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CONTINUOUS PLANKTON RECORDS:

FIRST REPORT ON THE DISTRIBUTION OF LAMELLIBRANCH LARVAE IN THE NORTH SEA

BY

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HULL

AT THE UNIVERSITY COLLEGE

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EDITORIAL NOTE.—It is thought that it may prove convenient for the reader to find this report on the distribution of the lamellibranch larvae next in the series to Mr. Rees' earlier account of his method of identifying the larvae. Consequently, to save repetition, it has been necessary for Mr. Rees to anticipate in his text the publication of the next 'Hull Bulletin,' No. 21, "Explanation and Methods, 1946–49."

CONTENTS.

INTRODUCTION AND METHODS.

IN a recent Hull Bulletin (Rees, 1950) the lamellibranch larvae obtained by the Continuous Plankton Recorder in the North Sea were described and named specifically or otherwise labelled. These descriptions and identifications were the essential first stage in the study of the distribution of the larvae in the North Sea. It has long been recognized that knowledge of the areas and times of main spatfalls would have considerable economic advantages. Whilst, perhaps, the distribution of larvae alone might not show *positively* these areas, the grabbing and dredging for spat areas could be guided by the distributions and much time and labour saved. Another important matter is that it is essential to know the larval history of a bottom-living lamellibranch to understand its biology fully.

As explained in 'Bulletin' No. 21 (Rae, 1951), only the odd numbered 10-mile blocks (1, 3, 5, etc.) have been analysed during the *routine* plankton analysis in recent years. It has been more convenient to investigate the lamellibranch larvae on the even numbered 10-mile blocks (2, 4, 6, etc.), and on these the proportions of the various species have been determined. This has been done more thoroughly than in initial or routine analysis, with the result that many more blocks have been found with larvae than without, which is the reverse to the finding during routine analysis. If, for example, there were only 10 larvae on a 10-mile block it is unlikely that one would be seen during routine analysis, and quite likely that some would be seen during the special analysis for lamellibranch larvae. The total numbers of larvae on these even blocks were not counted, but they were estimated by averaging the numbers found on the two adjacent odd numbered blocks for which counts were available. The number of larvae of each species on the even 10-mile blocks was then roughly estimated by splitting the total number according to the proportion of larvae of the various species. The quantitative estimate of the larvae is, consequently, indirect and quite approximate, but is adequate for the purposes of this report; our concern is with considerable differences in population density rather than with relatively minor ones.

A major difficulty has arisen from the fact that the silk in use is impregnated with an acid substance causing a fairly rapid deterioration of the larval shells in contact with the silk. Boiling the silk in water, the use of buffered formalin, and placing a bag of calcium carbonate in the tank of the Recorder have not entirely overcome this difficulty. Its effect has been minimized by analysing the larvae as soon as possible after arrival in the laboratory.

The distributions have been investigated thoroughly since August, 1948, but there is some scattered information prior to that. The 1949 distributions are chiefly used in this report, the earlier data being presented whenever it has appeared desirable.

Distribution of Total Lamellibranch Larvae.

In this section the results obtained during routine analysis are presented, irrespective of the specific content of the population.

The quantitative distribution of lamellibranch larvae in the southern North Sea during 1932–1937 is given by Henderson and Marshall (1944), and over the whole North Sea in 1938–39 by Marshall (1948). It is not proposed to publish similar maps for 1946–49. Instead, the distribution of blocks with more than 500 per 10 miles is shown in Text-fig. 1, using one symbol to cover the 1932–37 period, another for 1938–39 and others for each of the years 1946 to 1949.[1] As a result of the specific analysis of 1948 and 1949 some of the patches can be considered later in detail and, for ease of reference, these have been numbered in Text-fig. 1. In the meantime it should be stressed that in no year were all these patches found.

In Text-fig. 2 the distribution of blocks with over 1000 larvae per 10 miles is

[1] In recent years alternate 10-mile blocks only have been analysed. In preparing all the charts in this paper it has been assumed that if a certain distribution was found on alternate blocks the same distribution occurred on the unanalysed intermediate block, *e.g.*, if a certain symbol applies to blocks 5 and 7 on a line, the isolated symbols have been joined through block 6, though this latter block was not analysed. This procedure serves merely to simplify the visual appearance of a chart.

plotted. Many of the lesser patches of Text-fig. 1 have disappeared, but the patches east and northwards of the Dogger Bank remain distinctive.

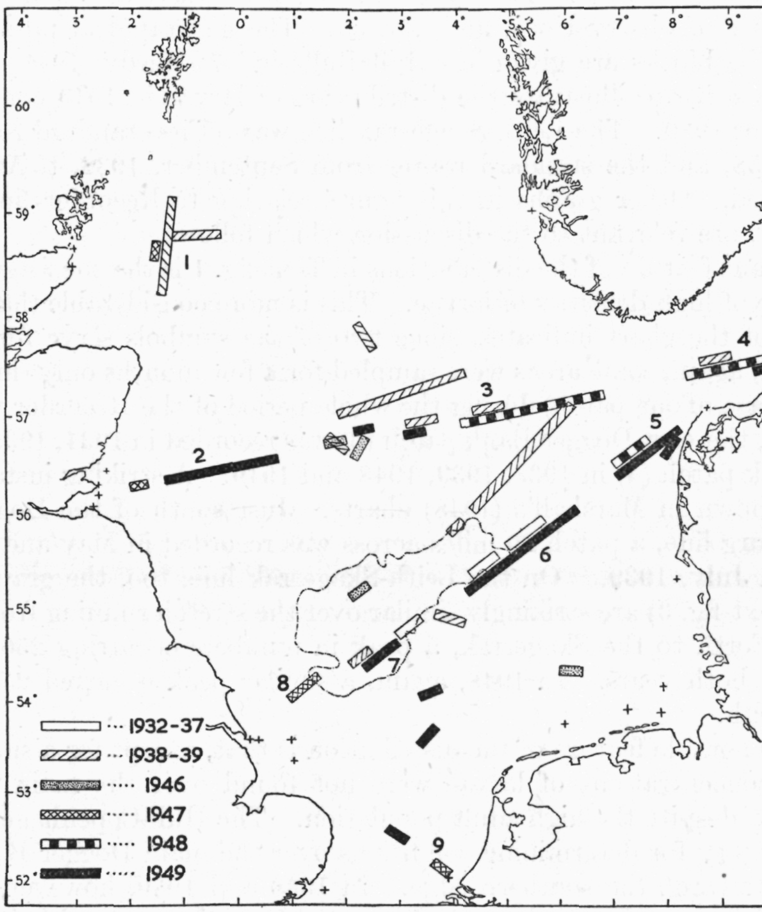
When the Recorder samples along a standard route, the same 10 miles over the sea bottom is, theoretically, analysed for plankton time after time. In Text-fig. 3 graphs are shown of the average number of lamellibranch larvae obtained on each analysed 10-mile block throughout various years on some standard lines; the larvae obtained over the same 10 miles of sea bottom have been summed, divided by the number of observations, and plotted. The geographical positions of the various 10-mile blocks are given in 'Hull Bulletin' 7 (Hardy, 1941, Text-fig. 1). These graphs serve to illustrate the distribution of larvae in 1949 compared with that of 1938 or 1939. The Leith-Skagerrak line was off its standard route in June and July, 1938, and the standard routes from September, 1938, to August, 1939, have been used. Other graphs in this figure, relating to Recorder lines taken in 1938–39 only, are relevant to the discussion which follows.

An important feature of the distributions in Text-fig. 1 is the consistency in place of occurrence of high densities of larvae. This is more considerable than the visual appearance of the chart indicates, since two of the symbols serve for more than one year and, again, some areas were sampled for a few months only (in one month only in the case of one patch) during the whole period of the Recorder programme. For example, the east Dogger Bank patch (6) was recorded in 1934, 1935 and 1949; the Skagerrak patch (4) in 1938, 1939, 1948 and 1949. A striking instance of consistency is shown in Marshall's (1948) charts. Just south of the Dogger, on the Leith-Hamburg line, a patch 20 miles across was recorded in May and July, 1938, and again in July, 1939. On the Leith-Skagerrak line, too, the graphs for 1939 and 1949 (Text-fig. 3) are strikingly similar over the stretch running from 190 miles east of the Forth to the Skagerrak, a peak in numbers occurring 250 miles from the Forth in both years. In 1948, again, a similar peak occurred 250–270 miles from the Forth.

Another notable feature of the distribution is that, except for a small patch in 1946, high concentrations of larvae were not found over the main area of the Dogger Bank, despite the high adult population. The Hull-Copenhagen line is not quite satisfactory for determining conditions over the main Dogger Bank, since it runs rather towards the southern edge. In 1938 and 1939, however, there were two lines which crossed over the main Bank, the Hull-Norway and Leith-Hamburg lines (see Text-fig. 1 in Hardy, 1941). On these two lines the average number of the larvae found on each block throughout the year is shown in Text-fig. 3, the position of the Dogger Bank being indicated. These graphs show clearly the scarcity of larvae over the Dogger. During 1946 and 1947, before ships resumed their standard routes, many Recorder lines crossed the main Dogger but, apart from the slight patch in 1946, no concentrations were found. In 1947 the Hull-Copenhagen route passed 15–20 miles north of the standard route and provided a good series of lines passing over the main Dogger; the high numbers at the western end of the line ended abruptly at the edge of the Bank (Text-fig. 3).

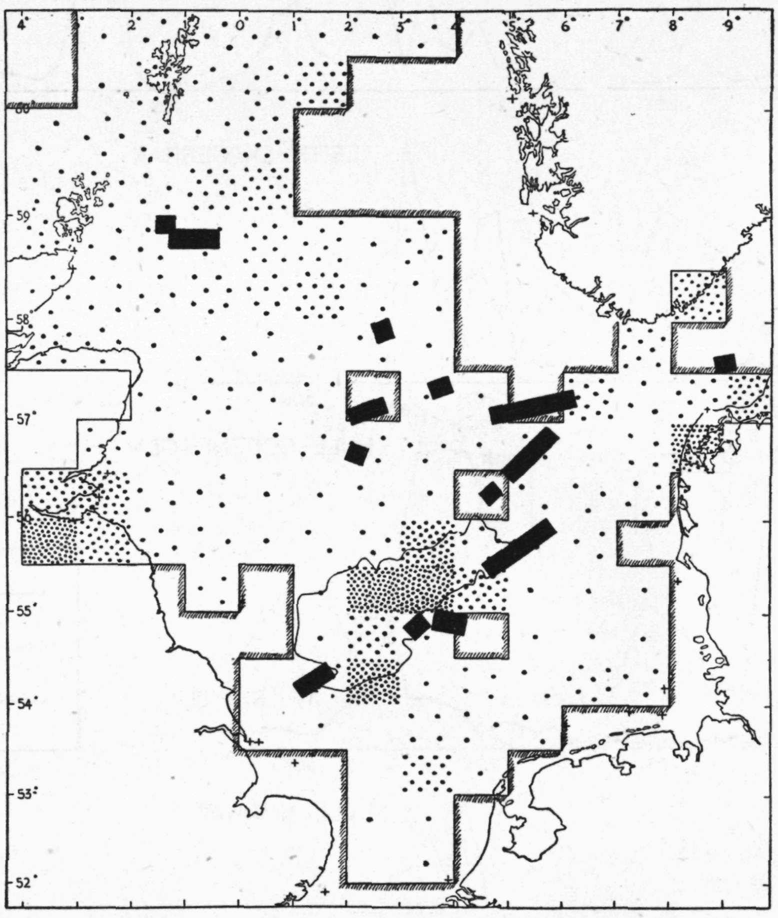
Regarding the comparison of the years, attention may be directed to the very high numbers east of the Dogger Bank (Hull-Copenhagen) in 1949 and off the Humber in 1947, the high numbers off the Forth (Leith-Skagerrak) in 1949, and the scarcity of larvae on the Aberdeen-Lerwick line in 1949.

It would be of interest to compare the numbers of larvae obtained by the Recorder with other results. The highest number ever attained per 10-mile block



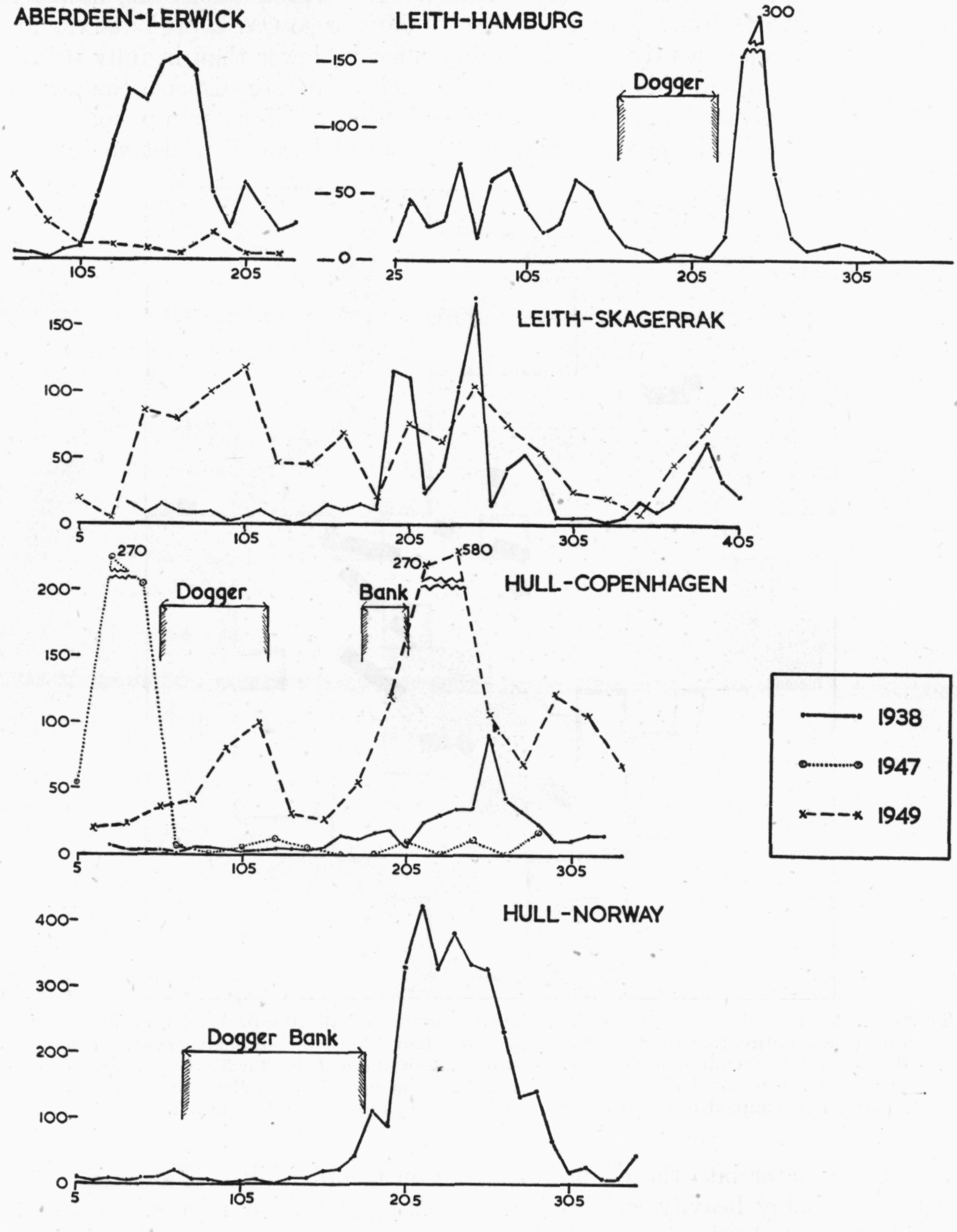
TEXT-FIG. 1.—Chart showing the distribution of 10-mile blocks with more than 500 lamellibranch larvae during the periods 1932–37, 1938–39, and each year from 1946 to 1949. The Dogger Bank is shown. Some patches have been numbered for convenience of reference in the text.

was estimated to be 9000. In passing through 10 miles the Recorder filters nearly 3 m^3 of water, thus giving the average density at 10 m through these 10 miles as 3000 per m^3. It is certain that "smoothing" occurred and that the density over a shorter tow than 10 miles was higher. This value can be compared directly with those for larvae of *Ostrea edulis*. Gaarder and Spärck (1932) found 2000–6000 oyster larvae per m^3. Korringa (1941) gives a few thousand at the height of the season, with 10,000 or more during swarming. These productions are, however, conserved by two factors: (*a*) for the first 10 days or so *Ostrea edulis* larvae are incubatory and consequently early mortality must be lower than in fully pelagic larvae, (*b*) the hydrographic conditions were such as not to disperse the larvae. Thorson (1946) gives figures from pump collections. These pump collections probably contained a large proportion of "**D**-shaped larvae," whilst such small



TEXT-FIG. 2.—The black rectangles show the distribution of all 10-mile blocks, obtained during the entire Recorder survey, with more than 1000 lamellibranch larvae. The density of bottom adults is represented by dots, each dot standing for 5 adults (nearest) per m² per international square (see p. 111). The hatched boundary line encloses squares not sampled during the quantitative surveys of the bottom fauna.

larvae rarely enter into the counts of larvae on recorder silk. Thorson's figures are thus probably heavily weighted in comparison with our results. Out of 74 individual pump hauls Thorson had 1 which exceeded 3000 per m^3, this being 3380 per m^3, of which 86% were not identified to species and were, presumably, at the **D**-shape stage.



TEXT-FIG. 3.—Graphs giving the average number of lamellibranch larvae obtained on each analysed 10-mile block throughout one year on some standard Recorder routes. The position of the 10-mile blocks can be seen by comparing the horizontal scale of miles with the chart in Text-fig. 1 of 'Hull Bulletin' 7. The Dogger Bank is indicated.

Marshall (1948) has charted the number of bottom-living lamellibranchs per m^2 for each international square of the North Sea as derived from Davis (1923, 1925) and Stephen (1933). Since this chart will be used later in this report some of the empty squares may be filled in by adding the results of Petersen (1914) off the Danish coast and mouth of the Skagerrak: 17 in L11, 46 in M14, 14 in M13, 20 in M12, 24 in M11 and 320 in N13. The international squares are shown in the key chart on Plate VIII.

Distribution of the Species.

The approximate quantitative distribution of larvae is shown in the series of maps in Plates VI–VIII. For one reason or another some of the larvae described by Rees (1950) are omitted. The same nomenclature is used as in the descriptive report, and attention should be drawn to the method used to indicate uncertain identifications, *e.g.* (? *Limopsis*).

The coverage of the North Sea month by month is a matter of much importance, and for proper consideration of the maps of distribution the coverage shown in Rae (1951) should be consulted. It depends on the particular species whether the absence of a certain line during a month is likely to be important or not. For example, the absence of a Leith-Skagerrak line in April and May is important in the case of a spring larva, such as *Ensis ensis,* but not in the case of an autumn form like *Montacuta ferruginosa.*

It was hoped to present in figures the known quantitative distribution of the relevant bottom-living species in the North Sea since, apart from the chart of all species combined given by Marshall (1948), the results are in tabular form. This would require, however, the publication of many more maps. Furthermore, only Davis (1923, 1925) and Petersen (1914) give full quantitative data, and it is possible that their results are now inapplicable to large stretches of the North Sea.

The alternative adopted is to show by means of a dot, on the maps of larvae (Plates VI–VIII), those international squares where the particular species were found by one or more of the four authors, Davis (1923, 1925), Stephen (1933), Petersen (1914) and Schrader (1911).[1] A key is given in Plate VIII showing the squares sampled by the four workers. It should be noted that Stephen (1933) gives only the more numerous or interesting species obtained by him. Some quantitative information on adults is given in the text, this, normally, being the highest density found by the authors referred to.

Seasonal Occurrence.

The seasonal distribution of the various species is presented in tabular form in Table I, the criterion being the number of blocks in each month of 1949 on which the species was found. The alternative of taking the total number of larvae of a species obtained in each month as the criterion has been rejected, since, by this

[1] A few adult occurrences have been omitted where it has been inconvenient to extend the area of a chart to include them. Mention is made in the text of omissions that appear to be important.

method, it is possible that an intense breeding of a dense, but local, adult population in one month would overshadow a more widespread breeding in another month. For the purpose of an overall picture a widespread breeding is of greater interest than a localized breeding. Species observed on less than 10 blocks throughout the year are not listed, but the season of occurrence of most of these can be read from the charts, which also give fuller information for the species included in the table. Thus, no particular month is marked out in the table for *Zirfaea crispata*, but the charts show that April and May were the peak months.

TABLE I.—*The Number of* 10-*mile Blocks on which Larvae were Observed in Each Month of* 1949.

	J	F	M	A	M	J	J	A	S	O	N	D
(*a*)												
Ensis ensis	.	.	.	*	*	+	+	.	.	.	.	.
Zirfaea crispata	+	+	+	+	+	+	.	.	.	+	+	+
(? *Lyonsia*)	.	+	+	+	+	+	.	.	.	.	.	.
(*b*)												
" *Montacuta* "	.	.	.	.	.	+	*	+	+	+	+	.
Cardium A	.	.	.	.	.	+	+	.	+	+	.	.
Hiatella gallicana	.	.	.	.	+	+	+	+	.	+	.	.
(*c*)												
Glycymeris glycymeris	+	.	+	.	.	+	+	+	●	●	●	*
(? *Limopsis*)	.	.	.	.	.	.	.	.	+	+	+	.
Adula simpsoni	.	.	.	.	.	.	.	.	+	+	+	.
Modiolus modiolus	.	+	.	.	.	+	+	+	+	*	*	+
Lima	.	.	.	.	.	.	.	+	+	+	+	.
Montacuta ferruginosa	.	.	.	.	.	.	+	+	●	■	*	.
Cardium D	.	.	.	.	.	.	.	.	+	+	+	.
Venerid A	.	.	.	.	.	.	.	.	*	*	.	.
Venerid B	.	.	.	.	.	.	.	.	.	+	+	.
(? *Paphia*)	.	.	.	.	.	.	.	.	+	+	+	+
Abra prismatica	.	.	.	.	+	+	+	+	●	●	*	.
Abra nitida	.	.	.	.	.	.	.	.	+	*	+	+
Cultellus pellucidus	+	+	+	+	+	+	+	+	*	■	*	+
Hiatella arctica	.	.	.	.	.	+	+	+	+	*	*	+
(? *Pholas dactylus*)	.	.	.	.	.	.	.	.	+	+	+	.
(*d*)												
(? *Mactra corallina*)	+	+	+	*	+	.	.	.	.	+	.	.
(? Mactrid E)	.	.	.	*	+	.	.	.	.	.	+	.
(*e*)												
Mytilus edulis	.	.	.	.	+	*	*	+	+	+	*	+
Cardium B	.	.	.	.	.	+	.	.	+	+	+	.

(*f*)	J	F	M	A	M	J	J	A	S	O	N	D
Mytilid A	.	+	.	.	.	.	+	+	+	+	.	.
Anomiacea	.	.	+	.	.	+	+	+	+	+	+	+
Cyprina islandica	.	+	.	.	.	.	.	.	+	+	+	.
(? *Spisula subtruncata*)	.	.	+	.	.	.	.	.	+	●	*	+
(? *Spisula elliptica*)	.	.	.	.	+	.	.	+	●	■	+	+

+ = 1–9 blocks ; * = 10–19 blocks ; ● = 20–29 blocks ; ■ = 30 blocks or over.

The grouping employed in the table will have to be reviewed as data accumulate in later years, but larvae seem to fit more or less well into six groups. In three groups there is only one main breeding season, (*a*) in spring, (*b*) in summer, or (*c*) in autumn/winter. Breeding may extend over many months as in *Zirfaea crispata*, *Glycymeris glycymeris* and particularly in *Cultellus pellucidus*, but the period of the *main* breeding is distinct. In the three remaining groups there are two recognizable breedings ; (*d*) a major spring and a minor autumn, (*e*) a summer and autumn and (*f*) a minor spring and a major autumn breeding. These double breedings will be discussed later (p. 124).

Werner (1939) has collected together the earlier information on the breeding season of lamellibranchs in the North Sea, and it can be seen from his list that little information is available. Lebour (1938) lists the breeding season of many Plymouth lamellibranchs, but in several cases this is judged by the presence of ripe sperm and eggs. Thorson (1946, p. 422) comments, however, that ripe sexual products may be present for a long time (months) before being shed, and successful artificial fertilization may take place outside the actual breeding season. Jørgensen (in Thorson, 1946) gives the monthly frequency of larvae in the Sound (Øresund), but his table must be reconsidered in several cases in view of the alternative identifications in Rees (1950).

Notes on Species.

It does not seem necessary to describe in detail the distributions, which, it is hoped, will be sufficiently clear from the charts and from Table I. Some notes on species are given below. The following species have received no comment : *Musculus marmoratus* (Plate VI), *Cyprina islandica* (Plate VI), *Kellia suborbicularis* (Plate VI), (? *Lepton squamosum*) (Plate VI), *Mya truncata* (Plate VIII). The distributions of a few species have not been charted but have been noted in the text.

Glycymeris glycymeris (Plate VI).—The larvae were widespread and comparatively numerous, far more widespread than the charted distribution of the adults suggests; also they, certainly, were not all derived from the north-west, where the adult records are concentrated, since they were found as early as August in the Southern Bight. However, the adult *Glycymeris* has also been found off the east English and Belgian coasts (Haas, 1926). Ford (1923) defined *Glycymeris* as an inhabitant of gravel deposits, and such gravel deposits cover wide areas down the east English coast, right into the Southern Bight (Borley, 1923). Since its distribution in depth ranges from 30–150 m (Haas, 1926), it would seem that there is an abundance of favourable areas for the species, at least on the western side of the North Sea. Stephen obtained 12 per m^2 in C18 (private communication).

(? *Limopsis*) (Plate VI).—If this should in fact prove to be the larva of *Limopsis* the relative abundance of the larva is unexpected. The Forth observations were made in September–November, the southern ones in November. Such a distribution suggests invasion from the north.

Of the two North Sea species of *Limopsis* the larva is most likely to be of *Limopsis aurita.* This has been found only north of Shetland Islands, and Schrader (1911) suggests that it is in process of dying out. If the identification of the larva is correct the species appears to be, on the contrary, still vigorous.

Mytilus edulis and *Modiolus modiolus* (Plate VI).—The main concentration of *Mytilus* occurred off the Danish coast, that of *Modiolus* off the Forth. Regarding both, but *Modiolus* especially, it should be noted that the Leith-Skagerrak line started some 90 miles from the Forth in August and September.

Only three localities for adult *Mytilus* are given by the four authors whose results are being plotted here, but records of *Modiolus* are much more frequent. Despite the fact that Schrader (1911) frequently collected epifaunal species, it must be considered that such species were very inadequately collected. Dense colonies of *Mytilus edulis*, of course, occur in coastal areas, and some of the larvae arising from these colonies may well be carried into offshore water.

Adula simpsoni (Plate VI).—No larvae were observed prior to 1949. Stephen (1927) found adults on a skull of a bottlenose whale taken 210 miles north-east of May Island, Firth of Forth, whale skulls being its normal habitat.

MYTILID A (Plate VI).—The distribution of the adult *Modiolus phaseolina* is given in the chart.

Crenella sp.—Only a single specimen has been found, about 30 miles off the Danish coast in May.

PECTINIDS.—*Chlamys striatus* was obtained in the tank residue[1] of the Leith-Skagerrak line in August.

Pectinid B was obtained 200 miles east of the Forth in December. In 1948 it was obtained in the tank residue of the Leith-Skagerrak line (October), the Hull-Copenhagen line (September) and Hull-Bremen line (October).

Pectinid D was obtained on the Hull-Copenhagen line 40 miles from the Humber in October, 140 miles away in November, and also 20 miles off the Forth in October.

Pectinid E was obtained 100 miles east of the Forth in June.

[1] A small proportion of the plankton caught during any tow may be washed off the silk and found in the bottom of the formalin tank of the Recorder into which the silk is wound. Although it is not possible to declare at what point in the tow this plankton was taken, it provides a source of material for qualitative analysis.

Pectinid F was obtained 80–100 miles east of the Forth and 40 miles south of the Shetlands in September.

Schrader (1911) gives the distribution of several species.

Lima sp. (Plate VI).—All the larvae plotted in the chart appeared to be the same species, but it is possible that there were more than one.

Anomiacea (*Monia squamula* and *Heteranomia ephippium*) (Plate VI).—The two species were not separated, but it is worth while showing the distribution of the larvae, since both the species are epifaunal. The division of larvae between epifaunal, boring and burrowing lamellibranchs is of interest and will be considered below. The south-west Dogger observations were made in November, suggesting an occurrence there due to water movements, the larvae coming from the north.

The distribution of the adults of all species combined of Anomiacea, as given by Schrader (1911), is shown.

Myrtea spinifera (Plate VI). The occurrence of the larvae resembles that of (? *Limopsis*), having been found on the Leith-Skagerrak line in September and October and on the Hull-Copenhagen line in November. It was suggested that the distribution of (? *Limopsis*) was due to transportation southwards from the north-west North Sea. Taking into account the distribution of adult *M. spinifera* such an explanation seems even more likely in this case. The adult was found in most of the squares in the north-west between the Shetlands and Aberdeenshire. Stephen (1933) obtained 12 per m^2 in C15.

Montacuta (*Montacuta bidentata* and *Mysella substriata*) (Plate VI).—In the charts labelled "Montacuta" both these species are included. (Throughout the text "Montacuta" refers to both species combined.) The overall plot for 1948 is given to show that higher numbers were obtained in this year than in 1949. The distribution of adults of both species is shown in the 1948 chart. Schrader (1911) gives a chart showing his records for each species separately. Davis (1925) obtained 2 per m^2 of *Montacuta bidentata* in J10.

Montacuta ferruginosa (Plate VII).—This larva was more frequent in 1949 than in 1948. Davis obtained about 2 per m^2 in J7.

Cardium sp. (Plate VII).—In the chart for *Cardium* A the distribution of adult *C. ovale* is given, for *Cardium* B the adult *C. minimum*, and for *Cardium* D the adult *C. echinatum*. It is to be understood that there are no other reasons for linking the larvae and adults than are given in Rees (1950).

Two records of adult *C. ovale* near Fair Isle and another north of Flamborough Head are not shown in the diagram.

Venerids A and B (Plate VII).—The larvae of Venerid A have been linked, rightly or wrongly, with the adult *Venus ovata*, and Venerid B with the adult *V. striatula* as in Rees (1950). The consideration of the distribution suggests, in fact, that the linkages should be reversed, but the evidence is still insufficient.

The larvae of Venerid A occurred earlier than Venerid B, in September and October, with October being the peak month; Venerid B occurred in October and November with the latter as peak. Davis (1925) obtained 2 per m^2 of *V.*

striatula in K12. The density of *V. ovata* was very low. Stephen (1933) obtained 5 per m² of *V. striatula* in H15 and K12 and 5 *V. ovata* in L12.

VENERIDS C–F (Plate VII).—The larvae of each kind occurred very infrequently and are combined in one chart.

(? *Paphia*) (Plate VII).—No species of *Paphia* is listed by the authors in dealing with the distribution of adults.

(? *Mactra corallina*) (Plate VII).—The highest densities of adults were found by Davis (1925) to be in the south-west part of the Dogger. High densities were very localized. The overall density in F7 was 251 per m².

(? *Spisula solida*) (Plate VII).—The spatial distribution of the larvae was very similar to that of (? *Tellina crassa*). They were obtained in May and April and again in September. In 1948 they were found from September to November in the same region.

As regards the adult we cannot include the findings of Schrader (1911), since he lumped *S. elliptica* and *S. solida* together. Stephen (1933) gives a chart of the adult distribution. This chart includes Petersen's (1914) records of *S. solida* off the Danish coast. It would be fair to neglect these records, since Petersen, too, lumped *elliptica* and *solida*. Davis (1925) found nearly 2 per m² of *S. solida* in G3.

(? *Spisula subtruncata*) (Plate VII).—In view of the extremely high densities of adult *S. subtruncata* found by Davis (1925) it is surprising that the larvae should have been found in comparatively small numbers only. This was also true in 1948. The persistence of a larval population, though low in density, over the Great Fisher Bank, compared with the distribution of adults, is of interest in view of Marshall's (1948) suggestion that the Fisher Bank population in 1938–39 may have been due to translation of more southerly species northwards. Davis (1923) gives great detail on patches of the species. The overall density in G9 was 424 per m².

(? *Spisula elliptica*) (Plate VII).—This larva was easily the most common of all, reaching concentrations many times denser than any other species. Its great density would lead one to expect it to be *S. subtruncata*. It is not so identified because, however uncertain it may be that Kändler's (1926) and Jørgensen's (in Thorson, 1946) species agree with the larva named here as (? *S. subtruncata*), there can be no doubt that their larva is not this one. The square end of (? *S. elliptica*) is quite distinctive and unmistakable as emphasised by Rees (1950).

Concentrations of 1949 may be compared with those of 1948. The population off the Skaw was well developed in 1948, somewhat better developed than in 1949 and with August the peak month, two months earlier than in 1949. The north-east Dogger concentration of October, 1949, was very great, larvae of (? *Spisula elliptica*) being present to the extent of more than 5000 per 10-mile block. The 1948 Great Fisher Bank concentration was small.

The distribution of adults is repeated from Stephen's (1933) chart with the slight modification of taking Petersen's "*Spisula solida*" to be *S. elliptica* since he did not separate the two. Schrader (1911), also, did not distinguish *S. elliptica*. The number found by Davis (1925) was very low, much less than 1 per m². Stephen

(1933), on the other hand, found high numbers off the Danish coast. He has kindly provided further details beyond those published. These include densities of *S. elliptica* of 35 per m^2 in L13, 15 in N13 and 10 in O14.

MACTRID E (Plate VII).—The larva was recorded off the Skaw in November. All the other records were obtained in April and May (when the Leith-Skagerrak line was not sampled).

In view of the suggestion in Rees (1950) that this may be the larva of *Spisula truncata* the two records of the adult *S. truncata* (Schrader, 1911) are given, but it must be recognized that only Schrader, of the four authors with whose distributions we are concerned, separated *truncata* from other forms of *Spisula*.

(? *Lutraria lutraria*) (Plate VII).—It is by no means certain that only one species has been included in this group. Since records are so few any errors that may have arisen are not important.

Only Davis (1925) found the adult, at a density of 1 per m^2 in G7.

Tellina fabula (Plate VII).—The larva occurred infrequently. Specimens were obtained in the tank residue of the Leith-Skagerrak line in July. It was noted twice on the silk in 1948, midway along the Hull-Copenhagen line in August and again in September. Davis (1925) obtained over 3 per m^2 in G6 and G7.

(? *Tellina pygmaea*).—The larva was only twice noted on the silk, once off the Skaw in July, 1948, and again in June, 1949. Larvae were also obtained in the tank residue of the Hull-Copenhagen line in November.

(? *Tellina crassa*) (Plate VII).—The larvae were found only in the southern North Sea, in the same region as (? *Spisula solida*), and all in September. They were present in relatively high numbers over a short period. A high proportion of the specimens were very large, the dissoconch having begun to form.

There are only two records of adults, one by Davis (1925) in the north-west corner of the Dogger Bank, and one by Schrader (1911) 20 miles south of the Shetlands.

Abra prismatica (Plate VIII).—This species was more abundant in 1949 than in 1948. Davis (1925) obtained 2·5 per m^2 in J9 and Stephen (1933) 8 per m^2 in G15 and H12.

Abra nitida (Plate VIII).—Davis (1925) obtained slightly less than 1 per m^2 in C9.

Abra alba.—The larva was not found in 1949, but was obtained on the eastern ends of the two Hull-Bremen lines taken in October, 1948. It was also obtained in the tank residue of the Hull-Rotterdam line in October, 1947.

Stephen (1933) charts the distribution of the adult. Schrader (1911) provides no additional records. Taking regard of the distribution of the adults and the coverage of the Recorder lines it is not surprising that so few larvae have been obtained.

(? *Donax vittatus*) (Plate VII).—All three observations of this larva on silk were made on September records. The tank residue of the July Leith-Skagerrak record had a good number of specimens, a fact that may have resulted from the

Recorder being shot well inside the Forth on this occasion, although none were found on the silk pertaining to this part. Davis (1925) obtained 6 per m^2 in H4.

Ensis ensis (Plate VIII).—Larvae were occasionally found in the tank residue of the Aberdeen-Lerwick line. Davis (1925) obtained 1·7 per m^2 in M9, but considered that the species was inadequately collected. Petersen (1914) obtained 8 per m^2 in M12.

Ensis siliqua (Plate VIII).—This was of occasional and scattered occurrence appearing at the same season as *E. ensis*. Records of adults show that this species was rare in comparison with *E. ensis*.

Cultellus pellucidus (Plate VIII).—The larva was found in every month, but, up to August, it was mainly confined to the east central North Sea, off the Danish coast. Its distribution spread considerably in September, to reach its peak in October. It is of interest how, in the direction Hull to the Skagerrak, the observations in November and December form five distinct pairs. Davis (1925) obtained over 14 per m^2 in L10.

Hiatella arctica (Plate VIII).—Only Schrader (1911) gives information on the distribution of the adults.

In 1948 the highest numbers also occurred off the Forth, but in this year in August–September rather than in September–October as in 1949.

Hiatella gallicana (Plate VIII).—Records of the adult are comparatively rare. This may be partly due to the fact that it bores into soft rock and is therefore inadequately sampled. However, the larvae do give the same sort of picture, and it is quite clear that the larvae of *H. arctica* are much more common than those of *H. gallicana*.

MYACEAN B (Plate VIII).—This larva was found more abundantly than either *H. gallicana* or *H. arctica* off the Aberdeenshire coast. The only other record was about 120 miles off the Forth, a record that may well have resulted from transportation of the larvae from the coastal area.

Aloidis gibba.—Larvae were obtained in April only, midway between the north-east Dogger and the Danish coast, on the Hull-Copenhagen line.

From the results of Davis (1925) and Schrader (1911) the *Aloidis* area of the North Sea may be roughly defined as the eastern half of the North Sea south of the Hull-Copenhagen line and north of the Hull-Bremen line. Davis obtained 2·5 per m^2 in J7.

Zirfaea crispata (Plate VIII).—Larvae were absent only in the months July to September. The main Dogger Bank concentration occurred in April and May.

(? *Pholas dactylus*) (Plate VIII).—October was the peak month in 1948, a patch occurring along the southern edge of the Dogger almost identical in extent with that of November, 1949.

(? *Barnea candida*) (Plate VIII).—The larval distribution is similar to that of (? *Tellina crassa*) and (? *Spisula solida*).

Teredo sp.—The *Teredo* larva described in Rees (1950) was obtained 80 miles off the Forth in October.

(? *Thracia*).—Larvae have been seen only in tank residues, in those of the Hull-Bremen line in October and November, 1948, and the London-Copenhagen line in November, 1948. It was not observed in 1949.

(? *Lyonsia*) (Plate VIII).—April was distinctly the peak month.

Discussion.

General.

Such a survey as this, involving the pelagic larvae of bottom-living adults, raises the major question of the association between the distributions of the larvae and the parent adults. Another important question, the answer to which is the main purpose of this work, is the possibility of forecasting the distribution of the future adult population. For this first report the available information is clearly inadequate to deal with these questions. The distribution of the larvae has been thoroughly traced for one year only, and this year may well have been unusual. The insufficiency in information, however, is not confined solely to the larvae. There is a complete lack of information about the contemporary bottom fauna over the general North Sea, and widespread surveys have not been undertaken since the early 1920s. Considerable changes in the bottom fauna may have occurred since then.

Nevertheless, this is the first time that a survey of lamellibranch larvae of this nature has been attempted, and it is believed to be worth while to issue the results of this first year rather than wait for several years in the hope that these questions may be considered more adequately.

It would enlarge our understanding of the distributions if the factors determining the onset of breeding, presumably the critical spawning temperatures (Orton, 1920), and the apparent double breeding periods each year of a few species, were known for each species. Though this information is required to explain the distributions shown by the Recorder, the Recorder technique is not suitable to derive it. Such questions are best answered by direct observations of the adults.

However, one encouraging feature has been brought to light—the consistency in distribution. Attention has been directed to this in the distribution of the high densities of larvae (p. 107). Such a consistency is very clearly marked, too, both in the distribution of single species and the distributions of groups of species. This is a feature of such considerable importance that it is worth while giving several examples: (a) *Glycymeris glycymeris* (Plate VI) off the Aberdeenshire coast in June–November and off the Humber in January and September–December, (b) (? *Limopsis*), *Adula simpsoni* and *Lima* (all in Plate VI) off the Forth in September–November, (c) Anomiacea (Plate VI) off the Aberdeenshire coast in June–November, (d) *Monacuta ferruginosa* (Plate VII) over the Great Fisher Bank in July–October, (e) *Cardium* D (Plate VII) near the Great Fisher Bank in September–November, (f) (?*Spisula subtruncata*) (Plate VII) in the south-west Dogger in October–December, (g) (? *Tellina crassa*), (? *Spisula solida*) (both in Plate VII) and (? *Barnea candida*)

(Plate VIII) in the Southern Bight, (h) *Zirfaea crispata* (Plate VIII) along the southern edge of the Dogger Bank in April, May, October and December.

These examples form only a short selection.

Thus a definite pattern emerges, raising the hope that the distribution may be explained in terms of permanent or semi-permanent factors. The 1948 results are so well in keeping with those of 1949 (except that the numbers of individual species were higher in one year than the other) that we may justifiably speak of the characteristic larval communities of the various localities.

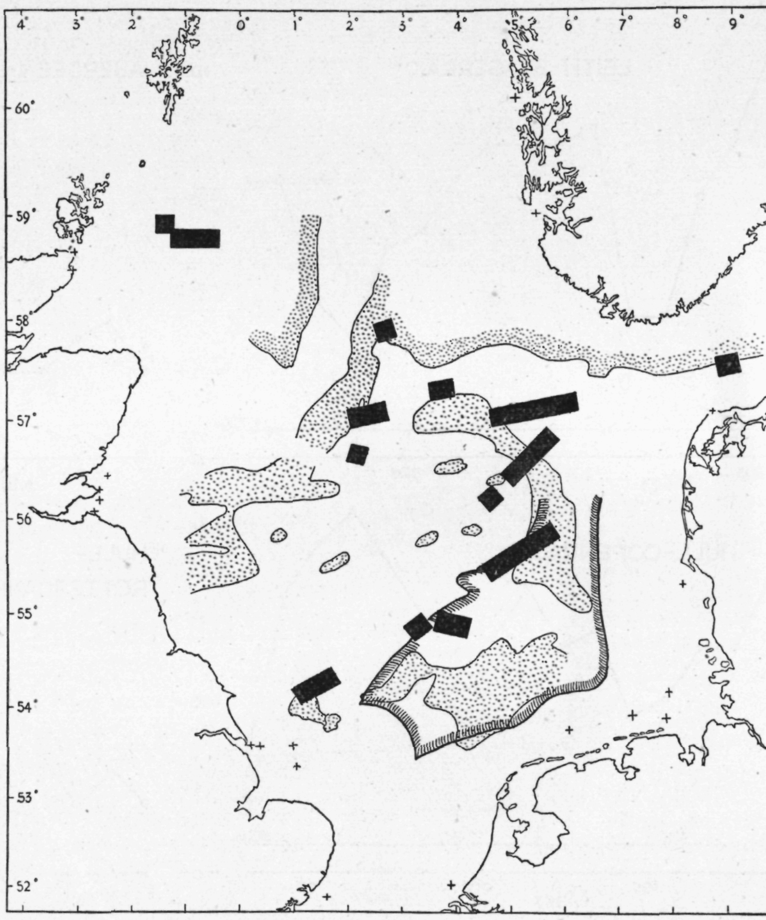
Distribution of Total Lamellibranch Larvae.

In the chart of larval distribution (Text-fig. 2) the density of adults is indicated by means of dots, one dot representing 5 adults per m^2 per international square. The adult densities are repeated from Marshall (1948) with the addition of Petersen's results (p. 111), and it should be noted that these adult densities were determined prior to 1925. The correlation between high adult and larval densities is poor. It is even less satisfactory when it is realized that the high density adult area south-east of the Shetlands is of no relevance, since it was mostly made up of *Thyasira flexuosa* (Stephen, 1933), which has no pelagic larvae. That patch would, in fact, disappear if only adults with pelagic larvae were considered.

Orton (1937) thought that *Cardium edule* and other organisms become concentrated in the plankton in localities where slack and eddy waters occur, and settle in vast numbers in such localities. He predicted that a rich planktonic area would be found over the north-east region of the Dogger, in the north-east Dogger Swirl. This prediction has proved correct for lamellibranch larvae, concentrations having been obtained near there in several years and, in fact, one of the highest densities ever obtained during the Recorder survey occurred there in 1949.

The existence of swirls will go a long way towards explaining the distribution of larval patches shown in Text-fig. 2. A comparison of this figure with the generalized water circulation given by Böhnecke (1922) and Tait (1937) shows, in particular, that major patches fit in with the south-west and north-east Dogger Swirls and with the Great Fisher Bank (Lindesnaes) Swirl. These swirls vary substantially in position, but are in part dependent on geographical features, the elevation of the Dogger Bank and narrow opening of the Skagerrak (Böhnecke, 1922), and we may regard these geographical features as being indirectly the permanent features determining the consistency in distribution of total lamellibranch larvae referred to above (p. 107). It can be supposed that the region from the south-east Dogger to the Great Fisher Bank may be covered by a swirl system at some time throughout the year, since in summer the north-east Dogger Swirl and Lindesnaes Swirls merge and another swirl develops south-east of the Dogger (Böhnecke, 1922). Tait (1937) says that in 1912 the north-east Dogger Swirl almost certainly travelled northwards in May–July to coalesce with the Lindesnaes eddy. It is clearly not to be expected that year after year a particular area will be marked out as a swirl by a concentration of larvae. Perhaps larvae may not be present to congregate, or perhaps the swirl may have moved away from the sampled area or even have disappeared.

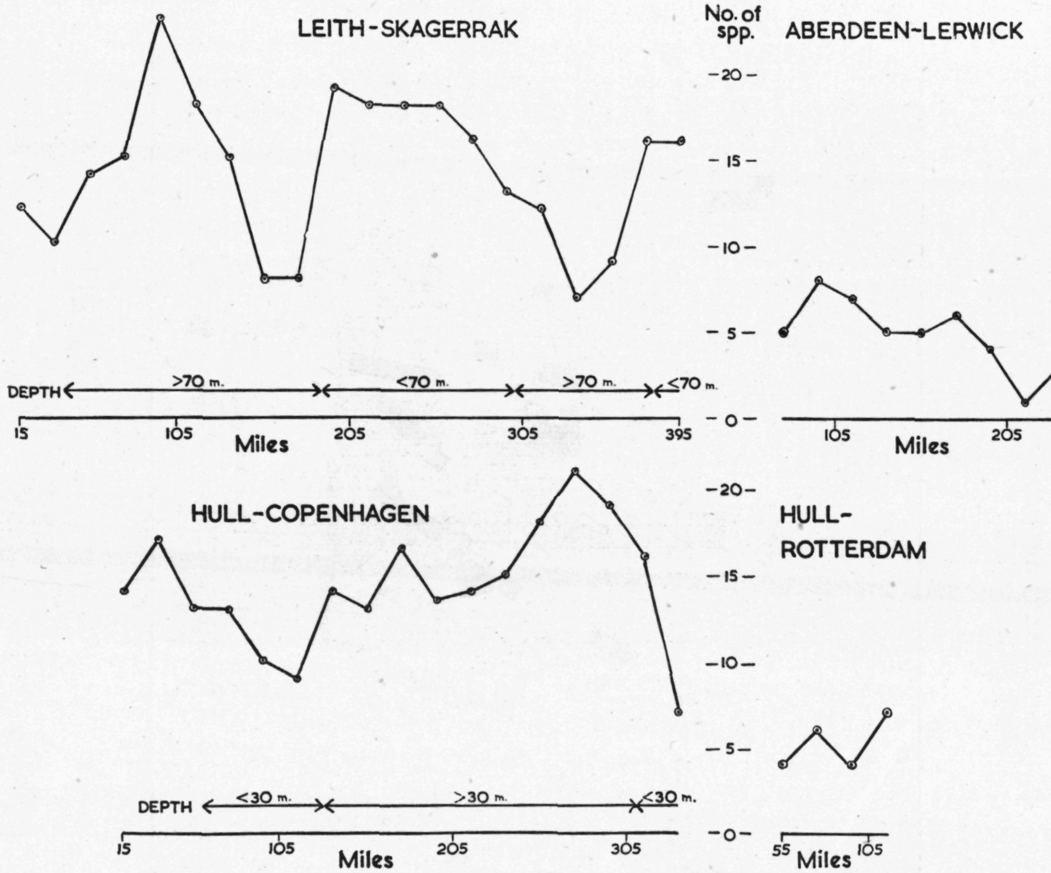
It is doubtful if all the patches in Text-fig. 2 can be explained by swirls. There is a likelihood that the limited patches west of the Great Fisher Bank are some-



TEXT-FIG. 4.—Chart showing distribution of 10-mile blocks with over 1000 lamellibranch larvae, repeated from Text-fig. 2, superimposed on a sketch map of deposits containing mud (dotted areas), derived from Close's Fishermen's Chart. The boundary of a silt area, derived from Borley (1923), is shown as a hatched line. Gaps in the boundary lines result from insufficient information.

how related to stream currents (cf. Tait, 1937, p. 54). However, this must remain a problem involving the whole plankton complex, and it is hoped to study this aspect in a later 'Bulletin.'

A line of approach to this question of larval distribution can be made through the bottom deposits. Borley (1923) mapped in great detail the deposits of the southern North Sea. Equally suitable data north of lat. 56° are not available and, instead, a sketch map, derived from Close's Fisherman's Chart, is given in Text-fig. 4, of the areas of deposits containing mud, whether listed as "sand and mud," or "mud" or "ooze." Superimposed on that derived from the Fisherman's Chart is the boundary of the large area of silt south of the Dogger as derived from Borley (1923).



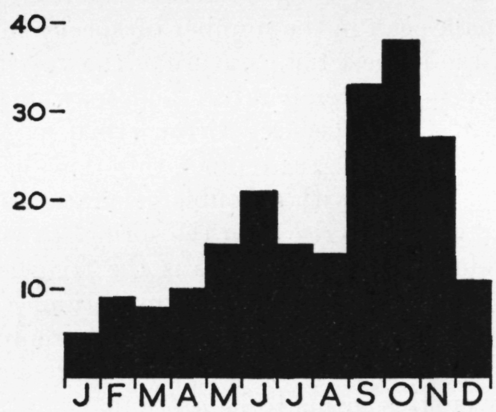
TEXT-FIG. 5.—Graphs showing the number of species obtained on each analysed 10-mile block on four Recorder routes in 1949. The position of the 10-mile blocks can be seen by comparing the horizontal scale of miles with the chart in Text-fig. 1 of 'Hull Bulletin' 7.

There seems to be a correlation between high larval densities and the presence of muddy deposits (cf. Text-fig. 1 with the silt area in Text-fig. 4). It is not suggested that the correlation is necessarily direct, through an accumulation of adults in muddy deposits. Mud is deposited where the bottom currents are weakest and one can return to Orton's view that larvae congregate in slack water or, to meet some cases, it may be better to express it negatively—larvae are not dispersed so much in slack water.

Distribution of Species of Larvae in 1949.

Qualitative.—The number of species found on each analysed block throughout the year on four Recorder lines is shown in Text-fig. 5. The depth profiles for these lines are given in 'Hull Bulletins' 1 and 7, and some of the depths are broadly indicated in Text-fig. 5. The lack of variety of species on the Aberdeen-Lerwick and Hull-Rotterdam lines is clearly brought out. The greatest variety occurred 100 miles off the Forth, on the Leith-Skagerrak line.

Though the values for the western end of the Leith-Skagerrak line are not reliable, being on the low side since the region off the Forth was not sampled in August and September, the line may be said to have three peaks and two troughs. The central peak occurred over the Great Fisher Bank, with depths less than 70 m,



TEXT-FIG. 6.—Histograms showing the number of species obtained in each month, taking in all samples from the North Sea in 1949.

and the eastern one in the Skagerrak, also over a depth less than 70 m. The two troughs occurred over depths exceeding 70 m. The western peak occurred over deep water, but this peak corresponded to the high numbers of larvae obtained, a feature which was unusual, since the high density occurred effectively only in one year (Text-fig. 1 ; see also total numbers for 1938 and 1949 in Text-fig. 3), and it will be maintained below that it was due to a great influx of larvae from the north. The Hull-Copenhagen line may be said to have two troughs, both over depths less than 30 m. Between the two shallow sections the depths varied down to 45 m.

Accepting, then, the unusual character of the off-Forth peak, there appears to be a rough correspondence between variety of species and depth, depths over 70 m and less than 30 m having a poorer variety.

The number of species of larvae obtained in each month over the whole North Sea is shown in Text-fig. 6. A major peak occurred in October and a minor one in June ; the minimum occurred in January. Thorson (1946, fig. 196) gives a similar diagram for larvae in the Sound, the trend of which is quite similar to that for the North Sea.

The most important generalization regarding spawning is that of Orton (1920), who maintained that sea temperature must be the factor of paramount importance controlling breeding in marine animals under normal biological conditions, and that breeding is dependent on the attainment of a critical temperature which is a physiological constant for the species. It would seem that some refinement of Orton's original hypothesis is required to meet some of Thorson's (1946, p. 422) objections, but, doubtless, the main features of the hypothesis will remain.

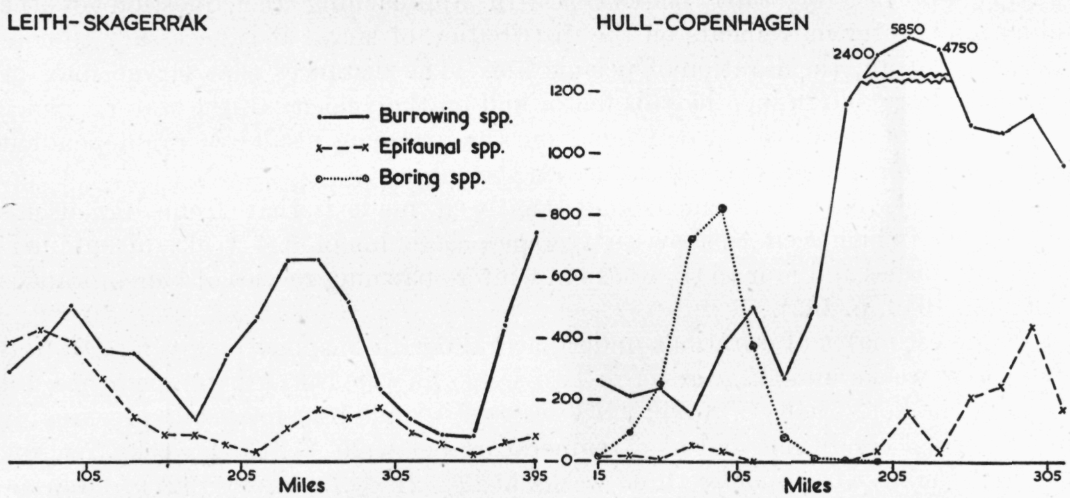
Little is known about critical spawning temperatures in lamellibranchs, apart from the various species of oyster. Nelson (1928*a*) gives 10°–12° as the critical temperature in *Mytilus edulis* and *Mya arenaria*. However, the higher the temperature the greater must be the number of species of lamellibranchs whose minimum critical temperature for spawning is exceeded. This would seem to account satisfactorily for the main peak in the number of species in October, a short time after the attainment of the highest temperature of the year in the North Sea.

Relevant to the question of temperature and spawning is that of the spring and autumn breedings in a few species. Orton (1920, p. 345) states that many animals continue to breed so long as the temperature remains above a certain value. It would appear that the species with a double generation are not amongst these, since the temperature continued to rise after the spring spawning, during the period when no larvae were found. If temperature is the trigger to spawning in these species in spring, is it the trigger to spawning in autumn ? According to Orton (1920) *Patella vulgata* breeds at about the maximum temperature and again at the minimum. Thorson (1946, p. 422) accepts this system for *Polydora ciliata*. On the face of it, however, this seems to be a peculiar phenomenon, and one may feel hesitant in advancing such an explanation of the case of the species we are dealing with. It is possible that the spring spat grows to maturity rapidly and spawns again within a few months. A rapid attainment of maturity is known in some species. Thus *Heteranomia squamula* (= *Anomia aculeata*) gives larvae on being fertilized at an age of less than four months (Orton, 1914), and it is probable that both *Abra alba* and *Cardium ovale* mature in summer in about three to four months (Orton, 1924). This, however, may not be a satisfactory explanation in those species with a minor spring and a major autumn breedings, *e.g.* (? *Spisula subtruncata*) and (? *S. elliptica*) (Table I). In these cases the main adult population possibly spawns twice, a quiescent period intervening whilst the sexual products mature.

In the case of *Mytilus edulis*, which had a peak of frequency in June–July and again in November, it is known that maturity is reached after one year (Field, 1923). However, Jensen and Spärck (1934, quoted by Thorson, 1946, p. 426) found that the older specimens breed in spring whilst the younger ones spawn later in the year.

Quantitative.—It should be noted that the relative numbers of the larvae of the various species do not give a true picture of the relative numbers of the corresponding species of adults in the North Sea, since some important species have non-pelagic larvae or larvae which are pelagic for a very short time only. Also, even in the case of species having pelagic larvae there is a difference in fecundity in the different species and a difference in time during which the larvae are pelagic. Of the species with no pelagic larvae which appear to be frequent in the North Sea, the species of the Nuculacea, *Modiolaria nigra*, *Astarte sulcata* and, above all, *Thyasira flexuosa*, may be mentioned.

Accepting, then, the fact that the relative numbers of larvae are not equivalent to the relative numbers of adults, a list is given of the ten most common larvae found. The number in brackets following the specific name refers to the number of hundreds of larvae estimated as collected by the Recorder in 1949. In order of frequency the list is: (? *Spisula elliptica*) (140), *Cultellus pellucidus* (26), *Zirfaea*



TEXT-FIG. 7.—Graphs showing the yearly number of larvae of epifaunal, burrowing and boring species obtained on each analysed 10-mile block of the Leith-Skagerrak and Hull-Copenhagen lines. The position of the 10-mile blocks can be seen by comparing the horizontal scale of miles with the chart in Text-fig. 1 of 'Hull Bulletin' 7.

crispata (23), *Abra prismatica* (21), *Glycymeris glycymeris* (20), *Ensis ensis* (20), *Mytilus edulis* (18), *Montacuta ferruginosa* (17), *Modiolus modiolus* (13), *Hiatella arctica* (11).

The very great dominance of (? *Spisula elliptica*) in 1949 was probably an unusual feature; in 1948 the comparable value was probably under 40. It may be mentioned, in addition, that the 1949 value for (? *Spisula subtruncata*) was 9.

Of these ten species, three are epifaunal (*Mytilus*, *Modiolus* and *Hiatella*) and one a borer (*Zirfaea*). To follow up this point, all the larvae obtained in two lines throughout the year have been separated into the three ecological groups, the burrowing, the boring and the epifaunal species. Text-fig. 7 shows the total number of larvae of each group on each analysed block of two lines.

On the Leith-Skagerrak line only the larvae of burrowing and epifaunal species realized appreciable numbers. It will be seen that the off-Forth peak (cf. Text-fig. 3) was made up of approximately equal numbers of both groups. Over the Great Fisher Bank the burrowing species easily predominated in 1949, but in years with a pronounced concentration of larvae over the Bank epifaunal species probably form a very substantial part of the total population. Epifaunal species formed a very minor part of the Skagerrak patch (4, Text-fig. 1). On the Hull-Copenhagen line the larvae of boring species, *Zirfaea* and *Pholas*, predominated over the shallow water of the south-west Dogger. Epifaunal species were almost absent over the Dogger, but increased in numbers towards the Danish coast. The epifaunal species, however, remained very low in comparison with the larvae of burrowing species along the eastern half of the line.

The influence of water movements.—In approaching the question of the influence of water movements on the distribution of larvae it is necessary to consider, first of all, the duration of pelagic life. The distances that larvae may be transported are determined by this factor and on the velocity of the water. Since no estimates of duration can be made from the foregoing results we are dependent on judging from the previous literature on the subject.

The most general statement that has been made is that from Jørgensen's calculations, which seem to show an average pelagic life of 3–4 weeks in summer-spawning species and four to six weeks in winter-spawning species of lamellibranchs (Thorson, 1946, p. 455).

Some estimates of durations under natural conditions may be given: *Mytilus edulis* four weeks and *Mya arenaria* two weeks in the Isefjord, temperature not known (Thorson, 1946, p. 453); *Mytilus edulis* and *Mya arenaria*, presumably under normal conditions and at a temperature below 20° C., three weeks (Nelson, 1928*b*); *Cumingia tellinoides* three weeks at 20°–21° C. (Grave, 1927). Larvae of shipworms last at least a month, perhaps more (Sigerfoos, 1908). *Teredo navalis* takes five weeks between spawning and settling at Woods Hole (Grave, 1928). The total larval life of *Ostrea lurida* is at least forty days at 17°–18° C. (Hopkins, 1937).

Much information is available about larval development in oysters. The literature has been reviewed by Korringa (1941), and is of interest in showing the general slowing down of development with decrease in temperature. As examples we may take firstly *Ostrea virginica*, which is non-incubatory—thirteen days at 23°–25° C., fifteen days at 21°–22° C. and seventeen days at 20° C. As a second example we can take *Ostrea edulis*. The larval life of this is divided into an incubatory phase lasting about ten days (more or less) and a pelagic phase. The pelagic phase at 22°–23° C. was six days, at 21° C. seven days, at 19° C. twelve days, at 16° C. fourteen days (Korringa, 1941, p. 134), *i.e.*, the pelagic life was doubled with a temperature change from 23° C. to 19° C.

All the examples are at relatively high temperatures, and it is generally agreed that the lower the temperature the greater the duration of the pelagic life. Most of the larvae dealt with in this report grow under much lower temperatures, at least during part of their breeding period. It is impossible to give precise values, since the whole range from surface to bottom is involved at any one time. However, the difference from the above results may be appreciated when it is realized that larvae develop during March, April and May at temperatures of 5°–10° C.

In the absence of more useful information it seems reasonable to expect a pelagic life of 6 weeks or so for larvae settling at 350–400μ. Indication of the surface drift velocities of the northern and middle North Sea may be obtained from Tait (1937, figs. 45–47). For purposes of illustration it is fair to work on an average drift velocity of 8 miles a day (the top velocity is over $12\frac{1}{2}$ miles per day). At this rate a larva spawned off Aberdeen could reach the Humber in about 25 days and if spawned just south of the Shetlands in about 43 days. It is clear, therefore, that larvae may be transported considerable distances in the North Sea, even allowing for marked variations in duration and velocity.

The distributions of several organisms, as shown by the Plankton Recorder, have been explained by a progressive translation from the north-west towards the southern North Sea (Rae and Rees, 1947 ; Marshall, 1948), the explanation being based on the current system described by Böhnecke (1922) and Tait (1937). These "north-west indicator" species follow approximately the same pattern. In August they are concentrated in the north-west and, subsequently, appear off the Forth in September–October and off the Humber in November–December. Allowing for the fact that larvae spawned in the path of a prevailing drift are too small to be identifiable during the first part of their journey, the larvae of (? *Limopsis*) and *Myrtea spinifera* appear to conform to this pattern of distribution. Though a composite group, the Anomiacea also conform. It will be suggested below that the larvae of *Modiolus modiolus* and *Musculus marmoratus* off the Humber in October were also translated from the north. The alternative explanation that there was a succession in time of spawning is hardly likely in these cases. If the initial stimulus to spawning is the attainment of a certain critical temperature (Orton, 1920), then, at this time of year, the succession in breeding should have been from south to north, whereas the succession in distribution was from north to south.

Instead of dealing with individual species we can consider the composition of patches shown in Text-fig. 1, with particular attention to the influence of water movements on them. This may be done, at present, only briefly and tentatively, but it is hoped to continue this work for some years and initial consideration of the data will serve as a useful background. The distributions will become very much clearer when knowledge of the contemporary bottom fauna, now being investigated at other laboratories, becomes available.

Patch 1 (Text-fig. 1).—This patch occurred very distinctly in 1938 and 1939, and only in 1947 in post-war years. In all these years it occurred in July, and there is little doubt that the population was mainly of epifaunal origin, chiefly

Mytilus edulis, but also *Modiolus modiolus*, *Hiatella arctica* and Anomiacea. It might well have been a swirl concentration (cf. Tait, 1937).

Patch 2.—This patch, occurring effectively only in 1949, was unusual. As far as the results go October was the important month, but it should be noted that the August and September lines did not start until some 80 miles from the Forth and the results are thus incomplete.

On the same record that had the main concentration of larvae the number of *Metridia lucens* was unusually high, much higher than obtained at any time in 1938 or 1946–48. The peak number occurred, too, earlier than in these years. Similarly, the peak number of *Candacia armata* in 1949 was much greater than in these previous years. The absence of collections near the Forth in August and September restricts the amount of guidance to be derived from these two useful north-west indicator species but the higher numbers of the two species appear to be associated with the Forth lamellibranch larval concentration. Dr. Tait has kindly informed me that he found that the southward movement of oceanic (or Atlantic) water into the North Sea reached its greatest intensity and penetration in August, in 1949. That this should occur in August is unusual, the maximum intensity of the autumn usually occurring later in the year. It appears, therefore, that the influx was earlier than usual, and occurred at a time when larvae, particularly of the epifaunal species *Modiolus modiolus* and *Hiatella arctica*, were still abundant. The early October community off the Forth consisted of 55% of epifaunal species and over 30% of *Glycymeris glycymeris*, whose adults were found in abundance in the north-west (Stephen, 1933). It can hardly be doubted that had the Forth end been sampled in September the early effect of invasion would have been shown, as may be seen from the distribution of *Adula simpsoni* and *Lima* (Plate VI). Several specimens of *Adula simpsoni* were found in the tank residue of the Leith-Skagerrak line in the autumn of 1949 ; it is significant that none were found in the tank residue in 1946–48 (since the silk collections were not analysed in these years, this is the only comparable information). The same southerly movement of water probably accounted for the October records of *Modiolus modiolus* and *Musculus marmoratus* off the Humber (Plate VI) ; it was noted during analysis that these specimens of *M. marmoratus* were unusually large.

Had the influx been delayed by, say, a month, the seasonal decrease in number of larvae would have removed the possibility of a Forth concentration appearing.

Patch 3.—The Great Fisher Bank concentration was poorly developed in 1949 in comparison with 1938, 1939 and 1948. The average number of larvae over the Bank in 1939 and 1949 (Text-fig. 3) was not greatly different in the two years, but when individual records are considered there was a pronounced difference between them. The June and July records of 1938, the June record of 1939 (Marshall, 1948) and the July record of 1948 had high numbers, records in other months being low. In 1949 no high density was recorded, but there was a persistent moderate density from July to October, the highest number being about one-tenth of those obtained in the peak concentration of earlier years.

It is unfortunate that no major concentration was obtained in 1949 since the data for 1948 are far from complete. It appears that the high density in early July of 1948 was due in large part to a high number of larvae of epifaunal species, chiefly *Modiolus*. Whilst preparing this paper the results for the earlier part of 1950 have become available and these have shown a very good development of the Fisher Bank population. In mid-May *Mytilus edulis* larvae were easily predominant, comprising over 70% of the population ; by the end of May *Mytilus edulis* had dropped to 35% and larvae of *Ensis* rose to over 40%. By June 10th the population had changed considerably, and Venerid D was the most common larva with *Abra prismatica* second. There were no less than 16 species in the well-marked Bank concentration of June 10th, 1950. No Bank concentration was shown on the record taken on July 8th.

There is, of course, nothing unexpected in this change of composition of the population with time. Such a change occurs through the normal seasonal succession of species and does not, in itself, imply a change in locality of origin of the population.

Marshall (1948) suggested that the Great Fisher Bank concentrations might be due to adult populations of the north-east half of the Dogger Bank, and that, in this case, a fair proportion of larvae of *Spisula* would be expected. As far as the *main* concentration is concerned this suggestion is not borne out. The Bank concentration has occurred within the May–July period, when *Spisula* larvae are low in number, and it is known that some of the main concentrations have been due to epifaunal species. Larvae of (? *Spisula subtruncata*) and of (? *Spisula elliptica*) have occurred over the Bank (Plate VII) even as early as June (1950), but never to an important extent. It is quite possible that these few larvae may have been brought from the south-west, but it is to be noted that (? *Spisula subtruncata*) larvae have also been found 100 miles from the Forth ; a southern origin of these is most unlikely. There is, probably, a local population of *Spisula elliptica* in the Fisher Bank.

There seems to be an association between *Clione* and high larval densities over the Fisher Bank, though the appearance there is not exactly coincident in time. Thus *Clione* was found over the Bank in July, 1938 (when larvae were abundant), and in August, 1939. Also, in 1948 *Clione* was found over the Bank on July 30th, on the record following the high larval density. Marshall (1948) considered that a northern origin for Bank *Clione* is more probable than origin from the Skagerrak. Yet a Skagerrak origin is quite possible. Graham (1934) visualized the possibility that the swirl over the Great Fisher Bank could act as an agent for transporting cod fry from Norwegian coastal waters into the North Sea proper. The only suggestion that can be made at present is that the direction of origin of the larval community was the same as that of *Clione*, allowance being made for larvae arising from the local adult population; it is still a matter of opinion that this was from the north.

Patch 4.—This was only slightly developed in 1949, in October, with (? *Spisula* *elliptica*) predominant and Venus A next in numbers. Non-burrowing species amounted to about 18%. The major development of this patch occurred in June–August, 1948. Over this period " Montacuta " was the most numerous larva, but was exceeded in numbers slightly by (? *Spisula elliptica*) in August. Epifaunal species were present to about 40% of the population in July, falling to a very small percentage in August. The concentration may have developed at the junction of the easterly current along the Danish coast and the westerly current along the Norwegian coast. It may well be related to the high adult concentration near the adjacent coast (Text-fig. 2).

Patch 5.—Though this developed twice in 1949, in May–June and again in October, this is not an important patch, since previously it was obtained only in 1948, in October, and even in 1949 the density was barely above the limit chosen to define patches. Its composition leads one to believe that it was a development largely from the local bottom population.

Patch 6.—As mentioned above, Orton (1937) predicted larval concentrations in this area. According to Böhnecke (1922) the Dogger Bank forms the southern boundary of the north-east Dogger Swirl and, this being so, the standard Hull-Copenhagen time runs rather south of the Swirl. This larval patch may, consequently, be more truly related to the south-east Dogger Swirl, which develops on the coalescence of the north-east Dogger and Lindesnaes Swirls (Böhnecke, 1922).

Over 2000 larvae per m^2 were found in the centre of the patch in October, 1949, and this estimate may have been on the low side. Of this very high number (? *Spisula elliptica*) accounted for about 95%.

Patch 7.—Though this patch was made up mostly of *Zirfaea crispata* in 1949, there is reason to believe that larvae of *Ensis* may form a considerable part of the population in spring and early summer patches near this region in other years.

Patch 8.—According to Böhnecke (1922) the south-west Dogger Swirl is bounded to the north by the Dogger Bank, so it is likely that the standard Hull-Copenhagen recorder lines run to the north of the Swirl. However, the larval patch found in 1947 occurred about 15 miles north of the standard Hull-Copenhagen Recorder route. This patch was made up predominantly of (? *Mactra stultorum*), together with some " Montacuta " and *Ensis*.

Patch 9.—This was obtained quite infrequently and never in really high density. In 1947 it was made up chiefly of (? *Spisula subtruncata*), together with (? *Spisula solida*) and (? *Tellina crassa*). One interesting feature of this area is the relatively great importance of species preferring coarser grades of bottom. Thus *Tellina crassa* and *Glycymeris* are given in Ford's Class B (Ford, 1923), and probably *Spisula solida* is to be considered in the same group (cf. Ford, 1925).

Summary.

1. The distributions of high densities of larvae from year to year, and of the species of larvae from month to month, were often repeated, in such a manner as to suggest a definite pattern of distribution.

2. Many of the major patches can be related to the existence of swirls. The concentrations of larvae seem to be correlated with silty or muddy deposits, and poorly correlated with the distribution of adults as shown in previous work. Larvae were uncommon over the main part of the Dogger Bank.

3. The maximum number of species occurred in October, with a secondary maximum in June. There was a poor variety of species in the north-west North Sea and the Southern Bight. In the central North Sea there appeared to be a correspondence between number of species and depth, depths over 70 m and less than 30 m having a poorer variety.

4. Most of the species encountered had only one *main* breeding period during the year, but a few species had two distinct breeding periods.

5. Whilst, generally, larvae of burrowing species predominated, in certain parts larvae of epifaunal and boring species were important, and sometimes exceeded in numbers larvae of burrowing species.

6. Rough estimates of duration of pelagic life and speed of surface water drift show that larvae may be transported considerable distances in the North Sea. Some species showed a southerly movement resembling that of " north-west indicator " species. There was an unusual influx, almost certainly due to water movement, of larvae into the off-Forth region in the autumn of 1949.

7. The month by month distributions of 47 species are given in charts and of 10 species, in addition, in the text.

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EXPLANATION OF PLATES VI–VIII.

Charts showing the monthly distribution of types of larvae during 1949. The numbers placed near the observations give the months of occurrence. The scale used to give broad indication of density is given in Plate VI. The dots show those international squares where the corresponding adults were found during quantitative bottom surveys in earlier years. The international squares sampled, and by whom, are shown at the bottom of Plate VIII.

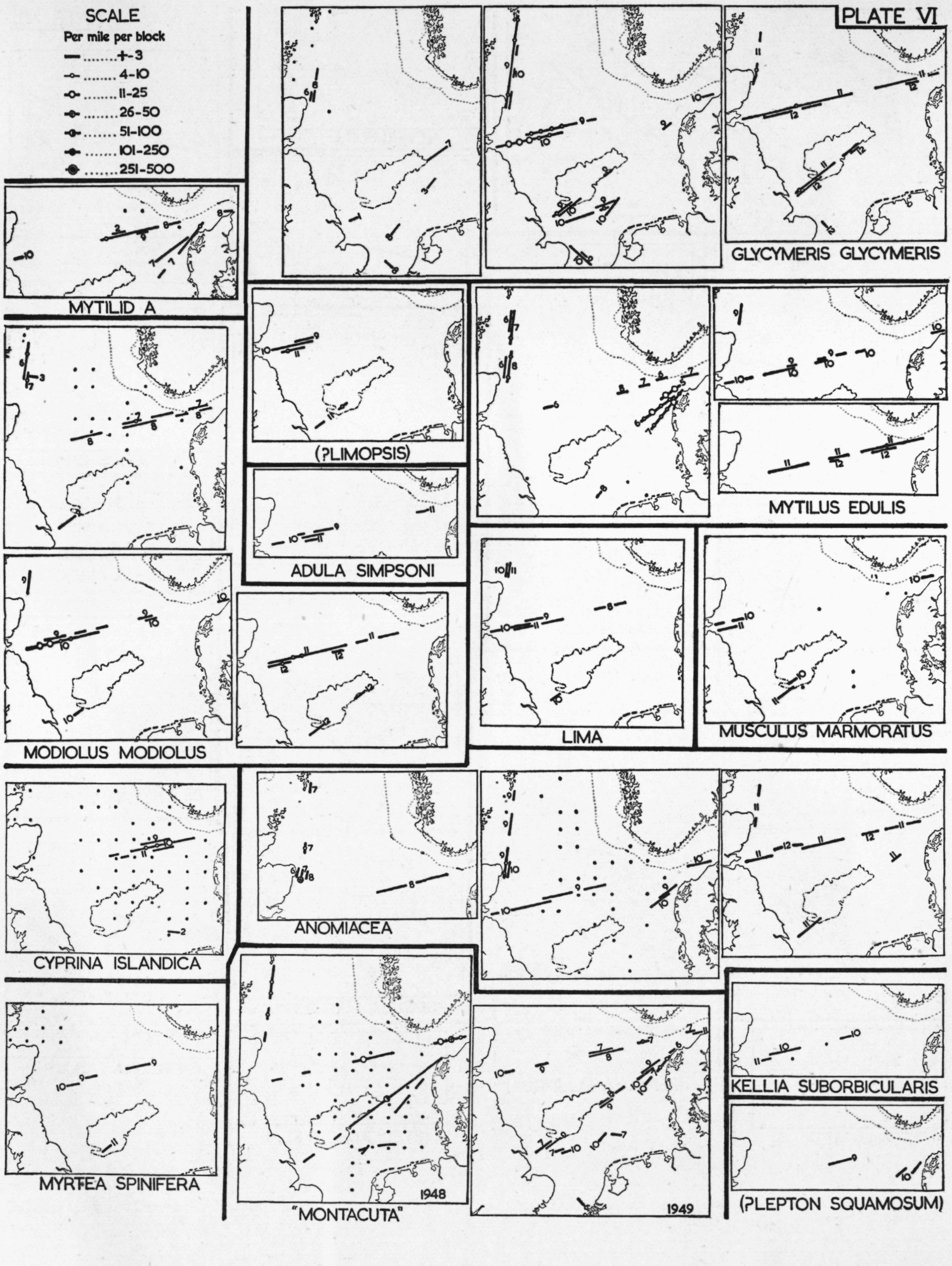
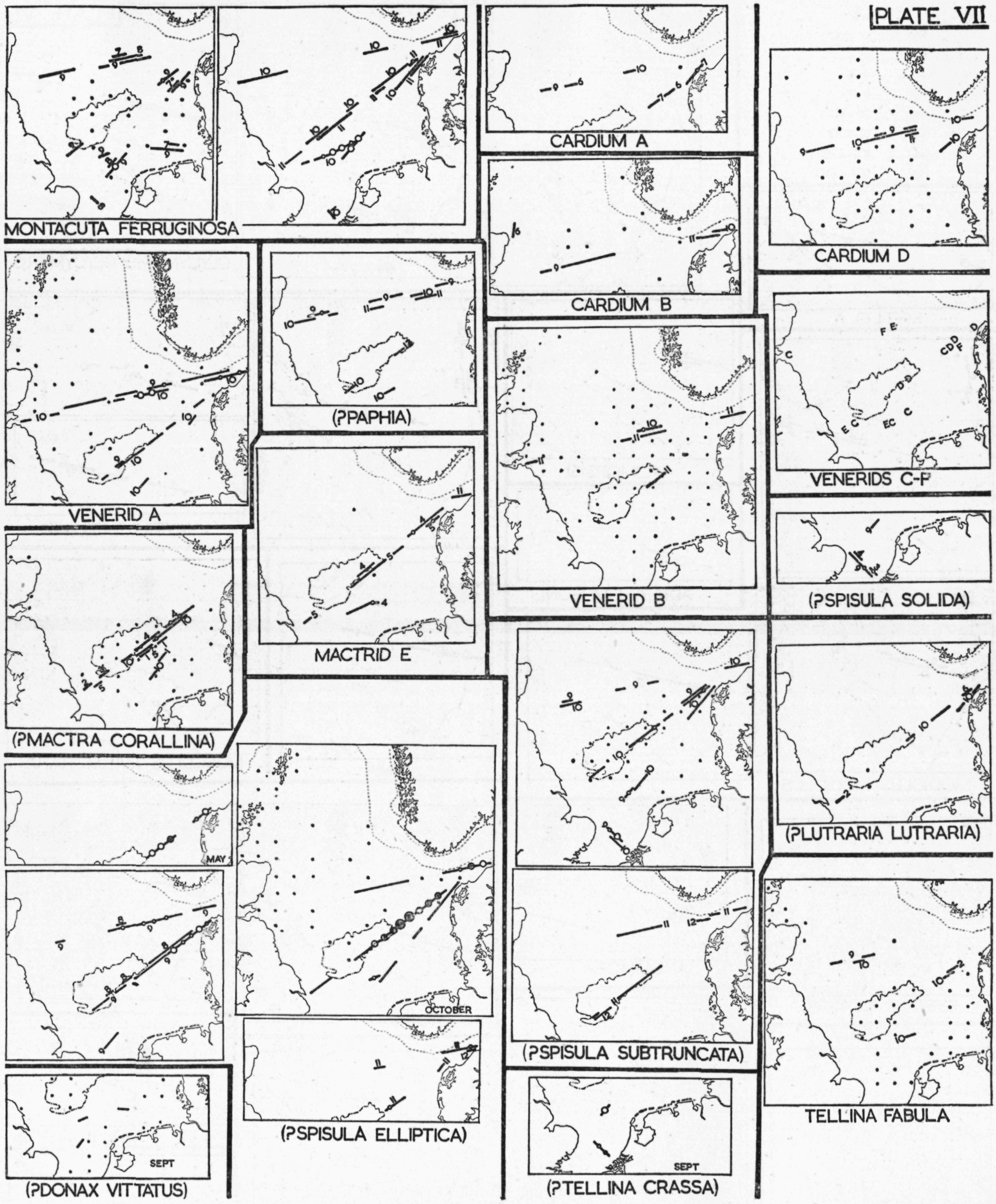


PLATE VI
SCALE
Per mile per block
........+-3
........4-10
........11-25
........26-50
........51-100
........101-250
........251-500
MYTILID A
GLYCYMERIS GLYCYMERIS
(?LIMOPSIS)
ADULA SIMPSONI
MYTILUS EDULIS
MODIOLUS MODIOLUS
LIMA
MUSCULUS MARMORATUS
CYPRINA ISLANDICA
ANOMIACEA
KELLIA SUBORBICULARIS
MYRTEA SPINIFERA
1948
"MONTACUTA"
1949
(?LEPTON SQUAMOSUM)

PLATE VII


MONTACUTA FERRUGINOSA
CARDIUM A
CARDIUM B
CARDIUM D
VENERID A
(?PAPHIA)
VENERID B
VENERIDS C-F
(?SPISULA SOLIDA)
(?MACTRA CORALLINA)
MACTRID E
(?LUTRARIA LUTRARIA)
MAY
OCTOBER
(?SPISULA SUBTRUNCATA)
TELLINA FABULA
(?SPISULA ELLIPTICA)
SEPT
(?DONAX VITTATUS)
SEPT
(?TELLINA CRASSA)

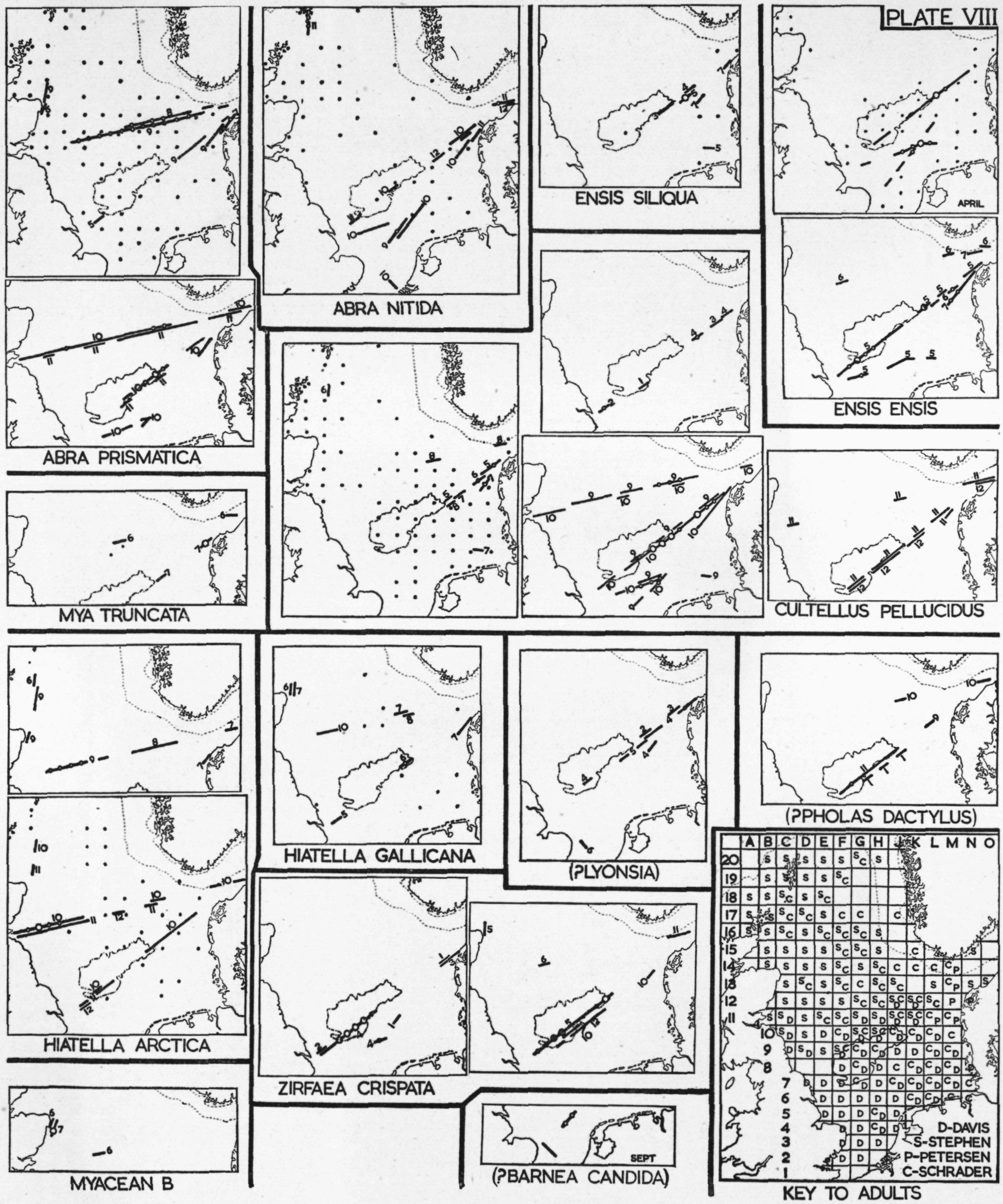


PLATE VIII
ENSIS SILIQUA
APRIL
ABRA NITIDA
ENSIS ENSIS
ABRA PRISMATICA
MYA TRUNCATA
CULTELLUS PELLUCIDUS
(?PHOLAS DACTYLUS)
HIATELLA GALLICANA
(?LYONSIA)
HIATELLA ARCTICA
ZIRFAEA CRISPATA
MYACEAN B
SEPT
(?BARNEA CANDIDA)
D-DAVIS
S-STEPHEN
P-PETERSEN
C-SCHRADER
KEY TO ADULTS

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