

113673

CONTINUOUS PLANKTON RECORDS : THE DISTRIBUTION OF LAMELLIBRANCH LARVAE IN THE NORTH SEA, 1950-51

BY

C. B. REES, D.Sc.

CONTENTS.

	PAGE
INTRODUCTION	21
DISTRIBUTION OF TOTAL LAMELLIBRANCH LARVAE	22
NOTES ON IDENTIFICATION AND NOMENCLATURE OF LARVAE	25
DISTRIBUTION OF THE SPECIES	27
<i>Seasonal Occurrence</i>	28
<i>Notes on Species</i>	30
DISCUSSION	31
SUMMARY	44
REFERENCES	45

INTRODUCTION.

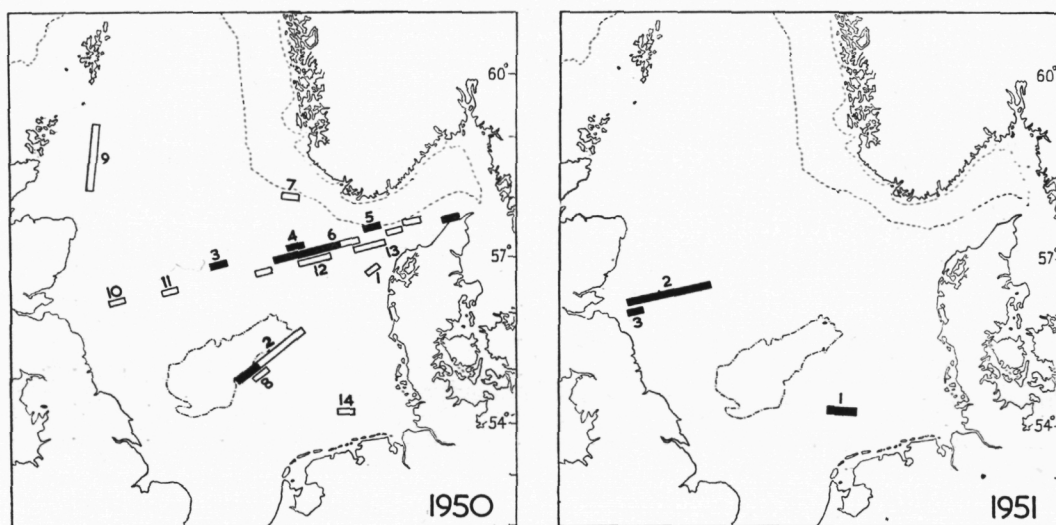
THE distribution of lamellibranch larvae in the North Sea has now been investigated in considerable detail over a period of three years, 1949-51. The distributions found in 1949 have already been presented, although it was fully realized whilst preparing the report that the conditions in that year might have been unusual (Rees, 1951). Many of the identifications of lamellibranch larvae in a previous paper (Rees, 1950) were, however, largely based on the distributions found in 1949 and it was thought that delay in presenting this evidence would be undesirable.

This account of the distributions in 1950 and 1951 is a continuation of the former one and completes the first phase of the investigation. The method of analysis and the derivation of the estimates of numbers have been explained in the first report. From 1952 onwards only major concentrations of larvae will be investigated, a change which will greatly reduce the amount of information acquired. Essentially, only a dozen or so species will be involved in the restricted analysis as against about 50 during 1949-51.

In addition to the Recorder material, the lamellibranch larvae in all Hensen net samples from the North Sea taken in 1950 for the Scottish Home Department, Marine Laboratory, Aberdeen, have been made available to me. It is a pleasure to record my gratitude to the planktologists at Aberdeen for undertaking the tiresome task of extracting the larvae. The contents of these samples will not be fully reported on here but information bearing on specific problems will be used.

DISTRIBUTION OF TOTAL LAMELLIBRANCH LARVAE.

Text-fig. 1 shows, for 1950 and 1951, the distributions of total lamellibranch larvae above the two levels of concentration used in Text-figs. 1 and 2 of the first report (Rees, 1951).

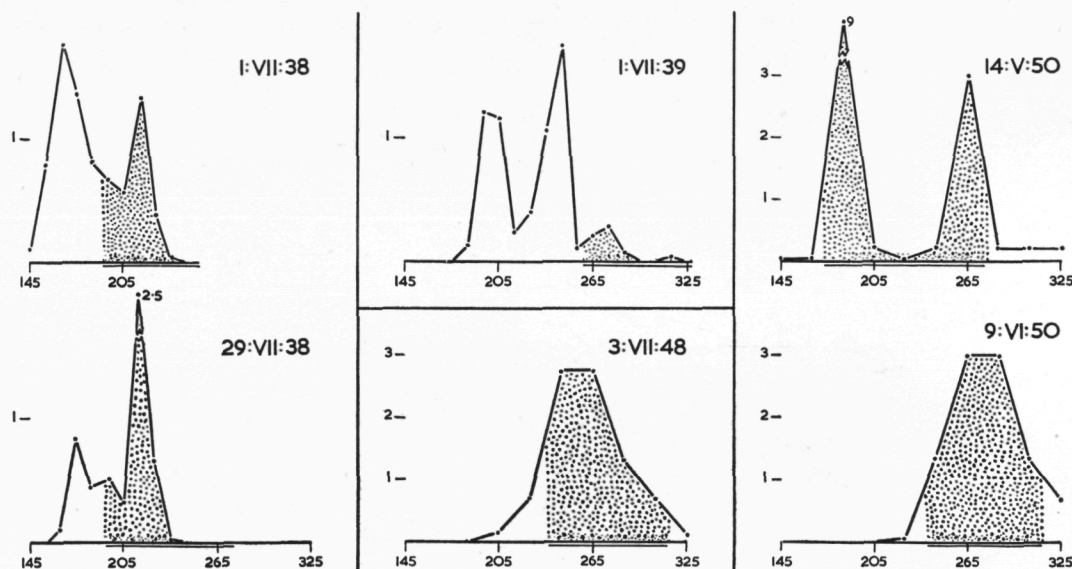


TEXT-FIG. 1.—Charts showing the distribution, in 1950 and 1951, of 10-mile samples with 500–1000 (white rectangles) and more than 1000 (black rectangles) lamellibranch larvae. Patches have been numbered for the purpose of Table III, p. 35.

A patch on the Aberdeen-Lerwick route was found in 1950; such a patch has been found in four years (1938, '39, '47, '50) out of the eight years of Recorder sampling in this area. A concentration off the Forth, with very high numbers of larvae, was found in 1951, and perhaps a minor concentration should be recognized in 1950, comparable with one in 1947. Whilst it can no longer be considered that the patch off the Forth in 1949 was particularly unusual (Rees, 1951, p. 128) it should be noted that the larvae were very much more numerous in 1951 than in 1947 and 1950. We cannot be quite certain about 1949 since the August and September Leith-Skagerrak records were short at the Forth end, but the numbers found on the available samples support the view that the Forth concentration of 1949 was comparable with that of 1951.

A concentration over the Great Fisher Bank was found again in 1950. If we take only the higher level of numbers (over 1000 larvae per sample, equivalent to about 350 per m^3) the years can be classified as (a) Great Fisher Bank patch and no Forth patch recorded: 1938, 1939, 1948, 1950; (b) Forth patch and no Great Fisher Bank patch recorded: 1949 (assumed for Forth patch), 1951; (c) neither patch recorded: 1946, 1947.

It has already been indicated that there is a similarity from year to year in the distributions found within the Great Fisher Bank patch (Rees, 1951, p. 107).

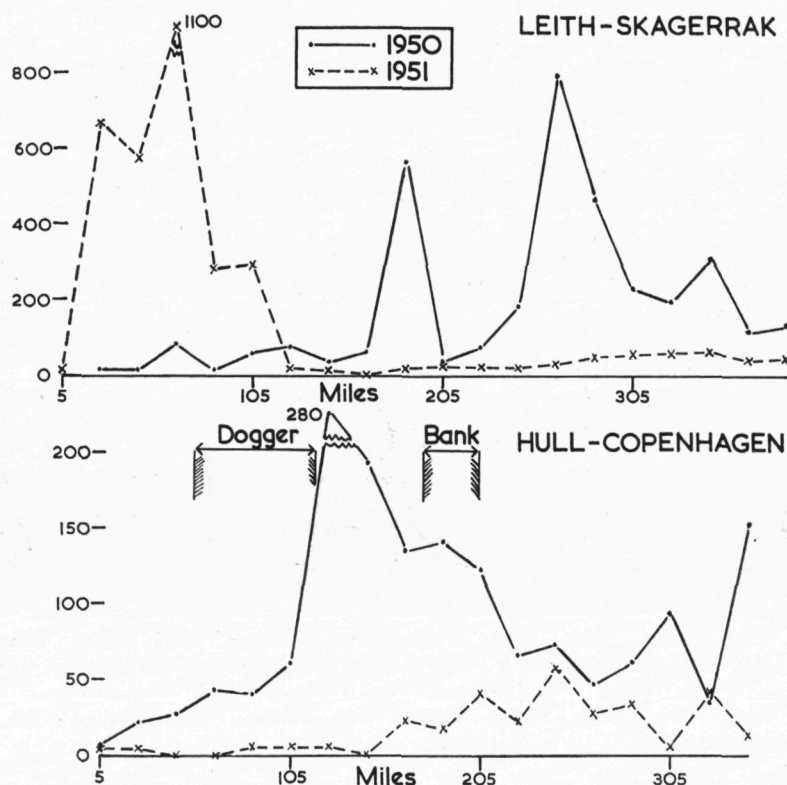


TEXT-FIG. 2.—Graphs giving the number of lamellibranch larvae in each 10-mile sample of a section, 140–330 miles from the Forth, of some of the Leith-Skagerrak records. The vertical scale is in thousands. The parts of the routes sampled between sunset and sunrise are shown by a double base line and the sections of the graphs showing larvae collected at night dotted.¹

The addition of the 1950 results allows more detailed consideration of this point. Text-fig. 2 shows the number of larvae in each 10-mile sample within a section (140–330 miles from the Forth) of each Leith-Skagerrak record that sampled such a concentration. From 1939 onwards there were two positions where peak numbers were found; at a position 190 miles from the Forth and at a position 265 miles away or in one of the two adjacent samples. Two peaks are shown in the 1938 records, one 165–175 miles from the Forth and the other 215 miles away. These two Leith-Skagerrak tows were off the standard route (see Hardy, 1941, plate II)

¹ The distinction between samples taken by night and by day which is made in this and some other text-figures is not considered to be relevant to this report. It is anticipated, however, that this information will be required on a future occasion.

and there is no reason to doubt that the 1938 peaks correspond to the two in 1939 onwards. This occurrence, time after time, of high numbers more or less at the same positions suggests a regular cause. What is particularly noteworthy, apart from the apparent regularity of the pattern, is the sharpness of the peaks. A good illustration is the westerly peak on the record of May 14th, 1950, where the number in one sample exceeded those in the adjoining samples by about 80 and 30 times (Text-fig. 2).



TEXT-FIG. 3.—Graphs giving the average number of lamellibranch larvae per 10-mile sample throughout 1950 and 1951 along the Leith-Skagerrak and Hull-Copenhagen routes. This text-figure corresponds to Text-fig. 3 of Rees (1951).

We shall return to a consideration of this patch later but, meantime, note should be made of the dates. In three years out of four the concentration was found about July 1st. In 1950, however, it was found more than a month earlier, May 14th and June 9th, and it had disappeared from the route by July 7th.

Of the other concentrations in Text-fig. 1, only the patch along the southern edge of the Dogger Bank in 1950 need be mentioned. Attention has been called to a striking consistency in distribution in the recurrence of a narrow patch on the

Leith-Hamburg line in 1938-39 (Rees, 1951, p. 107). The 1950 patch is as near to this earlier one as can be recorded with the routes at present in use.

The average number of larvae per 10-mile sample throughout each of the two years on two Recorder routes is shown in Text-fig. 3. In comparing this with Text-fig. 3 of the first report it should be noted that the vertical scale for the Leith-Skagerrak line has been altered to cope with the much greater numbers obtained in 1950-51. The values for the Hull-Copenhagen route for 1951 are possibly vitiated by the absence of records in September and October; but, if so, it is likely that it is the section between the Dogger Bank and Danish coast which is most affected. Concentrations on the western half of this route have previously been recorded earlier than September.

NOTES ON IDENTIFICATION AND NOMENCLATURE OF LARVAE.

The larvae included in this and the first report were described in an earlier Bulletin (Rees, 1950). Many of these were named specifically, others tentatively, as for example (? *Tellina pygmaea*), and the remainder labelled within a family or superfamily (e.g., Pectinid E). It is now possible to add the descriptions of a few more. The number of illustrations do not really justify the expense of publishing photomicrographs, desirable as this is; instead, line drawings which are tracings of photomicrographs are given. It is also possible to improve and revise some of the labels hitherto adopted. Apart from those items which follow, the same nomenclature has been used in this report as in the earlier descriptive account.

Arcacea.

Glycymeris glycymeris.—A rounder, more symmetrical larva than that described (Rees, 1950) is found occasionally. This is believed to be of the variety *pilosus* (Jeffreys, 1862).

Mytilacea.

MYTILID A.—The widespread distribution of Mytilid A in 1950 and 1951 leaves little doubt that it is the larva of *Modiolus phaseolinus*.

MYTILID F (Text-fig. 4).—The shell is brown and rather convex. The inner edge of the shell is regularly serrated all round except at the hinge and for an arc of about 5° between the dorsal and postero-lateral sides. The fossette for the ligament is deep and central and, in consequence, the intermediate teeth are very small and by no means easy to make out.

MYTILID G (Text-fig. 4).—The concentric lines are fine and close set in shells up to a length of about 320 μ . In larger larvae the outer concentric lines are well-marked and well-separated. A characteristic feature is the presence of irregular external ridges on the shell which disappear in hypochlorite. Several specimens of this species have been found amongst the Aberdeen net samples.

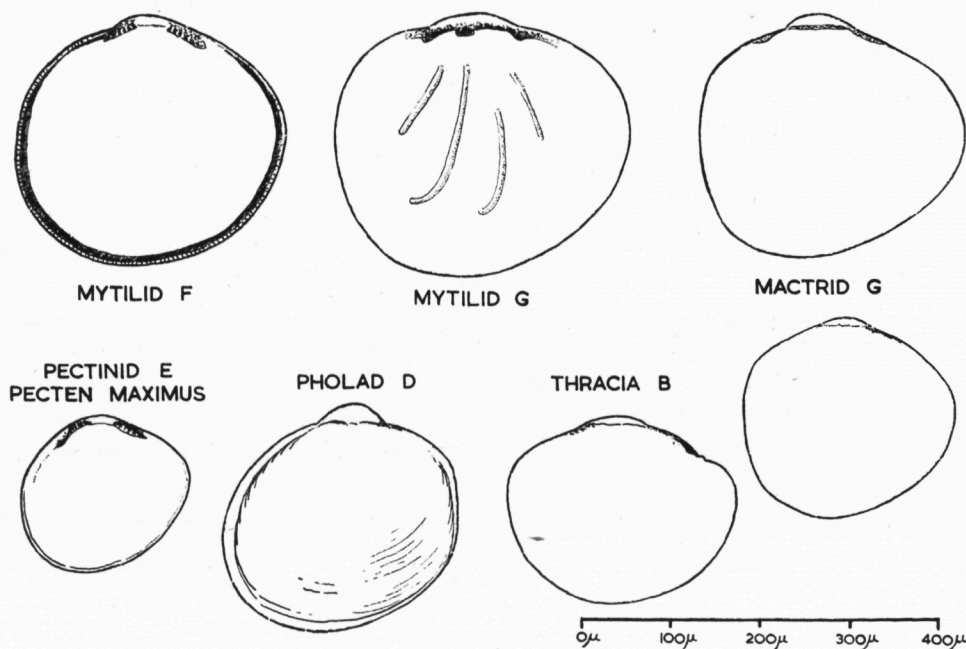
Pectinacea.

PECTINIDS C and E.—It can now be said that Pectinid C is the larva of *Chlamys opercularis* and Pectinid E that of *Pecten maximus*. This has been possible through the kindness of Mr. J.

Mason in supplying plankton samples, young spat stages and information about the spawning of these two species at Port Erin.

It was indicated in the original description that the two specimens shown of Pectinid E might not both be of the same species. It would be best to cancel altogether the smaller of the two photographs; this does not show the backward droop shown by the larger larva and which is distinct even in small larvae (Text-fig. 4).

Paphia.—Quayle (1952) has now published a description of the larva of *Venerupis* (*Paphia*) *pullastra*. This is so like the larva hitherto labelled as (? *Paphia*) that the identification may now be regarded as correct. Whilst the larva which has been described (Rees, 1950) is very like that of *P. pullastra*, it is advisable to await the descriptions of one or two other species of *Paphia* before identity is accepted.



TEXT-FIG. 4.—Tracings of photomicrographs of larvae which are described in the text.

Mactracea.

MACTRIDS A-D.—The identification of several of the Mactrid species were given tentatively only because the numbers of larvae which had been obtained did not agree with the fauna of the Dogger Bank as found by Davis (1923, 1925). A resurvey of the Dogger Bank (Ursin, 1952) has shown a very different fauna from that found by Davis and, in consequence, there is no further cause to regard the original identifications as merely tentative. The following identifications may be regarded as probable: *Mactra corallina*, *Spisula solida*, *Spisula subtruncata*, *Spisula elliptica*.

MACTRID G (Text-fig. 4).—The larva has a Type C hinge which places it akin to *Mactra corallina* but differs from it in shape. Specimens have sometimes been found in the southern North Sea. If these have been transported from the English Channel, they may possibly be of *Mactra glauca*.

Pholadidae.

PHOLAD D = (? *Panomya arctica*) of Rees (1950) (Text-fig. 4).—The larva previously called (? *Panomya arctica*) was placed in the Saxicavacea on the basis of the hinge structure in one valve only. The hinge in a complete specimen shows that it belongs rightly to the Pholadidae and is consequently relabelled Pholad D.

Pandoracea.

THRACIA A.—This is the larva previously designated as (? *Thracia* sp.).

THRACIA B (Text-fig. 4).—An occasional larva has been found which is sufficiently like (? *Thracia* sp.) to be regarded as an allied species. It is characterized by a distinct notch on the dorsal side of the narrow end.

Probable identification to *Thracia* follows from the fact that no other genus of the Pandoracea is represented by two species in the southern North Sea.

DISTRIBUTION OF THE SPECIES.

The approximate quantitative distribution of larvae is shown in Plates VII–X which are directly comparable with Plates VI–VIII of the first report. The distributions of a few of the uncommon species are given only in the notes below. Little will be said about these charts; they are included for record purposes since, with the end of the detailed study of distribution in 1951, it is unlikely that comparable information will again become available through the Recorder Survey. The records taken during 1950–51 are listed by Rae (1953).

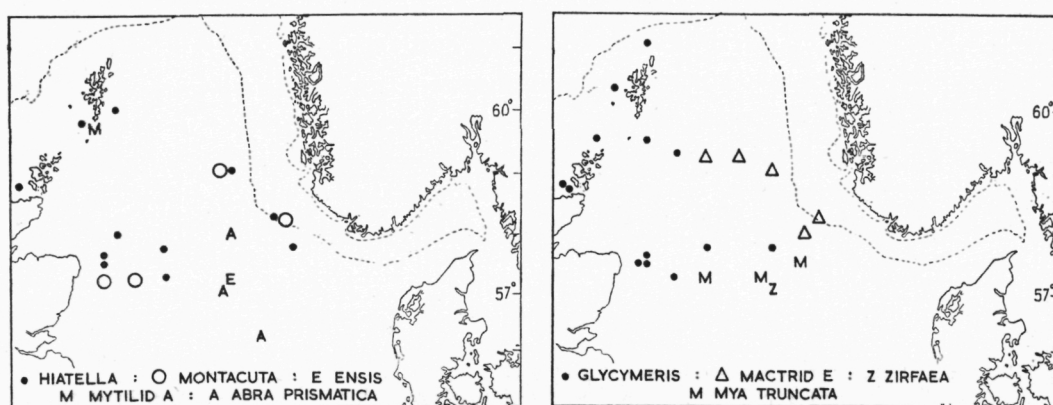
Some information derived from the Aberdeen net sampling is given in Text-fig. 5. The station positions of all samples containing over 50 specimens of various larval forms are shown.¹ *Mytilus edulis* is not included in this text-figure since full information on this species is given later.

Note should be made that the larvae of *Ensis ensis* and *E. siliqua* are here combined under the genus. The distributions of these larvae in 1949 (Rees, 1951) agreed well with the findings of Davis (1923, 1925) and Stephen (1933) that *Ensis ensis* was much more common than *E. siliqua*. However, the estimations for 1950, which was a particularly good year for *Ensis* larvae, give *E. siliqua* as more abundant than *E. ensis*. As will be seen below, some features in the distributions of various larvae early in 1950, particularly of *Mytilus edulis*, suggest a reason for the abundance of *E. siliqua*. On the other hand, it is possible that the material was inaccurately assigned to the two species; it is impossible, unfortunately, to return to the material for revision. In view of the doubt about the accuracy of the estimations, it has been decided to combine the two species and to refer only to the genus.

¹ It should be noted that the numbers of larvae obtained by the Recorder and by vertical net have a different meaning. The number obtained by the Recorder gives the concentration per unit volume of water at 10 m. depth (theoretically 3m³ in a 10-mile sample), whereas the net sample gives the number below a unit area of sea surface (approx. 0.4 m²), both within limits of sampling errors.

Seasonal Occurrence.

Table I gives the seasonal results in the same way as in Table I of the previous report (Rees, 1951, p. 112). For convenience the same order and grouping has been used, but *Mya truncata* has been added to the spring breeders and many species removed, particularly from the list of autumn breeders; the charts (Plates VII-X) contain all the information though in a less convenient form. Interest chiefly centres on species with apparently two breeding seasons in the course of the year. Certainly these species stand out most clearly in groups *d*, *e* and *f* of Table I of the previous report. That this feature is less apparent in the Table here is due on the one hand to the widespread distribution of the species in 1950,



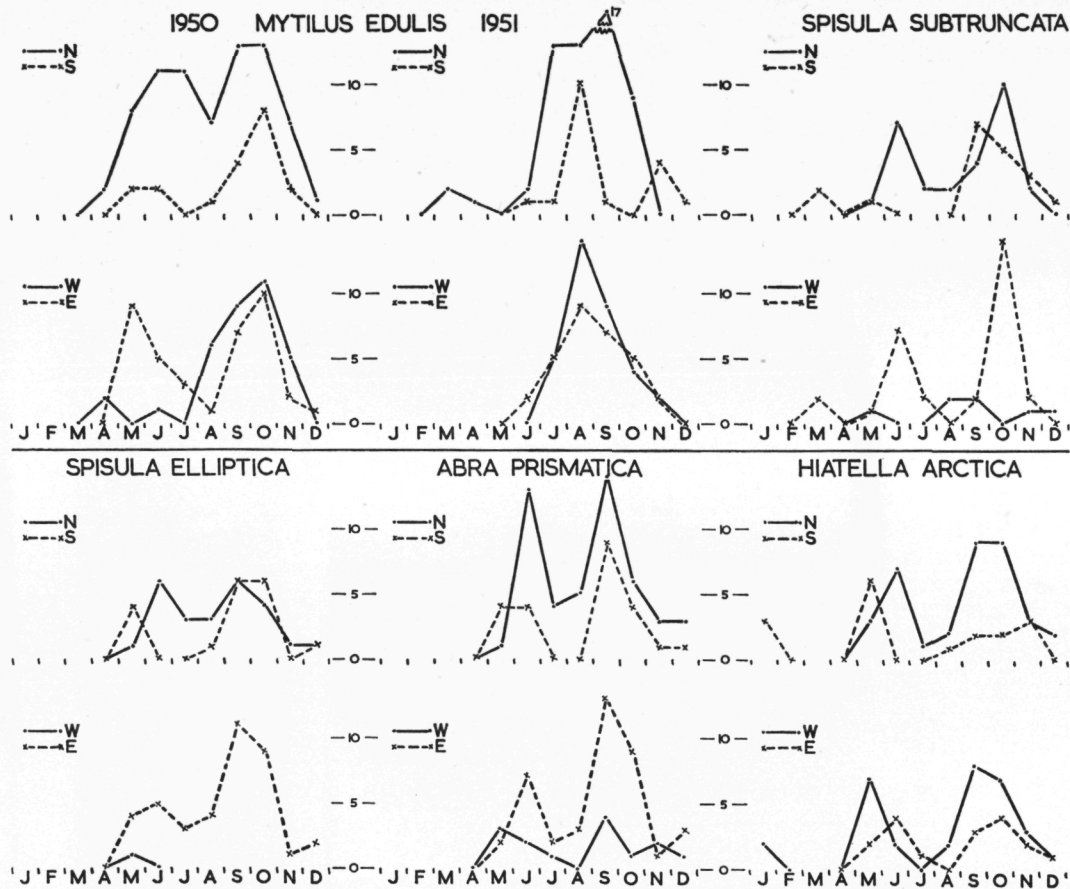
TEXT-FIG. 5.—Charts showing the distribution of samples containing 50 or more larvae of various forms in the Hensen net collections taken for the Scottish Home Department, Marine Laboratory, Aberdeen, during 1950.

so that what were two distinct periods are joined into one in the method of presentation,¹ and on the other hand to the relative scarcity of larvae in 1951. In reconsidering 1950, the greater number of samples, compared with 1949, which contained larvae of some of the more common species allows a subdivision of the North Sea so that the geographical factor may be partially eliminated. It is, of course, possible that a species may breed at different times in the north and south, so that the combination of the results may give the appearance of a double breeding, or, for that matter, continuous breeding. This point was not specially raised in the first report but a cross check between the table and the charts does not support this possibility.

Text-fig. 6 shows, for various species, the numbers of samples containing the species in each month in four subdivisions of the North Sea: north and south of a line from Newcastle to the Skaw (north; south) and the combined western

¹ If the number of samples containing larvae in successive months is 1, 9, 3, 1, 9 the same symbol (+) is used for each month though there are two distinct maxima.

halves (west) and eastern halves (east) of the Leith- and Hull-Copenhagen routes. Almost every curve may be interpreted most easily as bimodal. This is true not only for species previously recognized as showing this feature (the *Spisula* spp.) but also for *Abra prismatica* and *Hiatella arctica*, which were previously accepted as



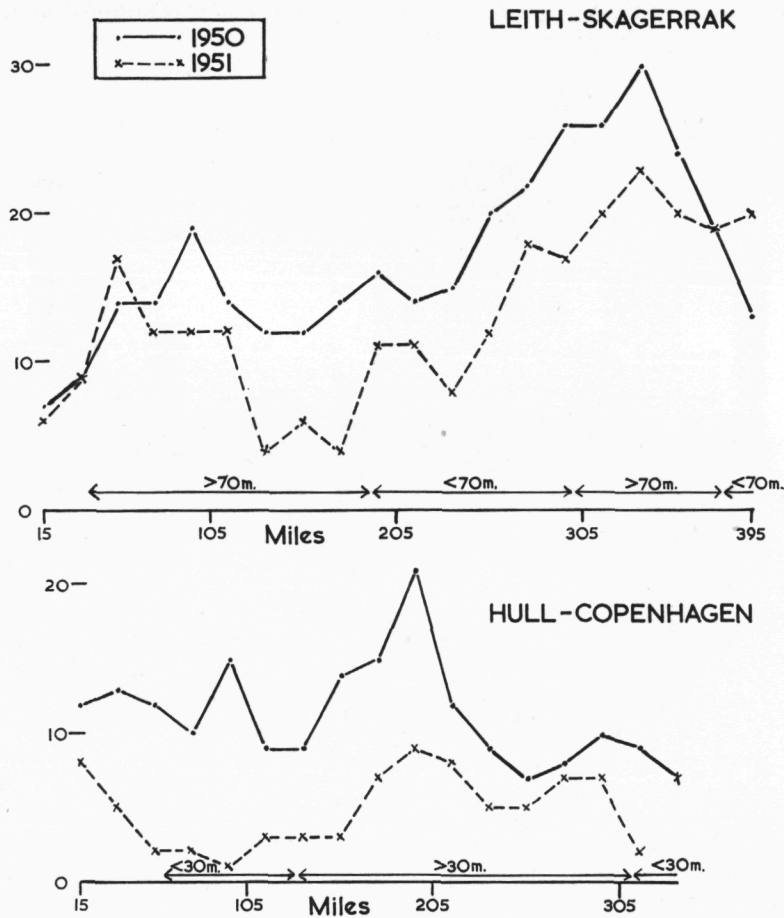
TEXT-FIG. 6.—Graphs giving the number of 10-mile samples containing larvae of various species in each month of 1950 (also 1951 of *Mytilus edulis*) in four sub-divisions of the North Sea. The sub-divisions are north and south of a line Newcastle to Skaw and east and west of the central North Sea.

single, autumn breeders (Table I in Rees, 1951). There is, at least, no evidence here that the geographical factor is involved.

This feature of the apparent double breeding, in the course of the year, of some species has already been discussed (Rees, 1951, p. 124). The three years results suggest that the phenomenon is not restricted to a distinct set of species and it may be further tentatively suggested that the feature is related to the Atlantic influx into the North Sea and the reciprocal influx through the Dover Straits.

DISCUSSION.

Text-fig. 7 corresponds to Text-fig. 5 of the first report (Rees, 1951, p. 122) and shows the number of species found in each block analysed throughout each year on the Leith-and Hull-Copenhagen routes ; depths along the routes are broadly indicated. On both routes there was a marked reduction in the variety of species in 1951 compared with 1950.



TEXT-FIG. 7.—Graphs giving the numbers of species obtained in the 10-mile samples along the Leith-Skagerrak and Hull-Copenhagen routes in 1950 and 1951. Depths along the routes are broadly indicated. This text-figure corresponds to Text-fig. 5 of Rees (1951).

The spatial trend in the two years on the Leith-Skagerrak route was very similar ; the greatest variety occurred at the same position, 335 miles from the Forth, and the lowest at about 140 miles from the Forth. The 1950-51 trends were, however, markedly different from that of 1949 from about 195 miles from the Forth eastwards, although to the west of this point all three years agreed. An

association between depth and number of species was suggested in 1949 (Rees, 1951, p. 123); this was not maintained in 1950-51.

The trend on the Hull-Copenhagen route in each year was also similar, the greatest variety occurring at the same position, 195 miles from the western end. This is just over the south-eastern edge of the Dogger Bank in the region that heavy larval concentrations have previously been found (see Text-fig. 2 of Rees, 1951). Again, the 1950-51 trends depart markedly from that of 1949 and here also the association between depth and number of species, suggested in 1949, was not maintained.



TEXT-FIG. 8.—Histograms giving the number of species obtained in each month of 1950 and 1951, taking in all Recorder samples from the North Sea. This text-figure corresponds to Text-fig. 6 of Rees (1951).

The number of species obtained in each month over the whole North Sea is shown in Text-fig. 8, corresponding to Text-fig. 6 in Rees, 1951, p. 123. The trends in all three years are in general agreement. The dip in October, 1951, in the diagram probably has no ecological significance; it might well be due to reduced sampling in that month.

A list was given in the first report (p. 125) of the 10 most abundant larvae. This list is incorporated in Table II here, which gives the approximate number of hundreds of larvae of the most abundant species in each year, and the yearly averages for 1949-51. The species are placed in descending order of yearly averages. An estimate of total larvae is also given. The letters N and S have been used to indicate those forms in which at least three-quarters of the larvae were obtained north or south of a line from Newcastle to the Skaw.

The numbers in this table must be taken with some reserve. The larval populations can change rapidly so that dates of sampling and the extent of sampling both have a substantial effect on the numbers obtained. A typical example is

TABLE II.—Giving, in Hundreds, the Numbers of Larvae of Various Forms Obtained in Each Year 1949 to 1951, and the Average of the Three Years. N stands for North, S for South as Explained in the Text.

	Average. 1949-51.	1949.	1950.	1951.
<i>Mytilus edulis</i> . . .	173N	18	210N	292N
<i>Spisula elliptica</i> . . .	52S	140S	13	3
<i>Ensis</i> . . .	46	22S	110	4S
<i>Abra prismatica</i> . . .	24N	21	41N	11
<i>Cultellus pellucidus</i> . . .	19	26S	25N	6
<i>Glycymeris glycymeris</i> . . .	17	20N	20	11
<i>Montacuta ferruginosa</i> . . .	17S	17S	22S	11
<i>Zirfaea crispata</i> . . .	15S	23S	21	1
<i>Modiolus modiolus</i> . . .	11N	13N	11N	10N
<i>Spisula subtruncata</i> . . .	9	9S	17	3
<i>Mya truncata</i> . . .	9	1S	26	+
<i>Venus D</i> . . .	9N	+	26N	+
<i>Hiatella arctica</i> . . .	8N	11N	10N	4N
<i>Abra nitida</i> . . .	7	3	12	5
Other species . . .	56	65	62	42
Total larvae . . .	472	388	627	405N

the low number of *Mytilus* in 1949. It is possible that this number would have greatly increased if the first 80 miles off the Forth in August and September had been sampled. Nevertheless, the table shows many points of interest.

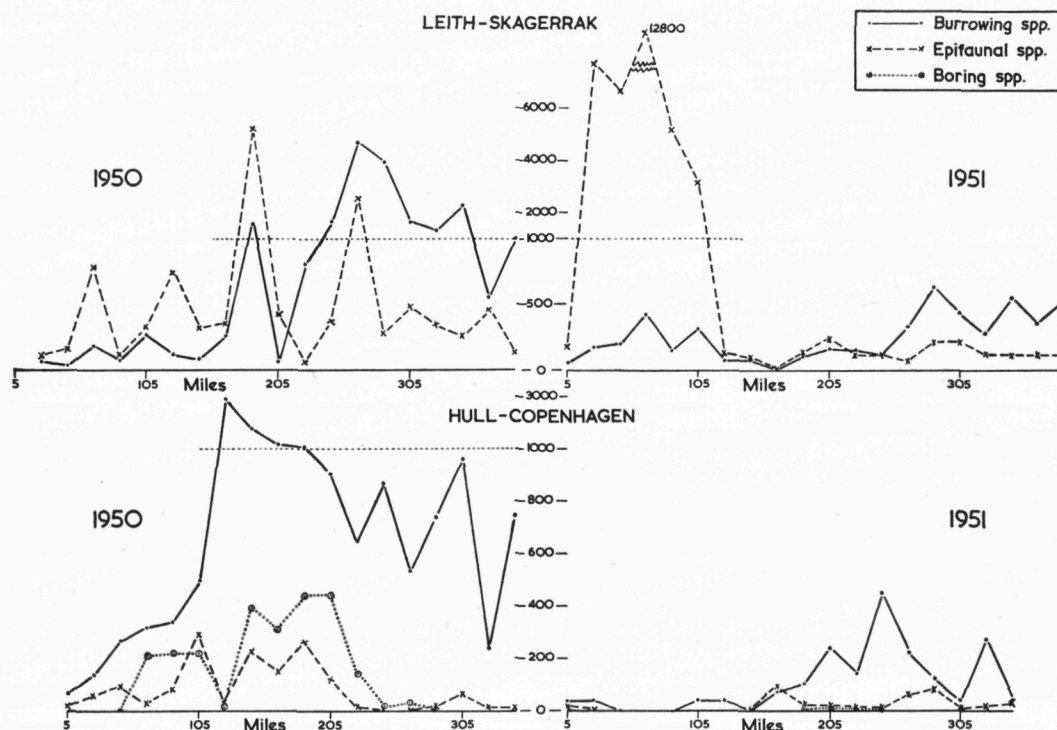
An outstanding feature is the marked predominance of *Mytilus edulis* which, overall, was more than three times as common as any other species. Since it was almost entirely northern in its distribution, the quantity of "total larvae" in the north was substantially greater than in the south. Forms more common in the south than in the north were *Spisula elliptica*, *Ensis*, *Montacuta ferruginosa*, *Zirfaea* and *Abra nitida*.

In several respects the years were very different. Despite the much lower total number of larvae in 1949 compared with 1950, several species were obtained in almost identical numbers: *Cultellus*, *Glycymeris*, *Zirfaea*, *M. modiolus*. The very great success of *Spisula elliptica* was, however, limited to 1949.

Apart from *Mytilus* larvae, the year 1950 was especially noted for the relative abundance of *Ensis*, *Mya truncata* and *Venus D*, all three occurring in spring and early summer. *Spisula subtruncata* was nearly twice as common as in 1949 and 73% were found towards the north, compared with 17% only in 1949. The relative success of *Abra nitida* in 1950 is partly accounted for by the fact that the Heligoland Bight was more thoroughly sampled than in 1949.

1951 was a poor year for larvae as a whole, even the very great number of *Mytilus* failing adequately to balance the scarcity of other species. Species notably scarce were *Spisula elliptica*, *Ensis*, *Cultellus* and *Zirfaea*.

As in the first report (Rees, 1951, Text-fig. 7), all the larvae on the Leith- and Hull-Copenhagen routes have been separated into three groups, those belonging to the burrowing, boring and epifaunal species. Text-fig. 9 shows the total number of larvae of each group in each sample of these two routes.



TEXT-FIG. 9.—Graphs giving, for 1950 and 1951, the total numbers of larvae of epifaunal, burrowing and boring species obtained in the 10-mile samples along the Leith-Skagerrak and Hull-Copenhagen routes. The vertical scale alters at 1000 larvae and a second base line (dotted) is drawn at this level. This text-figure corresponds to Text-fig. 7 of Rees (1951).

These graphs confirm the suppositions expressed in the first report that larvae of epifaunal species probably constitute a very substantial part of any pronounced concentration over the Great Fisher Bank (Leith-Skagerrak route, 1950), and that larvae of *Ensis*, a burrowing genus, may form a considerable part of the population in spring and early summer along the southern edge of the Dogger (Hull-Copenhagen route, 1950). The graphs for the Leith-Skagerrak route in 1951 reveal the tremendous dominance of the larvae of epifaunal species in the concentration off the Forth.

The main concentrations found in 1949 were briefly considered in the first report and the specific composition of the concentrations indicated. Most of the main concentrations obtained in 1950 and 1951 have been numbered in Text-fig. 1, and the percentage composition of these numbered patches given in Table III: only the dominant species are included.

TABLE III.—*Giving the Percentage Composition of Patches of Larvae in 1950 and 1951. The Patches are shown and numbered in Text-fig. 1.*

Patch.	Month.	<i>Mytilus</i>	<i>M.</i> <i>modiolus.</i>	<i>Mytilid</i> <i>A.</i>	<i>A.</i> <i>prismatica.</i>	<i>Ensis.</i>	<i>Cultellus.</i>	<i>Zirfaea.</i>
1950.								
1*	IV	—	—	—	—	72	—	—
2	V	4	2	—	—	74	1	10
3	V	82	—	—	2	—	—	4
4	V	73	—	—	—	10	—	—
5	V	—	—	—	—	89	—	2
6*	VI	—	—	3	20	14	5	—
7	VI	13	—	20	20	27	—	20
8	VI	—	—	—	—	80	—	20
9	VII	94	—	6	—	—	—	—
10	IX	6	78	—	2	—	—	—
11*	IX	74	5	2	4	—	—	—
12*	IX	—	—	—	35	—	45	—
13*	IX	5	—	—	35	—	29	—
14*	IX	—	—	—	1	—	1	—
1951.								
1*	VI	—	—	—	26	9	5	—
2	VIII	99	+	+	+	—	+	—
3	IX	55	37	—	—	—	—	—

* Also in 1950, Patch 1, *Macra corallina* 18%; Patch 6, *Spisula subtruncata* 10%, *Venus* D 28%; Patch 11, *Glycymeris* 9%; Patch 12, *Cardium* D 10%; Patch 13, *Spisula elliptica* 8%; Patch 14, *Abra nitida* 63%, *Montacuta ferruginosa* 24%: in 1951, Patch 1, *Macra corallina* 45%.

A brief account has recently been given of a resurvey, in 1950 and 1951, of the bottom fauna of the Dogger Bank (Ursin, 1952). Birkett (1953) has commented on this account and, in the main, confirmed the findings of Ursin. The available results on the bottom fauna are, however, as yet too meagre and from too restricted an area to allow any useful comparison between larval distribution and the contemporary bottom fauna. It would seem, from the larval results, that it is important to establish the age composition of the bottom fauna, to establish, in fact, whether there are dominant year classes. There can be very great differences in the numbers of larvae obtained from year to year, differences which may be reflected in the bottom fauna. As examples, we can note the great number of larvae of *Spisula elliptica* in 1949, of *Ensis* and *Mya truncata* in 1950, and the scarcity of larvae of *Cultellus* and *Zirfaea* in 1951 (Table II).

Distribution of Mytilus edulis larvae.—A question which arises is whether the Fisher Bank concentration of 1950 and the Forth concentration of 1951 were made

up of larvae which had originated *in situ* or whether larvae had been carried to these regions; and if carried, from which direction had they come? The concentrations as a whole consist of heterogeneous assemblages of species, but the distributions of the larvae of *Mytilus edulis* hold particular interest, partly because these larvae played a dominant part in both concentrations and partly because of the distribution of adult mussels, which, on the evidence, is closely restricted to coastal waters.

Schrader (1911) referred to *Mytilus edulis* as a coastal form. He did find a young specimen as deep as 42 m. but assumed that this must have developed from a larva which had been carried from the coast. He pointed out that the species occurs down to a depth of 20 m. off the Norwegian coast. The general absence of mussels in Schrader's North Sea samples cannot be explained by unsatisfactory means of collecting, for other epifaunal species were found in numerous samples.

At first sight it might seem that the grab surveys of Davis (1923, 1925) and Stephen (1933) are not really relevant to the question of the distribution of adult *Mytilus* in the North Sea. This, however, is not so. The mussel community shows its greatest development, not on rocky ground, but in sand and mud regions (Remane, 1940), that is, on bottoms such as are sampled by the grab. Davis (1925) did find *Mytilus* at one station, in 35 m. of water but less than three miles from the coast.¹ The grab is, in fact, capable of taking samples of *Mytilus*. At about 200 grab-stations, Petersen (1914) found *Mytilus* at 18% of the stations and the horse mussel, *Modiolus modiolus*, at another 7%. Excluding the half-dozen stations taken in the "true Baltic," where conditions cause an unusual distribution of animal communities, Petersen obtained *Mytilus* in 50% of the stations less than 14 m. in depth. The deepest station where *Mytilus* was found was 18 m. We may, therefore, accept the absence of *Mytilus* in the offshore samples taken during the grab surveys of the North Sea as evidence of its scarcity or absence in this region.

Hargreaves (1910) compiled a long list of lamellibranch species which had been recorded on the Dogger Bank. *Mytilus* was not included in this list.

White (1937) gives the usual habitat as from high water mark to a few fathoms. Jensen (1912) said that it belongs to the littoral belt.² He found young specimens at greater depths, down to about 100 m., but considered that such specimens must have been carried out into deep water with seaweed. In the western Atlantic it is said that mussels live down to a depth of about 30 m. (Anon., 1952).

Verwey (1952) states that the mussel is usually limited to shallow water, down to a depth of 6-9 m.; exceptionally, however, large banks may occur in somewhat deeper water of up to 17 m. or more. In the North Sea, at some distance from the coast, mussels are absent except near the surface, on buoys or lightships.

These results, as well as those of many other workers, show that we can discount

¹ Dr. A. C. Stephen has very kindly looked through his records and checked that he found no *Mytilus*, either living or as empty shells, at a greater distance than two miles from the coast.

² The term "littoral" is variously used, but it is implicit elsewhere in his report that Jensen did not consider a depth of 13 f. to be in the littoral region.

the possibility that adult *Mytilus edulis* occur in appreciable numbers, if at all, in depths greater than 40 m. in the North Sea, or, in shallower water, on the Dogger Bank. The 20 m. and 40 m. depths contours are shown in Text-fig. 12 and it is clear from these that we may regard the occurrence of appreciable numbers of mussels as limited to a few miles off the coasts.

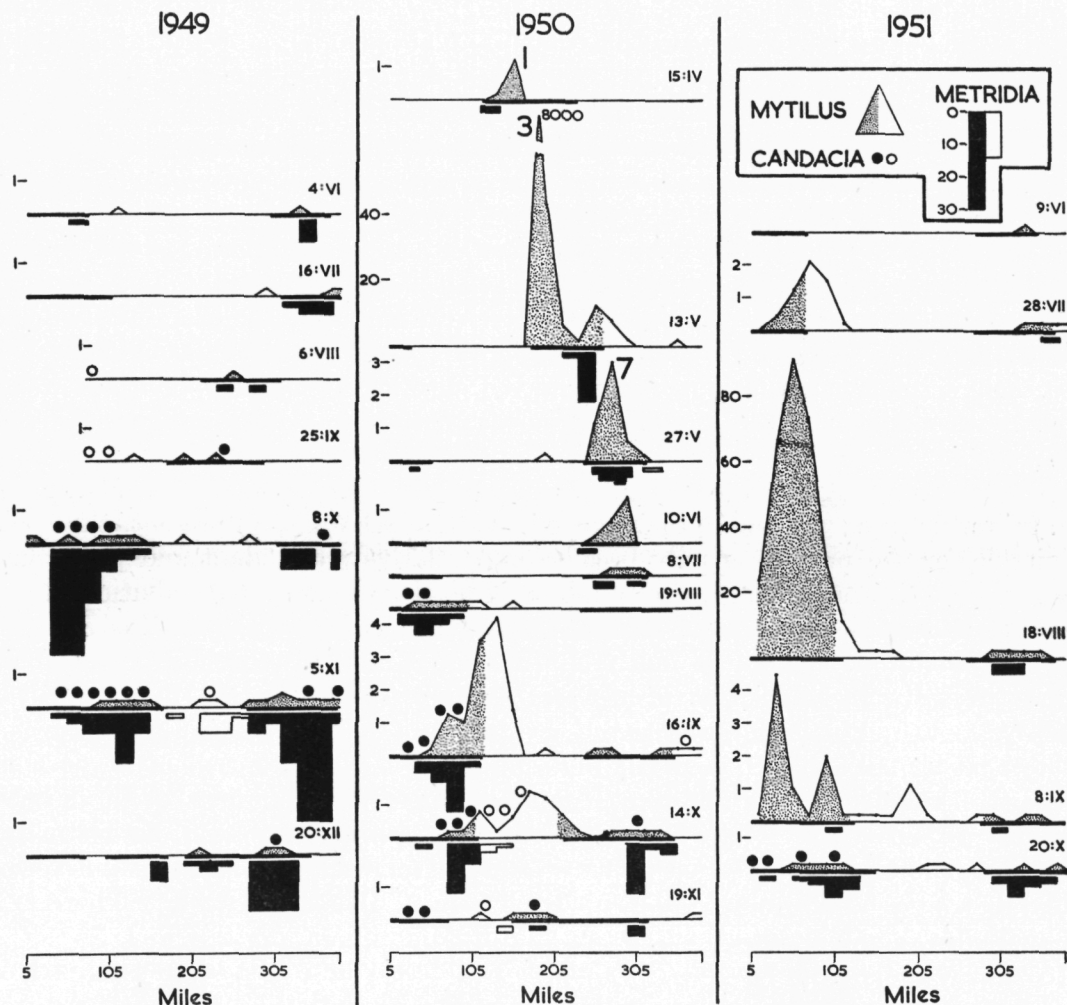
A preliminary scrutiny of the distribution of *Mytilus* larvae gives a partial answer to our question of origin. It can be seen on Plate VII that a very heavy concentration of *Mytilus* larvae was obtained in the centre of the North Sea in May, 1950. This particular concentration, of about 3000 larvae per m³, was found to compare favourably with high population densities of lamellibranch larvae obtained elsewhere and by other methods of collecting (Rees, 1951, p. 108). These *Mytilus* larvae were large and must have been several weeks old. There can be little doubt that these old larvae, in such a great concentration, must have originated in inshore waters where *Mytilus edulis* occurs in dense colonies.

An apparent association between *Clione*, which is regarded as an indicator of north-west North Sea water (Marshall, 1948), and high larval lamellibranch concentrations over the Great Fisher Bank was referred to in the first report (Rees, 1951, p. 129). Also, several examples were given (p. 127) of larvae which appeared to show a southwards movement during the autumn, at a time when it is usual for north-western indicator species to show a similar southwards progression. We should, therefore, attempt to relate the distributions of *Mytilus* larvae, which are taken to typify the two major concentrations, to the north-western North Sea indicator species. Of these, the copepod *Metridia lucens* is, at present, the most suitable for the purpose, partly because it is relatively abundant and persistent, much more so than *Clione*, for example, and partly because its distribution in the years under review is readily available from the results of the routine analysis of the plankton. Although much less numerous, the distribution of *Candacia armata* closely resembles that of *Metridia lucens* in the North Sea (Rae and Rees, 1947).

Text-fig. 10 shows (above the line) graphs of the distribution of *Mytilus* on each Leith-Skagerrak record which contained appreciable numbers of the larvae. Underneath the base line, which represents the record, are placed histograms of the numbers of *Metridia lucens* found on each 10-mile sample analysed and, above the base line, circles mark the samples containing *Candacia armata*. There is a remarkably good agreement between the distribution of *Mytilus* and *Metridia*. 1950 provides the best series. Patches of *Metridia* and *Mytilus* overlapped or coincided from April to July and, from an easterly position of coincident patches in July, a switch over to the west was shown in both species on the August record. From August to November both species showed an easterly trend along the line. *Candacia* also occurred in the association from August onwards and also showed the easterly trend.

In 1951 the agreement between *Metridia* and *Mytilus* is again well shown in the easterly patch from July to October. *Mytilus* appeared suddenly in the west,

off the Forth, in late July but *Metridia* was not recorded with it until September and, even then, only one specimen was found. *Candacia* was not obtained until October. On the whole, the occurrence of *Mytilus* larvae off the Forth in 1951 conformed to the distribution of *Metridia* most commonly found. *Metridia* and/or *Candacia* were first found off the Forth, after a summer absence, in August 1946, 1948, 1949 and 1950 but not until later than August in 1938 and 1947. In 1949



TEXT-FIG. 10.—Graphs and histograms giving the number of larvae of *Mytilus edulis* and of the copepod *Metridia lucens* in each 10-mile sample of a series of Leith-Skagerrak records in three years. The samples containing *Candacia armata* are indicated by circles. Each base line represents a Leith-Skagerrak line in its full length from the Forth to the Skagerrak and the thickened parts of each base line show the sections of the record which sampled between sunset and sunrise. The dotted parts of the graphs for *Mytilus* and the black histograms for *Metridia* show specimens taken during sampling at night. The vertical scale to the graphs is in hundreds of larvae. See footnote p. 23.

there was a reasonably close agreement between *Mytilus*, *Metridia* and *Candacia* on the eastern side, but, unfortunately the information was lacking at the western end of the route in August and September.

The similarity between the two distributions is close. It may therefore be said that the *Mytilus* larvae whose distributions are shown in Text-fig. 10 were contained in water inhabited by *Metridia lucens*. It was clear from our pre-war results that *M. lucens* is an indicator of mixed oceanic and coastal water, "elegans" water, in the North Sea (Rae and Rees, 1947), and this has been fully confirmed by the post-war results (Rae, 1949-52). It appears, then, that *Mytilus* larvae which occur off-shore in the northern North Sea (Text-fig. 10) are to be found in mixed water. It is, of course, obvious that we cannot generalize from this and say that *Mytilus* larvae are everywhere to be found only in mixed oceanic and coastal water. The fact that the adult is essentially a coastal and very shallow water form clearly precludes any such generalization.

Supplementary records were taken in May, 1950, besides the normal routine records. The records which now concern us are shown in the chart on the left of Text-fig. 11. In addition to Recorder samples, there were the Hensen net samples taken by the research vessels of the Marine Laboratory, Aberdeen. Consideration of the distribution of *Mytilus* larvae during this period requires that particular attention is given to the dates of sampling; these are given in the chart in Text-fig. 11.

No *Mytilus* larvae were found on the Aberdeen-Lerwick (A) and 12 TA records. The distributions on the three Leith-Skagerrak (K) records are given in Text-fig. 10. The distribution on the 7 TB record is shown in Text-fig. 11, the north leg and south leg being given in separate graphs; it also shows the distribution of larvae on the eastern half of the Hull-Copenhagen (C) record.

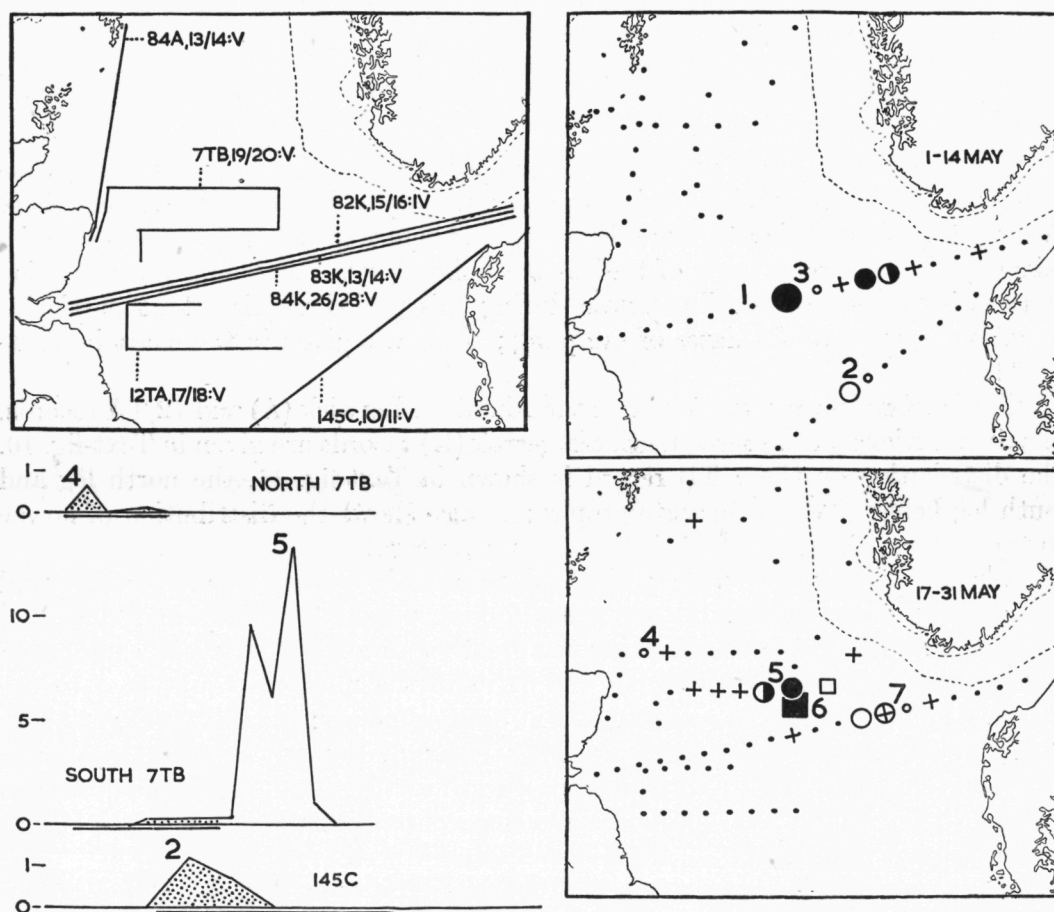
Charts showing the number of *Mytilus* larvae in each sample, Recorder and net, are given in Text-fig. 11, one chart for the period 1-14 May and the other 17-31 May. The samples containing the greatest number of larvae in each graph have been numbered (Text-figs. 10 and 11) and the numbers transferred to the charts. The numbers are more or less in date sequence: 2, May 10th; 3, May 13th; 4, May 21st; 5, May 20th; 6, May 24th; 7, May 27th. In addition, the concentration numbered 1 (April 15th record in Text-fig. 10) appears to be relevant to the distributions we are considering and the geographical position of this is shown in the chart for 1-14 May.

The symbol numbered 6 in the chart for 17-31 May in Text-fig. 11 refers to a Hensen net sample. This was an exceptional sample for it contained twice as many total larvae as any other net sample taken throughout the year. The measurements of one hundred *Mytilus* larvae from this net sample fell into the range 360-470 μ with an average of 413 μ . All the larvae were, in fact, very large, larger than the normal settlement size. They must have been several weeks old, sufficiently old to have allowed transportation over a considerable distance.

It is clear from the charts, that the axis of highest concentrations found on

records and Hensen net samples lies in the general direction WNW.-ESE. Since sampling took place irregularly over a relatively long period, any expectation that the numbers obtained would decrease with increasing distance from the source could hardly be realized.

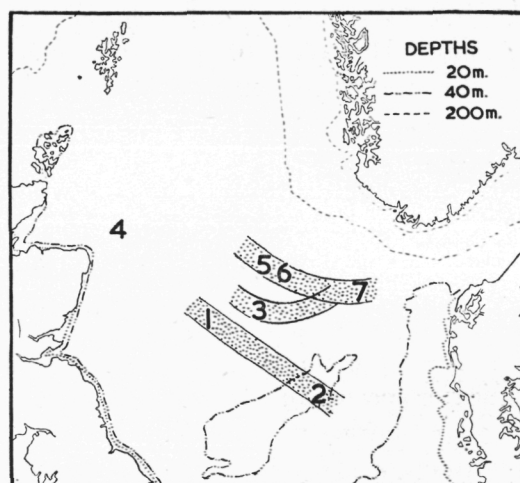
The concentrations found on the Recorder routes were relatively narrow in their west-east axes (Text-fig. 10 and 11). The implication is that the distributions were narrow and elongated, that is, they took a form which we can, for convenience, refer to as "band" distributions. A schematic representation of this feature is shown in Text-fig. 12 where boundary lines are drawn to enclose samples containing



TEXT-FIG. 11.—The chart at the top left shows the routes and dates of records taken in May, 1950. The charts on the right show the distribution of *Mytilus* larvae in Recorder and net samples in the periods May 1st–14th and May 17th–31st; the scale for the symbols is as shown in Text-fig. 13. The three graphs show the number of *Mytilus* larvae in samples along sections of records, the vertical scale being in hundreds of larvae. Peaks in these three graphs, and in the appropriate records in Text-fig. 10, have been numbered and the location of the peaks shown by similar numbers in the two charts on the right. See footnote p. 23.

appreciable numbers of larvae. It is not suggested that Text-fig. 12 is an accurate representation of the positions of the bands; one cannot allow for the distribution changing in association with the successive times of sampling. Other, perhaps equally acceptable, ways of representation could be chosen but they would present essentially the same features of long, narrow distributions.

Such features accord well with the accepted idea of the water circulation of the North Sea at this season, and cannot fail to remind one of the stream currents described by Tait (1937). However, we cannot conclude from this evidence alone that the incoming water was confined to narrow streams. Given a continuous spawning of *Mytilus*, an elongated distribution of larvae might form near the



TEXT-FIG. 12.—The suggested distributions of *Mytilus* larvae in the spring of 1950.

edge, say the western one, of a much wider inflow of water. The water carrying the larvae must, however, have moved comparatively rapidly to have carried larvae some hundreds of miles during their period of pelagic life.

Even without the extra samples which have suggested such a picture as Text-fig. 12, there is strong circumstantial evidence of the *Mytilus* larvae being distributed in narrow bands. On five successive Leith-Skagerrak records between April 15th, and July 8th, 1950, there were patches of *Mytilus* larvae restricted to a distance of about 30 or 40 miles in their east-west axes (Text-fig. 10). One cannot accept the premise that these five records sampled the same population; a generous estimate of the larval life of *Mytilus* is five weeks (Chipperfield, 1953) and, in fact, the larvae taken even in the earliest record, April 15th, were already large and in the later stages of pelagic life. One must, therefore, postulate a more or less continuous recruitment of larvae in the region of the Great Fisher Bank over a period of some three months. Since these larvae must have originated in shallow waters it is only reasonable to conclude that these shallow waters were to the north and

west, in view of the accepted idea of circulation in the North Sea (Tait, 1937). The picture, therefore, is of a distribution of *Mytilus* larvae some 200–300 miles long in its NW.–SE. axis but only 30–40 miles in its E.–W. axis, that is, a “band” distribution.

It seems, then, that the *Mytilus* larvae in the central North Sea in May, 1950, originated off the north British coast (including, possibly, the Orkneys and Shetlands), at least 200 miles away. The similarity in distribution between *Metridia lucens* and *Mytilus* larvae, which was particularly close in 1950 (Text-fig. 10), strongly suggests that the band distribution of *Mytilus* was, in some way, due to the movement of mixed Atlantic and North Sea water.

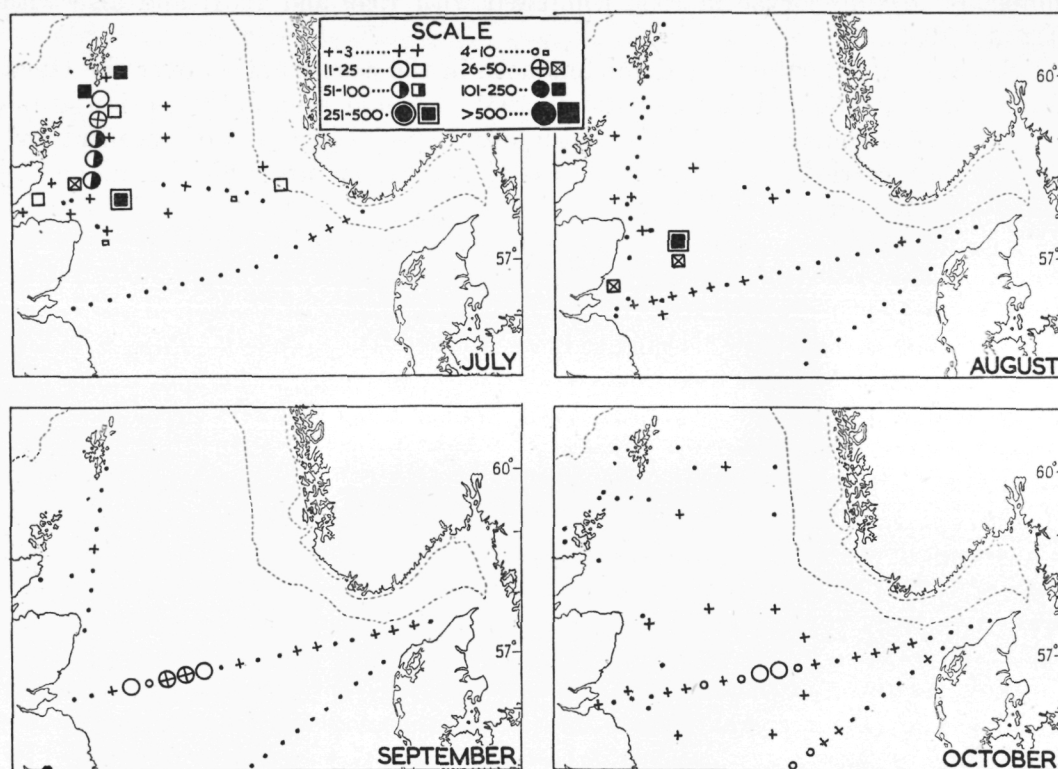
As regards the occurrence of an exceedingly heavy concentration of *Mytilus* larvae off the Forth in August, 1951, the only information available is given in the charts of distribution in Plate VII. It is, of course, inherently likely that these larvae had also been carried southwards in mixed water which had come from the north-west North Sea. More often than not, the indicator species of such mixed water re-appear off the Forth in August; the way *Metridia lucens* illustrates this feature is noted on p. 38. Although, in 1951, *M. lucens* was not observed off the Forth until September 7th, the high numbers of *Calanus finmarchicus* and *Limacina retroversa* here in mid-August indicated that mixed water had, in fact, reached the area from the north.

It must be recognized that some, at least, of the larvae originating from the numerous *Mytilus* colonies in the Forth are, doubtless, carried into the North Sea. On the evidence of the indicator species, one would expect the larvae of August and September to be carried in a southerly or south-easterly direction. It is very unlikely that many larvae would be transported, at this season, for any appreciable distance directly eastwards, that is, along the Leith-Skagerrak route. Even in August, 1951, when a Forth origin may most readily be suspected, the greatest population density of larvae was found 60–70 miles east of the entrance to the Forth and very large numbers were found up to 100 miles eastwards (Plate VII, Text-fig. 10). In fact, it is most likely that these larvae came from the north in the southerly or south-easterly drift.

A partial demonstration of an actual southwards drift is given by the distribution of *Mytilus* larvae in July–October, 1950, using the Hensen net samples as well as Recorder samples (Text-fig. 13). *Mytilus* larvae were very abundant in the north-west in July and became scarce in August. Larvae were absent off the Forth in July and a moderate concentration was found some distance east of the Forth in September and still further east in October. Appreciable numbers were found east of the Dogger Bank, on the Hull-Copenhagen route, in October.

It is worth while looking more closely at Text-fig. 13 with the distributions of the previous May in mind. The patches on the Leith-Skagerrak routes of September 16th and October 14th may reasonably be compared with the concentrations numbered 1 and 3 in Text-fig. 10 and 11, and that near the Dogger Bank on October 22nd with 2 in Text-fig. 11. The same considerations apply as in the

case of May 1950; the *Mytilus* larvae in the centre of the North Sea must have been transported many miles from coastal waters and, because of the duration of larval life, it is very unlikely that a single concentration sampled on September 16th was re-sampled further to the east on October 14th. It would seem that we should here again postulate a continuous recruitment of larvae. The alternative is to accept the coincidence that successive Leith-Skagerrak records sampled discrete



TEXT-FIG. 13.—Charts showing the distribution of *Mytilus* larvae in each month from July to October, 1950, in Recorder samples and in Hensen net samples of the Scottish Home Department, Marine Laboratory, Aberdeen. The circular symbols stand for number per mile per 10-mile Recorder sample and the square symbols for number per net sample in tens.

patches of larvae, each patch having travelled many miles from the coast. Clearly, we do not have at this time anything like so detailed a picture as in the spring; that region north of the Forth, which was sampled reasonably well in May, not only in number of samples but also within short intervals of time, was sampled very sparsely in the summer and autumn. There were, at best, hardly more than four or five net samples in a month over some thousands of square miles and, of particular importance, there was no suitable Recorder run to give a continuous traverse of the area. Even so, both in July and August a very large number of

larvae was found in one net sample whilst neighbouring samples had few or none, as happened also in May. There are, in fact, strong indications that in the autumn, as well as in the spring of 1950, the drift which had picked up *Mytilus* spawn in some coastal water had retained the larvae in a narrow, elongated distribution some hundreds of miles further down its course into the North Sea.

It may be as well to point out that there was a prolonged supply of large number of *Mytilus* larvae in 1950 compared with 1949 and 1951, and also with 1952 and 1953.

Since *Mytilus* larvae were dominant both in the concentration over the Great Fisher Bank in 1950 and off the Forth in 1951, it would seem, by extension of the argument, that some of the larvae of the other species in the two concentrations had also been carried in mixed water, and that these larvae originated along the route from the north-west North Sea.

The probable transport of larvae from the direction of the north-west North Sea explains the occurrence of larvae of other shallow water species, besides *Mytilus edulis*, in the central North Sea. In this connection, the distribution of the larvae of *Spisula subtruncata* may be noted (Plate VIII). The species of *Paphia*, which occurred especially in 1949, is not known but is probably a shallow water one. The estimated number of larvae of *Ensis siliqua* in 1950 was very great but there remains some doubt about the accuracy of this result (p. 27). However, it is stated in the report of the Council of the Marine Biological Association of the U.K. for 1951-52 that Mr. N. A. Holme finds that *E. siliqua* is typically a shore or shallow-water species, and *E. ensis* a typically offshore species. It is, therefore, possible that the larvae of *E. siliqua*, as well as those of *Mytilus edulis*, were unusually abundant in the central North Sea in 1950, both species being coastal forms which spawn in the spring.

Any discussion of the mechanism involved in the concentration and transport of larvae had better await the presentation of the available information on the distribution of other organisms, besides lamellibranch larvae, in May, 1950.

SUMMARY.

1. This report presents the distributions of lamellibranch larvae in the North Sea in 1950 and 1951 and follows the earlier one on the distribution in 1949 (Rees, 1951).

2. A few additional species of larvae have been described and some of the names given in the previous report have been revised (p. 25.)

3. A major concentration of larvae was found over the Great Fisher Bank in May-June, 1950. A comparison of concentrations here in four years reveals a regular form and placing of their profiles. A major concentration was found off the Forth in August, 1951.

4. In the course of a year, two main breeding periods were shown by some species.

5. The spatial trends shown by the number of species found in each sample along both the Leith-Skagerrak and Hull-Copenhagen routes were very similar in 1950 and 1951, but many more species were obtained in 1950. The trends differed from those found in 1949 and the association with depth, previously noted, was not maintained.

6. The total number of larvae of *Mytilus edulis*, obtained during 1949-51, was three times greater than the number of any other species. The numbers obtained, from year to year, of the dominant species were in several cases very different. Noted particularly were the great number of *Spisula elliptica* in 1949, of *Ensis* and *Mya truncata* in 1950 and the scarcity of *Cultellus* and *Zirfaea* in 1951.

7. Larvae of epifaunal species constituted a substantial part of the concentration over the Fisher Bank in 1950 and greatly dominated the concentration off the Forth in 1951.

8. The distributions of larvae of *Mytilus edulis* and the copepod *Metridia lucens* along the Leith-Skagerrak route were similar; the similarity was particularly close in 1950.

9. *Mytilus* larvae appear to have been distributed in narrow, elongated formations, termed "band" distributions, in May, 1950. Their cross-sections appear to have occurred in succession from west to east associated in some way, with the movement of mixed oceanic and North Sea water. The WNW.-ESE. lie of the bands indicates that *Mytilus* larvae in the central North Sea had come from the north British (including, possibly, the Orkneys and Shetlands) coast.

10. A southwards movement of *Mytilus* larvae from the north-west to the region off the Forth between July and October, 1950, is partially demonstrated.

11. The distributions of *Mytilus* larvae indicate that the concentrations of lamellibranch larvae over the Fisher Bank in 1950 and off the Forth in 1951 were due to the movement of mixed water, the larvae involved having originated along the route from the north-west North Sea.

REFERENCES.

- ANON. 1952. Marine Fouling and its Prevention. U.S. Naval Inst., Annapolis, Maryland, pp. 1-388.
- BIRKETT, L. 1953. Change in the Composition of the Bottom Fauna of the Dogger Bank Area. *Nature*, CLXXI, p. 265.
- CHIPPERFIELD, P. N. J. 1953. Observations on the Breeding and Settlement of *Mytilus edulis* (L.) in British Waters. *Journ. Mar. Biol. Assoc.*, XXXII, pp. 449-476.
- DAVIS, F. M. 1923. Quantitative Studies on the Fauna of the Sea-bottom. No. 1: Preliminary Investigation of the Dogger Bank. *Min. Agric. and Fish., Fish. Invest.*, Ser. II, VI, 2, pp. 1-54.
- 1925. Quantitative Studies on the Fauna of the Sea-bottom. No. 2: Results of the Investigations in the Southern North Sea, 1921-24. *Min. Agric. and Fish., Fish. Invest.*, Ser. II, VIII, 4, pp. 1-50.
- FRASER, J. H. 1949. Plankton Investigation from the Scottish Research Vessel. *Ann. Biol.*, IV, 1947, p. 66.

- HARDY, A. C. 1941. Continuous Plankton Records: General Introduction to the 1938-39 Survey. Hull Bull. Mar. Ecol., II, 7, pp. 1-18.
- HARGREAVES, P. 1910. The Marine Mollusca of the Yorkshire Coast and the Dogger Bank. Journ. of Conch., XIII, pp. 80-88.
- JEFFREYS, J. G. 1862-9. British Conchology. London.
- JENSEN, A. S. 1912. Lamellibranchiata. Danish Ingolf-Exp., II, 5, pp. 1-119.
- MARSHALL, N. B. 1948. Continuous Plankton Records: Zooplankton (other than Copepoda and Young Fish) in the North Sea, 1938-39. Hull Bull. Mar. Ecol., II, 13, pp. 173-213.
- PETERSEN, C. G. J. 1914. Valuation of the Sea. II. The Animal Communities of the Seabottom and their Importance for Marine Zoogeography. Rep. Dan. Biol. Stat., XXI, 1913, pp. 1-44.
- QUAYLE, D. B. 1952. Structure and Biology of the Larva and Spat of *Venerupis pullastra* (Montagu). Trans. Roy. Soc. Edin., LXII, Pt. I, 8, pp. 255-297.
- RAE, K. M. 1949-1952. The Continuous Plankton Recorder Survey: The Plankton round the North of the British Isles. Ann. Biol., V, VI, VII, VIII.
- 1953. Continuous Plankton Records: List of Records, 1950-53. Bull. Mar. Ecol., IV, 25, pp. 1-6.
- and REES, C. B. 1947. Continuous Plankton Records: The Copepoda in the North Sea, 1938-39. Hull Bull. Mar. Ecol., II, 11, pp. 95-132.
- REES, C. B. 1950. The Identification and Classification of Lamellibranch Larvae. Hull Bull. Mar. Ecol., III, 19, pp. 73-104.
- 1951. Continuous Plankton Records: First Report on the Distribution of Lamellibranch Larvae in the North Sea. Hull Bull. Mar. Ecol., III, 20, pp. 105-134.
- REMANE, A. 1940. Einführung in die Zoologische Ökologie der Nord- und Ostsee. Die Tierwelt der Nord- und Ostsee, I, pp. 1-238.
- SCHRADER, E. 1911. Lamellibranchiaten der Nordsee. Wiss. Meeresunters., N.F., Abt. Kiel, XII, pp. 1-71.
- STEPHEN, A. C. 1933. Studies on the Scottish Marine Fauna: The Natural Faunistic Divisions of the North Sea as shown by the Quantitative Distribution of the Molluscs. Trans. Roy. Soc. Edin., LVII, Pt. III, 22, pp. 601-616.
- TAIT, J. B. 1937. The Surface Water Drift of the Northern and Middle Areas of the North Sea and in the Faroe-Shetland Channel. Fish., Scot., Sci. Invest., 1937, No. 1, pp. 1-60.
- URSIN, E. 1952. Change in the Composition of the Bottom Fauna of the Dogger Bank Area. Nature, CLXX, p. 324.
- VERWEY, J. 1952. On the Ecology of Distribution of Cockle and Mussel in the Dutch Waddensea. Their Role in Sedimentation and the Source of their Food Supply. With a Short Review of the Feeding Behaviour of Bivalve Mollusks. Arch. Néerl. Zool., X, 2, pp. 171-239.
- WHITE, K. 1937. *Mytilus*. L.M.B.C. Memoirs, No. 31, 177 pp. Liverpool.

EXPLANATION OF PLATES VII-X.

Charts showing the distribution of types of larvae during 1950 and 1951. The numbers placed near the observations give the months of occurrence. When both the 1950 and 1951 distributions are shown in a single chart, the arabic numerals refer to 1950 and the roman numerals to 1951. A few of the specific names differ from those used in the charts of Rees (1951), in accordance with the revisions given on p. 25. The scale of symbols used to give broad indications of numbers is given in Plate VII.

