

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* T. Soot-Ryen (1932) has recently found in North Norwegian fjords minima around mid-winter and mid-summer and maxima in April and October. The distribution in waters of corresponding depth is very similar to that of E1.

VIII. AMMONIA.

The importance of ammonia in the sea both as an intermediate in the conversion of decaying organic matter to nitrate and as a possible direct source of nitrogen assisting the growth of phytoplankton is widely recognised. The earlier methods for its determination involving distillation with alkali are suspect owing to the possible liberation of free ammonia from proteid material (cf. Buch, 1923, 1928 ; Wattenberg, 1928). Hagen (1931) has recently claimed that his method of distillation with magnesia and subsequent microtitration with acid avoids this difficulty.

Buch and Witting (Buch, 1928), Ibañez (1929) and Wattenberg have evolved methods which enable ammonia in sea-water to be determined without prior distillation. Wattenberg's procedure (1928) has been used by the writer in this investigation and is discussed in more detail in the later section on Methods (p. 717). It is not ideal for determinations on the waters of the English Channel for the following reasons :—

Wattenberg claims an accuracy of 5–15 mg. nitrogen per cubic metre, and the lower limit has usually been attained by the writer. Nevertheless, since the waters of the open Channel commonly contain less than 30 mg., the percentage error of any one determination is at least 20% and may be as high as 100% or more on a determination of, say, 5 mg. Thus, highly significant variations in ammonia may fail to be detected or observed differences may not inspire sufficient confidence. This criticism, if it is a criticism, applies not only to Wattenberg's method, but probably with equal force to any method, such as that of Buch and Witting, that makes use of the Nessler reagent. This reagent seems to be somewhat capricious, gives a yellow colour less suitable than a red or a blue for colorimetric comparison, shows large deviations from Beer's Law at such low concentrations of ammonia and is not quite sufficiently sensitive for its task as this presents itself in the English Channel. Unfortunately it is the only colorimetric reagent that even approaches the required sensitivity to ammonia. Also with methylamine it appears to give a colour about one-tenth as intense as that given by an equivalent amount of ammonia.

SEASONAL CHANGES IN AMMONIA.

All the winter profiles for E1 (Fig. 6) and E2 (Fig. 7) are of similar form showing ammonia highest at the surface, least at 25–50 metres, with the bottom results lying in between. This accords with ammonia formation being mainly a surface phenomenon with lesser activity at the bottom. Nitrite, presumably formed from ammonia, shows a similar trend although the differences are not very marked (Fig. 5). Wattenberg has already established that ammonia formation in the East Greenland

Sea is mainly a surface phenomenon. The data for L4 also show the ammonia content of the surface in winter to exceed that of the bottom.

In the spring ammonia showed a general tendency to decrease in the surface layers leading to more uniform distribution throughout the water column. Two reasons may be adduced for this. Firstly, the stock of organic material left over from the preceding year and forming the source of the ammonia would be expected to be less, and secondly, there is evidence (see p. 713) that ammonia may be directly utilised by the spring plankton outburst which would especially affect the surface and deplete the excess found in winter.

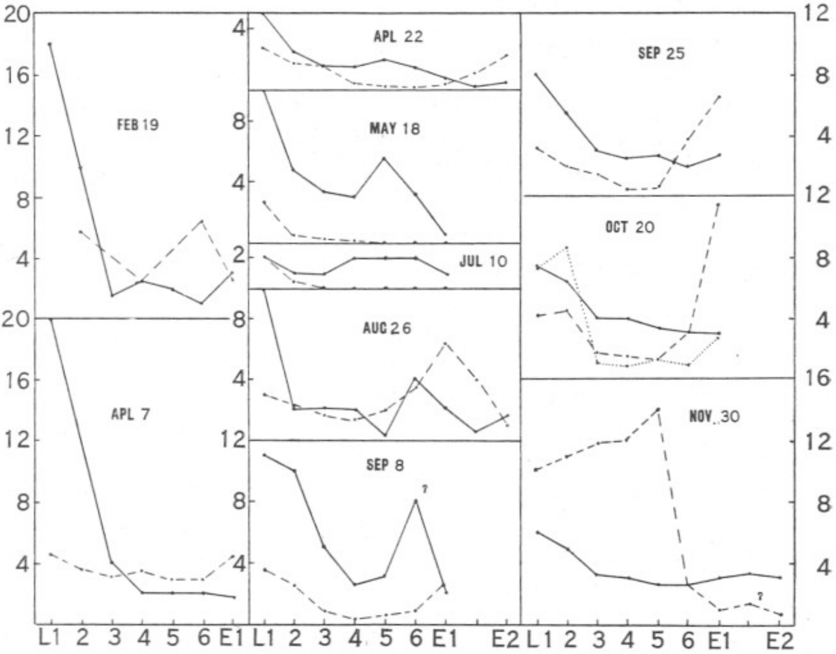

FIG. 15.—Relation between ammonia (full line) and nitrite (pecked line) content of surface water as the shore is approached, 1931. The scale for ammonia is ten times that shown for nitrite (mg. N per m³). Nitrate data are available for October 20th (dotted line) and are shown on same scale as for ammonia. Distances between stations are not shown to scale. They are in nautical miles :—

L1–2–L2 (Breakwater)–3–L3–3–L4–4–L5 (Eddystone)–5–L6–5–E1–17–Midway–17–E2.

During the summer and autumn a general trend upwards can be traced, although ammonia never exceeded 30 mg. at the more seaward Stations L6 (not graphed), E1, and E2. In general 30 mg. appears to be the upper limit in the open Channel and higher figures such as some of those at L4 may be attributed to land or urban drainage.

On the cruise of February 4th–5th determinations of the order of 200 mg. nitrogen per cubic metre were made on the deeper water from Station E3, 7 miles north-west of Ushant. Further data are not available for this Station where the complex water movements make a certain explanation difficult.

That land drainage may be of great importance is shown by the surface data from the L stations (Fig. 15). On most occasions the effect of land drainage was not apparent beyond L3, three miles outside the Breakwater. The ammonia content of the water in Plymouth Sound bears some relation to the state of the tide (Table IX). When, as on September 8th, ammonia was high on the first of the flood, the salinity was comparatively low, showing return of much water from the preceding ebb. The figures show the influence on a tidal Sound of a fair-sized river and of the sewage of a large town which is discharged only on the ebb, as well as the rapidity with which ammonia, like phosphate and nitrate, is dissipated on mixing with the open sea.

TABLE IX.

Comparison of Surface Ammonia in Plymouth Sound and in the Open Channel, 1931.

(L1, Mallard Buoy; L2, Breakwater; E1, Open Channel.)
Ammonia as mg. Nitrogen per cubic metre.

Date	19/2	23/3	7/4	22/4	18/5	10/7	26/8	8/9	25/9	20/10	30/11
L1	180	150	ca100	50	100	20	100	110	80	75	ca60
L2	100	ca120	–	25	48	10	20	100	55	65	50
E1	30	5	17	7	5	10	20	20	27	30	30
State of Tide Hours Flood or Ebb	1½ E.	1½ E.	1 E.	5 F.	2¾ E.	1½ F.	2 E.	2 F.	2 E.	1½ F.	1½ E.
Salinity, L1	31·97	33·08	32·57	34·58	33·42	32·76	31·23	30·72	33·67	33·48	29·45

IX. THE INTERCONVERSION OF AMMONIA, NITRITE, AND NITRATE.

The store of nitrate in the water is probably replenished through some such bacterial or chemical chain of reactions as the following:—

Dead proteid matter⟶polypeptides⟶aminoacids⟶ammonia ⟶nitrite⟶nitrate.

To obtain information as to the last two stages, a series of 44 experiments was made on water samples collected in the Sound (L1) at high and at low water and also at E1 at different depths. To certain of these known amounts of ammonia and of nitrite were added and determinations of ammonia, nitrite and nitrate were made after 10–13 days. Some samples were also preserved with mercuric chloride. In all cases the changes in nitrite were small, little more than the experimental error. The organic matter present in the L1 low-water sample had no effect on nitrite. Nitrate in the E1 bottom samples, including one preserved with mercuric chloride, decreased for a reason which is not clear. There was no correlation between the changes in ammonia and in the two oxy-acids, nor between the distribution of nitrite and the state of the tide at L1. The investigation of the oxidation of ammonia requires a longer period than ten days.

Examination of Fig. 13 which shows the changes in the average contents of ammonia, nitrite, and nitrate in the water columns at L4 and E1 brings out some interesting correlations. At E1 from January onwards the increase in ammonia seems to have been followed by increasing nitrite and nitrate. Indeed, the fact that nitrate went on increasing in March when phosphate and silicate were being depleted by photosynthesis is in excellent agreement with these prior-related increases in nitrite and ammonia.

During the period in mid-April when the salts definitely known to be of nutritional value were suffering rapid depletion, nitrite and ammonia did the same. This favours the view that both may be used as immediate sources of nitrogen for plant life, at any rate when nitrate is nearing exhaustion. Although ammonia increased during the midsummer period, nitrite remained very low, probably on account of the simultaneous dearth of nitrate. During this period scarcity of phosphate was exerting a second independent control over the growth of diatoms so that it is quite likely that the reserves of ammonia were never called upon.

During the early autumn a further increase in ammonia to about 25 mg. nitrogen per cubic metre took place and was followed by nitrite formation. Still later nitrate also began to increase towards its winter maximum. However, there was a short period at the beginning of September when both nitrate and nitrite showed marked falls whilst ammonia was lower in the surface than in the deeper waters. This is in accord with consumption of all three by plankton.

Decisive laboratory experiments on marine phytoplankton to establish the suitability for growth of different nutrient salts require bacteria-free pure cultures. Schreiber (1927), with such a culture of the unicellular alga, Carteria, has shown conclusively that nitrite and ammonia are utilised as readily as nitrate.

Further pure cultures of centric diatoms, such as *Biddulphia mobiliensis* and Melosira, showed luxuriant growths with each of the above sources of nitrogen, but since they were not free from bacteria the results were less conclusive. Harvey (unpublished work) has also found that cultures of Nitzschia were able to assimilate ammonia in the Laboratory.

Braarud and Föyn (1931) have carried out a series of experiments, similar to Schreiber's, using absolutely pure cultures of Chlamydomonas, with 5 to 10 mg. per 100 c.c. of the appropriate nitrogen compound added. They found that it, like Carteria, was able to utilise ammonia even more efficiently than nitrate, but glycine although usable was by no means as effective as for Carteria. Alanine, asparagine (optical rotation not stated), and urea gave yields of the alga roughly comparable with that given by glycine.

Although these algæ might still prefer nitrate if they could get it, there can be no doubt that they are well able to utilise nitrite, ammonia, and even aminoacids. This conclusion is probably of general application so that the evidence for their utilisation in the English Channel receives strong support.

From these results in 1931 the following conclusions may be tentatively deduced :—

(1) Ammonification of proteid matter is primarily a surface phenomenon which receives some assistance from the bottom waters. It is most evident in winter, but in spring and summer it may be masked by simultaneous direct utilisation by the plankton.

(2) An increase in ammonia would seem to be followed by an increase in nitrite and later in nitrate, although the necessary interval of time cannot be stated with any degree of certainty. It is not more than one or two months. The process of nitrification appears to go on throughout the water column and not merely at the bottom.

(3) Both ammonia and nitrite seem to be utilisable by the phytoplankton in the spring and autumn when nitrate is low.

(4) As the shore is approached, ammonia increases, but there is no correlated change in nitrite.

X. THE GRAM-ATOM AS A COMMON RATIONAL UNIT FOR NUTRIENT SALTS.

Phosphate and silicate have usually been given in terms of mg. P_2O_5 and mg. SiO_2, and nitrogen compounds in terms of mg. N, the unit of volume being the cubic metre. It has also been suggested that phosphate and silicate be given as mg. P and mg. Si or as mg. PO_4''' or mg. SiO_3''. Any advantages these changes might bring seem scarcely sufficient to warrant departure from well-established custom.

In the earlier work on the minor constituents of sea-water the method of presentation of results was of no great importance, but now that more and more work is concerned with comparison between the different chemical factors a more rational method seems to be called for. The need promises to become still more marked.

In the same way that the concept of the chemical equivalent simplifies volumetric analysis, a similar concept would probably simplify oceanographical chemistry. But, since the unit with which plants build is the atom, the gram-atom of phosphorus, silicon or nitrogen seems preferable to the gram-equivalent. In practice a sub-multiple such as the milligram-atom (10^{-3} gram-atom) or $\frac{1}{100}$ milligram-atom (10^{-5} gram-atom) per cubic metre would need to be used.

In studying the seasonal plankton outbursts, comparison of changes in phosphorus, silicon or nitrogen in terms of the milligram-atom would give a direct measure of the elements in terms of the common significant unit with which the plants themselves are concerned. It follows that the atomic ratios P : Si : N : N : N will be numerically identical with the molecular ratios $H_3PO_4 : H_2SiO_3 : HNO_3 : HNO_2 : NH_3$ or the ionic ratios $PO_4''' : SiO_2'' : NO_3' : NO_2' : NH_4^{\bullet}$, a point of definite practical importance. A similar concept might also prove useful for other constituents of sea-water such as calcium and iron. For oxygen and carbon dioxide the present method of presentation in c.c. per litre at N.T.P. is already based on a similar idea since, according to Avogadro's hypothesis, equal volumes of different gases at N.T.P. contain the same number of molecules.

It is felt that such a radical change in the method of presenting results, before being put into service, requires the concurrence of the majority of oceanographical chemists, as uniformity in practice above all else is desirable. In consequence the conventional method has been used in this paper, with the exception of Section VI.

XI. METHODS.

PHOSPHATE.

The cœruleomolybdic method of Denigès as adapted by Atkins for determinations in sea-water (1923 (1) *et seq.*) has been used. The solution of stannous chloride used for reduction requires to be strongly acid. The blank correction for the blue colour inherent in sea-water and for impurities in the reagents (usually nil) has been applied as described by Atkins (1930, p. 848).

A practice has been made in all work with Hehner tubes not to run down the standard column below 40 c.c. (compared with 100 c.c. of sample) as the differing fields of view make an accurate colour match difficult of achievement. Since in finding the blank correction this condition is infringed with any standard stronger than 10 mg. P_2O_5 per cubic metre, such a standard is usually prepared. But when two standards of different strengths are available, an alternative method of calculating the blank correction, *k*, may be used.

Suppose that 61·5 c.c. of a standard containing 20 mg. of P_2O_5 per m^3. matches 100 c.c. of another standard containing only 10 mg.

Then equating the two sides to the colour match :—

$$10 + k = \frac{61 \cdot 5}{100}.(20 + k)$$
$$38 \cdot 5k = 230$$
$$k = 6 \cdot 1$$

Standards have always been so compared not only for this purpose but as a check on one another. The lower limit of sensitivity of the method has been found around 1 or 0·5 mg. P_2O_5 per m^3. No correction has been made for salt error.

Denigès (1929) has recently stated that the blue compounds derived from the two " phosphoroïdes : P ou As " upon which his method is based have been isolated as rhombic crystals, analysing in accordance with

$$[4(MoO_3.MoO_2)]_2\ \phi\ O_4H_3,\ 4H_2O$$

where ϕ represents the phosphoroïde. He has proposed a structural formula.

The high molecular weights of these compounds (1578 for that from phosphorus) are about 50 and 22 times greater than the atomic weights of P and As, thus facilitating the determination of traces. Denigès also discusses the solubility of the molybdenum blues in organic solvents (cf. also Wu, 1920).

SILICATE.

The method of Diénert and Wandenbulcke, introduced into sea-water analysis by Atkins has been used. The colour produced by neutral ammonium molybdate in presence of dilute sulphuric acid is compared with that of standard picric acid solutions. The results are correct according to King and Lucas's standard (Atkins, 1930, p. 848, and slip in Journ. Mar. Biol. Assoc., Vol. XVII, No. 3).

Results quoted from earlier papers have been corrected to this standard by multiplying results in the above reference by 1·10 and in the other papers by 1·44.

Hehner tubes were not considered too satisfactory for the comparison, since inshore waters and certain E1 plankton rich surface waters were found to possess an inherent marked yellow colour. Instead, the apparatus described and illustrated by Harvey (1928 (2)) was used. The horizontal tubes were 60 cm. long and 1·6 cm. wide with a capacity of only 120 c.c. These have side-arms through which they can be filled. The presence of turbidity is countered by the presence of a similar sample of sea-water in the twin tube. No blank correction is required, but since acid tends to precipitate the plankton and sediment in the sample, the same amount of sulphuric acid was added to the contents of the twin tube, and both were allowed to settle for five minutes before effecting comparison. A distinct brown deposit formed with very turbid water, in which case an error of 50–100 mg. SiO_2 per m^3. may be introduced if the settling be omitted. In some cases, indeed, it may be necessary to wait until a lapse of a further 5–10 minutes causes no change in the reading.

If the wedges are calibrated in millimetres width, calculation of results is very simple.

Let the wedge reading at colour match be y mm.

And let the picric acid colour standard be equivalent to a solution of silicate containing c mg. SiO_2 per m^3.

Then since the tubes are 600 mm. long the strength of the unknown solution of sea-water, x, is given by :—

$$x = \frac{c.y}{600}$$

By this means the smallest amount of silicate which can be determined with certainty is about 20 mg. SiO_2 per m^3. At about 200 mg. per m^3. the results in general are accurate to within about ± 10 mg. The mean of 3–4 readings has been taken. Since a "daylight" lamp was found unsuitable, comparison was always effected by bright diffused daylight.

Waxed bottles have been found essential for storing samples for silicate determination (cf. Atkins, 1928). Several discordant results have been obtained with samples taken from the standard dark-green sample bottles in use at Plymouth.

Thayer (1930) has recently examined the molybdimetric methods for silicate and phosphate with respect to cross-interference and interference by iron. Their results appear to support Atkins that no trouble should be experienced at the concentration in which these substances are usually present in sea-water, but the paper may be of interest to investigators who have to study waters much richer than those on the European continental shelf.

AMMONIA.

The method of direct Nesslerisation of sea-water in presence of sodium hydroxide and Rochelle salt introduced by Wattenberg (1928) has been used. Since the samples have to be stored in the laboratory for a week or more before analysis, four drops of saturated mercuric chloride solution have been added to each sample (170 c.c.) on collection. This has no effect on the determination and has been shown to keep the water unchanged up to at least four months.

The method used is essentially as described by Wattenberg although one or two small changes in technique have been made. Reagents, other than Nessler, are made up the night before they are required for use in order to avoid contamination. The Nessler reagent has been made up exactly as described by Wattenberg except that it is two-thirds the strength and 1·5 c.c. instead of 2 c.c. is used for each analysis. It is believed that a slight increase in sensitivity is thus achieved. Further decrease in the amount of reagent seems to lead to inaccurate colour development with the stronger solutions of ammonia.

When the method was first examined it proved difficult to get clear solutions. Indeed, most of the troubles since recorded by Braarud and Klem (1931) were experienced. One or two small changes in technique were made and since then cloudiness has not interfered. It is true that the solutions sometimes begin to cloud after an hour, but within this time the comparisons may be easily effected. A detailed account of the routine adopted here may be useful.

One 350 c.c. conical flask or conical beaker and one 250 c.c. or 350 c.c. open beaker are required for each sample or standard. The series of labelled flasks is placed along the bench, each with a beaker and sample bottle behind. The appropriate amount of a standard ammonia solution is then added to each standard flask followed by 100 c.c. of the standard sea-water to which a small but definite excess of ammonia-free hydrochloric acid (e.g. constant boiling acid) has been added. If the sea-water after boiling with alkali has been brought only to neutrality, turbidity may ensue due to colloidal calcium and magnesium compounds remaining undissolved. Into each sample flask 100 c.c. of the sample is measured with a cylinder. The next operation is to add 10 c.c. of 20% boiled out caustic soda to each open beaker.

Instead of adding all the Rochelle salt (5 c.c.) to the sea-water, about 0·5 to 1 c.c. is added to the caustic soda and the remainder to the sea-water. This appears to give a test solution which remains clear longer. Each flask of sea-water is then poured into the corresponding beaker of caustic soda at first slowly and then rapidly while imparting a rapid swirling motion to the contents, which are finally poured quickly back into the flask. As a further check against development of turbidity the addition of Rochelle salt and mixing may be made in groups of six at a time.

The addition of Nessler reagent is made from a quick delivery burette so as to reduce the time interval between the first addition and the last to a minimum. The solutions are best transferred at once to the comparator although 15–20 minutes must be allowed for the development of colour. Attention to detail has been found essential to success with this method, and the work must be carried through with the greatest speed compatible with accuracy.

The early type of comparison tube evolved by Harvey and described by Wattenberg (1928) was first used. Optically it is excellent, but it was found dirty to work with since alkaline mercurial solution was often spilt in fitting the lens. The apparatus at present in use avoids this completely. The total length of the tube is 38 cm. and width 1·7 cm., except that it has a parallel-sided bell-top, 3·2 cm. wide. Its length is 3 cm. The bell-top is filled in each case to the same extent and avoids all spilling. The tube is viewed vertically through the centre of the bell where the meniscus is only very slightly concave. No lens is required.

The stand which holds thirteen tubes simultaneously consists of an open wooden box with a sliding front for use if required. Internal measurements: length, 58 cm., height, 53 cm., breadth, 8 cm. The tubes are held vertically by spring clips screwed to a strengthening piece fixed across the back of the box. The bottom of each tube is supported on a clear glass plate, 58×6·4 cm. carried on rests at the back and sides and 18 cm. above the bottom of the box. This plate bears no appreciable weight, serving mainly to adjust all the tubes to the same height. Light from a north window is reflected up through the tubes by a matt opal-glass plate, 58×10·5 cm., held at a suitable angle in the bottom by a slat of wood. In this apparatus standards and samples may be quickly arranged in sequence.

The following close series of standards was usually made up, viz. 0, 0, 5, 10, 10, 15, 20, 20, 25, 30, 40, 60, 80 mg. N per m^3. By comparison of these together any untrustworthy standards may be at once rejected. Duplication of some of the standards is very desirable. Interpolation is dangerous. Also after April 22nd, 1931, the sets of duplicate analyses were always made independently with different sets of standards.

It is possible to use Hehner tubes with advantage for comparing samples containing more than 40–50 mg. N per m^3. Since Beer's Law is quite invalid a special calibration curve must be constructed by comparing lower with higher standards. The departure from Beer's Law appears to increase with age of the Nessler reagent so that a fresh curve must be constructed on each occasion.

Determinations of less than 100 mg. N per m^3. are thought to be accurate to about ±5 mg. A series containing 0, 3, 5, 7, and 10 mg. N per m^3. can be placed in sequence with a fair degree of certainty, but agreement between independent duplicate determinations is not always quite so good.

Possible Interference by Organic Nitrogen Compounds.

It seemed possible that amino-acids and alkylamines which may be present in sea-water might be able to form a yellow complex with the Nessler reagent sufficient to upset ammonia determinations. Known amounts of glycine, aspartic acid, methylamine hydrochloride, dimethylamine hydrochloride, and ethylamine hydrochloride were therefore added to standard sea-water and compared with ammonia standards at the same time as the samples from the cruise of October 20th. Only the glycine was a B.D.H. analytical reagent. The other amines were ordinary B.D.H. products taken direct from the laboratory stock. The dimethylamine hydrochloride was very wet. The results are given in Table X.

TABLE X.

EFFECT OF AMINO-ACIDS AND ALKYLAMINES IN SEA-WATER ON NESSLER REAGENT.

Substance.	Amount of Amine added as mg. N per m^3.	Amount found as Ammonia mg. N per m^3.	Ratio $\frac{\text{N present in amine.}}{\text{N found as ammonia.}}$
Glycine	50	3	17
(A.R.)	200	7	29
	1000	7	140
Aspartic	50	5	10
Acid	200	7	29
	1000	22	45
Methylamine	50	15	3·3
Hydrochloride	200	22	9
	500	55	9
	1000	76	13
Dimethylamine	ca 50	5	ca 10
Hydrochloride	ca 200	3	ca 70
Ethylamine	53·5	5	11
Hydrochloride	214	7	31

Unless present in very large amounts, the effect of glycine and dimethylamine appears to be unimportant, but aspartic acid and ethylamine both impart a slight yellow colour to the reagent. Methylamine gave one-tenth of the colour given by an equivalent amount of ammonia. The smaller observed influences may have been due to ammonia present in the materials. In the case of methylamine this explanation would involve the presence of 10% of ammonium chloride as impurity which seems highly unlikely. On one occasion trimethylamine coming from a barrel of herrings on the floor below was found to upset ammonia determination. Thus, excepting methylamines, it seems safe to ignore the influence of amino-acids and alkylamines on the Nessler reagent.

NITRATE.

The determination of nitrate is described elsewhere (Harvey, 1928 (2); Cooper, 1932).

NITRITE.

The standard Griess-Ilosvay reagent (Orr, 1926; Wattenberg, 1931) has been used. The distilled water used for making up reagents and standards has been redistilled from caustic soda or baryta immediately before use into a Winchester bottle. This was fitted with a soda lime tube to stop ingress of nitrous gases always present in a laboratory in which gas burners are in use. No burners were allowed to be used when colour comparison was being made.

A special routine was developed to avoid change in nitrite whilst bringing the samples to the Laboratory for analysis. A box of 36 standard sampling bottles has been kept solely for nitrite samples. The series of standards required was prepared in these bottles on the morning of the cruise. About 100–120 c.c. of water was then collected in the remaining bottles at each station as required. The two Griess-Ilosvay reagents were mixed on the ship and 4 c.c. of the mixed reagent measured in a cylinder was added at once to each sample and standard. The colour was allowed to develop overnight and comparison made next morning. The idea that nitrite in the sea is very fugitive has since been found to be open to doubt but since the method is very expeditious it has been retained. Colour development in the actual sample bottle has a further advantage in that transference to laboratory glassware is avoided, thus eliminating an ever-present risk of contamination. Little change occurs in the colour of the dyestuff up to 4 or 5 days in darkness after which it begins to turn brown, thus vitiating results obtained. After cruises to E2, satisfactory comparison has been effected when addition of reagent had been made 40 hours earlier.

The following series of standards, each in duplicate, has usually been prepared: 0, 1, 2, 5, 10, 25 mg. N per m^3. Preliminary comparison of each pair with one another and with the next higher standard enables any untrustworthy standard to be discarded and gives an alternative means of calculating the blank correction. The reagent itself has always been found free from detectable colour, but since, in contrast to phosphate, the correction factor applies to nitrite present in the distilled water used for making the standards and not to any pink colour inherent in sea-water, it is calculated differently.

Thus, suppose that 20 c.c. of a nitrite standard containing 1 mg. N per m^3.+reagent matches 100 c.c. of redistilled water+reagent.

Let the amount of nitrite present as impurity in 100 c.c. of redistilled water, and consequently in the standard also, be x mg. per m^3.

Then
$$x = \frac{20}{100}(1 + x) = 0{\cdot}25$$

Then every standard will also contain 0·25 mg. N per m³., more than its nominal content.

If y c.c. of a nominal 2 mg. standard matches 100 c.c. of sea-water sample, then its nitrite content, c, will be given by

$$c = \frac{y}{100}(2 + 0{\cdot}25)$$

0·3 mg. per m³. has been regarded as the maximum permissible nitrite content of the distilled water, usually it was less than 0·1 mg. and it was often not detectable.

With about 5 mg. N per m³. present, the determinations are accurate to about 0·1 mg. At the lower limit using distilled water completely free from nitrite, 0·02 and 0·04 mg. may be just distinguished under very favourable conditions. This degree of accuracy is not usually necessary nor has it been often attained owing to the presence of a positive blank correction. However, on July 10th, 1931, at the surface Stations, L3 to L6, at L4, 50 metres, and at E1, 0, 5, and 10 metres, nitrite was shown definitely to be less than 0·02 mg. N per m³., i.e. less than 1 part in 50,000,000,000. The colour of the sea-water plus reagent was indistinguishable from distilled water with or without reagent.

In all cases where nitrite has proved undetectable, a drop of 0·1% sodium nitrite has afterwards been added to the test sample to confirm the presence of the reagent added on the ship.

Germuth (1929) recommended the replacement of α-naphthylamine by its dimethyl derivative. Amongst other advantages, it was claimed that the resulting dyestuff does not fade appreciably in 60 days in light. A sample (5 g.) of dimethyl-α-naphthylamine obtained commercially was a dark brown liquid insufficient for purification by distillation and when made up in the same way as α-naphthylamine gave a faintly pink solution. The tint developed with sulphanilic acid and nitrite was almost identical in intensity and quality of tint with the standard Griess-Ilosvay colour. Similar solutions when exposed to diffuse daylight for one week showed a similar amount of fading and discoloration. Dimethyl-α-naphthylamine is much dearer and as obtained commercially was less pure than α-naphthylamine over which for sea-water analysis it seems to have no advantage.

AVERAGE NUTRIENT SALT CONTENT OF THE WATER COLUMN.

The total nutrient salt (e.g. phosphate) content of the water column is first found and then divided by the depth to give what is termed in this paper *the average phosphate content of the water column.*

For purposes of calculation and generally in the construction of depth profiles, adjacent points are joined by straight lines to give a discontinuous curve (Figs. 1–7). The distribution of nutrient salts in the sea is probably seldom accompanied by such a discontinuity. However, such profiles seem as legitimate as any of the possible smooth curves which might be fitted to the points.

The total nutrient salt may be found in several ways, e.g. with a planimeter or by counting squares, the method used by Atkins. In this paper it has been calculated directly from the data.

Suppose determinations are made at depths $y_1, y_2, y_3 \ldots y_n$ metres apart and give nutrient salt contents $a, b, c \ldots n$ milligrams per cubic metre.

Then the total salt content between the surface and y_1 metres will be $\frac{a+b}{2} . \, y_1$. Similarly for the other depths.

Then the total nutrient salt content of the whole water column,

$$\Sigma \; Nutrient \; Salt = \frac{a+b}{2} . \, y_1 + \frac{b+c}{2} . \, y_2 \ldots + \frac{m+n}{2} . \, y_n .$$

This summation may be quickly made in practice since certain terms may often be taken together to give a convenient numerator, e.g. when $y_1 = y_2$, then

$$\frac{a+b}{2} . \, y_1 + \frac{b+c}{2} . \, y_2 = \frac{a+2b+c}{4} . \, 2y_1 .$$

$2y_1$ is often equal to 10.

The summation equation may be transformed to give :—

$$\Sigma \; Nutrient \; Salt = \tfrac{1}{2}[y_1 a + (y_1 + y_2)b + (y_2 + y_3)c \ldots + y_n n].$$

If D is the total depth in metres $= (y_1 + y_2 + y_3 \ldots + y_n)$, then the average nutrient salt content is $\frac{\Sigma \; Nutrient \; Salt}{D}$.

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XII. SUMMARY.

Determinations of phosphate, silicate, nitrate, nitrite and ammonia have been made at frequent intervals at two Stations, L4 and E1, in the English Channel off Plymouth between the autumn of 1930 and January, 1932. Determinations were also made quarterly at E2 in mid-Channel.

The year 1931 was an early one from the point of view of plankton production. The chemical data show that there was a small mid-winter outburst which gathered momentum during January and February. The main spring outburst started, however, early in March, carrying on fairly steadily until about the middle of May. The summer was characterised by exceptionally low phosphate and nitrate right through the water column due to very efficient utilisation in the spring and to the unusual hydrodynamical conditions. There was also a small autumn outburst.

The outburst at E2 in mid-Channel in 1931, as in several former years, began earlier than at E1, but by mid-April production at E2 had been far surpassed by that at E1, again in agreement with former years.

The date of the winter maximum has varied fairly regularly for different salts. That for silicate has been about a month later than that for phosphate and its magnitude has varied greatly from year to year. Nitrate in 1931 showed three maxima, one at mid-winter, one in March when the plankton outburst was well under way, and one in the late summer. Thus nitrate, whose formation is the last stage in the long nitrogen regeneration cycle, was unreliable as a criterion of plankton production in the early spring although it was valuable at other seasons.

In three seasons out of four silicate has shown a summer maximum about August due to re-solution at the bottom of siliceous matter, including the skeletons of diatoms dying off after the spring outburst. A minimum usually followed related with the autumn outburst.

Almost complete exhaustion of nitrite was found at E1 in January, May and July. Nitrite in the sea has been found to be fairly stable, although its distribution in the Channel is exceptionally localised. The amount seemed to be dependent on the amount of ammonia present a few weeks before. In the autumn the distribution of nitrite has been very dependent on hydrodynamical conditions.

The determination of ammonia in sea-water is discussed. Ammonia formation was mainly a surface phenomena which received some assistance from the bottom waters (at about 70 metres). In spite of vertical mixing this was most apparent in winter. The mechanism of the interconversion of ammonia, nitrite and nitrate and the utilisation of ammonia and nitrite by plants are discussed.

The first two months of 1931 were sunny leading to an early diatom outburst, but the late spring and summer were unusually sunless and stormy, the effect of which on the utilisation and distribution of nutrient salts is clearly brought out.

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Chemical Constituents of Biological Importance in the English Channel, November, 1930, to January, 1932. Part II. Hydrogen ion concentration, excess base, carbon dioxide, and oxygen.

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With 2 Figures in the Text.

CONTENTS.

The measurements of hydrogen ion concentration, excess base and oxygen described in this paper were carried out simultaneously with those of nutrient salts described in Part I. From these measurements, values for the partial pressure and total amount of carbon dioxide have been derived by methods described by Buch, Harvey, Wattenberg, and Gripenberg (1932).

I. Hydrogen Ion Concentration.

The method of determining pH and the correction to be applied to the measurements to give the pH at the temperature of collection, pH_w, or at a standard temperature of 12°, $pH_{12°}$, is given in the section on methods (p. 749). When the results are to be used for the calculation of total carbon dioxide or of any of the various functions concerned in the carbonate equilibrium in the sea, pH_w is the more suitable quantity, since the interpolation tables of Buch *et al.* take account of temperature. For the calculation of partial pressure, pH_w is essential. Values of pH_w are given in Tables I to III. For comparison of pH values amongst themselves it is best to correct to a standard temperature, say, 12°.

Profiles of $pH_{12°}$ for Stations L4 and E1 are given in Fig. 1. The minimum for the year was reached in January–February, 1931. At E1, $pH_{12°}$ increased steadily from mid-February until mid-summer. The effect of photosynthesis on the surface layers was most clearly shown in March.

The August gales not only led to vertical mixing and consequent levelling-up of pH values throughout the water column, but to a general lowering of pH due to absorption of carbon dioxide from the atmosphere. This effect of storms on pH has previously been observed by Atkins (1922, p. 763). The diatom outburst in September led to a slight increase in pH. The results are in general agreement with the seasonal changes at E1 already found by Atkins (1922, '23, '24). He, however, applied the McClendon temperature coefficient which applies at constant CO_2-tension and not at constant ΣCO_2, and is of opposite sign to that of Buch. But since his measurements were commonly made within one or two degrees of 12°, the amount of the correction is small so that a general comparison may be made with the present set of results.

The seasonal change in pH at the surface at E1 is also plotted in Fig. 2. The differences between the curves for $pH_{12°}$, and pH_w is shown. By the definition of $pH_{12°}$, the two curves cross at 12° C. The effect of increasing temperature, apart from other changes in the water, is seen on comparison of the two pH curves with the temperature curve between May 18th and July 10th.

The profiles for L4 are peculiar. $pH_{12°}$ shows a tendency to be lower at the surface than at the bottom (50 m.) even during the spring period of plankton growth. Station L4 is shallower than E1 and more subject to river influence and vertical mixing is probably more effective. There will thus be more tendency for the surface water, depleted of carbon dioxide by photosynthesis, to re-absorb the gas from the atmosphere, whereas the pH of the bottom waters may be raised by mixing with the waters from around 20 metres. The values of pH_w (Table I) show a tendency to approach 8·15–8·16, the pH of sea-water in equilibrium with the air. The results for November 30th show that the effect may be confined to the surface five metres. On this date the surface salinity was reduced to $33{\cdot}6°/_{oo}$. The lower surface pH was particularly apparent after the very stormy period in mid-August. The phenomenon was observed on six occasions, and in most cases it was confirmed by re-determinations.

Similar lower surface values have been found in winter by Atkins (1922, p. 763).

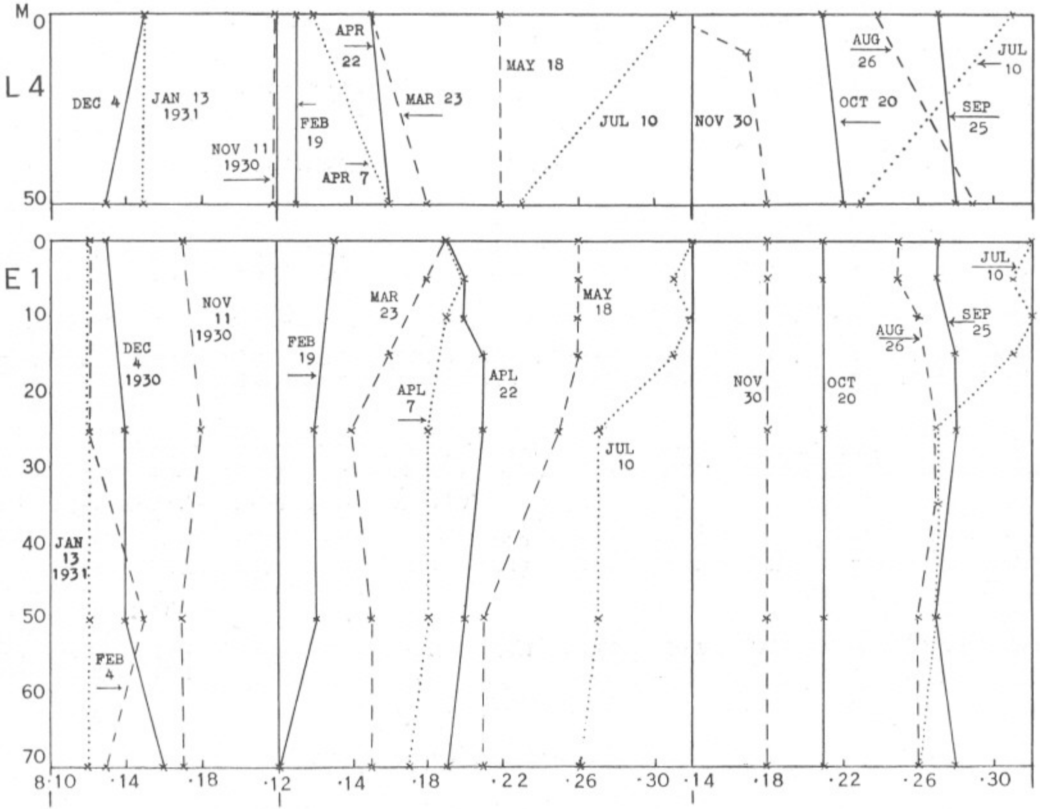

Fig. 1.—pH at Stations L4 and E1 corrected to 12° C. The depth scale for L4 is half that for E1.

TABLE I.

STATION L4. DEPTH SERIES.

Date	1930 11/11	4/12	1931 13/1	19/2	23/3	7/4	22/4	18/5	10/7	26/8	8/9	25/9	20/10	30/11
pH at temperature of collection (pH_w).														
M 0	8·21	8·15	8·16	8·15	8·19	8·16	8·19	8·23	8·27	8·21	–	8·23	8·18	8·13*a*
50	8·21	8·13	8·16	8·19	8·22	8·20	8·20	8·25	8·23	8·26	–	8·24	8·19	8·19
EXCESS BASE (by Wattenberg's Method, milli-equivalents per litre) (*b*).														
0	–	–	2·382	2·383	–	2·353*	2·372*	2·380	2·355	2·347*	2·343*	2·360*	2·370	2·282†
50	–	–	2·378	2·388	2·395	2·364	2·372	2·418	2·398	2·382*	2·389*	2·377*	2·381	2·365
Σ CO_2 (c.c. per litre at N.T.P.).														
0	–	–	45·9	46·3	–	45·7	45·6	44·8	43·2	44·0	–	43·8	44·7	44·5
50	–	–	45·9	46·3	45·7	45·4	45·5	45·4	45·8	43·8	–	44·0	44·9	46·0
Partial Pressure of CO_2, pCO_2 (Atmospheres $\times 10^{-4}$).														
0	*g* 2·6	*g* 3·0	2·9	3·0	2·6	2·9	2·6	2·3	2·1	2·5	–	2·4	2·7	3·1
50	2·6	3·1	2·9	3·0	2·4	2·5	2·5	2·2	2·4	2·2	–	2·4	2·7	2·6

Additional data and notes.

a, 5 m., 8·17.

b, Station L6; 25/9, 0 m. 2·367*; 62 m. 2·387*; 20/10, 0 m. 2·370; 67 m. 2·386*.

g, From pH and salinity.

* Mean of duplicate analyses. † Mean of quadruplicate analyses.

TABLE II.

STATION E1. DEPTH SERIES.

Date	1930 11/11	4/12	1931 13/1	4/2	19/2	23/3	7/4	22/4	18/5	10/7	26/8	8/9	25/9	20/10	30/11
pH at temperature of collection (pH_w).															
M															
0	8·15	8·13	8·14	8·15	8·16	8·22	8·22	8·22	8·27	8·28	8·21	–	8·23	8·18	8·17
5	–	–	–	–	–	8·21	8·23	8·23	8·27	8·27	8·22	–	8·23	8·18	8·17
10	–	–	–	–	–	–	8·22	8·23	8·27	8·28	8·23	–	–	–	–
15	–	–	–	–	–	8·22	–	8·24	8·27	8·28	–	–	8·24	–	–
25	8·17	8·14	8·14	8·15	8·15	8·20	8·21	8·24	8·27	8·28	8·24*d*	–	8·24	8·18	8·17
50	8·16	8·14	8·14	8·17	8·15*c*	8·21	8·21	8·23	8·24	8·28	8·23	–	8·23	8·18	8·17
68–71	8·16	8·16	8·14	8·16	8·14	8·21	8·20	8·22	8·24	8·27	8·24		8·24	8·18	8·17
A	When possible same night, otherwise first thing the following morning.														
	EXCESS BASE (Wattenberg's Method ; milli-equivalents per litre).														
0	–	–	2·377*	–	2·388*	2·384*	2·380*	2·382	2·384*	2·360	2·365*	2·357*	2·370*	2·375	2·370*
5	–	–	–	–	–	2·394*	2·380	2·395	2·384	2·355	2·357	2·379	2·384	2·370	2·381
10	–	–	–	–	–	2·384*	–	2·391	2·397	2·355	2·362	2·379*h*	–	–	–
25	–	–	2·384*	–	2·394*	2·394*	2·384	2·391	2·390	2·360*e*	2·384	2·379	2·384	2·372	2·392
50	–	–	2·380*	–	2·388*	2·400*	2·370	2·391	2·395*	2·364	2·379	2·382*	2·384	2·370	2·384
68–71	–	–	2·381*	–	2·393*	(2·373)	2·384	2·397*	2·391*	2·365*	2·376	2·411	2·395	2·375	2·378
A			16/1	–	23/2	26/3	14/4	28/4	28/5	22/7	22/9	22/9	3/10	28/10	5/12
OXYGEN (c.c. O_2 per litre at N.T.P.).															
0	–	–	–	–	6·43	6·49*	6·66*	6·92*	6·44*	–	5·71*	5·84	5·81*	5·76*	5·86*
5	–	–	–	–	–	6·48	6·68*	7·00	6·40	–	5·67*	5·80*	5·74	5·71*	5·81*
10	–	–	–	–	6·46	6·48	6 58	7·04	6·50*	–	5·62*	–	–	–	–
15	–	–	–	–	–	–	6·66	–	6·55	–	5·58	–	5·75	–	–
25	–	–	–	–	6·35	5·42*?	6·56*	6·92*	6·70*	–	5·54*	5·75	5·71*	5·68*	5·79*
50	–	–	–	–	6·37*	6·30	6·58*	6·75	6·54	–	5·52*	5·62*	5·66*	5·68*	5·79*
60	–	–	–	–	6·36	–	–	–	–	–	–	–	5·64	–	–
68–71	–	–	–	–	6·46*	6·40*	6·51*	6·81*	6·61*	–	5·47	5·38*	5·64*	5·64*	5·78*
B	–	–	–	–	19/2	23/3	7/4	23/4	18/5	–	27/8	8/9	25/9	20/10	1/12

TABLE II—*continued.*

Date	1930		1931												
	11/11	4/12	13/1	4/2	19/2	23/3	7/4	22/4	18/5	10/7	26/8	8/9	25/9	20/10	30/11
	Σ CO_2 (c.c. CO_2 per litre at N.T.P.).														
0	–	–	46·1	[g]46·4	46·1	45·4	45·2	45·4	44·3	43·0	44·1	–	44·0	44·7	45·2
5	–	–	–	–	–	45·6	45·1	45·4	44·3	43·2	44·0	–	44·1	44·7	45·3
10	–	–	–	–	–	–	45·2	45·3	44·3	43·1	43·9	–	–	–	–
15	–	–	–	–	–	45·5	–	–	–	43·2	–	–	44·1	–	–
25	–	–	46·1	46·4	46·4	45·8	45·4	45·2	44·6	43·6	44·1	–	44·1	44·7	45·5
50	–	–	46·2	46·2	46·4	45·7	45·3	45·3	45·1	43·6	44·2	–	44·2	44·7	45·4
68–71	–	–	46·3	46·3	46·5	45·3(?)	45·6	45·6	45·0	44·0	44·2	–	44·2	44·7	45·3
	Σ CO_2+O_2 (c.c. per litre at N.T.P.).														
0	–	–	–	–	52·5	51·9	51·9	52·3	50·7	–	49·8	–	49·8	50·4	51·1
5	–	–	–	–	–	52·1	51·8	52·4	50·7	–	49·7	–	49·8	50·4	51·1
10	–	–	–	–	–	–	51·8	52·3	50·8	–	49·5	–	–	–	–
15	–	–	–	–	–	52·0	–	–	–	–	–	–	49·8	–	–
25	–	–	–	–	52·7	(51·2)	52·0	52·1	51·3	–	49·6	–	49·8	50·4	51·3
50	–	–	–	–	52·8	52·0	51·9	52·1	51·6	–	49·7	–	49·9	50·4	51·2
68–71	–	–	–	–	53·0	(51·7)	52·1	52·2	51·6	–	49·7	–	49·8	50·3	51·1
	Partial Pressure of CO_2, $\mathrm{P}CO_2$ (Atmosphere × 10^{-4}).														
0	[g]3·0	[g]3·1	3·0	[g]3·0	2·9	2·4	2·4	2·4	2·1	2·1	2·5	–	2·4	2·7	2·8
5	–	–	–	–	–	2·4	2·3	2·3	2·1	2·1	2·5	–	2·4	2·7	2·8
10	–	–	–	–	–	–	2·4	2·3	2·1	2·1	2·4	–	–	–	–
15	–	–	–	–	–	2·4	–	2·3	2·1	2·1	–	–	2·4	–	–
25	2·9	3·0	3·0	3·0	3·0	2·5	2·4	2·3	2·1	2·1	2·4	–	2·4	2·7	2·8
50	2·9	3·0	3·0	2·8	3·0	2·4	2·4	2·3	2·3	2·1	2·4	–	2·4	2·7	2·8
68–71	2·9	2·9	3·0	3·0	3·0	2·4	2·5	2·4	2·3	2·1	2·4	–	2·4	2·7	2·8

* Mean of duplicate analyses.

A. Date of analysis.
B. Reagents added when collected on board. Acidified and titrated same night or following day as shown.

Additional data.
c. 60 m. 8·14.
d. 35 m. 8·24.
e. 20 m. 2·360.
g. From pH and salinity.
h. 15 m. 2·379.

TABLE III

STATION E2

	pH at temperature of collection (pH_w).				EXCESS BASE (milli-equivalents per litre).			Σ CO_2 (c.c. per litre at N.T.P.).				pCO_2 (Atm. $\times 10^{-4}$).			
Date	1931 4/2	22/4	26/8	30/11	22/4	26/8	30/11	4/2	22/4	26/8	30/11	4/2	22/4	26/8	30/11
								g				g			
M															
0	8·17	8·19	8·22	8·17	2·381	2·368	2·374*	46·0	45·5	44·0	45·2	2·8	2·6	2·4	2·8
5	–	8·19	8·23	8·18	2·381	2·373	2·389	–	45·5	44·0	45·4	–	2·6	2·4	2·7
10	–	8·20	8·23	–	2·376	2·397*	–	–	45·3	44·5	–	–	2·5	2·4	–
25	8·17	8·20	8·23*f*	8·18	2·376	2·378*	2·392	46·0	45·3	44·2	45·4	2·8	2·5	2·4*f*	2·7
50	–	8·21	8·25	8·18	2·386	2·394	2·392	–	45·4	44·4	45·4	–	2·4	2·3	2·7
70	–	–	8·27	8·18	–	2·379	2·381	–	–	43·9	45·3	–	–	2·2	2·7
87–91	8·16	8·19	8·25	8·17	2·404	2·384	2·384*	46·1	45·9	44·3	45·4	2·9	2·5	2·3	2·8

Additional data.

f	metres	15	35	40	45
	pH	8·25	8·24	8·24	8·26
	pCO_2	2·3	2·3	2·3	2·2

g. Calculated from pH and salinity.
* Mean of duplicate analyses.

STATION E3, 5/2/31.

	pH_w	Σ CO_2	pCO_2
		g	g
M			
0	8·16	46·1	2·9
103	8·16	46·1	2·9

II. Partial Pressure of Carbon Dioxide.

The partial pressure and total amount of carbon dioxide (Tables I to III) have been found from pH_w, excess base and temperature by means of interpolation tables (Buch, *et al.*, 1932). Failing excess base, salinity has been used on a few occasions.

It will be seen that the partial pressure showed no very large variation with depth. The changes at 5 metres have been plotted in Fig. 2. The partial pressure of carbon dioxide in the atmosphere is about $2{\cdot}95 \times 10^{-4}$ atmospheres (Krümmel, 1907). For three months during the winter, the water column as a whole was in equilibrium with the atmosphere or very slightly supersaturated. With the onset of the spring plankton outburst, the partial pressure fell rapidly during March. Since the sea had become decidedly unsaturated with respect to free carbon dioxide, further fall due to photosynthesis was offset by solution from the atmosphere. The consumption of nutrient salts during April was not therefore accompanied by proportionate apparent consumption of carbon dioxide. That carbon dioxide was actually being used in quantity was shown by the rapid rise in oxygen.

The August gales with the resulting vertical mixing and surface turbulence resulted in a rise in partial pressure. During the autumn there was a trend upwards towards the winter maximum although this had not been reached when observations ceased.

Thus for nine months of the year the sea was unsaturated with regard to carbon dioxide which presumably it was dissolving from the atmosphere. During three winter months it was just saturated or slightly supersaturated. Since exchange of carbon dioxide with the atmosphere in either direction is probably greatly aided by stormy weather, a disturbed equilibrium is likely to be restored more rapidly in winter than in summer. Nevertheless, the period of unsaturation was much longer and the degree of unsaturation was greater than the period and degree of supersaturation (if any) during winter.

III. Total Carbon Dioxide.

The total carbon dioxide, ΣCO_2, in sea-water is the sum of the concentrations existing as CO_2 (or H_2CO_3) and as bicarbonate and carbonate ions. The results in Tables I to III are reduced to normal temperature and pressure. The average CO_2 contents of the water column have been calculated by the method described in Part I, p. 722. The maximum for the year was reached in January and February when the partial pressure was also at a maximum. At L4 and E1 a fall due to consumption by plankton followed, and the minimum was reached by July or August.

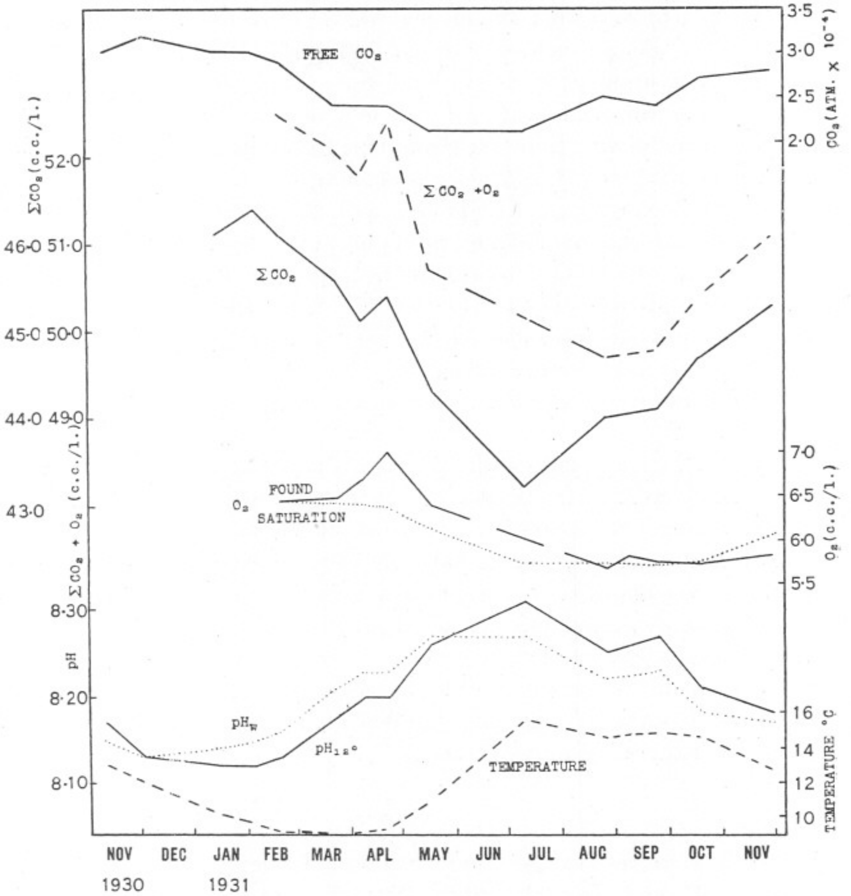

FIG. 2.—CO_2–O_2 system at Station E1. November, 1930–November, 1931. Depth 5 metres, except November–February for which surface values only are available.

(1) CO_2 partial pressure.

(2a) Oxygen found.

(2b) Volume of oxygen required to saturate the water at the temperature *in situ* under one atmosphere pressure.

(3) Total (Σ) carbon dioxide dissolved in the water.

(4) Sum of total volumes of carbon dioxide and oxygen.

(5a) pH of the water at the temperature of collection.

(5b) pH of the water if the temperature is changed to 12° C. without gain or loss of CO_2.

(6) Temperature, °C.

The figures do not show a straightforward relationship with nutrient salts since, between April 7th and 22nd, when these all showed heavy consumption, total carbon dioxide showed no great change. From then onward there was a much more rapid fall, particularly above the thermocline, even between mid-May and early July when nutrient salts remained very low. The values for $\Sigma\ CO_2$ at 5 metres at E1 in Fig. 2 may be compared with those for the nutrient salts in Part I, Fig. 8.

At Station E2 in early February both total carbon dioxide and partial pressure were lower than at E1, agreeing with the earlier start of the spring outbreak in mid-Channel deduced from phosphate data. Nevertheless, in the succeeding two months total carbon dioxide fell by 1·1 c.c. per litre at E1 compared with only 0·5 c.c. at E2. This again agrees with the deductions from nutrient salts that the early start at E2 was not followed up so effectively as the later start at E1.

In the autumn total carbon dioxide increased towards the winter maximum.

The daily change in carbon dioxide throughout the year is graphed in Fig. 14 in Part I. The results are there expressed in terms of the microgram-atom (10^{-6} gram-atom) of carbon for comparison with the data for phosphorus, silicon, and nitrate-nitrogen. Between mid-May and early July consumption of carbon was very marked, yet during this period phosphate and nitrate remained practically exhausted.

Since the total seasonal change in $\Sigma\ CO_2$ represents only about 3% of the whole, its measurement affords a less accurate criterion of changes in the sea than do determinations of phosphate and nitrate, for which the percentage changes are much greater.

IV. Oxygen.

Determinations of oxygen were made only for E1 and between February 19th and November 30th, 1931. Weather did not permit of the preparation of oxygen samples on board on July 10th. The resulting lack of data between May 18th and August 26th is unfortunate. During the height of the plankton outburst oxygen increased rapidly, reaching 8% supersaturation at the surface on April 22nd (cf. Fig. 2; 5 m.). During May, with rising temperature, the degree of supersaturation fell. Examination of the data for $\Sigma\ CO_2+O_2$ below shows that this was mainly due to loss of oxygen to the atmosphere.

V. Loss of Oxygen to the Atmosphere.

The measurements of oxygen alone record a loss of 1·35 c.c. per litre between April 22nd and August 26th. During most of this period the surface of the sea was supersaturated with respect to oxygen. Since the figure is affected by the balance between photosynthesis and respiration it gives but a rough guide to the real loss to the atmosphere. But the reactions $CO_2 \underset{\text{respiration}}{\overset{\text{photosynthesis}}{\rightleftharpoons}} O_2$ involve no change in the sum of the two gases, $\Sigma\, CO_2+O_2$.

Between February 19th and August 26th the partial pressure of carbon dioxide in the surface of the sea was always less than that in the atmosphere. In spite of this the sea suffered a loss of $\Sigma\, CO_2+O_2$, particularly during May and June. This loss (2·5 c.c. per litre from the whole water column) may be attributed to loss of oxygen to the atmosphere and to removal of carbon dioxide as calcium carbonate by plants and by deposition. From the small variation in excess base it has been possible to arrive at a rough measure of the amount of calcium and consequently of carbon dioxide removed during the summer to form calcium carbonate in the various possible ways. The biggest observed difference at the surface in the ratio $\frac{\text{excess base}}{\text{chlorinity}}$ during the year was between February 19th and September 8th (see Section VII). It amounted to 8×10^{-4}, when excess base is expressed as milli-equivs. per litre and Cl. as $^{\circ}/_{\circ\circ}$. From this the loss of CO_2 as $CaCO_3$ is 0·18 c.c. per litre. Since the figure depends on a difference in the third place of the measurement of excess base, it is very approximate, is probably maximal, and shows little more than the order of magnitude of the effect. Nevertheless, it is small compared with the loss of $\Sigma\, CO_2+O_2$. If the figure for the latter, 2·5 c.c per litre, is corrected for the loss as $CaCO_3$, 2·3 c.c. per litre remains as the net loss due to evasion of oxygen to the atmosphere during the course of the summer. This amounts to 161 litres from a column, 1 sq.-metre cross section and 70 metres deep. This loss of oxygen is greater than that due to rise of temperature alone. Between the dates of minimum and maximum temperatures at the surface or maximum and minimum oxygen saturation values, 0·75 c.c. per litre could have been lost from the surface layers, due solely to rising temperature. From this a maximum figure may be calculated for the whole water column on the assumption that all the excess oxygen was able to come to the surface and pass into the atmosphere. It is 52·5 litres per sq. metre × 70 metres. It would seem too large since vertical mixing of the water column was hindered by the thermocline and diffusion in a liquid is an exceedingly slow process. But even so, at least (161–52·5) = say, 110 litres per sq. metre × 70 metres of the oxygen given off to the atmosphere, was the product of photosynthesis.

Taking the figures for the area and average depth of the Channel given on p. 744, this is equivalent to the liberation of 9 cubic kilometres of oxygen due to photosynthetic activity in the whole of the Channel.

If events in the Channel can be regarded as occurring in a closed cycle, the carbon dioxide in the sea should be maintained by solution from the atmosphere, i.e. the water of the English Channel was able to replace 9 cubic kilometres of carbon dioxide by an equal volume of oxygen. This is the total volume of carbon dioxide in 30,000 cubic kilometres of air. Stated in another form, it implies that the sea, in effect, had removed the entire CO_2 content of a stratum of air 370 metres in thickness.

These quantities of oxygen and carbon dioxide involve large transfers of gases across the surface of the sea to and from the atmosphere. Application of the evasion coefficient of C. Bohr for oxygen and of the laboratory results of Adeney and collaborators (1918 *et seq.*) for the rate of absorption of oxygen by sea-water, show that the loss of oxygen can be easily accounted for. For carbon dioxide, however, the case is quite otherwise.

According to the invasion coefficient of Bohr (quoted by Krogh, 1904), the total volume of carbon dioxide invaded,

$$V = \gamma(P_a - P_w)t \text{ c.c. per sq. cm. of surface,}$$

where γ = invasion coefficient
P_a = partial pressure of CO_2 in the atmosphere
P_w = ,, ,, ,, ,, surface of the sea
t = time in minutes
γ for $CO_2 = 0{\cdot}1$ (Bohr, cited by Krogh, 1904).
P_a has been taken as $2{\cdot}95 \times 10^{-4}$ atmosphere.

In Fig. 2, the partial pressure in the 5-metre layer is plotted against time. A similar curve may be plotted for the surface. The area between this curve and a horizontal at $2{\cdot}95 \times 10^{-4}$ atmospheres (the partial pressure in the atmosphere, P_a), is a measure of $(P_a - P_w)t$ in (atmospheres $\times 10^{-4}$)-days. Between February 19th and November 30th, 1931, it amounted to 151·5 (atmospheres $\times 10^{-4}$)-days or 21·8 atmosphere-minutes. (1440 minutes=1 day.) This value may be substituted for $(P_a - P_w)t$ in the above invasion equation.

$$\therefore\ V = 0{\cdot}1 \times 21{\cdot}8 = 2{\cdot}18 \text{ c.c. per sq. cm.,}$$

or, say, 22 litres per sq. metre between the dates noted.

Since the sea-water is buffered with regard to CO_2, a fairly large amount of CO_2 may be absorbed without greatly altering the partial pressure in the surface water. But even so, and granting the applicability of the Bohr invasion coefficient and formula to the present problem, the figure, 22 litres per sq. metre, would seem to represent the maximum possible absorption. The presence of a fair amount of carbonate should not effect the initial solution of carbon dioxide which is primarily a physical transfer across the surface layer. That this is the case is supported by the work of Williamson and Mathews (1924) who found that the rate of absorption of carbon dioxide by distilled water and by solutions of potassium carbonate was dependent only on the partial pressure of the gas in the two phases and of course on the type of apparatus.

In the autumn as the water cools, oxygen will be redissolved, but this may be set off against the loss of oxygen with rising temperature in the early summer which was allowed for above.

The net result is that the amount of carbon dioxide which it would seem necessary for the sea to absorb from the atmosphere to make up for the amount converted to oxygen during photosynthesis, is six times as great as the invasion coefficient permits. But it must be remembered that, during rough weather with much churning and frothing of the surface water, the effective area of contact between air and water will be very much increased. Conditions will be very different from those of a laboratory experiment.

From another point of view also the result appears strange, for the conversion, year after year, of carbon dioxide to oxygen would lead to accumulation in the sea of organic material, which does not appear to be the case. Some other influence must therefore be at work. Since the summer of 1931 was unusually stormy in the Channel, it may have been characterised by unusually great loss of oxygen to the air from the disturbed waters. Again, there is a definite although slow drift up-Channel of water having its ultimate origin in the Atlantic, so that it may not be permissible to treat of events as occurring in a closed system. But after making all allowances, the order of magnitude of the oxygen loss in 1931 remains much the same.

VI. CALCULATION OF THE PLANKTON CROP FROM CHEMICAL DATA.

Atkins (1922) has measured the plankton crop off Plymouth from the change in CO_2 as measured by a titration method and also from change in phosphate. From the data for carbon dioxide, oxygen, phosphate, nitrate, and silicate collected in 1931, the author has made further estimates of the plankton production.

(1) *From change in carbon dioxide.*

The depth at Station L4 is about 53 metres, at E1 72 metres, and at E2 90 metres. The average depth of the Channel, determined from an Admiralty chart, between lines drawn from Dover to Cap Grisnez on the east and Land's End to Ushant on the west is about 72 metres.

The fall in carbon dioxide, determined from pH and excess base, has been measured between the winter maximum and the summer minimum. The subsequent calculation has been made as by Atkins (1922) ; 2·226 c.c. of CO_2 is equivalent to 4·4 mg. CO_2, 1·2 mg. carbon or 3·0 mg. dextrose or other hexose. Atkins used the assumption that the carbohydrates of the algal cell, including protein carbon, amount to 15% of the wet weight.

Station.	Between	Fall in CO_2 c.c./l.	Dextrose formed mg./l.	Phytoplankton formed, wet weight. g./m³.	Phytoplankton formed, wet weight. Metric tons per sq. km. of surface calculated on a mean depth of 72 m.
L4	19/2–10/7	2·4	3·24	21·6	1,550
E1	,,	2·7	3·63	24·2	1,730
E2	4/2–26/8	1·8	2·43	16·2	(1,160)
Mean					1,640

Since for E2 only quarterly data are available, it has been ignored in calculating all means. The figures are minimal since an increase in CO_2 will occur, due to respiration of plants and animals, and the gas will be dissolved from the atmosphere during the period under consideration.

(2) *From oxygen lost to the atmosphere.*

It was found above that in the course of the spring and summer, at least 110 litres of oxygen was given off from a column 1 sq. metre in cross section and 70 metres deep. This was formed from an equal volume of carbon dioxide so that by similar reasoning to the above the following calculation may be made :—

Station.	Between	Loss of O_2 litres per sq. m. × 70 m.	Dextrose formed g. per sq. m. × 70 m.	Phytoplankton formed, wet weight. Metric tons per sq. km. of surface calculated on a mean depth of 72 m.
E1	19/2–26/8	110	150	1,000

This figure is certainly too small since much of the oxygen set free by photosynthesis will be quickly re-utilised in respiration. Although based on different data, this result is not independent of (1) since certain steps in the argument are common to both.

(3) *From consumption of phosphate.*

Atkins (1923, p. 140) calculated the plankton crop from the seasonal fall in phosphate. On a similar basis the writer has arrived at the following results for 1931 :

Station.	Between	Fall in P_2O_5 mg./m³.	Phytoplankton formed, wet weight. g./m³.	Phytoplankton formed, wet weight. Metric tons per sq. km. of surface calculated on a mean depth of 72 m.
L4	19/2–10/7	22	14·8	1,070
E1	4/12–26/8	26·3	17·6	1,260
E2	4/2–26/8	19·9	13·2	(950)
Mean				1,170

(4) *From consumption of nitrate.*

In order to calculate the plankton crop from the consumption of nitrate, it is necessary to know the amount of nitrogen in a given wet weight of plankton. Suitable figures are available in "Fertilizer Resources of the United States" (U.S. Senate Document, No. 190), pp. 223–231.

As a mean of a number of analyses by Barlow, by Russell and by Tom of a number of British seaweeds, collected at different places and at different seasons, nitrogen constitutes about 2% of the dry weight. The dry weight is about 24·2% of the wet weight. This figure is based on Tom's results and was used in the above phosphate calculation. The nitrogen therefore constitutes about 0·5% of the wet weight of algæ. The extension of the result to the plankton seems admissible, so that from the known consumption of nitrate-nitrogen the minimum crop production may be calculated :—

			Phytoplankton formed, wet weight.	
Station.	Between	Fall in N mg./m³.	g./m³.	Metric tons per sq. km. of surface calculated on a mean depth of 72 m.
L4	4/12–10/7	116	23·2	1,670
E1	23/3–10/7	88	17·6	1,270
E2	4/2–26/8	39	7·8	(570)
Mean				1,470

(5) *From consumption of silicate.*

Wailes (1929) states that half a dozen nearly pure gatherings of plankton diatoms, mostly small species of Chætoceros, collected in Departure Bay, Vancouver Island, and dried for one hour at 110° C., contained on an average 40% of silica. Gatherings mostly composed of Coscinodiscus gave a percentage around 55%. When dried until there was no further loss of weight, the percentage of silica was about 75%. If the wet weight is taken as four times the dry weight, silica thus constitutes approximately 13% of the wet weight. The following calculation may therefore be made :—

			Phytoplankton formed, wet weight.	
Station.	Between	Fall in SiO_2 mg./m³.	g./m³.	Metric tons per sq. km. of surface calculated on a mean depth of 72 m.
L4	19/2–18/5	200	1·54	110
E1	13/1–18/5	208	1·60	115
Mean				110

The minimum production calculated in these five ways may be summarised :—

Basis.	Minimum production of phytoplankton wet weight, metric tons per sq. km.
CO_2	1,600
O_2	1,000
Phosphate	1,200
Nitrate	1,500
Silicate	110

The agreement between the first four of these figures is striking. The earlier calculations of Atkins gave 1,400 metric tons per sq. km., both from titration CO_2 and from phosphate. All the figures are minima and would be increased by the substances taking part in the life-cycle more than once. No exact figures for the proportion of siliceous diatoms to the total phytoplankton in 1931 are available. The above results, at first sight, point to the proportion being one-tenth or less. This is highly improbable, so that alternatively silica would seem to go through the life-cycle several times in one season. This is quite likely.

No such high concentration of plankton as here calculated is actually found at the end of the spring outburst. Some of it dies off and much of it is eaten by animals. Organic material, phosphorus and nitrogen are all required by the animals for their own purposes, and so for the time being are removed from the sea-water. But inasmuch as the animal organism requires little silica, almost the whole of it would be excreted at once. The speed with which silica can redissolve in sea-water is still a moot point, but the evidence presented in Part I, Section IV, points to re-solution being quite rapid. If then the excreted silica can be rapidly redissolved and made available for a second growth-cycle, the above low apparent crop production is explained as well as the fact that silicate in the sea is seldom found completely exhausted and functioning as a limiting factor in diatom growth.

A representative figure for the minimum phytoplankton production in the Channel would seem to be 1,400 metric tons per sq. kilometre for an area 72 metres deep. This is the average depth of the whole Channel. Its area is about 82,100 sq. kilometres. The minimum production for the whole area is therefore 115 million metric tons. It is interesting to compare this with the total landing of commercial fish from the English Channel at English and French ports during 1928 (Conseil International p. l'Expl. de la mer. Bull. Statistique des pêches maritimes, XVIII, p. 49). The amount was 71,000 metric tons. This figure seems suitable for the present purpose. Thus,

$$\frac{\text{Fish landed}}{\text{Phytoplankton produced}} = \frac{71{,}000}{115{,}000{,}000} = 0{\cdot}0006$$

Thus, only 0·06% of the phytoplankton produced each year is harvested as fish for the use of man and this in a region where the fishing has become so intense that many large English steam trawlers now find it unprofitable.

VII. Variation in Excess Base with Depth.

The most appropriate function to consider is $\frac{\text{Excess Base}}{\text{Chlorinity}} = \frac{\text{A}}{\text{Cl}}$. It will be seen from Table IV that the observed variations are small. The year has been divided into two parts, viz. (*a*) Winter, including determinations made between January 1st and April 15th and between October 10th and November 30th (6 cruises) and (*b*) Summer, including determinations made between April 16th and October 9th (6 cruises). During the winter vertical mixing is usually thorough. In the summer period, by contrast, the warmer surface water makes the water layers much more stable, so that a differential distribution is more likely to persist for a considerable time.

In Table V arithmetic means are calculated for each station and depth. When duplicate determinations of the excess base in the same sample exist, these have been treated as distinct. In the winter there was no difference between surface and bottom, but in the summer the arithmetic means showed a positive gradient downwards. The differences are admittedly small, but seem to be real, particularly as similar independent trends are shown by all four stations investigated.

The results have been examined statistically. Each group has been treated as measures of one quantity. The standard error, $\sigma_{\text{m}} = \sqrt{\frac{\Sigma \text{d}_{\text{n}}^2}{\text{n}(\text{n}-1)}}$, calculated from the observed deviations ($\text{d}_1, \text{d}_2, \ldots \text{d}_\text{n}$) from the mean, therefore incorporates experimental errors in the determination of excess base and of chlorinity and also any seasonal changes of whatever nature. For statistical purposes the distribution about the mean should be approximately normal, but this is by no means always the case. The standard error is given in each case where the number of data warrants. The observed differences between different pairs of depths are given in Table VI together with the standard error, $\sigma_{\text{m}_{\text{a}-\text{b}}} = \sqrt{\sigma^2_{\text{m}_\text{a}} + \sigma^2_{\text{m}_\text{b}}}$.

In summer at L4 and E1 the differences are as much as four times the standard error and are in the same direction. The quarterly results for E2 and the early autumn results for L6 agree very well with the more frequent determinations at L4 and E1. Some of the biggest deviations from the mean for the bottom samples (Table VII) occur in the early autumn, and it would seem very likely that these are real since regeneration and re-solution processes are very active at this season (cf. Part I).

TABLE IV.

$$\frac{\textsc{Excess Base (milli-equiv. per l.)}\times 10^4}{\textsc{Chlorinity}\ (^\circ/_{\circ\circ})}=\frac{\mathrm{A}}{\mathrm{Cl}}\times 10^4$$

		Winter.				Summer.						Winter.	
Station.	Depth.	13/1	19/2	23/3	7/4	22/4	18/5	10/7	26/8	8/9	25/9	20/10	30/11
L4	0	1237	1231	–	1223	1221 1226	1234	1228	1212 1212	1228 1225	1220 1224	1225	1228 1224
	50	1227	1232	1232	1215	1222 (1242?)	1248	1237	1230 1233	1239 1234	1236 1228	1229	1221
											(Autumn)		
L6	0	–	–	–	–	–	–	–	–	–	1224 1221	1222 1222	–
	50	–	–	–	–	–	–	–	–	–	1230 1234	1230 (1241?)	–
E1	0	1233 1215	1225 1224	1222 1223 1224	1225	1224	1224 1224	1223	1225 1215	1215 1220	1223 1220	1214 1221	1217 1217
	5	–	–	1224 1231	1225	1231	1227	1221	1216	1228	1229	1217	1224$_5$
	10	–	–	1223	–	1228	1238 1236	1222	1218	–	–	–	–
	15	–	–	–	–	–	–	–	–	1227	–	–	–
	20	–	–	–	–	–	–	1214	–	–	–	–	–
	25	1227 1227	1227 1225	1231 1226 1224	1227	1225	1229	1218	1230 1244 1244	1229	1229$_5$	1220	1226
	50	1224 1229	1228 1228	1230 1226	1219	1228	1233 1228	1219	1227 1231	1228 1231	1228	1219	1224
	68–71	1226 1218	1230 (1242?)	(1206)	1227	1236 1229	1233 1225	1218	1234 1219	1244 1244	1233 1235 1238	1222	1221
E2	0	–	–	–	–	1223	–	–	1216 1216	–	–	–	1218 1218
	5	–	–	–	–	1224	–	–	1219	–	–	–	1226
	10	–	–	–	–	1222	–	–	1232 1236	–	–	–	–
	25	–	–	–	–	1222 1238?	–	–	1227 1222	–	–	–	1226 1226
	50	–	–	–	–	1228	–	–	1223	–	–	–	1227
	70	–	–	–	–	–	–	–	1223	–	–	–	1222
	87–91	–	–	–	–	1237	–	–	1225	–	–	–	1220 1224

TABLE V.

NORMAL VARIATION OF $\frac{A}{Cl} \times 10^4$ WITH DEPTH.

Station.	Depth.	Winter. 1/1 to 15/4 and 10/10 to 30/11.			Summer. 16/4 to 9/10.			E2, Summer.		L6, Early Autumn	
		$\frac{A \times 10^4}{Cl}$	Standard Error.	N. of Detns. of A.	$\frac{A \times 10^4}{Cl}$	Standard Error.	N. of Detns. of A.	$\frac{A \times 10^4}{Cl}$	N. of Detns. of A.	$\frac{A \times 10^4}{Cl}$	N. of Detns. of A.
L4	0	1227·0	2·16	6	1221·9	1·87	10	–	–	1222	4
	50	1225·7	2·74	6	1234·9	2·32	10	–	–	1234	4
	Mean	1226·4	–	–	1227·4	–	–	–	–	–	–
E1	0	1221·7	1·59	12	1221·3	1·17	10	1218	3	–	–
	5	–	–	–	1225·3	2·12	6	1222	2	–	–
	10	–	–	–	1228·4	3·87	5	1230	3	–	–
	25	1226·2	1·01	9	1231·1	2·60	8	1227	4	–	–
	50	1225·2	1·39	9	1228·1	1·32	9	1226	2	–	–
	70	1224·0	3·64	8	1232·3	2·20	12	–	–	–	–
	Arithm. Mean	1224·3	–	–	1226·6	–	–	(90 m.) 1231	2	–	–
	Average Content of Water Column*	1224·8	–	–	1229·1	–	–	–	–	–	–
All Stations, Summer.											
	Surface	–	–	–	1221	–	–	–	–	–	–
	Bottom	–	–	–	1233	–	–	–	–	–	–

* For an explanation of this term, see p. 722.

In the statistical treatment these fluctuations have been treated as random errors, so that the standard error is increased and the normal form of distribution is upset.

TABLE VI.

Variation in Excess Base with Depth.

A positive difference means a greater value at the lower depth.
B means bottom depth.

Season.	Station.	Depths Compared (in m.).	Observed Differences and Standard Errors $\frac{A \times 10^4}{Cl}$	Significance.
Winter	L4	0 and 50(B)	$-1{\cdot}3 \pm 3{\cdot}49$	Not significant
,,	E1	0 and 70(B)	$+1{\cdot}23 \pm 3{\cdot}97$	,,
Summer	L4	0 and 50(B)	$+13{\cdot}0 \pm 3{\cdot}0$	Significant
,,	E1	0 and 70(B)	$+11{\cdot}0 \pm 2{\cdot}50$	,,
,,	,,	0 and 50	$+6{\cdot}8 \pm 1{\cdot}76$	,,
Stations not admitting statistical treatment :—				
Summer	E2	0 and 90(B)	$+13$	—
Early Autumn	L6	0 and 65(B)	$+12$	—

TABLE VII.

	Depth in m.			Depth in m.			Depth in m.		
Station		E1			L4			L6	
Date		8/9	25/9		8/9	25/9		25/9	20/10
	25	1229	1229	0	1226	1222	0	1222	1222
	50	1229	1228						
	68 or 70	1244	1235	50	1237	1232	62 or 67	1232	1230
Sounding	70 or 73			53			65 or 70		

TABLE VIII.

Variation of Calcium with Depth in Summer.

Station.	Excess of calcium at bottom over surface (with Standard Error) mg. Ca/m³.
L4	$+500 \pm 115$
E1	$+425 \pm 95$
Mean	$+460 \pm 105$

Wattenberg (1930), on the basis of work in the Atlantic, concluded that removal and solution of $CaCO_3$ was the principal cause of fluctuations in excess base. If this was the case in the English Channel, the data of Table VI may be converted to show variation of calcium content in summer with depth. Table VIII shows such data calculated for $35{\cdot}05\,^{\circ}/_{\circ\circ}$ S. ($19{\cdot}40\,^{\circ}/_{\circ\circ}$ Cl.). The average difference between the surface and bottom waters of the Channel off Plymouth in the summer of 1931 was about 460 ± 110 mg. Ca per cubic metre. On September 8th the difference between the calcium content of the 50 m. and 70 m. (bottom) layer may have been as great as 600 mg./m^3. On this date phosphate, silicate, and nitrite all showed quite marked increases towards the bottom although salinity and temperature changed little, so that regeneration of phosphate, silicate, nitrogen, and calcium seem to have been proceeding simultaneously at the bottom.

TABLE IX.

SEPTEMBER 8TH, 1931. STATION E1. (ALL IN MG./M^3.)

Depth in m.	P_2O_5	SiO_2	Nitrite N	Ca
50	9·5	165	3·6	—
70 (bottom)	13·5	220	9·8	
Difference	+4	+55	+6·2	+600 (v. approx.)

When compared with the total calcium content of sea-water of $35\,^{\circ}/_{\circ\circ}$ salinity (about $4{\cdot}2 \times 10^5$ mg./m^3) the percentage variation between surface and bottom in summer amounts to $(0{\cdot}11 \pm 0{\cdot}03)\%$.

The statistical treatment lends support to the conclusion, but it should be remembered that the number of analyses was small and the dispersion about the means was greater than was desirable. Nevertheless, it is felt that the agreement between the results for the different stations affords fairly strong evidence in favour of a slight increase in excess base between the surface and bottom in the English Channel in summer, equivalent to 0·1% of the total calcium content. To establish the conclusion with absolute certainty requires further work. The author is indebted to Mr. J. A. Harris, of Christ's College, Cambridge, for assistance in the statistical analysis of the results.

VIII. METHODS.

Concentration of Hydrogen Ion. Measurements of pH have been made colorimetrically with McClendon (1917) boric-borate buffers as described by Atkins (1923, Part II). In general, cresol red has been used as indicator with thymol blue and xylenol blue for confirmatory determinations over the more alkaline range. Since the buffers contain the appropriate amount of sodium chloride, salt error is automatically corrected for when salinity is near to $35{\cdot}2\,^{\circ}/_{\circ\circ}$. Samples have been preserved on collection with mercuric chloride (4 drops of saturated solution per 170 c.c.) and brought to the Laboratory in the standard dark green bottles, full or with but a small air space over the water. The pH was commonly determined the same night or occasionally on the following morning. Under these conditions Ibañez (1931) has shown that there is little or no change in the CO_2 content of the water.

The temperature of the Laboratory is usually higher than that of the sea. Buch (1929, 1 and 2) has shown that when loss or gain of CO_2 is precluded :—

$$pH_w = pH_b + \alpha(t_b - t_w) + \beta(t'_w - t_w)$$

where t_w = temperature of water on collection
t'_w = ,, ,, when compared
t_b = ,, buffer ,, ,,
pH_w = pH of water at temperature t_w
pH_b = pH of buffer at temperature t_b.

In the present case $t'_w = t_b$ = temperature of the Laboratory

$$\therefore \quad pH_w = pH_b + (\alpha + \beta)(t_b - t_w)$$

i.e. a positive correction factor must be applied when the temperature of the Laboratory is above that of the sea.

When cresol red is used $(\alpha+\beta) = +0{\cdot}011$.

This correction, which is based on an extensive spectrophotometric and electrometric examination, is in the opposite direction to that of McClendon (1917), which is for carbon dioxide equilibrium at the temperature of the water. In Tables I to III, the values of pH observed at the temperature of the Laboratory have been corrected by the Buch factor to the pH at the temperature of collection.

The value, pH_w, has a real physical meaning since it is the actual pH of the water in the sea. Since the interpolation tables of Buch, Harvey, Wattenberg, and Gripenberg (1932) take account of temperature, it is most suitable for calculation of the partial pressure and total amount of carbon dioxide.

But comparison of the pH values amongst themselves can only be made if all readings are corrected to a standard temperature. The temperature, 12°, is convenient since it is roughly the middle point of the annual range. The true pH of sea-water decreases by 0·011 unit for a rise of temperature of 1° C.

Chlorinity and excess base, which also affect pH, may, for this purpose, be taken as practically constant at Station E1. At L4, however, there may be a small error involved. The figures for pH_{12° are intended to show variations due to biological activity and exchange of CO_2 with the atmosphere independently of temperature changes.

In a private communication received since this paper went to press, Buch and Gripenberg suggest that the following temperature corrections should be applied :—

(1) The Walbum correction, if the buffers do not have the same

temperature as that at which they were calibrated (positive if $t_{calibr.}>t_b$) (Buch, 1929, (2)).

(2) Correction α to correct for indicator displacement if the water and the buffers have different temperatures (positive if $t_b>t'_w$).

(3) Correction 0·011 if the pH of the water at any other temperature (e.g. *in situ* or at 12°) is wanted.

In the present case (2) does not apply. The third correction is equivalent to that actually made above. The Walbum correction (which was worked out for Sörensen's borate–HCl buffers) was not made. It probably applies also to McClendon's buffers. These were calibrated at 20°. To make the Walbum correction, the following factors must be added to the figures given in Tables I to III and the curves in Fig. 1 must be moved to the right by the same amount:—Nov. 11, 1930, to Feb. 19, 1931, April 22 and Nov. 30, 1931, 0·03 unit; April 7, May 18, Sept. 25 and Oct. 20, 0·02 unit; Mar. 23 and Aug. 26, 0·01 unit; and July 10, nil.

Oxygen has been determined by Winkler's method. No correction has been applied to compensate for the volume of sea-water displaced by the reagents without reaction therewith. If made it would increase all values by about 0·07 c.c. per litre. Fox's table (1907) has been used for calculating the saturation values at the temperature and salinity found at the surface on each occasion. Most of the results appear to be accurate to within ±0·03 c.c./1. But on one or two cruises, when working conditions on the ship were not of the best, considerably greater differences between duplicates were shown.

Excess base (Alkalinität) has been determined by Wattenberg's method (1930).

IX. SUMMARY.

(1) In general, the changes in pH were similar to those observed in previous years. On six occasions the pH at the surface at Station L4 was lower than at the bottom.

(2) The changes in carbon dioxide in the spring agree with the conclusion, formed in Part I from nutrient salt data, that the early start in plant production in mid-Channel was not maintained and that by the middle of April production had become much greater nearer the shore.

(3) The partial pressure of CO_2 during nine months out of twelve has been observed to be lower than that of the atmosphere and equal or slightly higher during the remaining three months.

(4) It is suggested that the fall in (Total CO_2+O_2) during the course of

the summer was due mostly to loss of oxygen to the atmosphere. After allowing for carbon dioxide possibly removed from the sea as calcium carbonate and for the loss of oxygen due solely to rising temperature of the water, a net loss of 110 litres of oxygen was found from a column 1 sq. metre in cross-section and 70 metres deep; or 9 cubic kilometres from the whole of the Channel. If this is regarded as a closed system, the oxygen must have been formed during photosynthesis from an equal volume of CO_2 dissolved from the atmosphere. But the required transfer of CO_2 across the surface of the sea is too great to be accounted for by existing data on the rate of invasion of CO_2 into sea-water as calculated for a small bubble of gas in water.

(5) Estimates of the phytoplankton crop have been made, based on the seasonal consumption of carbon dioxide, of phosphate and of nitrate and on the oxygen lost to the atmosphere. All four are of the order of 1,400 metric tons wet weight per sq. km. of surface, in close agreement with the figure calculated by Atkins. The crop production calculated from consumption of silicate is less than one-tenth of this. This is attributed not only to the presence of planktonic organisms requiring no silica but to the silicate being used several times over in the course of the season.

(6) About 0·06% of the wet weight of phytoplankton produced is harvested as fish.

(7) A small variation in excess base, equivalent to about 0·1% of the total calcium present, has been detected between the surface and bottom in summer. The result requires confirmation.

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