J. mar. biol. Ass. U.K. (1961) 41, 17–35
Printed in Great Britain

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

I. SAMPLES TAKEN WITH STRAMIN NETS IN 1955 AND 1957

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(Text-figs. 1–6)

Our knowledge of the distribution of plankton in the English Channel and farther west has never been complete since work at Plymouth does not normally include routine surveys made over a long period. Recently, an opportunity was taken to carry out further discontinuous surveys in the hope that enough evidence could be gained to allow comparison with previous work and allow re-assessment of the long-term changes in distribution that appear to have occurred in the area during the past fifty years.

This first contribution describes the results of samples taken with stramin young fish trawls. The cruises were probably the last occasions that the young fish trawls will be used from Plymouth for other than qualitative sampling; and on later cruises, to be dealt with in another paper, high-speed samplers were used. It has been thought worth while therefore to give a brief outline of previous investigations with conventional nets, before the account of the work in 1955 and 1957.

PREVIOUS PLANKTON RESEARCHES AT PLYMOUTH

The earliest surveys were those carried out by the M.B.A. on behalf of the Government, as part of the International Investigations begun in 1903. The work in the English Channel ended in 1909 when the International programme was transferred to the newly established Government Fisheries Laboratory at Lowestoft. From 1903 to 1909 four cruises were made each year to a gradually increased number of stations at which hauls were taken with horizontal and oblique townets and the vertical quantitative Hensen net (Gough, 1905, 1907; Bygrave, 1911). The results were reported by these authors in a somewhat compressed form on a semi-quantitative basis, but with a detail of species never attempted since. Unfortunately, organisms were classed only as oceanic or neritic and it is difficult to compare the results with later investigations in which emphasis was given to different types of organisms (e.g. Russell, 1935).

Plankton work started again at Plymouth in 1924 and continued in detail up to 1935. As part of his now classic researches on the local plankton, Russell (1935) revised some earlier observations of Meek (1928) on the distribution of *Sagitta* in relation to hydrography and the herring fishery. The work was expanded to include several macroplankton species occurring off Plymouth, and later in other regions, and their relationship to different water masses demonstrated (Russell, 1935, 1936, 1939). Russell discovered the great change that took place in the macroplankton in Plymouth coastal waters in 1930–31, when many animals (including young fish) disappeared or became rare coincidently with a fall in nutrient salt levels in the water during the winter. The weekly plankton hauls, planned to follow these changes, using the 2 m stramin ring trawl, have been continued at less frequent intervals to the present day, but not all have been analysed or reported upon.

After 1935, further surveys, using the 1 or 2 m stramin ring trawls were made in the Western Approaches to the Channel, as part of an International Investigation of the mackerel fishery (Corbin, 1947). Since the war stramin ring trawl hauls have been taken west of Plymouth on several fishery and hydrographic cruises, but the results have not been presented. There is a growing appreciation that the stramin ring trawl is not a good quantitative sampler, in part owing to the variation in mesh size of manufactured samples of stramin supplied since 1945.

THE STRAMIN RING TRAWL AND METHODS

The method of operating the young fish trawl, to give it its common name, has been described by Russell (1930); the maximum depth reached in a haul varies from 30 to 50 m. There are several advantages compared with ordinary tow-nets (and even the larger types of quantitative Hensen or Helgoland net) in using the ring trawl for studying the distribution of young fish, their eggs, and large plankton animals. It takes a big sample, theoretically 4000 m^3 being filtered in a half-hour oblique haul at an estimated two-thirds efficiency; it collects the larger 'indicator' species, especially the coelenterates, in good condition; it does not capture the large mass of herbivorous copepods which are less useful as 'indicators', but retains some at least of the more useful spiny predatory forms such as *Euchaeta* and *Candacia;* and in theory its filtration efficiency (not yet measured) should be good because of the proportionately long bag (6 m) compared with the aperture of 2 m.

There are several disadvantages apart from the post-war variation in mesh. The most serious defect is that the depth of fishing and the volume of water filtered is critically dependent on the weight of warp and the speed of the ship through the water. Since oblique hauls are made at very low speed (*ca* 2 knots) the ship is affected by the weather, and is difficult to maintain on course or at a given speed. In the M.B.A.'s latest vessel, 'Sarsia', the main engines cannot be operated below 5 knots; the auxiliary drive of 20 h.p. is therefore employed for ring trawl hauls, and speed through the water, if any, is an unknown variable. Even hauls made by the smaller diesel ships, 'Sula' and 'Sabella', which are (or were) better powered than 'Sarsia', can hardly be compared with Russell's work with the steamboat 'Salpa', on which the warp angle could be kept reasonably constant. Another serious defect, which applies to all slowly hauled nets, is the difference between day and night hauls, even those designed to fish as deep as 30 fathoms. To some extent, especially in summer, part of this variation is due to diurnal migration of animals away from the surface in the daytime, but recent work with high-speed samplers towed at 6 knots confirms that in the daytime macroplankton can escape from, or evade, the mouth of slow-moving nets, even those of 2 m diameter. The young fish trawl, it must be rembered, is preceded in the centre line by the warp, shackle and swivel, and then three rope bridles, while high-speed samplers have unobstructed entry in front. The earlier observations on the agile young clupeoids (Russell, 1926, 1928) illustrate well the defective catching power of the young fish trawl in daylight. Finally, the construction of the young fish trawl prevents it being turned inside out between stations, and since it is too big to be hosed down outside as with other gear, there is considerable 'spread' of plankton from one station to the next and the sorter has to have a very critical eye for damaged or 'hung-up' specimens.

In the absence of better samples one must make use of ring-trawl hauls. The inherent errors can be minimized in several ways: by treating each cruise separately, or by analysing only the work of one ship during a short time; by plotting contours at intervals of more than × 10. When choice is possible somewhat better numerical evidence can be got by hauling the ring trawl vertically instead of obliquely; this reduces differences in towing speed and vertical migration.

However, since possible errors are so large, no great accuracy is claimed for the results given below. Wherever possible I avoided tedious counting by subsampling. Successively larger samples were taken (the smallest with Stempel pipettes) and viewed in a squared dish under a low-power binocular microscope, until about 10 or more individuals had been counted. The actual counts, converted to total number per haul, are shown on the charts, with contours plotted at intervals of × 10 or more, but it must be borne in mind that the actual distribution may be more or less irregular than that shown.

In discussing the practical use of indicator species for distinguishing different bodies of water Russell (1939) has remarked that though probably many species form the characteristic association of plankton accompanying one or two more striking animals, it is the latter that should be selected as indicators, for the rapid examination of large numbers of collections. Many species, both holoplanktonic and mesoplanktonic, have been suggested as 'indicators' by Russell (1935, 1936, 1939) and by other workers (Fraser, 1952; Glover, 1957; see also Abramova, 1956). In this and subsequent papers Russell's precepts have been followed with one or two exceptions. Thus I regard it as essential that an indicator species such as *S. elegans* should be present in all the samples from a supposed 'elegans' water area; and I have not been able to place so much reliance on medusae, which may be damaged in high-speed sampling and are often too scarce to be taken unless the large filtering capacity of the oblique 2 m ring trawl haul is employed.

In the case of the ring trawl samples described here, practically all the organisms are indicator species, and have been identified. The exceptions were young fish; euphausids; some copepods; certain medusae; and the oceanic siphonophores. These forms constitute a very small part of the daytime catches taken in the ring trawl off Plymouth.

THE 1955 SAMPLES

In the early months of 1955 sea-water samples taken at station E1, 20 miles S.S.W. of Plymouth, were found to contain more phosphate-phosphorus than in any year since 1929 (Armstrong, 1957). Dr Cooper made a cruise in March, to try to trace the source (if any) of this nutrient-rich water, and worked a number of stations with the 2 m ring trawl in addition to a chemical programme (see Fig. 1A). The following month part of the same area in the Western Approaches was worked by Dr Steven, assisted by Mr L. B. Pradhan, also with the 2 m ring trawl. Because of the possible significance of the high phosphate levels (cf. Kemp, 1938; Russell, 1939), I have examined the hauls from these two cruises and have compared them with some of the routine hauls taken at E1 and the Eddystone throughout the same year.

In describing some of the chemical results of Dr Cooper's cruise, Armstrong (1957) remarks 'although notably high phosphate concentrations were found in surface waters over the continental slope south-west of Ireland, there is no evidence that water from there has ever entered the English Channel, and no satisfactory source for the high phosphate water was found within the area surveyed'. This was evidently Dr Cooper's opinion at the time (Report of Council for 1955–56, Vol. 35 of this *Journal*, p. 653). The plankton results, however, allow us to suggest an origin for both the 'western' plankton and the high phosphate water, and thus emphasize the usefulness of biological indicators in comparison with the cruder chemical methods available for distinguishing water masses.

The distribution of the commoner indicator species at the cruise stations is given in Figs. 1 and 2, while the seasonal variation of these animals off Plymouth is presented in Table 1. The more interesting changes and distributions are described on pp. 22 and 25.

TABLE 1. ZOOPLANKTON INDICATOR SPECIES, 1955

(Daytime catches made with the 2 m stramin ring trawl off Plymouth: ½ h oblique hauls. 'Eddystone': 2 miles east of Eddystone light; E 1: 50° 02′ N., 4° 22′ W.)

		Species											
Date	Station	*Aglantha digitalis*	*Liriope tetraphylla*	*Nanomia* sp.	*Muggiaea* sp.	*Tomopteris* sp.	*Sagitta elegans*	*S. setosa*	*Candacia armata*	*Euchaeta hebes*	*Themisto gracilipes*	Larvae of Decapoda	Pilchard eggs
12. i.	Eddystone	—	80	—	—	—	44	1,300	—	—	—	—	—
18. i.	Eddystone	—	24	—	—	1	68	988	—	—	—	12	—
16. i.	Eddystone	—	10	—	5	28	292	1,892	4	—	—	—	—
16. ii.	E 1	1	1	—	4	48	104	1,324	1	—	2	—	—
1. iii.	Eddystone	2	32	*	—	8	64	1,304	24	—	4	*	—
15. iii.	E 1	1	—	*	—	60	1200	16,240	1680	—	—	*	—
30. iii.	Eddystone	—	—	—	—	20	40	3,270	—	—	—	*	—
9. v.	E 1	—	—	—	—	—	2	3	12	—	—	384	8150
11. v.	Eddystone	—	—	—	—	—	—	16	—	—	—	1200	576
13. vi.	E 1	—	—	—	—	—	—	10	—	—	—	*	4500
11. viii.	E 1	—	200	—	576	—	—	12	—	—	—	832	—
15. ix.	E 1	—	200	—	*	—	—	40	1	4	—	384	1920
17. xi.	E 1	—	5	—	2900	—	4	1,730	2	4	—	576	480
21. xii.	E 1	—	20	—	1060	—	7	376	—	—	—	144	—

* Present, not counted.

January

At the start of 1955 the plankton off Plymouth was not much different from other recent years (Russell, 1947; Corbin, 1948, 1949). The presence of *Liriope* suggests the remains of a south-western fauna of the previous autumn, but a small number of *Sagitta elegans* and *Tomopteris* indicated some western influence.

February

The following month the western component was much more marked, the significance of the increased numbers of *Tomopteris* and *S. elegans* being strengthened by the appearance of *Aglantha*: by this time the phosphate content exceeded 0·6 μg at./l. at the surface.

March

Aglantha was still present in March, and the phosphate level remained high. The disappearance of *Liriope* and *Muggiaea* left the western forms dominating the plankton, apart from continued numbers of *S. setosa*. From the maps (Fig. 1), it is clear the oceanic forms such as the salps were present only to the south-west, over the La Chapelle Bank (stations 3 and 9) while the more or less oceanic form *Sagitta serratodentata* was common at most of the stations along the edge of the continental shelf. The limits of this species may be compared with Corbin's results, for example April 1938 (Corbin, 1947, fig. 11 D): the area of dominance seems to have extended appreciably farther to the east. *S. setosa* was very much confined to the eastern stations. The 'western' indicators shown in Fig. 1, all have somewhat similar distributions. An area of abundance in the west (stations 10, 13 or 14, according to species) was partly separated by an area of scarcity (stations 8 and E3) from the English Channel (Eddystone, E1 and E2) where the species were again abundant. The phosphate (Armstrong, 1957) showed a similar distribution pattern.

It may be noted that the presence of an oceanic component at stations 3, 4, 7 and 8 to judge from the plankton, appears to have had no connexion with the distribution of *Sagitta elegans*. This species occurred in large numbers in association with *S. serratodentata* only at the more northerly stations.

April

There were no samples from the Plymouth stations in April, but on 30 March, at the Eddystone, the western forms were obviously declining. In addition to a small percentage of *Sagitta elegans* only *Tomopteris* was present. The network of stations to the west was closer than in March and the distribution can be shown in more detail (Fig. 2). Among the oceanic forms *Rhincalanus* and *Sagitta serratodentata* were present along the edge of the continental shelf, while salps were still restricted to the most southerly deep-

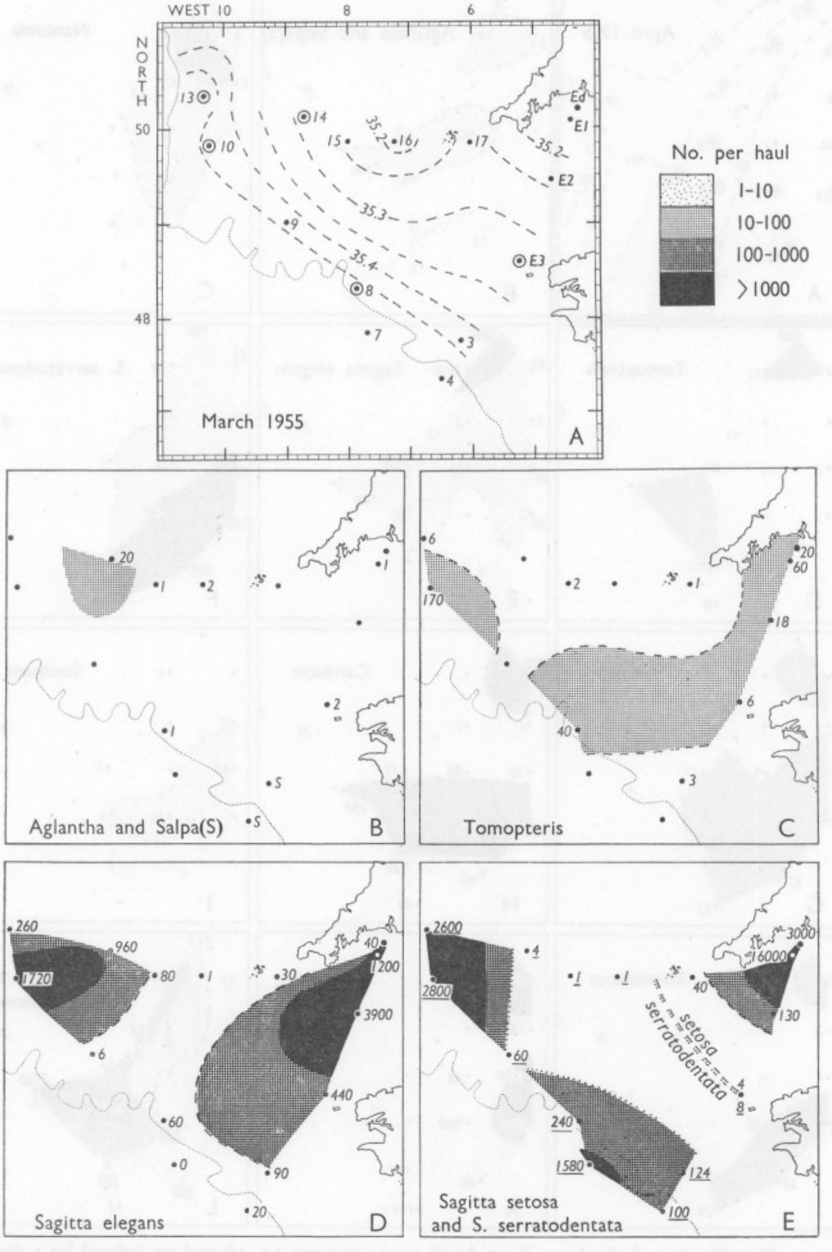

Fig. 1. Distribution of plankton and surface salinities 14–20 March 1955, with station at the Eddystone (Ed) on 30 March: A, position of stations (night hauls marked with a double circle) with approximate salinity contours at 10 m depth based on these stations and on others worked by Dr Cooper; B, *Aglantha digitalis* and *Salpa* spp; C, *Tomopteris* spp. (mostly *T. helgolandicus*); D, *Sagitta elegans*: E, *S. serratodentata* (to the west, numbers underlined) and *S. setosa* (to the east). The contour shading for this and subsequent maps is shown.

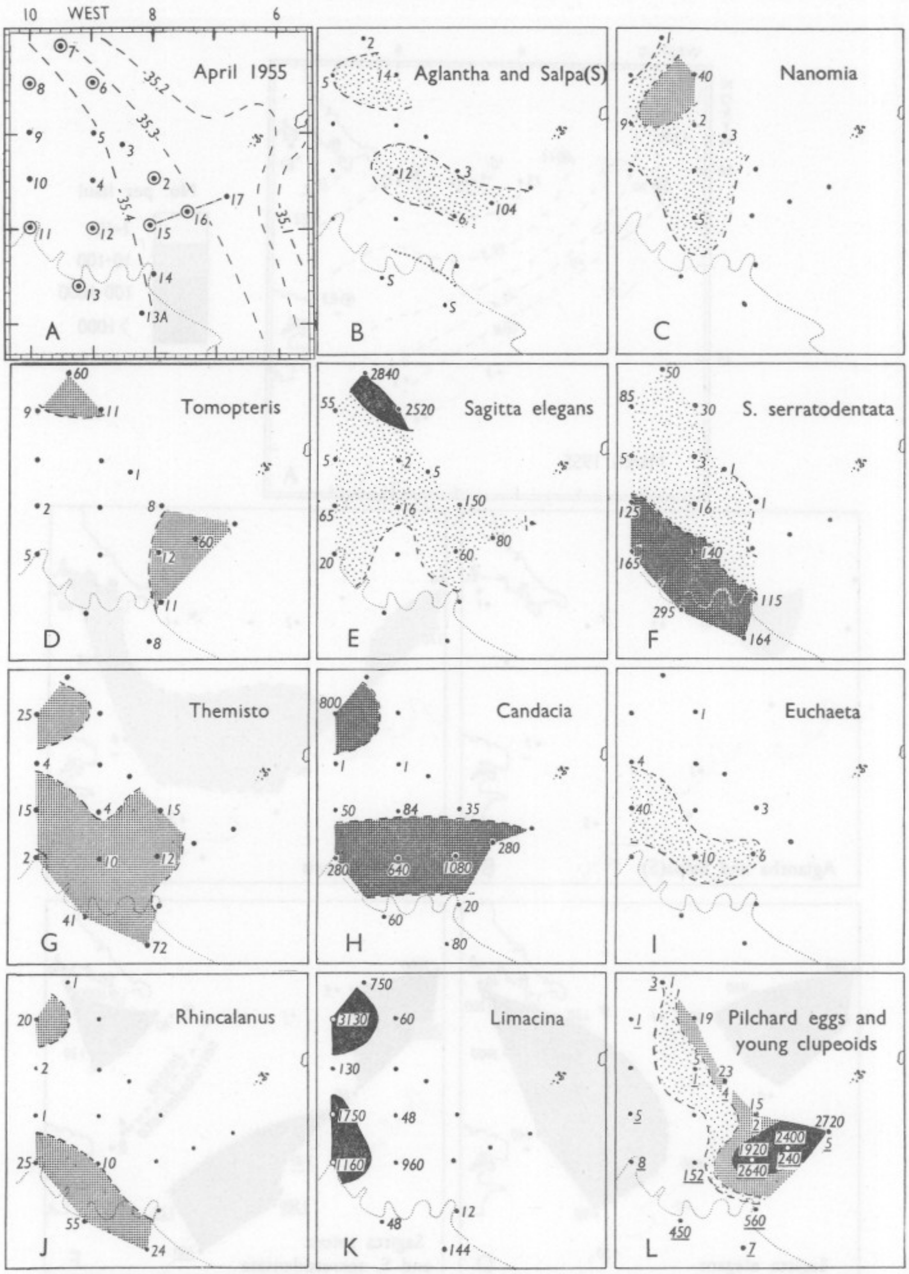

Fig. 2. Distribution of plankton, 8–12 April 1955: stations 15, 16 and 17 (joined by a dotted line on map A) were worked on 27–28 April. A, station positions (night hauls shown by double circle) with salinity contours taken from the International Council Synoptic Hydrographic charts (Smed, 1955) showing the surface monthly mean: *B*, *Aglantha digitalis* and *Salpa* spp; C, floats of *Nanomia* sp.; D, *Tomopteris* spp. (mostly *T. helgolandicus*); E, *Sagitta elegans*; F, *S. serratodentata*; G, *Themisto gracilipes*; H, *Candacia armata*; I, *Euchaeta hebes*; J, *Rhincalanus* sp.; K, *Limacina retroversa*; L, eggs of *Sardina pilchardus* (contoured) and young clupeoids (figures underlined).

water stations. The 'western' indicators show a pattern comparable with that of March, particularly *Aglantha*, *Tomopteris* and *Candacia*. The centre of abundance of *Sagitta elegans* would appear to have shifted farther north: south of the 50° parallel it exceeded 100 per haul only at one night station. A similar northern centre is suggested for *Nanomia*, and neither species seems to have any relationship with the oceanic component. *Themisto* and *Euchaeta*, from their geographical distribution, as far as it is known, are southern forms, and the patterns shown in Fig. 2 are probably falsified by the absence of stations off Brittany. In March they were present at most stations, without a clear pattern and have not been shown in Fig. 1. Russell (1935) regarded *Themisto* as a 'western' form, but recent investigations with the high-speed samplers show it as both a western and south-western form at times. He identified *Euchaeta* with 'south western' or 'Biscay water', but the present report shows that it now penetrates into the preserves of western forms (see p. 31). The distribution of the remaining southern form, *Sardina pilchardus*, is shown as eggs and post-larvae, and the pattern suggests a north-eastward progression of spawning. In March, pilchard eggs were taken at some of the more southerly stations (E3, 3 and 9; over 100 at the latter two) and together the two 1955 cruises indicate a possibly earlier start and more northerly extension of the spawning area compared with 1937–9 (cf. Corbin, 1947).

May and June

The last traces of western forms disappeared from the Plymouth stations in May, to be replaced by the usual dominance of pilchard eggs.

August and September

The pilchard dominance continued into the autumn. In August the usual appearance of south-western forms (Russell, 1935) occurred, and both *Liriope* and *Muggiaea* remained in the Plymouth area to the end of the year. They seem to have been accompanied by some *Candacia* and *Euchaeta* in September and November.

November and December

The numbers of *Liriope* were reduced at the end of the year, when slight signs of western influence were suggested by the reappearance of *Sagitta elegans* in small numbers. The numbers of all *Sagitta* increased at this time, coincident with the cessation of pilchard spawning.

1957

Two cruises were made to the west of Plymouth in 1957, vertical hauls being taken with the 1 m net in May, and with the 2 m net in September. Other work restricted the programme in May, and bad weather curtailed the later cruise. On both trips additional samples were taken with horizontally towed

TABLE 2. ZOOPLANKTON INDICATOR SPECIES, 1957

(Daytime catches made with the 2 m stramin ring trawl off Plymouth: ½ h oblique hauls.)

Date	Station	*Liriope tetraphylla*	*Muggiaea* sp.	*Nanomia* sp.	*Tomopteris* sp.	*Sagitta elegans*	*S. setosa*	*Candacia armata*	*Euchaeta hebes*	Other copepods	*Themisto gracilipes*	Pilchard eggs	Other fish eggs	Young clupeoids	Other young fish	Decapod larvae
1. i.	Eddystone*	—	—	—	13	—	1830	—	—	170	—	—	23	2	2	135
24. i.	E 1	—	33	1	—	18	1140	—	—	60	—	—	90	8	2	120
19. ii.	Eddystone	1	15	—	—	90	900	7	—	6	—	1	90	63	9	690
5. iii.	E 1	30	12	†	—	183	180	9	—	58	1	21	1410	—	—	1830
11. iii.	Eddystone	—	3	—	1	—	102	6	—	21	—	—	150	105	15	780
18. iii.	Eddystone‡	—	—	—	—	—	—	(27)	—	(21)	—	(45)	(99)	—	—	—
1. iv.	Eddystone	—	—	—	—	—	—	—	—	660§	—	11,100	60	180	126	2280
24. iv.	E 1	—	—	—	—	15	—	54	—	840	—	6,000	240	—	90	7560
9. v.	E 1	—	4	—	—	—	300	8	—	800	—	6,560	80	32	76	4500
12. vi.	Eddystone	—	†	—	—	—	192	—	—	1500	—	10,560	120	180	54	780
25. vi.	Eddystone	—	—	—	—	—	360	—	—	180	—	5,460	60	45	45	3000
16. vii.	E 1	—	†	—	—	—	234	—	—	180	—	1,620	450	30	—	180
21. viii.	E 1	—	2400	—	—	—	720	3	—	180	—	180	36	162	30	1140
27. viii.	Eddystone	—	1890	—	—	—	30	—	—	252	—	15	24	9	9	480
17. ix.	E 1	—	1800	—	—	—	12	2	1	12	—	1,260	—	3	18	360
9. x.	Eddystone	—	360	—	—	—	306	5	—	132	—	252	—	15	—	1200
25. x.	Eddystone	—	900	—	—	—	120	3	—	45	—	25	5	96	3	282
6. xi.	E 1	—	240	—	—	—	600	48	13	42	—	30	3	150	—	12

* Night haul. † Present. ‡ Not well preserved. § Includes 600 *Anomalocera patersoni*.

high-speed samplers based on the Hardy indicator (Glover, 1953) but it has been found impossible to relate the catches of these small samplers with the vertical hauls. The volume of water filtered was of the order of 1 or 2 m^3, and thus several of the larger 'indicator' species were not taken at all, others being distributed erratically. The samplers were run day and night at only 10 fathoms depth, the limit of the equipment at the time, and their catches appeared to be affected by diurnal migration.

The results of the May cruise are shown in Fig. 3, and Table 3 gives the results for the September cruise. In Table 2 are presented the main species found in the oblique hauls of the 2 m ring trawl off Plymouth throughout the year.

January to March

In the spring of 1957, the Plymouth samples showed a trend comparable to that in the spring of 1955. Some 'western' indicators were present in January and February, accompanied by some 'south-western' forms. At the beginning of March *Sagitta elegans* was found in some numbers, but no further increase in western forms took place.

April

Except for the sample at E1 on 24 April, *Sagitta elegans* was not present off Plymouth for the rest of the year. Pilchard spawning began earlier than in 1955, the surface temperatures at E 1 in February, March and April being 1 to 2° higher than in 1955. The activity of the pilchard and the higher temperatures may have had an effect on the numbers of *Sagitta elegans* and *Candacia*, but the absence of *Aglantha* suggests that there had been very little communication with the apparent source of the 'western' forms.

May

The results of the cruise in May appear to confirm the presence of a 'western' component in the Channel, for though by then absent off Plymouth, some western forms were found at the stations near and south of the Lizard (1 and 2). Apart from this area there was a generally reciprocal distribution of 'western' and 'south-western' forms. Species such as *Aglantha*, *Tomopteris* (excluding the unidentified oceanic species at stations 7 and 25), *Sagitta elegans*, *Candacia* and *Limacina* were all most abundant along the northern and western line of stations, while *Liriope*, *Muggiaea*, *Euchaeta* and pilchard eggs occurred only at, or were most numerous at, the southern stations. The oceanic forms, salps, *Rhincalanus*, *Sagitta serratodentata* and certain species of *Tomopteris* were found only at the extreme south-western stations. *Sagitta setosa* was restricted to the northern side of the Channel, but was in fact most abundant at the stations north of Scilly, where *S. elegans* was also abundant.

Compared with March and April 1955, May 1957 showed a closer approach to the area of abundance of the 'western' fauna to the Isles of Scilly; there was no region of poor macroplankton just to the west as in 1955.

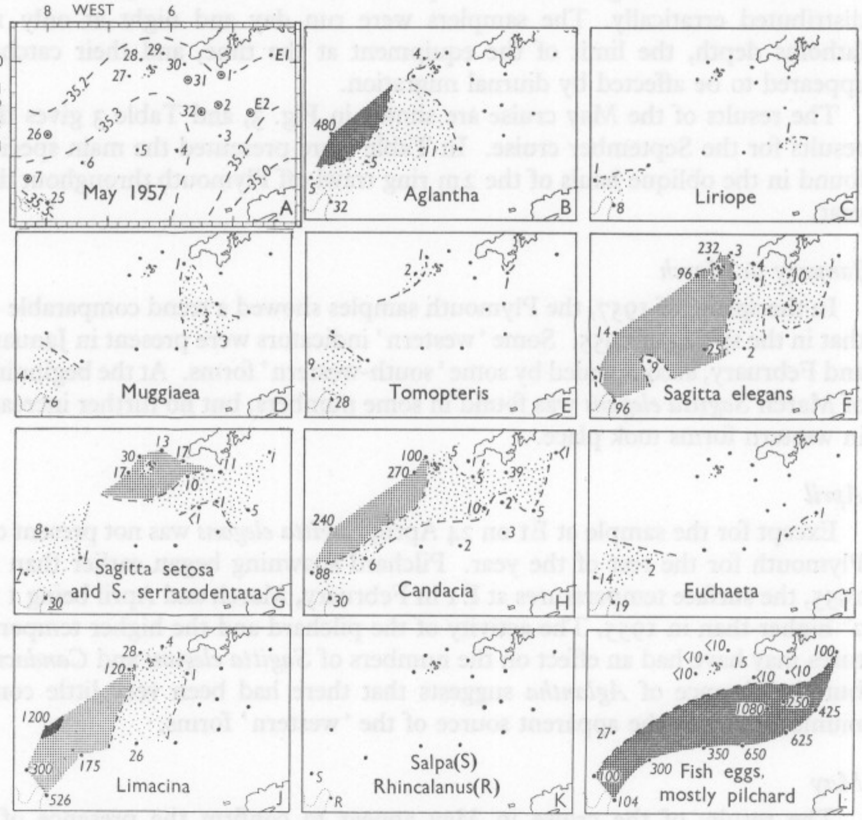

Fig. 3. Distribution of plankton and surface salinity, 1–9 May, 1957. A, position of stations, night hauls shown by double circles, and salinity contours at 0–10 m, derived from the International Council charts (Smed, 1957) modified by samples taken on the cruise by Mr F. A. J. Armstrong; B, *Aglantha digitalis*; C, *Liriope tetraphylla*; D, *Muggiaea* spp., probably all *M. kochi*; E, *Tomopteris* spp.; F, *Sagitta elegans*; G, *Sagitta serratodentata* (to the west, figures underlined) and *Sagitta setosa* (to the north); H, *Candacia armata*; I, *Euchaeta hebes*; J, *Limacina retroversa*; K, *Rhincalanus* sp and *Salpa* spp.; L, fish eggs, more than 95 % *Sardina pilchardus* at stations with over 100. For this cruise, with vertical nets, the numbers given are those per haul, i.e. in the column of water below a circle of 1 m diameter (ca 0·785 m^2) to within 10 m of the bottom.

April–July

Pilchard dominated the Plymouth plankton hauls for the summer, until the appearance of 'south-western' forms again in August.

August–November

Liriope was not found in the autumn but *Muggiaea* and *Euchaeta* appeared, again accompanied by small numbers of *Candacia*. Pilchard spawning continued to the end of the season's sampling and 'western' forms did not reappear in the area until March the following year (to be reported upon in a later paper). On the curtailed cruise in September, however, the 'western' forms *Aglantha*, *Tomopteris* and *Sagitta elegans* were found at station 2, 30 miles south of the Lizard (Table 3). Presumably this influence did not reach Plymouth for 6 months, or else it died away without travelling much farther eastwards.

TABLE 3. ZOOPLANKTON INDICATOR SPECIES FOUND DURING THE SECOND PLANKTON CRUISE IN 1957

(Vertical hauls with 2 m stramin ring trawl, 10 September.)

Station and depth of haul	*Aglantha digitalis*	*Muggiaea sp.*	*Tomopteris helgolandicus*	*Sagitta elegans*	*S. setosa*	*Candacia armata*	*Euchaeta hebes*	*Themisto gracilipes*
(1) 49° 55′ N., 5° 11′ W. from 40 f.	—	—	—	2	83	32	—	—
(2) 49° 27′ N., 5° 9′ W. from 50 f.	12	—	5	88	360	45	5	8

E 1 and Eddystone oblique hauls during same period are given in Table 2.

The series of samples off Plymouth in 1957 illustrate how deceptively unchanging the plankton at the Eddystone may appear compared even with that at E 1, 10 miles to the south. As the cruises show, the latter station itself is by no means representative of the northern half of the Western English Channel.

POSSIBLE MOVEMENTS OF PLANKTON AND WATER MASSES

There is great danger in trying to attribute some meaning to the limited number of samples taken in 1955 and 1957. However, some tentative suggestions as to the course of events, both biological and hydrographical, can be made.

In the spring of 1955 a macroplankton community containing some 'western' indicators, and accompanied by a characteristic water mass with high winter phosphate levels appeared in the Western Channel. The stations worked in the Western Approaches suggest that the plankton and water mass may have been derived from an area to the south of Ireland, i.e. to the north and west of the entrance to the English Channel. Distribution of surface salinities (10 and 0 m) suggests that a typical cyclonic swirl (cf. Matthews, 1914; Harvey, 1929) occupied most of the area south of Ireland to the latitude of Scilly, in March and April. The 'western' body may have been drawn in as part of this swirl at some preceding time, but as communication had been partly severed at the time of the cruise, it is not possible to say when and along what parallel it entered the English Channel. It is worth noting that the survival and spread of these 'western' forms, which are all of north Boreal character, may have been favoured by the cold summer of 1954, and winter of 1954–5, when the surface temperatures observed at E1 were among the lowest since the 'twenties. Moreover, the autumn of 1954 was marked by a succession of westerly winds which would be expected to strengthen the southern track of the cyclonic swirl. The more normal southerly and easterly winds of recent years did not supervene until the early spring of 1955; they may well have produced the separation observed in March.

After April 1955 the 'western' component soon disappeared, and there appeared to be no local benefit from the extra phosphate which may have entered the Channel.

In the spring of 1957 a cyclonic circulation was also present, to judge from the salinities in May. It appears, however, that the plankton had less southerly spread from the Irish region and that fewer 'western' forms were drawn into the Channel from the north-west.

Origin of 'western water'

From his own material taken near Plymouth, supplemented by samples from French and Irish stations farther west, Russell (1935, p. 315) deduced that his 'western water' originated from a source to the south of Ireland. The 1955 and 1957 samples are entirely consistent with this view, and, as far as it goes, the chemical evidence is also in agreement. Thus, the 'western water' is to be regarded rather as 'north-western' water, and, therefore, not now in the path of what might be thought to be the normal inflow into the English Channel from the west.

Neither the earlier work nor the recent investigations provide any evidence that the source of the 'western water' is a result of upwelling of deep, nutrient rich water along the edge of the continental shelf (for hypotheses see Russell, 1935, p. 322; Cooper, 1955*a*, *b*). Nevertheless, if upwelling does occur, a study of the bottom topography between France and Ireland suggests that it is more likely to occur, or have more effect, in the area just to the south of Ireland. On recent cruises of R.V. 'Sarsia' I have confirmed the difference shown on Admiralty charts and by Day (1959): the shelf from 49° N. to the Irish coast is bounded by long, relatively smooth slopes (of sandy or oozy nature, difficult to dredge over), whereas the southern edge of the Celtic Sea has a steeper slope dissected by many deep canyons, with rock exposures bearing an abundant epifauna. The effect of internal waves in deep water 'beating' along the end of the shelf may be compared with heavy waves on an open coast. Against a steep cliff the water-level rises and falls comparatively little at each wave, and where the rock is broken the energy is dissipated as spray. But on a smoothly sloping rocky ledge or beach the wave energy is translated almost completely to forward (and upward) motion and the water dashes a long way up the shore. By analogy then, we might suggest that upwelling of water from below 400 m would be more probable in the north Celtic sea, provided other factors were equal and that internal waves occurred. However, it is possible to explain the ecosystem found off the southern Irish coast in other ways, and of course, it does not follow, as some workers believe, that upwelling of water with a high phosphate content would necessarily produce the zooplankton community observed.

THE DISTRIBUTION OF *EUCHAETA HEBES*

The warm-water copepod *Euchaeta hebes* Giesbrecht was first recorded from the south-western entrance to the English Channel during the International Investigations. In November and February in some years it was found also though less abundantly, as far north as station E6 (Gough, 1905, 1907; Bygrave, 1911). According to Farran (1911) the species was not taken at the Irish stations in those years, and his chart of the limits of regular occurrence of the species based on Gough and Bygrave was used by Russell (1935) to illustrate the distribution of south-western water. The distribution in 1903–5

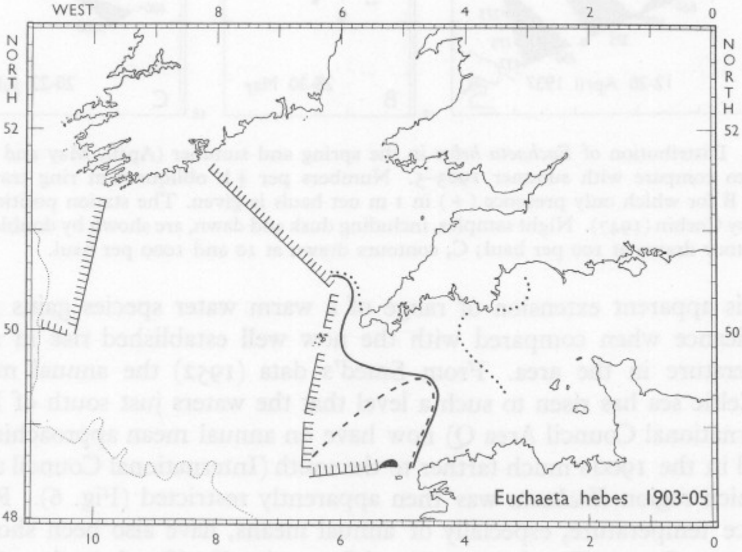

Fig. 4. The distribution of *Euchaeta hebes* in 1903–5, according to Gough (1905, 1907). The southern and western limits of the area investigated by the English and Irish Research vessels in 1903–11 is also shown. Small black area: species present at all seasons. Broken line: extreme northern limit found in summer (May and August) in certain years. Solid line: usual northern limit in winter (November and February). Dotted line: extreme northern and eastern limit in winter in one year.

when the species reached its farthest north during the period 1903–11 is shown in Fig. 4.

If we accept the previous evidence, then in 1955 and 1957 *E. hebes* ranged over a much wider area of the English Channel and western approaches than it did 50 years earlier. This extension of range continued in later years (to be described fully in another paper). For example, in 1959 small numbers were taken as far north as Bardsey Island in the Irish Sea, and the same species was reported from more oceanic waters to the north of Scotland.[1] Some further evidence on the distribution of *Euchaeta* has been provided by the mackerel cruises. Mr P. G. Corbin has kindly allowed me to examine his records for 1937, when *E. hebes* was included among the animals counted, and the results are shown in Fig. 5, at stations listed by Corbin (1947). Even in 1937 *Euchaeta* occurred over a wider area than in 1903–8.

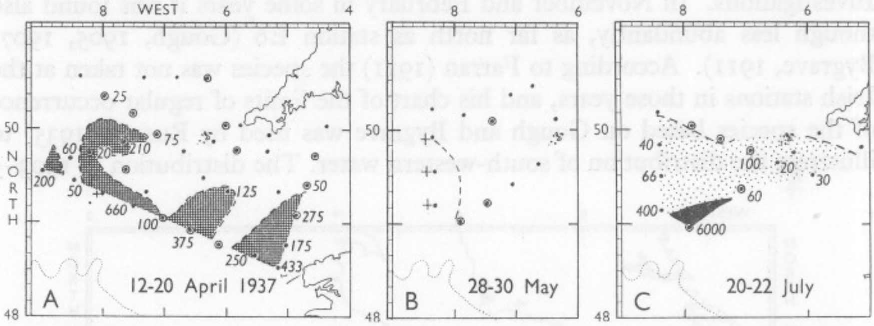

Fig. 5. Distribution of *Euchaeta hebes* in the spring and summer (April, May and July) of 1937, to compare with summer 1903–5. Numbers per $\frac{1}{2}$ h oblique 2 m ring trawl haul, except B for which only presence (+) in 1 m net hauls is given. The station positions were given by Corbin (1947). Night samples, including dusk and dawn, are shown by double circles. A, contour drawn at 100 per haul; C, contours drawn at 10 and 1000 per haul.

This apparent extension of range of a warm water species gains greater significance when compared with the now well established rise in surface temperature in the area. From Smed's data (1952) the annual mean in the Celtic sea has risen to such a level that the waters just south of Ireland (International Council Area Q) now have on annual mean approaching that found in the 1900s much farther to the south (International Council area P), to which region *Euchaeta* was then apparently restricted (Fig. 6). Rises in surface temperature, especially of annual means, have also been shown for the Seven Stones (Bowden, 1955) and for station E 1 (Southward, 1960), and the trend is obviously applicable to the whole English Channel and western approaches.

The idea of an increased occurrence of warm-water species in the English

[1] Personal communication R.S. Glover.

Channel was first suggested by Russell (1939, p. 186), and confirmatory evidence has now accumulated (Russell, 1953). An advance of southern forms and retreat of northern forms has definitely occurred on the shore (Crisp & Southward, 1958). Similar changes connected with the general warming up seem to have taken place in other habitats, for example among the commoner demersal fishes (unpublished observations of the late G. A. Steven) as well as with the rarer pelagic forms mentioned by Russell (1953), and it would be surprising if plankton organisms were unaffected. It might be assumed, then, that the extension in range of *Euchaeta* is not an isolated occurrence, and that there might have been a general northward shift of distributional limits in the

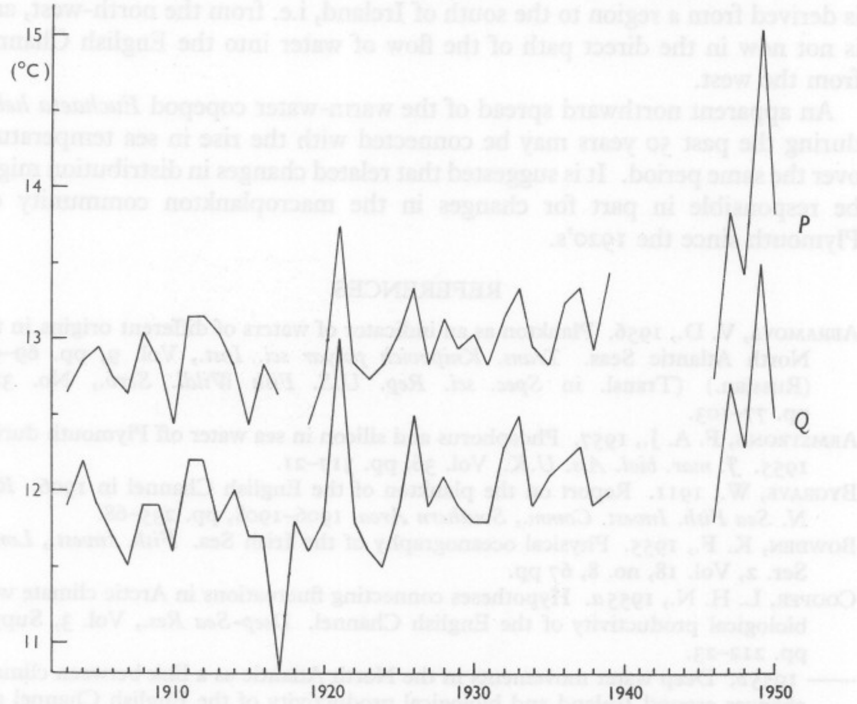

Fig. 6. Annual means of sea-surface temperature for International Council areas P (South Celtic Sea) and Q (north Celtic Sea, South of Ireland) 1903–50. Based on Smed (1952).

area. We may have, in the temperature change, a possible explanation, if only indirect, and in part, of the reduced occurrence off Plymouth since the 1920's of the western forms and the larger macroplankton species. Many of these (e.g. *Aglantha*, *Sagitta elegans*, *Meganyctiphanes*) are of northern origin and thus near their southern limits[1] at the entrance to the English Channel. Other factors, of course are involved; a full discussion will be given later.

[1] Excluding deep-water communities.

I am greatly indebted to Dr F. S. Russell for advice and discussions on this problem. Thanks are due to Dr L. H. N. Cooper and Mr A. D. Mattacola for the 1955 samples.

SUMMARY

Previous plankton work at Plymouth is reviewed briefly, and the limitations of the stramin ring trawl as a quantitative sampler discussed. The distribution of certain zooplankton 'indicator' species caught in hauls of the 2 and 1 m ring trawl during cruises in 1955 and 1957 is described in comparison with regular 2 m hauls taken throughout the same years at two stations near Plymouth.

The results support previous suggestions that 'western' water at Plymouth is derived from a region to the south of Ireland, i.e. from the north-west, and is not now in the direct path of the flow of water into the English Channel from the west.

An apparent northward spread of the warm-water copepod *Euchaeta hebes* during the past 50 years may be connected with the rise in sea temperature over the same period. It is suggested that related changes in distribution might be responsible in part for changes in the macroplankton community off Plymouth since the 1920's.

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