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CONTINUOUS PLANKTON RECORDS: THE DISTRIBUTION OF ECHINODERM AND OTHER LARVAE IN THE NORTH SEA, 1947-51

BY

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CONTENTS.

Introduction and Methods.

This report on echinoderm larvae is a further contribution in the general study of the distribution of the pelagic larvae of benthic animals in the North Sea, as shown by continuous plankton records. A section, placed at the end of this report, consists of a brief account of the distribution of larvae of the Polychaeta, Cirripedia, Bryozoa and Phoronidea. Earlier reports concerned the larvae of lamellibranchs and decapod crustacea (Rees, 1951, 1952, 1954).

The records obtained in each month from 1946 to 1951 are given by Rae (1952, 1953), who has also described the routine methods of plankton analysis employed. The plankton in every alternate 10-mile sample is analysed and estimates derived of the numbers of various organisms in each sample. Echinoderm larvae are at first treated as a single group and the estimate derived is not of the actual number of larvae in a sample but of the range of numbers in which the actual number lies.

For the purpose of calculation it is then assumed that the number of larvae in the sample is equivalent to the calculated mean of the range. A concrete example may be given by way of illustration. Suppose there are 4000 larvae in a sample. In routine analysis the number of larvae would be estimated to be in the range 2040–5000 larvae. In applying this estimate it is assumed that the number of larvae present is 3000, which is the calculated mean of this range. Clearly, therefore, the quantitative estimates are very approximate ; continuing the example, no distinction is made between samples containing 2100 and 4900 larvae.

Whilst the identification of the echinoderm larvae is by no means so formidable a problem as that of the lamellibranch larvae, some initial difficulty was encountered because of the damaged state of the larvae on the silk. With experience, however, the identification becomes easy and all can be identified. Since it was desired to identify larvae over the same period, 1949 to 1951, as that for which lamellibranch larvae were identified, the delay in acquiring experience made it necessary to return to material that was two or three years old. So much material had accumulated that it was not possible to study the distribution of echinoderm larvae in such detail as in the case of lamellibranch larvae. For the latter, every alternate sample taken was re-examined even though none had been found in the routine analysis. For the echinoderms, only samples known to have at least a certain number of larvae were re-examined for species, the limit being placed at 480 larvae in the 1949 and 1950 material and reduced to 160 in the fresher 1951 material. In the course of re-examination of samples, only a fraction or subsample of the echinoderm larvae were identified to species. This fraction was usually about one-fortieth, which approximated to the number seen in one microscope traverse of the silk (Rae, 1952). The number of larvae of each species in a sample has then been calculated on a proportional basis.

This difference between the method used for the echinoderm and for the lamellibranch larvae should be noted, especially as it affects the scarce larvae. Since every alternate 10-mile sample was examined for species of lamellibranch larvae there was, theoretically, the same number and distribution of samples in each month. For the echinoderm larvae, however, the effective number of samples varied from month to month according to the incidence of the more abundant larvae. A scarce echinoderm larva occurring in the winter months would probably not be observed, since so few samples were re-examined during this season. On the other hand, an equally scarce larva, which occurred in the summer, might be observed several times because of the increase in the number of re-examined samples, due to the abundance of other species of larvae.

Table I gives the number of samples re-examined for echinoderm larvae in each month in two halves of the North Sea, the boundary being conveniently placed along a line Newcastle–Skaw.

Only echinoplutei and ophioplutei were estimated and identified. Larvae of the other classes of echinoderms have not been studied. Few, however, appear to have been taken in the Recorder samples.

TABLE I.—*The Number of Samples Re-examined in each Month for Species of Echinoderm Larvae.*

	Northern North Sea.			Southern North Sea.		
	1949.	1950.	1951.	1949.	1950.	1951.
February	2	—	—	—	—	1
March	—	11	5	—	—	—
April	—	10	6	—	1	1
May	—	15	1	12	6	—
June	3	6	5	4	11	21
July	—	7	6	23	14	15
August	—	4	16	10	5	17
September	6	3	19	1	5	7
October	3	—	3	—	—	3
	—	—	—	—	—	—
Total	14	56	61	50	42	65

DISTRIBUTION OF TOTAL ECHINODERM LARVAE.

The distributions of total echinoderm larvae in Recorder collections from 1932 to 1939 are given by Henderson and Marshall (1944) and Marshall (1948). In the years 1932–37 the survey was confined to the southern part of the North Sea. These distributions, as well as those in each year from 1946 to 1949, are shown in summarized form in Text-figs. 1 and 2. Similar summary distributions have been given for lamellibranch larvae (Text-figs. 1 and 2 of Rees, 1951) and decapod larvae (Text-figs. 2 and 3 of Rees, 1952).

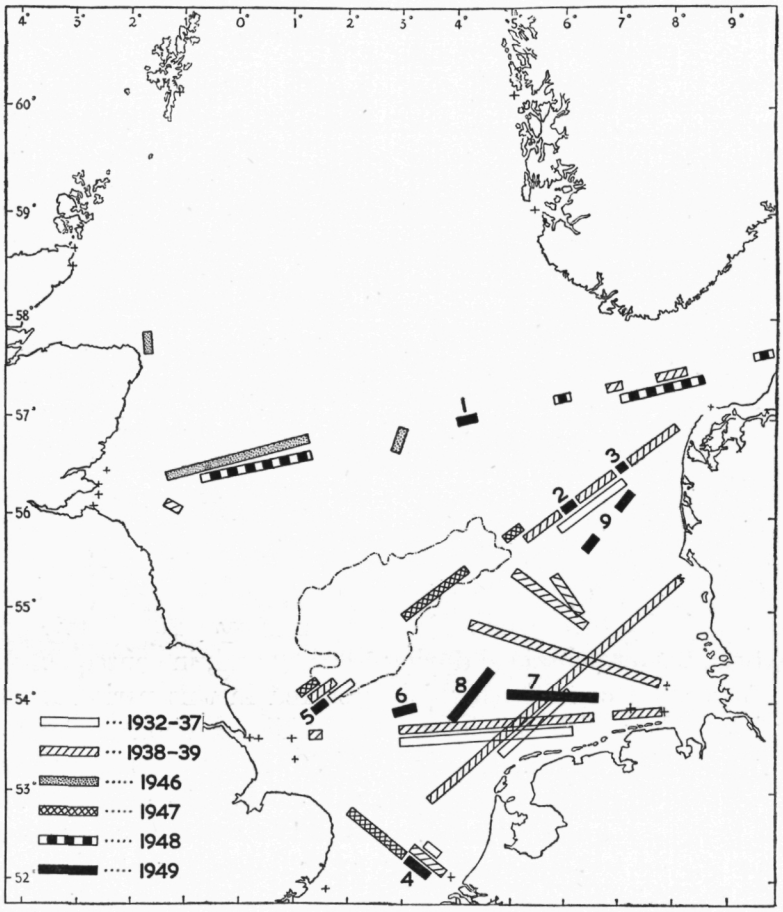
The great majority of the samples, containing over 2000 larvae, which go to make up Text-fig. 2, were obtained during 1938–39 and, in consequence, Text-fig. 2 may represent unusual conditions which occurred in this period rather than the generalized picture for which it is intended. Whilst echinoderm larvae were very numerous in the southern North Sea in 1938–39, it is particularly to be observed that several Recorder routes converged into the Heligoland Bight. There was little sampling into the Bight in 1946–49. In 1950–51 the Bight was more thoroughly sampled, although not to the extent of 1938–39, and the distributions, which are shown in Text-fig. 3 in a form comparable with similar charts for lamellibranch larvae (Text-fig. 1 of Rees, 1954), do confirm that the greatest concentrations of echinoderm larvae in the North Sea are found in the Heligoland Bight.

There is a clear difference between the distributions of the three main groups of larvae. The main concentrations of lamellibranch larvae have been found within an arc stretching from the south-west Dogger Bank to the Great Fisher Bank and westwards to the Forth ; of decapod larvae within the southern North Sea, west as well as east ; and of echinoderm larvae within the eastern half of the southern North Sea and particularly within the Heligoland Bight.

Marshall's (1948) charts of distribution of echinoderm larvae in 1938 and 1939 illustrate the general rule that the greatest numbers of larvae in the southern North Sea occur in June and July. Larval patches in Text-figs. 1 and 3 have

been numbered and the month of occurrence of the patches are given in Table IV (p. 59); all the southern North Sea concentrations of 1950 and 1951 were found in June and July.

The seasonal occurrence on two parts of the Leith–Skagerrak line is shown in Text-fig. 4, which gives the average number of larvae per sample in each month

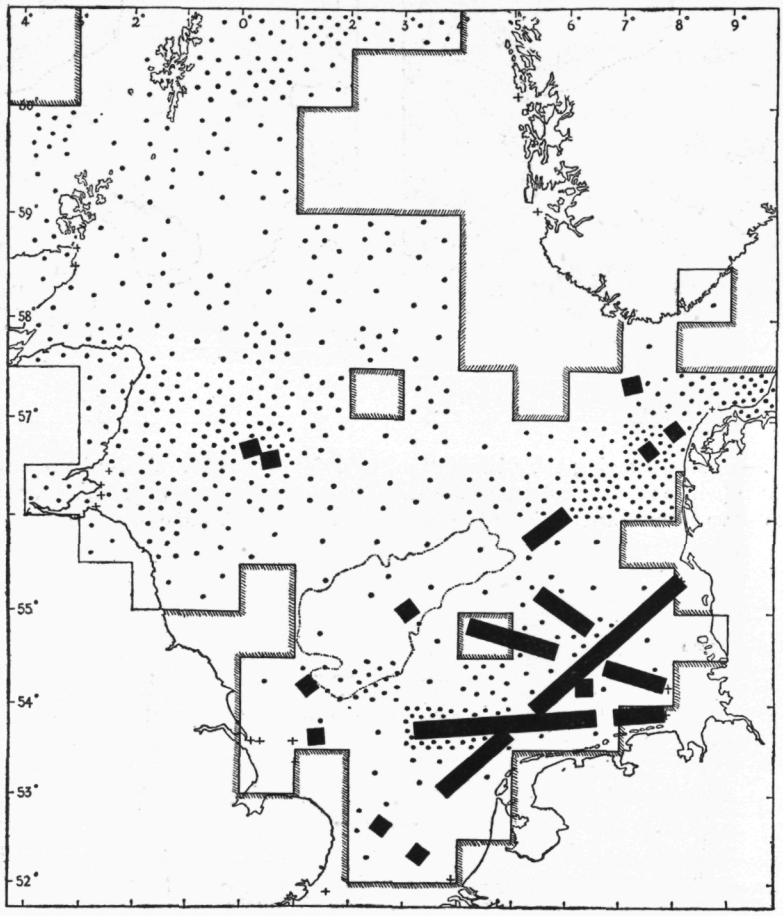


TEXT-FIG. 1.—Chart showing the distribution of 10-mile samples with more than 1000 echinoderm larvae during the periods 1932–37, 1938–39 and each year from 1946 to 1949. It should be noted that during the period 1932–37 only the southern part of the North Sea was sampled. The patches found in 1949 have been numbered for the purpose of Table IV, page. 59.

in the section off the Forth (0–170 miles from the Forth) and in the Fisher Bank section (170–350 miles from the Forth). The values for 1948 are given in preference to 1949 since this line was not sampled in April and May, 1949.

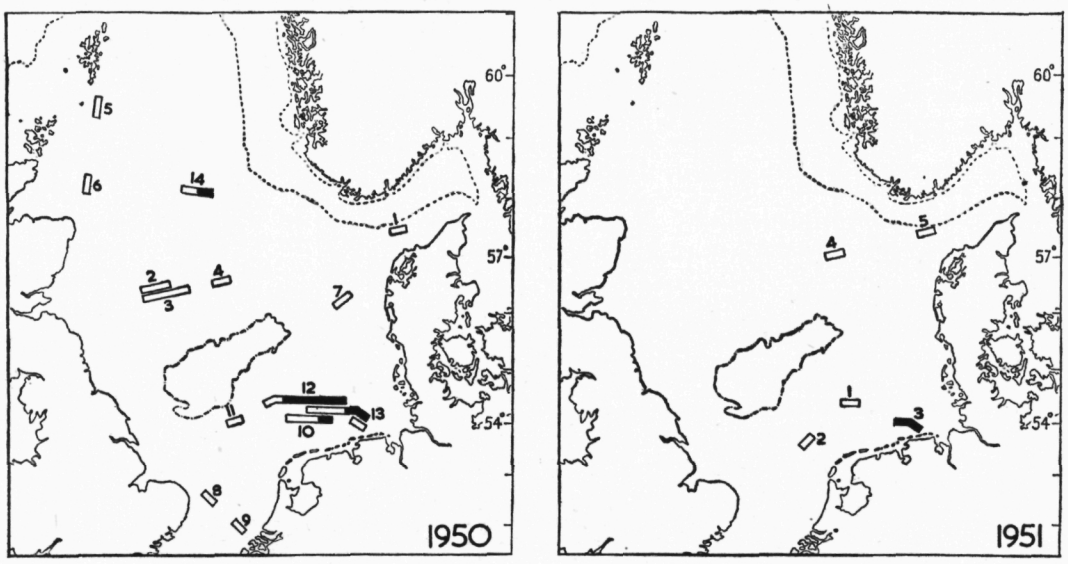
The greatest numbers off the Forth were obtained in April and May in 1948 and 1950, and there was a secondary maximum in August. In 1951 the numbers from March to October were more or less steady. In the Fisher Bank section larvae

were most plentiful in April and May in 1948 and 1950. In 1951 the main concentration occurred in September. In contrast, it may be noted that any concentration of *lamellibranch larvae* off the Forth occurs in August-September and over the Fisher Bank in June–July (Rees, 1954).

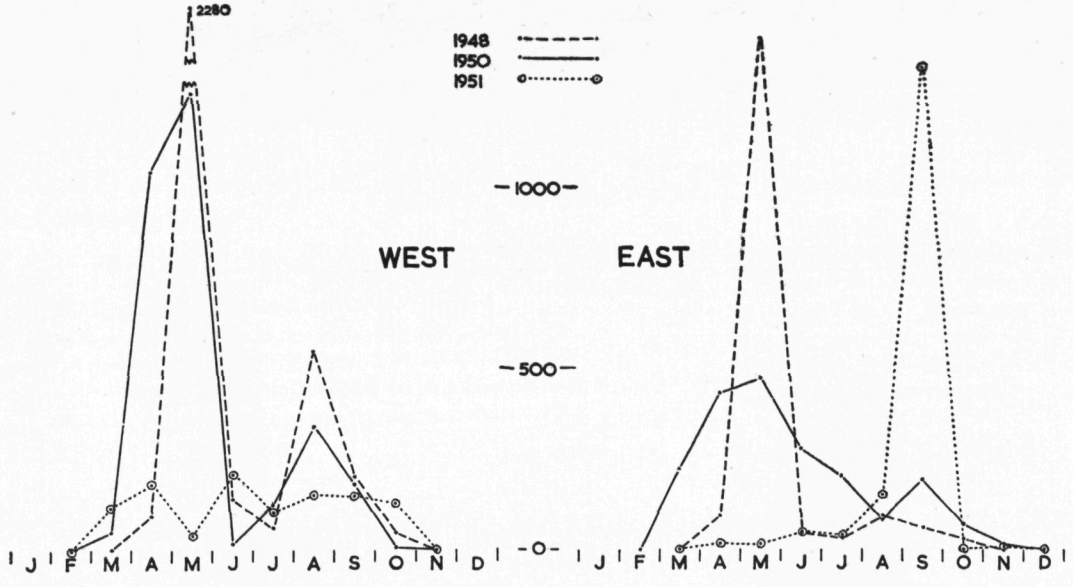


TEXT-FIG. 2.—The black rectangles show the distribution of all 10-mile samples, obtained during the entire Recorder survey, with more than 2000 echinoderm larvae. The density of adults on the bottom, as found in earlier surveys by other workers, is represented by dots, each dot standing for 5 adults (nearest) per m^2 per international square (see p. 57). The hatched boundary line encloses squares not sampled during the quantitative surveys of the bottom fauna.

Of the eight years, 1938–39, 1946–51, during which the Leith–Skagerrak route has been sampled, there was no effective sampling during April–May in three years, 1938, 1947 and 1949. Of the remaining five years, an April–May concentration of echinoderm larvae was found off the Forth in 1946, 1948 and 1950 and no concentration in 1939 and 1951. A heavy concentration over the Great Fisher



TEXT-FIG. 3.—Charts showing the distribution, in 1950 and 1951, of 10-mile samples with 1000–2000 (white rectangles) and more than 2000 (black rectangles) echinoderm larvae. Patches have been numbered for the purpose of Table IV, page 59.



TEXT-FIG. 4.—Graphs showing the average number of echinoderm larvae per 10-mile sample in each month for three years in two sections of the Leith-Skagerrak route. " West " refers to the section off the Forth, " east " to the section over the Great Fisher Bank.

Bank in the autumn has been found only in 1951 of the seven years of adequate sampling, 1938, 1946–51.

The Identification of Larvae.

The larvae of the following species have been found :

Ophiothrix fragilis (Abildgaard).
Ophiocomina nigra (Abildgaard).
Ophiactis balli (Thompson).
Ophiopholis aculeata (Linn.).
Amphiura Forbes.
Ophiura texturata Lamarck.
Ophiura albida Forbes.
Ophiura robusta Ayres.
Ophiopluteus dubius Mortensen.
Psammechinus miliaris (Gmelin).
Echinus acutus Lamarck.
Strongylocentrotus dröbachiensis (O. Fr. Müller).
Echinocyamus pusillus (O. Fr. Müller).
Spatangus purpureus O. Fr. Müller.
Echinocardium cordatum (Pennant).
Echinocardium flavescens (O. Fr. Müller).

On the whole, these larvae have been adequately described ; the literature concerning nearly all the species has been listed by Thorson (1946). The main fault with the literature lies in the fact that usually only a single stage of a species has been described, generally the latest. For many species, those in which the larva changes considerably during growth, several stages ought to be described before the description is regarded as complete. As an example, the diagnostic character for the larva of *Ophiopholis aculeata* was given as the presence of two median rods (Mortensen, 1927). The majority of larvae of this species observed in Recorder material possessed no median rods, these being present only in the older larvae. However, this particular species has been fully described more recently by Olsen (1943).

Whilst the larva of *Amphiura filiformis* (O. Fr. Müller) has been described (Mortensen, 1931), the larva of *A. chiajei* Forbes is still unknown. The experience of Thorson (1946, p. 350) seemed to show that the larvae of the two species closely resemble each other. The Amphiura larvae taken by the Recorder from many parts of the North Sea, and from various times of the year, have also been looked at closely, but no way of separating the larvae of the two species has been found.

Chadwick (1914) referred to the presence of central channels in the skeletal rods of some larvae of *Ophiura albida*. It is possible that these result from poor preservation and may indicate that the material in the core of the processes differs from that on the outside.

Thorson (1946) gives good reason for accepting *Ophiopluteus compressus* as the larva of *Ophiura robusta*.

The larva tentatively assigned to *Ophiura affinis* Lütken has a very simple form (Mortensen, 1927). It is probable that if such larvae have been taken by the Recorder they were unrecognized or unrecognizable as echinoderm larvae. *O.*

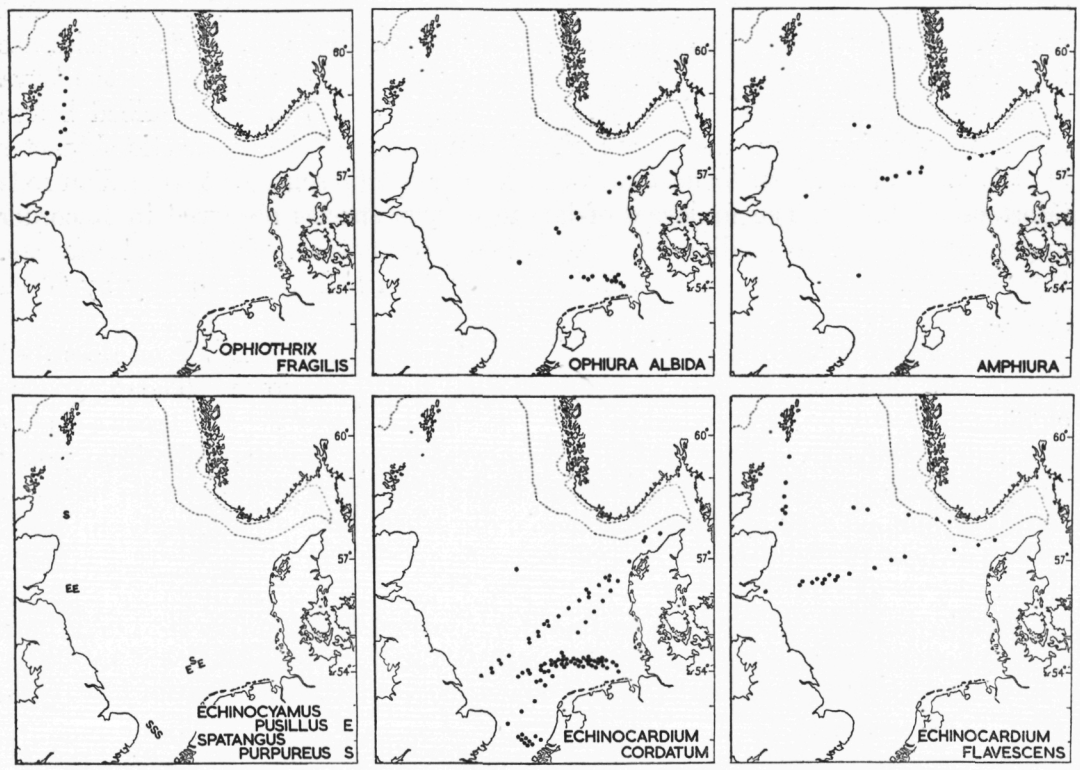
affinis larvae would be expected to be fairly common, but nevertheless no echinoderm larvae have yet been seen in the Recorder material which cannot be assigned to some other species. This could be taken as very indirect evidence that *O. affinis* larvae do not have a well-developed ophiopluteus form.

The characters used for the identification of the larvae of *Spatangus purpureus*, *Echinocardium cordatum* and *E. flavescens* have recently been described (Rees, 1953).

Distribution of the Species.

The approximate quantitative distributions of the larvae of various species are shown in Plates XI and XII. In most cases the month of occurrence is indicated by the use of circular, square or triangular symbols.

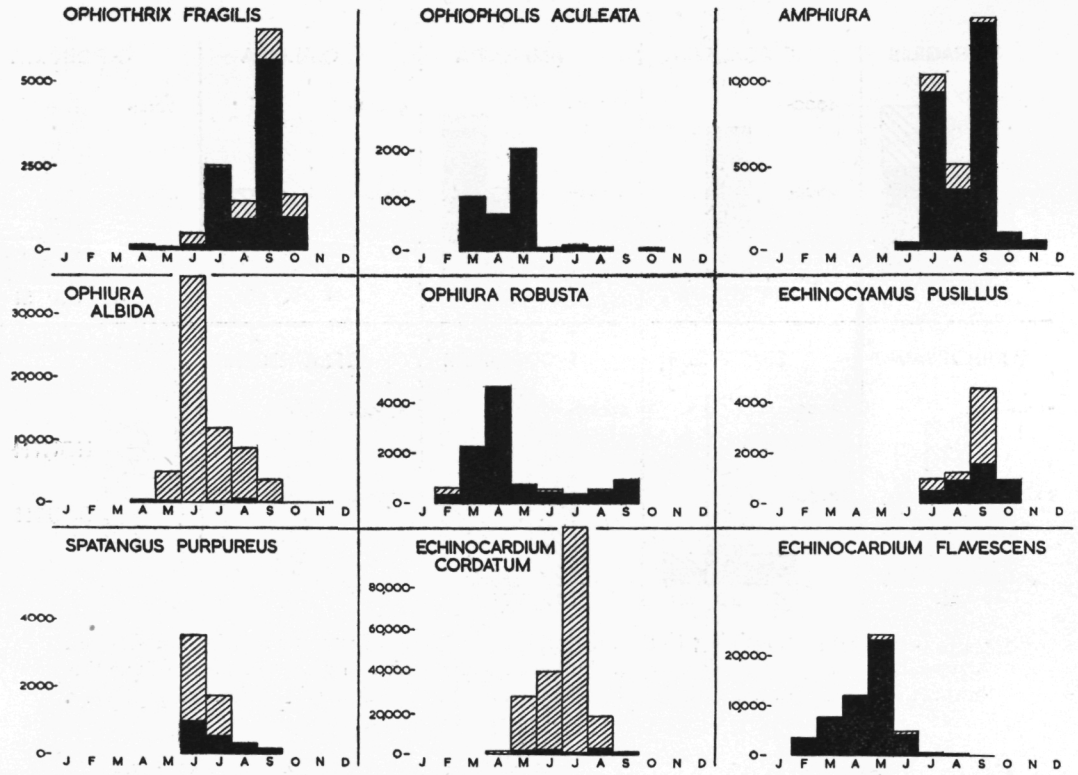
It was explained above that only samples containing more than 480 larvae in the 1949 and 1950 material, and more than 160 larvae in the 1951 material, were re-examined for species. The reduction in the lower limit in the 1951 material introduces a difference into the charts of distribution. If every sample had been re-examined, as in the case of the lamellibranchs, the number of small white and



Text-fig. 5.—Charts showing the distribution of all samples taken in 1949, 1950 and 1951 which contained more than 500 specimens of various species.

small black symbols (see Scale Key in Plate XI) would have greatly increased in the 1949 and 1950 charts, but there would have been no increase in the large white and higher symbols. In the 1951 charts the number of small white symbols would have increased, but the small black and higher symbols would not have increased.

Text-fig. 5 gives a simple overall picture of the distribution of various species. Dots show the positions of all samples which contained more than 500 larvae of the species illustrated.

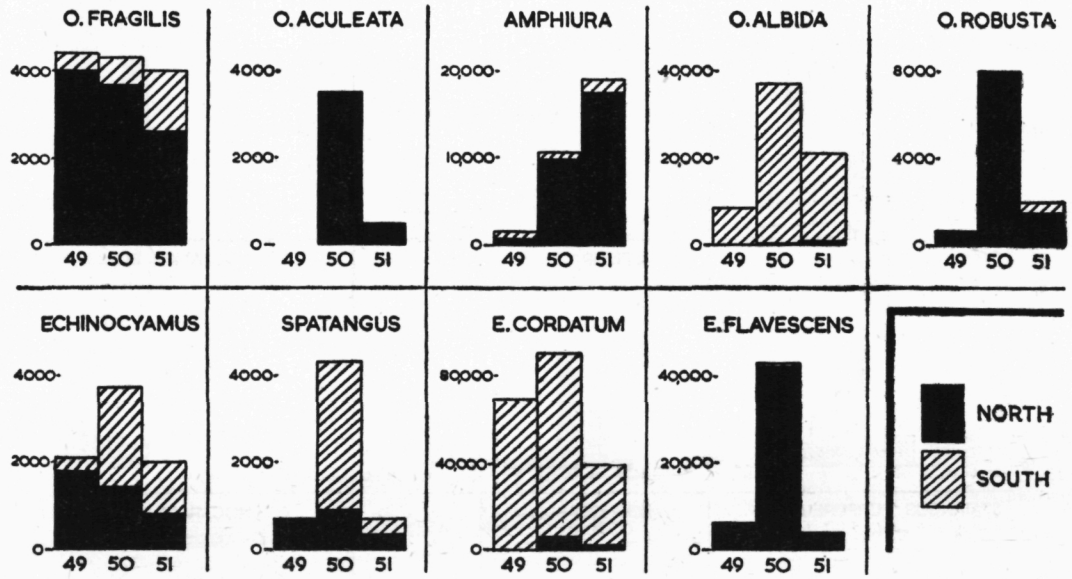


TEXT-FIG. 6.—Histograms giving the total number of larvae of various species obtained in each month, 1949 to 1951 combined, over the entire North Sea. The numbers obtained north and south of the line Newcastle to the Skaw are distinguished by the solid and hatched portions respectively.

The histograms in Text-fig. 6 show the estimated number of larvae of various species obtained in each month, 1949 to 1951 combined. The black portion shows the number north of the line Newcastle to the Skaw, and the hatched portion the number south of this line.

Text-fig. 7 shows the estimated total number of larvae of the species, included in Text-fig. 6, which have been obtained in each year, north and south of the Newcastle-Skaw line. The values for 1949 are affected, in comparison with those for

1950 and 1951, by some differences in the taking of records. There were no Leith-Skagerrak records in April and May, 1949, so that the numbers of the northern forms which thrive in the spring (*Echinocardium flavescens, Ophiura robusta, Ophiopholis aculeata*) are probably too low in comparison. Furthermore, the London-Copenhagen (G) line did not sample into the Heligoland Bight in 1949, whereas it did so in 1950 and 1951. In consequence, the larvae which occur in immense numbers in the Bight (*E. cordatum, Ophiura albida*) are probably too low in number in 1949 compared with the two following years.



TEXT-FIG. 7.—Histograms giving the total number of larvae of various species obtained in each year over the entire North Sea. The numbers obtained north and south of the line Newcastle to the Skaw are distinguished by the solid and hatched portions respectively.

Comment on the species will be restricted to features not immediately apparent from the distributions illustrated:

Ophiocomina nigra.—Only a single specimen was seen, 30 miles off the Forth in October, 1951.

Ophiactis balli.—Larvae were found from July to September, with most observations in September.

Amphiura.—Very few larvae were obtained after September (Text-fig. 6). Mortensen (1920) found, at Kristineberg, that *A. chiajei* began to breed about the middle of September. If the breeding time in the North Sea agrees with this, it would appear that the very great majority of Amphiura larvae obtained were those of *A. filiformis.*

This is the only larva which was more common in 1951 than in the two previous years (Text-fig. 7). It was responsible for the considerable population of total

larvae on the Leith-Skagerrak line in September. This was an unusual occurrence for no comparable concentration occurred at this time during the earlier years, 1938, 1946–1950.

Ophiura texturata.—Larvae were observed in thirteen samples only, from May to September, with no clear indication of the season of maximal abundance.

Ophiura albida.—There is considerable resemblance between the distribution of these larvae and those of *E. cordatum* (Text-fig. 5), but *O. albida* larvae occur in greatest number rather earlier, in June.

Ophiura robusta.—The larvae of this species have been found in the southern North Sea (Plate XI) although it is said that *O. robusta* is distributed on the east British coast only from the Shetlands to Durham (Mortensen, 1927).

Ophiopluteus dubius.—Larvae were observed in two samples over the Norwegian Channel, south-west of Norway, in March, 1950.

Psammechinus miliaris.—Larvae were obtained from June to October, but were always scarce.

Echinus acutus.—Larvae were observed only in March and April.

Strongylocentrotus dröbachiensis.—Larvae were recorded only in March and May.

Discussion.

Marshall (1948, Text-Fig. 7) charted the population densities of bottom-living echinoderms as determined in the surveys of Davis (1923, 1925) and Stephen (1934). This chart may be further filled by also using Petersen's (1914) results for the region off the Danish coast in the same way as was done for bottom-living lamellibranchs (cf. Rees, 1951, p. 111) : 0 in L13, 140 in L11, 7 in M14, 36 in M13, 140 in M12, 110 in M11, 5 in N15, 67 in N13, 25 in N12, 95 in O13.

It was noted that the major concentrations of lamellibranch larvae were poorly correlated with the distribution of adults as found in the bottom surveys (Rees, 1951, p. 120). In Text-fig. 2, dots have been inserted to indicate the adult echinoderm population as given in Text-fig. 7 of Marshall (1948), each dot representing five individuals per square metre per international square. Here again a poor association between adults and larvae is shown. In particular, the adult population density in the Heligoland Bight did not reflect the intense larval concentrations which have been found here.

There is a marked difference between the composition of the larval populations in the northern half and in the southern half of the North Sea, Newcastle to the Skaw being taken as the arbitrary boundary. This difference is brought out in Table II which gives the estimated total number (to the nearest 100) of larvae of the dominant species obtained during 1949 to 1951, and the percentage that each is of the total. The species are arranged in order of abundance over the entire North Sea.

In the north *Echinocardium flavescens* and Amphiura were the dominant larvae. Over a longer period of years it is likely that the percentage of Amphiura

TABLE II.—*Giving the number of Hundreds of Larvae, and the Percentages, of the Dominant Species obtained during* 1949 *to* 1951.

	North Sea.		Northern North Sea.		Southern North Sea.	
	Hundreds.	%.	Hundreds.	%.	Hundreds.	%.
Echinocardium cordatum	198	51	8	7	190	71
Ophiura albida	65	17	1	+	64	24
Echinocardium flavescens	52	13	51	43	1	+
Amphiura	31	8	28	24	3	1
Ophiothrix fragilis	13	3	10	9	3	+
Ophiura robusta	10	3	10	9	+	+
Echinocyamus pusillus	8	2	4	3	4	1
Spatangus purpureus	6	1	2	1	4	1
Ophiopholis aculeata	4	1	4	3	0	0

would be lower; the abundance of total echinoderm larvae, of which the great majority were Amphiura, on the Leith-Skagerrak line in September, 1951, was an unusual feature in comparison with the seven earlier years. It is also possible that many more *E. flavescens* larvae would have been obtained if the Leith-Skagerrak records of April and May, 1949, had been taken. In the south *Echinocardium cordatum* predominated by far, and *Ophiura albida* was the only other species which occurred in abundance.

A rough idea of the composition of the echinoderm bottom fauna of the southern North Sea can be obtained by summing the number of specimens of each species obtained by Davis (1925, Appendix 1) and expressing it as the percentage of the total echinoderms obtained. Similarly, the results of Stephen (1934, Table II) can be used for the northern North Sea. Table III compares the percentages of species of adults in bottom fauna surveys and of larvae obtained in the Recorder survey during 1949 to 1951.

TABLE III.—*Comparing the Percentage Composition of the Bottom Fauna and that of the Larvae obtained during* 1949 *to* 1951.

	Northern North Sea.		Southern North Sea.	
	Adults.	Larvae.	Adults.	Larvae.
Echinocardium cordatum	2	7	63	71
E. flavescens	24	43	4	+
Echinocyamus pusillus	9	3	2	1
Ophiura albida	+	+	4	24
Ophiura affinis	28	0	+	0
Amphiura	28	24	25	1
Echinus acutus	7	+	0	0

In the north, the percentage of *Ophiura affinis* differed greatly between adults and larvae. The possibility was raised above (p. 53) that the presumed larva of this species is so simple that it is unrecognized or unrecognizable in the damaged

Recorder material. During the grab surveys only material from soft bottoms was taken and species confined to hard bottoms were not obtained; this fact probably explains the fairly high percentages of larvae of *Ophiothrix fragilis* and *Ophiura robusta* in the north (Table II), without any corresponding adults in the grab survey. In the south, there was an interchange of the percentage values between *Ophiura albida* and Amphiura.

The main concentrations found in 1949 to 1951 have been numbered in Text-figs. 1 and 3. The percentage composition of the larval population in each numbered patch is given in Table IV, together with the month in which it was found.

TABLE IV.—*Giving the Percentage Composition of Patches in* 1949 *to* 1951. *The patches are shown and numbered in Text-figs.* 1 *and* 3.

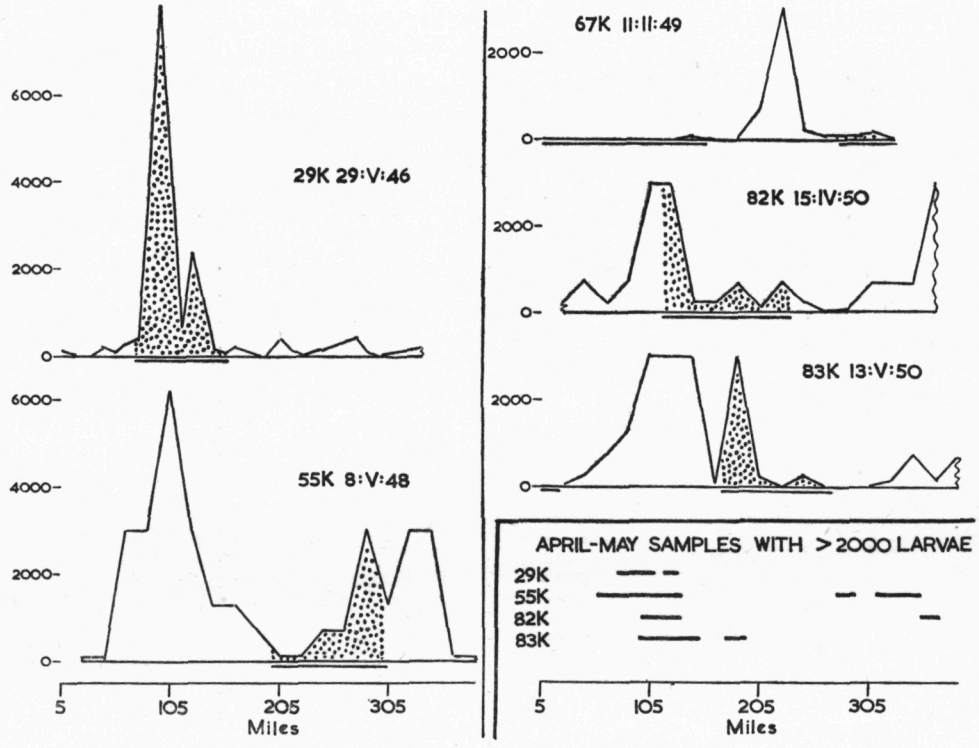
Patch.	Month.	*E. cordatum.*	*E. flavescens.*	*Spatangus.*	*O. albida.*	*O. robusta.*	Amphiura.
1949.							
1	II	—	93	—	—	7	—
2	V	76	10	—	14	—	—
3	V	76	7	—	17	—	—
4	V	99	—	.	—	—	—
5	VI	100	—	—	—	—	—
6*	VII	83	—	—	—	3	—
7	VII	100	—	—	—	—	—
8	VII	100	—	—	—	—	—
9	VII	98	—	—	2	—	—
1950.							
1*	IV	—	70	—	—	17	—
2	IV	—	96	—	—	4	—
3	V	—	100	—	—	—	—
4	V	—	96	—	—	4	—
5*	V	3	65	—	—	6	—
6	V	5	95	—	—	—	—
7	V	93	7	—	—	—	—
8	VI	73	—	22	5	+	—
9	VI	93	—	—	—	—	—
10	VI	27	—	—	73	—	—
11	VII	84	—	7	7	—	—
12	VII	99	—	1	—	—	+
13	VII	98	—	+	2	—	+
14	VII	—	—	2	—	2	94
1951.							
1	VI	53	—	—	47	—	—
2	VI	95	—	—	5	—	—
3	VII	50	—	—	50	—	—
4	IX	—	—	—	—	—	100
5	IX	—	—	—	—	—	100

* Also in 1949, 6, *Echinocyamus* 14%; 1950, 1, *O. aculeata* 10%; 5, *O. aculeata* 20%.

The table shows clearly the predominance in the northern half of the North Sea, of *E. flavescens* in the spring (Feb., April-May) and of Amphiura later in the

year (July, September). In the south *E. cordatum* was, of course, predominant, but *O. albida* was more abundant in one or two of the early patches in the Heligoland Bight.

It can be said that *E. flavescens* is by far the dominant species in any major concentration of larvae in the northern half of the North Sea before the end of May. It is, in fact, permissible to regard the numbers of total echinoderm larvae as virtually the numbers of *E. flavescens* during the first five months of the year.



TEXT-FIG. 8.—Graphs giving the number of echinoderm larvae in each 10-mile sample of all Leith-Skagerrak records, taken from January to May, which had in any sample over 2000 larvae. Sections of records taken at night are marked by a double base line and portions of graphs relating to larvae taken at night dotted.[1] At the bottom right, lines mark the position of all April-May samples with over 2000 larvae.

Text-fig. 8 shows the distribution of larvae along all Leith-Skagerrak records, taken before the end of May, which contained more than 2000 larvae in any sample. Of the years under review, April-May records were obtained only in 1946, 1948. 1950 and 1951, and a major concentration was found in May in all except 1951. Inset in Text-fig. 8 are shown the positions where samples containing over 2000

[1] The distinction between samples taken by night and by day which is made in Text-figs. 8–10 is not considered to be relevant to this report. It is anticipated, however, that this information will be required on a future occasion.

larvae have been found on April-May records. There is clearly a regularity here which may be illustrated by the fact that, in all four records, the sample taken 105 miles from the Forth contained a great number of larvae, in 1946 and 1948 the greatest number. In February, 1949, on the other hand, the concentration was found over the Great Fisher Bank.

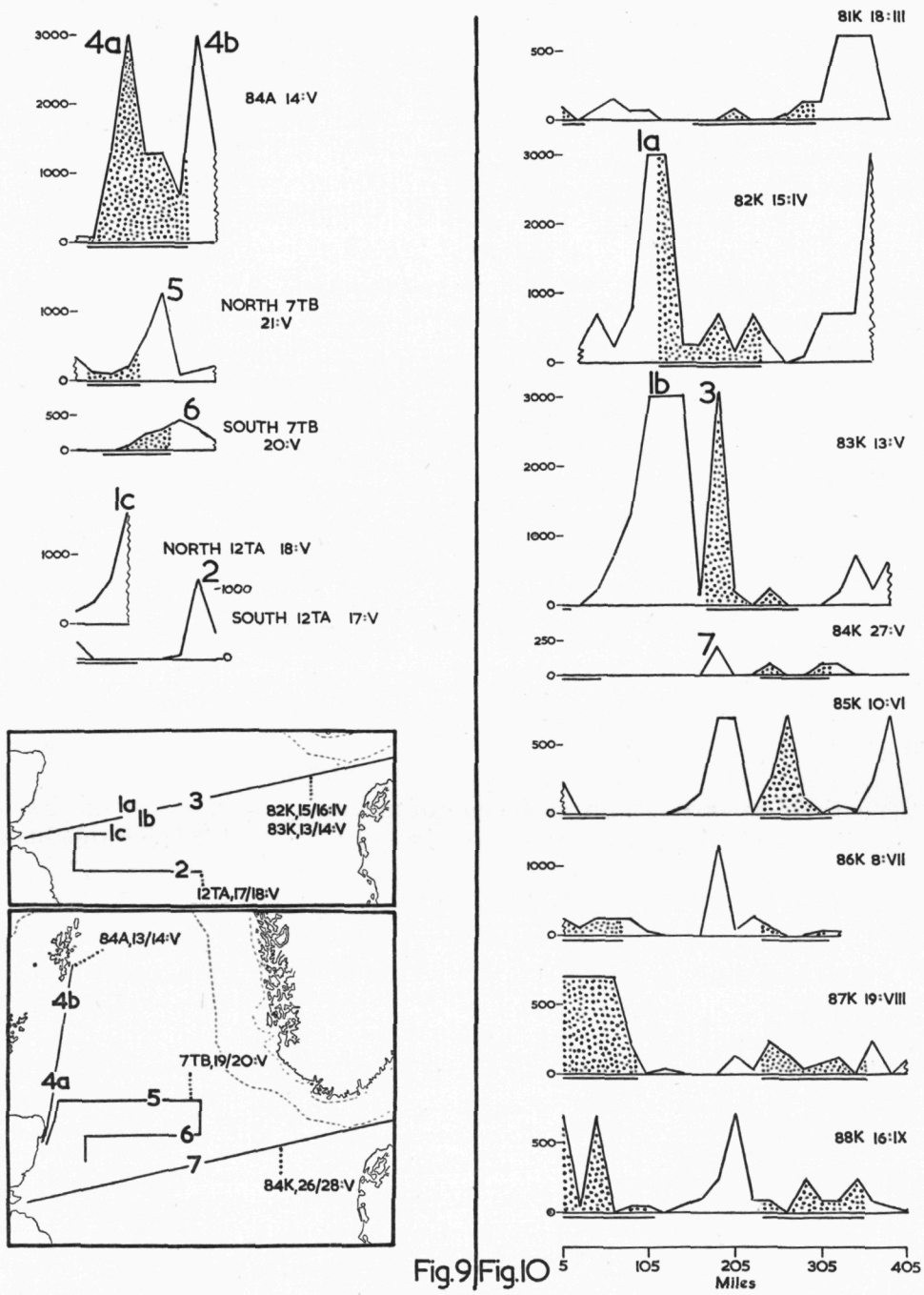
Text-fig. 8 shows that these concentrations were not only heavy but also narrow along the west-east axis. A detailed consideration of the distribution of the larvae of *Mytilus edulis* in May, 1950, when extra records were taken, led to the conclusion that similar narrow patches of *Mytilus* larvae on the Leith-Skagerrak records were due to sampling across elongated, narrow distributions. These were called band distributions (Rees, 1954). The data concerning *E. flavescens* have been similarly treated. The distributions of *E. flavescens* on the Aberdeen-Lerwick (A) record, and on the north and south legs of the special records, 7 TB and 12 TA, are shown in Text-fig. 9 (see charts in Text-fig. 9 for courses and dates). The distributions of total echinoderm larvae on the Leith-Skagerrak records from March to September are shown in Text-fig. 10. Various peaks in abundance have been numbered in Text-figs. 9 and 10 and the numbers transferred to two charts in Text-fig. 9.

The patches numbered 1*a*, 1*b* and 1*c* occurred in a closely confined area ; the 12 TA record was not long enough to sample right through concentration 1*c*. The great majority of the larvae in patch 1*a* were old, with well-developed postero-lateral arms. Whilst the larvae in patches 1*b* and 1*c* were distinctly more developed, it is very unlikely that the population of larvae in patch 1*a* was still planktonic 28 and 33 days later to be re-sampled as patches 1*b* and 1*c*. MacBride (1914) found that the entire development, up to the end of metamorphosis, of the allied species *Echinocardium cordatum*, took only four weeks in culture and it is improbable that the rate of development of *E. flavescens* larvae was so much slower that 1*a* and 1*b* were samples of the same population. It seems, then, that there was a recruitment and loss of larvae in the area where patches 1 were found. This change over of the larvae fits in well with the view that patches 1 and 2 were transections of a single band distribution, as in the examples of *Mytilus* larvae (Rees, 1954) and other organisms to be dealt with in a later ' Bulletin.'

The sharp peak of numbers comprising patch 3 (83K) occurred in the same sample which contained a very great number of *Mytilus* larvae. This was the most striking concentration of *Mytilus* larvae obtained during this period and is that numbered 3 in Text-fig. 10 of Rees (1954).

The patches 4 (*a* or *b*), 5 and 6 may, perhaps, be sections of a single band distribution. Numbers decreased greatly from north-west to south-east, and it is possible that larvae had become too scarce for this band to be shown further south, on the Leith-Skagerrak route (84K). It is uncertain whether the very small patch 7 (84K) should be regarded as an extension of patches 5 and 6 or the surviving residue of the earlier concentration here (3).

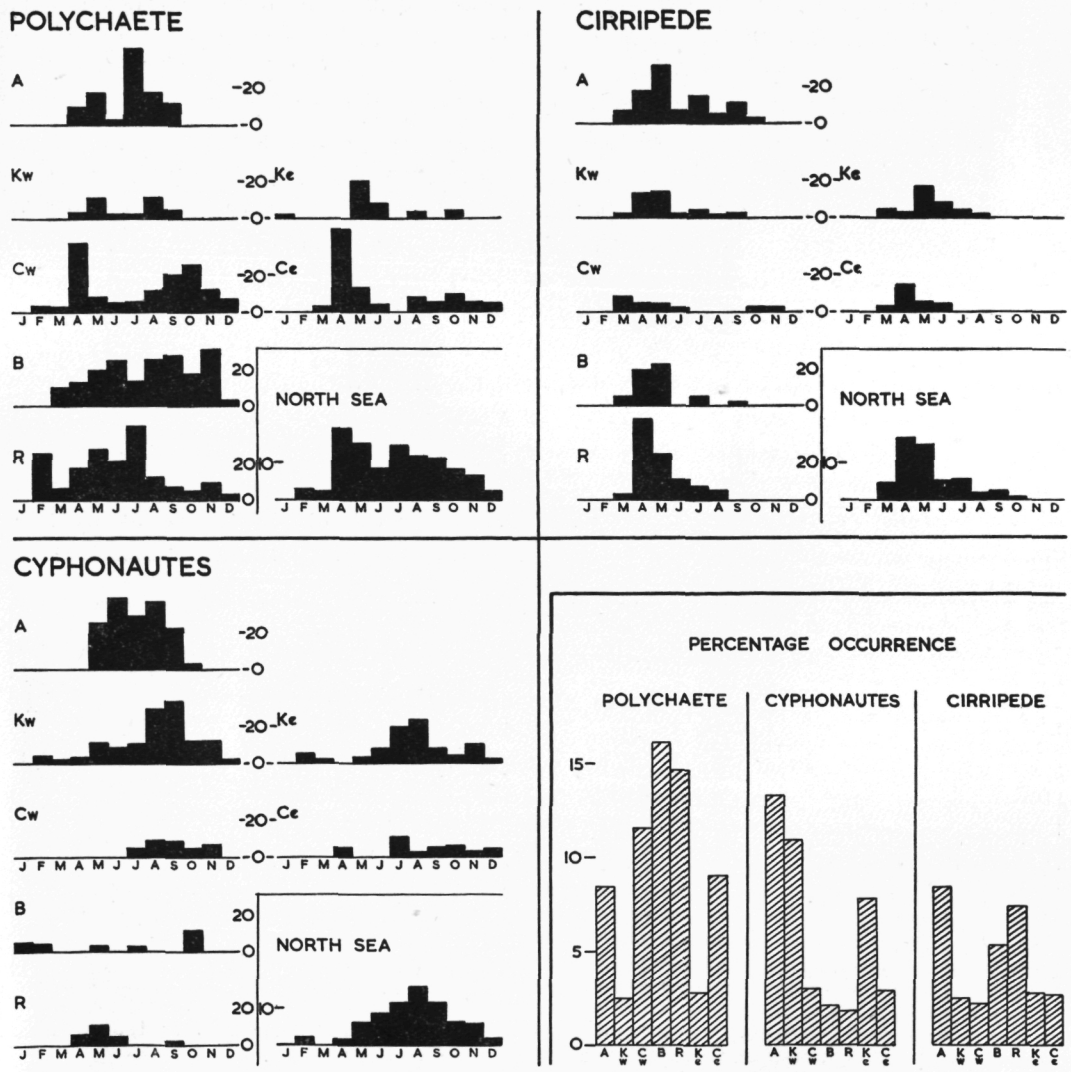
The distributions of larvae of *E. flavescens* and *Mytilus edulis* only partially



TEXT-FIGS. 9 and 10.—The charts in Text-fig. 9 show the routes and dates of records taken in May, 1950, the graphs show the number of echinoderm larvae in each 10-mile sample along some of these records. The graphs in Text-fig. 10 show the number of larvae in each sample of the Leith-Skagerrak records from March to September, 1950. Appropriate peaks in the graphs in Text-figs. 9 and 10 have been numbered and the location of these peaks shown on the charts in Text-fig. 9. In all graphs the sections taken at night are shown by a double base line and the dotted portions of the graphs. See footnote p. 60.

ments have been made to avoid bias due to the taking of more than one record along a route in a month.

The histograms in Text-fig. 12 show the percentage of the samples which contained these larvae in each month, 1947 to 1951 combined, along the main Recorder routes, the Leith-Skagerrak and Hull-Copenhagen lines being divided into western and eastern halves. The percentage for the entire North Sea is also



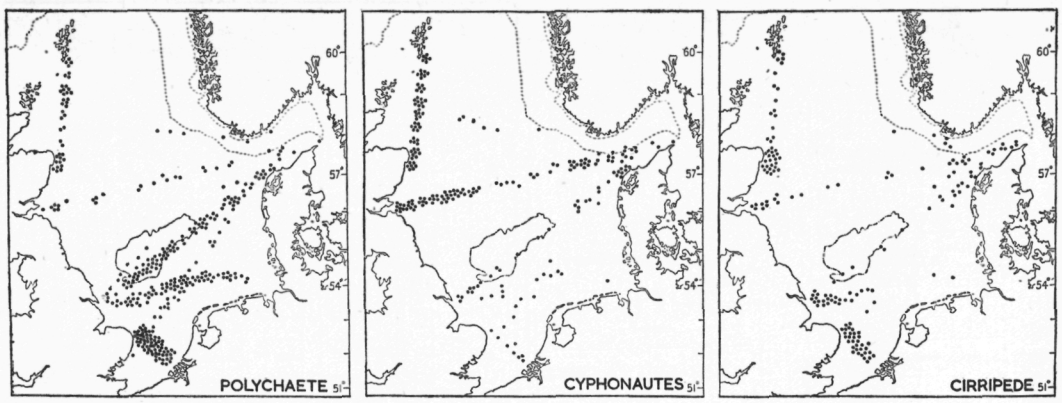
TEXT-FIG. 12.—Histograms giving the percentage of samples in each month, 1947 to 1951 combined, in which polychaete, cyphonautes and cirripede larvae were found along the Aberdeen-Lerwick (A) route, the western (Kw) and eastern (Ke) parts of the Leith-Skagerrak route, the western (Cw) and eastern (Ce) parts of the Hull-Copenhagen route the Hull-Bremen (B) route and Hull-Rotterdam (R) route. At the bottom right, the number of samples which contained these larvae along the various routes are expressed as a percentage of the total number of samples taken.

coincided over this period ; the only concentrations of *E. flavescens* which coincided with concentrations of *Mytilus* larvae are those numbered 3 and 6 in Text-figs. 9 and 10. In this connection, two points may be noted. The first is that the seasonal occurrence of *E. flavescens* larvae was earlier than of *Mytilus* larvae. On the earliest of the records, 82K, April 15th, *E. flavescens* larvae were abundant whilst Mytilus larvae were as yet rare, and very few *E. flavescens* larvae were found at the end of May when *Mytilus* larvae were still abundant (cf. Text-fig. 10 with Text-fig. 10 of Rees, 1954). The second is that the *E. flavescens* and *Mytilus* larvae concerned may have originated from different places. *Mytilus edulis* is essentially a coastal form whereas *E. flavescens* normally lives in deeper water.

A tentative representation of the distribution of *Mytilus* larvae in the spring of 1950 gave successive bands as occurring further towards the east (Rees, 1954, p. 41). Text-fig. 10 shows that there was a similar apparent movement of echinoderm patches on the Leith-Skagerrak line from April to June. A comparison between the graphs for 83K and 85K illustrates this feature very well. As in the case of *Mytilus*, a switch of the main concentration from the centre of the route in July to the Forth side in August was also shown It may be noted that *E. flavescens* was not a dominant species in the concentrations from June onwards.

Distribution of Other Larvae.

Polychaete, cyphonautes, cirripede and actinotrocha larvae have rarely been found in appreciable numbers in Recorder samples. Almost the whole of the



Text-fig. 11.—Charts showing the distribution of all samples taken during 1947 to 1951 in which polychaete, cyphonautes and cirripede larvae were found to be present.

post-war information available consists of records of only the presence, with no statement of numbers, of these larvae in the samples.

Text-fig. 11 illustrates the distribution of all samples taken in 1947 to 1951 in which the larvae of the first three groups have been recorded. Some minor adjust-

given. Also in Text-fig. 12 (bottom right) are histograms giving the overall percentage of samples containing larvae along each route.

Polychaete larvae.—These larvae were most frequently found in the southern half of the North Sea and rarely in the central North Sea (Text-figs. 11 and 12). Larvae were found most frequently in April along the southern edge of the Dogger Bank (C west) and towards the Danish coast (C east). There is an indication of a north to south succession in high frequency starting in July in the north-west (A), in August off the Forth (K west), in October off the Humber (C west) and in November in the southern North Sea (B).

One major patch of larvae has been recorded, off the Aberdeenshire coast in July, 1946, when two adjacent samples contained more than 2000 larvae.

Cyphonautes larvae.—Marshall (1948) has given the distribution of these larvae during 1938 and 1939. He pointed out that the north-west was by far the most important productive area, the entrance to the Skagerrak being the only other region where larvae were found in any quantity. This is generally confirmed by the distributions of 1947 to 1951 except that records were relatively frequent off the Forth (Text-figs. 11 and 12). Records off the Forth occurred most frequently in August and September which, related to the monthly frequency in the north-west, suggests that larvae may have been transported southwards in the early stage of the autumn influx. Of the years 1947 to 1951, larvae occurred least frequently off the Forth in August and September in 1947, a year in which the autumn influx was much delayed (Tait, 1949). The greatest frequency in these months was in 1951, at a time when a major concentration of lamellibranch larvae was sampled off the Forth, a concentration which appeared to be related to the autumn influx (Rees, 1954).

Cirripede larvae.—Cirripede larvae were mainly restricted to coastal areas and, in all regions, the greatest frequency occurred early, around April-May (Text-figs. 11 and 12).

The early maxima of larvae in the North Sea correspond with findings in other areas. At Millport the greatest number of cirripede nauplii were obtained in March in each of four years (Pyefinch, 1948, Table VIII) and at Port Erin in March and April over many years (Johnstone, Scott and Chadwick, 1924).

Actinotrocha larvae.—The larvae of Phoronis were found rarely, altogether in less than 40 samples throughout 1946 to 1951. A distinct patch occurred in July, 1946, off the Aberdeenshire coast, more than 1000 larvae being obtained in the same samples, mentioned above, which contained the large numbers of polychaete larvae. Elsewhere, larvae were obtained off the Forth and along the southern edge of the Dogger Bank, mostly in August.

SUMMARY.

1. The main concentrations of echinoderm larvae occurred in the eastern part of the southern North Sea, particularly within the Heligoland Bight.

2. The distribution of larvae as a whole was poorly correlated with that of the adults as found in earlier bottom surveys.

3. The greatest numbers of larvae in the southern North Sea occurred in June-July. Along the Leith-Skagerrak route the greatest numbers occurred, as a rule, in April-May, with secondary maxima in August-September.

4. The approximate quantitative distributions of larvae of various species during 1949–51 are presented in charts (Plates XI and XII), the seasonal occurrence in Text-fig. 6 and the comparative numbers from year to year in Text-fig. 7.

5. Larvae of *Echinocardium flavescens* and Amphiura were dominant in the northern half of the North Sea, and larvae of *Echinocardium cordatum* and *Ophiura albida* in the southern half.

6. There was a fairly good agreement between the specific composition of the larval populations and the adult populations taken in the early bottom surveys, except that *Ophiura albida* was the second most abundant echinoderm in the larval population of the south, whereas Amphiura occupied this place in the bottom fauna.

7. *Echinocardium flavescens* was by far the dominant species in any major concentration of larvae in the northern North Sea in the first five months of the year. The profiles of concentrations found in April-May along the Leith-Skagerrak route show marked uniformity.

8. The distributions of *E. flavescens* larvae in May, 1950, have been presented. The distributions may be interpreted as being narrow and elongated, or band distributions, as in the case of larvae of *Mytilus edulis* (Rees, 1954). *E. flavescens* larvae appeared in large numbers distinctly earlier than *Mytilus* larvae.

9. There was an apparent west to east movement of concentrations of echinoderm larvae along the Leith-Skagerrak route from March to June.

10. The larvae of Polychaeta, Cirripedia, Bryozoa and Phoronidea have rarely been found in appreciable numbers in Recorder samples. The distributions of these larvae are presented only very briefly.

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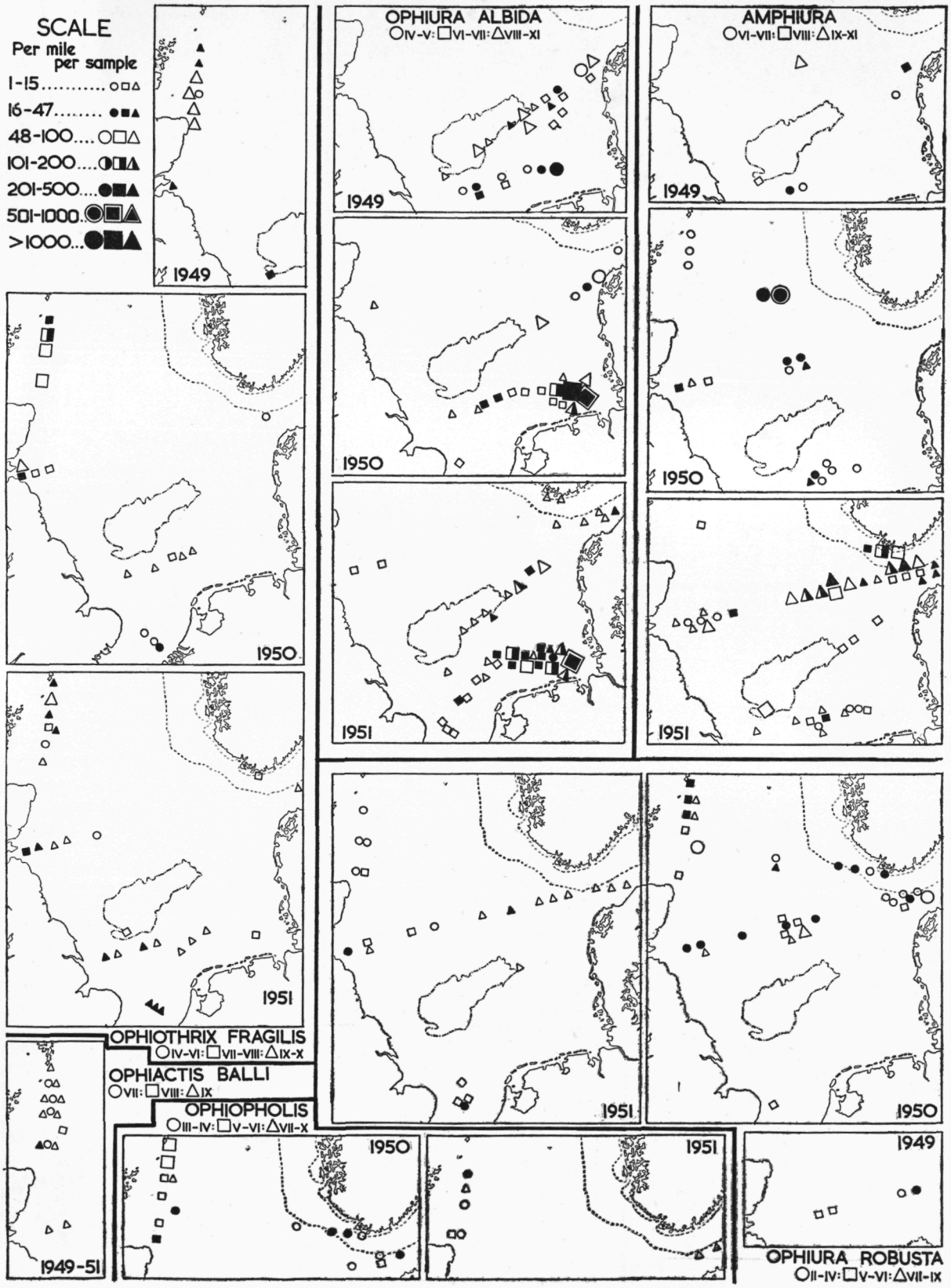
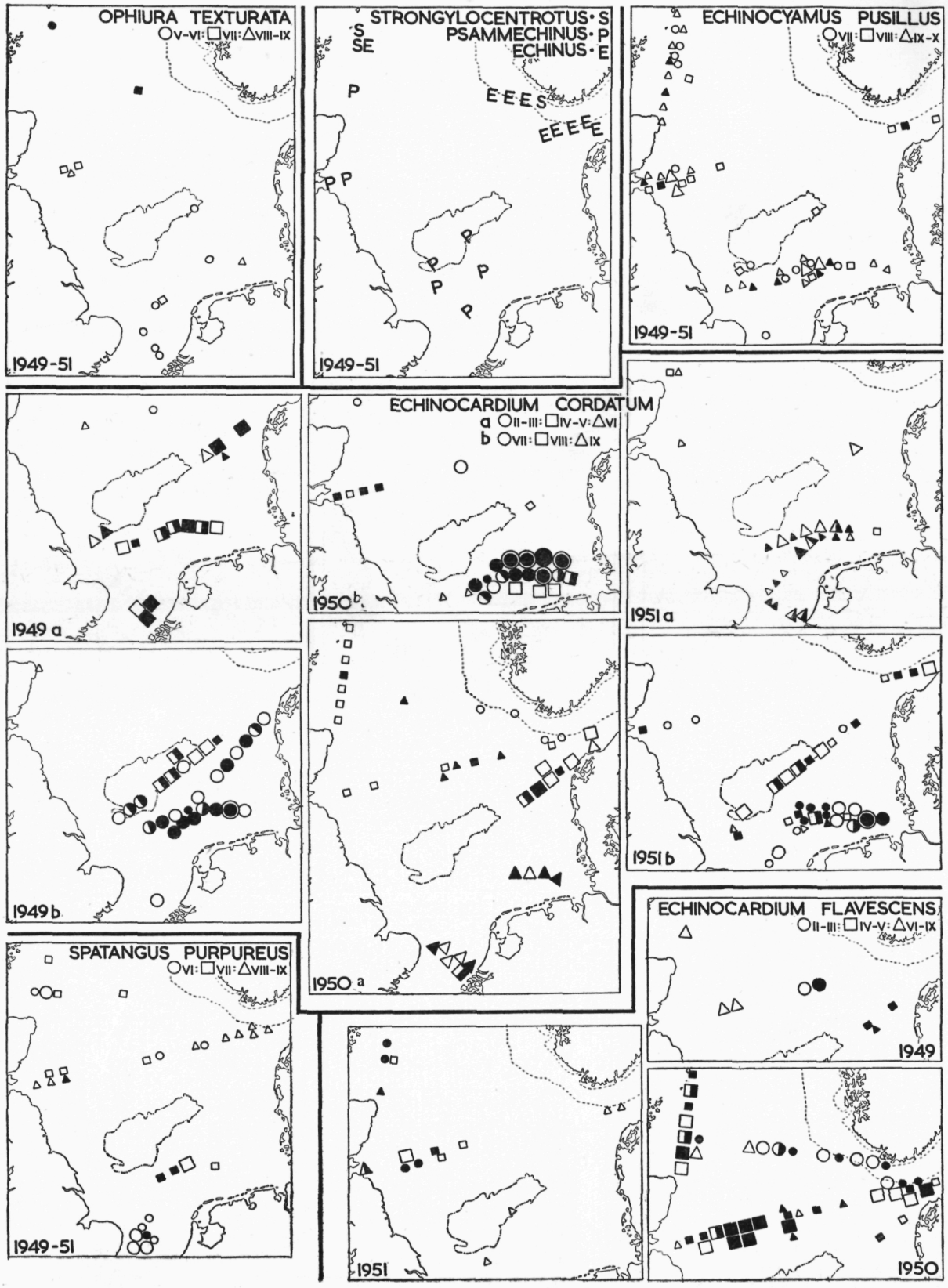
EXPLANATION OF PLATES XI AND XII.

Charts showing the distributions of species of echinoderm larvae in 1949 to 1951. In some cases the distributions in all three years are combined into single charts, in others the years are charted separately. The months of occurrence are indicated by the use of circular, square and triangular symbols, as shown near each specific name. The scale of symbols used to give broad indications of numbers is given on Plate XI.


SCALE
Per mile per sample
1-15.....
16-47.....
48-100....
101-200....
201-500....
501-1000.
>1000...
1949
OPHIURA ALBIDA
IV-V: VI-VII: VIII-XI
1949
1950
1951
AMPHIURA
VI-VII: VIII: IX-XI
1949
1950
1951
1950
1951
OPHIOTHRIX FRAGILIS
IV-VI: VII-VIII: IX-X
OPHIACTIS BALLI
VII: VIII: IX
OPHIOPHOLIS
III-IV: V-VI: VII-X
1949-51
1950
1951
1949
OPHIURA ROBUSTA
II-IV: V-VI: VII-IX


OPHIURA TEXTURATA
○v-vi:□vii:△viii-ix
1949-51
STRONGYLOCENTROTUS·S
PSAMMECHINUS·P
ECHINUS·E
S
SE
P
E E E S
E E E E
P P
P P
P P
P
1949-51
ECHINOCYAMUS PUSILLUS
○vii:□viii:△ix-x
1949-51
1949 a
ECHINOCARDIUM CORDATUM
a ○ii-iii:□iv-v:△vi
b ○vii:□viii:△ix
1950 b
1951 a
1949 b
1950 a
1951 b
SPATANGUS PURPUREUS
○vi:□vii:△viii-ix
1949-51
ECHINOCARDIUM FLAVESCENS
○ii-iii:□iv-v:△vi-ix
1949
1951
1950