

THE DISTRIBUTION OF SOME PLANKTON ANIMALS IN THE ENGLISH CHANNEL AND APPROACHES

II. SURVEYS WITH THE GULF III HIGH-SPEED SAMPLER, 1958-60

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(Plate I and Text-figs. 1-26)

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In discussing the results of sampling with stramin nets in earlier years (Southward, 1961) it was noted that the 'western' plankton of Russell (1935*b*, 1936*b*, *c*) was to be considered more as north-western with regard to the Plymouth area. It was suggested that changes in macroplankton populations off Plymouth during the past 50-60 years were due, in part at least, to an advance of the northern limit of southern forms and a corresponding retreat of northern forms as the sea warmed up during the period.

More evidence was needed for this hypothesis, and sampling was obviously required over large areas, notably to the north-west and south-west of the entrance to the Channel, in order to trace the origin of northern and southern species respectively. For such work new methods of quick survey were needed, and during 1957-58 trials were carried out to find a suitable gear with which to replace the stramin nets. The decision to stop work with the ring trawl was taken with great reluctance in view of the amount of sampling carried out previously (for references, see Part I), and one of the factors governing the choice of a new net was that it must provide a reasonable sample of the type of organisms captured by the ring trawl. After several trial cruises the modified Gulf III sampler described below was selected. This instrument takes satisfactory samples of the larger macroplankton species used as indicators in previous work, is quicker and easier to use, and gives more consistent results.

During 1958, 1959 and part of 1960, fifteen cruises, of varying length, were made with the Gulf III sampler, each cruise being fitted into the programme of R.V. 'Sarsia' when she was free of other work. No sampling was ever possible in April, August or September. More trips were available in the winter half of the year (10) than in the summer (5), since fewer other scientists wished to go to sea in the winter. The relative sparseness of summer samples causes some difficulty in comparing the results with earlier work and when trying to elucidate seasonal changes.

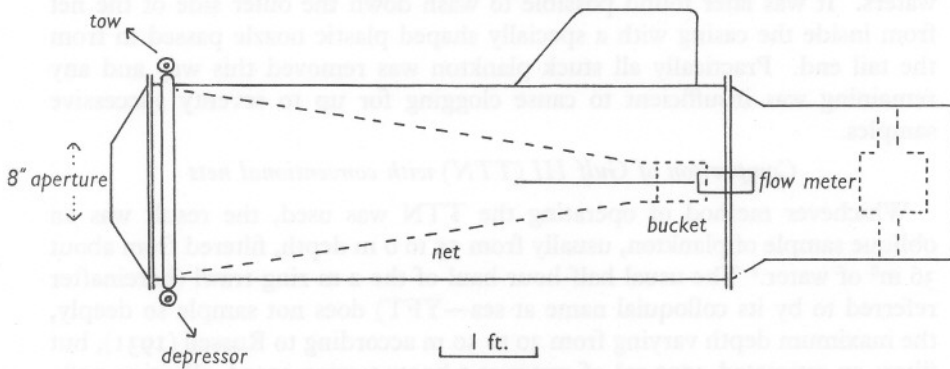
Many people have assisted me in various ways to carry out the field-work and prepare this account. I am indebted to Dr F. S. Russell for much discussion; the Director of Fisheries Research, Ministry of Agriculture, Fisheries and Food, for loan of equipment and permission to take part in a cruise of F.R.V. 'Sir Lancelot'; Dr D. H. Cushing, Mr A. C. Burd and Mr J. Bridger of the Pelagic section of the Fisheries Laboratory at Lowestoft for generous advice and supply of high-speed plankton samples; Mr A. J. Lee and the staff of the Hydrographic section at Lowestoft for analyses and supply of hydrographic data; Dr G. Hempel of the Biologisches Anstalt, Helgoland, for high-speed samples taken by F.F.S. 'Anton Dohrn'; Mr R. S. Glover, Dr B. Bary, and Dr M. H. Williamson of the Oceanographic Laboratory, Edinburgh, for advice on high-speed sampling and loan of equipment; Dr D. I. Williamson, Mr N. A. Holme, and Mr P. Foxton for helping in sampling; Mr G. M. Spooner for identifying Amphipoda, and Mr J. H. Wickstead for advice on copepods. Mr F. A. J. Armstrong and Mr E. I. Butler have carried out various analyses and dealt with the supply of hydrographic gear, while Mr A. D. Mattacola and Mr A. E. Stoaate have given invaluable assistance at sea. Mr G. C. Battin has greatly improved the original charts and other figures. Finally I would like to thank Lt.-Cdr. C. A. Hoodless, R.N.R. and

the crew of R.V. 'Sarsia' for their labours, often short-handed, in all weathers, on work that was not contemplated when the ship was designed.

The manuscript has been read and criticized by Dr D. I. Williamson, to whom I am indebted for invaluable suggestions.

METHODS

The original Gulf III high-speed sampler was described in a preliminary report by the designer (Gehringer, 1952). It was later modified by Bridger (1958) for quantitative sampling of young clupeoids, and in modified form is now in use for young-fish sampling by several workers in N.W. Europe (e.g. Hempel, 1959). In principle the modified Gulf III (hereinafter referred to by its colloquial name at sea, TTN = tin tow-net) is similar to all high-speed samplers (see, for example, Hardy, 1936; Glover, 1953; Bary, de Stefano, Forsyth & van den Kerkhof, 1958; Ahlstrom, Isaacs, Thraillkill & Kidd, 1958).



Text-fig. 1. Diagram of modified Gulf III high-speed sampler or TTN.

The instrument is towed faster than conventional nets, water is admitted by a narrow opening which is *in front* of the towing wire, and the plankton is filtered off by a stout net of proportionately large area (Text-fig. 1). The standard TTN has a galvanized steel outer casing fitted with an inner net of monel metal mesh (*ca.* 40 m.p.i.) ending in a detachable bucket of the same metal. The nose cone has an aperture of 8 in. diameter. The tail cone, of 18 in. internal diameter, is hinged at one side to permit easy access to the bucket and also carries the Lowestoft pattern flow-meter, which is an improved version of the Harvey net meter (Harvey, 1935).

The TTN is forced under water on tow by a cast-bronze depressor of the Scripps Oceanographic Institution pattern (supplied by the Oceanographic Laboratory, Edinburgh) attached 1 m below, assisted by the weight of the towing wire. Two methods of sampling were used. During the first year (1958) the ship was stopped on each station: the TTN and depressor hanging

ready from the davit were then lowered quickly to 55 m, or to the bottom; the ship was restarted at 6 knots and the warp hauled in very slowly over a period of 10 min. According to depth-gauge records¹ this method gives a sample slightly biased in favour of the upper layers (0–25 m) compared with deeper water (25–55 m). After some experience, a second method was used during 1959 and 1960. The ship was merely slowed down on course to 6 knots, and the TTN payed out slowly to 180 m of wire; it was then immediately hauled in again at the same speed to give approximately 10 min in the water. The amount of warp payed out was determined by depth-gauge records, but with Sarsia's $1\frac{3}{8}$ in. circumference wire, 55 m depth was obtained with 180 m wire.

In using the TTN the net should be well washed-down before removing the sample in the bucket. In the first cruise it was found that a hose passed in from the front end was not sufficient, but Gehringer's (1952) method of complete dismantling and scrubbing down is not feasible in N.W. European waters. It was later found possible to wash down the outer side of the net from inside the casing with a specially shaped plastic nozzle passed in from the tail end. Practically all stuck plankton was removed this way and any remaining was insufficient to cause clogging for up to seventy successive samples.

Comparison of Gulf III (TTN) with conventional nets

Whichever method of operating the TTN was used, the result was an oblique sample of plankton, usually from 55 to 0 m depth, filtered from about 36 m³ of water.² The usual half-hour haul of the 2 m ring trawl (hereinafter referred to by its colloquial name at sea—YFT) does not sample so deeply, the maximum depth varying from 30 to 50 m according to Russell (1931), but filters an estimated 4000 m³ of water at 2 knots towing speed, allowing 75% efficiency. It might be expected therefore that the TTN would collect only $\frac{1}{100}$ th of a YFT sample. In practice it was found that with many organisms the TTN catch approached $\frac{1}{10}$ th that of a YFT; i.e. the whole TTN catch was equivalent to the $\frac{1}{10}$ th subsample of a YFT which is all that is normally examined under the microscope.

It is, however, difficult to compare in detail the performance of the TTN and YFT at the same station. The two instruments are used from the same winch, but on different wire, and during change-over the ship drifts many miles. Furthermore, the use of the YFT at all during the surveys was always undesirable because of the short time available as a result of the low average cruising speed of R.V. 'Sarsia' (8 knots). A few hauls of the TTN and other gear, including the YFT, were made on a few occasions, and the results are

¹ Obtained with Admiralty Pattern recorder type HC4, Mk. III; Kelvin sounding tubes were occasionally used.

² I am indebted to Mr J. Bridger for supplying me with calibrations of TTN and flow-meters. There was never time to carry these out with 'Sarsia'.

set out in Table 1. These hauls were not planned comparisons, and only single samples were taken; for this reason the table shows only species captured in reasonable numbers in both types of gear.

In the first example (Table 1), some of the *Sagitta* probably went through the YFT mesh, but this cannot have happened to the euphausiids and young clupeoids which were all much larger. The relative catch of these organisms in the TTN was considerably higher than in the YFT. In the second example,

TABLE 1. COMPARISON OF CATCHES OF PLANKTON IN GULF III SAMPLER (TTN) AND IN THE 2 M STRAMIN RING TRAWL (YFT)

(Both used obliquely.)

Species	Number in TTN reduced to meter reading of 37 m ³	Number in YFT of estimated volume 4000 m ³	Factors for same volume*
On 8. i. 58, 14.00-15.00 h			
<i>Sagitta setosa</i>	6	178	3
<i>S. elegans</i>	61	952	6
<i>Nyctiphanes couchi</i>	36	65	18
Young pilchards, 20 mm	2	65	3
On 11. iii. 60, 10.00-11.00 h			
<i>Liriope tetrphylla</i>	3	16	20
<i>Sagitta elegans</i>	13	168	9
Large copepods	13	7	200
Decapod larvae	850	6000	15
Fish eggs, including sprat	490	2400	22
Young clupeoids	5	64	8
Other young fish	13	16	90

TABLE 2. COMPARISON OF SINGLE HAULS OF GULF III (TTN) AND VERTICAL NETS

(Midnight to 01.00 h, 8. i. 58.)

Species	Number in TTN reduced to meter reading of 37 m ³	Number in vertical 1 m stramin net; volume estimated as 63 m ³	Number in Hensen net; volume estimated as 31 m ³	Factors for same volume*	
				TTN 1 m	TTN Hensen
<i>Muggiaea</i> sp.	9	8	4	2	2
<i>Sagitta setosa</i>	137	63	123	4	< 1
<i>S. elegans</i>	10	6	10	2.5	< 1
<i>Nyctiphanes couchi</i>	11	2	4	10	2.5
Mysids	10	2	2	10	5

a difference in numbers of jellyfish and decapod larvae is probably due in part to their sticking to the stramin of the YFT, which cannot be hosed down after hauling in. Some other differences are again due to mesh differences, but there remains a strong indication of greater catching power by the TTN in daylight.

On another occasion the TTN was used at night together with vertical hauls of the 1 m stramin net and the 70 cm International Hensen Net (Table 2).

* That is, number in TTN divided by number in YFT or other nets for same volume.

There was no significant difference in numbers of *Sagitta* caught by the TTN and Hensen nets, which suggests that the smaller catch of the stramin net was due to the wide mesh. However, with fast-moving euphausiids and mysids both slowly hauled nets were inferior to the TTN. The relatively higher catch in the Hensen net compared with the 1 m net probably reflects the more efficient filtration ratio of the former and better retention of the catch by the nose cone.

On another cruise hauls of 'side-pin' samplers of the Hardy indicator pattern (Glover, 1953), towed at $8\frac{1}{2}$ knots, were taken within short distances of TTN stations. The number of organisms caught was very small, and it is not easy to compare horizontal with oblique hauls, nevertheless, for some species it appeared that from 2 to 10 times as many were captured by the side-pin samplers. Though towed at only 6 knots, a fully streamlined and slightly smaller version of the Gulf III (Bary *et al.*, 1958) was capable of catching about twice the quantity of some species compared with the standard TTN (pers. commun. Dr B. M. Bary). From these results it appears that both increased speed of towing and streamlining of samplers can increase the catch of macroplankton organisms. Presumably, a reduction in the shock-wave which is believed to precede the nose cone is as important as high speed in preventing evasion by fast-moving animals, while a smoother internal flow would be expected to increase filtration efficiency.

Even the standard TTN, crude though it is, indicates a greater apparent density of organisms than do tow-net samples (Cushing & Richardson, 1956), and a re-appraisal of production data for inshore waters is probably needed.

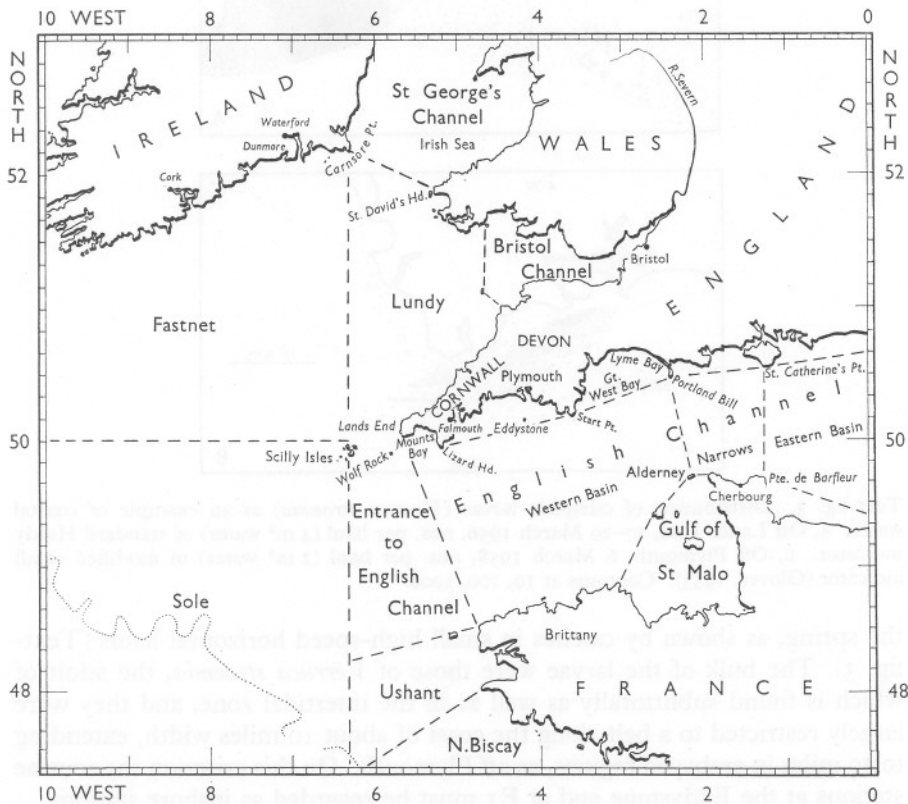
Echo-sounding

The echo-sounder is the only instrument capable of giving an indication of the extent of the shoals of pelagic fish which prey on macroplankton (Hodgson, 1950; Richardson, 1951; Cushing, 1952; Cushing & Richardson, 1955; Cushing, 1957*a*). Work since the war has shown how large these shoals may be, both adult fish and young too agile to be captured by conventional nets (Hodgson & Richardson, 1948; Burd & Lee, 1951; Cushing, 1957*b*). 'Sarsia' is not fitted with an echo-sounder capable of showing fish in detail and recording scattering layers. However, records were taken from time to time with two dry-paper 15 kc/s units, a Marconi Graphette and Kelvin and Hughes MS 26B, neither working at full efficiency. When both were run together they gave substantially similar records of the larger fish shoals, hence it was possible to employ one when the other broke down at sea. Any scattering-layer records are noted in the text where appropriate (see also Appendix, p. 373); the fish shoals were analysed in the usual way as echo units (mm of trace thickness—see Cushing, 1952, 1957*a*; Tungate, 1958; Richardson, Cushing, Harden-Jones, Beverton & Blacker, 1959) but for convenience are reported as units between stations rather than

for a given distance, most of the stations on each cruise being spaced at even intervals. The trace thicknesses reported are very much less than those that would be shown on a wet-paper recorder, in which the paper speed is usually much higher.

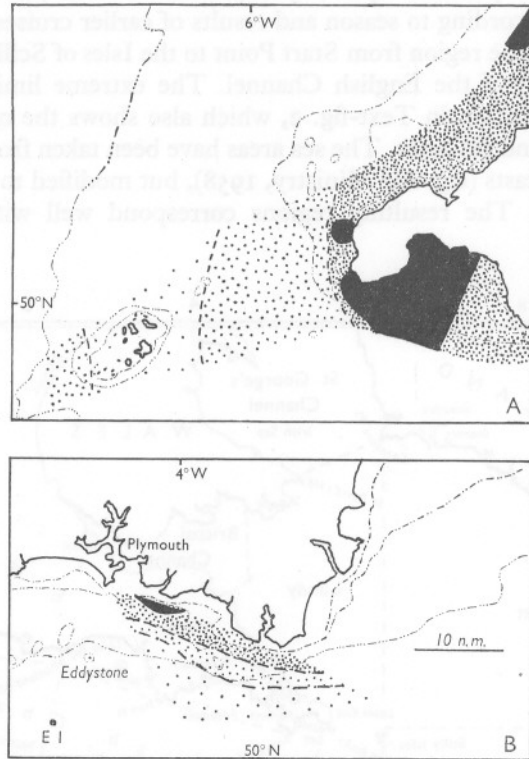
Area sampled

Each cruise was planned separately to provide the best information in the time available, according to season and results of earlier cruises. Most attention was given to the region from Start Point to the Isles of Scilly and part way across the mouth of the English Channel. The extreme limits of the area investigated are shown in Text-fig. 2, which also shows the names used for coastal features and sea areas. The sea areas have been taken from those in use for weather forecasts (e.g. Air Ministry, 1958), but modified to fit better with natural features. The resulting regions correspond well with major zooplankton areas.



Text-fig. 2. The extreme limits of the area investigated in 1958-60. The names used for sea areas are based on those used for weather forecasts (Air Ministry, 1958).

Except for a few occasions, notably during work off the south-east coast of Ireland in collaboration with the Fisheries Laboratory, Lowestoft, stations were kept well clear of the land to reduce the effect of inshore factors. The chief criterion of inshore waters, in the present instance, is the occurrence of large numbers of larvae hatched in the intertidal and immediately sublittoral zones. Such waters can be defined by the distribution of cirripede larvae in



Text-fig. 3. Distribution of cirripede larvae (*Verruca stroemia*) as an example of coastal water. A, Off Lands End, 27–29 March 1956, nos. per haul (4 m^3 water) of standard Hardy indicator. B, Off Plymouth, 6 March 1958, nos. per haul (2 m^3 water) of modified small indicator (Glover, 1953). Contours at 10, 100, 1000.

the spring, as shown by catches in small high-speed horizontal hauls (Text-fig. 3). The bulk of the larvae were those of *Verruca stroemia*, the adult of which is found sublittorally as well as in the intertidal zone, and they were largely restricted to a belt along the coast of about 10 miles width, extending to 20 miles in embayed regions, as off Plymouth. On this criterion the routine stations at the Eddystone and at E I must be regarded as inshore stations.

The species investigated

The preserved samples were subsampled whenever possible, but for the more critical indicator species the whole sample was examined (see Part I). Time was not available for identification of many species of medusae, small copepods, decapod larvae, fish eggs, and young fish. Only four to five copepods were run down to species, the rest being lumped into larger and smaller sizes to give a rough guide to standing crop. However, most of the indicator species used by Russell (1935*b*) have been included, and any deficiency has been made up by the inclusion of small forms not taken by the YFT. One of them, the larva of a lamellibranch, has not yet been identified.

The species¹ observed regularly are listed in Table 3, grouped into categories according to their general geographical distribution in relation to the English Channel. More attention has been paid than previously to defining the north-south distribution, since the mouth of the Channel forms the boundary of many northern and southern forms. Without such a definition the attribution 'Atlantic' to a species could cover all categories from tropical-warm-water to arctic-cold-water, according to the depth at which the species was living in the ocean. The grouping is partly based on Ostenfeld (1931) and Russell (1936*a*) but has been altered to fit recent observations. It is not to be taken as necessarily applying to any other sea area outside the English Channel and Approaches.

Some points in connexion with individual species of the table may be mentioned.

Doliolum species were not identified, but all are regarded as tropical-subtropical by Ostenfeld (1931) and warm-water Atlantic by Russell (1936*a*). *Muggiaea* species are not designated in the text but all found in 1958-60 appeared to be referable to *M. kochi*. Russell (1934) regarded both *M. kochi* and *M. atlantica* as warm-water species found in some coastal waters as well as the ocean, but noted that off Plymouth *M. atlantica* was replaced by *M. kochi* from 1925 onwards. Corbin (1947) reported mainly *M. atlantica* in 1937-39, and pointed out that the facility of *Muggiaea* for rapid reproduction made caution necessary in ascribing distribution patterns to water movements. *M. atlantica* was still dominant in 1946 (Russell, 1947).

Apherusa species, probably mainly *A. clevei* and *A. ovalipes*, made up the bulk of total Amphipoda other than hyperiids, but the samples included a few specimens of other genera. Of *Centropages* species, *C. typicus* was the commonest form, but small numbers of *C. bradyi* and *C. hamatus* may have escaped notice. The latter were recorded in number on one cruise only. *Nyctiphanes couchi* can occur in large numbers in association with N2 and N3 group forms, particularly in the Fastnet area, and probably for this reason was regarded as oceanic² by Russell (1936*a*). The distribution found in 1958-60 agrees well with Ostenfeld (1931), who noted it as a temperate species with restricted temperature/salinity requirements indigenous to the western basin and Fastnet areas, and penetrating into the North Sea in winter. It is now regularly found in the North Sea

¹ Names of species are those used in the Plymouth Marine Fauna (Marine Biological Association, 1957), except for *Parathemisto* (Bowman, 1960).

² But noted as the least oceanic of the euphausiids.

TABLE 3. GROUPING OF INDICATOR SPECIES ACCORDING TO GEOGRAPHICAL DISTRIBUTION

SOUTHERN FORMS		NORTHERN FORMS	
S1	Oceanic, but not really enough evidence to determine distribution off English Channel with any certainty: <i>Sagitta serratodentata</i> <i>Salpa</i> species		N1
	<i>Rhincalanus nasutus</i> <i>Candacia</i> sp. (not <i>armata</i>)		North-western forms only common to north and west of English Channel entrance, and not occurring in the Channel with any regularity. Present in coastal water of Fastnet area and in Irish Sea; some also taken in deeper water over the edge of the continental shelf to the west:
S2	South-western oceanic forms of fairly regular occurrence off the English Channel: <i>Liriope tetraphylla</i> larva of a lamellibranch		
	<i>Doliolum</i> spp.		<i>Tomopteris helgolandica</i> <i>Meganyctiphanes norvegica</i> <i>Spiratella retroversa</i>
S3	South-western warmer water species present for long periods in the western basin and N. Biscay, and capable of breeding there: <i>Muggiaea</i> spp. <i>Euchaeta hebes</i>		
	<i>Spiratella lesueuri</i>		N2 Forms as N1, but not present in the Irish Sea, and not abundant in Fastnet area every year: <i>Aglantha digitale</i> larva of <i>Luidia sarsi</i>
S4	Western basin species, present there all year round, but often more common in the colder months off the south-west entrance: <i>Apherusa</i> spp. <i>Nyctiphanes couchi</i>		
	<i>Centropages typicus</i>		N3 Northern forms occurring regularly in western basin each year, but otherwise as N1: <i>Sagitta elegans</i>
S5	English Channel neritic species; largely restricted to eastern basin: <i>Centropages hamatus</i>		This northern group includes herring, <i>Clupea harengus</i>
S5a	As S5, but occurring regularly along the northern side of the western basin and farther north, but not north of northern North Sea: <i>Sagitta setosa</i>		
The southern group also includes pilchard, <i>Sardina pilchardus</i>			
			FORMS OF UNCERTAIN NORTH-SOUTH DISTRIBUTION
			X1 Appearing often as N3, but sometimes as S4: <i>Candacia armata</i>
			X2 Present as N1 in summer, but more often as S3: <i>Parathemisto gracilipes</i>

independently of the English Channel stock (see p. 347). The genus as a whole seems to be of warm-temperate distribution (Hedgpeth, 1957). *Sagitta setosa* is best regarded as a temperate species with restricted range, and restricted temperature requirements with rather high maxima. It is not entirely coastal.

The adults of *Luidia sarsi* are definitely of northern distribution with regard to Plymouth (cf. Mortensen, 1927); they can be taken along the continental slope as far south as 48° 30' N. at 10° W. (personal observations). *Nanomia* species were not identified; counts refer to terminal floats of the colonies, not isolated nectophores. One species is apparently indigenous to the Fastnet area, but others are possibly present in the area investigated, and forms referable to *Physophora* and *Agalma* may be included. *Thysanoessa inermis* was not captured very often, but like *Meganyctiphanes norvegica* it appears to be indigenous to the Fastnet area. Unlike the latter it is not common in Lundy or the entrance to St George's Channel. It is probably a stenothermal arctic-boreal species with low temperature optima (Ostenfeld), fully neritic in the Arctic, and is certainly not oceanic. *Spiratella retroversa* was regarded as north-boreal-oceanic by Ostenfeld (1931), with a southern limit off the Brittany coast. It appears to be indigenous, in some years at any rate, to the Fastnet area, and a comparable centre of abundance is found in certain north and central parts of the North Sea (Vane, 1961).

Sagitta elegans is also at the southern limit of its distribution at the entrance to the English Channel. Regarded as a north boreal Atlantic species by Russell (1936a), it is perhaps more truly a boreal-arctic species with a low temperature optimum. It is present in inshore waters in the Arctic, Baltic Sea, North Sea and Fastnet area. *Parathemisto (Euthemisto) gracilipes* was regarded with some suspicion by Ostenfeld (1931), because of the doubtful identity of this and other species of the genus recorded in earlier years of the International Investigations (e.g. Gough, 1907). Those recorded included *P. gaudichaudi* (as *E. compressa*) which is a northern form (Hurley, 1955; Bowman, 1960) and *P. oblivia*, now regarded as a synonym of *P. gracilipes*. The latter species was the only one found in the 'twenties and 'thirties (Russell, 1937; pers. commun.). As far as can be ascertained only *P. gracilipes* was present in 1958-60; it should be classed as a southern form, in contrast to *P. gaudichaudi* which does not apparently occur in the area now, although shown on a chart by Bowman (1960).

It will be seen from the table and the above notes that some revision of the 'indicator species' concept is needed. Many species show obvious temperature relationships, and each sea area must be judged by itself. For example, salps are called oceanic off Britain, but are neritic in the Mediterranean, and almost so in Biscay; *Thysanoessa* could be called oceanic at times off the entrance to the English Channel but is neritic in the Arctic. For the Plymouth area the following species best fulfil requirements of indicator species:

Salpa spp. (S1); *Liriope tetrphylla* and *Doliolum* (S2); *Euchaeta hebes* (S3); *Sagitta setosa* (S5a); *S. elegans* (N3); *Tomopteris helgolandica* and *Spiratella retroversa* (N1); *Aglantha digitale* and larvae of *Luidia sarsi* (N2).

They do not meet all the requirements of a good indicator species which are: that it should be common enough in all samples from an area; easy to pick out under low magnification; capable of being linked with some projected centre

of origin or abundance from which it spreads or is dispersed; and it should not have too much facility for rapid reproduction.

The indicator concept assumes that a species is associated with some particular body of water, through temperature, salinity, nutritional or other ecological factors possessed by the water. An extension of the area occupied by the species then means under this concept either a movement of the particular body of water or a change in the character of an adjacent body of water permitting the species to live there. It is also assumed that when water movement ceases or conditions revert the indicator species disappears more or less completely.

RESULTS

The counts of organisms were corrected either to a flow-meter reading of 1200 revolutions¹ ($\equiv 36\text{--}37\text{ m}^3$ of water) or, in the absence of a flow-meter, a towing time of 10 min (very approx. 36 m^3). All 'Sir Lancelot' samples were converted to 1200 revs., but the 'Anton Dohrn' samples were corrected for time only. The corrected figures have been tabulated in full, and copies deposited for reference in the Library of the Marine Biological Association at Plymouth. Contoured maps derived from the tables are presented here instead (Text-figs. 4-17). Some hydrographic evidence is also shown as contoured maps, either based on Smed (1958, 1959), or on observations made during the cruises, supplemented by data supplied by the Fisheries Laboratory, Lowestoft.

The positions of the plankton stations are shown on the hydrographic maps, but the positions of other hydrographic observations used to construct the maps are omitted. With one or two exceptions due to lack of space, the species maps are arranged in systematic order for each cruise.²

Results of approximately monthly samples taken with the YFT at the inshore stations E1 and Eddystone are given separately (Tables 4-6). The more interesting features of the maps and tables are noted below, by years.

1958

In the first part of this series (Southward, 1961) it was stated that 'western' forms did not appear at the Plymouth stations in the autumn of 1957, although they were present at a station 30 miles south of the Lizard in September. These forms can now be referred to as north-western forms, in accordance with Table 3.

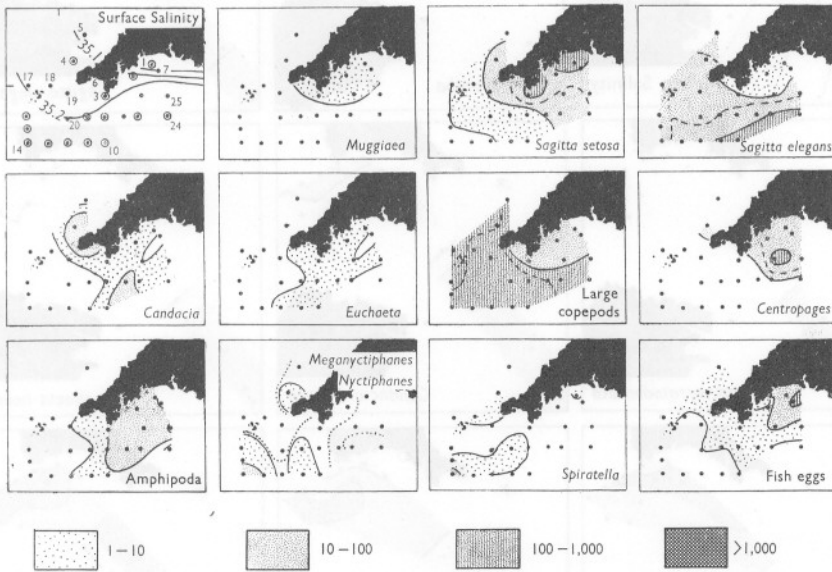
January

On the cruise in January 1958 fairly large numbers of *Sagitta elegans* were taken towards the centre of the western basin from due south of Plymouth to

¹ Mark 4 version of the Lowestoft flow-meter, now obsolete.

² For cruises requiring more than one page for the maps, the first time a species is mentioned it is followed by a reference to the page on which the appropriate map is figured.

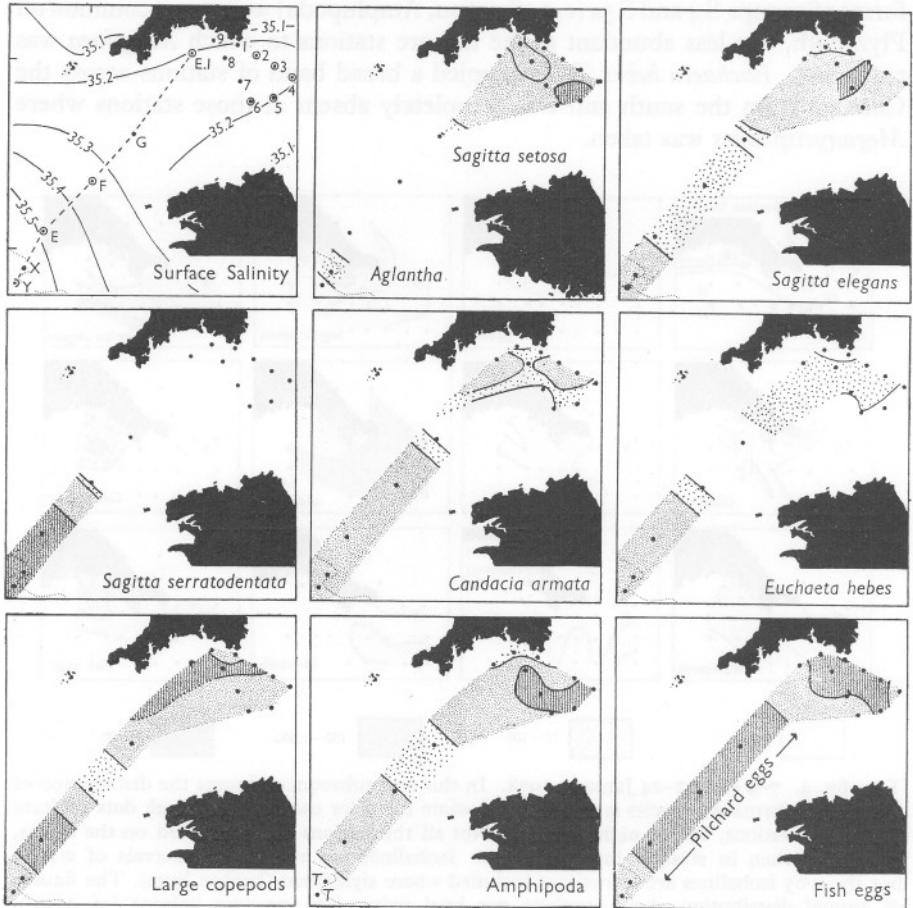
off Lands End (Text-fig. 4, p. 288). Other north-western forms were lacking, except at the most westerly stations where a few *Spiratella retroversa* and *Meganctiphanes* were found. The presence of the latter species south of the Scilly-Lands End passage is a comparatively rare occurrence; from the chart it will be seen that it was not taken in all hauls in which the other euphausiid, *Nyctiphanes*, was common (i.e. the night stations). More typical Channel forms of groups S4 and S5a (e.g. *S. setosa*, Amphipoda) were most common off Plymouth, but less abundant at the inshore stations to which *Muggiaea* was restricted. *Euchaeta hebes* (S3) occupied a broad band of stations across the Channel from the south and was completely absent at those stations where *Meganctiphanes* was taken.



Text-fig. 4. 7-9 and 22-24 January 1958. In this and subsequent figures the distribution of the more informative species is shown on separate maps for each cruise. Black dots indicate TTN day stations, circles night stations. Not all the stations are numbered on the charts, especially when in straight line sequences. Isohalines are usually at intervals of 0.1‰, but the 0.05 isohalines are sometimes included where significant (broken lines). The figures of animal distribution show numbers per haul reduced to constant volume (36-37m³), with contours and stippling at intervals of 1, 10, 100, 1000. Where significant, additional contours of approximate log values of 3, 30 and 300 are given for some species (broken lines). To economize on space some maps show more than one species: *Meganctiphanes* is shown as stipple, with the presence of adult *Nyctiphanes* also indicated (dotted lines).

None of the distributions in January 1958 is relatable to the very simple hydrographic pattern shown. By deduction, however, it is suggested that some movement had occurred from the north, possibly from the entrance to the Bristol Channel. Such 'meganctiphanes' water, though containing a

pure community of *Sagitta elegans*, was less rich in numbers of that species than water farther east in the western basin, and appeared to be comparatively poor in standing crop. From the distribution of fish eggs, the main population of breeding fish was present in Channel plankton off Plymouth. Pelagic fish were scarce, echo traces being found near Sts. 1, 7 and 19, again in typical Channel plankton, but extending to the edge of the rich patch of *S. elegans*.



Text-fig. 5. 5-6 and 18-19 March 1958. The dotted line joins a group of stations sampled by standard half-hour hauls of the 2 m stramin net. The catch from these hauls has been divided by 10 to agree with neighbouring TTN stations, although theoretically a factor of 1/100 should be used (see p. 278). T, presence of *Parathemisto* among amphipods.

February

All *Sagitta* were scarce in the YFT samples taken at the Plymouth inshore stations in February: a few south-western forms were present, with considerable numbers of fish eggs and clupeoid larvae (probably *Clupea sprattus*).

March

By March more north-western forms were found off Plymouth, and large numbers of *Sagitta elegans* were taken as far east as Start Point (Text-fig. 5, p. 289). Although sampling was very incomplete it appears that the north-western forms were restricted to the northern half of the western basin; *S. elegans* was comparatively scarce on the line of stations to the south-west, where *S. serratodentata* was dominant as far in as Ushant. Southern forms were poorly represented in the Channel, but *Euchaeta* was common south-west of Ushant. The typical Channel forms such as *S. setosa* and Amphipoda occurred together with *S. elegans* in the western basin, and showed no clear trend.

The YFT hauls at Stations E, F and G contained large numbers of pilchard eggs, and the adult pilchard were probably responsible for the lack of other macroplankton at these stations. Fish eggs other than pilchard were restricted to the remaining stations, with a maximum density off Start Point.

At the end of March small numbers of *S. elegans* and a lone *Parathemisto* were captured off the Eddystone, in an otherwise sparse macroplankton. A few pilchard eggs were found at E1 on the same date, and thereafter, as in previous years, pilchard dominated the local plankton until the autumn.

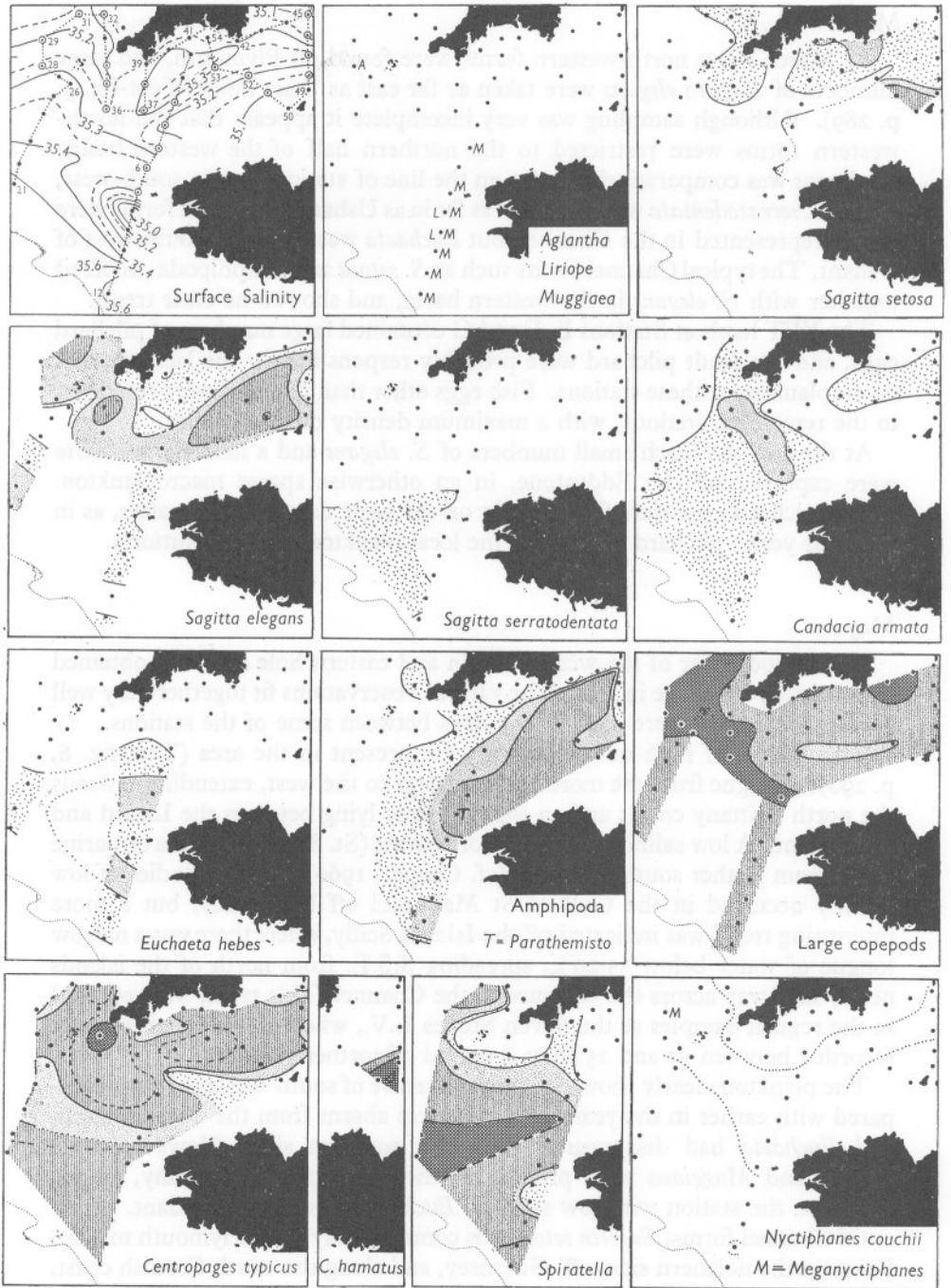
May

Quite good cover of the western basin and eastern Sole area was obtained from a two-part cruise in May. The various observations fit together very well even though there were gaps of 5-7 days between some of the stations.

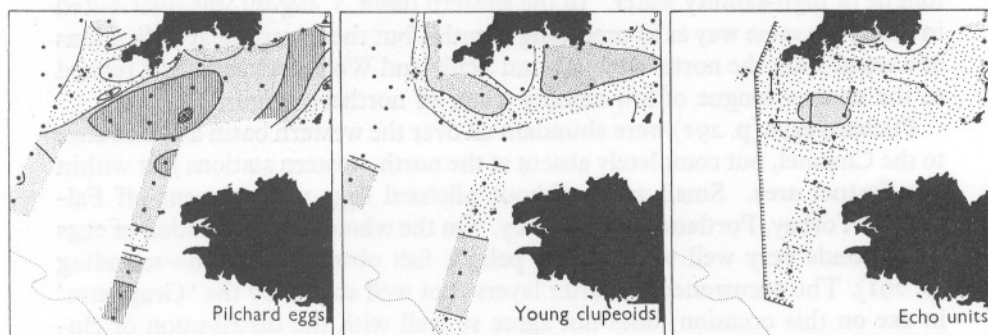
Two bodies of high-salinity water were present in the area (Text-fig. 6, p. 290): a tongue from the more oceanic water to the west, extending towards the north Brittany coast; and an isolated mass lying between the Lizard and Start Point. A low salinity area south of Ushant (St. 8) may indicate estuarine water from farther south in Biscay (cf. Cooper, 1960*b*). Other bodies of low salinity occurred in the Gulf of St Malo and off Lyme Bay, but a more interesting trend was indicated off the Isles of Scilly, where there was a narrow tongue of water below 35.20‰ spreading S.S.E. from north of the islands nearly half-way across the entrance to the Channel. This trend was reflected in the regular samples at the Seven Stones L.V., where lower salinities were recorded between 17 and 25 May, a period of northerly winds.

The plankton clearly shows a further decrease of south-western forms compared with earlier in the year. *Muggiaea* was absent from the western basin, and *Euchaeta* had disappeared from the northern side. However, both *Liriope* and *Muggiaea* were present off the west coast of Brittany, where, except at the station with low salinity, *Euchaeta* was most abundant.

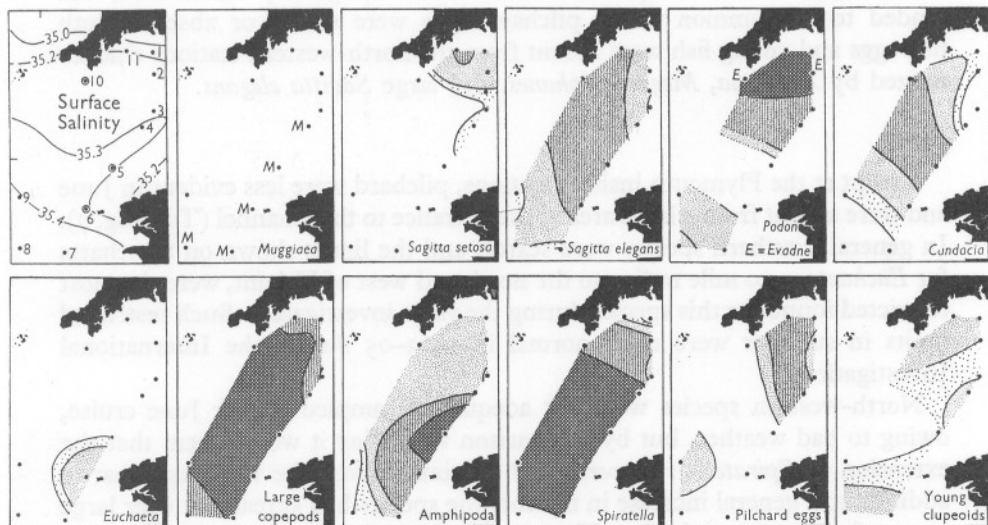
Of Channel forms, *Sagitta setosa* was common only from Plymouth to Start Point on the northern side, off Guernsey, and along the north Cornish coast.



Text-fig. 6 (part). For legend see facing page.



Text-fig. 6. 12-20 and 27-30 May 1958. In this and subsequent text-figures the hydrographic data includes much of the routine surface stations worked by MAFF, but space does not permit their positions being shown on the maps.



Text-fig. 7. 23-27 June 1958.

In contrast, Amphipoda and *Centropages typicus* were abundant all over the western basin, except off Guernsey where the latter species was replaced by *C. hamatus*.

North-western forms were quite common in the area, but their distributions were not in full agreement. *Aglantha* and *Meganyctiphanes* were truly north-western and found only at St. 29. *Spiratella retroversa*, however, was abundant both to the north-west and to the south-west, the trend of the contours suggesting that a big influx had occurred earlier from the west and north, the southernmost trend possibly in association with the indicated

tongue of high-salinity water. In the western basin *S. elegans* was distributed in much the same way as in preceding months, but there were clear indications of a trend from the north-west, around Scilly and Wolf Rock, possibly related to the narrow tongue of low-salinity water of northern origin.

Pilchard eggs (p. 291) were abundant all over the western basin and entrance to the Channel, but completely absent at the north-western stations just within the Fastnet area. Small areas without pilchard eggs were present off Falmouth, Torbay, Portland and Alderney. On the whole the distribution of eggs corresponds very well with that of pelagic fish observed by echo-sounding (p. 291). The occurrence of scatter layers (not well shown by the 'Graphette' in use on this occasion) does not agree so well with the distribution of clupeoid larvae (probably all pilchard) which outnumbered all other young fish, and another explanation such as the presence of young clupeoids too large to be captured by the TTN must be presumed.

Fish eggs other than pilchard were rather irregularly distributed, but tended to be common where pilchard eggs were scarce or absent. Both fish eggs and young fish were absent from the north-western stations characterized by *Aglantha*, *Meganyctiphanes*, and large *Sagitta elegans*.

June

Except at the Plymouth inshore stations, pilchard were less evident in June and were absent from a large area at the entrance to the Channel (Text-fig. 7). In general, southern species were scarce, and the limits shown on the charts for *Euchaeta*, a 20 mile radius to the north and west of Ushant, were the most restricted found for this species during the years investigated. Such restricted limits in summer were more normal in 1903-05 during the International Investigations.

North-western species were not adequately sampled on the June cruise, owing to bad weather, but by comparison with May it would seem that the extension of *Spiratella retroversa* had continued from the west, and that in addition to a general increase in number the species had spread out over large parts of the western basin. However, the species did not appear at the Plymouth inshore stations during the year, and the trend must soon have died out.

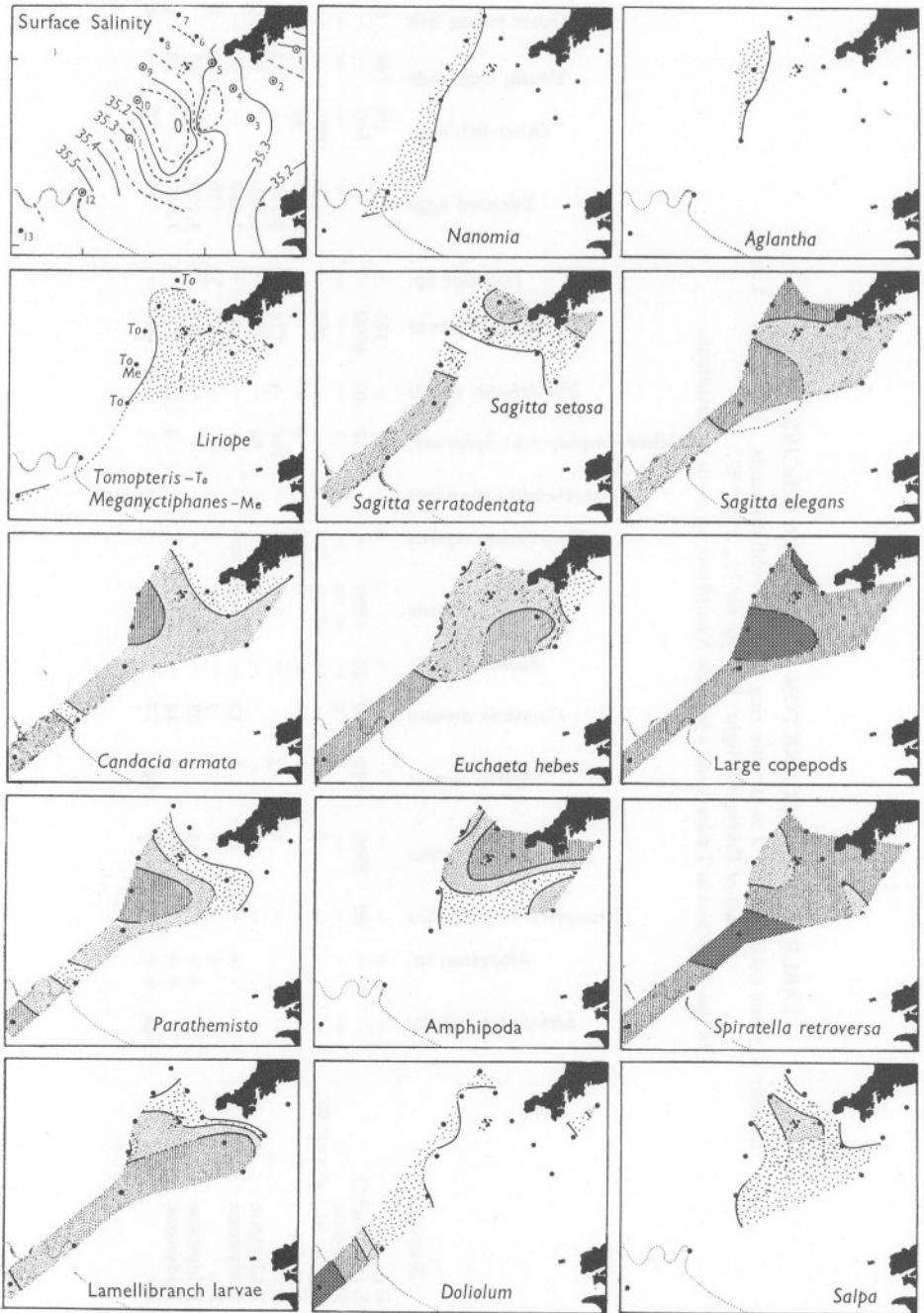
July-October

At the Plymouth stations some *Sagitta elegans* occurred during July, September and October. Numbers of copepods, including *Candacia*, increased considerably in September and October after pilchard spawning declined. *Muggiaea* was noted in September, but was not present in large numbers until October, when *Doliolum* was also found.

TABLE 4. MACROPLANKTON INDICATOR SPECIES, 1958
(Mostly daytime catches in the 2 m stramin ring trawl; $\frac{1}{2}$ h oblique hauls. 'Eddystone': 2 miles east of Eddystone light; E1: 50° 02' N., 4° 22' W.)

In this Table and in Tables 5 and 6 juvenile *Nyctiphanes* are given in parenthesis.

Date	Station	<i>Liriope tetraphylla</i>	<i>Mugilicia</i> sp.	<i>Tomopteris helgolandica</i>	<i>Sagitta setosa</i>	<i>Sagitta elegans</i>	<i>Candacia armata</i>	<i>Euchaeta hebes</i>	Large copepods	<i>Parahemisto gracilipes</i>	<i>Centropages typicus</i>	Other Amphipoda (<i>Aphersusa</i>)	<i>Nyctiphanes couchi</i>	Decapod larvae	<i>Doliolum</i> sp.	Pilchard eggs	Other fish eggs	Young clupeoids	Other young fish
18. ii.	E1	-	+	-	-	-	-	1	1	-	2	-	-	372	-	-	78	150	6
18. iii.	E1 (at night)	-	+	60	8800	1070	680	40	1600	-	-	20	40	4000	-	800	-	-	-
31. iii.	Eddystone	-	-	-	-	3	9	-	10	-	1	1	-	+	-	-	-	-	-
31. iii.	50° 04' N., 4° 11½' W.	-	-	-	3	6	-	-	10	-	1	1	-	+	-	-	-	-	-
10. vi.	E1	-	-	-	-	-	-	-	6	-	6	6	-	960	-	240	1000	-	-
9. vii.	E1	-	-	-	1	3	-	-	240	-	-	120	3	174	-	7,120	-	132	27
29. vii.	Eddystone	-	-	-	7	-	-	-	216	-	-	-	-	660	-	10,800	-	54	15
26. ix.	Eddystone	-	+	-	15	1	12	-	99	120	-	-	-	300	-	2,280	-	30	1
22. x.	E1	-	+	-	-	-	3	-	132	3	-	-	-	216	33	576	-	90	3
23. x.	Eddystone	-	+	-	12	4	28	-	28	-	-	-	-	72	2	3,100	-	96	1
28. x.	Eddystone	-	+	-	108	8	44	-	28	-	-	4	(4)	560	4	1,850	-	36	4
18. xi.	E1	42	+	-	36	640	72	-	45	-	-	-	-	600	-	21	45	-	9



Text-fig. 8. 24-26 November 1958.

November

Spawning of pilchard had practically ceased by the time E1 was sampled in mid-November, and large numbers of *Sagitta elegans* and *Candacia* were taken in the YFT. This was the earliest autumn appearance off Plymouth of north-western forms in quantity during the years studied (1955, 1957-60 inc.) and also represented the greatest number.

From the hydrographical evidence during a cruise towards the end of November, it appears that the usual cyclonic swirl (Matthews, 1914; Harvey, 1923, 1925, 1929) was well developed off the entrance to the English Channel, the low salinity area extending as far south as the latitude of Ushant, west of 6° W (Text-fig. 8, p. 294). A tongue of higher-salinity water reached right across the Channel from Ushant to Lands End, and projected to the north-west of the Isles of Scilly. The boundary between the regions of high and low salinity was very sharp, and the patches shown on the chart may well be due to serial error in the sampling. The distribution of plankton clearly followed the hydrographical pattern.

South-western species were dominant in the north-going tongue of high-salinity water, and the distributions of *Liriope*, *Muggiaea* and *Salpa* all indicate an extension from the south. *Muggiaea* was by this time generally abundant, with the greatest numbers near Plymouth.

The distribution of another south-western species, *Doliolum*, was largely complementary to that of *Salpa* and suggests that a former extension all over the region investigated had been interrupted by a recent influx of water from farther south.

All the north-western forms other than *Spiratella* were distributed similarly, being most abundant in or restricted to the lower-salinity region of the cyclonic swirl, and indicated clearly their north-western origin from the Fastnet area. Numbers of larger copepods were distributed in the same way. *Spiratella* was still fairly widespread over the area investigated but also showed signs of a north-western origin.

The large numbers of the larvae of a lamellibranch were present in the southern tongue of high-salinity water crossing the entrance to the Channel, but were also found far to the west at Sts. 11-13. The plankton at these stations, particularly the latter, contained oceanic, north-western and south-western elements, and it is presumed that the TTN sampled more than one layer of water.

Pilchard eggs were found only to the west, at St. 11. Few echo-sounder traces of pelagic fish were recorded, but 14 mm between Sts. 9 and 10, and 2 mm between 10 and 11 may be linked with the egg catches. Apart from this, pilchard seems to have been present only off Plymouth, and the shoals may well have been affected by the strong intrusion of *Salpa* and other southern elements.

December

No YFT samples were taken off Plymouth in December. A series of TTN stations worked by 'Sir Lancelot' in the eastern basin showed no trace of any penetration by north-western or south-western forms and need not be reported further.

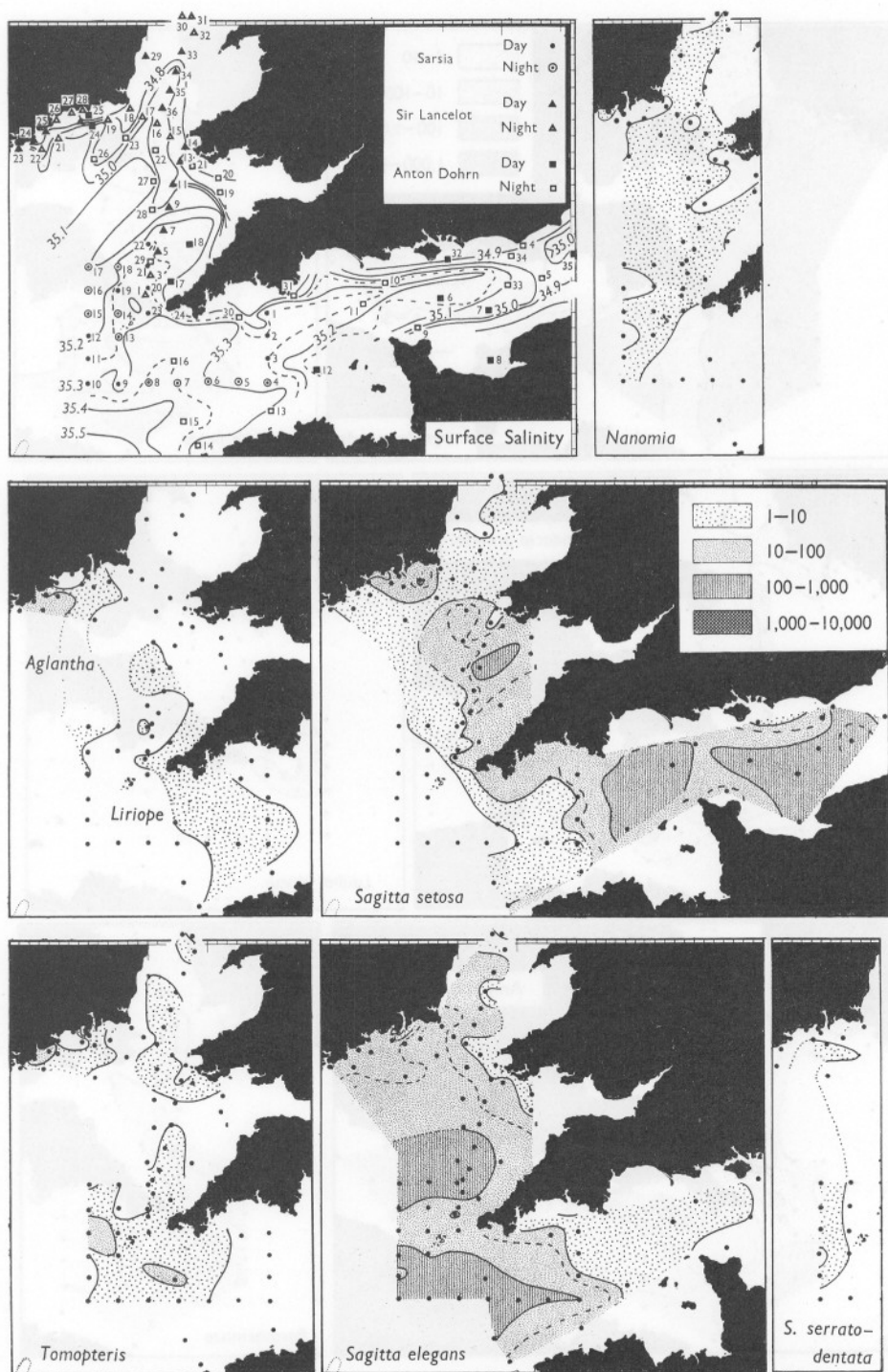
1959

Cruises undertaken in 1959 were planned on the basis of the previous year's TTN sampling, and showed more profitable results. In January and February R.V. 'Sarsia' and the F.R.V. 'Sir Lancelot' (Lowestoft) were working in the area, and in January were joined by the F.F.S. 'Anton Dohrn' (Hamburg). For these months there is very good cover, both biological and hydrographical, for a large part of the English Channel, Fastnet area, and the entrances to the Irish Sea and Bristol Channel.

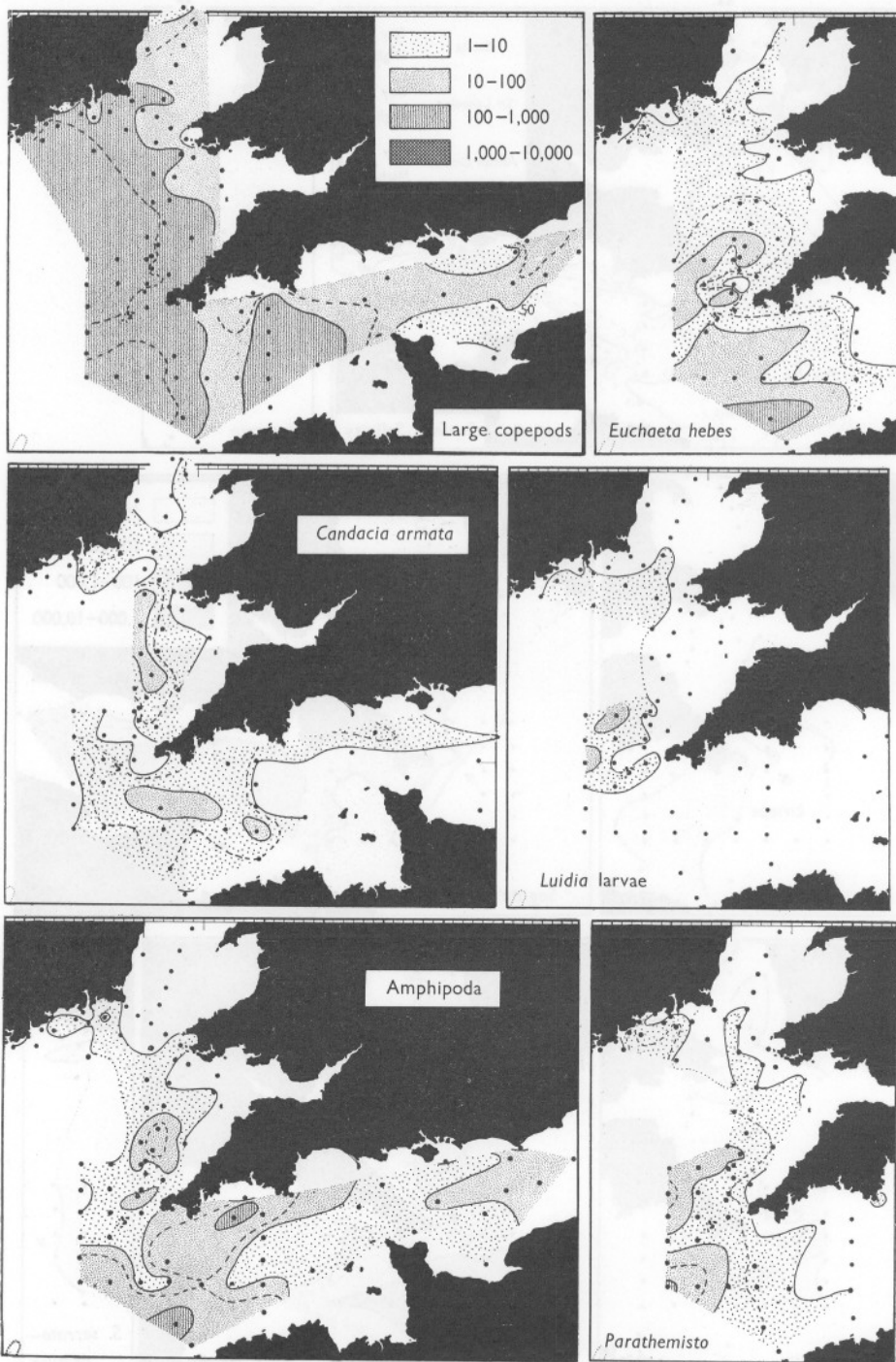
January

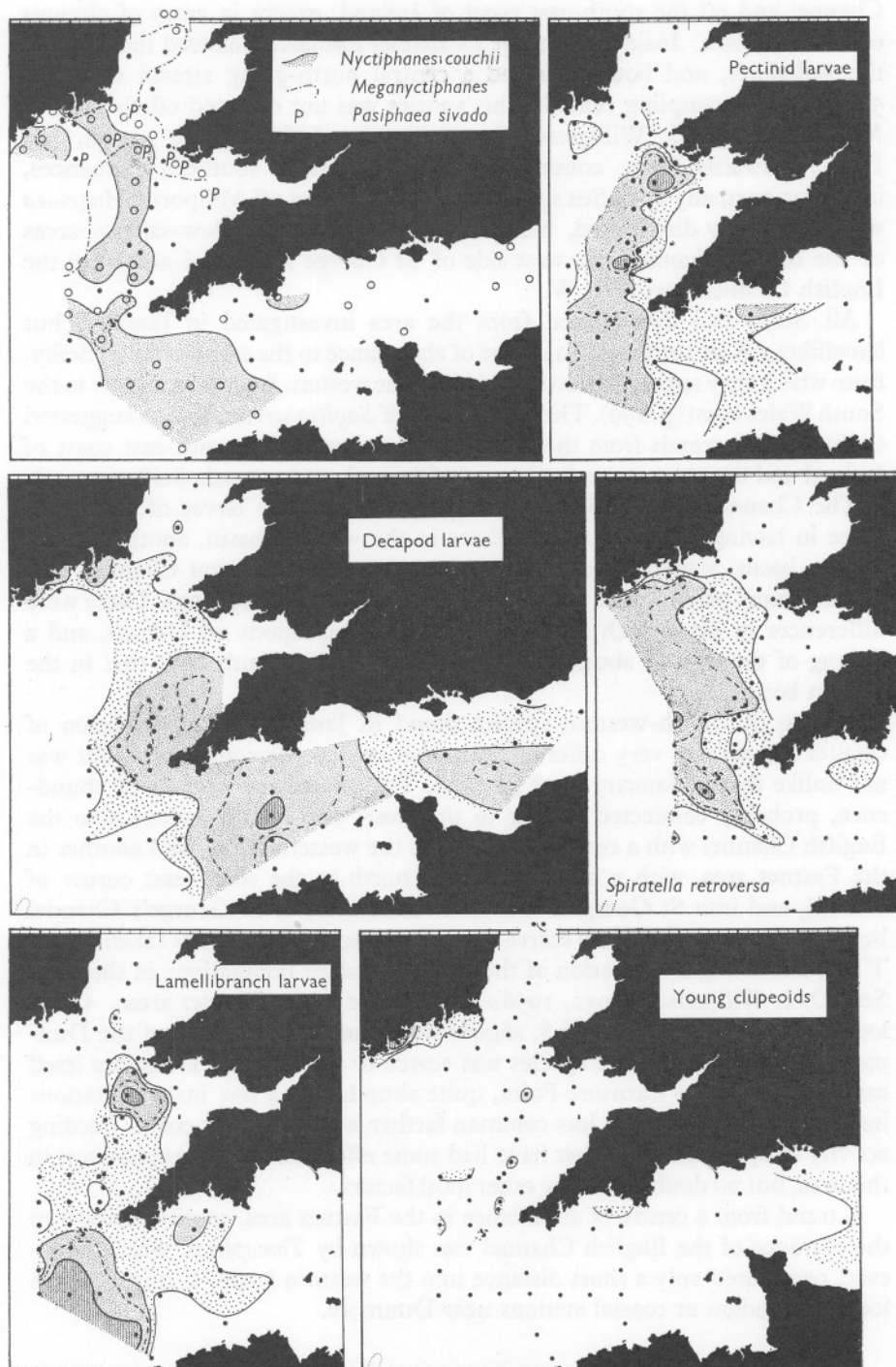
Comparison with November suggests that the intrusion of high-salinity water from the south continued, and extended to the entrance to the Bristol Channel, towards Plymouth and along the North Brittany coast (Text-fig. 9, p. 297). The body of lower salinity water from Fastnet area had retreated, but indications were still detectable as far as half-way across the entrance to the Channel. Around the Isles of Scilly the salinity was very complex, and suggestive of trends from several directions at different times, but there was a marked tongue of high salinity extending into Lundy. The few stations in the area of St George's Channel suggest a strong central flow of high-salinity water from the south-west, and a south-going tongue of low salinity, perhaps derived from the Severn estuary, between it and the north-east tongue of high-salinity water from the region of Scilly. Inside the English Channel, the main tongue of high-salinity water extending from the western basin east as far as Selsey tended to keep to the northern side.

The plankton evidence confirms and amplifies the hydrographical trends. *Liriope* was present in smaller numbers than in November 1958, and connexion with the presumed origin to the south-west appeared to have been severed (p. 297). The distribution does, however, illustrate the probable path of the spread, across the entrance to the Channel into the Lundy area across the Lands End-Scilly passage and there becoming dispersed by local movements including the outflow of Severn estuary water. There is fairly clear indication of a main centre of abundance of *Euchaeta hebes* to the south-west, just north of Ushant, and another, less marked off Scilly (p. 298). The trend of the contours of this species in the western basin agrees well with the isohalines for 35.3‰. North of the Isles of Scilly, the trend to the north-east follows the 35.1-35.2‰ isohalines off the north Cornish coast, but then differs. Small numbers of *Euchaeta* were present all over the entrance to St George's



Text-fig. 9 (part). For legend see p. 299.





Text-fig. 9. January 1959: 'Anton Dohrn' 15th-27th; 'Sarsia' 16th-20th; 'Sir Lancelot' 16th-22nd. For *Nyctiphanes* only the area with 10 or more adults per haul is stippled: the night stations on this map are shown in open circles.

Channel and off the south-east coast of Ireland, except in areas of obvious estuarine nature. Inside St George's Channel *Euchaeta* followed the trend of the isohalines, and both indicated a central north-going stream as far as 53° N. where sampling ceased. This species was not detected off the Isle of Man by Dr D. I. Williamson (pers. commun.) during the period, but Dr C. Edwards (pers. commun.) detected marked southern influences, including normally Irish Sea species, in the Clyde Sea off Millport. *Muggiaea* was extensively distributed, being absent only from the low-salinity areas of the Bristol Channel and west side of St George's Channel and from the English Channel east of 3° W.

All *Salpa* had disappeared from the area investigated in January, but lamellibranch larvae showed a centre of abundance to the south-west of Scilly, from which they appear to have spread into the western basin and almost to the South Wales coast (p. 299). The distribution of *Sagitta serratodentata* suggested slight oceanic trends from the Fastnet area towards the south-east coast of Ireland and the entrance to St George's Channel, and towards Scilly (p. 297).

The Channel species, *S. setosa*, amphipods, and also larvae of decapoda, agree in having a region of abundance in the western basin, another in the eastern basin, a smaller patch off the entrance to the Bristol Channel, and a rather small patch off the south-east coast of Ireland (p. 297-99). There were differences in detail such as an abundance of amphipods off Ushant, and a linking of the area of abundance of *S. setosa* off Plymouth with that in the eastern basin.

Among the north-western species found in January, the distribution of *Sagitta elegans* was very different from that on the previous cruise, but was not unlike that of January 1958 (p. 297). There were two regions of abundance, probably connected farther to the west; one off the entrance to the English Channel with a central tongue into the western basin; and another in the Fastnet area, with a broad extension north to the south-east corner of Ireland, and into St George's Channel. Over most of St George's Channel both species of *Sagitta* were scarce, and little macroplankton was taken by the TTN, indicating a separation of the more abundant populations in the Irish Sea (D. I. Williamson, 1952, 1956a) from those of the Fastnet areas. Great local variation in numbers of *S. elegans* was found in the region of the Dunmore herring fishery. The species was scarce or absent from Dunmore itself eastwards nearly to Carnsore Point, quite abundant at a few inshore stations just west of Dunmore but less common farther west along the coast. Feeding activity of spent herring must have had some effect on the macroplankton in this area, but no doubt there are other local factors.

A trend from a centre of abundance in the Fastnet area, south-eastward to the entrance of the English Channel was shown by *Tomopteris*, which, however, penetrated only a short distance into the western basin (p. 297). It was locally abundant at coastal stations near Dunmore.

Parathemisto was also present at coastal stations in the Dunmore area: its centre of origin for the indicated entry into the English Channel was somewhat farther south, from north of Scilly to just south of Scilly, and there appeared to be two tongues extending into the western basin (p. 298).

Both *Aglantha* (p. 297) and *Spiratella* (p. 299) showed centres of abundance in the Fastnet area, with extensions south-east towards the Isles of Scilly. A tongue of *Spiratella* extended past Scilly to the entrance of the English Channel in the centre line, and a few specimens were found within the western basin; *Aglantha* did not occur south of Scilly, and its distribution in the Fastnet area and Lundy was complementary to that of *Liriope*. The larvae of *Luidia sarsi* were found at a few stations just to the south of the Isles of Scilly, but otherwise were restricted to the Fastnet area, with a possible centre of abundance just to the north-west of the Islands. They were absent from the Lundy area but penetrated a short distance into St George's Channel from the south.

Nanomia appeared to have had a similar distribution to the larvae of *Luidia*, but extended farther into the Lundy area and St George's Channel (p. 297). In 1959 it did not enter the western basin of the English Channel.

The distribution of euphausiids revealed by the extensive sampling in January 1959 is worth comment. From the chart, which distinguishes day and night stations, it will be seen that in the western basin large numbers of *Nyctiphanes* were taken at all night stations, but few or none in the daytime (p. 299). In the shallower water east of Portland, however, the difference between day and night stations was very much less, but the average abundance was lower and densities over 10 per haul were not found. In the Fastnet and Lundy areas there was no systematic relation with day or night, large numbers being taken at some day stations and few at some night stations. It is probable therefore that a regular diurnal migration of *Nyctiphanes* is found only in the clearer, deeper, waters of the western basin.

Nyctiphanes was scarce in St George's Channel where *Meganyctiphanes* was dominant. No day/night relationship was discernible in the catches of *Meganyctiphanes* (cf. Hickling, 1925), but it was clearly restricted to the north and was found only at one station as far south as the Isles of Scilly (p. 299). It was present at most stations in the Fastnet area, but absent from Lundy except along the coast of South Wales. The prawn *Pasiphaea sivado* was somewhat similarly distributed, but was more usual in night hauls, and was not taken south of the latitude of Lundy Island nor within St George's Channel.

Larger copepods appeared to be more abundant in the deeper water off the entrance to the Channel and in the central Fastnet area: patches of more local abundance were found in the centre of the western basin and in the eastern basin off Beachy Head. They were scarce off Dunmore, in the Bristol Channel entrance, off Plymouth, off the Solent and in the Baie de Seine, all areas with

local estuarine influence and/or a known pelagic fish population (herring or pilchard) at the time. A chart of echo-sounder records for this cruise has not been included owing to partial failure of the instruments fitted to 'Sarsia', and the detailed observations off Dunmore will be published elsewhere. As far as can be judged from faulty records, the only large shoals of fish present in the western basin were inshore off Plymouth. Few fish eggs were taken in the samples. The distribution of clupeoid larvae is indicated on p. 299: more local detail for the eastern basin has been published by Hempel (1959), and the samples off Dunmore will also be dealt with elsewhere. At the level of TTN sampling it is clear that there is complete separation of herring spawning grounds, the eastern basin larvae being found east of Cherbourg and the Isle of Wight, the Dunmore larvae only in a narrow strip along the south-east of Ireland. The few clupeoids taken at intermediate stations in parts of the Fastnet and Lundy areas and off Plymouth were all pilchard of considerably greater age than the young herring found in the above areas.

February

The inshore samples off Plymouth early in February (Table 4) indicated a decrease in south-western forms and an increase in *Sagitta elegans*. This development was not at all typical of the western basin, as shown by the cruises at the end of the month (Text-fig. 10). The weather was kind, good cover of the area was obtained, and so many coastal stations were worked by 'Sir Lancelot' off Ireland that the majority of them have had to be omitted from the present account; only details of the more offshore stations are shown on the charts.

From surface salinity it is obvious that much water movement had occurred since January (p. 304). Further high-salinity water had moved into the south-western entrance to the English Channel; tongues of water above 35.3‰ extended north-east to the vicinity of Plymouth, and north past the Isles of Scilly into the Lundy area. Simultaneously, encroachment of estuarine water seems to have taken place, south of Ushant, off the north coast of Brittany near Plymouth, and along the north Cornish coast; hence there were very abrupt changes in salinity in many places. Off the Irish coast well marked estuarine outflows were shown and an extensive patch of low salinity occurred about 20–30 miles offshore. Inflow from the central Fastnet area into St George's Channel was much less obvious than in January, and the area was dominated by outflow of Severn estuary water in a massive tongue. The isohalines for 34.5 and 35.0 extended well out to the west across the Lundy and Fastnet areas to 6° and 7° W. respectively.

Salinity trends were less obvious at the fewer bottom stations, but there was clear indication of a trend of high-salinity water from the south-west across the entrance of the western basin, through the Lands End–Scilly passage into Lundy. Somewhat similar trends were shown by phosphate and silicate

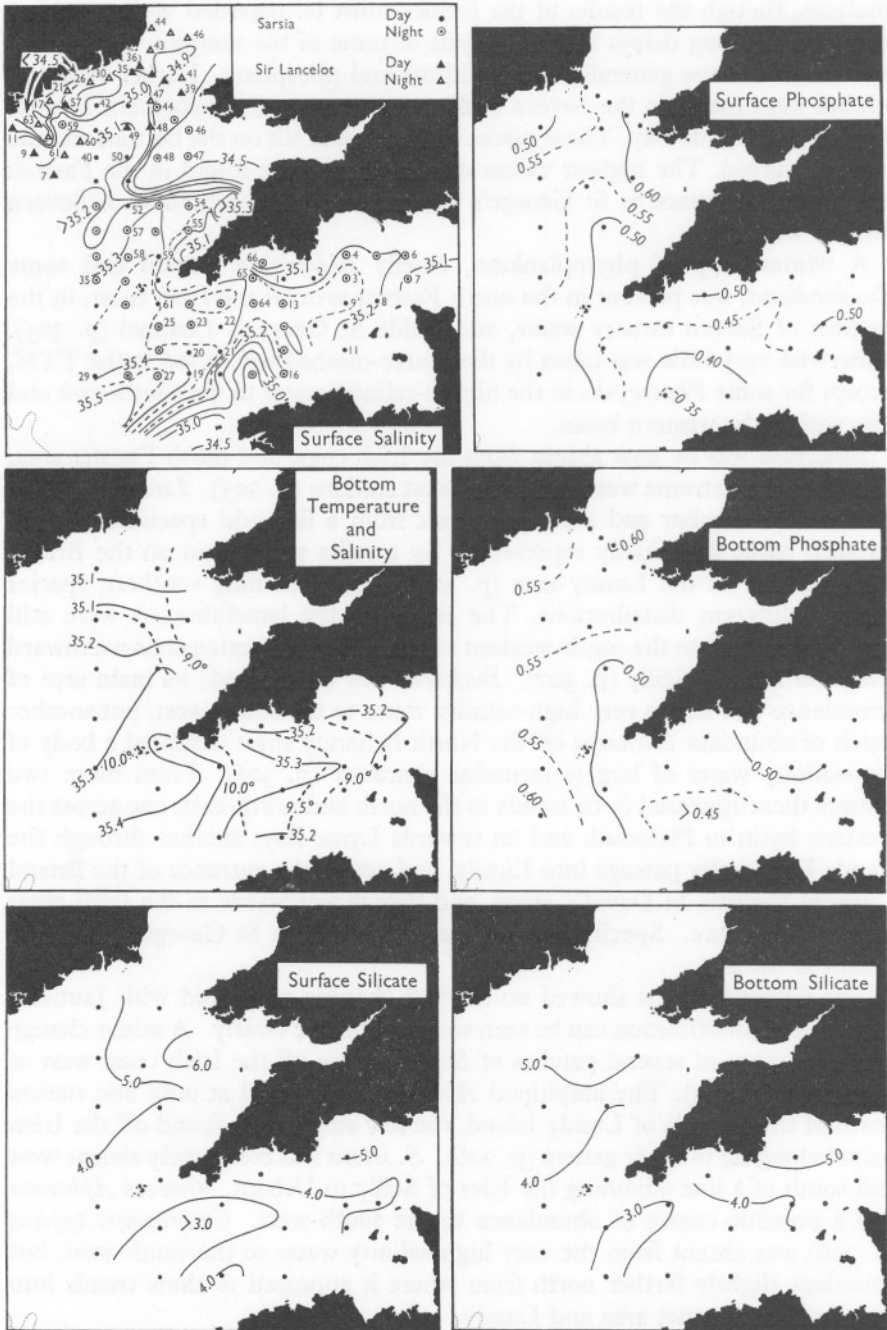
analyses, though the results of the former must be regarded with suspicion owing to the long delays before analysis of some of the samples. The south-western water was generally low in silicate and phosphate. Higher values of silicate were found in the Severn outflow, over most of the northern Fastnet area, and off Lyme Bay. These places all have some silt on the bottom and the water is turbid. The highest values of phosphate were found in the Fastnet area, in the entrance to St George's Channel, and in the outflow of Severn estuary water.

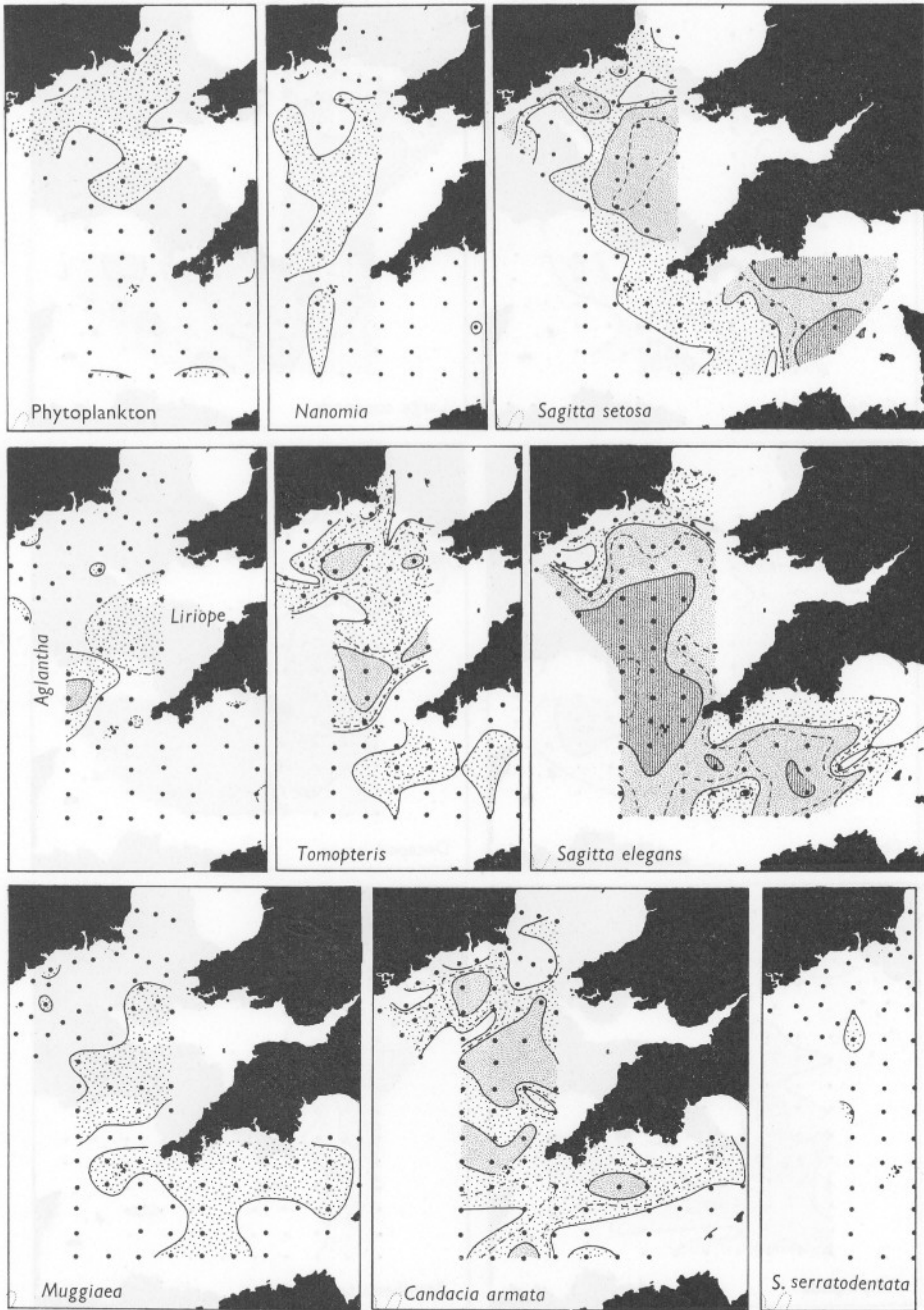
A winter crop of phytoplankton, chiefly *Biddulphia sinensis* and some *Coscinodiscus*, was present in the north Fastnet area off the Irish coast, in the outflow of Severn estuary water, and inside St George's Channel (p. 305). Otherwise very little was taken by the coarse-meshed nets fitted to the TTN, except for some *Phaeocystis* in the higher-salinity water to the south-west and just within the western basin.

Muggiaea was by now absent from the Irish coast and north Fastnet area, and from the extreme west and south-west stations (p. 305). *Liriope* had also declined in number and area, and apart from a few odd specimens in the western basin was chiefly represented by a relict population on the Bristol Channel side of the Lundy area (p. 305). The remaining southern species showed different distributions. The larvae of the lamellibranch were still largely restricted to the south-western stations, but with extensions northward from the Isles of Scilly (p. 307). *Euchaeta* was widespread; its main area of abundance was in the very high-salinity water to the south-west, but another patch of abundant *Euchaeta* off the North Brittany coast occupied a body of low-salinity water of largely estuarine character (p. 306). From these two centres there appeared to be trends to the north and north-east, one across the western basin to Plymouth and on towards Lyme Bay, another through the Lands End-Scilly passage into Lundy, and across the entrance of the Bristol Channel towards St David's Head, and thence westwards to the Irish coast beyond Dunmore. Specimens were not taken within St George's Channel, except at St. 46.

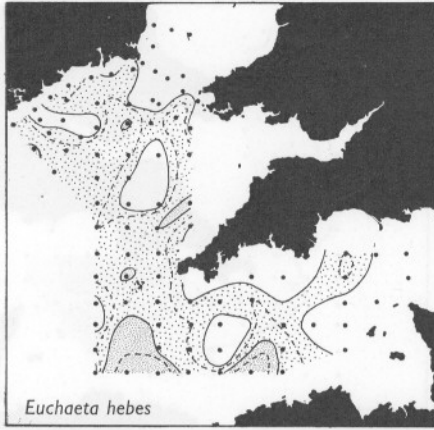
The Channel forms showed no marked changes compared with January, though their distribution can be seen somewhat more clearly. A minor change is the presence of several patches of *Sagitta setosa* off the Irish coast west of Dunmore (p. 305). The amphipod *Apherusa* was found at only one station north of the latitude of Lundy Island, the few amphipods found off the Irish coast belonging to other genera (p. 306). *S. setosa* was completely absent west and south of a line adjoining the Isles of Scilly to Ushant, whereas *Apherusa* had a possible centre of abundance to the south-west. *Centropages typicus* (p. 306) was absent from the very high-salinity water to the south-west, but abundant slightly farther north from where it appeared to show trends into the northern Fastnet area and Lundy.

All the forms classed as north-western showed typical distribution patterns.

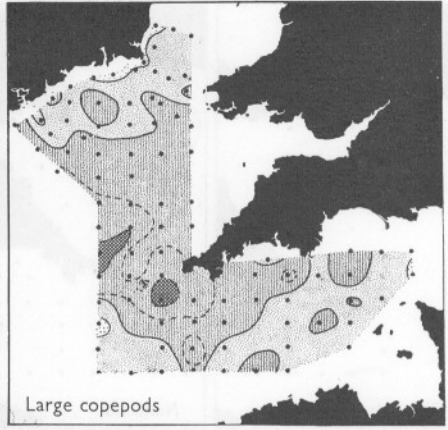




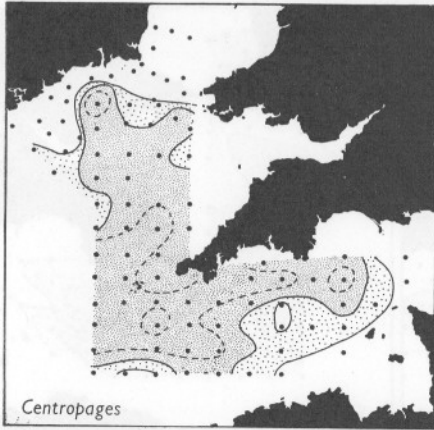
Text-fig. 10 (part). For legend see p. 307.



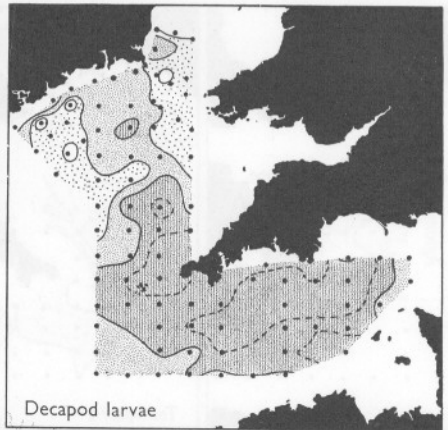
Euchaeta hebes



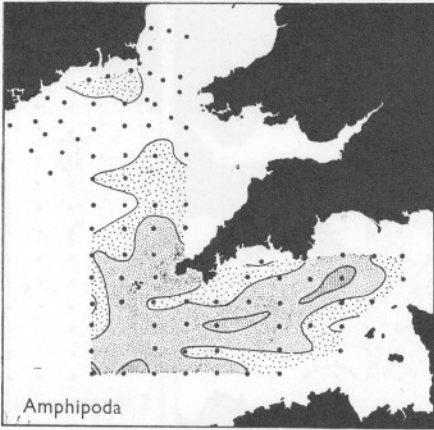
Large copepods



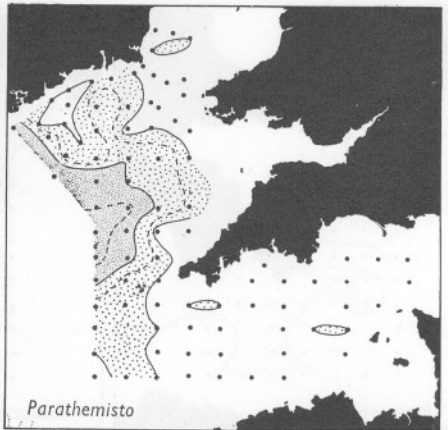
Centropages



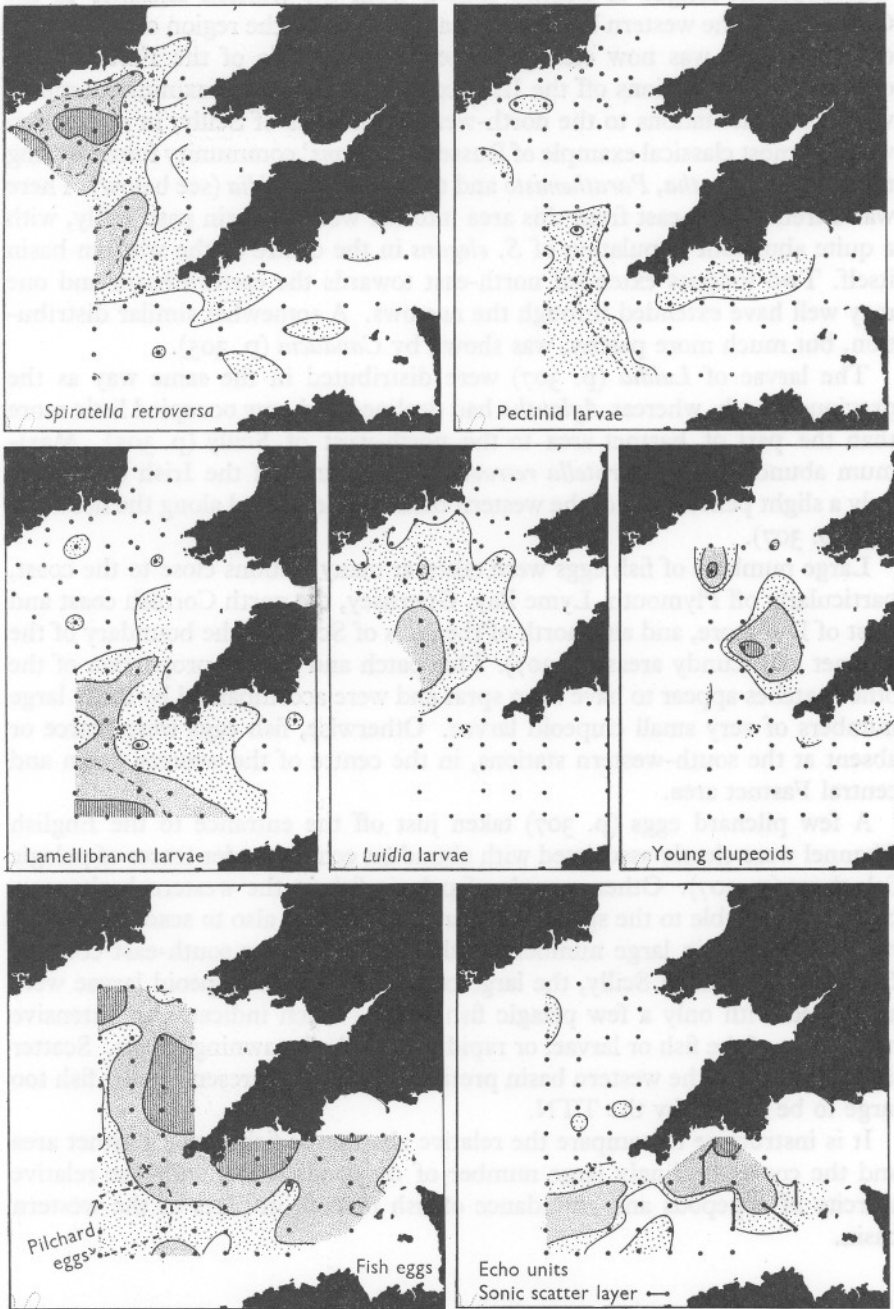
Decapod larvae



Amphipoda



Parathemisto



Text-fig. 10. February 1959: 'Sarsia', 18th-25th; 'Sir Lancelot', 22nd-25th. Phosphate and silicate samples are expressed in $\mu\text{g/at.}/\text{l}$. Phytoplankton and *Nanomia* as presence or absence only.

The apparent tongue of *Sagitta elegans* from the western entrance to the Channel into the western basin had disappeared, and the region of abundance of this species was now clearly defined as the whole of the Fastnet area, excluding a few stations off the Irish coast (p. 305). The maximum numbers were found at stations to the north-west of the Isles of Scilly, in association with the most classical example of Russell's '*elegans*' community found during the work—*Aglantha*, *Parathemisto* and the larvae of *Luidia* (see below). There was a trend south-east from this area into the western basin past Scilly, with a quite abundant population of *S. elegans* in the centre of the western basin itself. Two tongues extended north-east towards the eastern basin and one may well have extended through the narrows. A somewhat similar distribution, but much more patchy, was shown by *Candacia* (p. 305).

The larvae of *Luidia* (p. 307) were distributed in the same way as the previous month, whereas *Aglantha* had declined and now occupied little more than the part of Fastnet area to the north-west of Scilly (p. 305). Maximum abundance of *Spiratella retroversa* was found off the Irish coast, and only a slight penetration of the western basin was indicated along the northern side (p. 307).

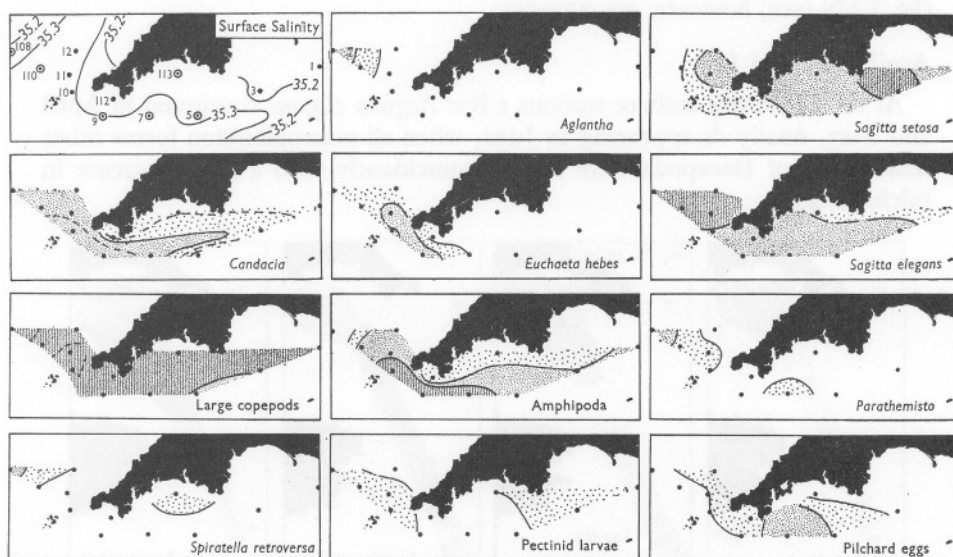
Large numbers of fish eggs were taken at many stations close to the coast, particularly off Plymouth, Lyme Bay, Guernsey, the north Cornish coast and west of Dunmore, and also north of the Isles of Scilly on the boundary of the Fastnet and Lundy areas (p. 307). This patch and a good proportion of the other patches appear to have been sprat and were accompanied by fairly large numbers of very small clupeoid larvae. Otherwise, fish eggs were scarce or absent at the south-western stations, in the centre of the western basin and central Fastnet area.

A few pilchard eggs (p. 307) taken just off the entrance to the English Channel were clearly associated with abundant echo-sounder traces of pelagic fish there (p. 307). Other records of pelagic fish in the western basin were partly attributable to the sprats (*Clupea sprattus*), and also to scad (*Trachurus trachurus*) taken in large numbers in the trawl. Off the south-east coast of Ireland and north of Scilly, the large concentrations of clupeoid larvae were associated with only a few pelagic fish traces, which indicates an extensive movement of the fish or larvae, or rapid dispersal of spawning shoals. Scatter layers present in the western basin presumably again represent young fish too large to be caught by the TTN.

It is instructive to compare the relative absence of fish in the Fastnet area and the correspondingly large number of copepods there, with the relative scarcity of copepods and abundance of fish records in parts of the western basin.

March

No very local samples were taken off Plymouth in March, but a few TTN stations were worked in the western basin from 'Sir Lancelot' (Text-fig. 11). Many additional stations were worked on the same cruise around the Irish coast, and it is hoped to present the results for these some other time.



Text-fig. 11. 'Sir Lancelot' 17-25 March 1959.

In the region covered the hydrographic situation was quite similar to that of the preceding months: a body of higher-salinity water extended across the entrance to the English Channel and north past the Isles of Scilly into Lundy, while another tongue extended eastwards in the centre of the western basin. *Euchaeta* was present only in the north-going tongue in the entrance to the Channel and was not found off Plymouth and the stations to the east. Pilchard spawning had now spread to the western basin and eggs were found from off Torbay to the Seven Stones Light Vessel, with a centre of abundance east of the Lizard.

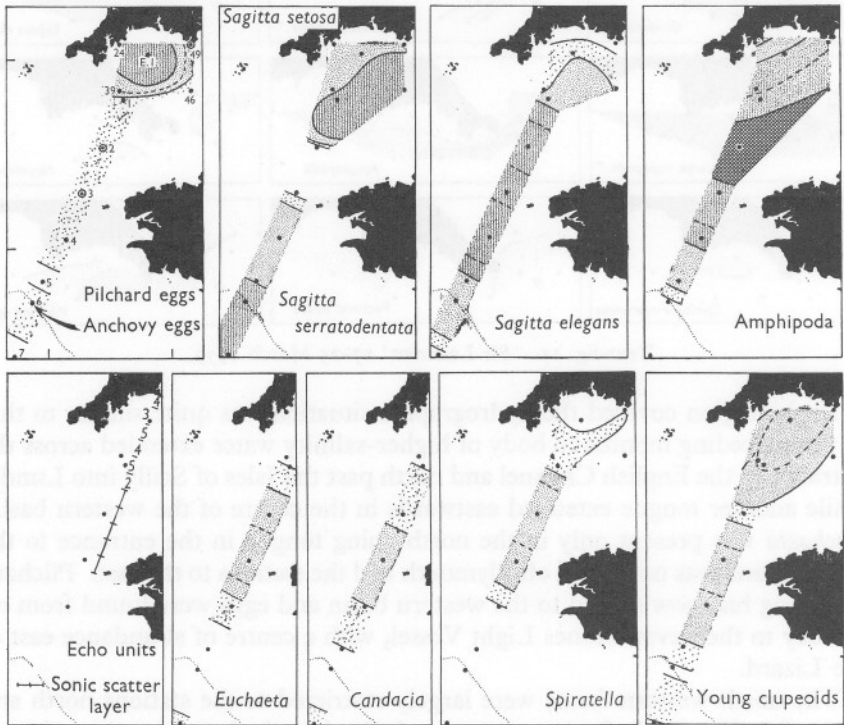
The north-western forms were largely restricted to the stations north and west of Scilly. Both *Sagitta elegans* and *Candacia* had trends suggesting an up-channel extension in the tongue of high-salinity water.

On this particular cruise the high sensitivity of 'Sir Lancelot's' M.S. 29 echo-sounder was available, and practically continuous diffuse scatter, not in the form of a layer, was found along the western basin and in the southern half of the Lundy area. On passage from Seven Stones towards South Wales the scatter records ceased abruptly on passing into a body of colder water shown

by thermograph records. This marked change, which was repeated on re-tracing the ship's track for a short distance, was later found to be due to transition from southern high-salinity water into Severn outflow water. The change in the macroplankton was less marked, though the total catch was less and the numbers of young euphausiids and decapod larvae reduced. The scatter effect may well have been due to organisms not effectively sampled by the TTN (see, however, pp. 373-75).

April, May and June

At the Plymouth inshore stations a few *Sagitta elegans* continued in April and May, finally disappearing in June, when all macroplankton forms other than larvae of Decapoda were scarce, coincidentally with a great increase in pilchard eggs.



Text-fig. 12. 30 June-3 July 1959.

A short cruise to the south-west was made at the end of June, and the results have been combined with those of a few TTN samples taken on a hydrographic survey around E1 at the same time (Text-fig. 12). It is clear that the great abundance of pilchard eggs in the YFT samples was restricted

to the Plymouth side, and was not typical of the western basin. Echo-sounder records made on the homeward run of the cruise to the south-west reinforce this conclusion. Although a strong scatter layer was present from St. 3 to half-way between Sts. 2 and 1, definite pelagic fish traces of the type attributable to pilchard were found only close to Plymouth, from St. 1 inwards. The young clupeoids taken by the TTN showed a less clearly defined trend, maximum numbers being found both off Plymouth and also just south-west of Ushant.

North-western forms were not at all common at the stations worked, but those present showed a good measure of agreement. *Sagitta elegans*, *Candacia* and *Spiratella* were all commonest at Sts. 2 and 3. However, *Euchaeta* was distributed in much the same way, and it is necessary to compare the situation with that of the more extensive cruise the following month. Oceanic forms including radiolarians, *Saphirina*, *Rhincalanus* and *Sagitta serratodentata* occurred at Sts. 5-7, and a single *Aglantha* at St. 5. Large quantities of *Liriope* were taken in a YFT at St. 7, and in smaller quantities in the TTN at St. 3 off Ushant.

July

The inshore samples off Plymouth in July showed the continued dominance of pilchard eggs and young, with decapod larvae and some *Muggiaea*, and very small numbers of copepods and *Sagitta setosa* (Table 5).

A successful cruise made in fairly good weather at the end of the month showed a very different distribution over most of the western basin (Text-fig. 13, pp. 314-17). The stations in the English Channel and the entrance followed those worked by Russell (1936*b*) the same month, 24 years earlier.

Surface temperatures are given, excluding the 'Sarsia' stations worked after a bout of bad weather (night of 28-29th), in order to show the full effect of the layering that had occurred during the preceding weeks' calm weather. Values over 18°, occasionally over 19°, were found inshore along the whole western basin and offshore over an extensive part of the Sole and Fastnet areas (p. 314). A markedly colder body of surface water was present on the southern side of the western basin, extending from south of Ushant to the Isle of Wight. Smaller areas of cold surface water were found off the north Cornish coast, in part of Biscay, and off south-east Ireland from Cork towards Dunmore. At 10 m depth there was surprisingly little difference in temperature distribution from the surface. Over most of the area investigated the upper edge of the thermocline, as detected by bathythermograph records, was between 10 and 20 m deep. Below this level, for example at 40-50 m, temperature trends were very different. The warmest bottom waters were found off the north coast of Brittany, north of Cornwall, and off the south-east coast of Ireland, areas where there was almost complete vertical homogeneity of the water. In the Fastnet area the main body of deep water had a temperature below 12°, some-

TABLE 5. MACROPLANKTON INDICATOR SPECIES, 1959
(Daytime catches in the 2 m stramin ring trawl, $\frac{1}{2}$ h oblique haul; supplemented by other samples.)

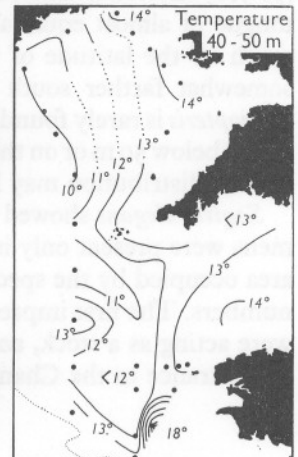
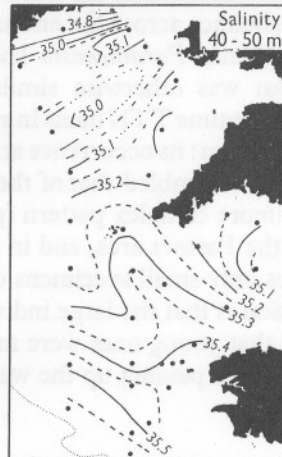
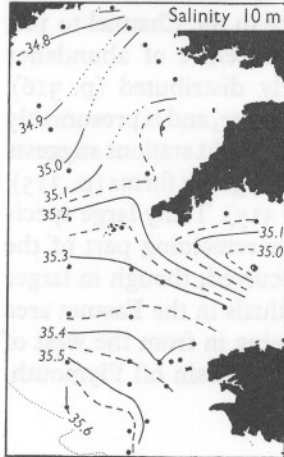
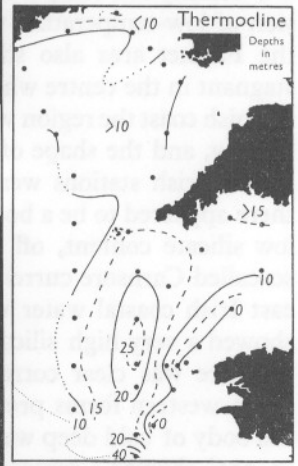
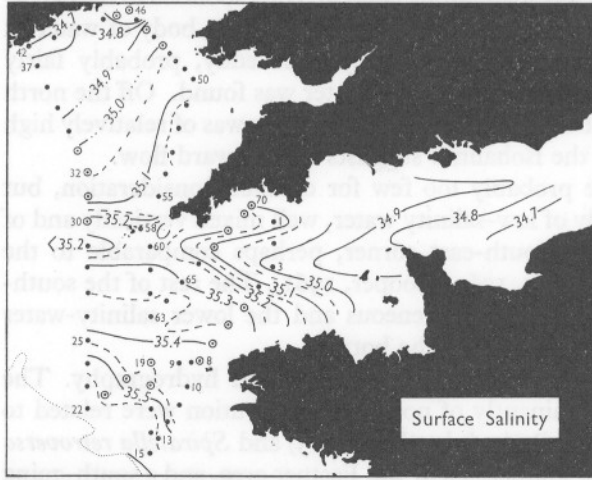
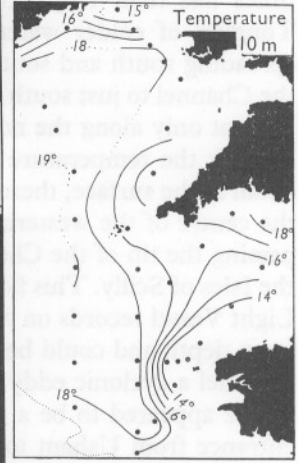
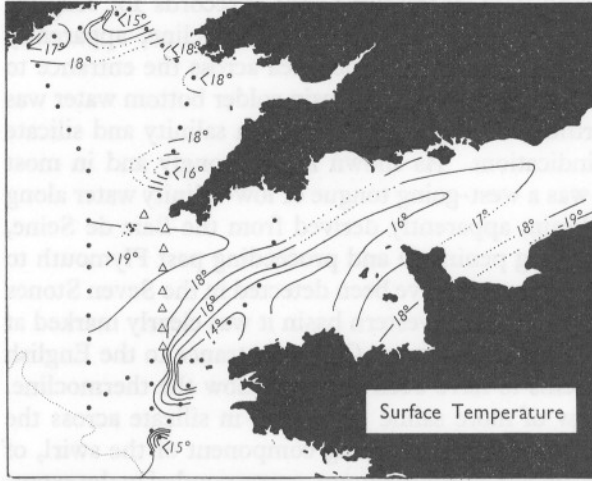
Date	Station	<i>Liriope tetraphylla</i>	<i>Muggiaea</i> sp.	<i>Sagitta serosa</i>	<i>Sagitta elegans</i>	<i>Gandacia armata</i>	<i>Euchaeta hebes</i>	Large copepods	<i>Centropages typicus</i>	Amphipoda (<i>Apherusa</i>)	<i>Nyctiphanes conchi</i>	Young euphausiids	Decapod larvae	<i>Spiratella retroversa</i>	<i>Doliolum</i> sp.	Pilchard eggs	Other fish eggs	Young clupeoids	Other young fish
8. i.	Eddystone	1	+	177	2														
12. i.	EI		+	250	12	11		20					350					1	2
10. ii.	EI	20	+	360	28	3		9		2			384				420	1	2
10. iv.	Eddystone	1	+	240	12	244		216		1			8160			240	400	64	40
12. v.	EI		+	108	4			1040					5520			1120	160	164	48
10. vi.	EI		+	60				120	20		1(20)		1100			9000		100	10
3. vii.	EI		+	12		40		120	80		1	600	720	40		7760		600	
15. ix.	10 miles south of EI (with Glover side pin samplers)		+	+	+	+	+	+	+	+		+	+		+				
13. x.	EI (vertical hauls of 1 m net, × 100)		+	1500		200		1000					300			4300			

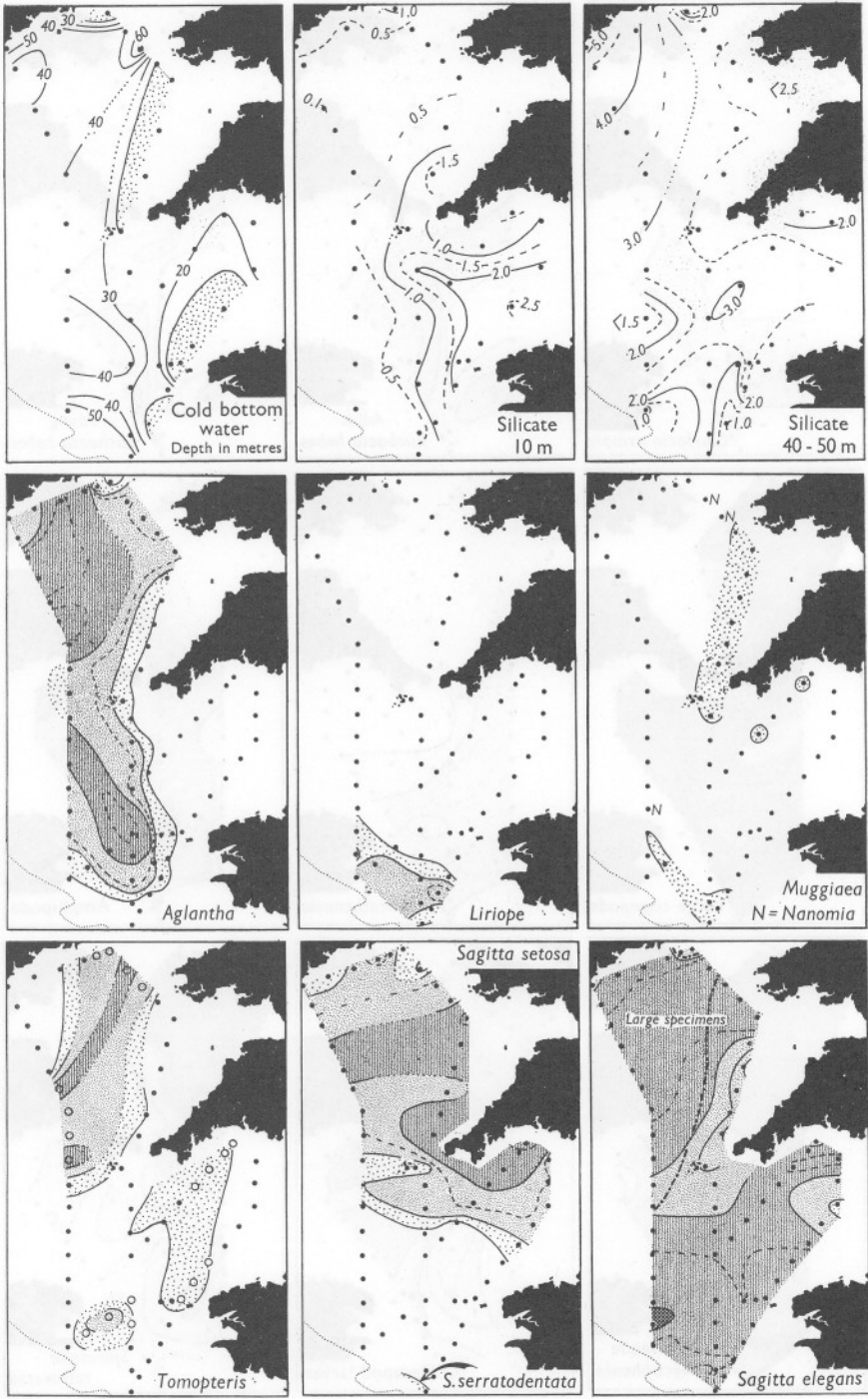
times less than 10° , agreeing with Matthews's (1914) records for August. Tongues of colder water were present below the thermocline, apparently spreading south and south-east from the Fastnet area across the entrance to the Channel to just south of 48° ; in the western basin colder bottom water was present only along the northern side (p. 314). Trends in salinity and silicate amplify the temperature indications. As shown most strongly and in most detail at the surface, there was a west-going tongue of low-salinity water along the centre of the western basin, apparently derived from the Baie de Seine, passing the tip of the Cherbourg peninsula and proceeding past Plymouth to the Isles of Scilly. This flow appears to have been detected in the Seven Stones Light Vessel records on 21 July; in the western basin it was clearly marked at 10 m depth and could be shown at 40–50 m. Off the entrance to the English Channel a cyclonic eddy seems to have been present below the thermocline. There appeared to be a flow of more saline water rich in silicate across the entrance from Ushant to Scilly: the south-going component of the swirl, of low-salinity and comparatively low-silicate content, corresponded to the extension of low-temperature water shown on p. 314. The main body of water in the Fastnet area also showed signs of the cyclonic eddy, probably fairly stagnant in the centre where the coldest deep water was found. Off the north Cornish coast the region where there was no thermocline was of relatively high salinity, and the shape of the isohalines suggests a northward flow.

The Irish stations were probably too few for detailed consideration, but there appeared to be a body of low-salinity water, well mixed vertically and of low silicate content, off the south-east corner, perhaps comparable to the so-called Carnsore current (Lee, 1960; Cooper, 1961). The rest of the south-east Irish coastal water was less homogeneous and the lower salinity-water showed a very high silicate content on the bottom.

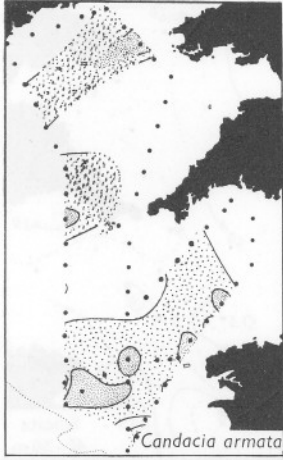
There was clear correlation of biological trends and hydrography. The north-western forms predominantly of northern distribution were related to the body of cold deep water. Both *Aglantha* (p. 315) and *Spiratella retroversa* (p. 316) showed a centre of abundance in the Fastnet area, and a south-going tongue of almost equal abundance across the entrance to the Channel to just south of the latitude of Ushant. *Parathemisto* had a centre of abundance somewhat farther south but was otherwise similarly distributed (p. 316). *Tomopteris* is rarely found in daytime TTN hauls in summer, and is presumably found below 50 m or on the bottom: its occurrence at the night stations suggests that its distribution may have resembled that of the foregoing forms (p. 315).

Sagitta elegans showed a more complex pattern (p. 315). Truly large specimens were present only in the Fastnet area, and in the remaining part of the area occupied by the species only small specimens occurred, though in larger numbers. The first impression is that the large individuals in the Fastnet area were acting as a stock, and that young ones were moving in from the west of the entrance to the Channel and passing up the western basin off Plymouth.

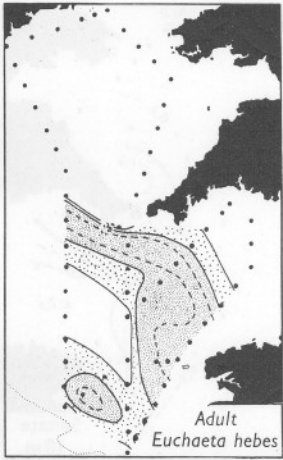




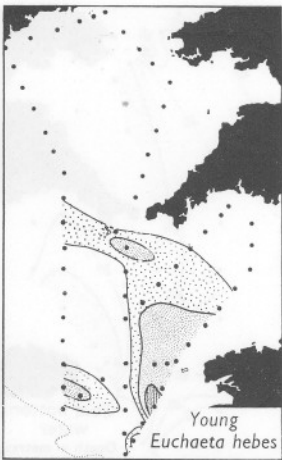
Text-fig. 13 (part). For legend see p. 317.



Candacia armata



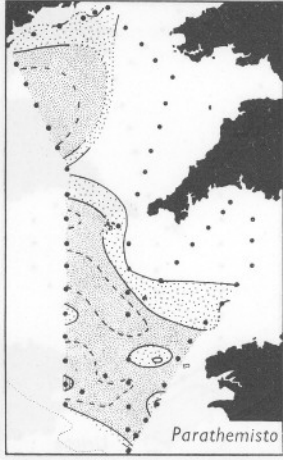
Adult
Euchaeta hebes



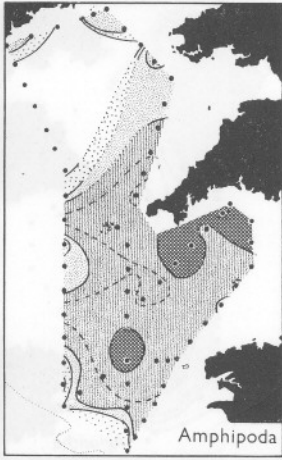
Young
Euchaeta hebes



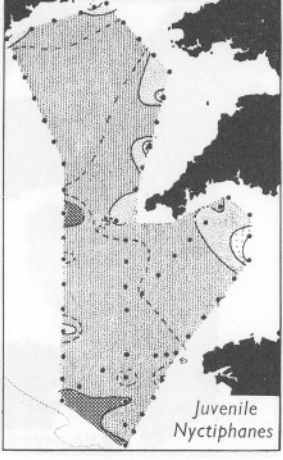
Large copepods



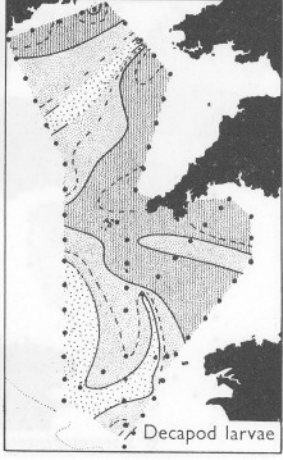
Parathemisto



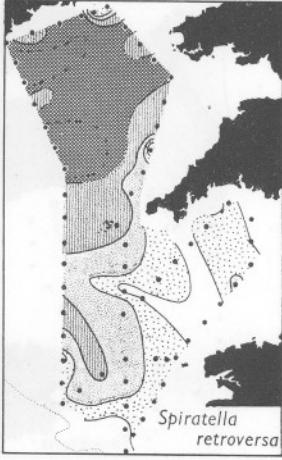
Amphipoda



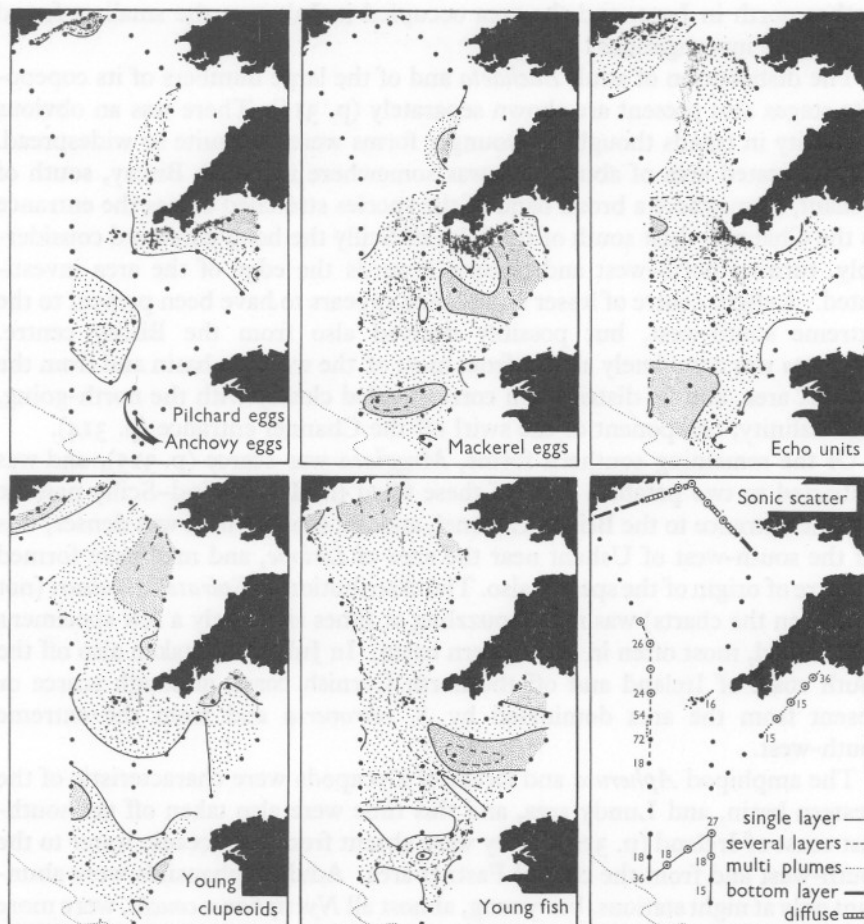
Juvenile
Nyctiphanes



Decapod larvae



Spiratella retroversa



Text-fig. 13. 23-29 July 1959. Silicate as $\mu\text{g/at./l.}$ The broken and dotted line on the map for *Sagitta elegans* encloses the area with large individuals. Figures alongside scatter layer symbols show depths in metres of upper edge of layer.

Such a view is probably false, however, and it seems more likely that these smaller specimens were derived from spawning animals much nearer. It is worth noting not only the almost complete absence of the species in the areas of very low salinity off the south-eastern corner of Ireland and in the centre of the western basin, but its equal scarceness in the relatively high-salinity water off the north Cornish coast.

Liriope was the most restricted of the south-western forms at this time, and was found only in the warm water of very high salinity in north Biscay (p. 315). It was obviously derived from farther south, though apparently not from the completely oceanic water to the south-west. The species had been found

farther north in June, and the area occupied in July was the smallest found during the investigations.

The distribution of adult *Euchaeta* and of the large numbers of its copepodite stages also present are shown separately (p. 316). There was an obvious similarity in trends though the younger forms were not quite so widespread. The indicated area of abundance was somewhere in North Biscay, south of Ushant, from where a broad band of the species stretched across the entrance to the Channel. Just south of the Isles of Scilly the band narrowed considerably, turning north-west and passing towards the edge of the area investigated. A slight centre of lesser abundance appears to have been present to the extreme south-west, but possibly derived also from the Biscay centre. *Euchaeta* was completely absent from most of the western basin and from the Fastnet area, and its distribution corresponded closely with the north-going, high-salinity, component of the swirl off the Channel entrance (p. 314).

Of the remaining southern forms, *Muggiaea* was scarce (p. 315), and was restricted to two patches. One of these filled the Lands End-Scilly passage and the entrance to the Bristol Channel, and the other, which was denser, was off the south-west of Ushant near the area of *Liriope*, and may have formed a centre of origin of the species also. The distribution of *Spiratella lesueurii* (not shown on the charts) was rather puzzling at times since only a few specimens were found, most often in the western basin. In July it was taken also off the south coast of Ireland and off the north Cornish coast, although scarce or absent from the area dominated by *S. retroversa* and from the extreme south-west.

The amphipod *Apherusa* and larvae of Decapoda were characteristic of the western basin, and Lundy area, and this time were also taken off the south-east coast of Ireland (p. 316). They were absent from the oceanic water to the south-west and from the central Fastnet area. Adult euphausiids were abundant only at night stations, but young, almost all *Nyctiphanes couchi*, were more generally distributed over part of the western basin and Fastnet area, and the entrance to the Channel (p. 316). They were scarce or absent at some stations off the Irish coast, and off the entrance to the Bristol Channel, and notably absent at Sts. 2 and 3 in the low-salinity water probably derived from the eastern basin.

In July 1959 pilchard eggs were scarcer than earlier in the year, and restricted to three areas (p. 317). The most extensive patch of pilchard eggs corresponded more or less with the area of abundant *Sagitta setosa* extending round the south-west of England from Plymouth and into the Lundy area. A smaller patch, but with nearly equal densities of eggs at some stations, was present off the south coast of Ireland from Carnsore Point towards Cork, a region where both species of *Sagitta* were scarce. The third patch was of much lower numbers of eggs, just to the west of the entrance to the English Channel. Young clupeoids, though rather more dispersed, tended to be

centred on these areas of pilchard eggs and on a patch of a few anchovy (*Stolephorus encrasicolus*) eggs to the south-west of Ushant. Echo-records of fish shoals showed much less agreement, except for the area off the south coast of Ireland, and the densest patch of fish echoes corresponded to the area of anchovy eggs (p. 317).

Fish eggs tentatively identified as mackerel (*Scomber scombrus*) by appearance only, were abundant over most of the western basin and approaches to the Channel, but absent from the Fastnet area with the exception of two stations off the Irish coast (p. 317). Young fish were also scarce in the Fastnet region, as well as in the Lundy area and approaches to the Channel; they were most abundant in the western basin, off Ushant and along the south coast of Ireland.

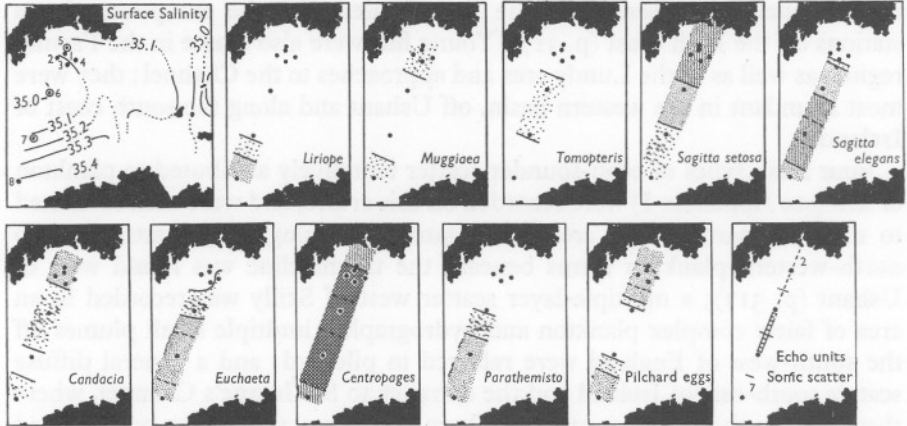
Four main types of echo-sounder scatter tentatively attributed to plankton or fish (see Appendix I) were recorded on this cruise, and were each restricted to different parts of the area investigated. The single layer attributed to north-western plankton forms beneath the thermocline was found west of Ushant (p. 317); a multiple-layer scatter west of Scilly was recorded in an area of fairly complex plankton and hydrography; multiple small plumes off the south-west of England were referred to pilchard; and a general diffuse scatter south-east of Ireland and the entrance to St George's Channel, where there was no thermocline, may have been due to macroplankton or dispersed fish.

September and October

No further YFT samples were taken in 1959 after July. However, a set of samples was taken with Glover side-pin samplers around E1 in September. *Euchaeta* was present just to the south-east, and a single *Sagitta elegans* was captured in one haul, otherwise the samples were too small for the plankton species being investigated. In October a series of 1 m vertical net hauls was made near E1, and a line of TTN stations worked running south-west to Ushant (Text-fig. 14).

From the surface salinities it appears that a considerable body of low-salinity water had been present in the western basin since July. By October this had been split by an intrusion of higher salinity water from the south-west, round Ushant, the influence reaching Plymouth from the south-east. This deduction is supported by the occurrence of *Euchaeta*, which was found to the south-east of E1 in both September and October, and was more common on the French side of the Channel. Of other southern forms, *Liriope* was found only off the Brittany coast, whereas in other years it had been taken off Plymouth in October. *Muggiaea* was present off Plymouth and off Ushant, but not at the stations of very low salinity on the line between. Pilchard eggs were similarly distributed, but with somewhat greater abundance on the English side around E1.

Of north-western forms present in October, both *Tomopteris* and *Sagitta elegans* appeared to be commonest in mid-Channel, in association with the lower salinity water, which may therefore be of north-western origin and not directly related to the west-going low-salinity water from the eastern basin found in July. *Parathemisto* appeared to be associated with south-western forms.



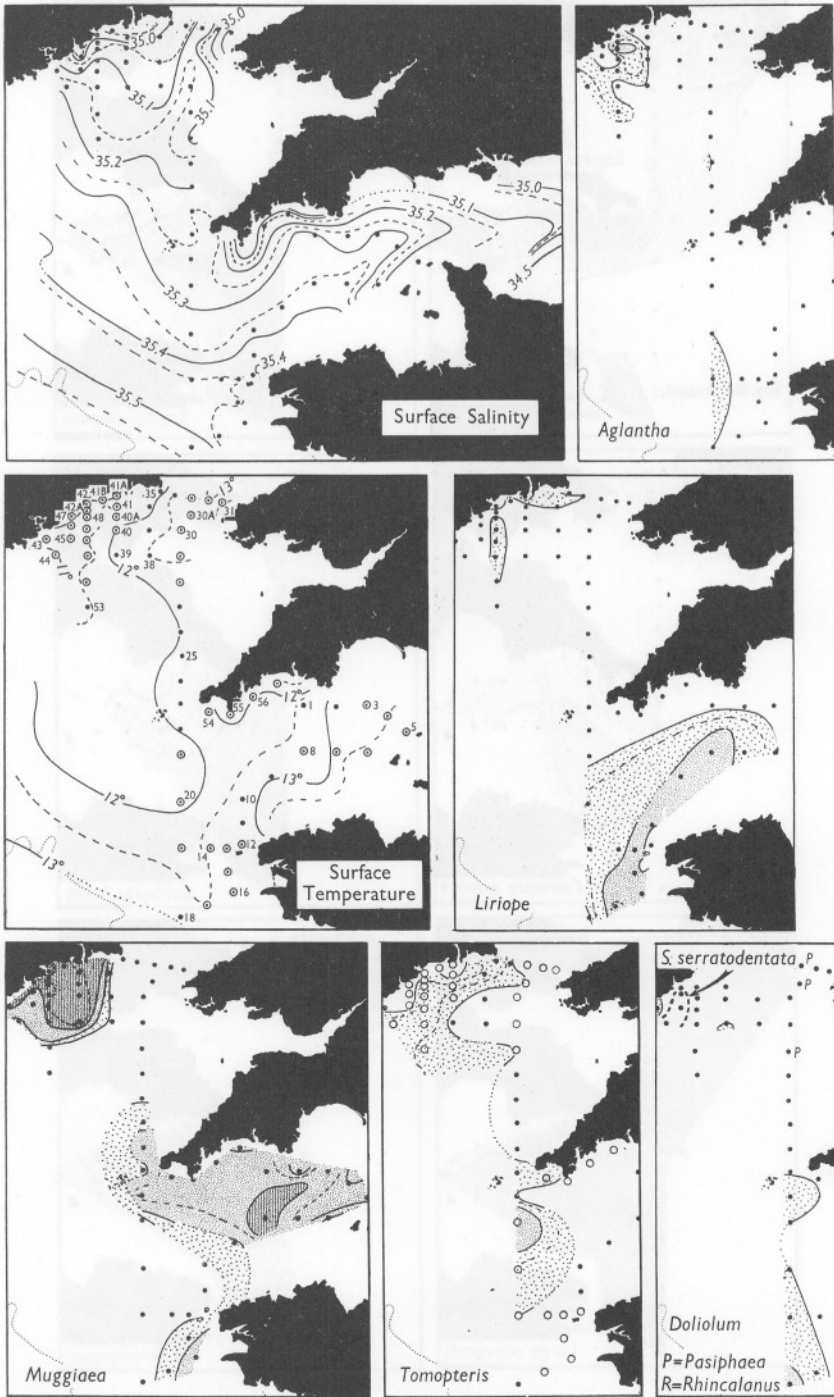
Text-fig. 14. 9-10 and 13 October, 1959.

Channel forms were fairly generally abundant, though *S. setosa* was, as usual, more abundant on the English side where clupeoid larvae were also commoner. The presence of some *Crystallogobius* at the central stations (6 and 7) strengthens the suggestion of a north-western element at these stations. Pelagic fish traces were not found in this central area but only on either side, in agreement with the pilchard-egg distribution. A general diffuse scatter was recorded in the region of low salinity in mid-Channel; multiple scatter layers from off Plymouth out to beyond E1 were probably associated with the slight thermocline still present at the latter station.

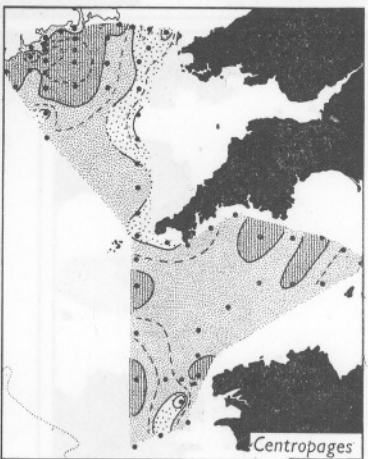
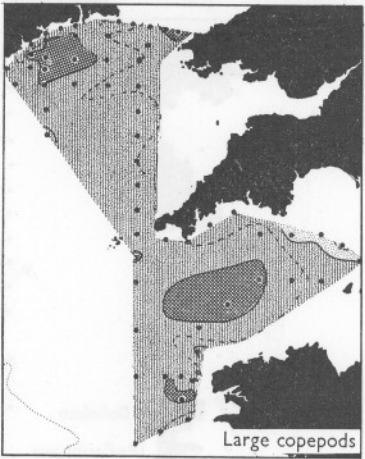
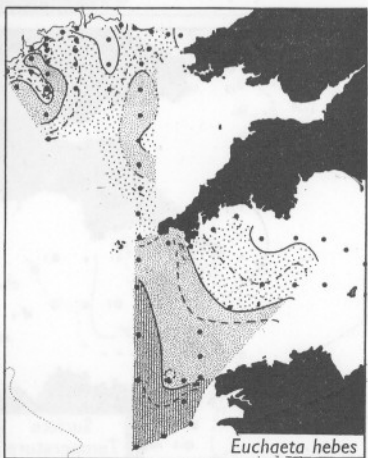
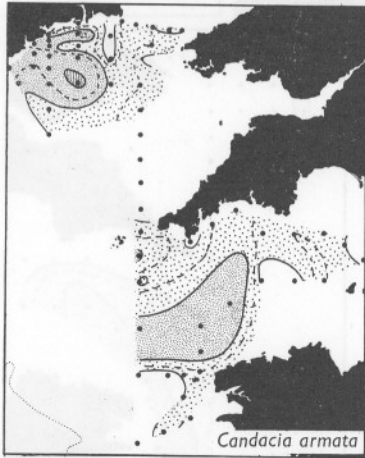
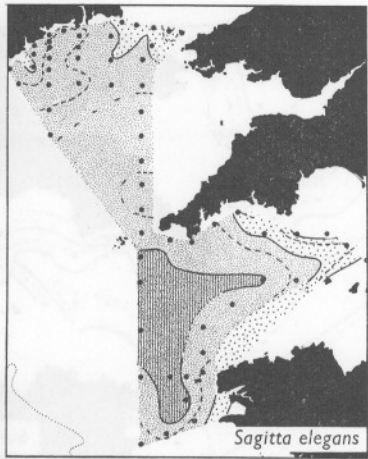
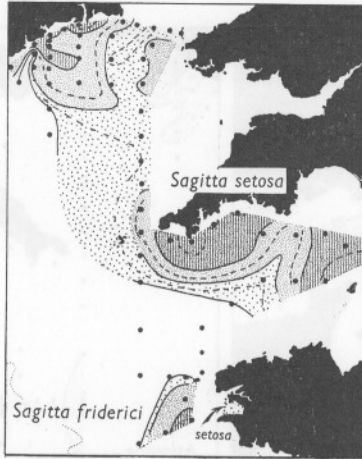
November and December

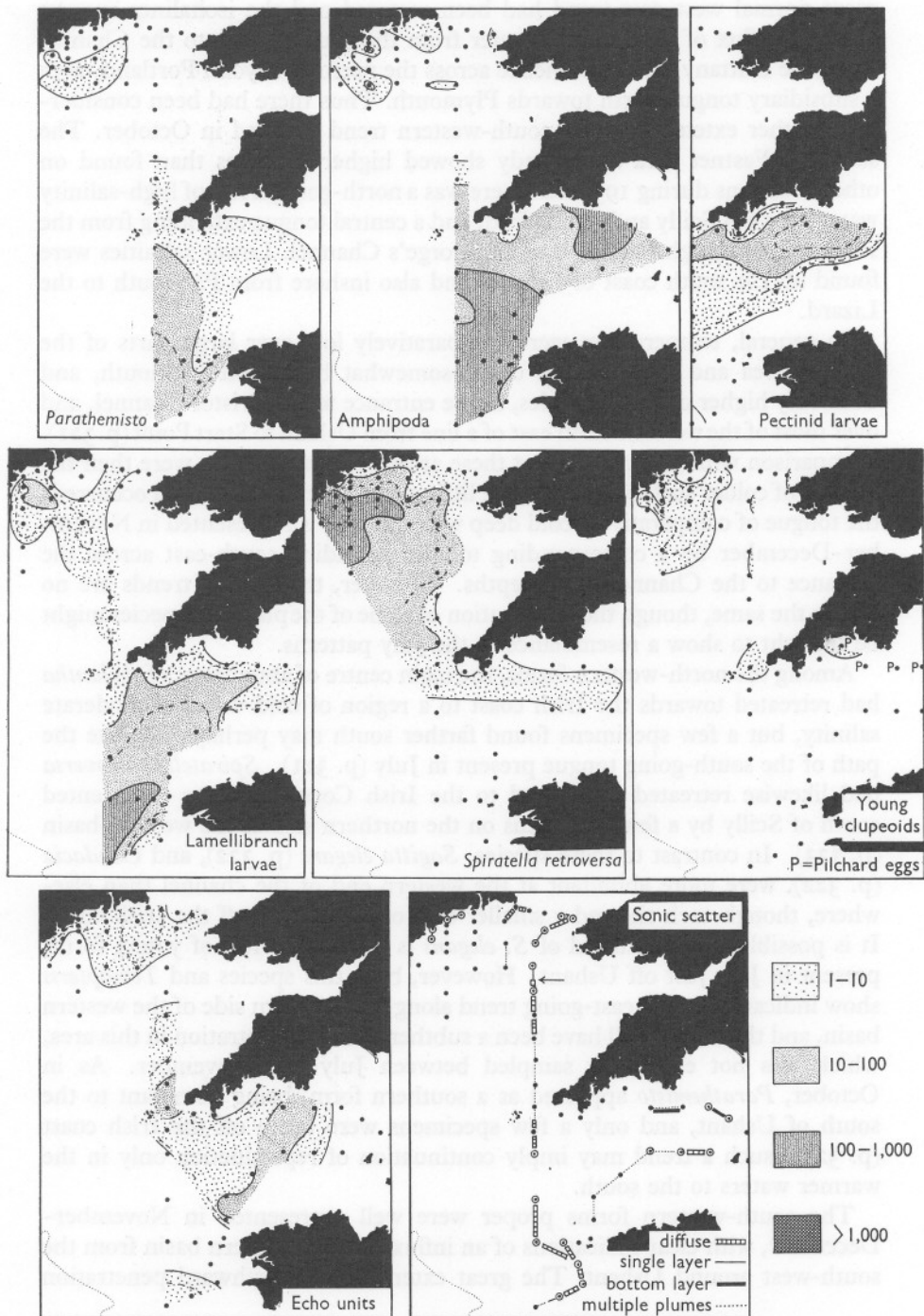
An extensive survey was carried out over the western basin and Fastnet area at the end of November and the beginning of December, but some very bad weather, with winds up to force 11, prevented sampling just to the north-west of Scilly (Text-fig. 15). The gap in the programme produced some uncertainty over trends and it has been necessary to draw inferences by comparison with hydrography, for which better cover is available from the routine surface stations in the area.

The water of the whole area appeared to be practically the same down to the bottom, and hence only surface salinities have been mapped (p. 321). The



Text-fig. 15 (part). For legend see p. 323





Text-fig. 15. 26 November-9 December 1959.

more normal west-east trend had been restored and the isohalines suggest a strong influx of high-salinity water from the south-west into the Channel along the Brittany coast and thence across the narrows beyond Portland, with a subsidiary tongue north towards Plymouth. Thus there had been considerable further extension of the south-western trend inferred in October. The southern Fastnet area and Lundy showed higher salinities than found on other occasions during 1958-60: there was a north-going trend of high-salinity water between Scilly and Lands End, and a central tongue extending from the south-west through Fastnet into St George's Channel. Lower salinities were found off the south coast of Ireland, and also inshore from Plymouth to the Lizard.

In general, temperatures were comparatively low over large parts of the Fastnet area and off the Irish coast, somewhat higher off Plymouth, and decidedly higher off South Wales, in the entrance to the Bristol Channel, and over most of the western basin east of a line from Ushant to Start Point (p. 321). Comparison with July shows that these areas of warmer water were then the regions of colder surface water where little vertical stratification had occurred; the tongue of comparatively cold deep water in July is represented in November-December by a corresponding tongue extending south-east across the entrance to the Channel at all depths. However, the salinity trends are no longer the same, though the distribution of some of the plankton species might be thought to show a resemblance to the July patterns.

Among the north-western forms, the main centre of abundance of *Aglantha* had retreated towards the Irish coast to a region of cold water of moderate salinity, but a few specimens found farther south may perhaps indicate the path of the south-going tongue present in July (p. 321). *Spiratella retroversa* had likewise retreated northward to the Irish Coast, and was represented south of Scilly by a few specimens on the northern side of the western basin (p. 323). In contrast to these species, *Sagitta elegans* (p. 322), and *Candacia* (p. 322), were more abundant at the western end of the channel than elsewhere, though each showed a smaller area of abundance off the Irish coast. It is possible that this trend of *S. elegans* is due to survival of young forms present in July just off Ushant. However, both this species and *Tomopteris* show indications of an east-going trend along the northern side of the western basin, and there may well have been a subthermocline penetration in this area, which was not effectively sampled between July and November. As in October, *Parathemisto* appeared as a southern form, being dominant to the south of Ushant, and only a few specimens were taken off the Irish coast (p. 323): such a trend may imply continuation of reproduction only in the warmer waters to the south.

The south-western forms proper were well represented in November-December, with clear indications of an influx into the western basin from the south-west around Ushant. The great extent of the northward penetration

outside the Channel is indicated by *Liriope*, which was found in a subsidiary tongue off the south coast of Ireland (p. 321). It was associated with *Doliolum* (p. 321) both in the Channel off Brittany, and off the Irish coast, but in the latter area the presence of a nearby tongue of *Sagitta serratodentata* suggests a more general oceanic effect not shown by the salinity trends (p. 321). The clearest evidence of a north-going trend of warm-water species is shown by the presence of numbers of *Sagitta friderici* off Ushant (p. 322). This species was once noted in north Biscay in the spring of 1954 (Corbin, pers. commun.), the northern limit of a distribution extending south to Morocco and West Africa (Furnestin, 1957, 1958; Fraser, 1960). In November–December 1959 it was found in a narrow tongue extending north from Biscay to the latitude of Ushant, and although the two species were separated by many miles of empty water, there had been a corresponding retreat of *Sagitta setosa* from parts of the western basin (p. 322).

Other southern species were widespread. *Euchaeta* showed the usual trend from a centre of abundance in the south-west, north across the entrance to the Channel, and also into the western basin along the Brittany coast and thence across towards Start Point (p. 322). The north-going trend across the entrance to the Channel extended through the Scilly–Lands End passage and up into the central trend of water into the entrance to St George's Channel. *Euchaeta* was also comparatively common over a large area of the south coast of Ireland except off Dunmore–Carnsore where a trend from the north was indicated. The denser patch of this species may perhaps be connected with the occurrence of *Liriope* in the same area, and a separate influx of south-western forms might be inferred from an area to the west of the region surveyed.

The larvae of the unidentified lamellibranch again showed the same trend from the south-west, extending over most of the western basin, but with a centre of origin somewhat more to the west than that of the other species noted above (p. 323). Another small patch of this form was found off the south coast of Ireland. By comparison with the other south-western species, *Muggiæa* was at this time more of a Channel type, absent only from those areas where *Sagitta elegans* was the dominant chaetognath, and, except for the entrance to the Bristol Channel, its areas of abundance agreed well with those of *S. setosa*, though in the western basin some signs of a trend from the south-west could be detected (p. 322). A patch of local abundance off the Irish coast agrees with the other south-western forms found there.

Very little sense can be made of the distribution of Channel forms, especially the copepods. *Apherusa* had returned to its former region of abundance off the south-west entrance to the Channel and in the western basin, though a few specimens off the south coast of Ireland, from which region the species was not recorded the previous winter, may be held to reinforce the southern trend there (p. 323). The most conspicuous western-basin form was in fact the larva

of a pectinid, most abundant along the north side, from Scilly to Start Point (p. 323).

Fish spawning had almost ceased. A few pilchard eggs were taken off Plymouth and eastwards, and a few other species were present between Plymouth and the Lizard, but the remaining area was devoid of fish eggs and young fish other than clupeoids (p. 323). Young clupeoids, probably pilchard, were present in small numbers inshore off Plymouth, and somewhat more commonly off the south-east corner of Ireland, where greater spawning intensity may have occurred later in the year (p. 323). (In July eggs were most numerous off Plymouth, and fewer were found off the Irish coast.) Echo-sounding records support the egg and young-fish distributions in showing a relative scarcity of pelagic fish except in the central western basin, in north Biscay, off north Cornwall and off southern Ireland (p. 323). Many of the fish records appear to have been of young specimens too large to be captured by plankton gear, to judge from the presence of multiple-plume type echoes. More diffuse scatter was obtained over a large part of the area, especially to the south. A very sharp boundary was found in scatter records off the entrance to the Bristol Channel, comparable to that noted in March (p. 323). The scatter ceased abruptly half-way between Sts. 28 and 29, where the warmer, lower salinity-water of the South Wales coast was encountered.

1960

A few restricted cruises were made in the western Channel and approaches in the first half of 1960 before the present sampling programme ceased, and some YFT hauls were made off Plymouth during the same period (Table 6). A few later samples were also available.

January

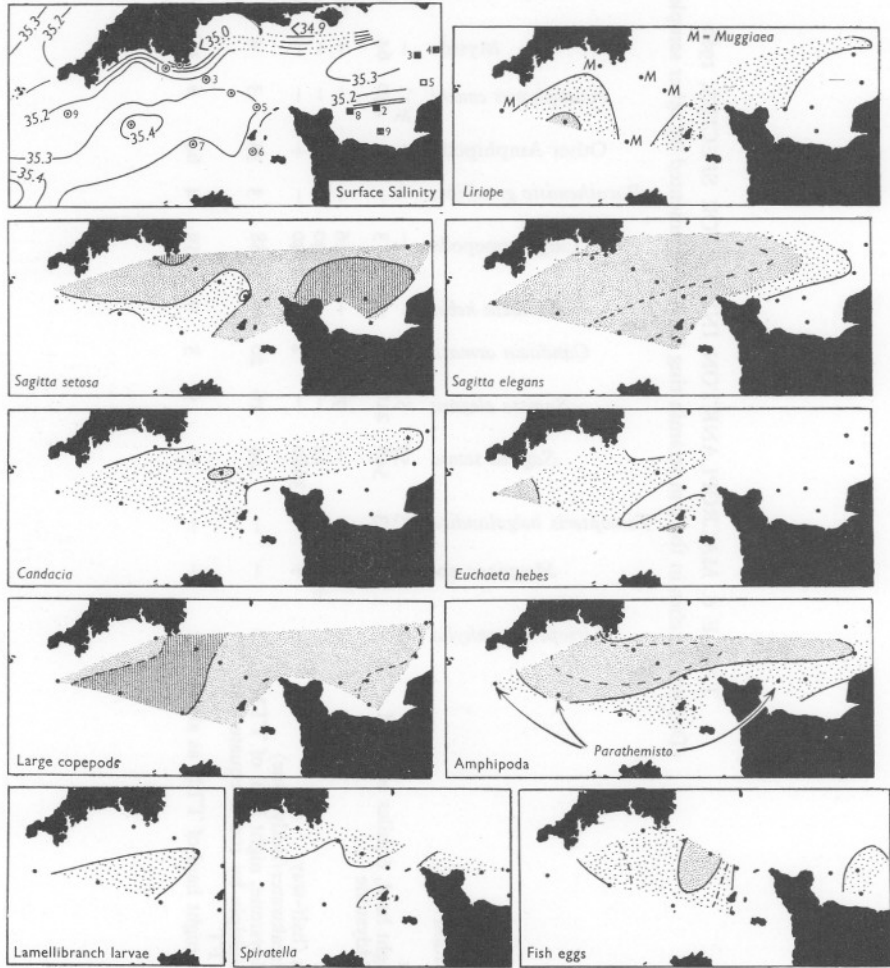
The strongest southern influence of the winter of 1959-60 reached Plymouth early in January, when *Liriope* occurred at E1. However, a north-western component, which persisted to February, is suggested by the comparatively large numbers of *Sagitta elegans* and smaller numbers of *Parathemisto* and *Candacia*.

The surface salinities at the time of the cruises show water of very high salinity at the south-west entrance to the Channel, well clear of Ushant, extending in a broad tongue up Channel towards Alderney (Text-fig. 16). High-salinity water was present in the eastern basin, and a few specimens of *Liriope* found there suggest that the southern influx was stronger than the previous year. The lower-salinity water was at this time confined to a narrow coastal strip off Plymouth, possibly extending some distance offshore west of the Lizard. A distinct trend from the south past Scilly into the Lundy area is clearly shown by the salinities.

TABLE 6. MACROPLANKTON INDICATOR SPECIES, 1960
(Daytime catches in the 2 m stramin ring haul, supplemented by other samples.)

Date	Station	<i>Liriope tetraphylla</i>	<i>Mugilicaea</i> sp.	<i>Tomopteris helgolantica</i>	<i>Sagitta serosa</i>	<i>Sagitta elegans</i>	<i>Candacia armata</i>	<i>Euchaeta hebes</i>	Large copepods	<i>Parathemisto gracilipes</i>	Other Amphipoda	<i>Nyctiphanes couchi</i>	Mysids	Decapod larvae	Doliolids	Pilchard eggs	Other fish eggs	Young clupeoids	Other young fish
4. i.	E1	2	+	5	59	53	-	-	-	2	-	3(1)	-	12	-	-	2	-	-
11. ii.	Night haul, 6 miles south of Eddystone	-	-	3	548	216	2	-	3	-	-	440	64	100	-	-	88	-	1
4. iv.	E1	-	-	-	-	96	-	-	116	-	-	-	-	3240	-	800	1320	160	121
8. vii.	E1	-	++	-	12	-	2	4	240	-	-	-	-	2460	-	9600	660	1080	60
28. ix.	L4 (half-way, Breakwater/Eddystone)	-	+	-	3680	-	2	-	1840	-	+	-	-	2460	160	-	240	4	-
19. xii.	Eddystone, night haul of TTN multiply by 100 to equate with YFT	1	-	-	44	16	20	10	88	3	35	3	4	26	-	-	3	-	-
19. xii.	E1 night haul of TTN as above	1	+	-	10	9	5	9	59	4	64	6	26	40	-	-	-	-	-

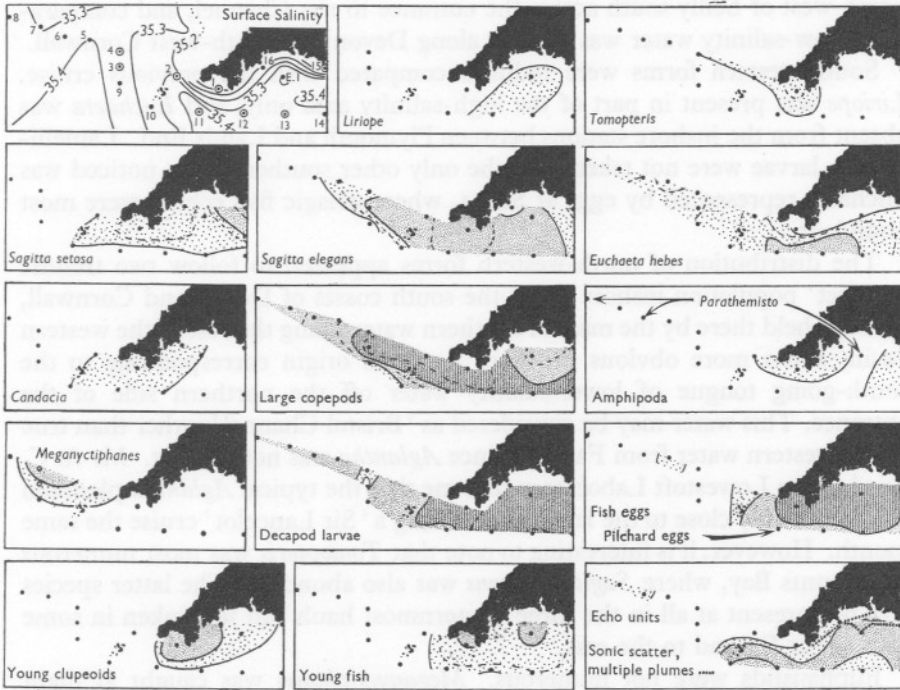
In the western basin *Liriopse* was still common, but was generally found at stations without *Muggiaea*, with which it appeared to have a reciprocal distribution. The body of high-salinity water to the south-west was clearly still dominant and equivalent to the area without *Sagitta setosa*. *Euchaeta* was quite widespread, but showed centres of abundance at Sts. 6 and 9, which were not in the area of very high salinity but on either side of it. *Euchaeta* did not penetrate into the eastern basin, but one specimen of *Parathemisto* was found east of Cherbourg. The distribution of the lamellibranch larva resembled that of the main body of *Liriopse*.



Text-fig. 16. January 1960: 'Sarsia' 11th-13th; 'Anton Dohrn' 12th-15th. Latter stations shown as squares.

Sagitta elegans was generally distributed in the western basin without a clear trend, but showed a broad tongue extending east through the narrows in the eastern basin. Another north-western form, *Spiratella*, was also fairly generally distributed in small numbers, but was absent from the most southern stations.

Fish eggs were present at most stations, but common only in mid-Channel. The echo-sounder records were unsatisfactory owing to aeration in a heavy sea, but pelagic fish were recorded only off Plymouth and Start Point.



Text-fig. 17. 7-11 March 1960.

On the map of *Meganyctiphanes* distribution, stations where *Nyctiphanes* was absent are shown as open circles.

February and March

North-western forms were very obvious in a night haul of the YFT off Plymouth in February, and were still present in the area in March when a short cruise was made to the west (Text-fig. 17). This cruise was planned to collect samples of so-called 'western water' (i.e. north-western water of high winter phosphate with large macroplankton species, notably *Sagitta elegans*, *Aglantha* and *Spiratella*), for Dr Wilson's experiments on rearing echinoderm larvae (Wilson & Armstrong, 1961). No such water could be found in the

short time available, and the maximum 'western' qualities, i.e. the largest numbers of north-western species, were found near E1.¹ From the surface salinities it can be seen not only that the western basin was occupied by high-salinity water, but that water of nearly as high salinity was present over parts of the Fastnet area in contrast to the situation in previous years. The more normal, cold, low-salinity water of the Fastnet area had apparently been pushed well back against the south coast of Ireland by the warmer high-salinity influx from the south. However, signs of some north-western influence were detectable in a tongue of medium-salinity water extending from north-west of Scilly south across the entrance to the Channel, and comparatively low-salinity water was present along Devon and south-west Cornwall.

South-western forms were reduced compared with the previous cruise. *Liriope* was present in part of the high-salinity area only, and *Euchaeta* was absent from the inshore stations between Plymouth and Lands End. Lamelli-branch larvae were not taken, and the only other southern form noticed was pilchard, represented by eggs at St. 11, where pelagic fish echoes were most abundant.

The distribution of north-western forms appeared to follow two trends: a 'relict' population inshore along the south coasts of Devon and Cornwall, perhaps held there by the mass of southern water filling the rest of the western basin, and a more obvious group of northern origin corresponding to the south-going tongue of lower-salinity water off the northern side of the entrance. This water may be considered as 'Bristol Channel' rather than true north-western water from Fastnet, since *Aglantha* was not present. Mr A. C. Burd of the Lowestoft Laboratory tells me that the typical *Aglantha* plankton was found only close to the Irish coast during a 'Sir Lancelot' cruise the same month. However, it is interesting to note that *Tomopteris* was most numerous off Mounts Bay, where *Sagitta elegans* was also abundant. The latter species was not present at all in the three westernmost hauls but was taken in some number at E1 and to the east.

Euphausiids were not numerous. *Meganycitiphanes* was caught at night stations in or near to the tongue of lower-salinity water off Scilly, but not at the other night stations, and *Thysanoessa inermis*, which is not shown on the charts, was similarly distributed. In contrast, the usual western Channel species, *Nyctiphanes couchi*, was found at only one of these low-salinity night stations, although present in good numbers at the other night stations where it was the sole euphausiid. This separation of the euphausiids reinforces the 'Bristol Channel' nature of the low-salinity water. Night hauls off the entrance to the Bristol Channel, and in eastern Lundy, usually show an abundance of *Meganycitiphanes*, whereas in water of obvious Fastnet origin *Nyctiphanes* is more abundant.

Channel forms were not well represented off Plymouth nor to the west in

¹ This may explain the comparatively good results with E1 water on this occasion.

March. *Sagitta setosa* was generally scarce, and was not found in any number except off Start Point, though present in small numbers inshore as far west as Scilly. *Apherusa* was also uncommon, and nothing can be made of the distribution of *Parathemisto*.

Considerable numbers of fish eggs, including many sprat, were taken at most stations between Start Point and Scilly, with an indicated centre of abundance off south Devon and south-east Cornwall, though a few eggs were also taken to the west. Both young fish in general and young clupeoids were similarly distributed, being absent from the high-salinity water to the west and from the lower-salinity water just west of St. 2. Echo-sounder records show very abundant pelagic fish traces from south of the Isles of Scilly to south of the Wolf Rock. It is presumed that these fish were largely pilchard and that the small number of pilchard eggs taken in the same area meant that spawning had just begun. A lesser abundance of fish echoes was recorded from this region eastwards to Start Point, and a fairly strong scatter layer of multiple plumes was obtained on lines of hydrographic stations (not shown on the charts) inshore from Lizard to Start. Some of this scatter must be attributed to the large shoals of sprat which were present at the time, as shown by their capture in fine-meshed trawl hauls off Plymouth.

June

A line of stations was sampled with the TTN in June, from just east of E 1 down channel and past Seven Stones across to Cape Clear and from there south-west into deep water (Table 7). Hydrographic information available suggests the occurrence of a very large cyclonic swirl in the Bristol Channel entrance, Lundy and Fastnet areas, with an intrusion of north-going higher salinity water from the south between the Isles of Scilly and two-thirds of the way across to Cape Clear. A westward movement of colder low-salinity water appeared to be taking place along the south coast of Ireland, extending round towards Dingle Bay. The English Channel was occupied by very low-salinity water (< 35.0‰), possibly related in some way to the high rainfall of the year.

In June, as in March, many indicator species were absent, and few *Sagitta* were taken at any stations. Except near E 1, *S. elegans* was dominant off the south Cornish coast, and was accompanied by small numbers of *Spiratella retroversa*. These stations also showed large numbers of western Channel species, including *Apherusa*, and abundant Cladocera. In accord with previous years, *Euchaeta* was at this time absent from the area sampled in the western basin, and was not encountered until St. 4 to the west of Scilly. Apart from this intrusion, possibly related to the higher-salinity water, the species was recorded only at Sts. 8 and 9 over deep water. Cladocera were abundant at these stations, and large numbers of *Salpa fusiformis* were found at St. 9. Apart from this, south-western forms were scarce and represented by a few

TABLE 7. LINE OF HIGH-SPEED SAMPLER (TTN) STATIONS, JUNE 1960

(Numbers per haul, reduced to flow-meter reading of 1200 rev. (\equiv 36-37 m³ water).)

Date	Station	Organisms																							
		<i>Nanomia</i> sp.	<i>Mugilataea</i> sp.	<i>Tomopteris</i> sp.	<i>Sagitta setosa</i>	<i>Sagitta elegans</i>	<i>Sagitta serratodentata</i>	<i>Podon</i> sp.	<i>Evadne</i> sp.	<i>Candacia armata</i>	<i>Euchaeta hebes</i>	Large copepods	<i>Centropages typicus</i>	Small copepods	<i>Parahemisto gracilipes</i>	Other amphipods	<i>Nyctiphanes couchi</i> *	<i>Meganyctiphanes norvegica</i>	Decapod larvae	<i>Salpa fusiformis</i>	<i>Dotillana</i> sp.	Pilchard eggs	Other fish eggs	Young clupeoids	Other young fish
20. vi.	A,	50° 08' N., 4° 10' W.	-	-	2	11	170	-	-	-	-	1040	260	2400	19	-	-	-	330	-	-	220	48	90	1
	1,	50° 01' N., 4° 41' W.	-	-	7	110	110	-	-	-	1020	250	4000	25	-	-	-	510	-	-	1050	70	160	4	
	2,†	49° 55' N., 5° 12' W.	-	-	-	140	140	-	4	-	680	410	720	10	-	-	(78)	510	-	-	1050	38	24	38	
21. vi.	3,†	50° 04' N., 6° 03' W.	-	-	-	500	+	-	-	-	1450	2400	4700	-	-	-	(72)	580	-	-	580	16	51	14	
	4,	50° 21' N., 5° 53' W.	-	-	-	+	+	-	-	2	1100	1580	3640	-	-	-	(330)	200	-	-	1	7	3	1	
	5,	50° 38' N., 7° 41' W.	-	-	-	+	+	-	-	-	980	260	1600	-	8	-	(50)	130	-	-	1	4	-	-	
	6,	50° 55' N., 8° 31' W.	-	-	-	+	+	-	-	-	3300	300	5750	-	-	-	(15)	25	-	-	-	1	15	-	
	7,	51° 12' N., 9° 21' W.	-	-	-	+	+	190	-	-	5400	-	3200	-	-	-	(92)	170	-	-	-	-	12	2	
22. vi.	8,†	51° 07' N., 10° 51' W.	11	-	-	22	92	260	-	-	220	4600	590	1120	-	-	58(550)	2	110	+	22	121	11	40†	
	9,	50° 37' N., 12° 19' W.	>10	-	-	>10	-	+	-	5	-	+	-	>10	-	+	-	+	+	-	-	>10	>10	>10	

* Figures in brackets show juveniles.

† Night stations.

‡ Including myctophids.

Muggiaea at Sts. A to 2, and small specimens of *Spiratella lesueurii* here and there. Very good echo-sounder scatter layers were observed, attributed to myctophid fish (see Appendix, p. 373).

July–December

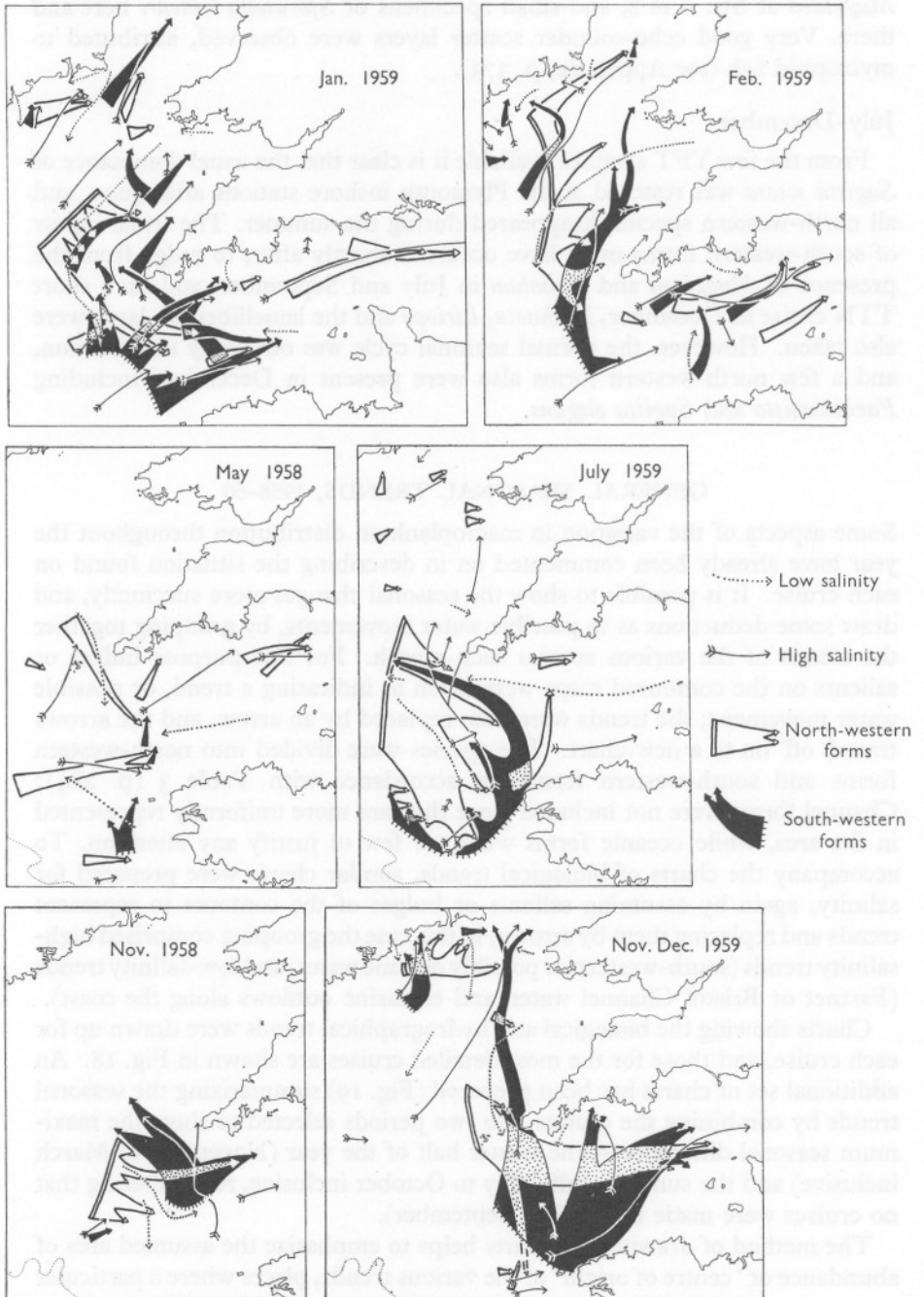
From the few YFT samples available it is clear that the usual dominance of *Sagitta setosa* was restored at the Plymouth inshore stations after June, and all north-western species disappeared during the summer. The usual inflow of south-western forms must have occurred shortly after, to judge from the presence of *Muggiaea* and *Doliolum* in July and September, and on a short TTN cruise in December, *Euchaeta*, *Liriope* and the lamellibranch larva were also taken. However, the normal seasonal cycle was obviously in operation, and a few north-western forms also were present in December, including *Parathemisto* and *Sagitta elegans*.

GENERAL SEASONAL TRENDS, 1958–60

Some aspects of the variation in macroplankton distribution throughout the year have already been commented on in describing the situation found on each cruise. It is possible to show the seasonal changes more succinctly, and draw some deductions as to possible water movements, by grouping together the trends of the various species each month. For this purpose bulges or salients on the contoured maps were taken as indicating a trend, or possible water movement; the trends were then replaced by an arrow, and the arrows traced off on to a new chart. The species were divided into north-western forms and south-western forms, in accordance with Table 3 (p. 284); Channel forms were not included since they are more uniformly represented in the area, while oceanic forms were too few to justify any attention. To accompany the charts of biological trends, similar charts were prepared for salinity, again by assuming salients or bulges of the contours to represent trends and replacing them by arrows; in this case the grouping comprised high-salinity trends (south-western or possibly oceanic water) and low-salinity trends (Fastnet or Bristol Channel water, and estuarine outflows along the coast).

Charts showing the biological and hydrographical trends were drawn up for each cruise, and those for the most detailed cruises are shown in Fig. 18. An additional set of charts has been prepared (Fig. 19) summarizing the seasonal trends by combining the cruises into two periods selected to show the maximum seasonal differences—the winter half of the year (November to March inclusive) and the summer half (May to October inclusive, remembering that no cruises were made in April or September).

The method of drawing the charts helps to emphasize the assumed area of abundance or 'centre of origin' of the various trends, places where a particular group of species is well represented and where a reasonably stable ecosystem

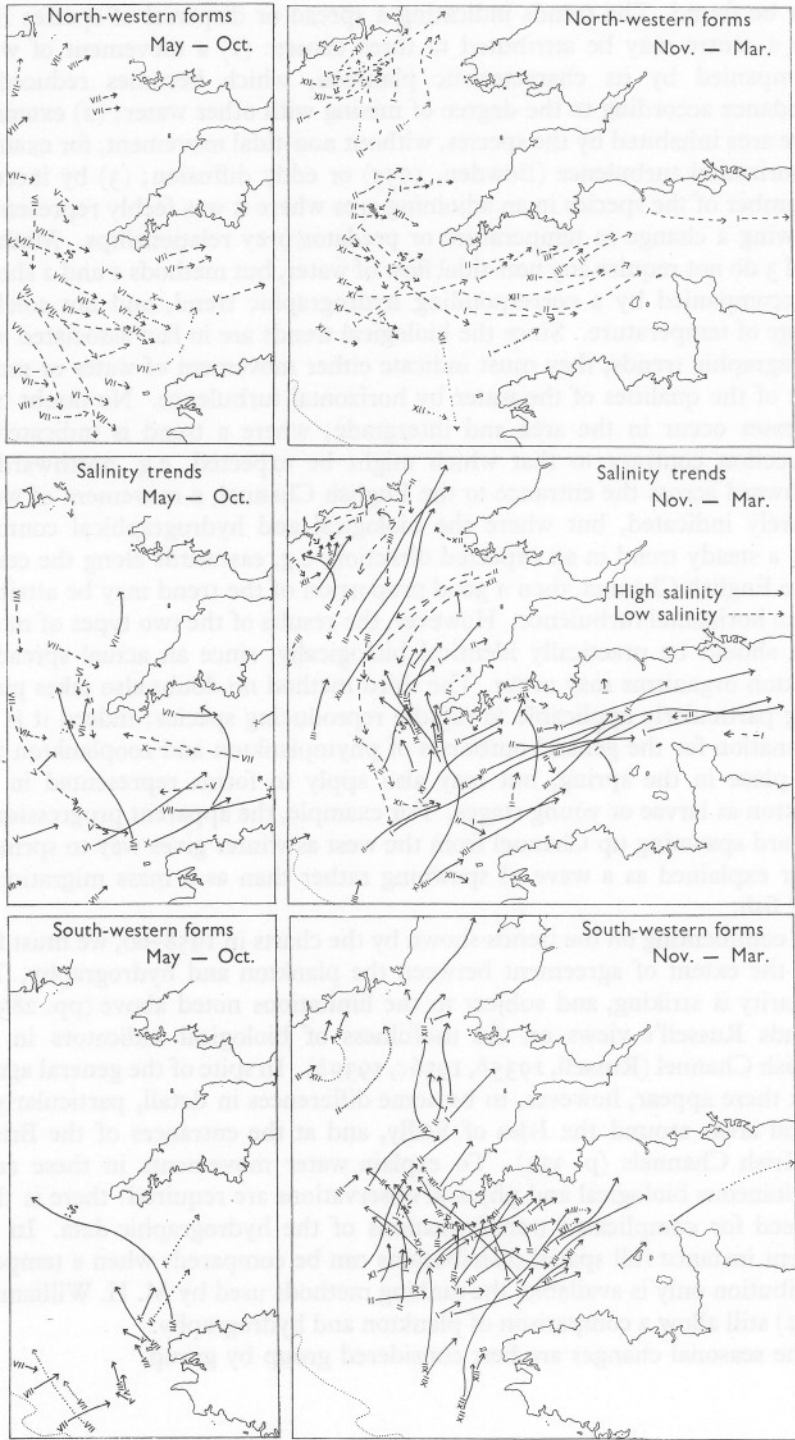


Text-fig. 18. Trends in plankton and hydrography. See text for full explanation.

must be found. The trends indicating a spread or dispersal of species from such a centre may be attributed to three causes: (1) a movement of water accompanied by its characteristic plankton, which becomes reduced in abundance according to the degree of mixing with other water; (2) extension of the area inhabited by the species, without non-tidal movement, for example by horizontal turbulence (Bowden, 1955) or eddy diffusion; (3) by increase in number of the species in an adjoining area where it was feebly represented, following a change in temperature or predator/prey relationships. Methods 2 and 3 do not require any non-tidal flow of water, but methods 1 and 2 should be accompanied by a corresponding hydrographic trend, and not solely a change of temperature. Since the biological trends are in fact associated with hydrographic trends, they must indicate either movement of water or movement of the qualities of the water by horizontal turbulence. No doubt both processes occur in the area and intergrade; where a trend is indicated in a direction contrary to that which might be expected, e.g. northward or southward across the entrance to the English Channel, a movement of water is surely indicated, but where the biological and hydrographical contours show a steady trend in an expected direction, e.g. eastwards along the centre of the English Channel, then a good proportion of the trend may be attributable to horizontal turbulence. However, the results of the two types of movement should be practically identical biologically, since an actual spread of plankton organisms may occur. The third method no doubt also takes place, being particularly applicable to rapidly reproducing species; indeed it is the explanation for the general outbursts of phytoplankton and zooplankton that take place in the spring, but may also apply to forms represented in the plankton as larvae or young stages. For example, the apparent progression of pilchard spawning up Channel from the west as winter gives way to spring is better explained as a wave of spawning rather than as a mass migration of adult fish.

In commenting on the trends shown by the charts in 1958-60, we must first note the extent of agreement between the plankton and hydrography. The similarity is striking, and subject to the limitations noted above (pp. 283-6) extends Russell's views on the usefulness of biological indicators in the English Channel (Russell, 1935*b*, 1936*c*, 1939*b*). In spite of the general agreement there appear, however, to be some differences in detail, particularly in critical areas around the Isles of Scilly, and at the entrances of the Bristol and Irish Channels (p. 334). To explain water movements in these areas simultaneous biological and physical observations are required: there is then no need for complicated transformations of the hydrographic data. In the present instance full spatial distributions can be compared; when a temporal distribution only is available, the ranking methods used by M. H. Williamson (1961) still allow a comparison of plankton and hydrography.

The seasonal changes are best considered group by group.



Text-fig. 19. For legend see facing page.

North-western forms

There was a clear centre of abundance for north-western forms in the Fastnet area, towards its junction with Lundy. In winter (i.e. December–March) the centre was comparatively small and in 1959–60, for example, it was reduced to a small patch off the south coast of Ireland, though in earlier seasons (1958–59 and apparently 1957–58) it occupied a larger area. As winter gave way to spring the centre of abundance appeared to extend to the south and south-east, the area of abundance entering the Sole area, until by June and July such forms as *Aglantha* and *Spiratella retroversa* were present in a broad band across the entrance to the Channel as far south as Ushant, sometimes entering the western basin from the south-west. After July a corresponding retreat northward began, the area of abundance contracting to its former small extent by December–January, when the south-western forms had reached their maximum. This movement was closely linked with a corresponding movement of the cyclonic swirl, and at all phases the distribution of the north-western forms was correlated with the south-going component of the, usually, cold low-salinity water.

South-western forms

The centre of origin of south-western forms was at its smallest and was most clearly delineated in summer at the north end of the Bay of Biscay, on the edge of the Sole and Ushant areas. At this time forms such as *Liriope* indicated a more western (oceanic) origin than others such as *Euchaeta* which appears to have been the dominant large copepod of the whole Biscay area. However, as the season progressed the area of abundance extended northward, and the distinction between these two types of south-western species disappeared. From July onwards all south-western forms showed north-going trends across the entrance to the English Channel, corresponding to the high-salinity component of the cyclonic swirl, then at its maximum. The south-western forms appeared to occupy the surface water in this area while the simultaneous trend of north-western forms seems to have occurred below the thermocline. A similar dual trend has recently (1961) been detected as late as October. Normally, however, the thermocline broke down earlier in the western basin, coincident with the appearance of south-western forms in some number off Plymouth. Apparently these forms were carried in a subsidiary

Legend to Text-fig. 19

Text-fig. 19. Summary of trends in hydrography and plankton 1958–60 divided into two seasons, summer (May–October incl.) and winter (November–March incl.). Excluding April, August and September when sampling was never possible. The roman numerals on the arrows show the month when the trend was observed. On the top charts, of north-western forms, weaker trends are shown dotted instead of broken. On the bottom charts weaker south-western trends are shown dotted instead of solid. For detailed explanation see text.

trend from a centre of origin to the south-west, the main trend in the autumn continuing northward beyond the Isles of Scilly into the Lundy area. By November and December south-western forms were dominant over the whole western basin, the Lundy area, and the entrance to the Bristol Channel. A month or two later the same forms had spread to the south-east Irish coast and had entered St George's Channel, the indicated centre of origin apparently including the whole of the entrance to the English Channel as well as Ushant, with subsidiary centres much farther north. By this time the cyclonic swirl had shrunk within the Fastnet area and, especially in 1959/60, much high-salinity water was spread out over the whole area investigated.

Channel forms

Although the common Channel species showed no obvious trends, they fluctuated in abundance according to season. *Apherusa* increased remarkably during the summer and was present in very large numbers, apparently in the surface waters, from July to October. Although declining again in November and December, it persisted at much lesser abundance through February and March. Somewhat similar changes were shown by *Centropages typicus*. Both species had a region of maximum abundance in summer (July–October) within the western basin, whereas in winter (January–March) they were most abundant off the south-west entrance to the Channel, where the water was warmest.

In contrast to these species, the area occupied by *Sagitta setosa* remained fairly constant, and there was less seasonal variation in numbers. *S. setosa* was very obviously restricted to the northern side of the western basin, where the surface waters show a greater annual variation of temperature than on the southern side.

Multiple trends

In many parts of the area investigated we can recognize simultaneous trends of north-western and south-western forms, sometimes apparently proceeding in different directions. The most obvious case was found off the entrance to the Channel in summer, when a north-going trend of south-western forms partially overlapped a south-going trend of north-western forms. Here there is always a stable thermocline, with temperature differences of the order of 5–6 C°, and it is possible to resolve the conflicting movements by depth as well as relate them to the cyclonic swirl (see Text-fig. 21, p. 343). A similar situation in part of the western basin in summer may be explained in a like manner. In the winter months, however, the water in these areas appears to be vertically homogeneous, yet conflicting multiple trends were present (Text-figs. 18 and 19). For example there were trends of south-western forms from Ushant across the entrance and north-eastward over the western basin towards Plymouth and Great West Bay, and at the same time trends of north-western

forms along the northern side of the western basin from the Isles of Scilly towards the narrows. It is presumed that these trends were not entirely simultaneous but represent the resultant of various intermittent movements of each component, as, indeed, an apparent zig-zag motion of the south-western trends would appear to suggest (e.g. January 1959). Beyond Plymouth these multiple trends were no longer resolvable, and for a large part of the year there was a single east-going trend offshore up Channel, of mixed north-western and south-western forms corresponding to a tongue of high-salinity water.

So far we have been discussing the evidence provided by detailed TTN sampling cruises. To what extent are these large-scale general movements displayed by the routine inshore samples from the Plymouth area?

Relevance of Plymouth inshore samples to seasonal trends in 1958-60

Only a part of the seasonal changes in the western basin was shown at the inshore stations. The extension of the north-western forms to the south during the summer had no effect at that time on the local samples, and north-western forms were detected in the YFT catches only in winter and late spring (December to April inclusive) when the TTN samples show evidence of an eastward trend of these forms along the northern side of the western basin. In summer only occasional finds of north-western forms were noted, and the catches were dominated by pilchard and the commoner Channel forms.

South-western forms were most frequent in the YFT samples in late autumn, continuing from November to February, though occasional earlier occurrences of one or two species were noted at times. Although this evidence confirms the results for 1930-38, when more YFT samples were taken (Russell, 1930, 1933, 1935*a*, 1936*d*, 1937, 1938, 1939*a*), it is obvious that the great spread of south-western forms across the entrance to the Channel in July was hardly represented in the local samples, which recorded only occasional offshoots to the east. The greater proportion of eastward spread of the south-western forms from October onwards was more clearly shown, as was their continued dominance until the re-appearance of north-western forms in the samples.

The average distribution, 1948-56

Recently the first parts of a plankton atlas of the North East Atlantic and the North Sea have been published. The average distributions of zooplankton established (Colebrook, Glover & Robinson, 1961; Colebrook, John & Brown, 1961; Vane, 1961; Barnes, 1961; Henderson, 1961) make a very interesting comparison with the results for 1955-57 and 1958-60, and reinforce some of the conclusions already drawn as to the distribution of some species.¹

¹ I must point out a possible mistake in the analyses for April 1955 (Southward, 1961) when the records of *Euchaeta* at Sts. 10, 12 and 15 may include *Euchaeta acuta* Giesbr.

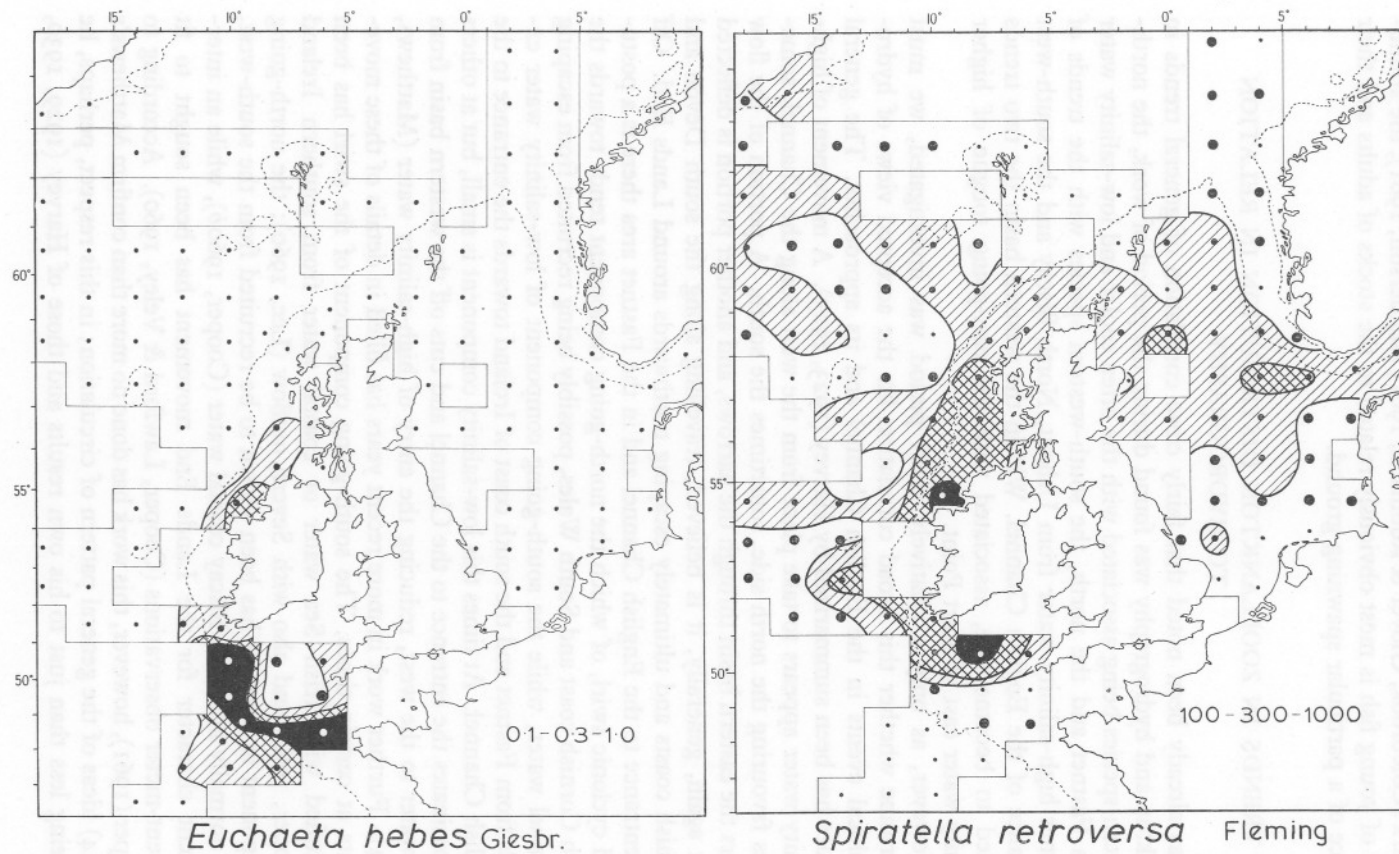
Excluding the oceanic species, which have little relevance to the present investigation, the results are in good agreement with the average distributions. The latter confirm that *Centropages typicus* is abundant over large areas to the west of the English Channel, as well as within the western basin, and emphasize the difficulty in classifying the status of *Candacia armata* in the area, though in the North Sea the species is obviously a northern form not common over the deeper water.

The most significant average distributions are those of *Euchaeta hebes* and *Spiratella retroversa*. The different centres of abundance in relation to Plymouth and in association with the cyclonic swirl are beautifully established (Text-fig. 20). The regular occurrence of *Euchaeta* in a tongue across the mouth of the Channel is confirmed; a very much stronger trend of this species is also shown, outside the area investigated from Plymouth, along the edge of the continental shelf in a broad band from north Biscay to south-west Ireland, and apparently extending north round the west coast of Ireland to the Hebrides. This trend probably explains the occurrence of *Euchaeta*, and related south-western forms, off the south coast of Ireland east of Cork in 1959, and confirms their origin from a centre of abundance separated from the origin of the same forms found in the Lundy area.

The average distribution of *Spiratella retroversa* illustrates its centre of origin in the Fastnet area near the centre of the cyclonic swirl (Text-fig. 20); the fewer records farther south show the occasional extensions south-east towards Ushant and indicate that the movement follows a more indirect route than some of the other north-western forms. This trend confirms the more westerly nature of the distributions found in the late spring and summer, e.g. in May and June 1958 and July 1959. It is remarkable that a form which reaches its southern limit off Ushant should be more abundant in the Fastnet area than in the northern North Sea, especially as average distributions suggest that it is a species of very limited temperature requirements.

The charts of average distribution of the oceanic species illustrate how infrequently such forms, even partly oceanic forms such as *Salpa fusiformis*, penetrate close to the English Channel. The recorded invasion of *S. fusiformis* in November 1958 must therefore be regarded as exceptional. In contrast, *Doliolum nationalis*, which is apparently the species recorded in 1958-60, seems to be a more regular inhabitant of the shallower waters of the Sole and Fastnet areas, though it is not found north of Shannon. This distribution agrees with its more regular occurrence in the English Channel, where it often appears off Plymouth in the autumn, with other south-western forms.

The relative scarcity of the young of most commercial fish in the Sole and Fastnet areas is well brought out by the average distributions of young fish, only mackerel and the clupeoids occurring regularly there. As the authors



Text-fig. 20. The average distribution of *Euchaeta hebes* and *Spiratella retroversa*, 1948-56, as shown by sampling over the continuous recorder routes. For full explanation see Colebrook, John & Brown (1961) and Vane (1961). Reproduced by courtesy of the Oceanographic Laboratory, Edinburgh.

remark (Colebrook, Glover & Robinson, 1961; Henderson, 1961), the abundance of young fish is most obviously related to the stocks of adults and their choice of a particular spawning ground.

TRENDS IN ZOOPLANKTON DISTRIBUTION IN RELATION TO HYDROGRAPHY

It has already been noted that fairly close correlation of general trends in plankton and hydrography was found during the period of work, the north-western species being associated with the often cooler and low-salinity water from Fastnet and the north, the south-western species with the trends of warmer high-salinity water from Ushant, North Biscay and the south-west entrance of the English Channel. Within the western basin the two trends tended to become one, associated with the east-going tongue of higher salinity water east of Start Point.

However, as only a relatively short period was investigated, we must determine whether this broad correlation fits the accepted views of hydrographical events in the English Channel and its approaches. The general picture has been summarized by Harvey (1923, 1925). A movement of high-salinity water appears to take place from the west along the Channel, sometimes favouring the north side, sometimes the south. A portion of the flow enters the eastern basin through the narrows, and another portion is deflected west again, generally, it is believed, travelling along the south Devon and Cornish coasts and ultimately escaping northwards around Lands End. Off the entrance to the English Channel and in the Fastnet area there is a postulated cyclonic swirl, of which the north-going component tends towards the north Cornish coast and South Wales, possibly being recruited from escaping Channel water, while the south-going component of low-salinity water extends from Fastnet and the south coast of Ireland towards the entrance to the English Channel. At times this low-salinity component is small, but at others it dominates the entrance to the Channel and cuts off the western basin from the water to the west, reducing the entry of high-salinity water (Matthews, 1914). Further work in more recent years has filled in details of these movements at certain times. The south-going component of the swirl has been identified with Irish Sea water or coastal water from southern Ireland (Cooper, 1961) and also with Severn outflow (Lee, 1960); the north-going component in summer has been shown to be recruited from the south-west, and normally not from Biscay coastal water (Cooper, 1960*b*), while an intermittent character for the Lands End movement has been sought to fit current-meter observations (Cooper, Lawford & Velej, 1960). According to Cooper (1961), however, this work has done no more than confirm Matthews's (1914) ideas of the general pattern of circulation; in this respect, perhaps, he is being less than just to his own results and those of Harvey (1929, 1930,

1934), Carruthers (1930), and Dietrich (1950). Nevertheless, within the western basin there is still a great deal of uncertainty. Harvey (1929, 1930) was of the opinion that much of the movement there is intermittent, a view supported by the recent biological evidence, but it has also become clear that there is no general flow from west to east, though such a movement may occur east of Start Point.

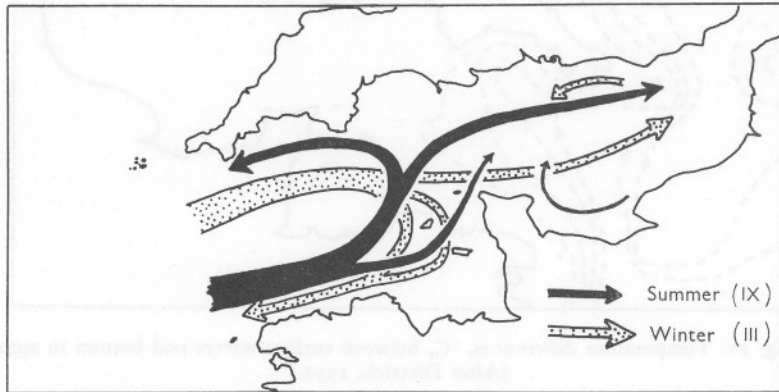


Text-fig. 21. Temperature differences, °C, between surface waters and bottom in summer. (After Dietrich, 1950.)

Once we have admitted that no general inflow from the west takes place it is easier to relate the seasonal trends found in 1958–60 with the rest of the deduced general pattern of circulation. It is obvious from Text-fig. 19 that there was more vigorous circulation of water and more marked biological trends in the winter half of the year, from November to March. For this period, or rather for March, Dietrich (1950) has postulated a flow from the west along the northern side of the western basin, with a portion of the flow entering the eastern basin and the remainder flowing west along the Brittany side (Text-fig. 22). Very little trace of such a movement was noted in 1958–60, the predominant trend being of the south-western type. The indicated centre of origin of the south-western forms was not restricted to the extreme south-west as it had been in summer, but was extended north across the entrance to the Channel, with the reduction of the cyclonic swirl. The only trace of a movement of the Dietrich pattern was represented by a minority trend of some lower-salinity water from the Fastnet area accompanied by characteristic north-western forms. In one or two cruises a movement of this pattern could be followed from north-west of the Isles of Scilly along the northern half of the western basin, or sometimes towards the centre, but there is little evidence for any westward flow along the Brittany side where there were still strong indications of south-western trends. As already noted, the north-western trend can

only be regarded as intermittent at this time of the year during the period of investigation.

The situation found from March to May was somewhat nearer to the Dietrich theoretical concept of winter circulation (e.g. Text-fig. 18, May 1958). The south-western influence had begun to decline, and the high-salinity water was retreating back across the entrance to the Channel as the cyclonic swirl expanded. At this point in the seasonal cycle it appears that there was a somewhat stronger trend of north-western forms, still intermittent, along the northern side of the western basin, soon coming to an end as the cyclonic



Text-fig. 22. Surface water movements in the English Channel in summer (September) and winter (March) according to Dietrich. (After Dietrich, 1950.)

swirl moved farther south and the flow entering the western basin was thrust back towards Ushant. The southerly movement of north-western forms developed strongly with thermal stratification of the water at the entrance to the Channel and part of the western basin and by June the south-western forms were pushed back towards the south-west entrance. A circulation corresponding to Dietrich's summer pattern started in July, though in some years, e.g. 1959, signs of a slight pause may be noticed when there might even be a reverse flow in the Channel from east to west. Such a pause may be due to the calmer weather of high summer, broken by the gales and more frequent winds of late July and August. As the south-western trends gathered force in the autumn the full Dietrich pattern developed, with high-salinity water and south-western forms moving anti-clockwise in the western basin, followed by an almost total disappearance of the north-western forms as the thermocline broke down. The latter forms appeared to remain as relics in certain areas, cut off from their origin to the north-west by the northward trend of the south-western forms.

From the routine samples taken off Plymouth, and from hydrographic data, it seems that a seasonal cycle of the above pattern is nearly always present in

the western basin and entrance to the Channel and can be recognized back to 1930. However, the strength of the south-western trend each autumn differs, as does the exact time of the change-over from the previous phase, while the north-western phase is obviously variable and not at all strongly developed in most years.

Turning to a more detailed comparison of the theoretical pattern of circulation with the results for 1958-60, we are handicapped by a rather wide spacing of stations in critical areas. Thus, none of the cruises provided evidence for an escape of water from the western basin around Lands End, though there was ample evidence of a general north-going flow in the Lands End-Scilly passage for a large part of the year. This flow, however, is derived from farther south, as part of the south-western trend. If the postulated flow from the Channel occurs, it must indeed be in a narrow stream close to the land, as Cooper *et al.* (1960) suggest. Moreover, its volume must be relatively small and hardly likely to have much influence near the north Cornish coast or in the entrance to the Bristol Channel, where the plankton is of a south-western type for a large part of the year. The general non-tidal flow in a S.S.E. direction found at the Seven Stones Light Vessel (Carruthers, Lawford, Veley & Gruning, 1951) can perhaps be related to the occasional occurrence just to the north-west of Scilly of a tongue of north-western forms in low-salinity water of Fastnet origin. There is evidence of a trend from this direction past Scilly into the western basin, though, as already noted, it is presumably intermittent, and a minority movement in comparison with the south-western trends. Such a trend from the north-west was more frequent in March-June when the flow at the Seven Stones has a greater south-going component.

Within the western basin, trends of south-western forms in late summer and autumn clearly conformed to the Dietrich pattern of summer circulation, hence in the Plymouth area, a large part of the south-west influence must approach from the south-east rather than from the south-west. It is easy to see how such a movement can be associated with a population of *Sagitta setosa* by the time it reaches the Plymouth inshore stations, by mixing with and carrying along with it part of the stronger population of *S. setosa* which appears to be always present east of Start Point and in Great West Bay. Later in the year the north-western influence appearing off Plymouth may be derived partly from the south-west and will be mixed with more obvious south-western forms, which will only disappear in the spring, when the north-western forms can approach more directly from the west.

As far as the trend of south-western forms from north Biscay and Ushant is concerned, there is no evidence that in 1958-60 they were limited to a narrow tongue of water off or near the Ile d'Ouessant. Even in July they were present on a relatively broad front in the surface water, and in later months, of course, dominated most of the entrance to the Channel.

The limited amount of evidence for the sea areas north and west of Scilly tends to emphasize the relative importance of the Severn estuary water. During the period, any flow of water from the Irish Sea, e.g. the Carnsore corner current (Lee, 1960; Cooper, 1961), was insufficient to influence trends in plankton, though detectable in the salinity trends. On some cruises the Severn outflow appeared to turn southward and contribute to the south-going component of the cyclonic swirl. It is debatable to what extent the Severn outflow causes the swirl and to what extent it is produced by the patterns of winds (cf. Cooper, 1960*a*). It is clear, however, that the centre of the swirl is relatively stagnant and that in some way this is connected with its function as a reservoir of the north-western forms and of lower-salinity water. The centre is so stable that a very strong thermocline is established, and the bottom water has an annual temperature range of only a few degrees around 9° or 10° (see Matthews, 1914), an obvious factor to be considered in the maintenance of a community of essentially cold-water animals. It seems that the Severn component is strong enough to influence the bottom deposits, possibly by heavy deposition of silt, for the few observations available suggest that the infauna is comparatively sparse, though the area obviously provides feeding for facultative detritus-eaters such as *Meganyctiphanes* (cf. Fisher & Goldie, 1959; Mauchline, 1960) and *Pasiphaea*.

There appears to be no biological indicator with which we can determine the nature of water movements off the south-east coast of Ireland and along the adjacent part of the south coast. From the charts it is obvious that the area is very complex and that a large number of different local habitats must exist for the macroplankton. There was an enclave of essentially southern character, with at times a dominance of *Sagitta setosa*, from Carnsore Point west to Dunmore. From Dunmore towards Cork a more north-western community with some *S. elegans* was usually found, but at certain times a strong oceanic component was detectable in the same area, in association with south-western forms. The area is not an especial preserve of herring from the commercial fishery of the region; pilchard are present, at least in summer, though their eggs are then commonest in the enclave of southern forms and *S. setosa* at the extreme south-east corner. This area of *S. setosa* does not seem to be influenced by the postulated Carnsore current, which originates from the Wicklow coast to the north. In that region there is a rather reduced plankton of the type more common in the Irish Sea, with *S. elegans*, and with large quantities of detritus held in suspension by the continually scouring currents in the shallow water. Mr A. C. Burd informs me that herring larvae believed to be spawned off Dunmore are present off the Wicklow coast, and hence there is likely to be a movement of water, at least at times, in this direction. From the plankton evidence there is a general trend from the south into St George's Channel in winter, involving both Fastnet water and south-western water; but in summer there is not yet enough evidence to show any trend.

DISTRIBUTION OF COMPARABLE MACROPLANKTON
SPECIES IN OTHER SEAS

Among the great spate of literature discussing the relationships of macroplankton distribution and hydrography, it is possible to select only a few examples for comparison with the English Channel, drawn from other areas with mixed arctic-boreal and warm-water communities. The most detailed information is available for the North Sea, where there has been practically continuous plankton research for over 50 years.

Immediate parallels can be drawn between the plankton communities of the eastern basin of the Channel and the southernmost parts of the North Sea, between the eastern side of the North Sea and the western English Channel, and between the Fastnet area and the central and north-western parts of the northern North Sea. The extreme southern North Sea, like the eastern English Channel, is generally poor in plankton species, and to a certain extent is influenced by movement of plankton and water from the eastern basin (Künne, 1937; Lucas & Rae, 1946). However, it is generally agreed that most of the non-resident species found at times over large parts of the North Sea are derived from the north, in a movement related to the general anti-clockwise pattern of circulation (Rae & Fraser, 1941; Rae & Rees, 1947; Marshall, 1948; Fraser, 1949, 1952, 1961; Glover, 1952, 1957; Glover, Cooper & Forsyth, 1961; Steele, 1961). This means that both cold-water and warm-water species may display similar trends—from the north-west down the east coast of Scotland and England and thence round to the Helgoland Bight—and has led to a good deal of discussion as to the biological significance of the indicator species.

It appears from the literature cited above and the Plankton Atlas (p. 339) that the central and north-western parts of the northern North Sea are dominated by a *Sagitta elegans* association comparable to the north-western species of the English Channel area, including, however, cold-water forms such as *Thysanoessa inermis* and *Aglantha*, together with *Parathemisto gracilipes* and *Nyctiphanes couchi*, which are more southern in distribution. The deeper water in this area is characterized by great temperature stability (cf. McIntyre, 1961) with a range of only one or two degrees around 7° C, and is thus a good deal colder than the subthermocline water of the Fastnet area which also acts as a reservoir of similar plankton. After the thermocline has been established in the northern North Sea in late spring and early summer, *Sagitta elegans* and associated cold-water forms begin to move south along the eastern side as they do in the Fastnet and Sole areas off the entrance to the English Channel. In late summer and autumn this movement is mixed with or replaced by an extension of warmer water forms following the same path, including, at times, species such as *Salpa fusiformis*. At the end of the autumn all these apparently migrant forms are widespread over the

whole North Sea as far as Helgoland, but gradually disappear before the spring.

The question as to whether some of the species taking part in this apparent migration are or are not resident forms showing local increases in abundance (the type 3 spread noted on p. 335) has been discussed, but is still not settled (e.g. Einarsson, 1945; Rae & Rees, 1947; Glover, 1952). The species most under contention is *Nyctiphanes couchi*, which has clearly extended its range since 1902-08 (Einarsson, 1945). It has always been resident in or near the English Channel; in 1958-60 it was abundant in the Fastnet area as well as in the western basin and off the south-west entrance, and there is no reason to suppose that it is any less capable of existing under equally diverse conditions in the North Sea.

The parts of the southern and central North Sea dominated by *Sagitta setosa* are generally those without marked thermal stratification in summer, and *S. elegans* occurs there only occasionally in autumn or winter. During the summer *S. setosa* has been recorded alone from the surface waters of the northern North Sea (Furnestin, 1938), presumably from above the thermocline, while *S. elegans* remained dominant in the deeper layers. Possibly comparable stratification takes place in the Fastnet area, when, as in July 1959, mixed populations of both species are present, but is less likely in the western basin where the distributions tend to be more distinct. Farran (1947) was able to detect a limitation of the copepod *Metridia lucens* to the colder water below the thermocline in the north Fastnet area in August, but at another station south-west of Ireland diurnal vertical migration of *Sagitta elegans* (other species of the genus apparently being absent) seemed to be unaffected by nearly as sharp a thermal boundary.

Some of the inshore areas of the North Sea appear to have self-maintaining local communities of *S. elegans* for a large part of the year, e.g. Northumberland (Meek, 1928; Burton & Meek, 1932), off the Humber estuary (Marshall, 1948), in the Thames estuary (Wells, 1938), and possibly near Helgoland (Künne, 1937; Caspers, 1939). These areas may perhaps be compared with the inshore region off Plymouth previous to 1931. In spite of its low salinity, the western part of the Baltic Sea is also inhabited by *Sagitta elegans*, with occasional occurrences of other related forms such as *Aglantha* and *Spiratella retroversa*, though *Sagitta setosa* may also occur in certain years of greater inflow of North Sea water (Mielck & Künne, 1935; Künne, 1937; Mankowski, 1951, 1959; Waldmann, 1959).

There is little doubt that the typical *S. elegans* community of the north-east Atlantic area is largely independent of salinity and that its distribution is chiefly limited by temperature, as it is in the Northern Pacific where *S. elegans* is said to be associated with Arctic water of low temperature and fairly low salinity (Bieri, 1959; Hida, 1957; cf. Fish, 1925; Bigelow, 1928a). Hence, though there may be local correlations in a few areas possibly through other

factors such as temperature, attempted general correlations of the occurrence of *S. elegans* with inflows of Atlantic water, are based on false premises. This is clearly true of the Irish Sea, where D. I. Williamson (1952, 1956*a, b*) has shown that *S. elegans* persists throughout the year, especially over the deeper water on the west side, though little trace can be found of some of the associated species that ought to be present also if the chaetognath population was maintained by recruitment from outside. From Williamson's data it seems that the distributions of *S. elegans* and *S. setosa* in the Irish Sea might well be influenced by temperature. In late summer and autumn, when temperatures are higher on the eastern side, *S. setosa* becomes abundant there; *S. elegans* is then practically confined to the western side, where the surface waters are cooler (Bowden, 1955), and, since there may be a thermocline offshore (Matthews, 1914) and a temperature gradient inshore (Slinn, 1959), the deeper waters are considerably cooler. In winter, when temperatures fall, *S. elegans* becomes more common on the eastern side together with smaller numbers of *S. setosa*, but it must be noted that in extreme inshore areas (Liverpool Bay and Morecambe Bay) only *S. setosa* is found. Although occurrences of *Nyctiphanes couchi* and *Centropages typicus* may be derived from the south, the Irish Sea plankton seems not to be influenced by the autumn trend of south-western forms into the Lundy and Fastnet areas (see p. 294-308), and the general absence of forms common in the Fastnet area is attributed to the slowness of the north-going flow.

On the opposite side of the Atlantic *Sagitta elegans* is the dominant chaetognath of the Gulf of Maine (Bigelow, 1928*a*), where it is endemic with such typical associated forms as *Tomopteris helgolandica* (as *T. catharina*), *Calanus finmarchicus*, *Parathemisto gaudichaudi* (as *Euthemisto compressa*), and *Spiratella retroversa*. *Aglantha* is possibly a resident species also, and *Meganyciphanes* and *Pasiphaea* sp. are found in the deeper layers. The predominant circulation pattern is roughly anti-clockwise (Bigelow, 1928*b*) and, as in the North Sea, immigrant species of different origin follow similar patterns. The influx of predominantly arctic species, including *Calanus hyperboreus* in the spring from the north, may be compared with the movement of north-western forms off the English Channel. The south-western trend in the Channel has a parallel in the influx of warm-water species, including surface 'Gulf Stream' forms such as *Salpa* and *Doliolum*, in late summer and autumn. Many of the endemic species and most of the cold-water forms are limited to the colder areas in summer though occasionally capable of appearing in the warmer surface waters at night. For example *S. elegans* was found mainly below the thermocline in summer, but more uniformly distributed vertically in winter. Many forms were larger in the colder water areas, a notable example being *S. serratodentata*, an oceanic form in the Gulf though found inshore off New York; this species reached a much larger size within the Gulf but apparently failed to breed there.

In the inshore waters of the Woods Hole area *S. elegans* appears to be abundant only during the colder months, disappearing in June or July when the water warms up and reappearing the following November as the temperature falls again (Fish, 1925). *Aglantha* occurred only in March and April, corresponding to the influx of northern forms in the Gulf of Maine (Bigelow, 1928a), and suggesting a parallel with the trend of north-western forms off Plymouth in February, March and April. However, off Plymouth *Sagitta elegans* is found for a much shorter period, the period of pilchard dominance in summer interposing between the north-western forms in the spring and the south-western forms in the autumn.¹

COMPARISON WITH EARLIER YEARS

It has already been made clear (p. 278) that the TTN data have no equivalent in the earlier work in the Channel which was generally of less quantitative value. Hence comparisons of distribution are not easy. Forms such as *Sagitta*, *Euchaeta* and the euphausiids are perhaps the most difficult to compare because of the variation in catching power of the gear and in depth of fishing in relation to diurnal migration. However, we can still compare less detailed trends in distribution. The data for 1937-39 are not of great quantitative value, owing largely to the use of stramin ring-trawls by day and night and the corresponding variation in catches (Corbin, 1947). Nevertheless, there seems to have been no significant difference in the main boundaries of distribution of *Sagitta* since then. As noted in Part I (Southward, 1961), *Euchaeta* was as abundant in parts of the western basin and approaches in 1937 as it was in 1958-60, and the average distribution for 1948-56 (Colebrook, John & Brown, 1961) confirms the regularity of its increase in area compared with earlier years.

The most useful parallels can be drawn from the results of Russell's cruise in July 1935.

Comparison between July 1935 and July 1959

The cruise in July 1959 was planned to follow the stations worked by Russell (1936b) at the mouth of the English Channel, but was also extended to cover the Fastnet and Lundy areas. Owing to a short period of bad weather some stations around the Isles of Scilly had to be omitted, and thus the comparison is less complete than hoped. In 1959 standard TTN hauls were used, but in 1935 hauls were made with metre-diameter nets, one of stramin and another of 58 m.p.i. silk, towed for 10 min. with 40 fathoms of warp out. Assuming a towing speed of approximately 2 knots, which would give a depth of fishing of at least 20 m, at two-thirds efficiency some 200 m³ of water must have been

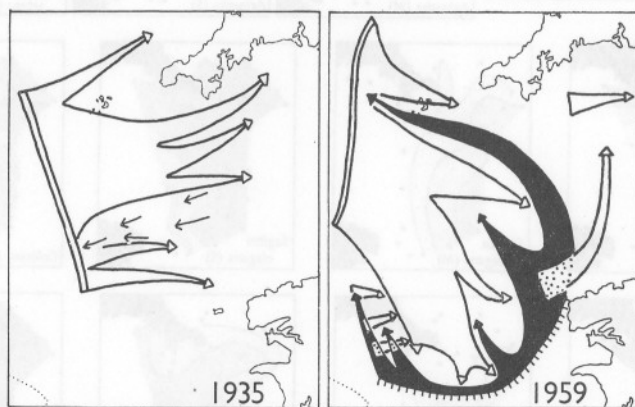
¹ This comparison with the western shores of the Atlantic relates to conditions nearly 40 years ago. There is increasing evidence of a northward shift of distribution boundaries on the coasts of Massachusetts and Maine (Taylor, Bigelow & Graham, 1957) and it is difficult to believe that the seasonal plankton changes have remained the same.

filtered by each net, compared with about one-sixth of this in the TTN. From the published data, and from Dr Russell's personal notebooks which he kindly lent me, I have drawn up some contoured charts of the distribution in 1935 to compare with the charts for 1959 (Text-fig. 23).



Text-fig. 23. 'St George', 23-27 July 1935. Samples taken with 1 m stramin net (M) or 0.5 m silk net (S) and shown as numbers per haul uncorrected. For some species data from a routine haul of the 2 m net at the Eddystone is also included, reduced to the equivalent of a 1 m haul. Except for *Sagitta elegans* the catches in the different nets did not vary significantly. (See text for further explanation and acknowledgements.) Surface salinities from routine stations (*Bull. Hydr.*, 1936).

Unfortunately, there was much less hydrographic information for 1935, and the lines of routine surface stations worked then allow only a general surface pattern to be made out, leaving vacant a large area off the Brittany coast. It can be seen that at the surface there were quite similar trends in the two periods, notably the position of the 35.4‰ isohaline in the south-west entrance and the 35.2‰ line off Plymouth and Lands End. In the earlier period, however, there was an extension of lower salinity water from the north-west across the entrance to the Channel towards Ushant: this extension was not present at the surface in 1959, but may perhaps be compared with a similar trend of low-salinity cold water below the thermocline. Tentatively we can say that in both periods the cyclonic swirl must have extended south across the mouth of the Channel, but that the north-going component was the weaker in 1935.



Text-fig. 24. Comparison of biological trends in 1935 and 1959. Heavily outlined arrows show north-western forms, black arrows south-western forms, the centre of origin of each being indicated by double lines. An apparent trend of some channel forms in 1935 is shown as thin arrows.

The biological trends show at least one major difference in an otherwise reasonably similar pattern (Text-fig. 24). In 1935 the north-western forms are clearly indicated in a broad tongue of water originating somewhere west of the stations sampled and extending around Scilly and across the mouth of the Channel towards Ushant, in association with the extension of lower salinity water. Such a trend, but apparently below the thermocline, was also present in 1959, but in the latter year there was no trace of a subsidiary trend that was clearly marked in the earlier cruise. In 1935 there was a strong east-going trend of north-western forms on the northern side of the western basin, from south-west of the Isles of Scilly towards Lizard Head, and from there apparently extending inshore towards Plymouth. Few north-western forms were taken in the YFT hauls off Plymouth in 1935, until the end of the year,

though *S. elegans* predominated from December 1935 to August 1936, and was accompanied by *Aglantha* (see Russell, 1936*d*, 1937).

In July 1959, the main boundary of north-western forms other than *Sagitta elegans* ran from west of Scilly S.S.E. across the entrance to the Channel to stations west of Ushant. From Ushant itself and from the south-west there were strong trends of south-western forms, one of them, *Euchaeta hebes*, extending right across the mouth of the Channel to the Isles of Scilly and beyond, corresponding to a trend of warm high-salinity water above the thermocline. A south-western trend of this type was not shown by the samples in July 1935, when *Euchaeta* was absent or present in too small numbers to be taken by the slowly hauled nets. However, from the distribution of clupeoid larvae, assuming these to be all pilchard, and classifiable as a south-western form, we can deduce a slight tendency for south-western influence of the same pattern though very much reduced. The sampling in 1935 did not disclose a centre of origin of south-western forms such as *Liriope* and *Muggiaea*, though the latter was recorded off Plymouth later, in October, and indicator species were practically absent from the stations in the north Biscay area. It is clear enough that south-western influence was very weak in 1935, confirming the inference drawn from the hydrographic data.

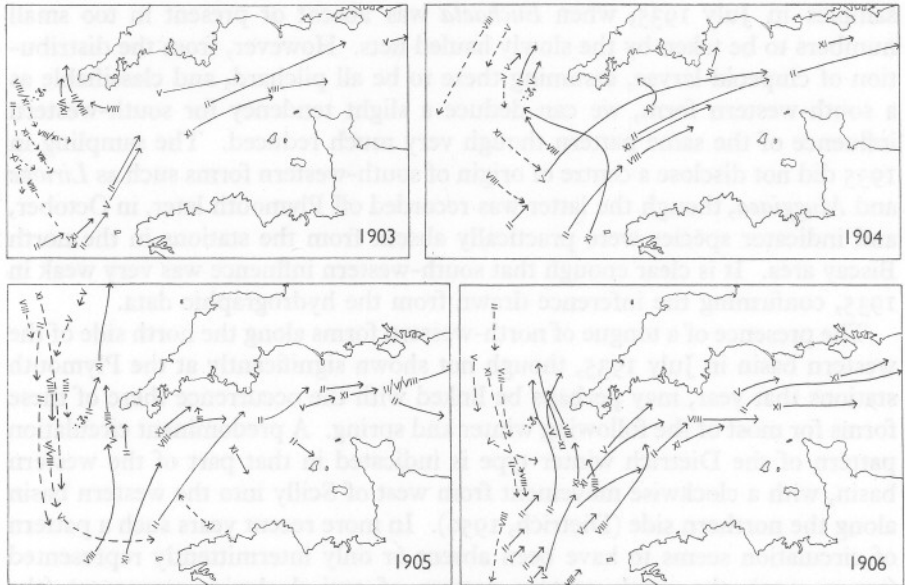
The presence of a tongue of north-western forms along the north side of the western basin in July 1935, though not shown significantly at the Plymouth stations that year, may perhaps be linked with the occurrence there of these forms for most of the following winter and spring. A predominant circulation pattern of the Dietrich winter type is indicated in that part of the western basin, with a clockwise movement from west of Scilly into the western basin along the northern side (Dietrich, 1950). In more recent years such a pattern of circulation seems to have been absent or only intermittently represented (see p. 343), the south-western pattern of anti-clockwise movement (the Dietrich summer pattern) being dominant. Can we infer that the abundance of north-western forms off Plymouth previous to 1931 was due to a dominance of a clockwise circulation in that part of the western basin, that the change-over has been associated with an increased importance of the anti-clockwise pattern, and that there has been a further strengthening of the latter since 1935? This and other theories are discussed later; it is first necessary to see what inferences can be drawn from the earliest cruises.

The International investigations, 1903-07

Although the quarterly cruises carried out from 1903 to 1907 were the most complete surveys ever made of plankton distribution and hydrography in the English Channel, the nets used were comparatively small and the stations were rather widely spaced, especially in the critical part of the western basin, from 4° to 6° W. Vertical hauls of the Hensen net were taken at most stations and the results are therefore nearer quantitatively to the recent TTN results than

to the intermediate period when large stramin nets were in use. At some stations horizontal closing-net hauls were taken at various depths, providing useful supplementary evidence.

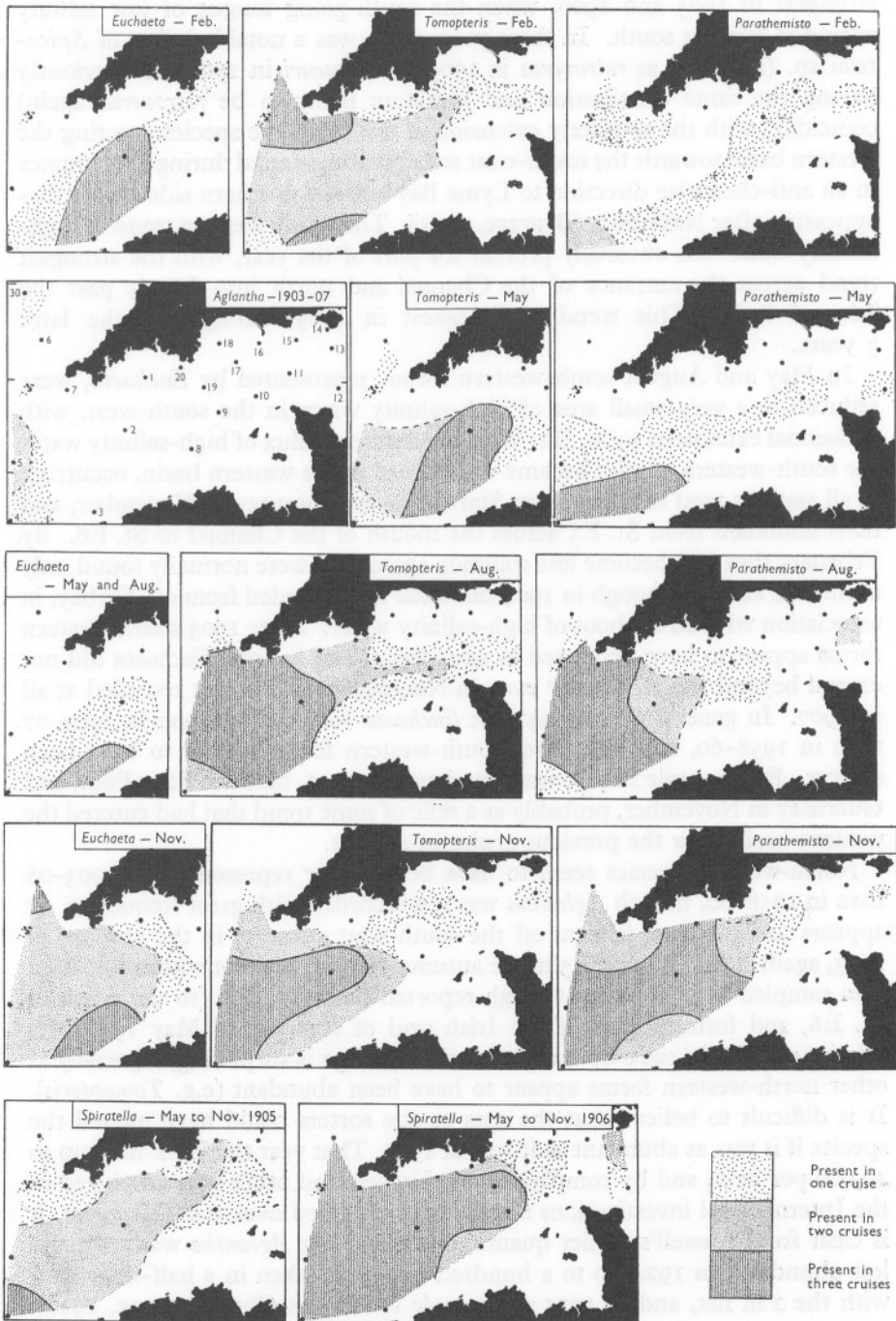
From the semi-quantitative data published (Gough, 1905, 1907; Bygrave, 1911; Int. Council, 1908, 1909) it has been possible to draw up some charts of seasonal distribution for a few species, chiefly the period 1903–05, representing the average conditions each quarter, by noting the presence or absence of the species in each of the three years. *Euchaeta* and *Tomopteris* are presented



Text-fig. 25. Salinity trends found on each of the quarterly cruises of the International Investigations in 1903–06, arranged by years. The roman numerals on the arrows show the month. High salinity solid arrows, low salinity broken arrows. Based on Matthews, 1905, 1909, 1911.

(Text-fig. 26) as indicators of south-western and north-western plankton respectively, and *Parathemisto* included to see if light could be thrown on its status as an indicator. *Spiratella retroversa*, another north-western species, but of more 'western' character, not recorded in 1903–04 is shown for 1905 and 1906. Hydrographic trends have been drawn up by the method described on p. 333.

From the hydrographic trends we see that the accepted pattern of general circulation was present each year (Text-fig. 25). The cyclonic swirl is clearly indicated off the entrance to the western basin in May and August, but more restricted to the edge of the Fastnet area in November and February. There were obvious differences in intensity of the swirl in different years: it was



Text-fig. 26. Seasonal distribution of certain species, 1903-06. For explanation see text.

strongest in 1905 and 1906, when the south-going tongue of low salinity extended farthest south. In these years there was a notable influx of *Spiratella* sp. (recorded as *retroversa* in 1905 and *lesueuri* in 1906, but obviously having the same distribution and therefore likely to be *retroversa* again) coinciding with the southerly extension of the swirl, the species entering the western basin towards the south-west and spreading round during the summer in an anti-clockwise direction to Lyme Bay and the northern side before disappearing after November (Bygrave, 1911). The south-western trend of high-salinity water was obviously present for part of the year, with the strongest trend across the entrance of the Channel and north into Lundy past the Isles of Scilly. This trend was weakest in 1903, stronger in the later 3 years.

In May and August south-western forms, represented by *Euchaeta*, were reduced to a very small area of high-salinity water in the south-west, with occasional extensions to St. E2. With the autumn influx of high-salinity water the south-western species became widespread in the western basin, occurring at all stations west of a line from Start Point to Guernsey in November, and most abundant from St. E3 across the mouth of the Channel to St. E6. By February they had become less common again, and were normally found only at Sts. E2 and E3, though in 1904 *Euchaeta* was recorded from off Torbay, in association with an offshoot of high-salinity water. After 1905 south-western forms appear to have decreased in abundance, and in 1906 *Euchaeta* did not extend beyond Sts. 2, 3 and 7 even in November. It was not recorded at all in 1907. In general we can say that *Euchaeta* was less common in 1903-07 than in 1958-60, and that other south-western forms appear to have been scarcer. For example *Liriope* was noted only in 1903, between Start Point and Guernsey in November, probably as a relic of some trend that had entered the western basin after the previous cruise in August.

North-western species seem to have been better represented in 1903-08 than in 1958-60, though *Aglantha* was not recorded with great frequency. It appears to have been present off the south-west entrance in the autumn of 1903, again at Sts. E4 and E5 in the autumn of 1904, but not within the usual area sampled in later years, though reported from St. E30 (to the north of St. E6, and forming part of the Irish grid of stations) in May 1907. Its relative scarcity in 1903-07 compared with 1924-31 is surprising, especially as other north-western forms appear to have been abundant (e.g. *Tomopteris*). It is difficult to believe that the nets or the sorters could have missed the species if it was as abundant as it was in 1930. That year the YFT took up to 40,000 per haul, and by comparison the Hensen and other nets employed in the International investigations should have captured over 100. However, it is clear from Russell's earlier quantitative work that *Aglantha* was normally less abundant; in 1924 up to a hundred might be taken in a half-hour haul with the 2 m net, and in 1925 only single specimens (Russell, 1925, 1927).

Low densities of this order would scarcely be taken in the volume of water sampled earlier. Obviously, therefore, 1930 was unusual for the abundance of extreme north-western forms, as Russell (1933) himself remarks, and conditions then are not to be taken as normal for 1924-31.

Tomopteris was much more frequently encountered in 1903-07 than in recent years. In February each year it was present at most stations in the western basin, extending in a narrow tongue through the narrows, but generally became somewhat reduced by May, and then appeared, like *Spiratella* in 1905-06, to have an origin more to the south-west, no doubt related to the extent of the cyclonic swirl. In August it had usually returned to its former abundance, once again with an extension through the narrows. It was still quite widespread in November, but rather patchy, as if its spread had been interrupted, as for example by the Autumn influx of south-western forms.

Forms such as *Meganyctiphanes* have a good chance of avoiding the slow-moving nets employed, and the species was not recorded in 1903-05. It was, however, present on occasion in 1906 and 1907 at Sts. 4, 5, 20 and 30, while a sure index to the southerly spread of north-western forms is provided by the occurrence of *Thysanoessa inermis* at Sts. 4 and 5 in the autumn of 1906.

In 1903-05 the distribution of *Parathemisto* appears to have had a pattern somewhat in between that of the south-western forms and the north-western forms. It was common at most stations in the western basin in August and November, rather uncommon in February and restricted to the central and southern stations in May. For a large part of the year this species, or possibly a related species, was also present as an apparently separate population, at some stations in the eastern basin.

At this point we may usefully sum up the changes in macroplankton distributions since 1903.

CHANGES IN DISTRIBUTION DURING THE PAST 58 YEARS

During the International Investigations both north-western and south-western forms were common at times throughout the western basin, and the cyclonic pattern of circulation was well established with clearly marked south-going and north-going trends. From 1903 to 1905-06 the south-western forms were commoner than they were in the late 1920's, but after 1905 they seem to have declined, leaving the north-western species dominant. During the period to 1936 we have no surveys of plankton distribution in the western basin as a whole, but inshore off Plymouth the north-western species tended to be dominant from 1924 to the summer of 1930. Thereafter there seems to have been a gradual increase in ascendancy of the south-western forms in the Plymouth region, with occasional slight resurgences of north-western forms at infrequent intervals (e.g. 1936, 1947, 1955). Not all the north-western

forms suffered equally. There was complete disappearance of *Meganycitiphanes*, and today this species very rarely occurs farther south than the Isles of Scilly. *Aglantha* has reappeared off Plymouth only a few times since 1930, e.g. in 1936 and 1955, but may be taken just within the western basin in some years. *Tomopteris*, however, occurs more frequently. In contrast to these species, and the rest of the north-western forms, *Sagitta elegans* is still a regular inhabitant of parts of the western basin, even though it is comparatively rare at the Plymouth inshore stations; its exact status needs examining carefully.

The status of Sagitta elegans

The most significant aspect of the change in distribution since 1930 is that *S. elegans*, formerly an inshore species of great abundance, became an offshore species of lesser abundance. At the same time the size of the individual specimens was reduced and the very large types that were once taken off Plymouth in the late spring (Russell, 1932) are now found only in the central and northern parts of the Fastnet area (e.g. as in July 1959). Unfortunately we do not know if these large specimens were widespread in the western basin before 1931, or whether they were introduced to the Plymouth area from outside by a strong north-western trend comparable in time and place (but obviously not in strength) to that found in late winter and spring of recent years.

The small specimens of *S. elegans* present in the western basin in 1958-60 fluctuated considerably from month to month, and trends were less obvious than with other north-western forms. It is impossible to say whether the species is endemic to the area. Although it was present in numbers exceeding 100 per haul at some of the stations in the western basin in about two-thirds of the cruises, the information is not as complete as desirable for the summer months (see p. 276). As far as the sampling goes, the trends suggest that *S. elegans*, like other north-western forms, increases its range and abundance in the western basin from January to May, and that later in the year, from June or July onwards, it becomes less common in the eastern parts although remaining abundant in the deeper water to the west until the autumn. To some extent this interpretation suggests a temperature association similar to that put forward to explain the seasonal trends in the Irish Sea (see p. 348), the species increasing in abundance during the coldest part of the year (January to May in the western basin) and decreasing when conditions are warmer. However, complications are introduced by the lack of comparable fluctuations in *S. setosa*, and the absence of a general reciprocal distribution of the two species for large parts of the year. Further investigations on their vertical distribution are obviously needed.

Strictly speaking, it is not true to say that there was a change from *S. elegans* to *S. setosa* in 1930-31. As already noted (p. 357), the spring and summer of 1930 seem to have been unusual for an abundance of more rarely found north-western species, and by inference it is likely that the almost pure population

of *S. elegans* found then was abnormal. A similar, almost pure, population of *S. elegans* was recorded in the summer of 1924, but in another year, 1926, up to one quarter of the chaetognaths consisted of *Sagitta setosa* (see Russell, 1931). Similarly, in most years since 1931 it has been possible to find some *S. elegans* off Plymouth. The change-over was therefore from a mixed population dominated by *S. elegans* to a mixed population dominated by *S. setosa*, and the process took several years to complete, a concomitant general reduction in abundance of chaetognaths taking place.

Chemical factors

Although only a few species have been discussed for the earlier years, it is clear that there must have been some changes in the distribution of both north-western and south-western forms in the western basin as well as at the Plymouth inshore stations. Yet the hydrographic evidence indicates that there has been no fundamental change in the pattern of water movements deduced (cf. Cooper, 1961), although a general association between water movements and plankton trends was demonstrable throughout the period. For this reason, Kemp (1938) and Cooper (1955*a, b*) were led to seek an explanation for the change in communities in a change of fertility connected with a decrease in the level of phosphate in the winter (see also Harvey, 1950), and related to events occurring well outside the area, for example by massive changes in the deep ocean. However, it is becoming increasingly evident (Cushing, 1959*a, b*; Menzel & Ryther, 1961) that the winter phosphate maximum need have very little relationship to the total production (including fish), or even total standing crop, and it is questionable if there has been any marked decrease in the fertility of the English Channel. In areas subject to seasonal variation in the standing crop of plankton the winter phosphate level governs the initial first few weeks' outburst of phytoplankton, most of which is, in any case, lost to the bottom (Riley, 1956); it does not control the level at which production is maintained for the remaining months (Cushing, 1959*a*; Parsons & Strickland, 1959). Moreover, the extent of the winter maximum is itself controlled by the rate at which the organisms die (if they do) as well as the rate of the chemical transformations taking place (Cushing, 1959*a*). It is obviously a better measure of this return than of potential fertility.

Nevertheless, the evidence for 1958-60 and some earlier years such as 1955 (see Pt. I) and 1947 (cf. Corbin, 1949; and Cooper, 1958*b*) reinforces the correlation found in 1924-38 (Russell, 1930-39*a*) between dominant populations of *S. elegans* and associated north-western species and the occurrence of high phosphate levels in the winter, as for example in the Fastnet area in 1959, off Plymouth in 1955 and before 1931. But it cannot be too strongly stressed that the converse is not true—high phosphate levels do not necessarily mean the occurrence of the north-western type of plankton, e.g. as in 1959 east of Plymouth, off the entrance to St George's Channel, and in the entrance to

Bristol Channel.¹ Moreover, the presence of *S. elegans* without the other indicator species, as for example off Ushant in certain years in winter in association with south-western forms, is not necessarily associated with high phosphate levels, e.g. February 1959 (cf. also Cooper, 1958*b*).

TABLE 8. SOME WINTER VALUES OF INORGANIC PHOSPHATE

As $\mu\text{g/at./l.}$ phosphorus, recalculated from Atkins (1925-30), and from Cooper (1938*a*, *b*). The figures show the range of values in the water column, excluding the surface sample which tends to be abnormal at times.

Winter	E 1	Half-way	E 2	E 3
1923/24	0.61	.	0.55-0.59	0.55-0.59
1924/25	0.59-0.63	0.36	0.36-0.40	0.42
1925/26	0.70-0.74	.	0.53	0.53-0.55
1926/27				
1927/28	0.53	.	0.46-0.48	0.48
1928/29	0.76	.	0.93	.
1930/31	0.53-0.60	.	0.40-0.60	.
1932/33	0.51-0.55	.	0.50-0.51	.
1933/34	0.48	.	0.48-0.53	.
1934/35	0.41-0.44	0.40-0.42	.	.
1935/36	0.44-0.48	0.37	.	.

Sampling was confined to E 1 after 1936.

There is a mistaken idea that the English Channel waters in the 1920's showed a uniform high level of winter phosphate. If, however, we tabulate the maxima for the routine stations (Table 8, from data in Atkins, 1923-30; Cooper, 1938*a*, *b*), it is apparent that in at least 3 out of 5 years there was a trend towards lower values along the line south-west from Plymouth, with the greatest phosphate content on the northern side of the western basin. A trend of this type was found in 1947 (see Cooper, 1958*b*) and in 1959 (p. 304), with relative differences of the same order as those of the earlier years, and a similar difference in 1932-36 is noted by Cooper (1938*b*). There is a strong possibility that the higher phosphate levels on the northern side of the Channel in 1924-31 were connected with a plankton of the north-western

¹ In Part I of this work, while discussing the distribution of plankton in March 1955, it was suggested that the presence inside the western basin of north-western species, including *Aglantha*, and high phosphate values indicated a movement of plankton and associated water from the region to the south of Ireland and that there may have been some connexion with the very high phosphate levels found over the edge of the continental shelf to the south-west of Ireland. There was, of course, no proof for this second theory, and Cooper (1961) has now suggested instead that the high phosphate values off Plymouth indicated a movement of water from farther east, possibly from Lyme Bay. Such an interpretation ignores the presence of the north-western plankton off Plymouth and in the western basin, species which could not have originated to the east of Plymouth, and which could not have arisen *de novo* in the middle of winter as a result of a brief rise in the phosphate content of the water. Moreover, high phosphate values were found at the other stations in the western basin showing north-western plankton, and well away from possible effects of Lyme Bay water. Thus, whether or not the very high phosphate values to the south-west of Ireland had any part in the situation, the indicated movement was from the north-west, and from an area close to the region with very high phosphate content.

type, certainly so off Plymouth (Russell, 1930-39*a*). By inference, and by comparison with the recent data quoted above, then the lower phosphate values sometimes found on the southern side of the western basin in the 1920's were possibly associated with a lesser dominance of north-western forms and a greater abundance of south-western forms. This suggests that most of the change in plankton communities in the 1930's was confined to the northern side, and that otherwise there was little alteration in the communities or the basic pattern of circulation. That is, the chemical evidence is in support of deductions made on physical and biological grounds, and indicates that the biological change, though drastic enough in the Plymouth region, was of lesser importance in the Channel as a whole and associated with comparatively minor changes in water movement. It is obvious that so delicate is the balance between species, and so cumulative the interaction between them, that even small changes in temperature and water movements might be responsible for the more significant biological changes, and hence there may be no need to seek an explanation farther afield.

Possible causes of the change in macroplankton

Let us first consider a system in which the pattern of water movement is unchanged, but subject to the rise in temperature that we know has occurred (e.g. Scherhag, 1937; Southward & Crisp, 1954; Bowden, 1955; Cooper, 1958*a*; Southward, 1960). Before 1931 there was, off Plymouth, and probably along part of the northern side of the western basin, a community of north-western forms, some probably resident all the time (but restricted to the colder water at the bottom in summer) others possibly continually recruited from farther west or north-west. During most of the year we can assume that the in-flowing water was also carrying a plankton of the same type, certainly so in winter (December to April), but possibly mixed with warmer-water species for a few months in the autumn (after August to judge from 1903 to 1907). Many of the species were living very close to their limit of distribution, especially in the warmer months. As the temperature slowly increased during the 1920's and 1930's, particularly as the annual range of temperature widened, many of these species would no longer be able to live so far south, especially in competition with warm-water forms or eurythermal species tolerant of higher temperatures. This would mean a general decline of cold-water species in the Plymouth area and a general shifting northwards of the boundaries of distribution in the western basin and approaches. Hence the water entering the western basin would be recruited more and more from plankton of the south-western type until, as today, the north-western trend was felt only in a few of the winter months. Evidence for a shifting of distributional boundaries has already been presented here and in Part I. Such a change is obviously not confined to the immediate area. The extension in range of *Euchaeta* to Scottish waters in 1948-56 (Colebrook, John & Brown, 1961)

compared with its Biscay limitation in 1903-06, the apparent increase of *Nyctiphanes couchi* in the North Sea (Einnarsson, 1945); the increase in abundance of pilchard in the eastern Channel and North Sea (Aurich, 1950; Corbin, 1950; Cushing, 1957*b*), and their appearance off the Hebrides (Rae, 1961): these are all more spectacular aspects of a change that has probably been too slow to be detected among less conspicuous forms of the plankton, but which is well known to have taken place among animals in other habitats (for references see Part III).¹

The process would be expected to be gradual, but liable to considerable fluctuation as the struggle between competing species developed (cf. Darwin, 1872, ch. 3). From the glimpses afforded by the regular samples off Plymouth (Russell, 1930-39*b*) there is a suggestion of a start in 1926, a big advance of south-western forms in 1931, a slight recession in 1935-36, and a more or less complete defeat of north-western forms in 1937 and thereafter. But it is almost certain that some slight change in water movements occurred as well, thus providing us with a more convincing explanation of the suddenness of parts of the change, such as that noted in 1930 and 1931. It seems possible that the rising temperature was accompanied by a strengthening of the north-going component at the expense of the south-going component of the cyclonic swirl off the entrance to the Channel, particularly after 1930. The wind records (Air Ministry, 1921-38; Dietrich, Wyrski, Carruthers, Lawford & Parmenter, 1952) suggest a comparable shift in direction of wind, which had a greater frequency of north and west components before and during 1930 and more south and east components afterwards, while the overall wind-strength declined considerably. Thus any trend of north-western forms into the western basin would be weaker than formerly (cf. July 1935, p. 352), and in most years opposed by a stronger trend from the south; it would be restricted to 1 or 2 months during a period when the centre of abundance was too far to the north for much influence to be felt off Plymouth.

Although the process may have been gradual enough on the whole, a slight movement of the 'front' of south-western forms, to take in the Plymouth inshore stations, as in the autumn of 1931 and after, would be sufficient to give a local impression of abrupt change. Moreover, since the south-western influence reaches Plymouth in an anti-clockwise direction the same slight extension would easily explain the sudden increases of *Sagitta setosa* off Plymouth in the autumn, drawn in from farther east and mixed with the south-western forms. The persistence of *S. setosa* would be favoured by the general warming up that had taken place, and withdrawal of the north-western forms would lead to its farther extension along the coast, perhaps at first only in the warmer months.

The change in communities that took place is itself sufficient explanation for the decreased abundance of larger macroplankton species, and there is no

¹ Part III may possibly appear in the third number of this volume (October, 1962).

need to assume a loss of fertility of the water. A cold-water plankton with large animals, was replaced, for most of the year, by a more diverse assemblage of less abundant smaller species, many of them warm-water forms or more eurythermal 'neritic' types (see p. 347). Such a change is in accordance with the general tendency for reduction in size of animals, of peak seasonal standing crop and of seasonal phosphate maxima that we find the farther we travel towards the tropics¹ (e.g. Bogorov, 1955; Cushing, 1959*a, b*; Menzel & Ryther, 1961; cf. also Wickstead, 1961). Although the decrease in winter phosphorus off Plymouth may be part of such a tendency, and a measure of the extent of the change in communities, it does not follow that there has been any marked change in primary production off Plymouth. Indeed, the major factor governing production in the English Channel in the winter appears to be light or turbulence and, as Dr Cushing has pointed out (personal communication), a rise in temperature would have very little influence on the length of the productive season. But, there is quite a latitudinal difference between the centre of abundance of north-western forms in the Fastnet area and of south-western forms in North Biscay—at least 120 miles—and the difference in primary production in these areas would be felt in the nutrient content of the respective water movements as well as in the longer-lived macroplankton species.

However, it is impossible to consider the fortunes of macroplankton animals without taking into account fluctuations in their largest predators, the pelagic fish, which we know underwent a comparable change in 1930–35; when herring were replaced by pilchard. This aspect is considered in more detail in Part III in relation to the various hypotheses that have been put forward to account for the changes.

In conclusion, the explanation offered here for the change in macroplankton communities does not necessarily require any alteration in the rate of flow of 'Atlantic' water entering the English Channel. The plankton distribution offers no conclusive evidence on this point; the south-western forms are no less 'Atlantic' than the north-western forms, indeed some may be more oceanic, and the south-western water is often of higher salinity than north-western water. It may be that the apparent correlation between the north-western plankton at Plymouth and the direction of mean water flow at the Varne Light Vessel (Russell, 1935*b*, 1936–39*b*) (see also Carruthers, Lawford & Veley, 1950) was fortuitous, or governed by the direction of winds rather than water movements. The Varne is situated in an eddy of the main flow, and the flow past it has been shown to have little relationship to the movement of water from the eastern basin into the North Sea (Lucas & Rae, 1946), which is in any case only a part of the movement taking place in the western basin (Gehrke, 1907; Harvey, 1923, 1925; Dietrich, 1950). The evidence on macroplankton distribution provided here does, however, stress the extreme importance of the cyclonic swirl and

¹ Excluding deep-water oceanic forms.

associated water movements taking place off the entrance to the western basin and in the Ushant and Fastnet areas. Until we can have more information on plankton and water movements in those areas, and more regular observations there, in the depths as well as at the surface, we can never do more than guess at the extent of seasonal or longer-term trends hinted at by observations made closer to Plymouth.

SUMMARY

In 1958–60 fifteen cruises were made in the area of the western English Channel and approaches, between lat. 2° and 8° W. and between long. 48° and 52° N. Plankton samples were taken with a modified Gulf III high-speed sampler fitted with a net of 40 m.p.i., and towed for about 10 min at 6 knots on an oblique haul between the surface and 55 m depth. A few additional samples from the eastern English Channel and southern Irish Sea have also been analysed.

The results for the larger or commoner macroplankton animals are presented as sets of contoured maps for each cruise. Accompanying maps show salinity and temperature data, and, when available, distribution of pelagic fish and scatter layers as recorded by 15 kc/s echo-sounders.

Although most of the animals studied were of use as indicator species, none of them were perfect. The indicator concept has been revised to take more account of north–south differences as well as oceanic–neritic effects. For this reason each area must be judged by itself, and the conclusions for the English Channel are not necessarily applicable to other regions.

The macroplankton of the western English Channel can be divided into four entities; north-western forms (the ‘western’ species of previous work), many of them northern species near the southern limits of their distribution; south-western forms, mostly warm-water species near their northern limits of distribution; oceanic forms; and Channel forms. The last two are not treated in detail, oceanic forms because so few of them were present, Channel forms because they were present most of the time and showed no distinct trends.

Both north-western and south-western forms showed well marked seasonal changes during the years studied. The north-western forms (including *Aglantha*, *Tomopteris*, *Sagitta elegans*, *Spiratella retroversa*) appeared to have a centre of abundance in the Fastnet region (51 – 52° N., 6 – 8° W.). They were restricted to this region, or part of it, in winter, particularly from December to March, but extended south across the entrance to the English Channel from May to July, and reached the latitude of Ushant ($48^{\circ} 30'$ N.) before retreating north again from July to November. The area of abundance of south-western forms (including *Liriope* and *Euchaeta hebes*) was restricted to the south-west of Ushant in May and June; from July to January/February they extended north across the entrance to the English Channel, eventually reaching 52° or 53° N. before withdrawing again from February to June.

These movements appeared to be related to the extensions and contractions of a well known hydrographic concept, the anti-clockwise swirl occupying parts of the Fastnet area and the entrance to the English Channel. In general, north-western species seemed to be associated with the south-going low-salinity component of the swirl, and moved south when the swirl expanded, south-western species with the north-going high-salinity warm-water component, moving north as the swirl contracted.

Within the western English Channel south-western forms were dominant from July to January, appearing off Plymouth from September/October to January/February or sometimes March. Their trends corresponded fairly well with the apparent movement of high-salinity water from the south-west entrance and with the anti-clockwise pattern of summer circulation suggested by Dietrich. North-western forms were not dominant in the western Channel, but some were present and appeared off Plymouth in January to March/April. They appeared to be associated with movements of lower-salinity water and showed some agreement with the clockwise winter circulation suggested by Dietrich; the ingoing trend was obvious along the northern side of the Channel, but the supposed outgoing trend along the Brittany coast was not clearly demonstrated.

Trends of north-western forms and south-western forms were not always separated in time, and in the western Channel and off the entrance to the Channel, opposing trends could be found at certain periods. In summer it was assumed that such trends would be separated by depth, and that the north-western forms were associated with the colder waters below the thermocline, the south-western forms with the warm surface water. In the winter the water appeared to be homogeneous and it can only be assumed that opposing trends found then were intermittent. East of 4° W. the south-western and north-western forms tended to become mixed, and both seemed to be identifiable with a tongue of high-salinity water passing up the centre of the Channel into the eastern basin.

Detailed comparison of plankton distribution and hydrography shows no evidence in connexion with the deduced movement of water from the western Channel around Lands End, but ample evidence for a general movement from the south across the Lands End-Scilly passage and for an occasional intermittent movement south-eastwards from north of Scilly. No planktonic evidence was found for a flow around Carnsore Point from the eastern side of St George's Channel, but the south-east coast of Ireland was obviously very complex, with many local habitats for differing types of plankton. The outflow of low-salinity water in the Bristol Channel appeared to have much influence on the plankton of the immediate area and may contribute to the south-going low-salinity component of the anti-clockwise swirl.

The distribution of the species studied is compared with their distribution in other areas, including the North Sea, Irish Sea, Baltic Sea and Gulf of

Maine. Common features to all areas are examined and it is suggested that many of the north-western forms (e.g. *Sagitta elegans* and *Aglantha*) are cold-water stenotherms whose distribution has little connexion with oceanic water. Further work is needed to determine the status of *S. elegans* in the western Channel.

Comparison of the recent surveys with investigations back to 1903 confirms earlier suggestions of a general tendency towards an increase in southern forms (including south-western species) and a decrease in northern forms (including north-western species) in the western English Channel, although there has been considerable fluctuation from time to time. These and other biological changes in the area during the past 58 years are believed to be largely a result of rising temperatures and a consequent general shifting of boundaries of distribution. There appears to be no real evidence that the changes in plankton distribution are due to a change in fertility in the water or of variation in strength of inflow of oceanic water. However, these aspects cannot be separated from the changes that have taken place in populations of fish, and will be discussed further in a later paper.

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APPENDIX

SONIC SCATTER RECORDS

MS 26B, 23-29 July 1959

In addition to the fish shoals plotted on the chart (Text-fig. 13, pp. 314-17) the instrument recorded four other phenomena which may be referred to loosely as scatter, and which have some relevance to the macroplankton distribution. Such scatter records were obtained at all night stations and also at morning and afternoon stations adjacent to the night station, i.e. the scatter was caused by diurnal movement of some sort.

From Sts. 16 to 24 there was a definite scatter layer, predominantly one single band with an upper limit varying from 15 to 27 m deep. The position of the layer corresponded very closely to that of the thermocline shown by the bathythermograph records, and the exactitude of the relationship is confirmed by the records at St. 19. The two positions of the thermocline shown on the BT slide (Pl. I, A) agree exactly with the depth of the scatter layer recorded on the echo-sounder as the BT unit and weight were recorded passing through it on the way down and on the way up again (Pl. I, B). The most probable interpretation of these records is that the scatter was caused by a congregation of animals normally undergoing vertical migration at night, but on this occasion unable or unwilling to pass through the boundary layer into the body of very much warmer water above (cf. Farran, 1947), i.e. some of them were probably cold-water forms of north-western origin, including *Aglantha*, but *Nyctiphanes* juveniles may also have contributed, as well, no doubt, as young fish too large to be captured by the sampler. If the position of the layer marks the thermocline, then the variation in depth of the layer from place to place, and while the ship was on station, represents internal waves in the thermocline. If this interpretation is true, the internal waves had a greater amplitude than suggested previously (cf. Harvey, 1954).

A second type of scatter consisting of multiple layers, each layer more or less similar to the single layer already noted, was found at Sts. 27-33. As the ship moved some of

the layers coalesced and then divided again and some developed into another type of scatter referable to fish. Most of the layers, however, gradually faded out in the morning without much change of depth, i.e. there was a general dispersal. It is assumed that these traces were also due to the same type of organisms as type 1, again largely below the thermocline, and that the multiple traces were due to variation in water layering in the region (west of the Isles of Scilly) where the plankton evidence suggests a good deal of mixing. The association between plankton, thermoclines and scatter layers has been discussed by Trout, Lee, Richardson & Harden-Jones (1952), Cushing, Lee & Richardson (1956), and by Richardson *et al.* (1959). At St. 19 there were about 40 large organisms per cubic metre of water sampled and thus 2200 in the water column below 1 m² to 55 m depth. If we assume only half of these were present within the scatter layer at an average depth (for the upper edge of the record) of 32 m and if we assume that one transmission of the echo-sounder covers an angle of 30° and hence an area of 23 m² at 32 m depth, then the number of organisms responding to one sound pulse might be of the order of 25,000, hence there is no improbability in attributing the scatter to plankton.

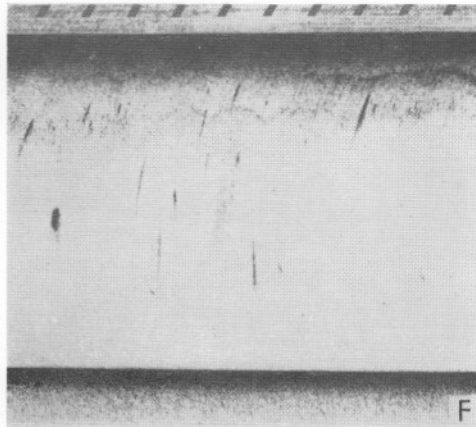
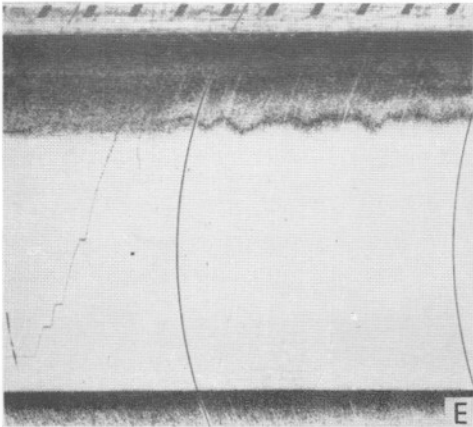
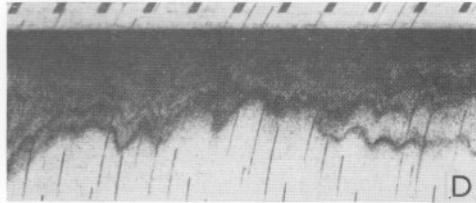
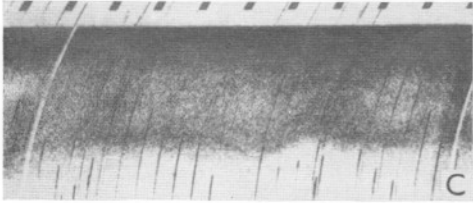
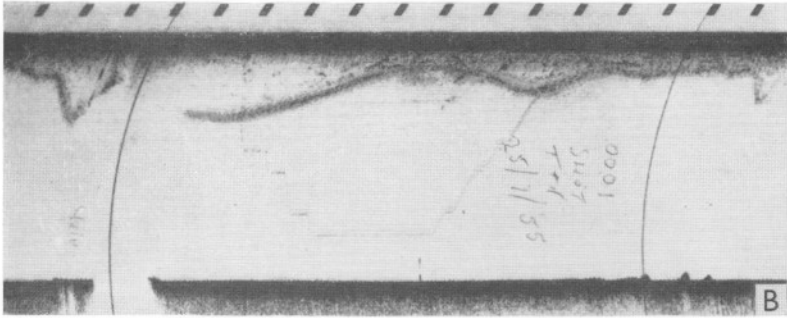
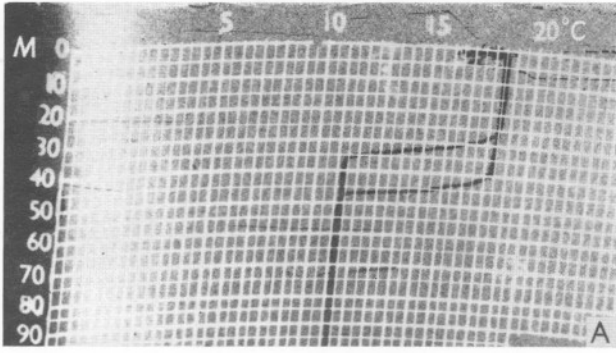
A very different type of scatter was found at Sts. 42-50. It appeared as a fairly discrete layer at the bottom in the late afternoon, and during the night became a general diffuse scatter from the surface down to 20 or 30 fathoms, and then went down again in the morning. In this region, off the entrance to St George's Channel, the thermocline is weak or absent, and a strong layer effect might not be expected. *Aglantha* was common at most of these stations, and fairly large numbers of young fish, including clupeoids were also taken in the TTN, while at the midnight stations large numbers of mysids and some *Meganycitiphanes* were also captured. All these forms, particularly the latter two, should be capable of giving some response to the sounder (cf. Cushing & Richardson, 1956), but on the other hand the area is known to contain adult herring, which can provide a diffuse scatter at times when they are not shoaling (cf. Cushing, 1957a).

The remaining type of scatter was obviously associated with fish, generally consisting of very large numbers of tiny plumes, which tended to thicken into more definite fish-shoal echoes before sinking to the bottom in the morning. These traces were recorded at Sts. 28 and 29, near St. 58 (after a rough night when no records were taken) and from St. 66 to Plymouth. There was some agreement between the depths of the

EXPLANATION OF PLATE 1

- A. Bathythermograph record of the position of the thermocline at St. 19, 24 July 1959. Depth in metres, temp. in °C.
- B. 15 kc echo-sounder record at same station as A, showing the depth of the scatter layer at the two positions through which the bathythermograph passed when lowering and raising. The triple echo from the bottom of the wire is caused by the weight and a reversing bottle as well as the bathythermograph.
- C and D. Scatter layers recorded 23 June 1960; C, while fishing Isaacs-Kidd Trawl at 4-5 knots; D, proceeding at 8½ knots after trawl haul.
- E. Record at TTN St. 8, 22 June 1960; left, while drifting on station, right, hauling TTN at 6 knots.
- F. Just previous to St. 8, scatter layer forming at dusk. Pelagic fish traces are present, many of them at the same depth as the scatter layer.

The depth scale, in fathoms, for all echo-sounder records, is given alongside B. The time marks at the top of the records are at approximately 2 min intervals. On C and D the sea-bottom was about 130-140 fathoms and just off the echo-sounder range in use: the vertical marks on these records are due to interference from the 10 kc deep sounder also in use.



(Facing p. 374)

plumes at Sts. 67-69 and the depth of the thermocline. For rather subjective reasons these traces are attributed to pilchard, possibly with younger age-groups predominant, but sprat and anchovies are also possible (cf. Cushing, 1957a).

MS 26b, 22 June 1960

Very conspicuous scatter was found in the evening and during the night on a run in towards Dingle Bay from St. 9 (see Table 7, p. 332). Patches of general diffuse scatter developed into very distinct multiple thick layers displaying internal waves (Pl. I, c and d). The bathythermograph was not available for this cruise, but the reversing bottle stations worked indicate several distinct temperature changes between 10 and 100 m corresponding to the layers at 18-55 m. The Isaacs-Kidd trawl was carried ready rigged on this occasion and a tow of 30 min was carried out at depths adjudged to be within the scatter layer region, but afterwards found from depth gauge records to be mostly below the thickest traces, 56-77 m compared with 18-55 m (Pl. I, c). During the estimated 18 min that the net was fishing at these depths 14 myctophid fish were captured, 10 of 30-90 mm length and the remainder about 15 mm. Very little else was captured, and although most euphausiids would not have been retained by the 5 in. shrimp netting, it seems probable that the scatter was due to large numbers of the myctophid fish, of which most managed to evade the slow-moving net in the dusk.

A similar scatter record was obtained the previous night near St. 8, at similar depths (Pl. I, e). The Isaacs-Kidd trawl was not ready, but the TTN haul at St. 8 contained some of the small myctophids in addition to large numbers of *Nyctiphanes* and a few *Meganyctiphanes*. It may well be that all these various organisms contributed to the layers, possibly taking up different depths according to the temperature boundaries. However, records taken while the ship was drifting on the night of the 23rd show very open 'crescent traces' characteristic of fish, and the myctophids are again indicated, while at dusk on the 22nd, typical fish plumes were associated with the start of the layers (Pl. I, f).

Fraser (1961) shows a somewhat similar type of scatter layer which he says is not due to small plankton organisms. As the layer was sampled only with a slow-moving 1 m net, myctophids and large euphausiids would not be caught.