[*Hull Bulletins of Marine Ecology, Vol. I, No. 4, pp. 171–238, Plates LXV–CXXV, September, 1941.*]

ECOLOGICAL INVESTIGATIONS WITH THE CONTINUOUS PLANKTON RECORDER:

THE COPEPODA OF THE SOUTHERN NORTH SEA, 1932–37

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CONTENTS

PART I.—GENERAL CONSIDERATIONS AND THE DISTRIBUTION OF THE COPEPODA AS A WHOLE (J. H. F.[1] and K. M. R.).

	PAGE
INTRODUCTION	173
METHOD OF ANALYSIS	175
ARRANGEMENT OF THE DATA	177
LIMITATIONS OF THE METHOD	177
THE DISTRIBUTION OF THE "TOTAL COPEPODA"	187

PART II.—THE DISTRIBUTION OF THE SPECIES OF COPEPODA (K. M. R.).

INTRODUCTION	195
METHOD OF ANALYSIS	195
LIMITATIONS OF THE METHOD	198
ARRANGEMENT OF THE DATA	203
THE DISTRIBUTION OF :	
1. *Paracalanus parvus* (Claus) + *Pseudocalanus elongatus* Boeck	205
2. *Temora longicornis* (Müller)	207
3. Acartia spp.	207
4. *Centropages typicus* Kröyer and *C. hamatus* (Lilljeborg)	208
5. *Isias clavipes* Boeck	212
6. *Corycaeus anglicus* Lubbock	213
THE SEASONAL VARIATIONS IN THE ABUNDANCE OF THE COMMONER COPEPODA	214
THE OCCURRENCE OF OTHER SPECIES OF COPEPODA	220
THE AUTUMN PROGRAMME OF 1937	224
A COMPARISON BETWEEN THE RECORDER RESULTS AND THE INTERNATIONAL COUNSEL SURVEY, 1902–1908	227
SUMMARIZED DISTRIBUTION OF THE COPEPODA IN THE AREA	232
A COMPARISON OF THE $5\frac{1}{2}$ YEARS	234
GENERAL SUMMARY	236
REFERENCES	237
PLATES LXV–CXXV.	

[1] Mr. Fraser was Leverhulme Fellow from 1932 until 1935, when he resigned to take up his present position with the Fishery Division, Scottish Home Department. He made the general analysis of a considerable proportion of the Recorder rolls taken during these first three years of the survey. The estimations of the constituent species which form the subject matter of the second part of this report were made by Mr. Rae.

Part I.—GENERAL CONSIDERATIONS AND THE DISTRIBUTION OF THE COPEPODA AS A WHOLE.

Introduction.

In 1932 Professor A. C. Hardy instituted a long-term survey of the plankton of the southern North Sea, using the Department of Zoology and Oceanography at University College, Hull, as a centre. The scheme departed from the conventional oceanographic methods by adopting the Continuous Plankton Recorder as the means of collecting the material. This automatic sampling instrument and the general methods and aims of the survey are fully described in 'Bulletin' No. 1.

The purpose of this report is to present a study of the varying distribution and abundance of the Copepoda in the southern North Sea from the middle of 1932 to the end of 1937. Part I deals with the copepod population as a whole and Part II with the more important constituent species or groups of species. That there are considerable variations in the numbers of the Copepoda in the area from season to season and from year to year has long been known from many previous cruises and particularly from the quarterly observations made in the plankton investigations of the International Council for the Exploration of the Sea during the years 1902–1908. The present investigation, by repeating continuous lines of observation across the area, as far as possible once a month, for five and a half years, aims at providing answers to such as the following questions: Is the seasonal sequence of changes in the population of the area broadly the same year after year? How great are the ranges of fluctuation usually encountered? Are phases of exceptionally high or low production usually only of short duration? Do two or more species tend to fluctuate together? Do some species tend to be more evenly spread throughout the area than others? When we find a markedly uneven distribution in the area, does such a pattern of distribution tend to be repeated at the same season in subsequent years?

It is intended that this Bulletin should be taken together with those dealing with the other zooplankton (Henderson and Marshall, *in the press*) and the phytoplankton (Lucas, 1940) to provide a picture of the changing plankton community as a whole. A discussion of the possible causes underlying the fluctuations found is reserved for a later paper when the results of all three reports will be considered in relation to the hydrological changes in these and adjacent waters.

With the co-operation of a number of steamship lines the Recorder was towed once a month when weather conditions and sailing schedules permitted on the following routes:

1. Between Hull and Rotterdam (East Dudgeon Light-vessel—Maas Light-vessel).
2. Between Hull and Bremerhaven (Outer Dowsing Light-vessel—Borkum Light-vessel).

3. Between Hull and Copenhagen (Humber Light-vessel—100 miles short of Hanstholm Light).
4. Between London and Esbjerg (Sunk Light-vessel—Graadyb Light-vessel).

The London-Esbjerg line was started experimentally in 1936, and did not run regularly until 1937. In the latter part of 1937 the Hull-Copenhagen line was extended as far as the Hanstholm Light, an extra 103 miles, and the Hull-Bremerhaven line to the Norderney Light-vessel, about 60 miles east of Borkum Light-vessel.

A list of the sailing dates, the times of shooting and hauling of the machine, the lengths of tow, the prevailing weather conditions and other particulars are published in ' Bulletin ' No. 2.

It may be recalled that in the Continuous Plankton Recorder the plankton is caught upon a long strip of silk gauze which is slowly wound across the flow of water passing through the internal mechanism as the machine is towed along. This silk strip is marked off into 2-in. divisions, each of which samples the plankton for a distance which can be estimated for each record, and is referred to as the " graduated silk." Directly after passing across the water flow it is met by a second band, known as the " plain silk," and together, sandwiching the plankton between them, they are wound on to a spool in a tank containing formalin. When the machine is returned to the laboratory this storage spool or " roll " is removed and put in neutral formalin to await analysis.

In the earlier years of the Department when the Continuous Plankton Recorder was only just emerging from what may be described as an experimental phase, a considerable amount of time had to be spent in designing and trying out minor modifications to assure the relatively high standard of working efficiency which has been a feature of the machine during the greater part of the survey. In addition to this the detailed correlations between the samples taken by the Plankton Indicator and herring catches (Hardy, Henderson, Lucas and Fraser, 1936) occupied a further considerable proportion of the time available, and consequently it was not possible to undertake a detailed analysis of the recorder material for the first few years. A number of arbitrary categories, which could be readily distinguished on the silk, had to be adopted as a basis for identification, although it was realized that some of them were not sufficiently specific to be ideal for ecological considerations. At this time specific identification of the Copepoda on the silk was deemed impracticable, so all species were included in a single category.

The economic importance of the Copepoda has been pointed out by a large number of workers. There is no space available here to review the literature, but we may remind the reader of one or two of the significant points in some of the more recent papers on the subject. Lebour (1921), referring to the herring, sprat and pilchard, writes, " They all eat much the same sort of pelagic food, copepods being the commonest in all after about 12 mm.," and states that the sprat still eats mostly copepods and larval molluscs after metamorphosis. Hardy (1924) lays particular stress on the importance of the smaller species, especially *Pseudocalanus* *elongatus*, in the diet of the developing herring, and shows what a large proportion of the food of the adult may be made up by the group. Savage (1931 and 1937) and Cambell (1934) give further evidence of this, while Hardy, Henderson, Lucas and Fraser (1936) show that the relative abundance of *Calanus finmarchicus* may be a good indication of the presence of herring, and give practical examples of how this inter-relationship may be used to assist the fishery. Ogilvie (1938) finds that the post-larval haddock in the Scottish area is also to a very large extent dependent on the copepod community as a source of food, almost 90% of the stomach contents of those from 3·5 to 17 mm. in length being comprised of ova, nauplii, copepodids and adults. Hart and Wailes (1932) correlate the oil content of the pilchards caught off the coast of British Columbia with the quantity of copepods in their diet; while Clarke (1934), in assessing the role of the copepods in the economy of the sea, lists mackerel, herring, pilchard, alewife, shad, blueback and pollack as fish which are known to feed chiefly on the group.

In view of these points it seemed possible that a long-term survey of the fluctuations in the combined copepod population might throw some light on the variations in the commercial fisheries, and for this reason we include in this report an account of the distribution of the Copepoda as a whole, although it must be realized that this category is comprised of many species with well known and pronounced ecological differences.

Method of Analysis.

The procedure followed in examining the Recorder rolls is described in detail elsewhere (' Bulletins ' Nos. 1 and 3). From the beginning of the survey until the beginning of 1936 the copepods were estimated in the following manner.

The graduated and plain silks were separated on a specially designed stage and each 2-in. division of silk was crossed by one traverse of a travelling microscope, using a $\frac{2}{3}$ in. objective and a $\times$ 6 ocular. The traverse was made near the centre of the division on the graduated silk and at a corresponding position on the plain. At times almost all the plankton was found to have remained on the graduated or filtering silk, but at others, especially when *Phaeocystis* was present, considerable quantities stuck to the plain or covering silk. In all cases those copepods seen in the traverse on the plain silk were added to those counted on the graduated. It was found that the area included in the field of these two traverses was a close approximation to 1/20 of the area of the 2-in. division and its corresponding 2 in. of covering silk, so the number of copepods per division was estimated by multiplying the number seen in the two cross traverses by 20.

As explained above, each division of the graduated silk had collected for a certain distance, which varied between 1·5 and 2·5 miles per division from record to record, but could be fairly accurately worked out in any one record. In order to make the data comparable for all records the numbers of copepods estimated on each division were converted to the numbers caught per mile of tow by dividing by this ratio.

A copepod was only included in the count when the proximal ends of its first antennae were in the field. This point was found to be a satisfactory criterion, as it is easily recognizable even in the most damaged specimens, and at the same time is sufficiently localized to overcome the difficulty of the size discrepancy in the group.

In addition to the total copepod estimate made with the microscope, a subsidiary examination was made with a low-powered lens or the naked eye. The purpose of this was to get as reliable value as possible for the larger species, which rarely occurred in numbers sufficiently high to be adequately estimated by the subsampling method. During this examination the late copepodids and adults of Calanus and Labidocera were counted.[1]

The plankton was then scraped from each division and its corresponding area on the plain silk with a razor-blade and placed, section by section, in separate tubes of formalin for the subsequent analysis of constituent species, when time became available.

After 1935 it was realized that data was accumulating faster than it could be analysed, and it became essential to reduce the scale of working. In order to do this, it was decided that after a roll had been analysed for phytoplankton, it should be cut up into lengths each representing 10 miles of tow. These lengths usually consisted of six or seven 2-in. divisions, and instead of taking a cross traverse on each division, only three were made, evenly spaced along the 10-mile length and, as before, three similarly spaced traverses were made on the plain silk. The copepods seen in these six traverses were again converted to an estimate of the number of copepods per mile of tow and were therefore directly comparable to the previous data.

Those records taken after May, 1937, were subjected to another modification. To economize in the quantity of silk used, the rate of winding through the Recorder was decreased by altering the pitch of the driving propeller blades, until a 2-inch division represented about 5 miles instead of about 2 miles. The 10-mile block now consisted of approximately two divisions of silk, and only one traverse was taken on the graduated part and one on the plain.[2] To prevent clogging of the silk as a result of the increased period of filtering, it was thought wise to replace the $\frac{3}{4}$-in. sq. aperture in the nose of the Recorder with one $\frac{1}{2}$-in. sq. This new aperture was calculated to allow only $\frac{4}{9}$ as much water to pass through the recorder as before, and so to compensate for the fact that on account of the reduced winding speed each division of silk was filtering approximately $2\frac{1}{2}$ times as long as previously. Such a double change, although keeping quantities of plankton deposited on the silk roughly constant, did of course reduce the numbers caught

[1] This was only adopted as part of the regular routine in 1934 after the Indicator work had shown the importance of the Calanus-herring correlations (Hardy, Henderson, Lucas and Fraser, 1936).

[2] These traverses were "staggered," *i.e.* taken in steps diagonally across the block.

per mile of tow by $2\frac{1}{4}$ times. This necessitated either raising the 1937 or reducing the 1932–36 estimates by this figure to make them comparable. The latter course was adopted, so that the figures presented here would be consistent with those in subsequent reports. All the scales appended to the diagrams indicate the numbers that would have been estimated had the $\frac{1}{2}$-in. sq. aperture been used from the beginning of the survey. These successive modifications of the Recorder have been described and discussed more fully by Professor Hardy in 'Bulletin' No. 1.

Arrangement of the Data.

Graphs of the varying abundance of the copepoda along each record have been prepared. The base line represents the length of tow in miles and the vertical scale the estimated number of copepods per mile. In the bulk of the records, all those earlier than 1936, an estimate is plotted for every section, *i.e.* at intervals of $1\frac{1}{2}$ to $2\frac{1}{2}$ miles, depending on the calculated mile-division ratio in each particular case. From the beginning of 1936 onwards only one estimate is plotted every 10 miles, but it should be remembered that this figure is derived from the analysis of all the plankton collected in those 10 miles and not from a single section or limited part of the 10 miles.

These graphs are arranged in two ways.

Firstly, each route is considered separately so that fluctuations along its length may be considered over the whole $5\frac{1}{2}$-year period and a comparison between years can be readily made. On Plates LXV–LXX the Rotterdam, Bremen and Copenhagen lines, and on Plate XCII the Esbjerg line, are taken in turn and for each the arrangement is the same. Down the side of each figure there is a time scale divided into the months of the year, and each record is placed against its appropriate date, so that the space between the base lines is proportionate to the time between the records. Each column of graphs represents one complete year from January to December, and the years are placed side by side.

Secondly, the same graphs are arranged together month by month on a series of small maps, with the base line of each in its correct geographical position. This enables one to see the distribution over the whole area at any one time. It must be remembered, however, that these maps are generalized impressions rather than instantaneous pictures of the distribution, because the records on any single map may cover a period as long as three weeks. This was inevitable on account of sailing schedules, bad weather and the limited number of machines available. The date of each record is placed under its right-hand end.

Limitations of the Method.

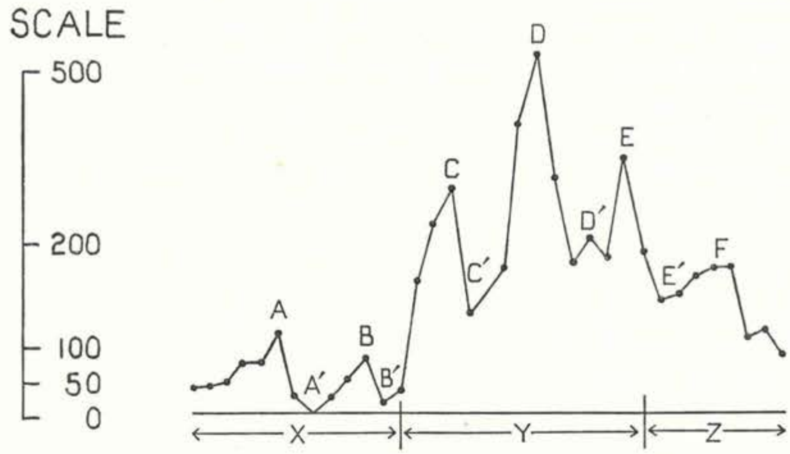
The advantages and deficiences of the Recorder method have been adequately discussed by Hardy ('Bulletin' No. 1) and Lucas ('Bulletin' No. 3). It is only necessary to mention here two of the limitations which affect more particularly the Copepoda. The first is the relatively poor catching power of the Recorder or the smallness of the sample at any one point of observation when compared with the more usual tow-net haul. This, of course, is inevitable if the machine is to be small enough to be easily handled, but at the same time is to take hundreds of samples without being hauled and reloaded; the ease and low cost with which vast numbers of samples can be taken is undoubtedly the outstanding feature of the Recorder. However, when the aperture has been reduced to prevent clogging on the length of silk that can be used in the mechanism, we find that the numbers of copepods caught per mile are low. The highest numbers estimated are of the order of 3000 individuals per mile when the $\frac{3}{4}$-in. sq. nosepiece is fitted to the machine or 1500 with the $\frac{1}{2}$-in. sq. nosepiece, but if all the results are considered it will be found that any figure over 1000 per mile is exceptional and the majority are of the order of 100 or less.

When such small samples are being used one must bear in mind the possibility of considerable variation from mile to mile due to the random sampling of the machine in the sea. Two samples may differ for two distinct reasons. In the first place they may have been taken from populations that are essentially different and so reveal the type of change sought in ecological study. Or secondly, they may have been taken from the same or a similar population, but nevertheless show a non-significant difference due to their random selection.

Superimposed on this possible error there is the experimental error entailed in the laboratory estimation of the number of individuals caught. As explained above, the method of estimation consisted of counting the number of individuals on a fraction of the silk, usually about one-twentieth, and multiplying the result by a suitable factor. Any such sub-sampling method introduces a random error, which at times may make the estimated total far from the actual total caught. Such discrepancies should not be frequent if the subsample is as large a fraction as one-twentieth, but subsequent comparison of the totals estimated on the silk and the check counts made of the scrapings showed that they did occur (see p. 199).

The smallness of the individual samples is a more serious matter in the consideration of the copepoda than the phytoplankton, as the range between the densest concentrations found and absence is so very much shorter. If the phytoplankton catches of the Recorder were analysed to the nearest 5000 individuals there would still be a clear distinction between the periods of abundance and scarcity, whereas a far less drastic procedure would tend to obscure all the seasonal variations of the Copepoda.

In view of these two sources of random error, the one in the sea and the other in the laboratory, both of which may on occasions combine to give a false impression of the actual concentration of the organism, it is clearly dangerous to put too much reliance on any single observation unless it is confirmed by others near it. It is impossible with the figures available to make any statistical estimation of the extent of these errors combined, because at no time has it been possible to take a large number of Recorder samples from a confined area to give a measure of the catching error, but some idea of their effect on the results may be derived from a consideration of the distribution graphs. It will be seen that these show a number of well-marked changes in concentration both in space and time, which are too large to be accounted for by any chance distribution, and further are shown by a number of successive but independent estimations. These are the major ecological variations that the survey was designed to reveal. Superimposed on these gross changes, there are, however, minor fluctuations which give the graph a wavy appearance. These may, of course, well be due to genuine minor patches or swarms only a mile or two in breadth, but it appears possible that they are artefacts produced by the errors entailed in the two random selections. Text-fig. 1 has been drawn to illustrate this point. The first forty divisions of record B. 3 have been replotted with a wider interval between each observation, so that each estimation is quite distinct from those on either side of it. Each division on this



TEXT-FIG. 1.—A graph of the estimated numbers of the " total Copepoda " on a part of a Bremen line record. For further explanation see text.

record represented 1·7 miles, so that each point plotted was this distance from its neighbour in the sea, but it should be borne in mind the number of copepods plotted on the vertical scale is an estimation of the number present in the 1·7 miles sampled and not the number at that particular isolated point.

In this figure it can be seen that the distribution graph is made up of a number of peaks (A, B, C, D, E, F) alternating with troughs (A′, B′, C′ . . .), superimposed on the general trend. Whereas, for example, one can place little confidence in the peak " E " or the trough " C′ " which are shown by only one and two estimations respectively, there can be no doubt as to the validity of the general trend if it is expressed broadly: that is to say there were many more copepods in the water sampled by the tow Y than by X. This is quite clear from the fact that all the 13 estimations included in Y are higher than any of the 13 in X, and that their mean value is more than six times as high. This report deals with major differences shown by trends of this sort, which are far too pronounced to be greatly affected by the inaccuracies entailed in the sampling techniques. See also p. 203.

The second, and what at first sight must be thought the most serious limitation of the Recorder method, is that all samples are taken at a single depth—10 metres. This depth was selected as a compromise in the hope that it would give a fair picture of the distribution of both the phytoplankton and zooplankton. Lucas (' Bulletin ' No. 3) has shown that for the phytoplankton at least it is fairly satisfactory. Using figures published by Savage and Wimpenny (1936), he found a reasonable approximation to a straight line correlation between the numbers of cells taken in horizontal hauls at depths between 5 and 25 metres and the corresponding vertical hauls, and again between the numbers of cells in mid-water hauls and the mean of surface, mid-water and bottom hauls. However, as has already been pointed out by Hardy (' Bulletin ' No. 1), this limitation is likely to be much more serious in the case of the zooplankton, as so many of the organisms are known to make diurnal vertical migrations. Most of the work that has been done in the past on the vertical distribution of the Copepoda has been confined to the larger forms, *Calanus finmarchicus* especially being selected. Data have been produced by many authors for this species, but in view of the fact that it is omitted in the present report, and that it is relatively scarce in the area under consideration, we have decided to postpone any analysis of their figures until the later report dealing with the distribution of Calanus.

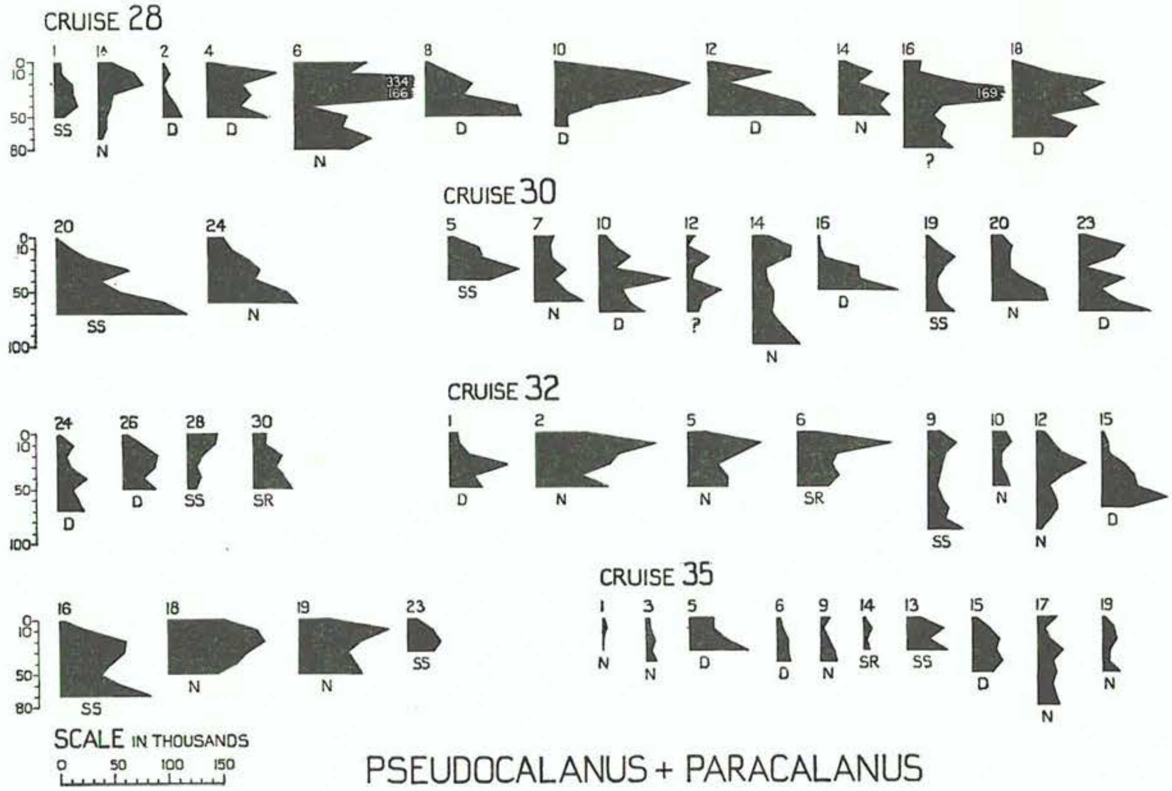
In order to form an estimate of the value of observations taken at a standard depth of 10 metres we must find out what proportion of the whole vertical population, for the commoner forms, we are likely to find at 10 metres at various times of day or at various seasons. Savage (1931) offers some very useful information on this subject. At a number of stations on four cruises in the summer and autumn of 1926, he took horizontal hauls at the surface and at 10-metre intervals to the bottom. His cruises covered the herring grounds and the bulk of his samples were taken from the Shields and Off-Flamborough areas, while a few of them came from further south off the East Anglian coast. They are then not far removed from a part of the area covered by the recorder survey, and although they are generally in slightly deeper water, they may be assumed to have sampled comparable populations. The vertical distributions of Pseudocalanus (+ Paracalanus) and *Temora longicornis* as found by Savage at these stations are shown diagrammatically in Text-figs. 2 and 3. There is in addition information for Centropages spp. from one cruise only. These diagrams bring out very well the variations there may be in the apparent density of the population between the surface and the bottom, and at the same time make it clear that the variations are of two types. Firstly there is the tendency for the bulk of the individuals to be nearer the surface or bottom, or at some mid-water level, and secondly, superimposed upon this, there are a number of irregularities in the distributions which are too pronounced to be accounted for by sampling or estimating errors. These may be described as examples of " vertical patchiness."

Under each diagram the letters D, N, SR or SS indicate whether the samples were taken in daylight or darkness, or within one hour of sunrise or sunset. It will be seen that generally, as might be expected, the majority of the copepods were deeper in the water during the hours of daylight, but that this was by no means invariably so. For example, the highest number of Temora taken was at 10 metres three-quarters of an hour before midday at Station 2 on Cruise 28, whereas on a number of occasions the larger numbers were found near the bottom after some hours of darkness, for example Pseudocalanus at Station 22 on Cruise 28, and at Station 20 on Cruise 30.

In order to test the probable effect of vertical migration or any other factor on the Recorder results, it is necessary to have some figures expressing the proportion of the copepods at 10 metres at each station. In the absence of more information we may average the horizontal catches from different depths to give an indication of the plankton there present, and so, by expressing the catch at 10 metres as a percentage of this average and comparing the percentages under various conditions, we can get an idea of the inaccuracies entailed in sampling at this depth only. To simplify the discussion, it is convenient to refer to this percentage as the "10-metre value."

It is clear that over the period worked by Savage, a number of false impressions would have been obtained, had only his 10-metre hauls been considered. In the first place Pseudocalanus (+ Paracalanus) had a different vertical distribution from Temora over the whole period. The mean of the "10-metre values" for all cruises was 98% for the former and only 54% for the latter, so that Temora would have appeared only about half as abundant as it should have done relative to the Pseudocalanus group. Secondly the vertical distribution of both forms varied from cruise to cruise. For Pseudocalanus (+Paracalanus) the average "10-metre value" for Cruise 28, which was made towards the end of June, was 90%, for Cruise 30 in early August 83%, for Cruise 32 in early September 120%, and for Cruise 35 in mid-October 102%. Variations of this order need not be considered very disturbing, especially in view of the fact that there happened to be a higher proportion of day stations in the first two cruises than in the latter two. The figures for Temora on the other hand appear far less satisfactory, the mean "10-metre values" for the four cruises being 57%, 13%, 70% and 85%. Differences of this kind might have a very serious effect on conclusions drawn from samples at 10 metres, as one would have had the impression that August was a particularly poor month for this species, when in fact it was quite as successful as September and October. It will be seen from Text-fig. 3 that at no time during Cruise 30 was there an appreciable proportion of Temora above 30 metres, with the exception of the very shallow Station 5, although it included three sets of night hauls and one near sunrise.

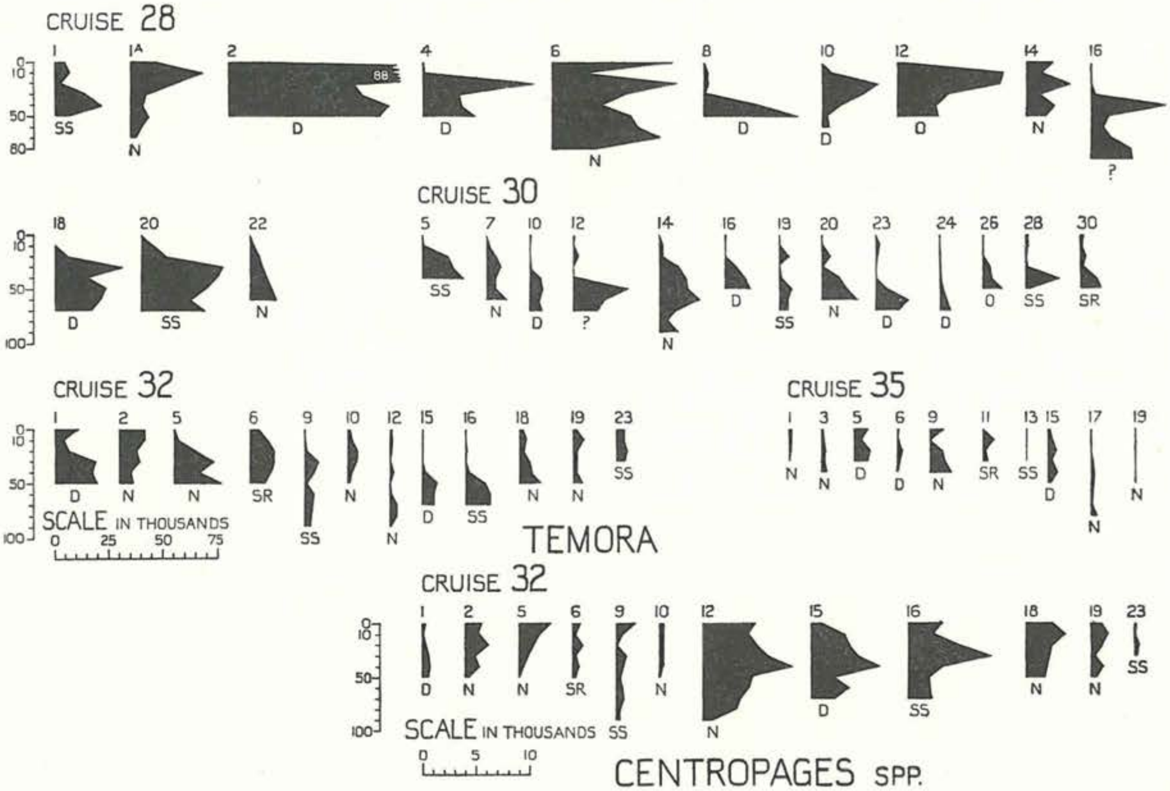
The effect of diurnal migration on the population at 10 metres can be summarized in the following way: The average "10-metre value" for Pseudocalanus (+Paracalanus) at the 19 stations sampled between sunrise and sunset was 90·6%,



TEXT-FIG. 2.—Diagrams showing the vertical distribution of Pseudocalanus + Paracalanus at points in the North Sea during the summer and autumn of 1926 drawn from the data of Savage (1931). Above each diagram is the station number, and below it is an indication of the time of day at which the samples were taken: D for daylight, N for darkness, SS for within an hour before or after sunset, and similarly SR for sunrise. The vertical scales represent depth in metres, the horizontal scale the number of individuals taken in the tow-nettings.

while the 25 stations sampled between sunset and sunrise gave an average of 98·8%. This certainly appears to support Professor Hardy's contention in ' Bulletin ' No. 1 (p. 48) that in these shallower waters the effect of vertical migrations would prove relatively unimportant. Again, however, the results for Temora are less satisfactory, the average value for day being 40·8%, and for night 69%.

We may note in passing that the eight sets of hauls which were taken within one hour of sunset gave a relatively low average " 10-metre value " for both forms: 72·6% for Pseudocalanus (+Paracalanus) and 37·5% for Temora. These figures are surprisingly low in view of the suggestion made by Michael (1911) and supported by Russell (1927A) that organisms tend to concentrate most in the surface layers about the hours of sunrise and sunset. There were only three stations sampled within an hour of sunrise and these did give high average values at 10 metres: 145·7% and 111·3% for the two forms respectively. But clearly

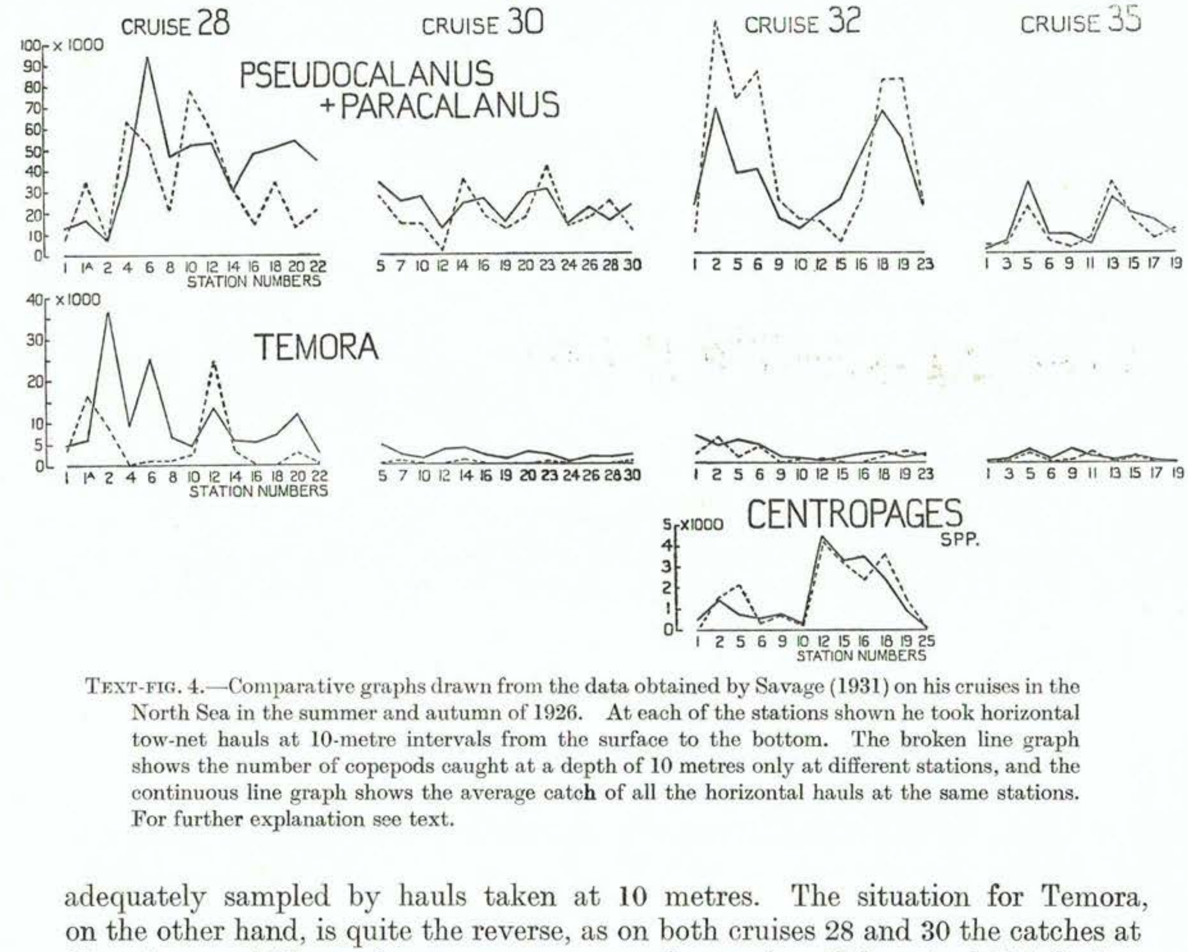


TEXT-FIG. 3.—Diagrams showing the vertical distribution of *Temora longicornis* and Centropages spp. at points in the North Sea during the summer and autumn of 1936 drawn from the data of Savage (1931) and arranged as explained under Text-fig. 2.

not much weight can be attached to figures derived from so small a number of observations available (either for sunset or sunrise).

We have also tried correlating the " 10-metre values " with the depth of the stations, with the density of the population, and with the spatial arrangement of the stations. There was apparently no relationship in the first case. From the second, although there was no significant correlation, it was clear that a large proportion of the low " 10-metre values " occurred when relatively few copepods were present at the station. This was especially so for Temora, as can be seen in Text-figs. 3 and 4. There was some suggestion that the third might have proved interesting had there been more stations spread over a larger area, as there was a tendency for groups of adjacent stations to have similar values, but the limited data available do not warrant the publication of the figures involved.

In Text-fig. 4 the numbers caught at 10 metres and the average catches of all the hauls at each station have been plotted together. The cruises have been considered as single straight traverses when in reality the stations are scattered over an area, but such an arrangement allows a convenient comparison between the apparent distribution that would have resulted from the consideration of the 10-metre hauls only and the nearer approximation to the true distribution. We find, as we might expect from the remarks above, that for the Pseudocalanus group, although at some stations the figures are widely discrepant the general picture is quite good. The two main concentrations on Cruise 32 are clearly shown and the overall changes from cruise to cruise are quite apparent. From the limited data available, it appears that Centropages would also be quite



TEXT-FIG. 4.—Comparative graphs drawn from the data obtained by Savage (1931) on his cruises in the North Sea in the summer and autumn of 1926. At each of the stations shown he took horizontal tow-net hauls at 10-metre intervals from the surface to the bottom. The broken line graph shows the number of copepods caught at a depth of 10 metres only at different stations, and the continuous line graph shows the average catch of all the horizontal hauls at the same stations. For further explanation see text.

adequately sampled by hauls taken at 10 metres. The situation for Temora, on the other hand, is quite the reverse, as on both cruises 28 and 30 the catches at 10 metres would have given a very erroneous impression of the actual distribution. It is true that on the whole the numbers for Temora were lower than those for Pseudocalanus, and so, it might be argued, must be expected to be less reliable, but these are in their turn relatively high when compared with Centropages. There is, however, some reason to suppose that Temora is an exceptional form, and that any conclusions drawn from its distribution should be treated with some reserve. Regarding this Farran (1910, p. 72) wrote : " This species has the habit, more marked than in most other copepoda, of forming swarms of great density but limited extent, so that conclusions as to its abundance in any region drawn from a small number of tow-nettings may be very misleading."

There is a second method of approach to the problem of the validity of observations taken at 10 metres—that of using the recorder material. Clearly such questions as whether the vertical distributions of the species vary from season to season or whether the species appear in their true proportions at 10 metres cannot be answered by analysis of information derived from this depth only, but nevertheless it is possible to assess the effect of diurnal migration and this might be expected to be the most serious factor. For this purpose, the parts of each record which were sampled in night and day, during the first $2\frac{1}{2}$ years of the survey, have been separated. As will be seen from the station list (' Bulletin ' No. 2), owing to the regularity of the sailing schedule, practically all the Rotterdam records were taken at night. On a few occasions the machine was not hauled at the eastern end of the tow until a few hours after sunrise, but these parts of records are too few and restricted to give a fair statistical comparison with the night records and can be more conveniently considered individually. In 1933 they consist of the following distances from the eastern ends of the records : In January 20 miles, August 20 miles and December 30 miles ; while the first 15 miles at the western end of the April record were also taken in daylight. It will be seen by reference to the various plates that these day observations, when compared with the rest of the line, were relatively high for all species in both January and December, and that Temora particularly was well represented on the August record during the daytime. In 1934 most records had some part of their eastern end towed during the hours of daylight, and although this was usually restricted to the last 20 or 30 miles, again it is quite clear from the plates that it does not appear less densely populated than the rest of the area which was sampled at night. In fact, by the chance that a number of day samples were taken in the region of the winter coastal concentration, they are on the whole higher than those taken at night. It may be pointed out, however, that the coastal concentration is still clearly shown when sampled at night, for example, on the April record of 1933 and the January record of 1934 with the exception of the last 5 miles.

There is a danger of obtaining a false impression when time and space are as closely correlated as they are on the Rotterdam line. For instance, if the day samples are always taken from an area with a population normally higher, the effect of vertical migration might only be to make the differences between this area and those sampled at night appear less than it should be. This becomes a much less serious possibility on the Bremen line, where, although there is some tendency for night observations to occur more frequently at either end of the record than in the centre, the sailing schedules are much less consistent. On this line in the first $2\frac{1}{2}$ years about 40% of the samples analysed for constituent species (see p. 196) were taken from parts of records towed at night and about 60% during day, the actual numbers being 157 and 234 respectively. The average number of

Pseudocalanus (+ Paracalanus) per mile in the night samples was 69·5 compared with 62·2 in the day, of Temora 28·8 compared with 35·8, and of Acartia 16·0 compared with 23·2 ; so that taking the three species together more individuals were taken by day than by night. We must bear in mind, however, that a few patches are sufficiently dense to have a considerable biasing effect on the result should they fall more frequently in the day than in the night, and there is, of course, a tendency for denser populations to occur during spring and summer when there are relatively more hours of daylight. To eliminate the effect of this, we can estimate the proportion of records on which the average number of individuals per mile was higher during the night than during the day. In doing this it has been thought wiser to neglect those records that had less than three samples in either category. There remain 22 records ; for Pseudocalanus (+ Paracalanus), Temora and Acartia the ratios of higher day and night values are 13 : 9, 12 : 10 and 9 : 13 respectively, or a combined ratio of 34 : 32. This, it may be argued, is sufficiently close to equality for us to conclude that diurnal migration has little if any effect on the apparent distribution of these forms at 10 metres. But before being confident of this we should make sure that these figures are not the result of the fairly regular sailing schedules and the consequent tendency for the night samples to be at either end of the line. Now if the arrangement of the day samples is effectively random in relation to the denser patches of copepods and vertical migration has no considerable effect at this depth, we can assume that each form has an equal chance of being higher in the day or at night on any record. Consequently, as there are three forms, the normal expectancy would be that out of any eight records, all three would be higher in the day on one, two forms would have higher day values on three records, one would be higher in the day on three, while on the remaining record all three forms would have higher night values.[1] If, on the other hand, vertical migration was causing considerable changes in the population at 10 metres, yet its effect was obscured through some correlation between the times of towing and the spatial distribution of the copepods, we should expect a considerably higher proportion of records on which all three forms behave in the same manner, giving in an extreme case a ratio of 4 : 0 : 0 : 4 instead of the 1 : 3 : 3 : 1 mentioned above. We find in fact that the 22 records available are divided into the four categories in the following way : 3, 7, 9 and 3, which is a close approximation to this 1 : 3 : 3 : 1 ratio. Therefore it is improbable that the distribution of day and night samples in the area is responsible for our result, and we can assume that vertical migration is an unimportant factor at this depth and in this area.

[1] If D and N are used to signify higher values for day and night respectively, the only possible combinations on the eight records are :

	1	3	3	1
Species "A" .	D	D D N	N N D	N
,, "B" .	D	D N D	N D N	N
,, "C" .	D	N D D	D N N	N

THE DISTRIBUTION OF THE "TOTAL COPEPODA."

The distribution over the $5\frac{1}{2}$-year period will first be considered for each line in turn and then that over the whole area will be discussed.

Rotterdam Line.

It will be seen (Plates LXV and LXVI) that in January, 1933, on the Rotterdam line, the bulk of the Copepoda were taken on the eastern end of the record, but that this had become less pronounced in March and April. During the summer months, with the exception of a central patch in July, the distribution appeared low and relatively even, and remained so until December. The records in December, 1933, and January, 1934, showed that there was again an eastern concentration similar to that found at the beginning of the year, but by March and April this, as in the previous year, had become less marked, and during the summer months the copepods were fairly evenly distributed. The first record in November showed a well-defined concentration near the Dutch coast, and from then until April, 1935, there remained some indication of the eastern preponderance, though this was not so marked as in the winter months of the previous years. From March, 1935, when the numbers found were very low, there was a steady increase in copepods, which was, in April, restricted to the eastern end, but was by June apparent across the line, and in July more were found in the west and centre than in the east. In August and September they remained relatively abundant and evenly distributed, but in October they had become much scarcer on the western half of the line, and decreased generally through November until in December the few that were found were taken near the Dutch coast. The same type of distribution persisted until April, 1936, practically none being found except in the east and there only few. The population remained sparse throughout this summer, though as in previous years there were indications of an extension across the line in June, July and August. By December there had been an improvement in the population on the eastern half of the line, and in fact the numbers taken then were higher than at any other time in the year. This distribution with the copepods restricted to the farther side of the Southern Bight remained fairly constant during the first half of 1937, but by July there were well-marked signs of a return to the usual summer arrangement. Unfortunately although there were two August records, both were short at the western end. The later one appeared to have sampled the edge of a very strong concentration about 50 miles from the English coast, but there was no further indication of this in the subsequent months, during which numbers decreased sharply until December, when practically none were found.

To summarize, as briefly as possible, the copepod distribution on the Rotterdam line, it may be said that in all the winters the copepod population was restricted to the Dutch coast—an arrangement which normally persisted from November until April. It will be seen that in January, 1933, December, 1933, and January, 1934, the copepods were relatively abundant in this region, but that in the following winters, although they were more numerous here than in the west and centre, they never occurred in such large numbers. During the summer months the population was always more evenly spread across the area, and during midsummer there were at times indications of a slight preponderance near the English side. This was pronounced in August, 1937. The most striking features of this series are the extremely poor summer population in 1936 when compared with those of 1935 and 1937, and the apparently progressive decrease of the density of the eastern population during the winter period, from 1932–33 until the end of the survey.

Bremen Line.

By reference to Plates LXVII and LXVIII, which show the distribution of the " total Copepoda " on the Bremen line, it will be seen that broadly the seasonal variation was the same as that on the Rotterdam line. There were no data for the beginning of 1932, but all the records taken in January, February, March and April of 1933–36 showed the tendency for the eastern half of the line to be richer than the western, as during the winters on the Rotterdam line. This was followed, with the exception of 1934, by a marked spring increase in the population, May being in fact on the whole the most prolific month of the year. In 1932, in the absence of any previous records, the copepods appeared most abundant in June. They were at this time situated in two well-defined patches on either side of the centre of the line. During July and August they were much scarcer, but in the latter month more abundant near the English coast than elsewhere ; this was less marked by September, and from October onwards there was a progressive change to the normal winter distribution with the majority at the eastern end. This was followed in May, 1933, by a spring increase, concentrated in a central patch, which appeared to persist in a lesser degree on the part record taken at the beginning of June. In July there was again a concentration near the English coast, as in the previous year, but also a second patch at the other end about the region of the Borkum Light-vessel. Far fewer copepods were taken in the later months of 1933 than in 1932, but as before, there were by November indications of a return to the winter arrangement. As mentioned above, there was no real increase in the spring of 1934, and the eastern restriction in the first three months was less noticeable than in other years, but there was, however, the apparent movement of the centre of concentration to the western side in June. The copepods remained unusually even both in space and time throughout this year, though there was a slight increase in August. It will be seen, however, that although there was no sudden change in the density of population on part of the line in the spring, as in other years, the numbers found throughout the year as a whole were quite as high as normal, and in fact considerably higher in the late summer than in either 1933 or 1937.

In the spring of 1935 the increase was very pronounced. At the beginning of May there appeared an enormous concentration at the eastern end of the line. At the end of the month there was a concentration still here, but, in addition, a very dense patch in the centre. The numbers decreased considerably after this, giving rise to a central arrangement in June, followed by a bimodal distribution in July, with the peaks situated at either end of the line in a manner somewhat similar to that shown in July, 1933. From September onwards there was a general depletion of the population.

The numbers were never high in 1936, when compared with the spring of 1935. In May there was a small but definite increase across the line, but the bulk were still taken in the east. By July the centre of concentration had moved well to the western half of the line, even more markedly so than in previous years, and as before, there was, from September until the end of the year, a gradual reversal to the winter distribution, which became established by the end of November.

During 1937 copepods were very scarce on this line except in May. Unfortunately in January, February and March the records were all short at the eastern end, but, as far as they sampled, they showed no significant indication of the eastern concentration, which normally occurred in the winter. In May, however, there appeared a very dense patch over the eastern half of the line. This had disappeared in the following month, and the numbers remained very low and even from then until the last record, which was taken at the end of November. There was in this year no patch near the English coast in mid-summer as previously, the only possible suggestion of this being a relatively low patch extending some 40 miles from the Outer Dowsing Light-vessel on the first September record.

The main points shown on the Bremen line may be briefly summarized as follows. There was, as on the Rotterdam line, a well-defined and typical winter distribution. From November onwards the copepods appear to be progressively restricted to the eastern end of the line, usually becoming concentrated in the last 40 or 50 miles in January and February. In May there was generally a spring increase, which might appear either in the centre of the line or in the east. Central concentrations in June were followed in 1932, 1933 and 1935 by low numbers in the centre and patches at either end of the line. Again, as on the Rotterdam line, the summer months showed a more even distribution than the winter ones, and a tendency for the higher concentrations to occur towards the English coast. The summer of 1935, as also on the Rotterdam line, is marked by an exceptionally high copepod population, whereas June, July and August of 1937 and August of 1933 show an abnormal poverty for summer months.

Copenhagen Line.

Plates LXIX and LXX show the " total Copepoda " data derived from the Hull-Copenhagen route. There were no satisfactory records for April, May or August in 1933 and no records had been taken prior to June, 1932, but nevertheless it is immediately apparent that numbers were far lower during these summers than during those of the subsequent years. There is, in fact, only a relatively small difference between the numbers taken during the summer and winter in 1932 and 1933. During these two years the distribution remained very even spatially, and with the exception of a slight western preponderance in October, 1932, and September and October, 1933, there is little of significance. It may, however, be worth drawing attention to the small patch situated directly over the south-west patch of the Dogger Bank in March, 1933, for comparison with later years.

From 1934–37 there is a well-defined difference between the summer and winter records. From the late autumn until March there was never more than a very sparse population, and no indication of the eastern concentration found on the two more southerly routes.[1] Throughout the summer, on the other hand, the copepods were relatively abundant. There appeared in April of each year, with the exception of 1936, when there were no data, a general increase over the Dogger Bank, which was usually maintained until August or September, before any marked decrease started to produce the winter scarcity. In this respect the Copenhagen line differed from the Bremen, because in the latter, a pronounced increase in May was generally speaking followed by considerably lower numbers in the next months.

At the end of April, 1934, the increase was well pronounced across the line, but the majority of the copepods were taken in a dense patch over the South-West Patch (*cf.* March, 1933). In the June and August records there was no sign of this patch, but the copepods remain fairly abundant across the line. From September onwards there was steady reduction.

In 1935 the late April record showed again the spring increase as in 1934. In this year, however, it was not so much localized but extended well across the Dogger Bank, although centred about the middle of the line. In May this broad single patch had given place to two large patches situated over either end of the Bank. The area of lower concentration between these two coincided exactly with that part of the line which passes just outside the 20-fathom contour. This can be seen in Plate C, where the 20-fathom contour of the Dogger Bank is included. The June record was unfortunately curtailed on account of fog and only sampled the western half of the line; it revealed, however, a dense patch about 50 miles from the English coast, and high numbers towards its eastern end. The July and August records showed a similar distribution to that found in May; the two patches were slightly less defined to the east and west, but still had their centres of concentration in the same places as before and still showed the region of

[1] In this respect it should be remembered that this line usually ended at least 100 miles from the coast. It may be argued that had it extended farther, coastal concentrations similar to those found on the Bremen and Rotterdam lines would have been sampled. This, however, was not found to be so in 1937 when the extra information was available, nor, to anticipate a later report, were there more than the slightest signs in 1938 and 1939.

lower numbers outside the 20-fathom contour. By September and October the distribution was far more even with the numbers decreasing and by December very few remained.

There was very little data available for the spring of 1936. Unfortunately in March, April, May and July a series of mechanical defects caused the records to be short. In the first three of these months only about 60 miles were satisfactorily sampled. The only facts apparent from these part records were that there was an increase at the extreme eastern end of the line from April to May, giving rise to a considerable concentration here in early July. Further, there were relatively few copepods over the Dogger Bank in the latter month. A record in August showed no indications of the high numbers over the Bank as in 1935, but rather that the bulk of the copepods were situated to the west and over its eastern end. By November the copepods were again scarce.

The spring increase in numbers was again apparent in April, 1937. There was only a slight increase over the major part of the line, but a dense concentration only a few miles broad was found about 60 miles from the English coast just west of the South-West Patch. At the beginning of May there was a further increase on the central and eastern parts of the line, slightly larger numbers being taken over the north-eastern end of the Bank than elsewhere. The following month there were similar numbers over the north-eastern end, but to the east and west of this two very dense concentrations had appeared. By July there were still two points of concentration comparable to those in June, but both further west. In August the numbers were lower in the area sampled, but the record stopped 90 miles short at the English end. During October, November and December very few copepods were taken, and it seemed that the winter distribution had appeared earlier than in previous years.

From July until the end of December the normal length of the Copenhagen-Hull tow was extended by 100 miles. This extra distance sampled revealed very little in these six months except a third centre of concentration in July.

Considering the results obtained on the Copenhagen line as a whole, one sees that 1932 and 1933 are probably comparable in their relative scarcity of copepods, that 1935 and 1937 are similar in their abundance, and that 1934 lies as an intermediate between the two pairs. In view of this it is interesting to note that there is a marked similarity in the seasonal spatial arrangement found in both 1935 and 1937. Early in both years there appeared a very wide patch centred over the Dogger, which gave place in subsequent months to two centres of concentration, which persisted for two months in 1937 and four months in 1935. This suggests some relationship between the density of the population in this area and the factors governing its spatial distribution. A series of short records in 1936 provide only limited data for the spring of that year and prevent comparison with other years, but the July and August records indicate that it may have been at least as successful as 1934.

Esbjerg Line.

In 1937 the Esbjerg line was instituted regularly. It was run from the Sunk Light-vessel to the Graadyb Light-vessel. The results obtained therefrom are presented on Plate XCII. It afforded a useful check for the Bremen and Rotterdam lines, and also gave some idea of the distribution across the Heligoland Bight.

It will be seen that the April record showed the winter arrangement of copepods which might be expected from the consideration of these other lines. There was a general low distribution with a slight preponderance towards the north-eastern end of the line in that part of the Bight sampled by the eastern end of the Bremen records. In May there was a very marked increase in this region, which, as has already been pointed out, was also revealed by the Bremen record for this month. This concentration stretched well up towards the Danish coast. The June record was short at both ends, but the 160 miles that were valid indicated that the centre of concentration was by this time south-west of the centre of the line, that the numbers were generally lower, and that the really dense patch found in the east in the previous month had moved away from this area or had died down.

The records for July and August showed relatively even distributions along their lengths, although a number of minor fluctuations were found. Numerically the population appeared slightly lower than in the two preceding months, but nevertheless was surprisingly high when compared with the contemporary Bremen records. It may be remembered that during this period very few copepods were found on the Bremen line, whereas the numbers on the Rotterdam records were quite as high as usual.

From September until the end of the year all the Esbjerg records caught very few copepods and the general sparse winter arrangement appeared to have returned.

Distribution in Area as a Whole.

It is hoped that by considering the fluctuations on the four lines together a better idea may be obtained of the general distribution of the copepods in the area. To facilitate this the graphs of the various records have been arranged month by month on a series of small maps. Each record is placed in its correct geographical position (see Plates XCIV–CVI).

It is convenient for this purpose to divide the year into four quarters and treat these independently.

During the first quarter, January, February and March, it will be seen that spatially the population is arranged in a similar manner in each year. There appears to be a band of relatively high concentration off the Dutch coast and following its contour. There is in different years a varying degree of westward extension of this community; for example, it is less pronounced in 1934 on the Bremen line than in other years, but, nevertheless, it would seem to be a very consistent feature of the winter distribution. Over the rest of the area, during these months the numbers are low and even. It must be borne in mind that there is no absolute evidence of continuity between the patches of copepods found at the eastern ends of the Bremen and Rotterdam lines, but in view of their persistence for several months of each year, they may be considered indicative of a general coastal concentration stretching at least between the points of observation.

The next quarter is characterized by an increase in the density of the population over the northern part of the area. The actual timing of the arrival of this increase is made difficult by the fact that April and May have been, throughout the survey, months in which, for some unknown reason, there has been a far higher incidence of unsatisfactory records than in any others. However, in the three years 1934, 1935 and 1937, in which data for April was available on the Copenhagen line, there were signs of a change from the general low winter distribution. In 1934 there appeared a dense patch over the South-West Patch, in 1935 a general increase over the Dogger Bank, and in 1937 a patch just to the west of the edge of the Bank. On the Bremen line satisfactory April records were only obtained in 1935 and 1936, and whereas there was an enormous concentration in the east on the former there was no indication of this on the latter. If, however, the maps for the months of May are considered there is evidence leading to the conclusion that this synchronous increase over the Dogger Bank and at the eastern end of the Bremen line is quite usual in the spring. It will be seen that the general picture for May, 1937, is rather similar to that shown for April, 1935, and by reference to the dates in 1935 it will be noticed that all the records were taken near the end of this month. Further, although there was no change found on the Bremen line by the middle of April, 1936, there was a higher concentration in May, and this was again more pronounced towards the eastern end. Generally speaking there is a tendency for the bulk of the copepods to be concentrated much nearer the centre of the area during this quarter than during the first.

The July-September quarter reflects the success or failure of the spring increase in population. By this time the copepods have become fairly evenly spread over the area and the patchiness which is typical of the spring months is less marked. It can, however, be a very lean period, as for example in 1933. One comparatively consistent characteristic of these three months is the tendency towards a bimodal distribution on the Bremen line. A region of lower concentration in the centre of the line appears in some degree at some time during the quarter in every year except 1936. It was most pronounced in July and August, 1935, but was also noticeable in July, 1932, July, 1933, August, 1934, and August and September, 1937.

The last quarter shows a transition from this relatively plentiful summer stock to sparse winter distribution and the tendency to the coastal concentration off Holland.

Without doubt the most striking feature of this series is the extent to which the density of the copepod population can vary from year to year. Although there is some variation in the success of the winter populations, that of 1932–

1933 being particularly good, these are insignificant when compared with the differences between the spring and summer months during the five and a half years. It is difficult to assess 1932, as no records were taken before June, but there can be little doubt that, if the July to September periods are compared, it was a more successful season than 1933. Unfortunately we are very short of information in April and May of 1933, but with the exception of the winter coastal concentrations, the May Bremen record was the only one that showed any indication of high numbers. 1934 showed an improvement. Again there was a run of bad luck with the spring records, but the June, July and August maps show clearly that the population was stronger than in the previous year and probably than in 1932. In April and May, 1935, after a comparatively poor winter, really high numbers of copepods were taken for the first time. These concentrations on the Copenhagen and Bremen lines were not only denser than any found before, but they were widespread when compared with the restricted patches found in May, 1933, and April, 1934. Further, in this year, the larger catches continued well into the autumn, and until August they remained higher than those in the most successful months of the earlier years. Although once again the spring information was spoilt by a series of short Copenhagen runs, 1936 obviously fell well below the 1935 level, but nevertheless appeared slightly more successful than 1934. Then following another lean winter period, there was between April and May, 1937, another sudden increase in the population very similar to that of 1935. Although the high numbers did not persist on the Bremen line as long as they did in the former year, the northern part of the area was still as successful in July.

With the copepods forming an important link in the food chain, fluctuations of this magnitude must almost inevitably be reflected in the general ecology of the sea. Almost certainly such changes will play a big part in determining the success or failure of the fry of many of the marketable fish which depend on the smaller copepods for a large part of their diet, and it is quite probable that a long-term study of such gross changes, especially over an extended area, will be of great assistance in forecasting the variations in the commercial fisheries.

PART II.—THE DISTRIBUTION OF THE SPECIES OF COPEPODA.

INTRODUCTION.

As has been pointed out earlier in this Report, during the first years of the survey it was only possible to identify and count the "total Copepoda" as a combined group and add to this an estimate of the number of larger species. Although knowledge of the seasonal production of the whole copepod population and more especially of the factors controlling long-term fluctuations in its success might well, with careful interpretation, be useful in helping to forecast the variations in the commercial fisheries, it is clear that an understanding of the ecology of the components of the population would make this a great deal more probable. Whereas there may be over-riding physical conditions controlling the entire stock, there will also be other minor factors affecting only those parts of it that have particular ecological idiosyncrasies. There is some evidence that as a result of selective feeding, some fish may be more dependent on certain copepod species than others. For example, Lebour (1919) described copepods as the chief food of larval and post-larval fish, and pointed out that although most fish eat one or more of the four commonest species, *Pseudocalanus elongatus*, *Temora longicornis*, *Acartia clausi* and *Calanus finmarchicus*, there is usually in each case a definite selection. The whiting up to 9 mm. show a preference for Pseudocalanus, but in the spring, when this species is less common, will take Acartia or Calanus but rarely Temora, even if it is very abundant. The soles and the dab eat Temora but hardly ever Pseudocalanus, while *Scophthalmus norvegicus* appears to select Pseudocalanus and Acartia. Again the particular importance of the single species, *Pseudocalanus elongatus*, in the southern North Sea was stressed by Hardy (1924). He showed that in that area the post-larval herring are almost entirely dependent on this species for food during approximately three months of their development, and suggested that variations in its success from year to year might play some part in controlling the fluctuations in the numbers of adult herring in subsequent years. It is also clear from his investigations that whereas older herring (*i.e.* those over 30 mm.) might be able to make up a deficiency of Pseudocalanus by taking, for example, Temora if it was more abundant, the smaller individuals would be unable to do so on account of its larger size.

Such considerations made it clear that it would be valuable to return to the material that had been scraped from the rolls and to attempt as detailed an analysis as possible. An opportunity to do this did not present itself until 1936, and then the time available prohibited the examination of more than a fraction of the samples available.

METHOD OF ANALYSIS.

For the purpose of this survey one record per month has been analysed for constituent species on the Bremen and Rotterdam lines and one every other month on the Copenhagen line whenever this was possible. In months when more than one record had been taken on a line, the longest was selected and an effort was made to select those rolls for analysis which were as evenly spaced in time as possible. At first every fifth tube was analysed, giving an observation at about every 10 miles along the length of the line, but after half the Bremen records had been completed it was found to be necessary to reduce the number of tubes analysed by half, so that from then on data for the relative abundance of the constituent species were only taken approximately every 20 miles. As described in ' Bulletin ' No. 1, after the first few months of 1936 the rolls were divided up into units or " blocks " representing 10 miles of tow. Every second " block " was analysed for the copepod species, so that from this point the observations are at exactly 20-mile intervals. It should be noted, however, that whereas previously each analysed sample only contained the plankton from approximately 2 of the 20 miles it was taken to represent, it now contained the plankton from 10 miles.[1] The scraping technique has been referred to earlier in this report. Briefly it was as follows: each 2-in. division of silk was thoroughly scraped with a razor-blade, and plankton from it was preserved in a tube containing 4 per cent. neutral formalin, to await any further identification or confirmation of the silk estimations that might be deemed necessary. During the earlier part of the survey the plankton from each division (*i.e.* 2 in.) was kept separately, but from the beginning of 1936 a number of divisions were added together, so that each tube represented the catch from 10 miles of tow (see p. 176).

The procedure adopted with each tube analysed was as follows: The tube contents were washed out into a round dish 4·8 cm. in diameter. Using a low-powered lens, a count was made of all the larger genera, such as Calanus, Labidocera, Metridia and Candacia to confirm the similar counts made on the rolls, and to provide data for those rolls which had been analysed before the practice of counting these on the silk was adopted and for those on which the abundance or type of plankton had made this count unreliable.

After the dish had been thoroughly shaken to give an even distribution of plankton over its area, it was placed on a " Murray " long range mechanical stage and traverses were made across two diameters at right angles to each other. The optical equipment consisted of a $\frac{2}{3}$-in. objective and a $\times$ 6 ocular. It was found by experiment that two such traverses included in their field a close approximation to $\frac{1}{8}$ of the area of the dish. Again, as in the roll, only those copepods showing the proximal ends of their antennae in the field were counted, and the number seen was multiplied by eight to give an estimate of the number present in the sample removed from the silk by scraping. The object of this estimation was primarily to give some measure of the normal loss due to the scraping operation. It was obvious at once that there must be some loss, and in the probability of this loss being more pronounced for the smaller or more fragile species, it seemed

[1] Following further modifications to the internal mechanism, it has become possible to identify the individual copepods while they are still on the silk.

advisable to base any figures of the relative abundance of different groups that were found in the tube on the number of individuals that were present in that tube rather than on the number that had been on the roll. It gave, however, some insight into the accuracy of the sub-sampling method used in estimating the copepoda on the roll. Although in a number of instances there was a disturbing discrepancy between the roll and the tube estimations of the number of copepods on any particular section, it was found that if they were all considered together they gave a correlation coefficient of ·89, which is felt to fall well within the limits of experimental accuracy normally expected or required in ecological work. The average loss from the roll to tube was found to be slightly below 15%, and there is some evidence that this was chiefly due to the single genus Oithona.

The dish was next traversed up and down progressively until 50 copepods had been seen and as many of these as possible identified. In order to avoid identifying as two individuals two parts of a single mutilated specimen, it was decided to include in the 50 copepods only those which had the anterior end present. In the tubes containing less than 50 individuals a proportion exceeding half of those present was identified.

The descriptions in G. O. Sars' 'Crustacea of Norway' were used in identification throughout and the material was divided into the following species or groups:

Calanus finmarchicus (Gunnerus) { over 2 mm. in length.
 under 2 mm. in length.
Pseudocalanus { *Paracalanus parvus* (Claus).
 Pseudocalanus elongatus Boeck.
Centropages typicus Kröyer.
Centropages hamatus (Lilljeborg).
Isias clavipes Boeck.
Temora longicornis (Müller).
Metridia lucens Boeck.
Candacia armata Boeck.
Anomalocera patersoni Templeton.
Labidocera wollastoni Lubbock.
Parapontella brevicornis (Lubbock).
Acartia { *Acartia longiremis* (Lilljeborg).
 Acartia clausi Giesbrecht.
Harpacticoidea.
Oithona spp.[1]
Corycaeus anglicus Lubbock.

In the majority of the samples the Copepoda were in a very bad condition, the bulk of them being completely flattened and often fragmented, and conse-

[1] As explained on the next page a treatment of the genus Oithona has been abandoned owing to the unsatisfactory nature of the material.

quently a certain number of genera and species had to be grouped together. It is hoped, however, that in the future with the improved mechanism this will be avoided and a more complete identification will be practicable.

It was found to be very difficult to separate *Paracalanus parvus* from *Pseudocalanus elongatus*, and adopting the recommendation of Gran, Hentschel and Russell (1936), they have been joined in a single category. Wherever possible some gross estimation of their proportions was made in the hope that any broad spatial or seasonal variation in their relative abundance might be apparent, and some indication might be gained as to the desirability of attempting to separate them in the future.

Acartia longiremis and *A. Clausi* were also combined, because the proportion found squashed in such a way that their diagnostic features were obscured was too large to warrant the time necessary to identify the relatively low numbers of identifiable individuals.

A certain number of Harpacticoidea were taken on the rolls. The majority were copepodid stages of Ectinosoma and Microsetella, but no estimation of the actual abundance of these or other genera was made. A reference to the occurrence of *Alteutha interrupta* will be found on p. 233.

Of the Cyclopoidea, only *Corycaeus anglicus* was identified specifically. The genus Oithona was not subdivided, because from the start it was apparent that the method was unsuitable for its study. There was a tendency for individuals to become embedded in the meshes of the silk, so that a disproportionately large number were left on the silk during the scraping, and it appeared far more susceptible to mutilation during this process than the larger and more robust genera. There were, in addition, a number of cyclopoid copepodid stages. A description of the distribution of these and of the genus Oithona has been abandoned owing to this unsatisfactory nature of the material.

If an attempt had been made to identify every individual seen specifically the percentage of unidentifiable copepods would have increased considerably, reaching a figure as high as 50% or 60% in some samples. While most of the species by the nature of their diagnostics are rarely damaged beyond recognition, the separation of *Acartia clausi* from *A. longiremis* and *Paracalanus parvus* from *Pseudocalanus elongatus* is dependent on diagnostics less pronounced and more easily destroyed by the crushing to which the Recorder material is subjected. So in order to keep the number of unidentified individuals as low as possible and to avoid obtaining disproportionately low values for Paracalanus, Pseudocalanus and Acartia, it was thought better to combine them into the two groups described above at the expense of detailed information.

Limitations of the Method.

Before considering the distribution of various species some further assessment of the validity of the method should be made.

The analysis of the individual species differed from the general recorder technique in a number of ways, which must be expected to cause some loss in accuracy and detail.

The first difference was that whereas the examination of phytoplankton, the " total Copepoda," and most other organisms was made on the silk, that of the copepod species was made from the plankton scraped from it. By comparing all the tube estimates of the total copepoda with the corresponding silk values, it was found that the average loss through scraping was about 15%. In isolated cases the discrepancy between tube and roll was much higher, but such exceptions must be expected when comparing two figures both susceptible to sampling errors. As stated above, the figure for any species was based on the total number found in the scrapings and not on the number estimated on the silk. This policy, although eliminating the effect of the disproportionately large loss of the genus Oithona, did open the possibility of an error due to a varying success of the scraping technique at different times. There was in fact little doubt that whereas the presence of Phaeocystis allowed almost every individual to be removed, when little other than copepods were on the silk a proportion higher than the average value of 15% might be left embedded in the meshes or rendered completely unrecognizable. However, usually Phaeocystis in quantity made an estimate of the number of copepods in the tube impossible, and so for want of a better method the roll totals, less 15%, were used in these cases and so cancelled the effect of the more successful scraping. It is clear that the variations in the efficiency of the removal of the plankton were very small when compared with the differences in numbers of individuals in both space and time, and so can safely be neglected.

For reasons stated earlier, it was only possible to analyse one division out of ten on the records examined for the individual species. There were exceptions to this, namely, that on every other Bremen record from 1932–35 every fifth division was taken, and that during the later part of 1936 and all 1937 each tube contained the plankton scraped from a length of silk equivalent to 10 miles of sampling. In order to interpret the results obtained by this method, it is necessary to consider this single observation in ten divisions, which may represent a distance varying between 12 and 25 miles, as typical of that distance. It is, therefore, important in assessing the validity of the method to determine to what extent we are entitled to do this.

Lucas (' Bulletin' No. 3, p. 83) raised this point when comparing the efficiency of the recorder with the more conventional method of taking vertical hauls at approximately 20-mile intervals. He showed that by taking a typical record and considering the various combinations of every tenth division, very different ideas of the distribution of *Rhizosolenia styliformis* might have been obtained. A certain patch might have appeared as much as ten times more dense in one series than another. While such differences may be fairly common in the phytoplankton material, they are not likely to be so for the copepoda, because they are obviously dependent on major changes in concentration occurring twice within 20 miles or, in other words, on the existence of dense patches not more than 20 miles in extent, and by reference to the "Total Copepoda" data it will be seen that such are exceptional, and it will be shown later that it is unlikely that they occur often with the individual species.

The point we wish to determine is to what extent we must expect the population to vary within the distance sampled by ten recorder divisions. Probably the simplest and most convenient method of doing this is that adopted by Gardiner (1931) in his comparison of successive vertical hauls taken by Savage (1931). It may be recalled that he divided the observations into arbitrary "groups," defined by the postulation that all the observations in any group were included in a certain period of time. He then took the average of these observations as the best measure available of the plankton sampled by them, and expressed the deviation of each observation from this "group mean" as a percentage of it. So he obtained a measure of the frequency with which any percentage deviation from the average was likely to occur. For our purpose we can take the estimate for "total Copepoda" in ten successive recorder divisions as a "group" and find how often the estimate made from a single division in a group will be sufficiently atypical to be misleading.

The records for the first six months of 1935 were used, as they appeared to include a good selection of the various types of distribution found during the survey. The policy adopted was to start with the first division of each record, and take successive groups of ten divisions until the end of the line. In Table I a sample group is set out to make the procedure quite clear.

TABLE I.—*A Sample Group Showing the Method Adopted in Estimating the Percentage Deviations of the Observations in a Group of Ten Divisions.*[1]

No. of division.	Estimated number of copepods ÷ 10.	Deviations from group mean (259).	$\frac{\text{Deviation} \times 100.}{\text{Group mean.}}$
51	314	+ 55	21%
52	278	+ 19	7%
53	274	+ 15	6%
54	286	+ 27	10%
55	290	+ 31	12%
56	212	− 47	18%
57	232	− 27	10%
58	206	− 53	17%
59	246	− 13	5%
60	256	− 3	1%

Group mean = 259

[1] All estimates refer to catches with the earlier aperture fitted to the recorder, *i.e.* $\frac{3}{4}$-in. square. They appear in the Plates expressed at $\frac{4}{9}$ths of the above values to make them comparable with the later catches taken with a $\frac{1}{2}$-in. square aperture (see p. 176). For obvious reasons it would have been unfair to make this correction in the tables.

The period tested included 55 groups, giving 550 observations. These are arranged in Table II, so that the frequency with which any percentage deviation occurred in any range of mean values can be seen at a glance. There is a higher incidence of larger deviations when the mean values are low. This is to be expected, but the occasional estimation of either 0 or 200 copepods when the value should have been 100 is not disturbing, as all numbers of this order fall into the category

TABLE II.—*Showing the Frequency Distribution of the Percentage Deviations (Signs Ignored) in the Various Ranges of Group Means.*[1]

% deviation from group mean	Group means ÷ 10. 0–9.	10–19.	20–29.	30–39.	40–49.	50–59.	60–69.	70–79.	80–89.	90–99.	>99.
0–9	34	13	8	13	3	6	2	3	4	4	15
10–19	8	9	10	19	4	3	2	2	3	3	23
20–29	34	11	14	13	..	5	..	2	9	1	13
30–39	39	7	4	7	..	3	4	1	3	2	10
40–49	10	10	2	2	2	2	2	1	3	..	4
50–59	38	4	6	5	..	..	..	..	2	..	1
60–69	12	5	4	1	1	1	..	..	2	..	2
70–79	13	2	..	..	..	..	..	..	1	..	2
80–89	..	5	..	..	..	..	..	..	1	..	..
90–99	..	..	..	..	..	..	..	..	1	..	..
>99	22	4	2	..	..	..	..	1	1	..	..

[1] See footnote to Table I.

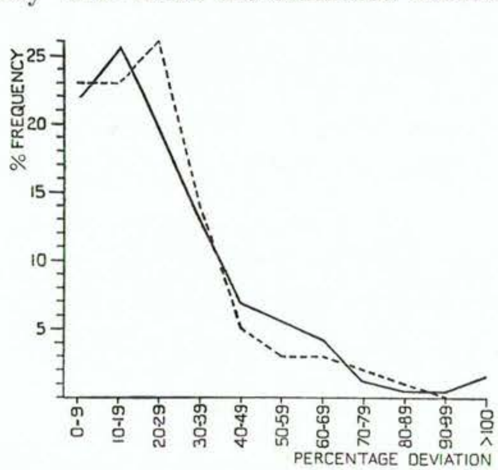
TABLE III.—*Showing the Frequency Distribution of the Percentage Deviations of All Estimates and of only those from Groups with Means Exceeding* 19.[1]

% deviation from group mean	All estimates. Frequency.	% Frequency.	% Cumulative frequency.	Estimates from groups with means > 19. Frequency.	% Frequency.	% Cumulative frequency.
0–9	105	19·1	19·1	58	21·5	21·5
10–19	86	15·6	34·7	69	25·5	47·0
20–29	102	18·6	53·3	57	21·1	68·1
30–39	80	14·5	67·8	34	12·6	80·7
40–49	38	6·9	74·7	18	6·6	87·3
50–59	56	10·2	84·9	14	5·2	92·5
60–69	28	5·1	90·0	11	4·1	96·6
70–79	18	3·3	93·3	3	1·1	97·7
80–89	6	1·1	94·4	1	·4	98·1
90–99	1	·2	94·6	1	·4	98·5
>99	30	5·4	100·0	4	1·5	100·0

[1] See footnote to Table I.

of " few present " (see footnote to Table I). It will be seen, however, from the summarized results in Table III that if we neglect areas with mean populations of this order, we need only expect one observation in every five to differ by more than plus or minus 40% from the average of the ten observations it is taken to represent.

In Text-fig. 5 the frequency of percentage deviations are plotted together with those found by Gardiner (1931). The continuous line graph shows the percentage frequency with which the analysis of one recorder division in a group of ten differs from the mean of the group by various percentages when the mean exceeds 20 (see Table III). The broken line graph, plotted from the data of Gardiner, shows the percentage frequency with which the estimated numbers of Calanus, Pseudo-



TEXT-FIG. 5.—For explanation see accompanying text.

calanus and Temora per metre caught in vertical hauls with an International Net differ from the mean of his " group " of such hauls taken over a restricted area. His definition of a " group " was that it contained at least five hauls taken within an hour from the drifting boat. It is impossible to estimate how far the boat would drift relative to the water column beneath it in one hour, but in view of the favourable weather conditions prevailing during the experiments, it can only have been a matter of yards. There is further evidence from the work of Herdman (1920), Gardiner and Graham (1925) and Winsor and Walford (1936), which suggests that fluctuations of this order in adjacent hauls are inevitable in the sampling techniques, regardless of how close together they are taken ; or that they are the result of a " patchiness " inherent in distribution of plankton in the sea.

We are then faced with the apparently anomalous conclusion that a single horizontal haul with the Recorder gives a sample as typical of the plankton over a distance of 12 to 25 miles, as a vertical haul is of other vertical hauls only a few yards away from it. This would be easily explained if we could assume that the normal distribution of the plankton was far more even from the surface to the bottom than it was in the horizontal plane. Then the vertical hauls would be subjected to a degree of patchiness that would not affect the horizontal ones, but this seems improbable in view of the very patchy vertical distributions found by Savage (1931), which we show in Text-figs. 2 and 3. A more probable explanation lies in the length of the hauls in the various methods of sampling. The vertical hauls only sample a column of water about 50 metres long, the conventional 10-minute horizontal hauls about $\frac{1}{4}$ of a mile, while in the Recorder each sample includes plankton from about 2 miles of water. This longer haul of the Recorder must have a considerable smoothing effect on the numbers found. A single division samples a distance equivalent to approximately four conventional horizontal hauls taken consecutively, and in doing so probably samples both high and low concentrations of plankton giving a smoothed value over the two miles, and we have seen from Gardiner's results that the population may vary considerably in shorter distances than this, at least when estimated with vertical hauls. The comparison of successive half-mile horizontal hauls taken on the *Discovery* Expedition shows in the deeper waters of the Antarctic (Hardy and Gunther, 1935, p. 255 *et seq.*) how large this smoothing effect would be in that area.

It would seem probable, however, that only on rare occasions will the division selected for complete analysis give a very misleading impression of the plankton it is taken to represent. In fact the suggestion is that it will give as fair a picture of the 12 to 25 miles as the vertical haul does of the area immediately around it.

It is thought probable that further consideration of the recorder material along these lines, augmented by some designed experiments using a reduced winding speed of silk, should be very useful in giving a better picture of the degree of patchiness in the sea and a better idea of the validity of isolated samples. It is hoped that such a study will be possible in the future.

Further confidence in the method is given by the detailed analysis of a series of weekly records in the autumn of 1937 (see p. 224), when, although the catches of some forms were low, the agreement between successive records is too consistent to be accounted for by chance.

Arrangement of the Data.

Graphs have been compiled for the main species and categories of copepods identified on each record that was fully analysed, in a similar manner to that used for the " total Copepoda " (see p. 177). As before, the graph is a measure of density of population plotted above a mile scale which stretches between the relevant lightships. In the case of the " total Copepoda " these graphs were arranged in two ways—as a chronological series for each route in turn to facilitate the comparison of the five years, and secondly on a number of maps to give an idea of the changes occurring over the whole area. The space available prohibits the publication of both series for all the forms identified, so it is thought advisable to use only the annual series for the more common copepods, such as the Paracalanus-Pseudocalanus group, Temora and Acartia, which it will be seen together constitute a very large proportion of the population and each of which follows fairly closely the spatial distribution of the total. These will be found on Plates LXXI–LXXXVIII and XCII–XCIII. It is comparatively easy to relate the various peaks in their distribution which are shown in the annual series with the corresponding patches on the map arrangement shown for the " total Copepods."

Isias clavipes and *Corycaeus anglicus*, on the other hand, were only found during a part of each year, were always scarce, and their relative abundance bore very little relationship to the fluctuations of the total population. They both showed characteristic and somewhat restricted spatial distributions, which are best illustrated by the map arrangement. They have been combined on a single series (Plates CXIX–CXXV). The comparison between their densities in the various years is not difficult from this arrangement because in each case there are only two or three months to be considered.

The significance of the two species of Centropages is thought, for reasons that will be given later, to warrant both methods of presentation. They can be conveniently plotted together and the two sets will be found on Plates LXXXIX–XCI and CVII–CXVIII as the annual series and maps respectively.

Calanus finmarchicus is not dealt with in this report. As has been mentioned before, the Recorder Survey was at first planned to investigate only the broadest changes in the plankton, and more particularly those changes which might have direct economic application to the fisheries. Originally the copepoda were treated as a single category on the assumption that their total number was an indication of the production of food available for the plankton-feeding fish. The comparison of the Indicator discs with herring catches (Hardy, Lucas, Henderson and Fraser, 1936), showed clearly that the relatively large size of Calanus made it the key copepod as far as the herring was concerned, and as was then pointed out the total copepod population could only be assessed as " available food " if the various constituent species were considered in relation to their respective sizes. At this stage it appeared impossible to analyse the recorder rolls in detail. As stated on p. 176 it was, however, thought possible to make a very rough estimate of the number of the larger stages of Calanus and other similar sized forms, such as Anomalocera, Labidocera, Candacia and Metridia, on the rare occasions when they appeared, by counting them on the silk with the naked eye, and so at least to separate the larger and smaller forms. The criterion used for a " larger Calanus " was that the length of its metasome exceeded 2 mm. This was only to be used as a rough guide and no actual measurement of individuals was undertaken. There can, in fact, be little doubt that the criterion varied both with the worker and at different times, and for this and a number of other reasons the estimates have since proved unsatisfactory. In view of the particular importance of this species it has been thought wiser to return to the material for more detailed information regarding both its total numbers and the proportions of the various copepodid stages. In the near future this revised data combined with the findings from the extended area sampled in 1938 and 1939 will be the subject of a report on the ecology of Calanus in the Southern North Sea from 1932–1939.

A generalized picture of the distribution of *Candacia armata*, *Metridia lucens* and *Parapontella brevicornis* will be found in Text-figs. 10 and 11. These species never appeared in appreciable numbers, so the arrangement used for the commoner forms was unsatisfactory for them. A more summarized picture was required to show merely the time and position of their various occurrences.

A diagram comparing the numbers of Labidocera caught in the various years is included in Text-fig. 9.

It is felt that the Plates show the general trends in the distribution clearly. There is in addition a description of the variations seen in the commoner forms (immediately following). It is suggested, however, that unless the reader is interested in the detail of these variations he should neglect this and refer to the more generalized sections following it which include a summarized account.

The Distribution of *Paracalanus parvus* and *Pseudocalanus elongatus*.

As has been explained in the introductory section, *Paracalanus parvus* and *Pseudocalanus elongatus* have been combined for this report into a single category. Together they constituted by far the greater proportion of the whole population during the major part of the year, so it is inevitable that any description of their distribution will follow fairly closely that of the total copepoda. In view of this it would only appear necessary to draw attention to a few of the more striking points.

It will be seen from Plates LXXI and LXXII that on the Rotterdam line Para- and Pseudocalanus exhibit the swing from west to east already pointed out for the Copepoda as a whole. Whereas there were pronounced concentrations on the eastern half of the line from January to the beginning of April, 1933, from December, 1933, to January, 1934, and from December, 1936, to March, 1937, there were in September and October, 1933, September, 1934, and October, 1937, definite preponderances on the western half. It is important to note that the winter months may be more productive than the summer. In fact the concentrations off the Dutch coast in January of 1933 and of 1934 were as dense as any found with the solitary exception of the western patch on the October record in 1933; and in 1936, following three of the poorest months of the survey, there is a pronounced increase in early December which persists until the March of 1937. This, together with the fact that during the period December, 1933, to January, 1934, the numbers were higher than those in November, 1933, indicates that there may be a considerable recruitment of the winter population either due to late autumn breeding or the accumulation of individuals carried here from some other region. There is some evidence awaiting confirmation in future years that the winter concentration is composed almost entirely of Paracalanus, whereas in the summer the more northerly form Pseudocalanus is predominant.

In Plates LXXIII and LXXIV are arranged the data for the Paracalanus-Pseudocalanus group derived from the Bremen records. It will be seen that here again its distribution follows closely that of the " total Copepoda " in as much as there is an easterly tendency during the winter and a westerly one during the summer.

The most striking point of the series is the enormous production in 1935. Throughout the summer of this year the numbers found were far higher than at any other time on this route. From January to March there was a low and fairly even distribution, with indications of the eastern preponderance not well pronounced. Towards the end of April, however, an enormous concentration had appeared in the east. A similar patch remained in May, separated by a narrow region of low numbers from a second equally dense patch over the centre of the line. The central patch persisted to some extent for the next three months, being reduced in June and July, but increasing again in August. In June there was no sign of the eastern one, but one appeared again as quite a dense concentration in July and the August record, although short, again suggests its presence.

It is interesting to note that the group was more abundant on the eastern end of the line in January and February in 1933 and 1934 than it was in these months in the later years. This was also found to be the case on the Rotterdam line, and so adds to the evidence already found in the consideration of the " total Copepoda " that there is some spatial continuity in the winter coastal population.

As has been stated earlier, fewer records were analysed for constituent species on the Copenhagen line than on the two more southerly routes. It will be seen, however, that from Plates LXXV and LXXVI a certain number of generalizations can be made. The summer months of 1935 and 1937 appear to be the outstandingly successful periods for the Paracalanus-Pseudocalanus group. In both May and July, 1935, there were two very dense patches covering the bulk of the line. In 1937 a very rich population in May, stretching across the Dogger Bank region, gave way in June to two more restricted patches at either end of the line. January, 1935, January and February, 1936, and from September to the end of 1937 appear to be periods of abnormally low numbers.

In 1937 information was available from the fourth route from the Thames estuary to Esbjerg. In the absence of earlier data this route has little comparative significance, but, as will be seen from Plate XCII, the high numbers taken on the eastern half of the June record help to delimit the very dense patch sampled by the Copenhagen line and the eastern end of the Bremen line in this month. Again on this line the period from September to the end of 1937 appeared to be a particularly poor one for Para- and Pseudocalanus.

Attention may be drawn to the fact that at no point in this series is there any indication of more than one increase in the Para- and Pseudocalanus population during the year. The low winter distribution gives place to the more abundant summer one quite suddenly in April or May, and from that time there is a steady decrease to the autumn and following winter.

The Distribution of *Temora longicornis*.

In Plates LXXVII and LXXVIII are arranged the data for the species *Temora longicornis* on the Rotterdam line. This species also reflects the distribution of the "total Copepoda," but to a lesser degree than the Paracalanus-Pseudocalanus group described above. The densest concentration of Temora was found on the centre of a record taken in late July, 1933, and it would appear that the months June and July are normally periods of relative abundance for the species in this region. The difference between these months and the subsequent ones is more pronounced than it is for Pseudocalanus. The records for January and December in 1933 and 1934, December, 1936, and February and March in 1937 show that Temora is well represented in the winter population off the Dutch coast.

On the Bremen line, Plates LXXIX and LXXX, Temora was again found to be abundant during the summer, the more successful months being August, 1932, May and July, 1933, May, 1935, June and July, 1936, and May, 1937. There were even higher numbers across the line in November, 1932, compared with the few taken after August or September in the other years. On the whole it may be said that the Temora population fluctuated far less from year to year than the Paracalanus-Pseudocalanus group. Although fairly high numbers were found in the mid-summer of 1935 and May, 1937, the difference between these and the normal density is not so marked.

It will be seen that the species shows plainly in every year except 1937 the apparent movement of the centre of concentration along the line from east to west and back again.

With the exception of the May records in 1935 and 1937 the numbers of Temora on the Copenhagen line were very low (see Plates LXXXI and LXXXII). There was a patch situated over the south-western edge of the Dogger Bank at the end of April, 1934, which suggests, together with the 1935 and 1937 observations, that this is the most successful month in this region, but it is clear that the species is generally more abundant on the two more southerly routes.

The Distribution of Acartia.

In Plates LXXXIII and LXXXIV the data for Acartia are presented. As stated above, it was found to be impossible to identify the species in the mutilated material in sufficient cases to warrant the time required. The impression gained is that *Acartia clausi* was far more common than *Acartia longiremis* and that *Acartia discaudata* occurred only very spasmodically, if at all.

On the Rotterdam line Acartia was not very well represented in the three winter periods successful for the forms mentioned above, *i.e.* January, 1933, December, 1933 and January, 1934, and February and March, 1937. It was more abundant then than in the winter months of 1935 and 1936, but the difference is not pronounced as in other species.

A slight increase in the density of population appeared about July in each year, while in 1935 relatively high numbers were found at the eastern end of the line in April and early June.

On the Bremen (Plates LXXXV and LXXXVI), as on the Rotterdam line, Acartia showed a summer maximum. June, 1932, July, 1933, May, June and July, 1934, April, May, June and July, 1935, May to July, 1936, and May, 1937, were the months when the genus was most successful. High numbers were taken at the eastern end of the line in October and November, 1932, after two months of scarcity, and after a depletion in December another increase was observed in this position in January and February, 1933. As stated above, this was the outstanding winter for the other Copepoda, but whereas they were again relatively abundant in the following winter, this proved to be a particularly poor period for Acartia.

It is interesting to note the frequent occurrence of coastal patches. These may be due to the predominance of *Acartia longiremis*, which is reported to be essentially a neretic form flourishing in low salinity water. It is hoped that in the future there will be time available to make a specific analysis of the denser patches of Acartia already recorded with a view to determining this.

Acartia appears to have been scarce in the more Northern parts of the area during the years under review, Plates LXXXVII and LXXXVIII. The only dense patch on the Copenhagen line was found off the north-eastern end of the Dogger Bank in July, 1936. In the two very successful copepod summers, 1935 and 1937, Acartia was relatively well represented on the Bremen line and Esbjerg line (see Plate XCIII), but on the Copenhagen line it appeared no more abundant than in the other years. There is, however, in each year some indication of a numerical superiority of the summer population over the winter.

The Distribution of *Centropages typicus* and *Centropages hamatus*.

In 1933 *C. typicus*, Plate LXXXIX, was first identified on the Rotterdam line in late July, towards the eastern end. It persisted here until January, 1934, being very abundant near the coast in October and December, 1933, and January, 1934, but never extending to the western half of the line.

In comparison with that of 1933–34 the winter of 1934–35 showed a very low *C. typicus* population. The species was present in the centre of the line in September and occurred in low numbers in the east in November and December. It was also recorded as present in the west near the Dudgeon light-vessel in November, and it is an interesting point that this is the only occasion on which the species was taken at this end of the line.

The only occurrence in 1935 was in June on the eastern half of the line, as the 1935–36 winter population failed to appear.

Moderate numbers were taken in the autumn of 1936. In 1936 the highest numbers appeared to be near the Dutch coast, but in 1937 the centre of concentration was further offshore. In 1937 the species disappeared earlier than usual, being recorded only as present in November and not at all in December.

On the Bremen line, Plate XC, *C. typicus* was again usually found on the winter records, appearing in August or September and at times persisting until March.

In 1932 the species was well represented. It first appeared in September, stretching well across the western half of the line, but centred in a patch about 60 miles from the English coast. The October record was short in the west, but it showed a high concentration to the east of the patch found in the previous month and a few individuals in the extreme east. The November record revealed a similar concentration, and also that the species extended well towards the English coast in the region not sampled by the October record. By December the species had decreased considerably, only low numbers remaining near the centre.

In the winter of 1933–34 *C. typicus*, although never occurring in numbers as large as those found in 1932, was both widespread and persistent. It first occurred in low numbers on the western half of the line in August, increased in the west in September and spread across the line in October and November. Unfortunately the December record was short on the English side, but there were still a number on the eastern half of the line and indications of it persisting in the west. By January, 1934, the species was restricted to a patch in the east, just west of the Borkum Reef, and a similarly placed patch was found in March. In February and March a few individuals were also found near the centre of the line.

The winter of 1934–35 showed a distribution very similar to the previous one, but the numbers were much lower ; the species was recorded as present in the west in September, spreading eastward in October and November to an easterly preponderance in December. In January, 1935, it was again recorded as present in a position corresponding to the patch found in the January of the previous year and also in the centre of the line in March.

As on the Rotterdam line, the 1935–36 population was even poorer than that of 1934–35. The species was present on the September record to the east of the centre, and in October, November and December occurred spasmodically across the line. In spite of the low numbers there was indications of the west to east restriction during this period.

In the winters of 1936–37 and 1937–38 *C. typicus* had a more easterly distribution. In both these seasons there was a concentration towards the eastern end of the line in September, October and November. In both years it first appeared in August, in the centre in 1936 and in the east in 1937. There were also other records of its presence in the area during these periods, but it was never in appreciable numbers. In October and November, 1937, when the line was extended to the Norderney Light-vessel, the species was found to extend to the end of the line, and in November there was a relatively high concentration outside the area normally sampled. It is probable, in view of this, that in 1933 and 1936 when the numbers were still increasing at the point where the Recorder was hauled, considerably denser populations would have been found had the record been continued.

The distribution of *C. typicus* on the Copenhagen line (Plate XCI) differs from that on the two southern lines in one striking respect. Whereas, as has been already pointed out, there is a spatial sequence or restriction on the latter, this is not apparent on the former. The distribution in fact although generally low is surprisingly even. The species occurred along the line during the second half of each year, and persisted until January in 1933, 1934, and 1937. It is difficult to pick out any year as either successful or unsuccessful for the species here. It is interesting to note, however, that the population may establish itself earlier on this line than on the others, for example, in August, 1934, 1936, and 1937, and July, 1935.

By reference to Plate LXXXIX it will be seen that on the Rotterdam line *Centropages hamatus* is essentially a summer form, though it may occur at any time in the year. In each summer the maximum was reached in July.

In 1933 it was taken from January until September, and the late July record of this year showed the densest population found on this line during the survey. 1934 was a poorer season; the species was taken only in April, July, August and September, and then in low numbers. 1935, although no numbers were found as high as those in July, 1933, was probably the most successful season for this species. It was present on the January record, from July to September extended across the line and persisted into October and December. In 1936 it was again taken in fair numbers in June and July, and from then on was recorded as present on various parts of the line until December. It reappeared in the eastern winter population in February and March, 1937, and subsequently showed the usual midsummer maximum in June, July and August, and was taken again in October.

On the Bremen line (Plate XC) the distribution of *C. hamatus* followed that on the Rotterdam line fairly closely, though here the maximum was reached slightly earlier, the richest month being May or June, rather than June or July. It is interesting to note that the three years in which it was taken in January and February, 1933, 1935, and 1937, coincide with the years of early occurrence on the Rotterdam line. Here, again, it was a regular member of the plankton during the midsummer months and occurred spasmodically in every other month excepting December. The summer population was in every year more abundant on this than on the Rotterdam line.

C. hamatus on the Copenhagen line (Plate XCI) again showed a well-defined summer maximum. The shortage of data makes it difficult to define within narrow limits the months of occurrence, but it is clear that it had a more successful if shorter season here than on the two more southerly routes, and that it reached its maxima slightly earlier in the year. It was abundant in July, 1933, May, 1935, June, 1936, May and June, 1937, and the only month in which it was found in 1934 was April. On the other hand, it was never recorded from the 15 records analysed between August and the end of the year. The appearance of a few specimens in January and February, 1936, is rather surprising, as this was one of the two years in which the species was not found in the early months of the year on the other two lines.

On the series of Plates CVII–CXVIII the two species of Centropages have been combined on a set of monthly maps. These serve to make clearer the distribution of the genus in the area, and at the same time show the exclusion between the species. This is thought to be important for reasons that will be explained later, but it may be pointed out here that it seems probable that these two species will prove to be valuable indicators.

As will be seen, there was only data for the Bremen line in 1932. In June, July, and to a lesser degree in August there was a relatively successful *C. hamatus* population centred about the middle of the line. This gave place in September to an equally successful *C. typicus* stock which persisted in October and November to decrease sharply in December. By January, 1933, it was no longer present in the Bremen line, though a few individuals were taken on the Copenhagen line over the Dogger Bank. We find, however, a certain amount of *C. hamatus* from January until April on the eastern ends of the Bremen and Rotterdam lines, forming a part of the coastal concentration of copepods typical of the winter, and it may be remembered that for the total copepod population this was a particularly successful winter in this region. There was an unfortunate shortage of records in May and June, but we can see that *C. hamatus* had become fairly common on the Bremen line in the former month and that by July it was found all over the area sampled. In August, September and November low numbers were recorded on the Rotterdam and Bremen lines. This autumn was marked by the outstanding success of *C. typicus*. Appearing as a few individuals as early as July, it increased to cover the whole area by October or November and persisted until the following March. It played a very important part in the winter coastal population, probably being the dominant species off the Dutch coast in December and January—a remarkable change from the previous January when it was not found there at all. In April, 1934, *C. hamatus* reappeared, and although not very abundant, spread well across the Bremen line in May, June and July. By August *C. typicus* was again present on the Copenhagen line and proceeded to replace *C. hamatus*, although the latter cropped up here and there until November. *C. typicus*, although widespread, was not this autumn nearly so successful numerically as in the previous one. In fact, except for two traces on the Bremen line in January and March it did not appear in the early months of 1935. The spring and summer of 1935 again found *C. hamatus* successful, especially in the centre of the area, and giving way in the autumn (October, November, and December) to a fairly sparse *C. typicus* stock. It is important to note for subsequent comparison with other species that this year *C. typicus* apparently failed to establish itself in the southern part of the area. Although it was well represented on the Copenhagen line in September and October and appeared in lower numbers on the Bremen line, it was only taken on the Rotterdam line in June, whereas *C. hamatus* was found in October and December.

1936 was in many respects similar to 1935. *C. hamatus* was as usual successful in June and July, while *C. typicus* appeared on the Copenhagen line in August and spread southwards. Unlike the previous year, however, it became well established in the winter population off the Dutch coast. Again in 1937 we find *C. hamatus* predominant from May to June. In July there was no Copenhagen record, but small numbers of *C. typicus* were mixed with the *C. hamatus* about the centre of the Esbjerg line. In August it was well established on the Copenhagen line, and subsequently covered the whole area to the exclusion of the other species. As in 1933 and 1936, it became a prominent constituent of the coastal population.

The Distribution of *Isias clavipes*.

Isias clavipes and the cyclopoid *Corycaeus anglicus* are plotted on a series of maps in Plates CXIX–CXXV. Such an arrangement is convenient for these two species, because by considering the three lines together it is possible to get a better idea of the pronounced seasonal and spatial restrictions which are the striking points of their distribution.

As is explained in the legend preceding Plate CXIX, these species only occurred in appreciable numbers during the later half of the year, and consequently for economy of space the maps representing the earlier part of the year have been omitted. Occasionally odd individuals of Corycaeus were recorded in January, February or March. These were most likely stragglers from the winter stock, and have been indicated by black circles on the December map, except in the case of the winter of 1933–34, when an extra map appeared necessary.

Considering first *Isias clavipes*, it will be seen that although none were found on the Bremen line in June and July of 1932, by August it had appeared in a relatively dense patch at the western end. This patch persisted to a lesser extent in September, but by November had disappeared. The October record was 60 miles short at the English end, but the species was present at its finishing point.

In 1933 Isias was again only recorded in three months, July, August and September. In July there was a patch on the western end of the Bremen line similarly placed to that found in August, 1932, although not so dense. In addition it had appeared at two points on the eastern end of the Rotterdam line. By August there had been an extension to cover the southern part of the area. There was no data for the Copenhagen line, but the species extended well out to the middle of the Bremen line and was present in low numbers over a broad stretch of the eastern half. The western population had extended south to the Rotterdam line, where a high concentration was found off the East Anglian coast and at the same time the numbers on the eastern half of this line had increased. There was a trough of low concentration in the middle of both lines. By the following month, September, there was little change in the western population, but those on the eastern half of the Bremen line had disappeared. Unfortunately there was no information from the eastern half of the Rotterdam line. A few individuals were found over the South-West Patch on the Copenhagen record.

In 1934 the season again lasted from July to September, but the distribution was not at first like that of the previous year. There was in July a fairly rich population in the middle of the Bremen line and a single record of presence on the Rotterdam line about 50 miles from Spurn Point. By August there were indications of a restriction to the region off Spurn, but the numbers were still low and stretched well across the Bremen line. In September, however, there was a marked improvement in the numbers and the well-defined restriction found in September, 1933, had re-established itself. A few records of presence were all that remained of this in October and November.

The appearance and subsequent behaviour of the Isias population in 1935 was very similar to that of the previous summers, but the stock was less successful. In July it was found in the centre of the Copenhagen and Rotterdam lines, and at a point towards the English end of the Bremen line. Through August and September there appeared a progressive restriction to the off-Humber region, which was found in the previous years. This was followed by the usual rapid decline, leaving only a few stragglers on the Bremen line in the following month.

In 1936 Isias was common only in the centre of the area. It never appeared on the Rotterdam line, and not until September was it taken on the Copenhagen line. In June there was a patch on the English side of the Bremen line which increased until it practically covered the line in August. The September records showed a decline on the Bremen line, but the species had widened its distribution sufficiently to cover the major part of the Copenhagen line.

In 1937 the species was first found on the Esbjerg line in July. It was taken at the southern end, where the line is near the Suffolk coast. In August, although it extended well across the Bremen line and was present on the far end of the Rotterdam line and the Dogger Bank, there were indications of the Western preponderance which seems to be the normal distribution at this time of the year. This persisted in September, and in October low numbers were taken across the western half of the Bremen line and on the centre of the Rotterdam line. Numbers were well below normal in 1937.

THE DISTRIBUTION OF *Corycaeus anglicus*. (PLATES CXIX–CXXV.)

Corycaeus anglicus was found to be a winter form, reaching its yearly maximum in November or December.

In 1932 it was well represented at the extreme eastern end of the Bremen line in October and November and was recorded as present here in December.

In 1933 it first appeared in September in low numbers on the western half of the Copenhagen line and on the extreme east of the Bremen line near the Borkum Light-vessel. For the next three months it was relatively abundant near the Dutch coast on the two southern lines and less abundant towards the centre of the area. There was only one Copenhagen line analysed during this period, that for

November, and Corycaeus was present along most of its length. This winter it was particularly persistent. There were four records of its presence in January, 1934, and one in both February and March.

In 1934 the species was again relatively successful, but its distribution differed from that of the previous year. Its centre of concentration was rather nearer the middle of the Bremen line than along the Dutch coast, and from October to December it was present along the whole length of the Bremen line and showed no signs of the restriction to the east found in 1933. Further it was only taken on the Rotterdam line in very low numbers. It appeared earlier, in July on the Bremen line and remained present there until February. It was well established on the Copenhagen line by September. During this year on two occasions it occurred in a patch of Isias on the July and September Bremen records. This rarely happened because usually the two species were separated both in space as well as in time.

1935 saw a very pronounced reduction in the Corycaeus population. It was recorded as present on the Bremen line in August, and in low numbers on the eastern ends of the September Bremen and Copenhagen records. It was scattered over the Bremen line in October, November and December, and present on the far end of the December Rotterdam record. It was later present on the centre of this line in March, 1936.

In 1936 the species had reached a very low level, constituting an insignificant part of the winter copepod population. There was a small patch on the eastern end of the Copenhagen line in September, as in 1935, but apart from this it never occurred in appreciable numbers. It was, however, present on the Bremen line in November and December at the eastern end, and on the Rotterdam line in October and December, and well scattered over the November Esbjerg record.

The following year saw a recovery in the area. Small numbers were taken as early as July on the Esbjerg line, by September the species had established itself on the far half of the Copenhagen line, and moderate numbers were taken there until the end of the year. In October and November high numbers were found in the Heligoland Bight, in fact higher than in 1933 and 1934. At first sight it appears that this period was the most successful for Corycaeus during the survey, but this is improbable in view of the fact that the bulk of them were taken on the extension of the Bremen line not previously sampled, and that the species did not extend so far south as in 1933 or as far west as in 1934. 1935 and 1936 were very lean years when compared with the other three.

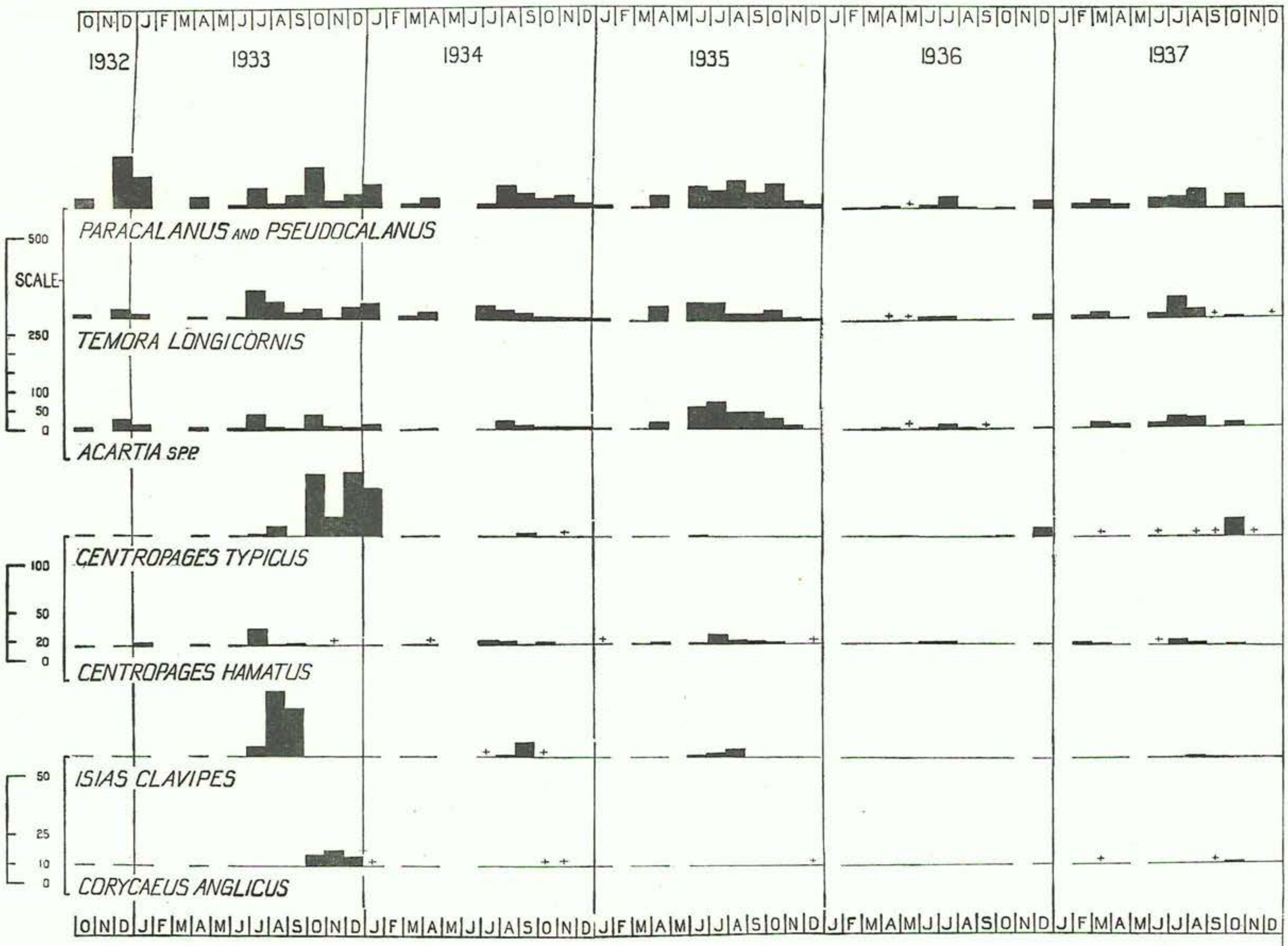
The Seasonal Variations in the Abundance of the Commoner Copepoda.

In the brief description of the distribution of the various genera and species some remarks have been made about their relative abundance in time. As it is not easy to correlate this information from the distribution graphs alone a pictorial summary has been made in the following manner : The number of individuals of each species caught in any month is totalled and divided by the number of miles sampled in that month. This procedure is followed for each line to give the average number of individuals per mile of tow for every month for which there is information. These figures are arranged as histograms in a chronological series. The various species are placed beneath each other for the three lines in turn (see Text-figs. 6, 7 and 8).

There are a number of points to be borne in mind when considering these diagrams, as false impressions can be made if they are treated too literally. For example, if a species has a very restricted spatial distribution, a single patch on the Copenhagen line will, on account of the relatively greater length of tow, give a far lower average value than a patch of similar dimensions found on the Rotterdam line. A similar situation arises when a record is considerably shorter than usual owing to a mechanical defect or to weather conditions. In such circumstances the mean value may be unfairly high or low according to whether the part sampled was one of higher or lower density than the part that was not. For this reason only those records that are valid for more than half their length have been used, but nevertheless it must be remembered that on some of the winter Rotterdam records practically all the copepods found were taken on quite a small fraction of the total length. Another point is that as the records could not be evenly spaced in time, on some occasions a sample taken in the first or last few days of a month has had to be used to give a value for the whole of the month. In spite of these limitations, which will only effect isolated cases, there are a number of trends which appear more clearly in this summarized arrangement of the data than in the distribution graphs.

Considering first the Rotterdam line (Text-fig. 6) it will be seen that the three main genera, Pseudocalanus (+ Paracalanus), Temora and Acartia did not vary much in abundance from year to year. The outstanding points are the weakness of the 1936 population for all three, and the surprisingly dense population of Pseudocalanus in December, 1932, and January, 1933. On the whole, 1933 and 1935 appeared to be the most successful years, though 1935 was more markedly so for Acartia than the other two genera.

Turning to the Bremen line (Text-fig. 7) it will be found that Pseudocalanus was far more abundant than on the Rotterdam line, even the least successful year, 1933, being comparable to the more productive years on the Rotterdam line. It is interesting to note, however, that the difference is more pronounced during the summer months of maxima than during the winter, or that there was a more even and stable population throughout the year on the southerly route. The outstanding year for this group was 1935. In this year the average for the maximum month, May, was approximately twice that of the maximum month of any other year, and further the averages for April, July and August were also in excess of the usual maxima. 1934 and 1936 were both comparatively successful years, and the autumn population of 1932 was, as on the Rotterdam line, surprisingly high.



TEXT-FIG. 6.—Histograms showing the average number of the commoner Copepoda caught per mile of tow on the Rotterdam line for each month from October, 1932, to December, 1937. The values represent the total catch per month divided by the distance sampled. Records of less than half their normal length are discarded, and months in which there is no valid average are indicated by a break in the base line. A " + " sign denotes that the form was present, but in numbers too small to be shown on the scale adopted. For further explanation see text.

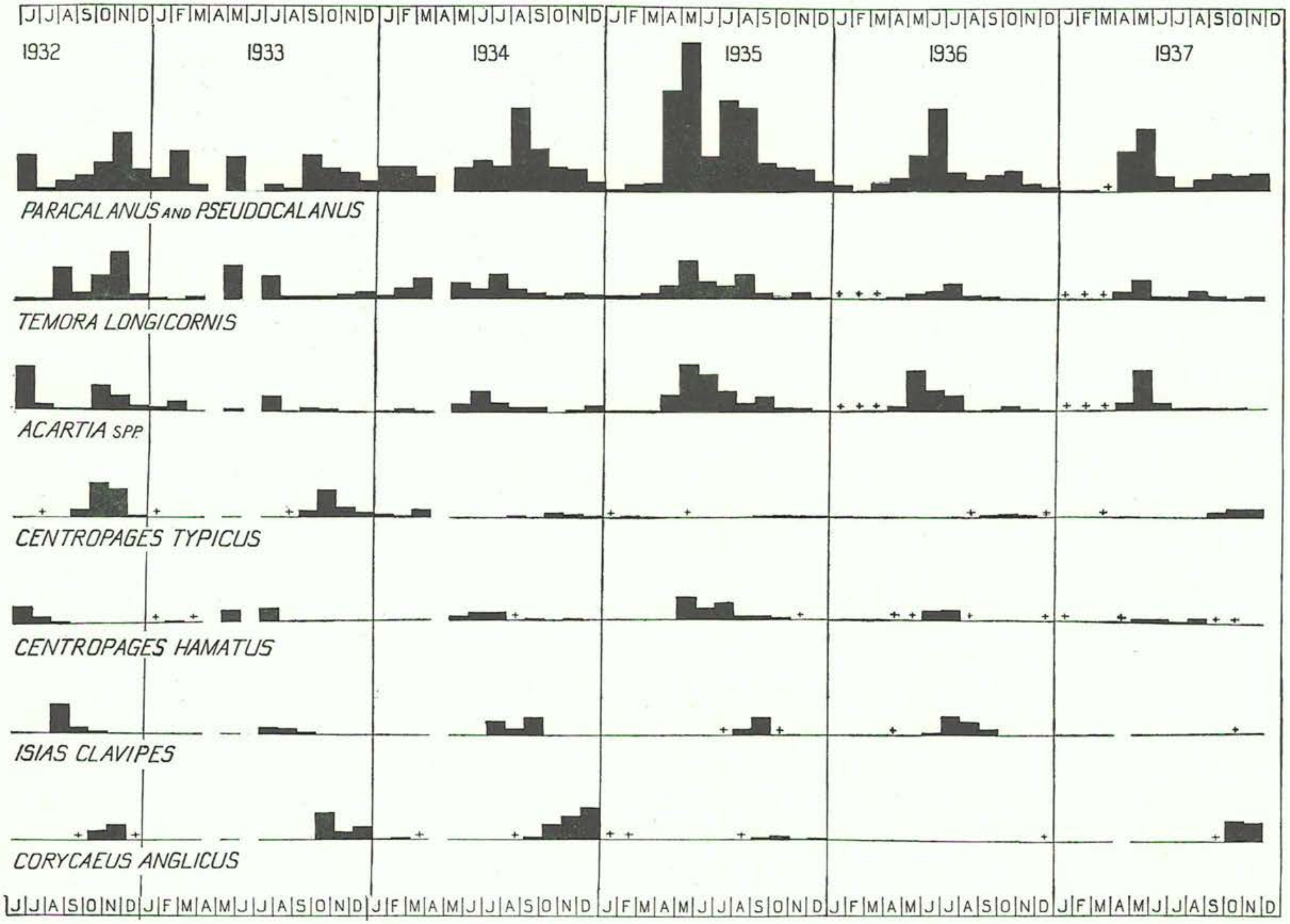
The numbers of Temora and Acartia taken were more comparable with those on the Rotterdam line, 1936 and 1937 being weak years for the former and 1933 and 1934 for the latter. The summer of 1935 and autumn of 1932 were the most successful periods.

The Copenhagen data (Text-fig. 8) are far less definite. There is a possibility of the maximum for a year occurring in a month not analysed and a false impression so being obtained. It is clear, however, that Pseudocalanus was very well represented on this line. From 1933–35 there was a steady increase in numbers, followed by a decrease in 1936. Whereas on the Bremen line in 1937 the lower numbers were maintained, in June, 1937, on this line the highest mean value of the survey was found. Of the other two genera one can conclude that either they had a far shorter season or else they were on the whole lower than on the Bremen line. The high concentration of Temora in June, 1935, is an exception to this generalization.

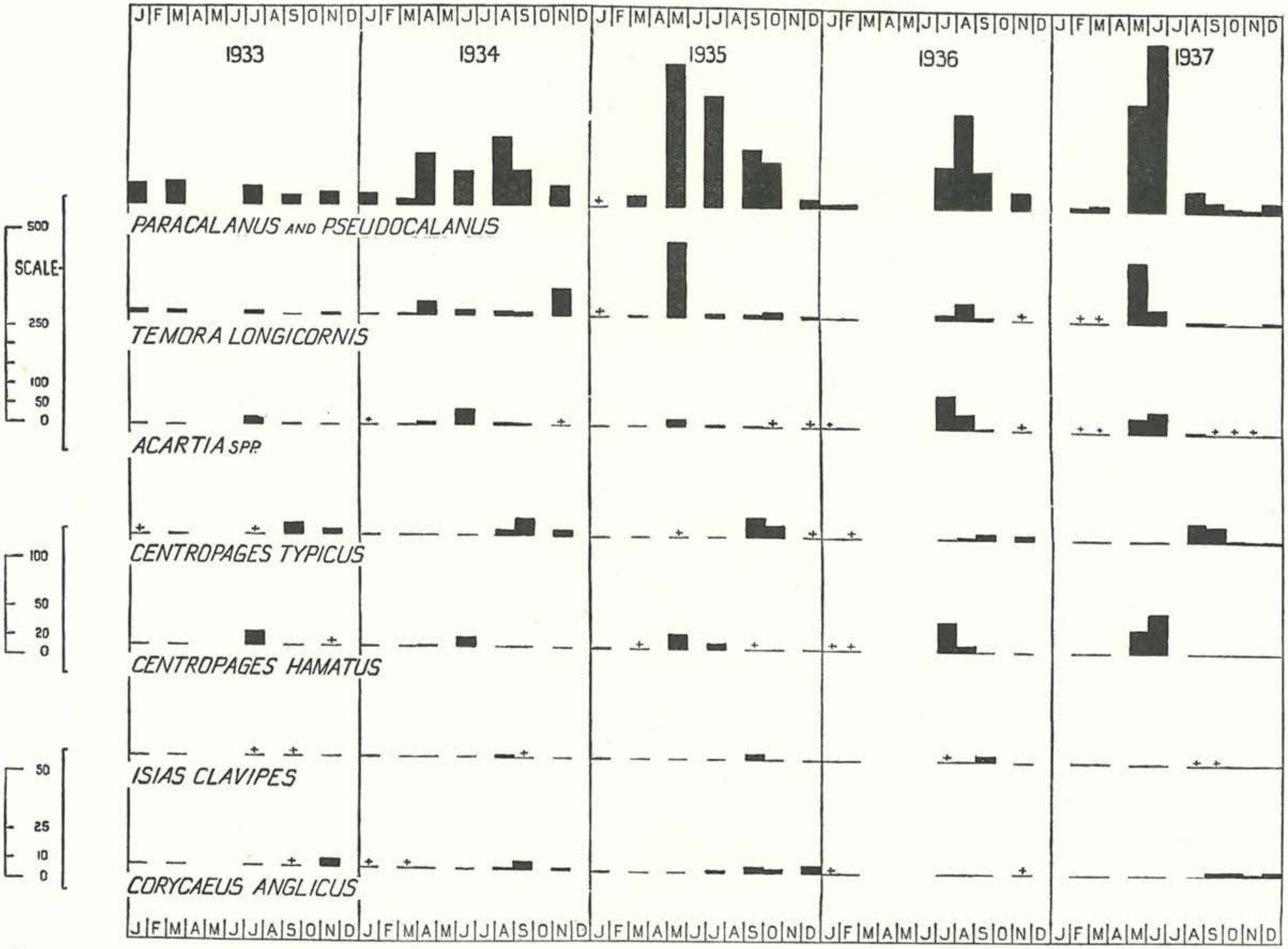
By far the majority of the Copepods taken during the survey belonged to the three genera, Pseudocalanus, Temora and Acartia. These are in Text-figs. 6, 7 and 8, plotted at $\frac{2}{5}$ of the scale used for the two species of Centropages and $\frac{1}{5}$ of that used for Isias and Corycaeus. It will be seen that they were present on practically every roll analysed. Centropages, Isias, and Corycaeus, on the other hand, appeared to have a far more marked periodicity, occurring annually only over a comparatively short season. Such a seasonal variation might be due to two distinct causes. Firstly these might be species that normally flourished in an area not sampled by the survey and carried on to the lines at certain times only, or they might have normally occurred in such numbers that they were only taken by the recorder or revealed by the process of analysis during those months in which they reached their maxima. The relative merits of these two possibilities will be discussed later (p. 233); at the moment it is sufficient to draw attention to the more striking points regarding their occurrence on the lines.

Centropages typicus and *Corycaeus anglicus* were winter forms, as has been pointed out above. They first appeared in appreciable numbers about September and persisted until the early months of the following year. These species showed similar fluctuations in their abundance as well as an agreement in the times of their occurrences. 1933 was by far the most successful year for both species on the Rotterdam line, and in the winter when *C. typicus* persisted into the following year, it was found that Corycaeus did the same. It will be seen that both were poorly represented on all three lines during the winter of 1936, and show a slight improvement in the following winter. It is interesting that neither species enjoyed the advantages that the conditions of 1935 appeared to give to the more common species.

Centropages hamatus and *Isias clavipes* were summer species. Considering *C. hamatus* first, it will be seen that it showed very little variation. It occurred every mid-summer on all three lines. The variations from year to year were slight, 1935 being the most successful year on the Bremen line, 1936 and 1937 on the Copenhagen line and 1933 on the Rotterdam line.



TEXT-FIG. 7.—Histograms showing the average number of the commoner Copepoda caught per mile tow on the Bremen line for each month from June, 1932, to November, 1937. General arrangement as in Text-fig. 6.



TEXT-FIG. 8.—Histograms showing the average number of the commoner Copepoda caught per mile tow on the Copenhagen line from January, 1933, to December, 1937. General arrangement as in Text-fig. 6.

Isias clavipes never showed a high average value on the Copenhagen line. This doubtless is in part due to the very marked restriction of the species to a region off the Humber mouth and the relatively short part of the Copenhagen line which samples this area. On the Bremen line its value remained fairly constant for the few months in which it occurred each year with the exception of 1937, when it hardly occurred at all on any of the lines. This is in contrast to the findings on the Rotterdam line, as there was there a very dense population in August and September, 1933 ; in 1936 the species was not taken at all on that line.

The seven groups of copepods dealt with above, although varying in their normal abundance, are the main constituents of the population in the area covered by the survey, and for the purpose of this report must be considered as the most important. *Calanus finmarchicus* is to be the subject of a special report (see p. 204), but neglecting for a time this species, there can be little doubt that the Pseudocalanus-Paracalanus, Acartia and Temora groups together must form the significant link in the food chain, simply because of their numerical superiority over the other copepod forms (see also p. 195). The species of Centropages, Isias and Corycaeus have been considered in some detail, because it is thought that their particular types of distribution both in space and time make them useful in the study of water movements and changes in the physical conditions of the environment which is an immediate objective of the investigations.

As was pointed out in the introductory section a number of other species were taken and identified. Although space would not permit any detailed consideration of their distribution even if they were ever present in numbers sufficiently high to warrant it, it is felt that some summarized account of their occurrence is valuable in an understanding of the ecology of the area. In order to do this as briefly as possible it has been necessary to adopt different methods of presentation at the expense of consistency.

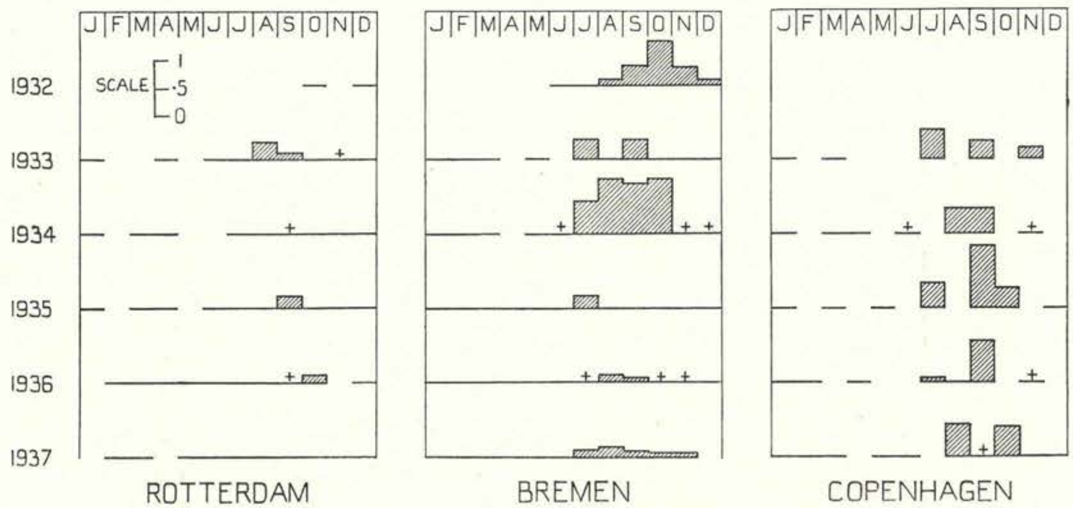
The Occurrence of Other Species of Copepoda.

(1) *Labidocera wollastoni.*

Labidocera wollastoni was never abundant when compared with the smaller copepoda. It was taken in ones and twos when the commoner species appeared in hundreds, but nevertheless occurred with regularity during certain months each year. This is illustrated in Text-fig. 9, where its monthly averages are presented. The average number caught per ten miles of tow in each month is estimated ; after adjustment for the size of aperture, these are plotted as histograms, one for each line in each year.

It will be seen that Labidocera was not so well represented on the Rotterdam line as on the other two. Not only were the average numbers lower, but the period of occurrence was shorter. In 1933 the species was taken in August, September and November, and the figures estimated for the former two months show this to be its most successful year on this line, whereas 1934 and 1937 were the poorest.

On the Bremen line the species was generally more persistent. It will be noticed that in four years out of the six, it was present for five or six successive months. 1933 and 1935 were the years in which the season was shorter, while 1932 and 1934 were particularly successful. In 1936 and 1937, however, although the species was found for periods of five months, it was never present in high numbers. The normal period of occurrence on this line seems to be the summer and autumn.



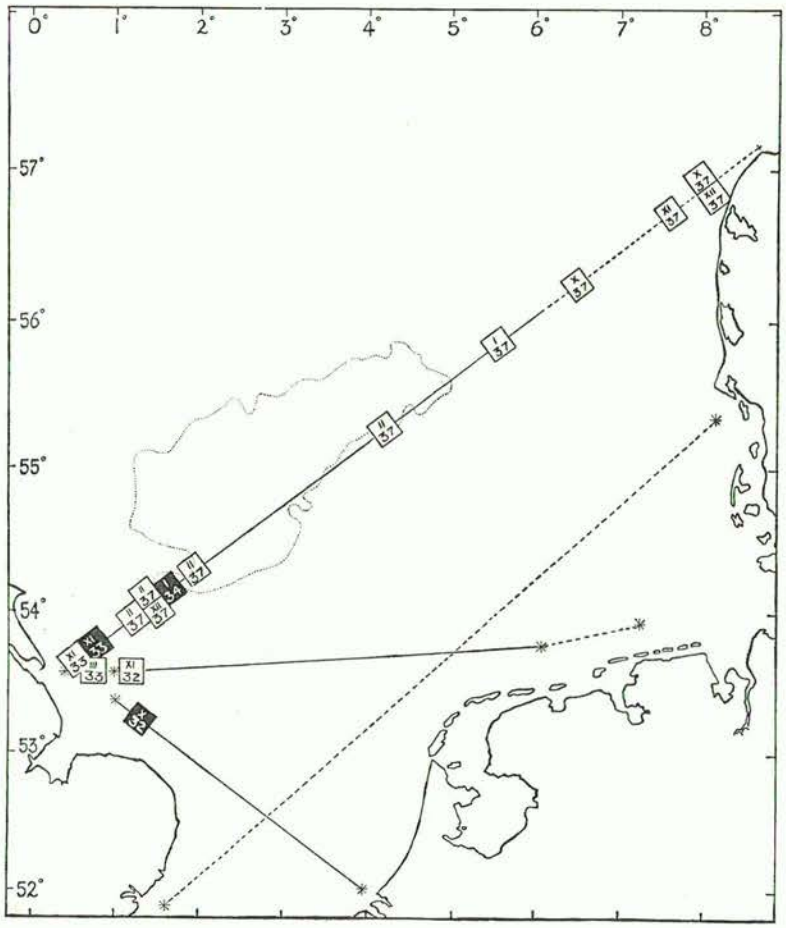
TEXT-FIG. 9.—Histograms showing the monthly fluctuations in the average number of *Labidocera wollastoni* caught per mile on the Rotterdam, Bremen and Copenhagen lines from 1932 to 1937. A break in the base line indicates that data were not available for at least half the usual mileage sampled. A " + " sign denotes that the species was present, but in numbers too small to be shown on the scale adopted.

The Copenhagen line was quite as productive as the Bremen, and here the species was taken over the same season. It is not easy to compare the years for the relative success of the population because a different series of months was sampled in different years, but judging by the September record it appears that 1935 was above the average, and that there was very little difference between the other years. This is rather unexpected because in 1935 as stated above the species hardly established itself on the Bremen line at all.

No diagrams are included in this report showing the spatial distribution of Labidocera. It was usually found at scattered points over the centre part of the lines, but might in its more successful months cover practically the whole area. As will be seen from the monthly histograms it was always more abundant in the more northerly records.

(2) *Anomalocera patersoni.*

This species was practically absent from the Recorder material, two isolated records of presence being the only indication of its occurrence in the area during the period of the survey (see p. 230).



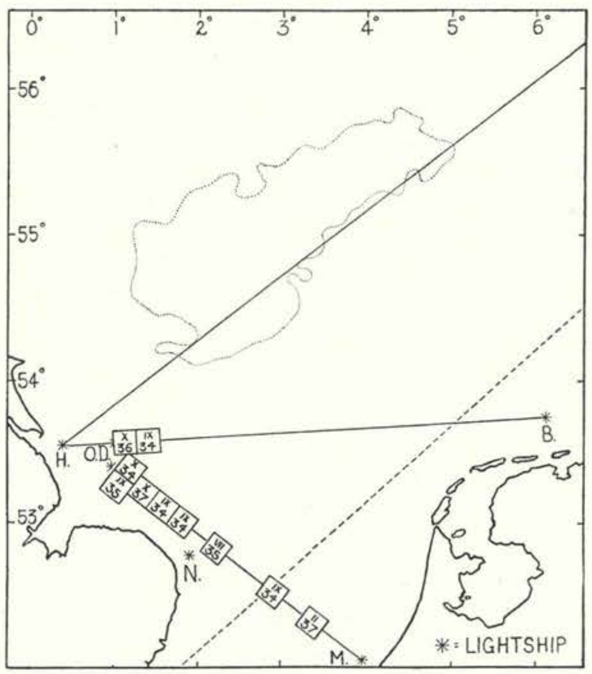
TEXT-FIG. 10.—A chart showing the occurrence of *Metridia lucens* (open squares) and *Candacia armata* (black squares) on the recorder lines from 1932 to 1937. The month and year of each occurrence are indicated by numerals in the squares. The broken lines represent additions to the survey only sampled during the latter half of 1937.

(3) *Metridia lucens.*

Metridia lucens was recorded as present on 13 occasions only. These are arranged on a map in Text-fig. 10. It will be seen that they all fall in the winter months, between October and March. In November, 1932, and March, 1933, the species was found on the Bremen line in the vicinity of the Dowsing and Humber Light-vessels. It reappeared in November, 1933, in a similar position near the Humber Light-vessel, but was not taken again until the beginning of 1937. 1937 was in comparison with the others a good year, as the species was present at ten stations. In the early part of the year it was taken at a point north-east of the Dogger Bank in January, and in February at three stations around the south-western end of the Bank and at one over the northern part. In December, 1937, the species was again found in the same place as the February observations, off the South-West Patch. From October to December, 1937, it was also found on the extension of the Copenhagen line, but there is, of course, no comparable data for this region in the earlier years.

(4) *Candacia armata.*

Candacia armata was very rare, only being taken on three occasions—October, 1932, November, 1933, and January, 1934. Each of these records fell in the western part of the area, on the Copenhagen line between the Humber Light-vessel and the Dogger Bank and about 20 miles south-east of the Dudgeon Light-vessel (see Text-fig. 10).



TEXT-FIG. 11.—A chart showing the occurrence of *Parapontella brevicornis* on the recorder lines from 1932 to 1937. Arrangement as in Text-fig. 10.

(5) *Parapontella brevicornis.*

Parapontella brevicornis was not found until 1934, when it was taken five times. It appeared twice in 1935 and 1937, and only once in 1936. The bulk of the observations come from the Rotterdam line (see Text-fig. 11).

(6) Oithona spp.

Any treatment of this genus has been abandoned for the reasons given on p. 198.

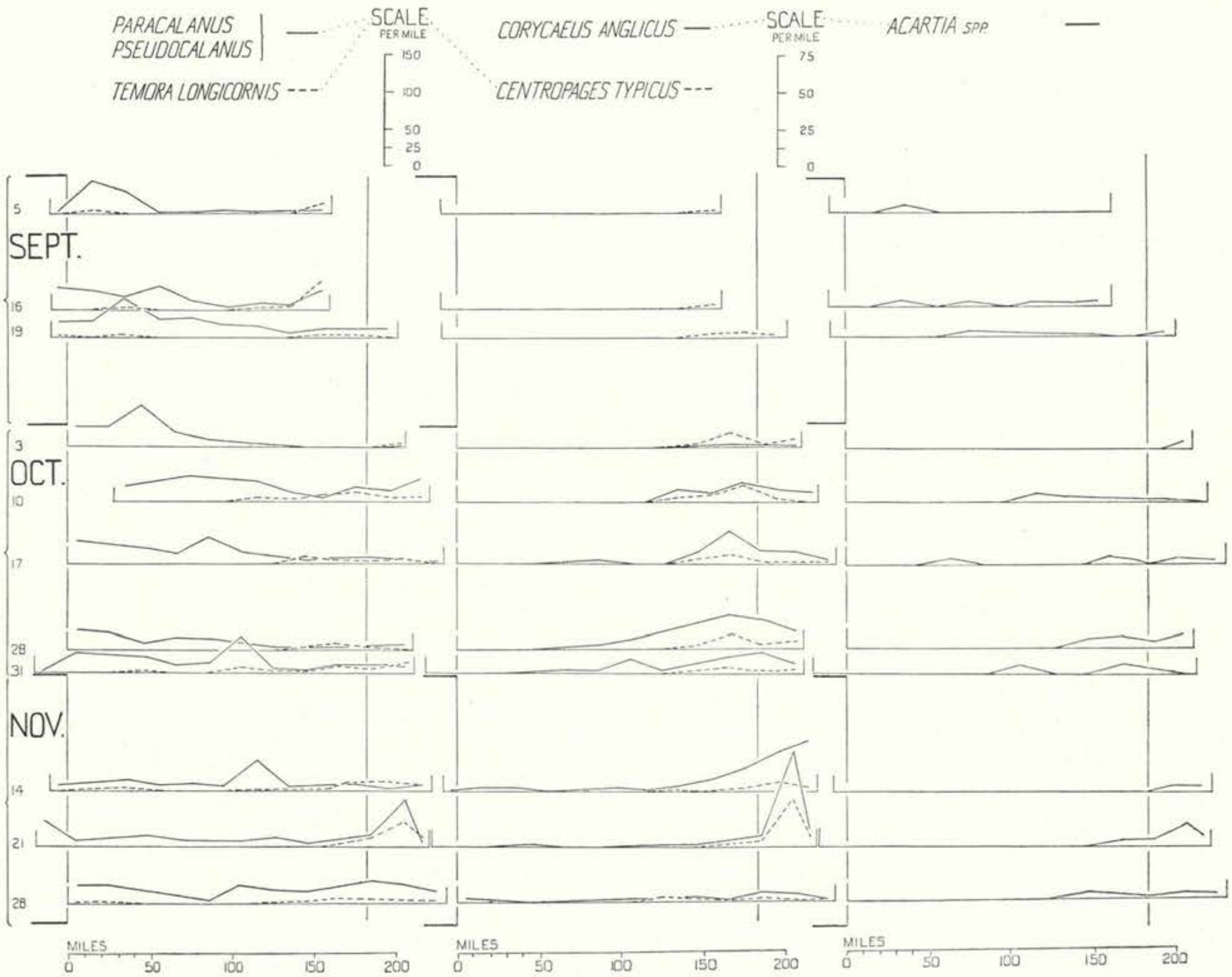
THE AUTUMN PROGRAMME, 1937.

In each year, during September, October and November, the usual monthly records were augmented by a weekly series on the Bremen line whenever the sailing dates and weather conditions permitted. The object of this was primarily to afford additional information about the extent and movements of the main autumn diatom patches, which have been shown under certain circumstances to control the movements of the herring and so affect the main fishing season (Savage and Hardy, 1935). As there was not sufficient time available to analyse even a complete monthly series of records for the individual copepod species, there seemed little point in dealing with these extra rolls, especially as they were taken at a time when the population was generally low, and also when the herring were not feeding in the area. Nevertheless it was realized that a weekly series would be valuable for giving some idea of the rate at which the copepod population might change at any one point, and the practicability of interpolation between the usual monthly observations. Further, such a series might, by the consistent appearance of any particular distribution over a number of records, give an added amount of confidence in the method.

For these reasons it was decided to analyse one autumn series fully. September, October and November, 1937, were selected because there was then a fairly comprehensive programme completed, and because during this period the bulk of the copepods had apparently moved from the western end of the line to the eastern end.

The results from these records are not all included in the annual diagrams for the various species, because they would there only cause a degree of congestion which would obscure the general distribution. They are presented independently in Text-fig. 12, where the vertical time scale is increased by three times. Only the Pseudocalanus-Paracalanus group, Acartia spp., *Temora longicornis*, *Centropages typicus* and *Corycaeus anglicus* occurred in appreciable numbers on these rolls. Acartia and Corycaeus are plotted at twice the scale used for the other three forms, and consequently appear in this diagram to be more dominant members of the copepod population than they really were.

There is a mile scale placed below each column of graphs, showing the distances from the Outer Dowsing Light-vessel, which is represented by a vertical line at 0 miles, to the Borkum Light-vessel, which is similarly marked at 182 miles. By comparing the general contours of the graphs with these scales, it will be seen that points are only plotted at 20-mile intervals and may fall either on the 15, 35, 55, 75 . . . or the 5, 25, 45, 65 . . . mile series from Outer Dowsing Light-vessel. This is due to the arbitrary selection of blocks for analysis on the basis of taking the first complete block and every other one thereafter until the end of the record. On account of this it is impossible in many cases to find an agreement closer than 10 miles for either the centre or the end of a patch. This point can be illustrated by reference to the western limit of the *Centropages typicus* patch throughout the series. On all three September records the even blocks were analysed giving data for 10–12, 30–40, 50–60 . . . miles east of the Outer Dowsing Light-vessel, and



TEXT-FIG. 12.—Graphs showing the distributions of the commoner copepods found along the Bremen line during the intensive autumn programme of 1937. The vertical lines on the left and right of each series mark the positions of the Outer Dowsing and Borkum light-vessels respectively. They also represent a time scale from September to November on which each graph is placed against its appropriate date (indicated at the left-hand side). Acartia spp. and *Corycaeus anglicus* are plotted at twice the scale used for the other forms. For further explanation see text, p. 224.

in each case the species was present on block 16 (*i.e.* between 150–160 miles east of the light-vessel), and was not taken on block 14 (*i. e.* 130–140 miles east of the light-vessel). For the first record in October, however, the odd blocks were analysed, and then the species was present on block 15 and absent on 13, so that there appears in the diagram a westward extension of the patch amounting to 10 miles, whereas in point of fact the agreement between the two records is as close as the method will allow.

The persistence of this *Centropages typicus* distribution is one of the most striking points in the series. Its western limit is surprisingly constant, as there is no significant movement of this boundary in the eight records for September and October, and very little if any in November. Quite apart from its biological interest this point is important, because it does reveal the capability of the Recorder method to show an agreement through sequences of observations even when the numbers concerned are low.

There are further points in these records which lend confidence to the method. It will be seen that there are a number of trends running through the series, so that each record appears as a reasonable mean of those preceding and succeeding it. For example, *Corycaeus anglicus* was first taken in very low numbers on the eastern end of the first record in October, had increased by the following week, and then appeared to spread progressively further westward in the next four records, until it extended to the English coast during the second week of November. *Temora longicornis* was found on the eastern half of all the records and also at the western end in September and November, though it was absent there during four successive October records. The distribution of the Paracalanus-Pseudocalanus group also shows a strikingly regular pattern. If the higher numbers are considered, it will be seen that at the beginning of the programme they were situated off the English coast and then moved offshore towards the centre of the line until November, when the highest concentration was found on the eastern side. The actual number of individuals present in this patch, which apparently moved from west to east, is so similar that one is tempted to consider it as a single concentration drifting along the line. Whether this is so or not, one is presented with an anomalous situation in the apparent movements of the various species during these three months. The Centropages population appears to remain stationary, while the Corycaeus population, which at first is conterminous with it, spreads westward against the direction of Pseudocalanus, which steadily moves from west to east. No discussion of the significance or explanation of this will be offered here. The matter will be considered fully and compared with the contemporary data for the phytoplankton in the report dealing with the relationship of the plankton to hydrology in the near future. This series is presented at the moment merely to show that had only one record per month been analysed during this period it would have given a very fair picture of the distribution which has been shown by the weekly records, and to show that the changes in the distribution are gradual ones. It does, however, at the same time go a long way towards convincing one that the errors entailed in the subsampling technique are not nearly as serious as might at first be expected.

A Comparison between the Recorder Results and the International Council's Survey, 1902–1908.

It is thought that at this stage a broad comparison between the findings of the International Council, 1902–08, and the Recorder data, 1932–37, will be of value. For this purpose the summaries of the species listed in the 'Bulletin Trimestriel '[1] will be used, and it is hoped that a more detailed comparison may be made using the figures in the 'Bulletin Planktonique' when later papers dealing with the ecology and life histories of the various species are published. Before this is undertaken, however, as has been pointed out earlier, it is wiser to wait until more information has been obtained from the extended area.

The area defined as "Southern North Sea" by the International Council[2] is practically speaking that sampled by the three Recorder lines in the first five and a half years of the survey. It extends from the mouth of the Channel (South Foreland–Cape Grisnez) in the south to the 60-metre contour in the north. The northern boundary may be considered as a line passing from about Flamborough just north of the Dogger Bank to a point in the mouth of the Skagerrak mid-way between Hanstholm and the Naze lights; this boundary is, in fact, nor far removed from the path taken by the Copenhagen line.

In the 'Bulletin Trimestriel' *Paracalanus parvus* was described as a neritic euryhaline species with a fairly high temperature optimum. It was, from 1902–1908, most abundant in the Channel and Southern North Sea, but there, as in adjacent areas, it was less successful in February and May than in August and November, though in the region off the Belgian coast this was not always so. The species should then be expected to be most abundant in the mouth of the English Channel, extreme south of the North Sea and the mouth of the Skagerrak in the autumn. *Pseudocalanus elongatus*, on the other hand, was considered to tolerate a very wide range of conditions. It was described as being "always present but usually scarce" in the North Sea south of 55° N.; the exception to this generalization being that in the extreme south of the area, the Dover Straits and off the coast of Belgium, it was often abundant. These periods of abundance appear to have occurred most frequently in the May quarter.

If these conclusions are combined to give a picture of the distribution of two species together, we may expect to find in the Southern North Sea a sparse population throughout the year except in a coastal strip of water stretching from the Dover Straits along the Belgian coast, where there may be relatively high concentrations of Pseudocalanus in the spring or summer and of Paracalanus in the autumn. In fact, if the period covered by the Recorder Survey was generally similar in physical conditions to these earlier years, we should find high numbers on the eastern end of the Rotterdam line throughout the bulk of the year, and a

[1] Farran (1910 and 1911), pp. 60–105, and Scott (1911), pp. 106–149.

[2] See Kyle (1910), p. viii.

relatively sparse distribution over the remainder of the lines. This, however, is very far from being the case. Throughout the survey the Pseudocalanus-Paracalanus group was found to be the predominant element in the copepod population. Further, one of the most striking points revealed was, as mentioned above, the relative success of the group on the Copenhagen and Bremen lines, when compared with that on the Rotterdam line. The pronounced numerical superiority of the "total Copepoda" during the summers of 1934–37 on the more northerly lines was almost entirely due to these species, which frequently constituted more than half of the entire catch. This is well illustrated in the monthly average histograms in Text-figs. 7 and 8. Although no accurate data is available for the relative proportions of Pseudocalanus and Paracalanus, there is no doubt that the former was by far the more common. Fairly large numbers of Paracalanus were found during the winters off the Dutch coast, but at no other time did it approach the density of Pseudocalanus.

It is very difficult to assess the criteria used for "common" and "scarce" in the 'Bulletin Trimestriel,' as the commonest species in the Southern North Sea might well be scarce when compared with its concentration in more productive regions, such as the Skagerrak. As all the Recorder material was taken from a comparatively restricted area, there is no opportunity of testing this, but nevertheless it is clear that during the period 1932–37 the copepod population was very different in constitution to that studied from 1902–08. A comparison between the International Council's findings and the Recorder results shows an important difference: in the earlier years Pseudocalanus was little, if at all, more successful than the other common species. It appears that the high concentrations of Pseudocalanus which were found by the Recorder in the Dogger Bank region in the summer months failed to establish themselves between 1902 and 1908. The significance of this change of distribution will be considered in relation to the broad changes in hydrological conditions in a paper dealing with water movements which is now being prepared. There is, however, a general agreement between the periods of maxima for the two species; Pseudocalanus in early summer, and Paracalanus in late summer or autumn.

Farran (1910) described *Temora longicornis* as a neritic species capable of surviving a wide range of physical and chemical conditions. He commented on the fact that it was absent from the Atlantic current and scarce on the shores which were directly under its influence. This species, like *Pseudocalanus elongatus*, was usually present throughout the year, but only in small numbers in the extreme south of the area, *i. e.* between the Norfolk coast and the Hague, and seemed to thrive more successfully in the channel than in the Southern North Sea. Here again the Recorder results are only in part agreement with his findings. It is true that a relatively higher proportion of the copepod population on the Rotterdam line was made up of Temora, but this was not due to a greater success of the species in the south, but due to the comparative weakness of the Pseudocalanus-Paracalanus group. In fact numerically the species was fairly evenly spread over the

Southern North Sea, and its variation from year to year was small in comparison with some species. The reason that this species did not share the successful summer periods on the Copenhagen and Bremen lines to the same degree as Pseudocalanus might have been in part due to its absence from inflowing Atlantic water. Such a possibility will be discussed more fully at a later date.

The group identified on the Recorder rolls as Acartia spp. is comprised almost entirely of the two species *Acartia clausi* and *Acartia longiremis*, the latter being definitely predominant. These two species are markedly different ecologically. The former is described as oceanic, being most common in the area affected by the inflowing high salinity water in the Straits of Dover and round the Shetlands, whereas the latter is strictly neritic, thriving in the mouth of the Skagerrak and off the Norwegian coast in the region of dilution by the Baltic effluent. In view of this it seems doubtful if a comparison between the two sets of observations has any value.

Scott (1911) found *Centropages hamatus* to be one of the more common calanoids in the North Sea from 1902–08. He decided that although it was a truly pelagic form, it was more abundant in coastal or restricted waters than in open sea. The 'Bulletin Trimestriel' showed that it was rare in winter, reached a maximum in May, persisted as common during the August quarter, and then declined. Giesbrecht (1882) described it as being frequent in the first part of the year and then rarer. The Recorder data fully confirm such a seasonal distribution. It was usually present on all the lines during the mid-summer months, reaching its maximum in June or July, and was rarely taken during the winter. It was, however, far less abundant than Pseudocalanus, Temora and Acartia spp.

The 'Bulletin Trimestriel' on *Centropages typicus* is interesting when compared with our present data. It was considered as an oceanic species and was only common in areas of Atlantic influence, such as the western part of the Channel and the Faroe-Shetland region, while it was only sparingly distributed over the central and Southern North Sea. It appeared to have a maximum in August or November. On all three Recorder lines in each year there were indications of a maximum towards the end of the year, usually in September or October. It may be remembered that it was usually during this period scattered fairly evenly along the Copenhagen line, but was restricted to the eastern ends of the Bremen and Rotterdam lines, and it was here in the Dutch coastal waters and the Heligoland Bight that the species was most successful. This area is well within the influence of the tongue of high salinity water flowing through the channel, and in view of the species' relative abundance in the channel and its high salinity optima, one might expect some agreement between the strength of inflow through the Straits of Dover and its concentration. Strangely the reverse seems to be the case. The most successful winters for the species were 1932 and 1933, which were years of comparatively weak flow of water past the Varne Light-vessel (see Carruthers, 1935). This is an apparent anomaly which requires further consideration. It will be dealt with when detailed figures for the changes of salinity in the area are available.

Unfortunately the 'Bulletin Trimestriel' contains no summary of the distribution of *Corycaeus anglicus*, which we have found to behave in a manner very similar to *Centropages typicus*, and might therefore afford confirmatory evidence in a comparison with the flow through the Straits of Dover.

Scott (1911) made no comment in the 'Bulletin Trimestriel' on the western restriction of *Isias clavipes*, which seemed to be a regular feature of its distribution on the Recorder lines, but if reference is made to the map summarizing the frequency of occurrence in the area from 1902–08, it will be seen that the species was more often taken in the channel and western half of the southern North Sea than off the Dutch coast or in the Heligoland Bight. There is agreement in the seasonal periodicity for the species, as between 1902–08 the maximum fell in the August quarter, and, as is shown in the histograms of monthly averages (Text-figs. 6, 7 and 8), we found August and September to be the most successful months.

Labidocera wollastoni was described from 1902–08 as an oceanic species, which reaches its maximum between August and November. This again is in agreement with the Recorder data, which showed August and September as the most successful months for the species.

As was stated earlier, *Anomalocera patersoni* was found in the Recorder material on two occasions only. This extreme scarcity was surprising in view of the International Council's findings, because it was then recorded to have had a similar distribution and periodicity to Labidocera, but to have been, if anything, more common. A possible explanation lies in the common supposition that the species usually swims near the surface, and if this is so the Recorder may, at 10 metres, pass too deep to catch it. Sars (1903, p. 141) stated that it might be found so near the surface that it might break the surface. Gough (1905) was more definite when he remarked that it rarely descended to 10 metres, and Savage (1926) took it only in surface hauls. Again, Gibbons (1936, p. 28), after commenting on its importance as a food of the herring, wrote: "It is . . . located almost entirely in the surface layers of the sea. Even when occurring in large numbers it is frequently found only in the surface net, the two lower nets, and especially the bottom net, rarely taking more than one or two individuals." Russell (1927b), on the other hand, found in the Channel in 1925 that the species was restricted to the upper few metres in April, May and June, but showed signs of spreading into deeper water in July and August, which was the time when it became more abundant in the area. If this is a general phenomenon and the conclusion that Anomalocera is almost exclusively a surface form is a fallacy based on observations which do not cover the whole year, one is compelled to assume that the 1932–37 period was a particularly unsuccessful one for this species. This seems unlikely in one respect, because in 1932 and 1933 and to a lesser extent in 1934 Savage (1937) found it to be quite well represented in the stomachs of herring taken from the Shields area, which is not far removed from the Copenhagen line. During this period, however, no Labidocera were recorded in the stomach contents. Hardy

(1924), on the other hand, showed that the North Sea herring would take both species, and as Labidocera did occur in appreciable numbers on the Recorder lines from 1932–34, the most reasonable assumption is that both species were present in our area, but the vertical distribution of Anomalocera prevented it being caught at 10 metres.

In the 'Bulletin Trimestriel' *Parapontella brevicornis* was described as a tychopelagic form recorded mostly from the southernmost North Sea and the English Channel. The Recorder findings are in agreement with this, as the species was almost entirely restricted to the Rotterdam line. There is some disagreement, however, in the seasonal distribution. Whereas from 1902–08 the maxima fell in the August quarter and the minima in the winter, all the appearances of this species between 1932 and 1937 were in October and November with the exception of two. This may be due to the fact that its appearance in the Recorder samples was correlated with the increased turbulence and vertical mixing associated with the winter, while during the summer months it remained too near the bottom to be caught.

From the 1902–08 data Farran decided that the presence of *Metridia lucens* was indicative of the presence of Atlantic water. He described it as an inhabitant of the North Atlantic which increased very rapidly on meeting favourable conditions in coastal waters, and suggested that the high concentrations so formed followed the oceanic current both round the Shetlands into the northern part of the North Sea and up to the western end of the Channel. He found that effectively the southern limit of its distribution was conterminous with the Scottish observations, which are well north of the 55° parallel.

Candacia armata was another species which appeared from the International Council's results to be oceanic, as it was generally present in the Channel and Northern North Sea. Scott, however, commented particularly on the fact that it was never caught in the North Sea south of a line drawn between the Firth of Forth and the Skagerrak.

Metridia lucens and *Candacia armata* should then prove to be two good indicators of the extent of the Atlantic influence. Apparently from 1902–08 they were not carried into the Southern North Sea.

Turning to the Recorder results it will be seen that although not common, these species were by no means absent from the area between 1932 and 1937. In fact they penetrated as far south as the Humber region during the winters of 1932–33 and 1933–34. Metridia was taken in November, 1933, and March, 1934, and again in the following November, while Candacia was taken in October, 1932, and in November and January of the 1933–34 winter. It is interesting to note that not only were these two species taken farther south during these winters than might be expected from the earlier results, but at the same time *Centropages typicus*, another oceanic form, was far more successful than usual. Metridia, however, was relatively abundant in January and February, 1937, when Candacia was not found, and when *Centropages typicus* was at a very low level.

These species will be considered in relation to the prevailing physical conditions and water movements in a future paper.

Summarized Distribution of the Copepoda in the Area.

Having presented the Recorder material and made some broad comparisons between it and earlier results, it remains only to draw attention to the more striking points arising from it.

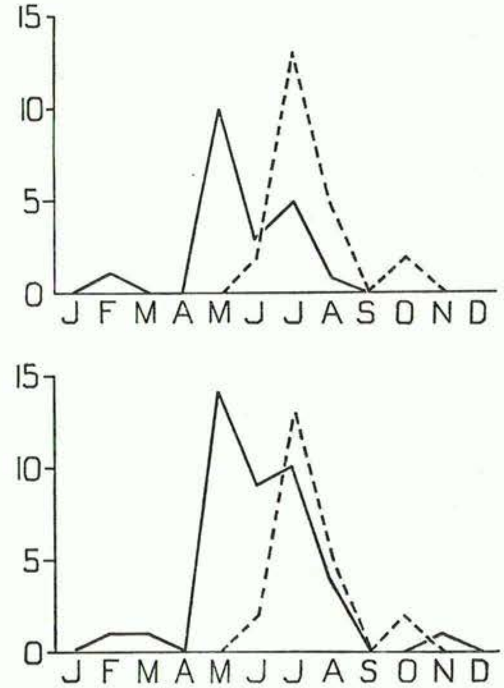
First we may consider the changes which take place during the year. There are quite obviously very marked and significant differences between the years, but nevertheless there are a number of common points which serve as a basis for comparison. It will be remembered that there is a degree of consistency between the winter months of all years and so the winter is a convenient time at which to begin. December or January are typical months, in which there appears a low and even distribution over most of the area, and a band of higher concentration off the Dutch coast. This coastal restriction has been shown by other workers. Savage (1923), during the 'Plaice Egg Cruises' of the 1920–21 winter, found in January and February higher numbers on the eastern side of the area, whereas in December he took more off the East Anglian coast, so that there appeared between December and January a swing of the main part of the population from west to east. He correlated this with the winds prevailing over the periods just previous to his observations, and concluded that the change was due to a heaping effect off the Dutch coast of the surface water driven by south-west winds. This is in agreement with the principle suggested by Gran (1912), who commented that the prevalent winds tended to drive the surface layers towards the coast in the autumn and so accumulate large quantities of plankton there. It is not easy to assess the degree of this restriction or apparent heaping effect in the various years, as it obviously is bound up with the number of individuals present, a number which varies very considerably itself, so it is not practicable to attempt at this stage any comparison between the distribution and wind data. It is interesting, however, that the composition of the eastern population on both the Bremen and Rotterdam lines is very similar to that in the rest of the area sampled, and although at times, as for example in the 1933–34 winter on the Rotterdam line, there is a comparatively sharp boundary between the regions of higher and lower densities, there is more often a quite gradual change from one end of the line to the other. There is, in fact, no evidence to suggest that these higher numbers are part of a distinct community of different origin to the individuals that are scattered over the rest of the area, but it seems more probable that it is the result of an accumulation of the type suggested by Gran and Savage. The way in which a more even autumn distribution gradually gives way to the eastern preponderance gives some confirmation of this; the best example is the autumn of 1937, when there is data for practically every week on the Bremen line, and the eastward movement of copepods appeared to be both gradual and continuous (see Text-fig.

12). In addition to the spatial arrangement there are other characteristics of the winter copepod population. A number of species appear in the area only at this time of year. These fall into two categories. The first includes *Centropages typicus* and the cyclopoid *Corycaeus anglicus*, both of which regularly appear in the autumn and persist until the end of the year. Reference to the maps illustrating the distributions of these two forms shows that they by no means invariably have similar spatial arrangements at first, but in every case they show signs of conforming to the typical winter pattern before they disappear. The second consists of two larger forms, *Candacia armata* and *Metridia lucens*, which are most certainly not indigenous to the area but have a natural habitat further north, and are only carried as far south as the Recorder lines by the influx of higher salinity water. Two other species occur almost exclusively in the winter, *Parapontella brevicornis* and *Alteutha interrupta*, but as both of these have a bottom habitat it is probable that their appearance in our records at this time is associated with the increased turbulence.

In the spring or early summer there occurs an increase which may in some years (1935 and 1937) be very pronounced. The dense population found over the Dogger Bank and on the Bremen line at this time is in the main composed of *Pseudocalanus elongatus*. *Temora longicornis*, *Acartia clausii* and *Paracalanus parvus* are well represented, although there is some evidence that the last named species does not reach its maximum until the autumn. In addition there are a number of less common forms, such as *Centropages hamatus* and *Acartia longiremis*, while by midsummer *Isias clavipes* and *Labidocera wollastoni* appear.

This spring improvement in the population in our particular area may be produced in two ways. Firstly there is the possibility of large numbers of copepods being carried into the area at this time of year from some more densely populated region adjoining it, and secondly the possibility of a sparse population that has wintered in the Southern North Sea breeding there to produce a new and more abundant stock. It is of course most probable that both of these occur and the summer population is the combined result of local breeding and invasion, but it would be valuable if possible to determine the extent of each effect in order to know where to look for the factors controlling the success of the population or the available fish food in any year. The distributions found during the years of the survey indicate that if not the actual individuals the factors controlling their production come from a region north of the Copenhagen line. On the maps showing the " total Copepoda " distribution (Plates XCIV–CVI) it will be seen that, if the Dutch coastal concentration is neglected, the first indications of higher numbers appearing amongst the general sparse winter population were usually found on the western half of the Copenhagen line: March, 1933, April, 1934, and April, 1937, being particularly good examples of this.

Another point in this respect is that the population in the southern part of the area sampled by the Rotterdam line was never affected by spring and summer to anything like the same extent as the two more northern lines. In fact, as has been pointed out earlier, the difference between the summer and winter populations on this line may not be very marked (see Text-fig. 6). In addition to this the various species tend to reach their maxima later here than on the Copenhagen and Bremen lines. This is illustrated by Text-fig. 13, where the continuous line graphs showing the frequency with which the summer species reach their annual maxima in the different months during the years 1933–37 on the Copenhagen line



TEXT-FIG. 13.—For explanation see accompanying text.

(upper graph) and the Bremen line (lower graph) are compared with broken-line graphs, each showing similar data for the Rotterdam line. The species included in this figure are all those given in Text-fig. 6 except the two winter species *Centropages typicus* and *Corycaeus anglicus*. It will be seen that whereas the maxima for the summer species on the Rotterdam line occurred most frequently in July and August, on the two northern lines the majority fell in May, June and July.

A COMPARISON OF THE FIVE-AND-A-HALF YEARS.

Finally, it may be convenient to sum up as briefly as possible the characteristic points of the various years investigated.

The information available for 1932 consists only of Bremen records for the later part of the year and Rotterdam records for November and December. This, however, is sufficient to show that it was a particularly successful autumn for most species. This was most marked in the case of *Temora longicornis* and Acartia spp. The Para- and Pseudocalanus group was above average and *Isias clavipes*, *Centropages hamatus* and *Labidocera wollastoni* were well represented. Of the winter species, *Corycaeus anglicus*, although quite abundant at the end of the November record, appeared to have a short season, but *Centropages typicus* was plentiful on the centre of the Bremen line over quite a long period. Both *Candacia armata* and *Metridia lucens* were taken.

Although the successful preceding autumn crops were reflected in the early months of 1933 for some species, this was, on the whole, the leanest year of the survey. All the summer species with the exception of *Isias clavipes* and possibly *Centropages hamatus* and *Labidocera wollastoni* were well below their usual level, the failure of the mid-summer Para- and Pseudocalanus population being most pronounced. There was, however, an improvement towards the end of the year, when *Centropages typicus* and *Corycaeus anglicus* were widespread and in places plentiful, and the two exotics, *Candacia armata* and *Metridia lucens*, again appeared.

1934 was an average year. The main species were well represented, but never particularly abundant. *Labidocera wollastoni* and *Corycaeus anglicus* were more successful than usual, while *Centropages typicus* was the less so.

1935 was marked by the very high production on the northern lines in the spring and summer. This was in the main due to the Para- and Pseudocalanus group, but the numbers of *Temora longicornis* and Acartia spp. were also much higher than usual. With the exception of *Labidocera wollastoni* on the Copenhagen line, however, this was not a successful year for the other less abundant species. *Isias clavipes* and *Centropages hamatus* were at about their normal density, while both *Corycaeus anglicus* and *Centropages typicus* reached a very low level, the latter only occurring on the Rotterdam line in June. In fact this winter appeared to be most unfavourable for the copepod population. A relatively small proportion of the enormous summer Para- and Pseudocalanus stock persisted through the autumn, but all the other species became sparse, and during the early months of 1936 this was the only group present in appreciable numbers.

The summer months of 1936 were rather like those of 1934. The main species were less numerous than in 1935, but more successful than 1933, and the winter species were again as in 1935 very poorly represented. *Centropages typicus* was never abundant and *Corycaeus anglicus* only recorded as present. Acartia spp. were outstandingly successful in the spring or early summer; with 1935 it was the most successful period for this group during the five-and-a-half years.

As in 1936, the early months of 1937 supported only a very weak population. Low numbers of Para- and Pseudocalanus were taken, but little else except in a restricted region off the Dutch coast, where a slightly stronger population was made up of this group, *Temora longicornis*, Acartia spp., and a few *Centropages hamatus*. By May, however, a great change had taken place. The Para- and Pseudocalanus group was as successful as in 1935 and *Temora longicornis*, Acartia spp. and *Centropages hamatus* were more abundant than usual. During the subsequent months these forms remained at a high level in the northern part of the area, but there was a marked decrease in their numbers on the Bremen line, while on the Rotterdam they were no more successful than usual. This was a relatively poor year for *Isias clavipes* and *Labidocera wollastoni*. Both *Centropages typicus* and *Corycaeus anglicus* showed a considerable improvement on the two previous poor winters, and the northern form *Metridia longa* returned to the area for the first time since the 1933 winter.

As a generalization it may be said that the years with a flourishing summer population were followed by a poor winter, for example, 1935 and 1937 ; whereas in those years characterized by the success of the winter species, the commoner summer forms were less abundant, *i.e.* in 1932, 1933 and 1934. It is interesting to note, however, that in 1935 and 1937 the particularly successful copepod communities appeared just after dense and varied crops of spring diatoms had been found over the Dogger Bank region (see Lucas, 1940).

General Summary.

1. The monthly changes in the distribution and abundance of the Copepoda in the southern North Sea have been investigated from June, 1932 to December, 1937, by using the Continuous Plankton Recorder ; this was towed at a standard depth of 10 metres, by ships sailing on regular lines from Hull to Rotterdam, to Bremen and towards the Skagerrak, and later from London to Esbjerg.

2. The methods are described and those limitations which apply more particularly to the Copepoda are discussed (pp. 175 to 186 and 198 to 203).

3. The first part of the report deals with the Copepoda as a whole, *i.e.* the total population. The difference between the summer and winter distributions is stressed. The variations in numbers from year to year are found to be considerable and it is suggested that they are sufficiently large to be reflected in the success or failure of the broods of those fish which are at some period of their development dependent upon the Copepoda for food.

4. The second part deals with the data concerning the constituent species or groups of allied species ; a list of these is given on p. 197.

5. The group Paracalanus + Pseudocalanus was by far the most abundant and together with the genera Temora and Acartia was found to be responsible for most of the fluctuations in the population (pp. 205 to 208).

6. The distributions, seasonal and spatial, of the other common forms are described, with the exception of that of *Calanus finmarchicus* which is to be the subject of a later report.

7. The recorder results are compared with the findings of the International Council survey from 1902 to 1908 ; some marked disagreements are discussed (pp. 227 to 232).

8. The appearance of the northern forms *Candacia armata* and *Metridia lucens* during the winters of 1932–33, 1933–34 and 1937 are recorded (pp. 222 to 223).

9. A summarized account of the main seasonal changes in the area is given (pp. 232 to 234) and followed by a brief comparison of the $5\frac{1}{2}$ years investigated.

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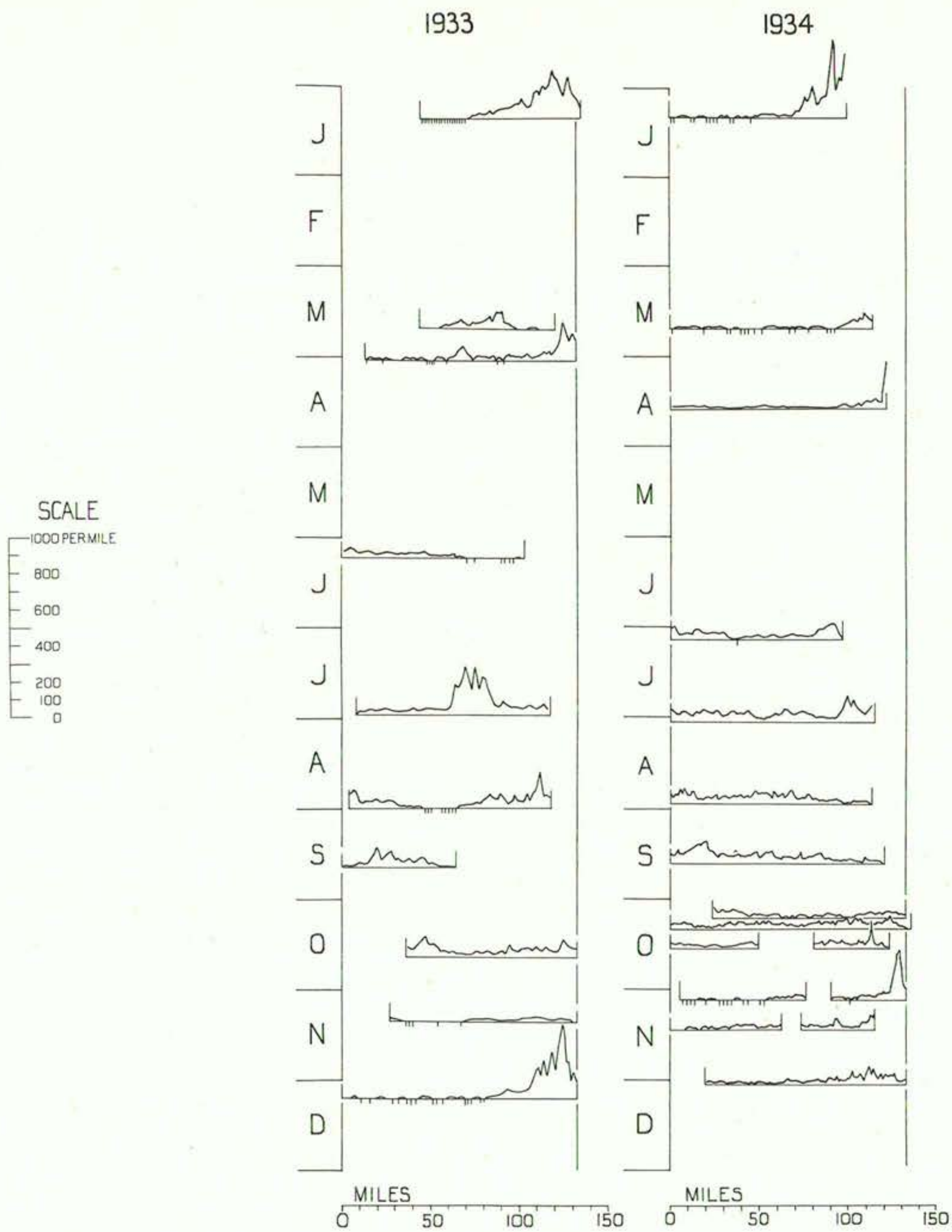
PLATES LXV-XCIII.

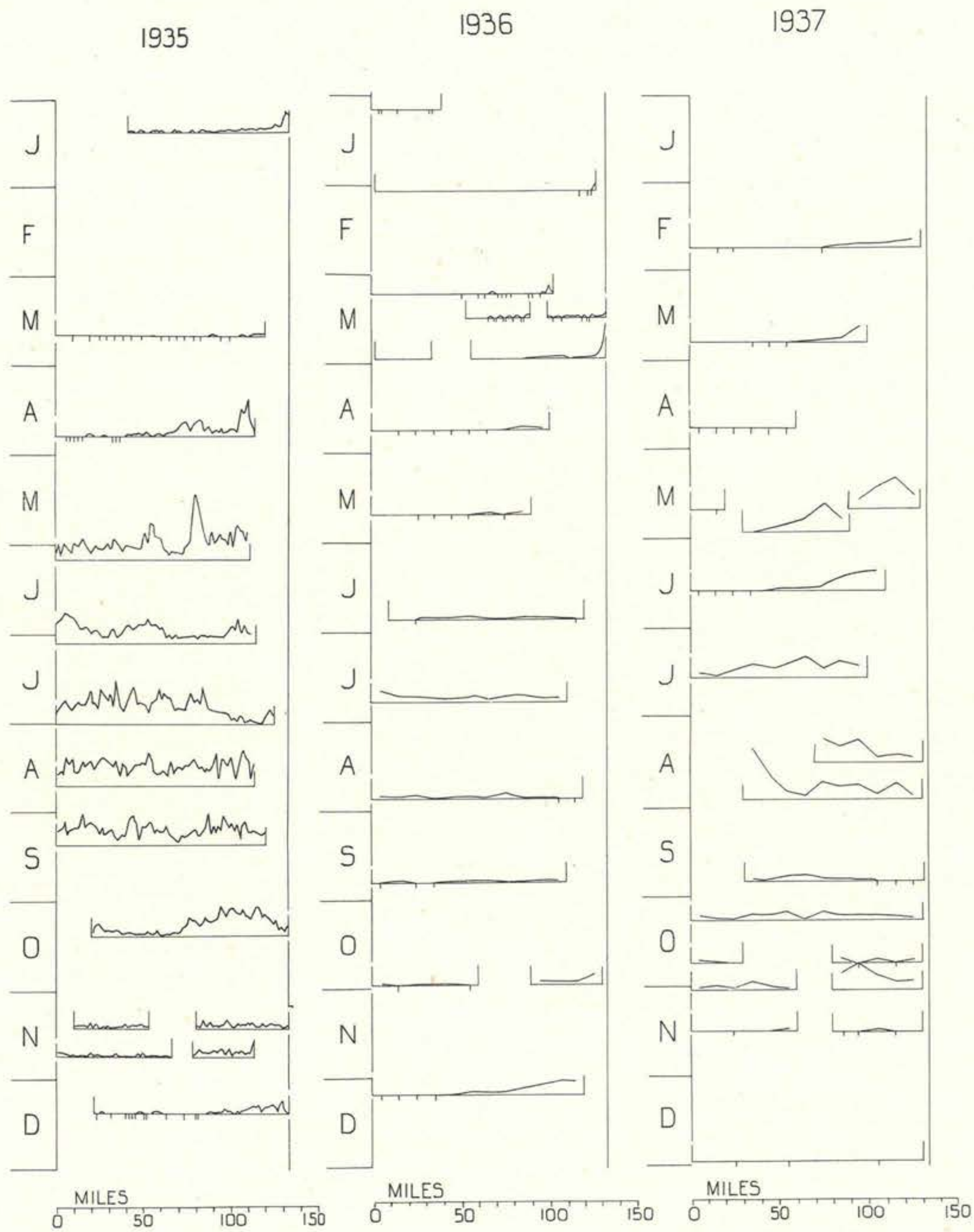
SERIAL GRAPHS COMPARING THE VARYING QUANTITIES OF THE PRINCIPAL COPEPODA FOUND YEAR BY YEAR ON THE DIFFERENT RECORDER LINES IN THE SOUTHERN NORTH SEA JUNE 1932 TO DECEMBER 1937.

PLATE LXV



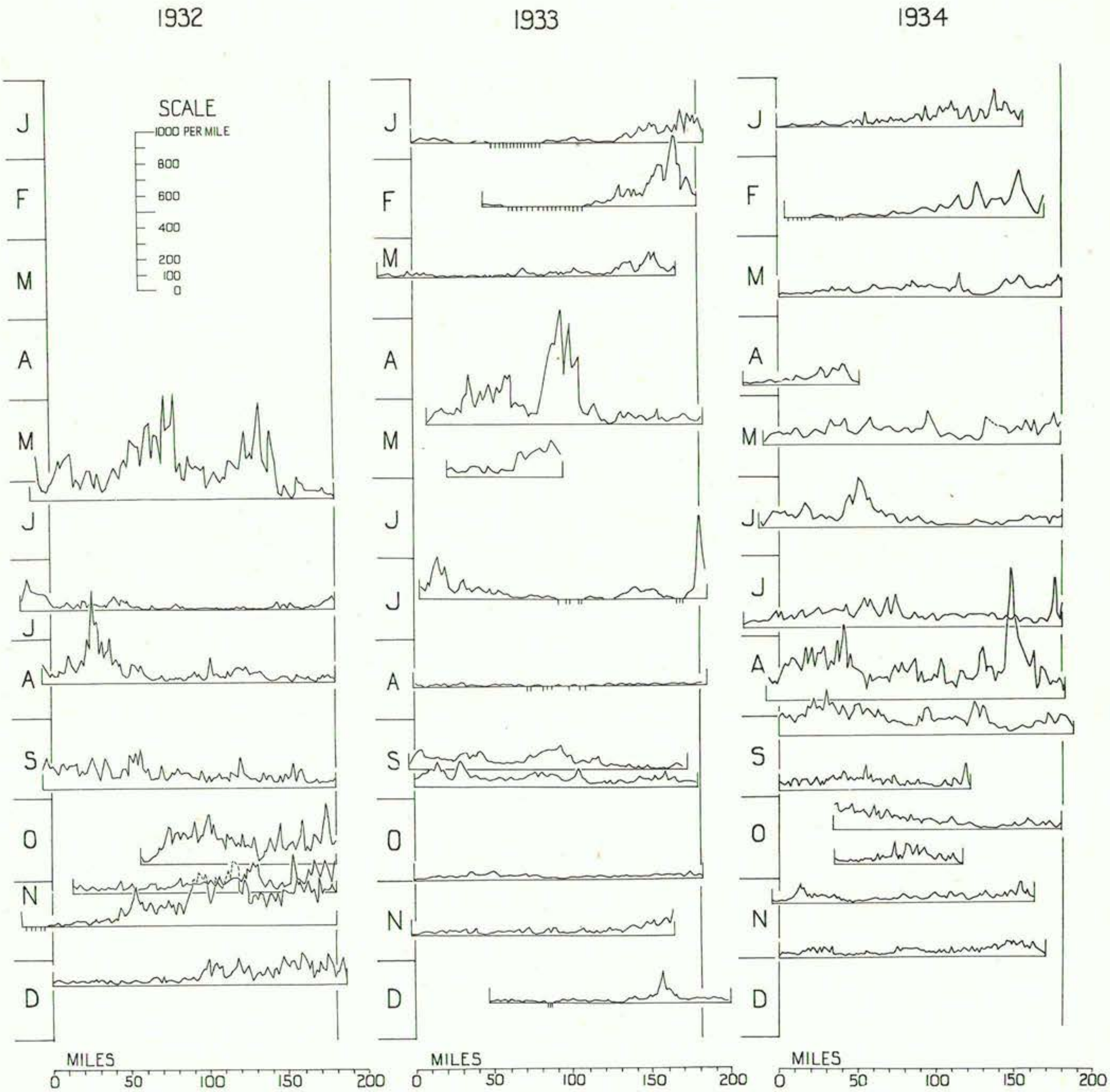
Records of **TOTAL COPEPODA** *on the* Rotterdam *line,* 1933 *and* 1934, *each placed in it's position of date against a vertical scale of months indicated by the letters J. F. M, etc. in each year. The vertical lines to the left and right of each annual series represent the positions of the* East Dudgeon *and* Maas *lightvessels. The estimated numbers per mile are shown as graphs above the base lines and traces (too small to graph) as small vertical strokes below them.*

PLATE LXVI



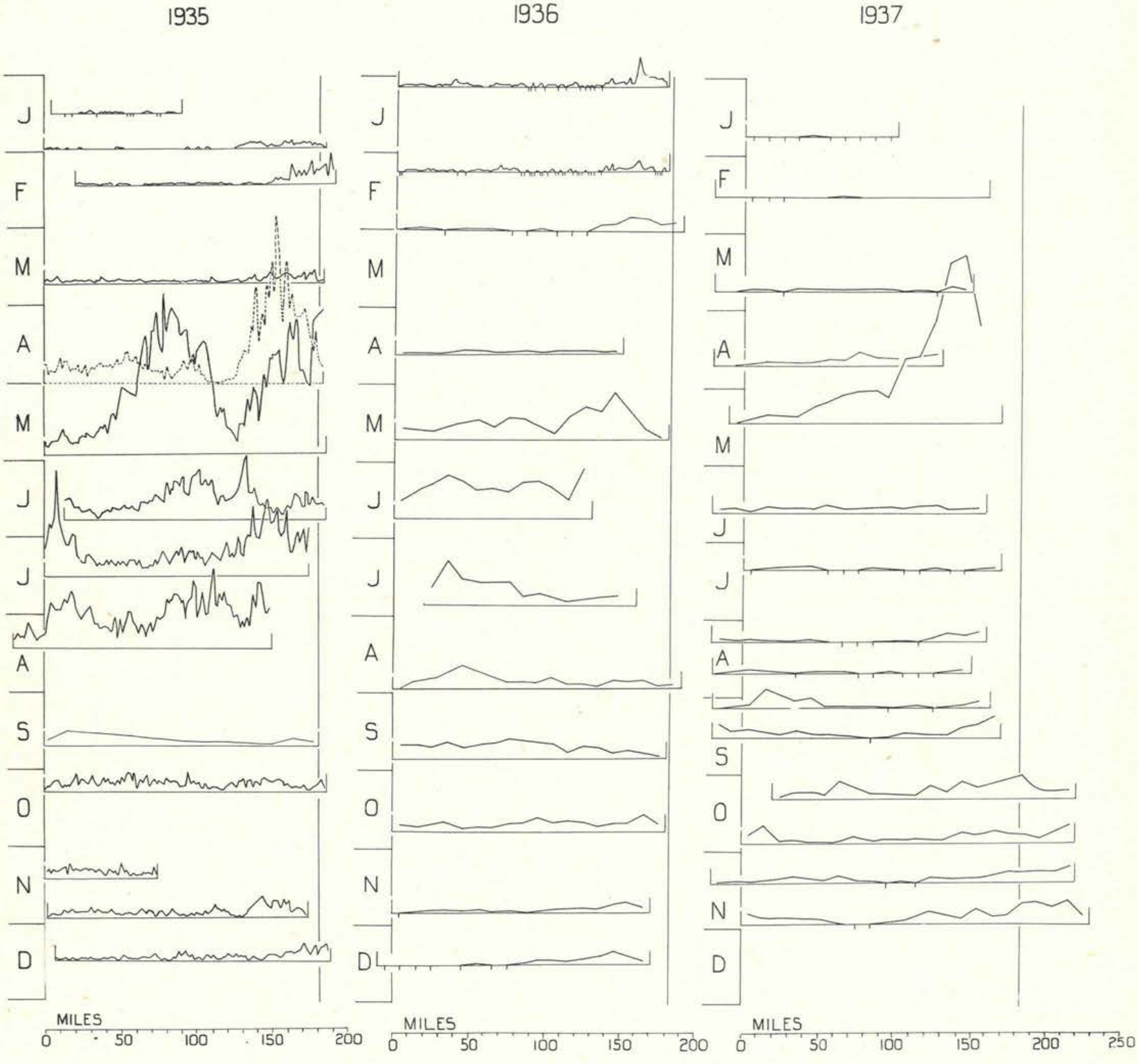
Records of the **TOTAL COPEPODA** *on the* Rotterdam *line,* 1935 – 1937, *arranged as on Plate LXV.*

PLATE LXVII

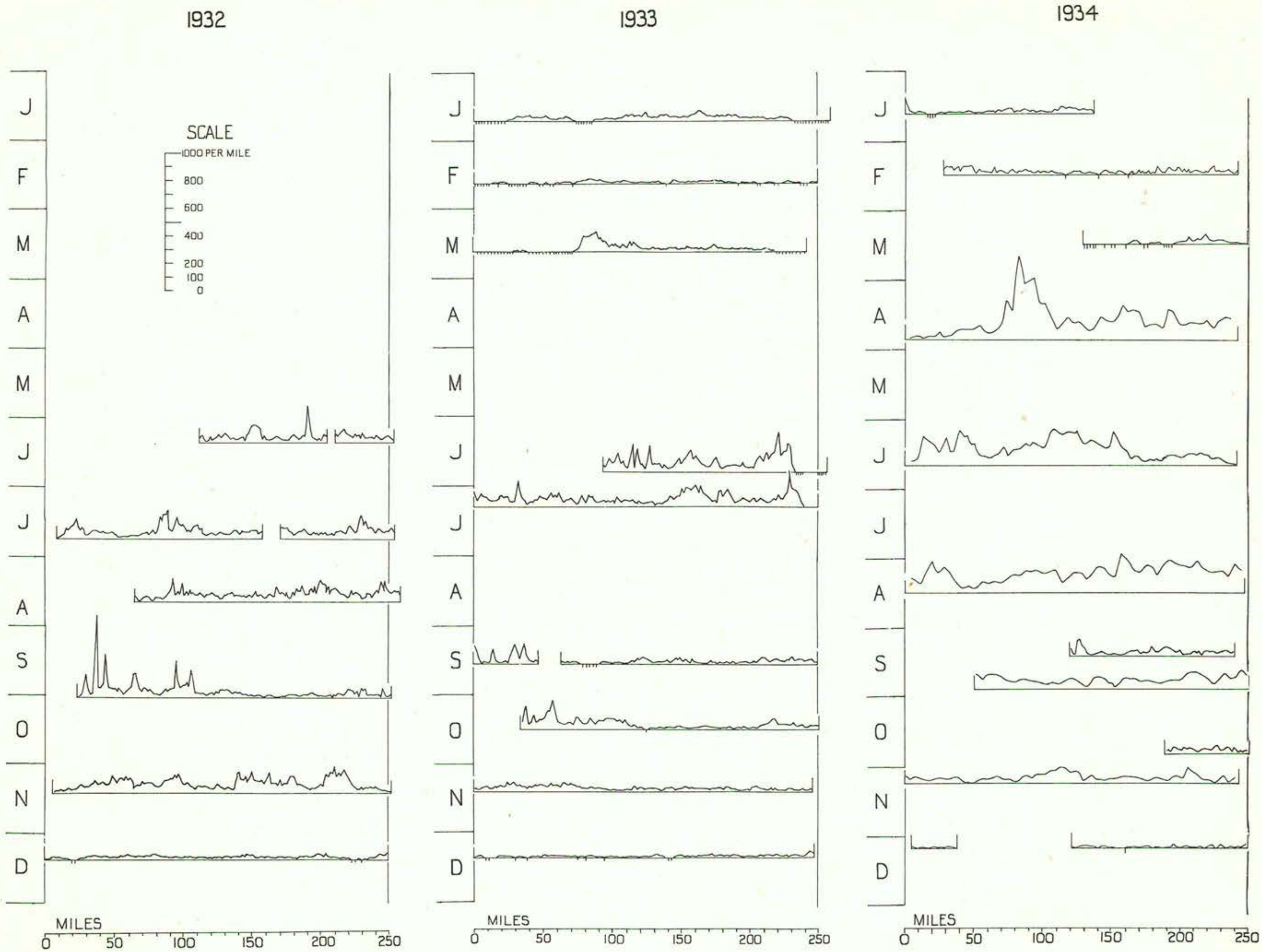


Records of the **TOTAL COPEPODA** *on the* Bremen *lines,* 1932 — 1934, *arranged as on Plate LXV except that the vertical lines to the left and right of each annual series represent the positions of the* Outer Dowsing *and* Borkum *lightvessels.*

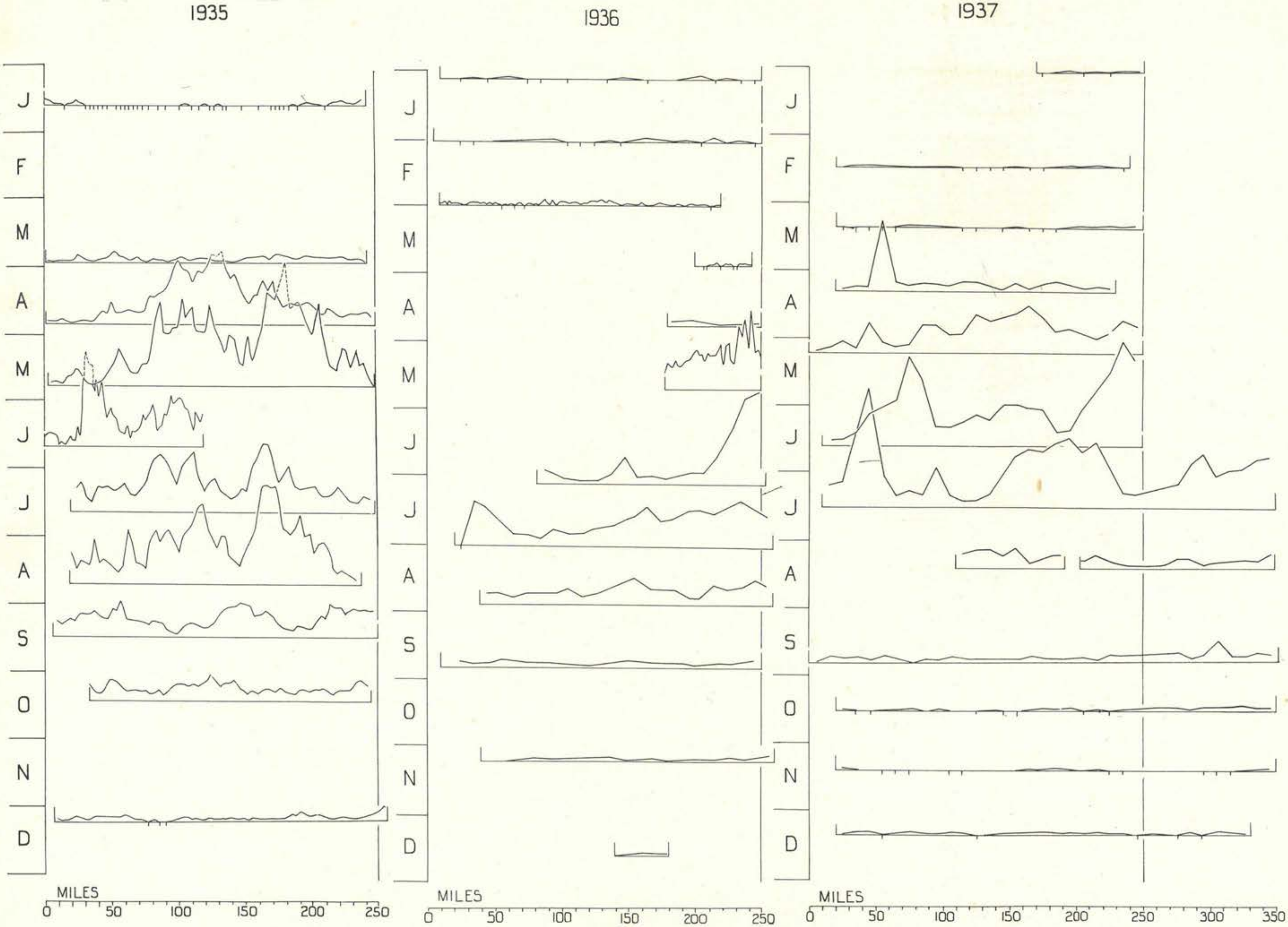
PLATE LXVIII



Records of the **TOTAL COPEPODA** *on the* Bremen *line,* 1935-1937, *arranged as on Plate LXVII. An overlapping graph is shown in broken line for clarity.*



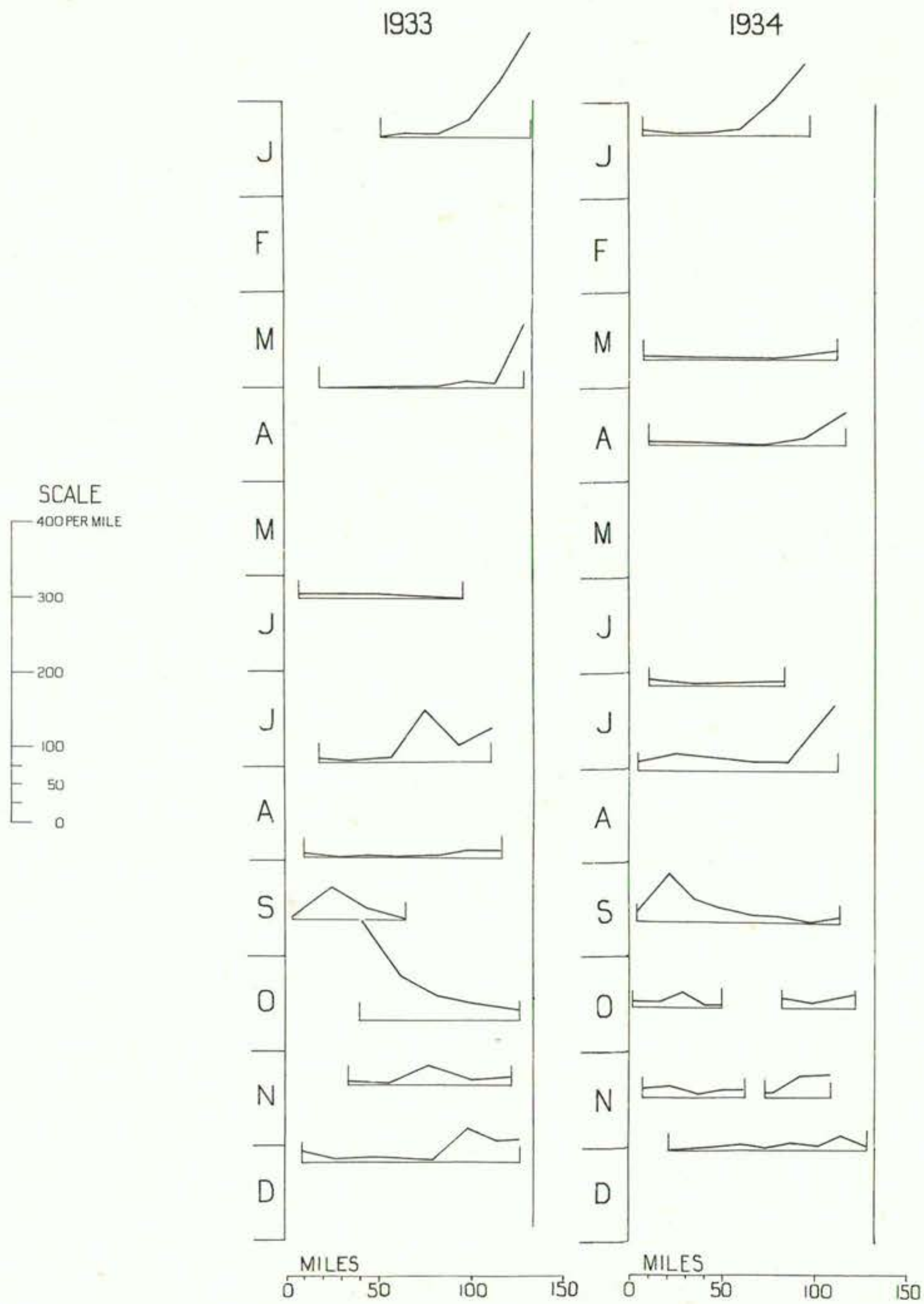
Records of the **TOTAL COPEPODA** *on the* Copenhagen *line*. 1932 – 1934, *arranged as in Plate LXV except that the vertical lines to the left and right of each annual series represent the positions of the* HUMBER *lightvessel and a point* 250 *miles from it.*



Records of the **TOTAL COPEPODA** *on the* Copenhagen *line, 1935 – 1937, arranged as on Plate LXIX.*

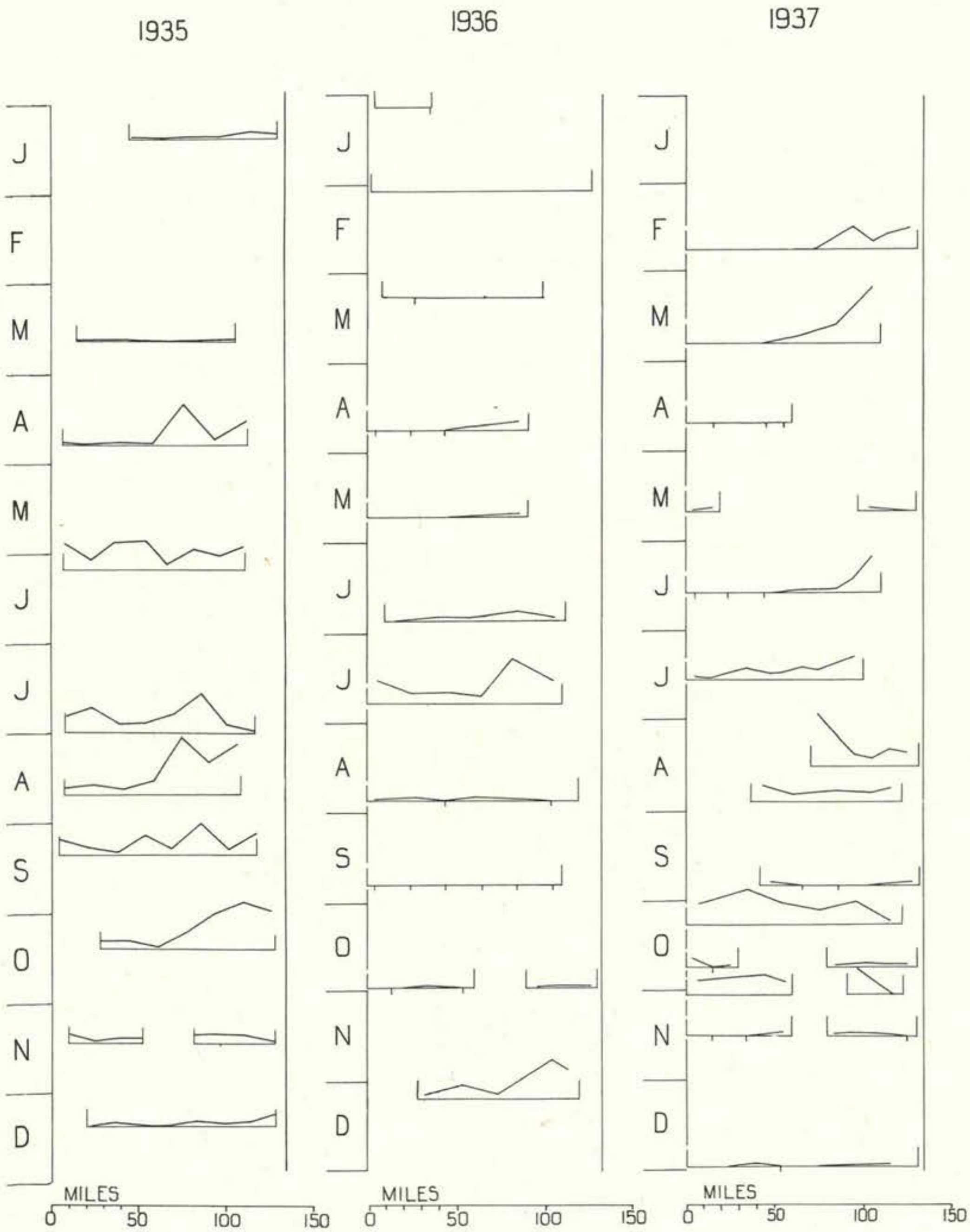
PLATE LXX

PLATE LXXI



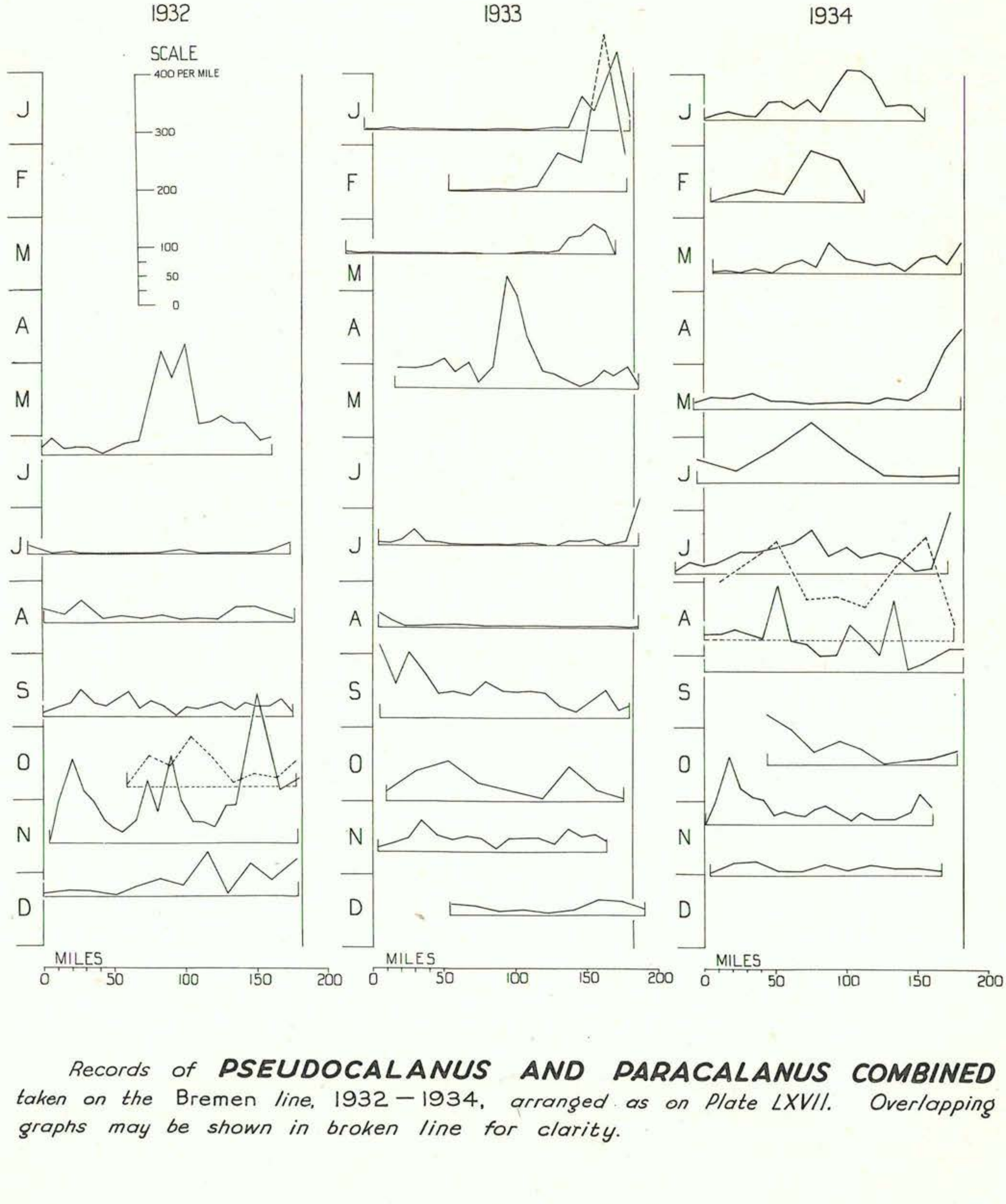
Records of ***PSEUDOCALANUS AND PARACALANUS COMBINED*** *taken on the* Rotterdam *line*, 1933 *and* 1934, *arranged as on Plate LXV.*

PLATE LXXII

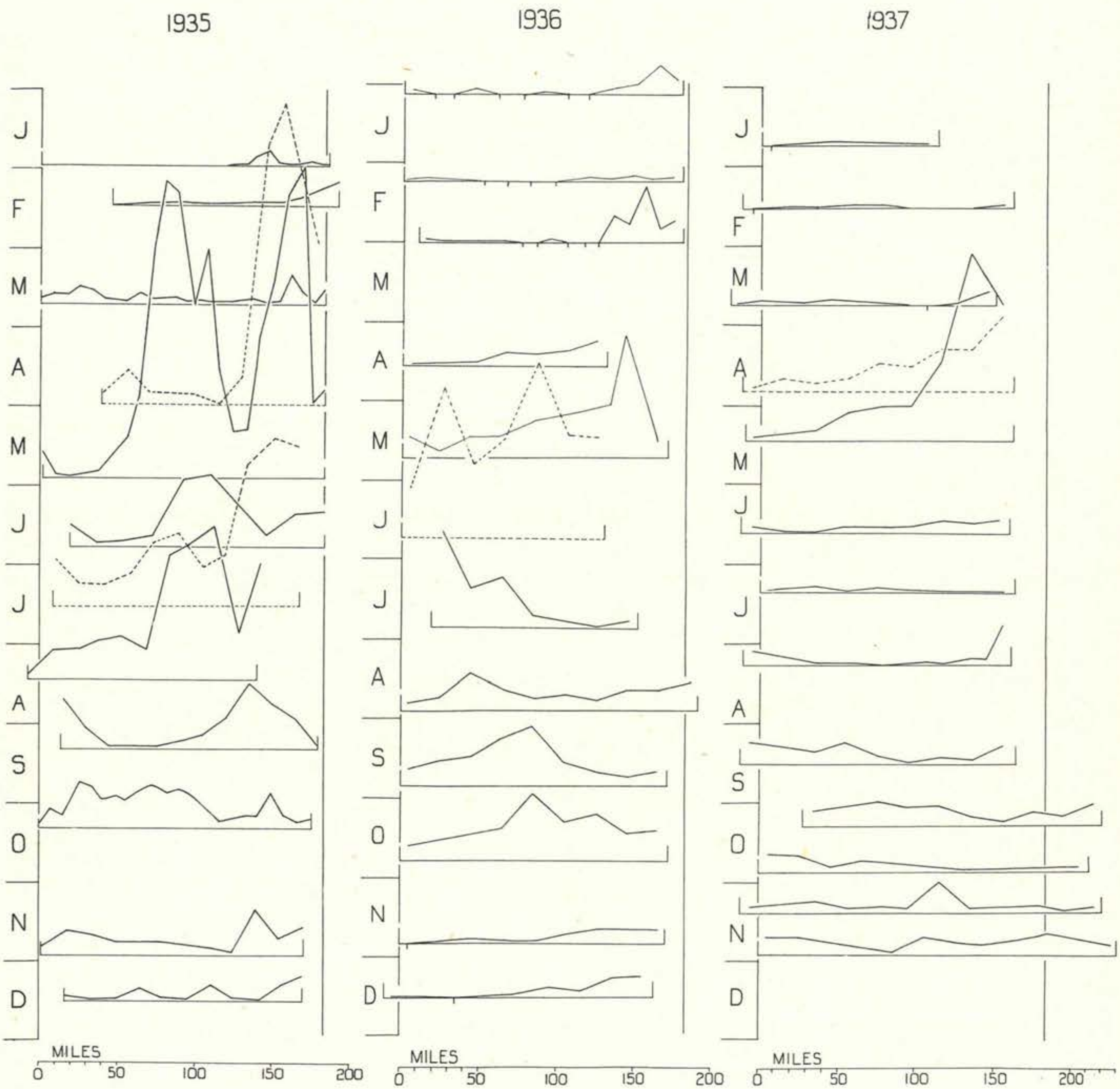


Records of ***PSEUDOCALANUS AND PARACALANUS COMBINED*** *taken on the* Rotterdam *line,* 1935 – 1937, *arranged as on Plate LXVI.*

PLATE LXXIII

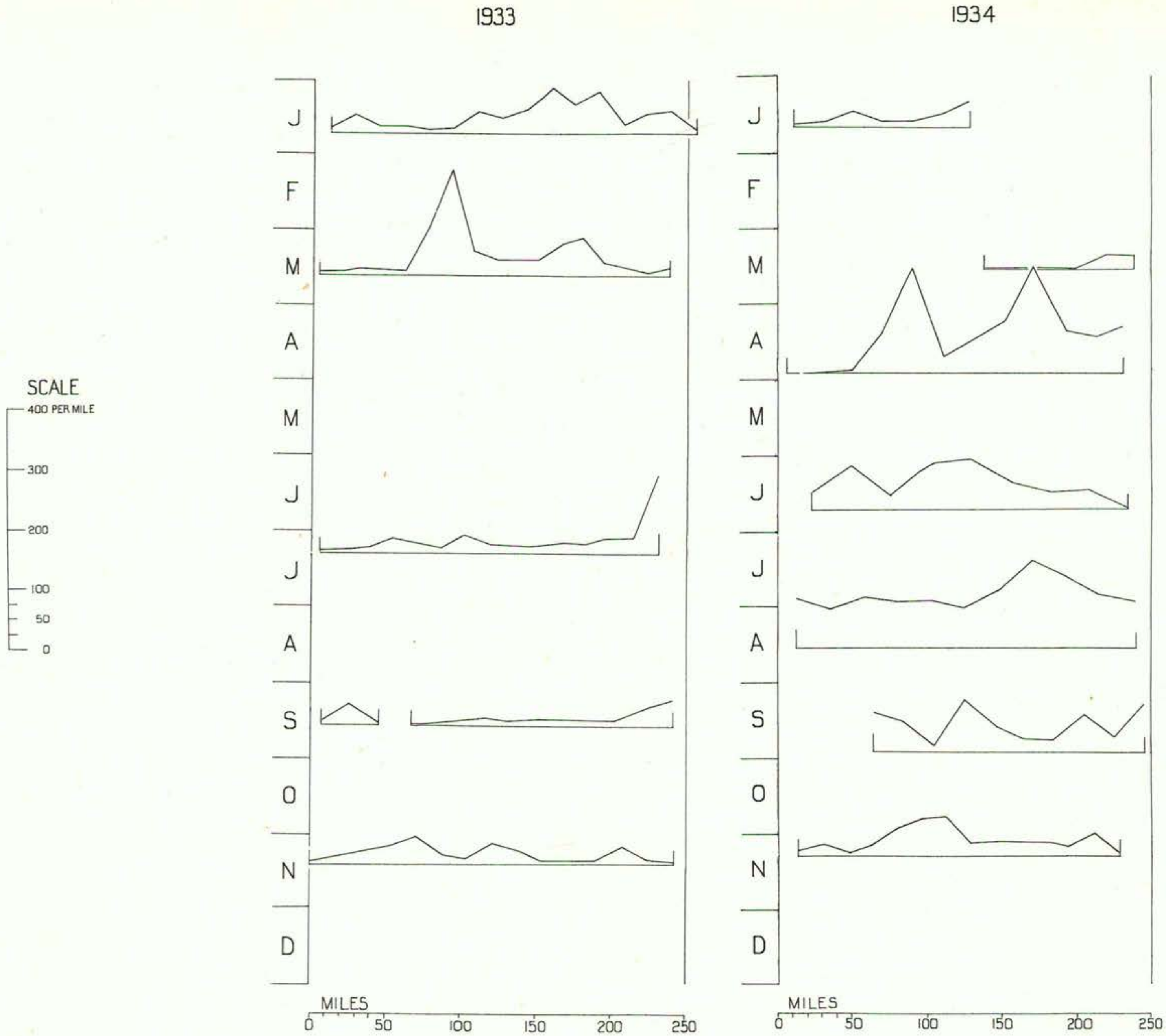


Records of ***PSEUDOCALANUS AND PARACALANUS COMBINED*** *taken on the* Bremen *line,* 1932 — 1934, *arranged as on Plate LXVII. Overlapping graphs may be shown in broken line for clarity.*

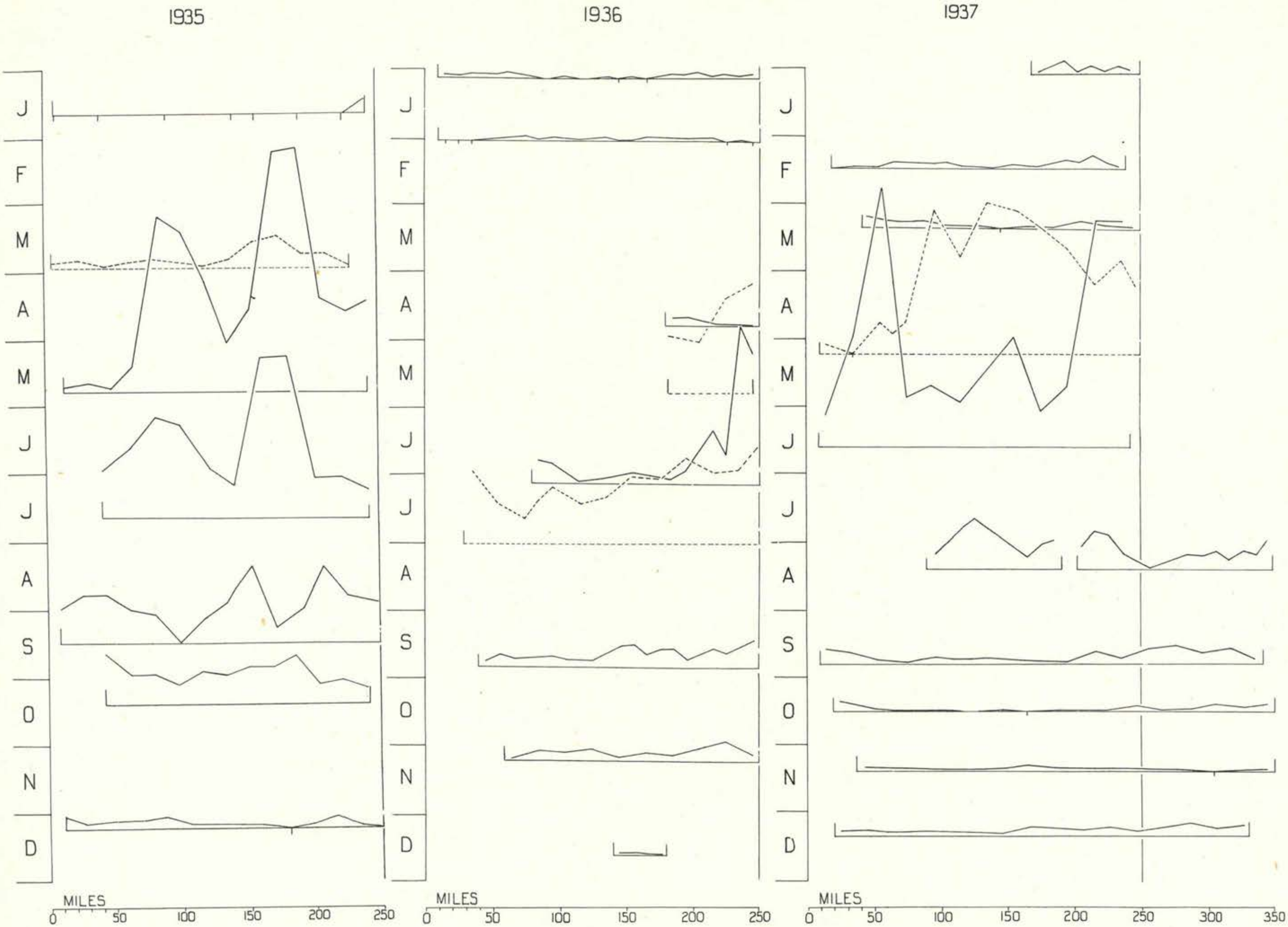


Records of **PSEUDOCALANUS AND PARACALANUS COMBINED** *taken on the* Bremen *line*, 1935–1937, *arranged as on Plate LXVIII. Overlapping graphs may be shown in broken line for clarity.*

PLATE LXXV



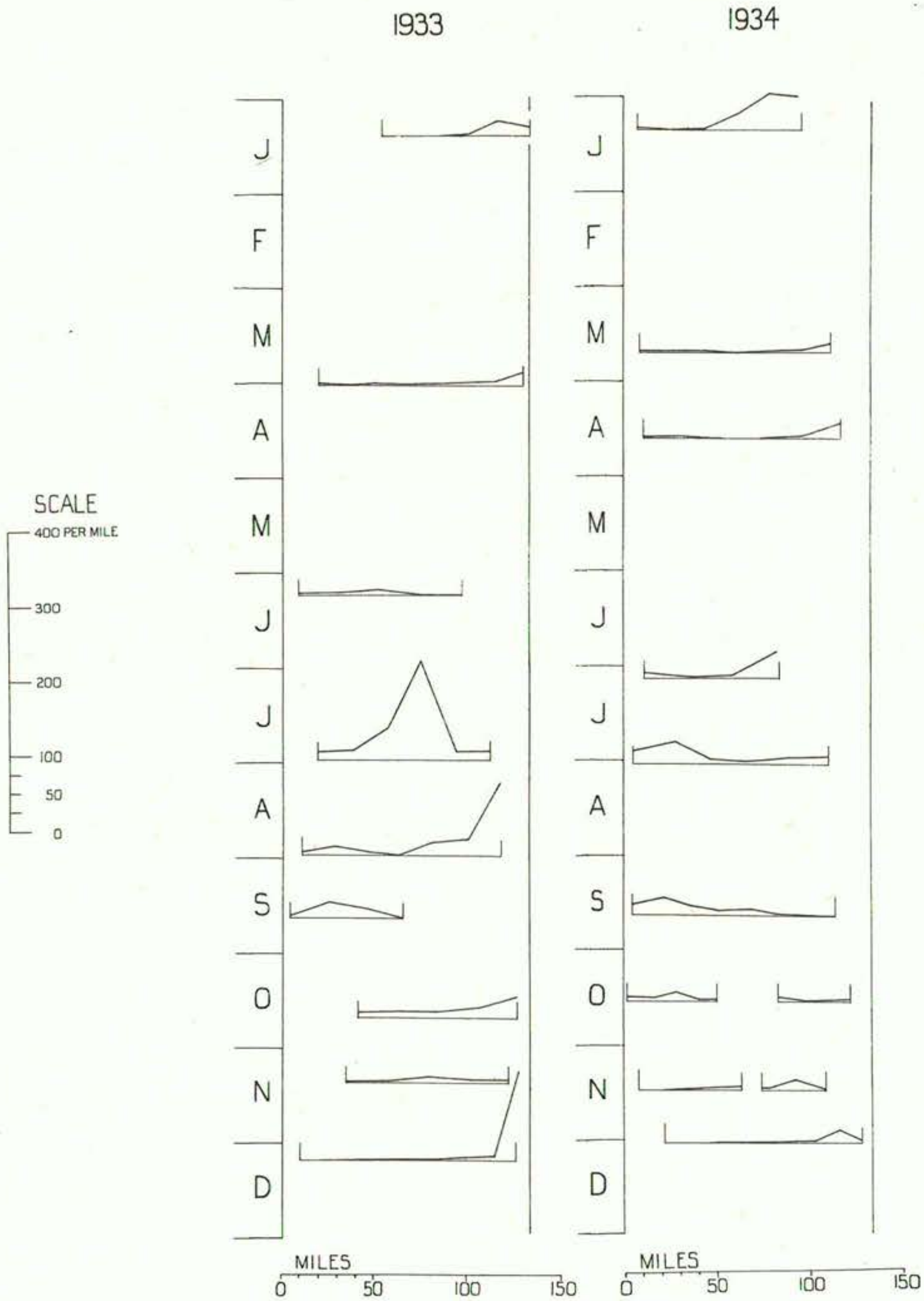
Records of **PSEUDOCALANUS AND PARACALANUS COMBINED** *taken on the* Copenhagen *line,* 1933 *and* 1934, *arranged as on Plate LXIX.*



Records of **PSEUDOCALANUS AND PARACALANUS COMBINED** *taken on the* Copenhagen *line,* 1935 - 1937, *arranged as on Plate LXX. Overlapping graphs may be shown in broken line for clarity*

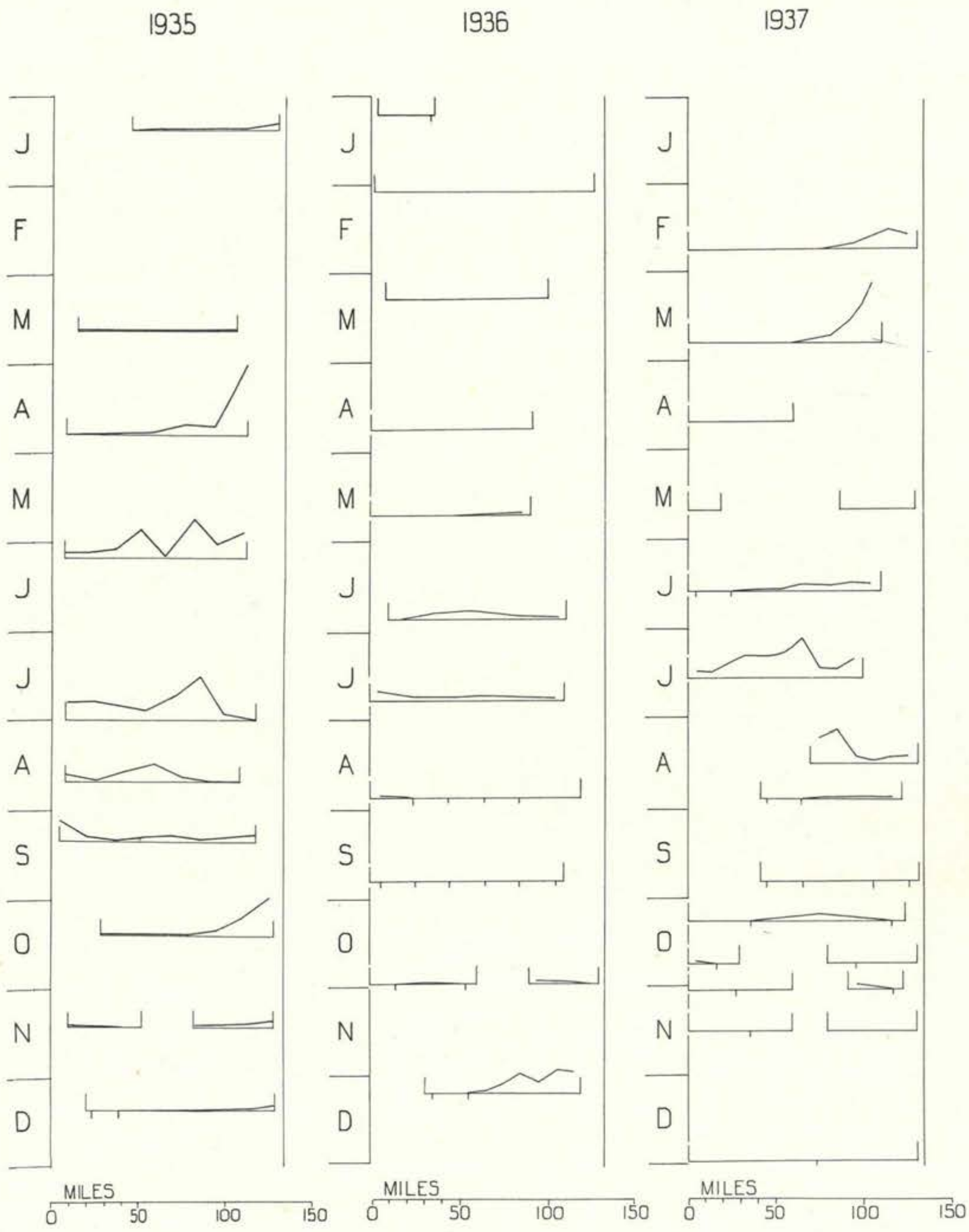
PLATE LXXVI

PLATE LXXVII



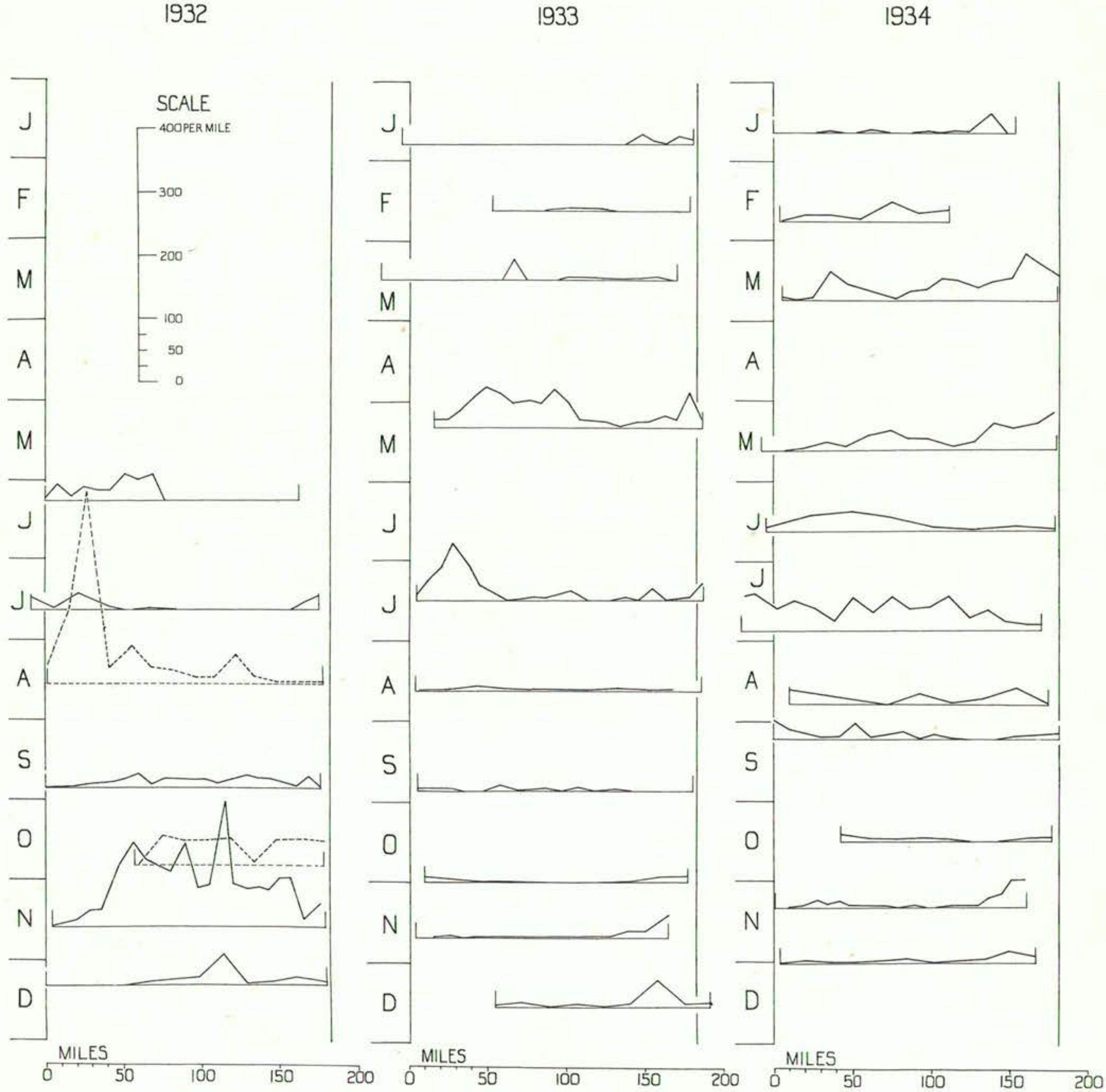
Records of **TEMORA LONGICORNIS** *on the* Rotterdam *line,* 1933 *and* 1934, *arranged as on Plate LXV.*

PLATE LXXVIII



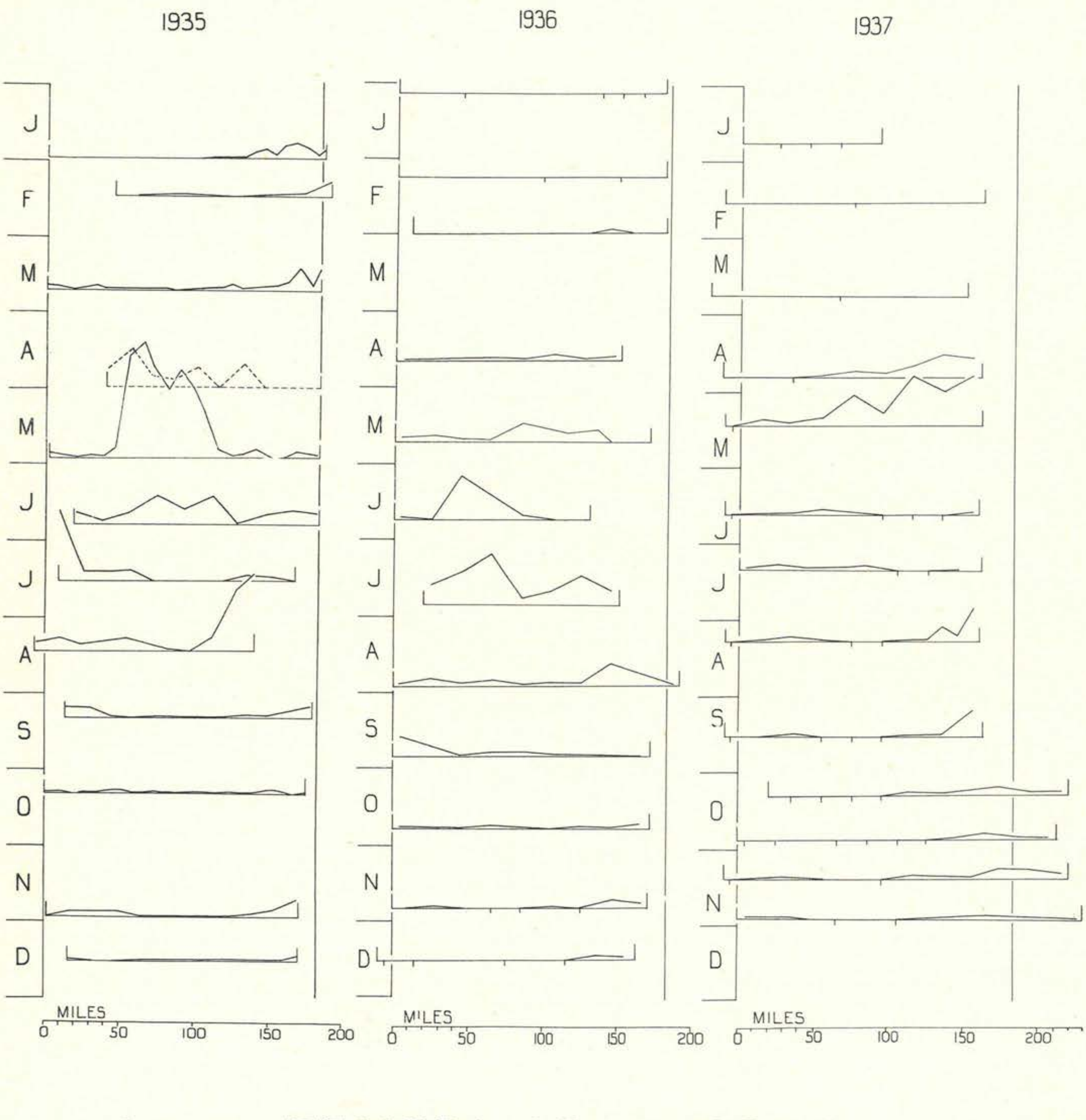
Records of **TEMORA LONGICORNIS** *on the* Rotterdam *line*, 1935 — 1937, *arranged as on Plate LXVI.*

PLATE LXXIX



Records of **TEMORA LONGICORNIS** *on the* Bremen *line*, 1932–1934, *arranged as on Plate LXVII. Overlapping graphs may be shown in broken line for clarity*

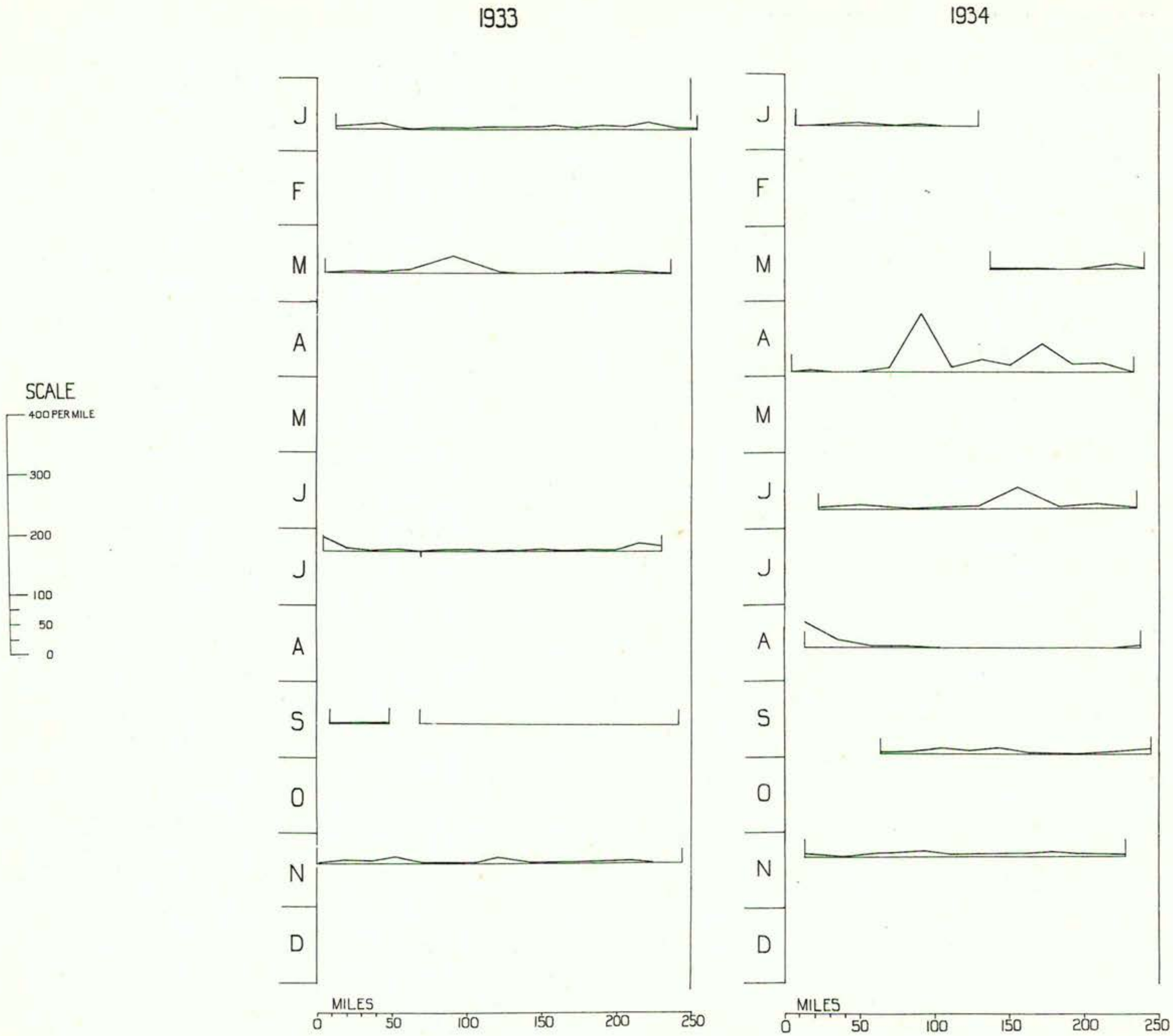
PLATE LXXX



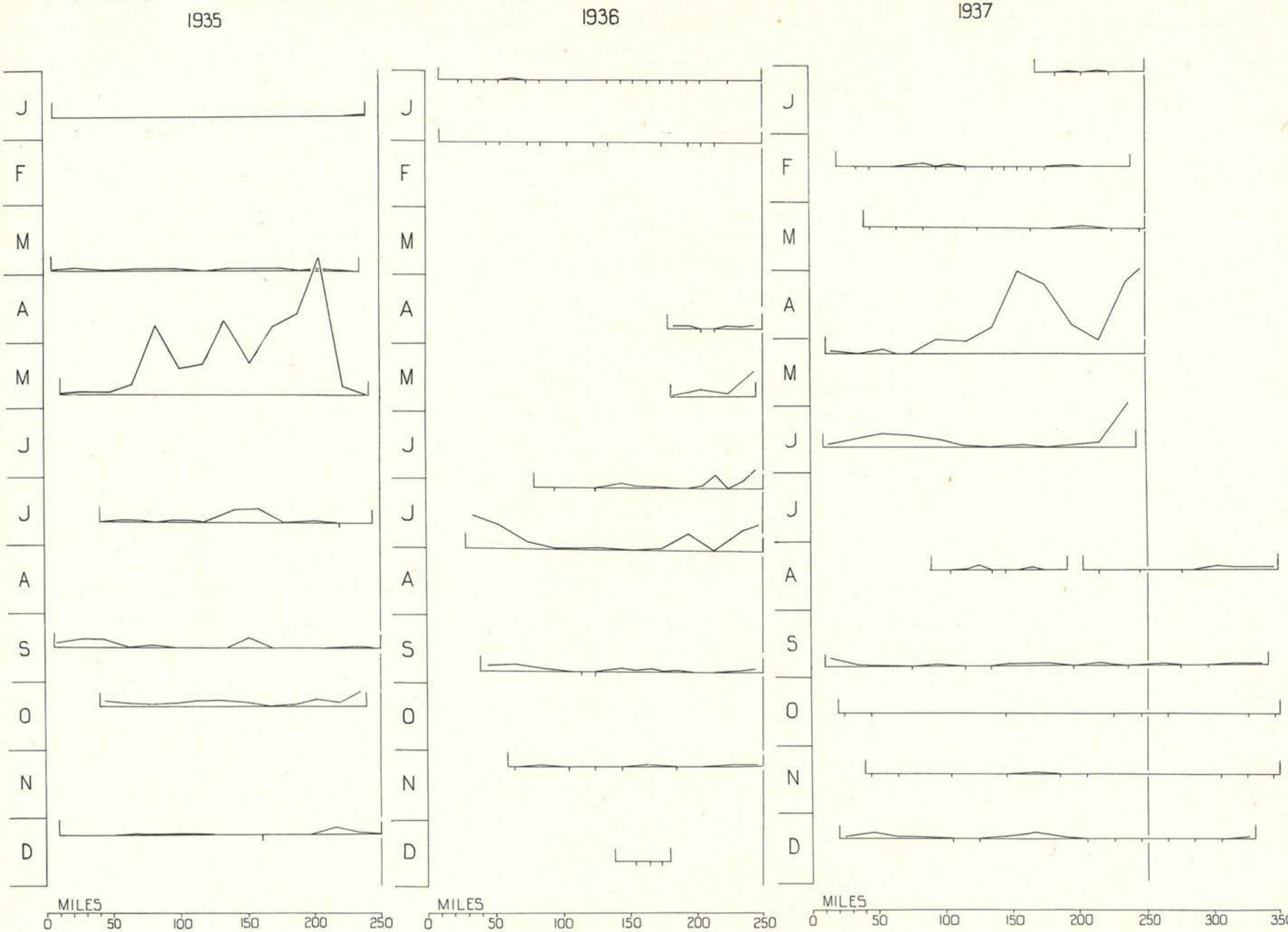
Records of ***TEMORA LONGICORNIS*** *on the* Bremen *line,* 1935 — 1937, *arranged as on Plate LXVIII.*

G

PLATE LXXXI



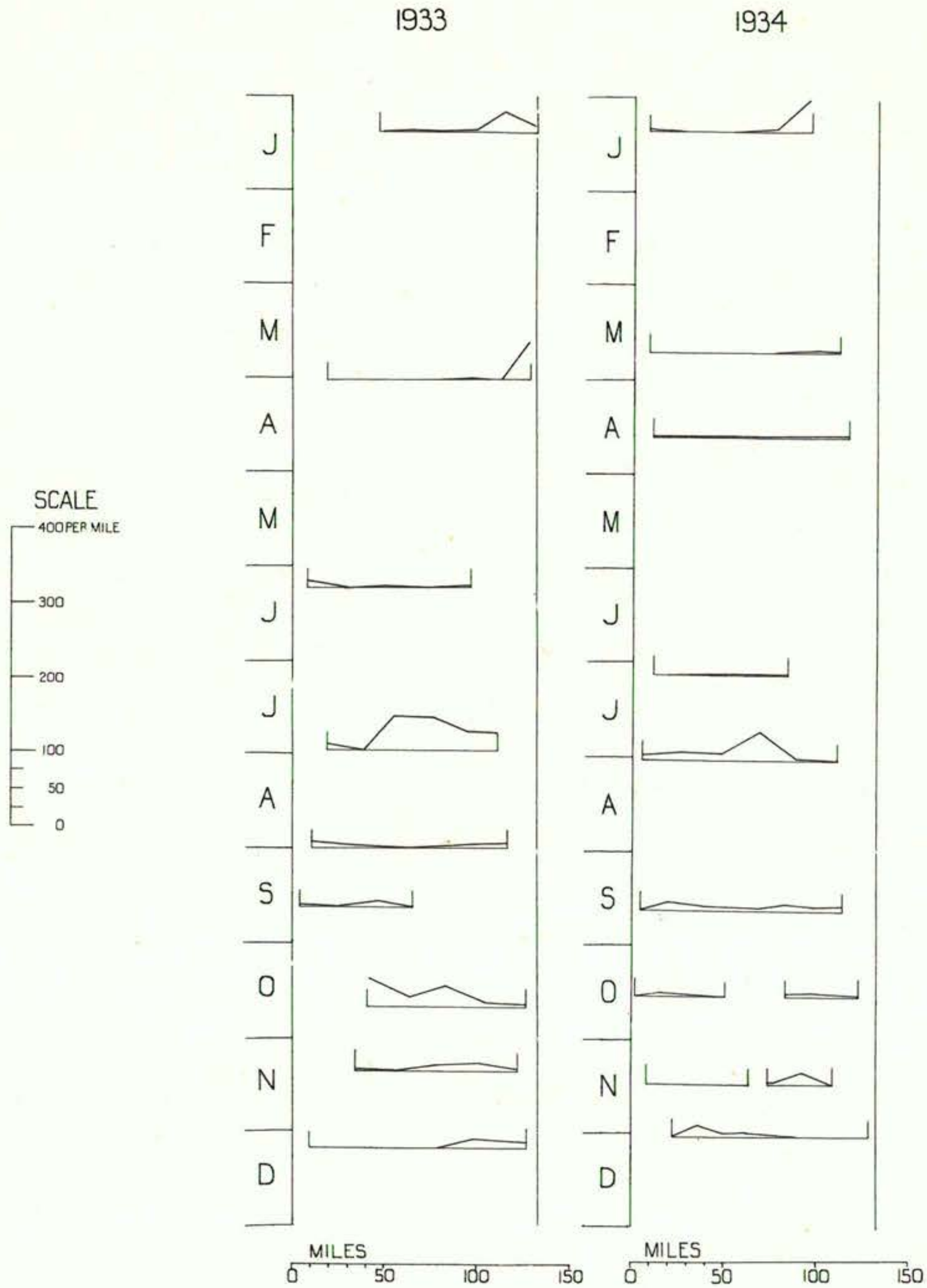
Records of **TEMORA LONGICORNIS** *on the* Copenhagen *line*, 1933 *and* 1934, *arranged as on Plate LXIX.*



Records of **TEMORA LONGICORNIS** on the Copenhagen *line* 1935 – 1937 *arranged as on Plate LXX.*

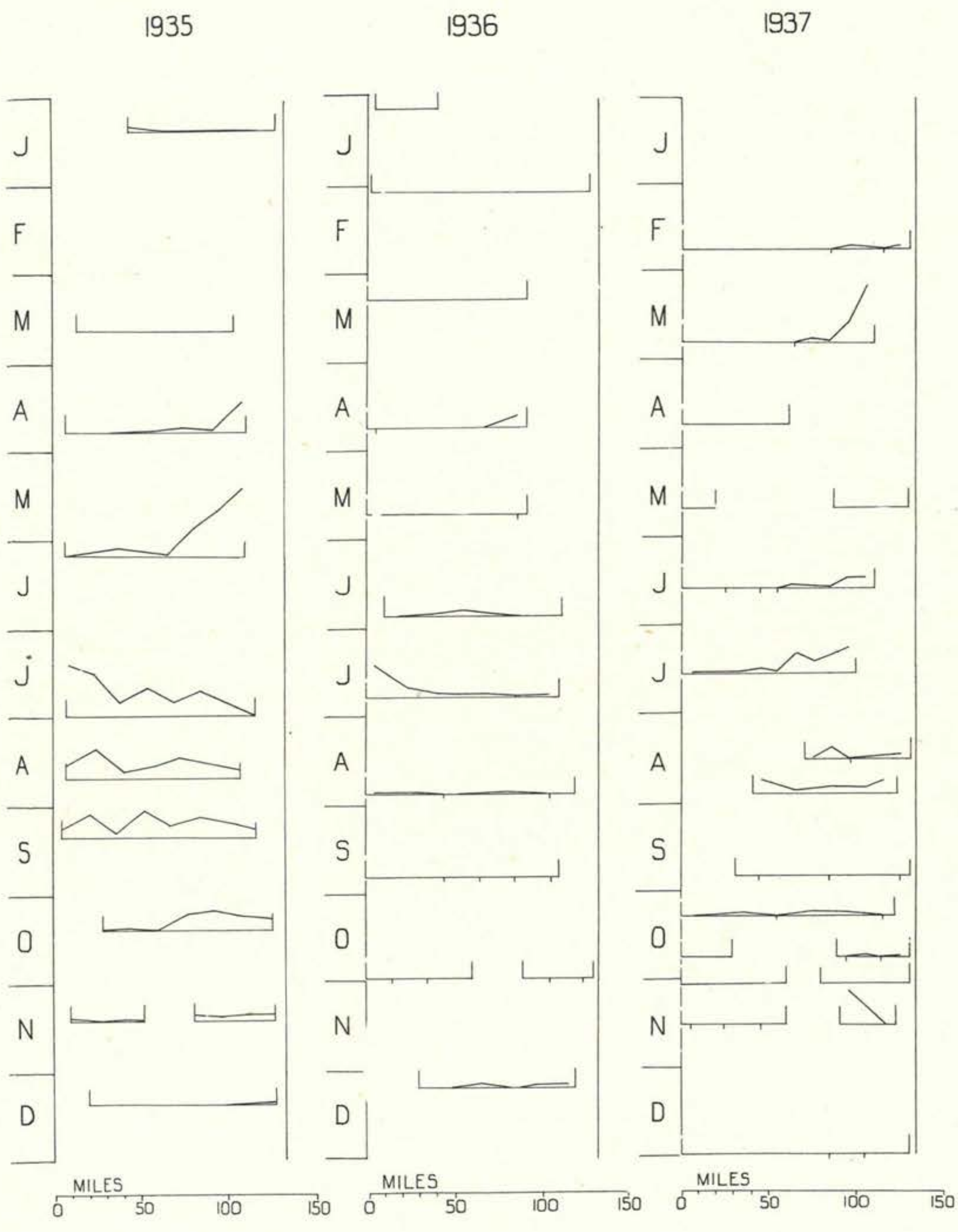
PLATE LXXXII

PLATE LXXXIII



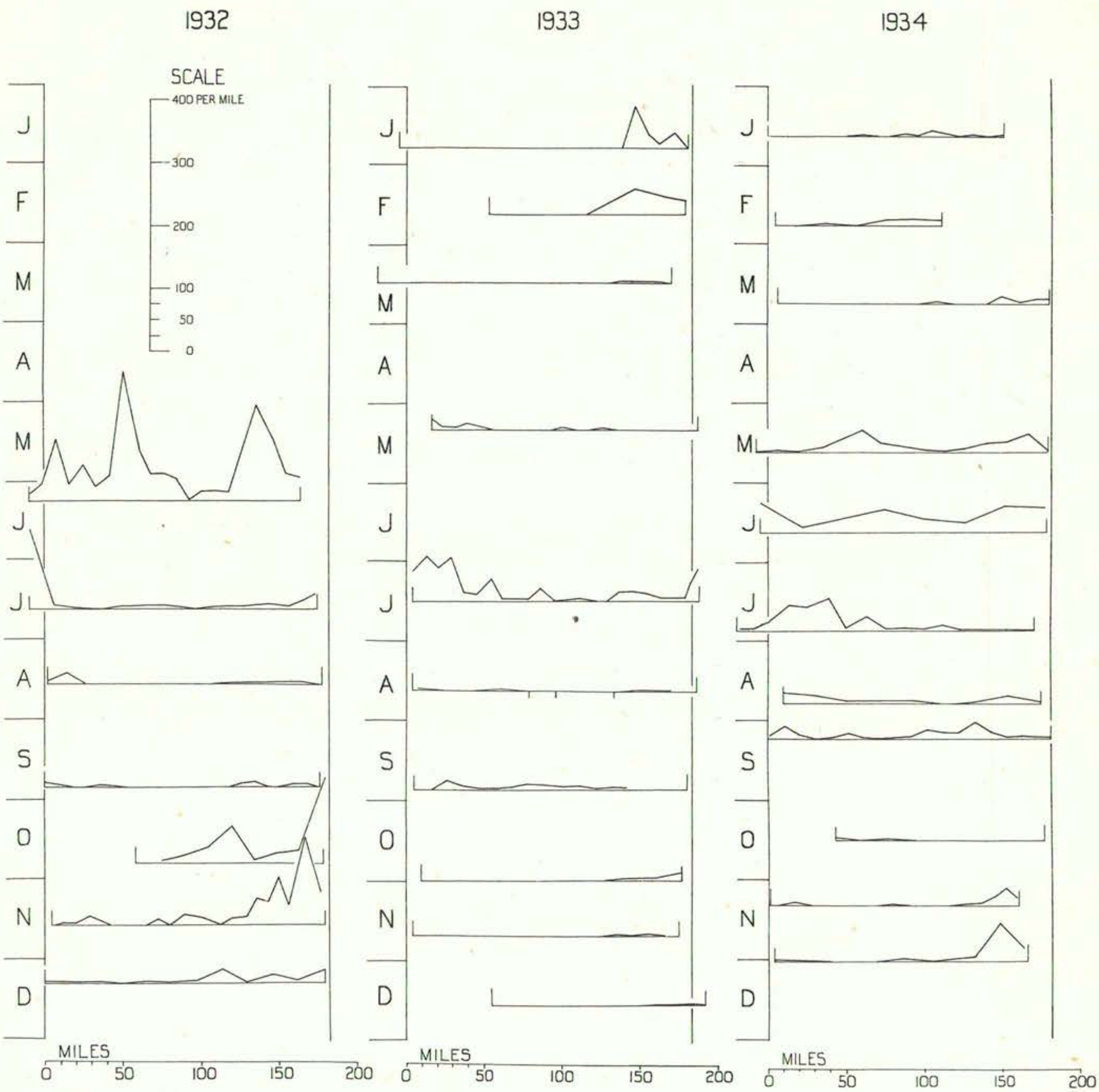
Records of **ACARTIA** *on the* Rotterdam *line,* 1933 *and* 1934, *arranged as on Plate LXV.*

PLATE LXXXIV



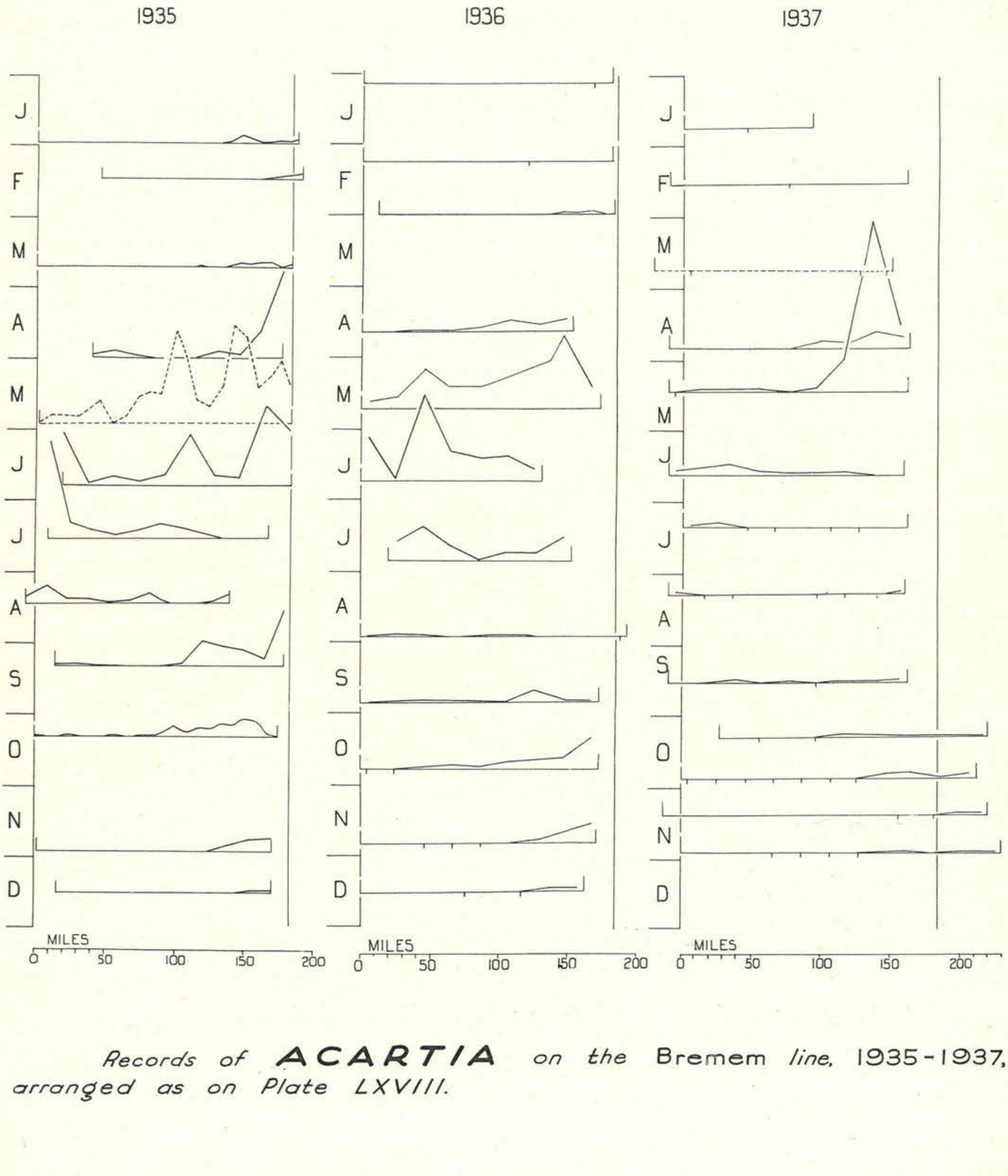
Records of **ACARTIA** *on the* Rotterdam *line,* 1935 — 1937, *arranged as on Plate LXVI.*

PLATE LXXXV



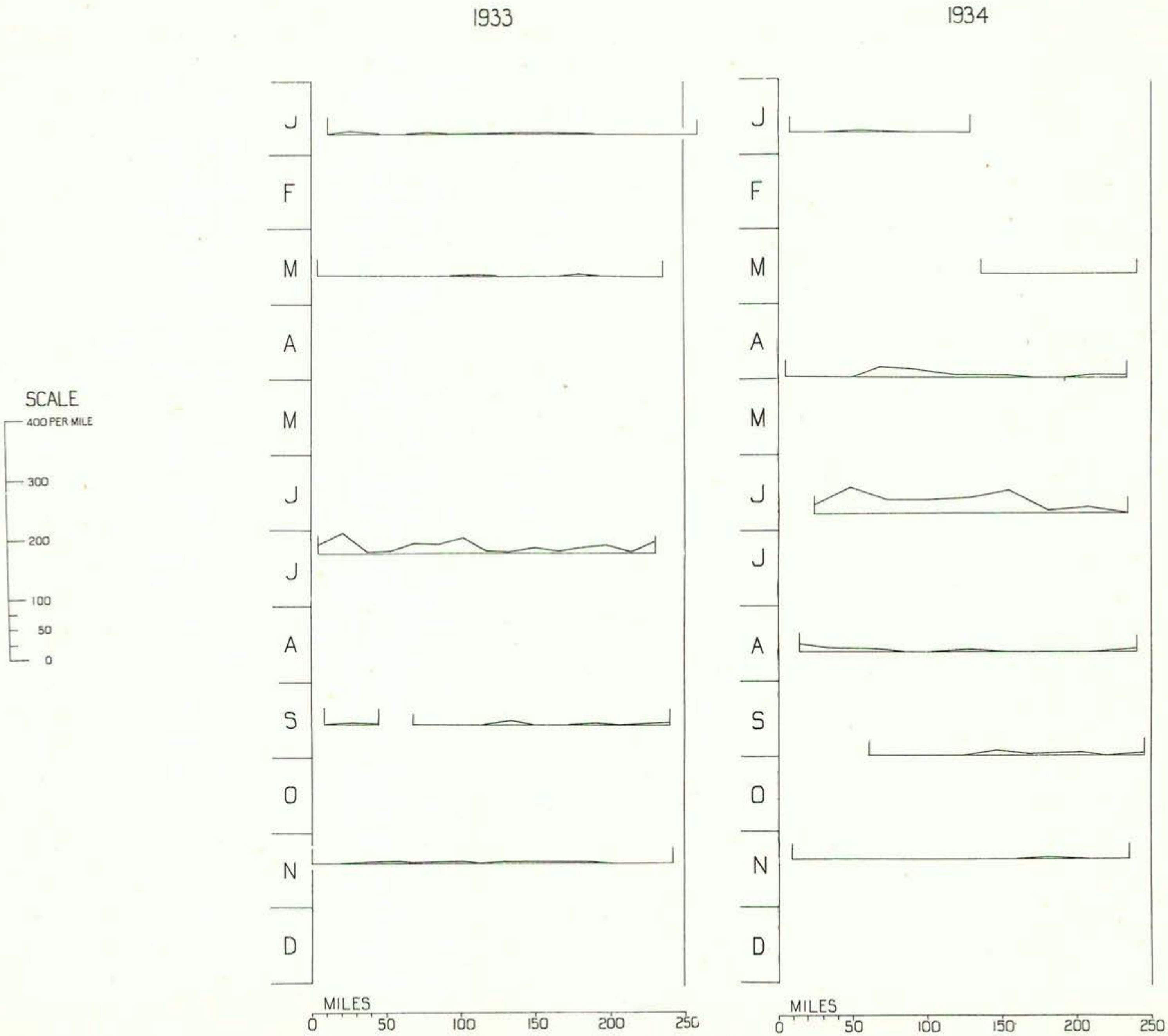
Records of **ACARTIA** *on the* Bremen *line*, 1932 – 1934, *arranged as on Plate LXVII.*

PLATE LXXXVI



Records of **ACARTIA** *on the* Bremem *line,* 1935-1937, *arranged as on Plate LXVIII.*

PLATE LXXXVII



Records of **ACARTIA** *on the* Copenhagen *line*, 1933 *and* 1934, *arranged as on Plate LXIX.*

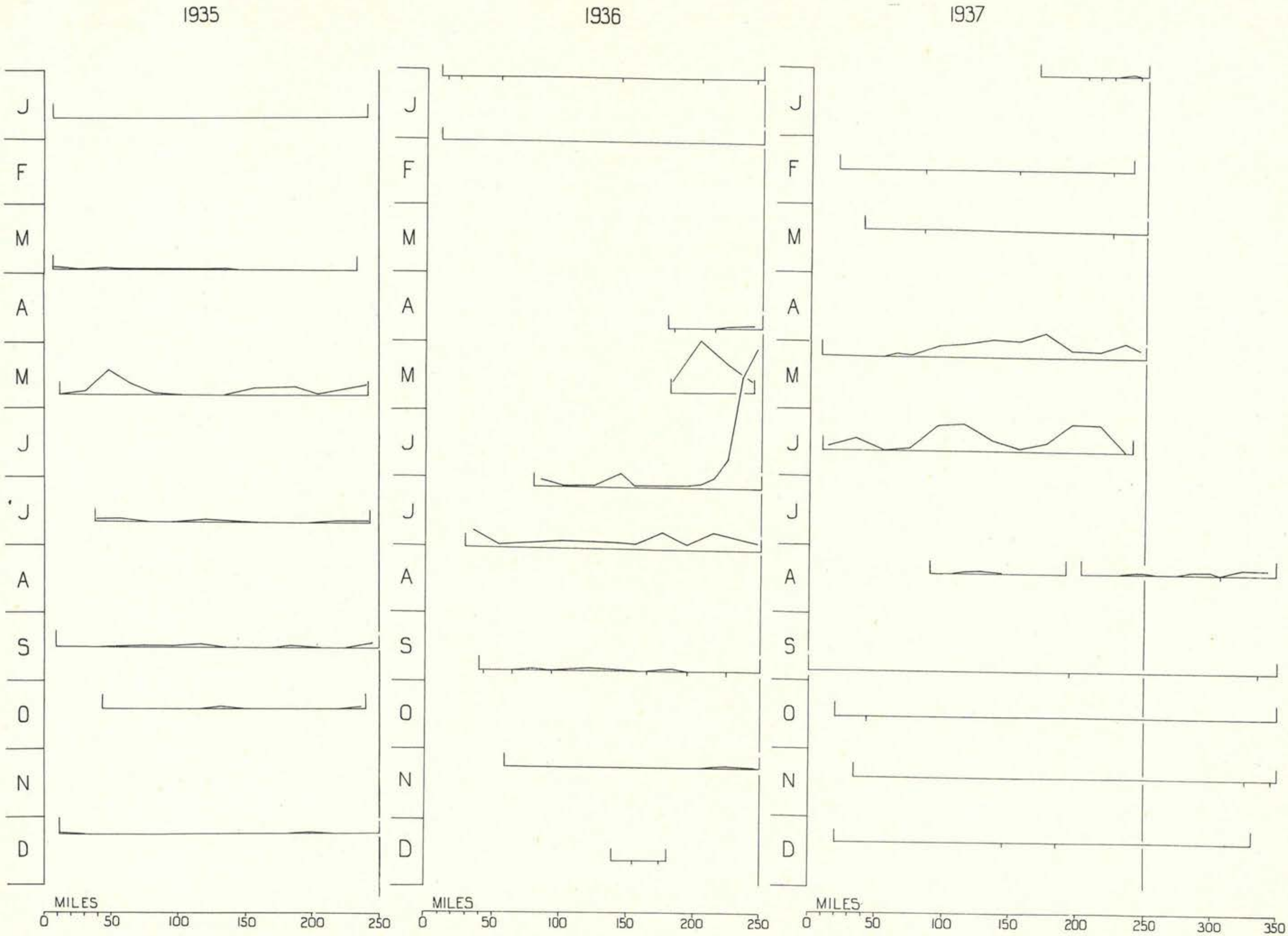
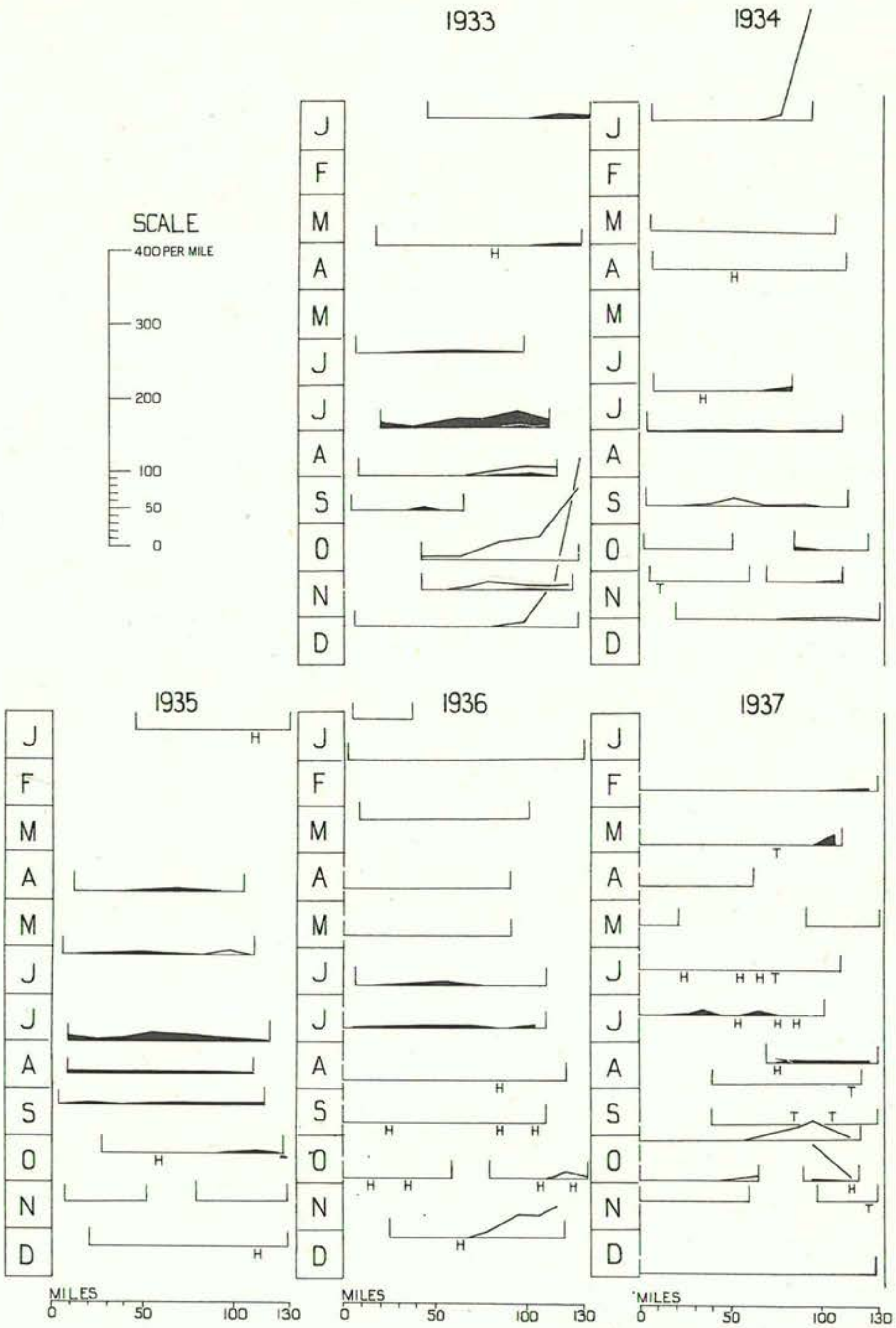


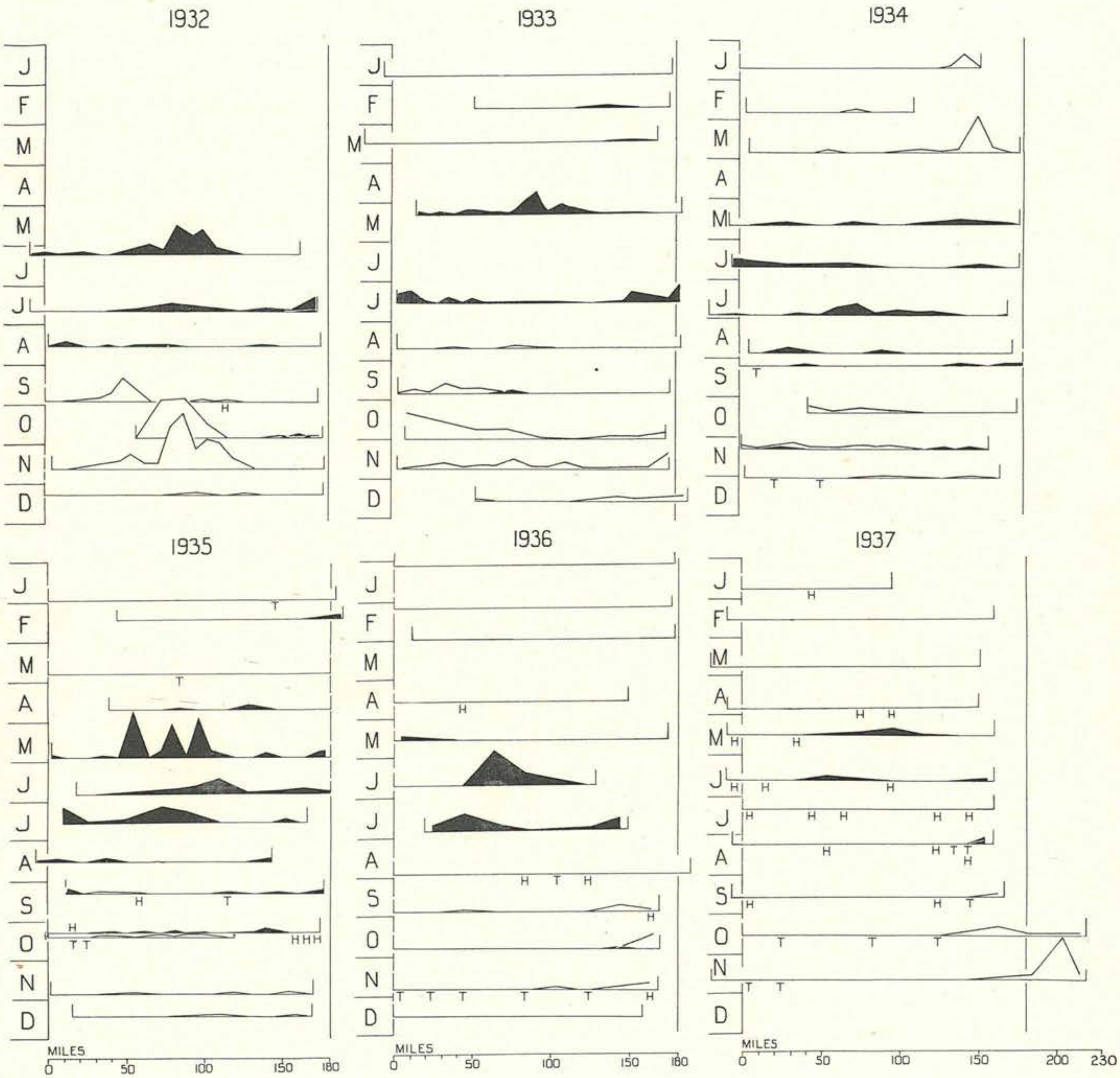
PLATE LXXXVIII

Records of **ACARTIA** *on the* Copenhagen *line.*, 1935 – 1937, *arranged as on Plate LXX.*

PLATE LXXXIX

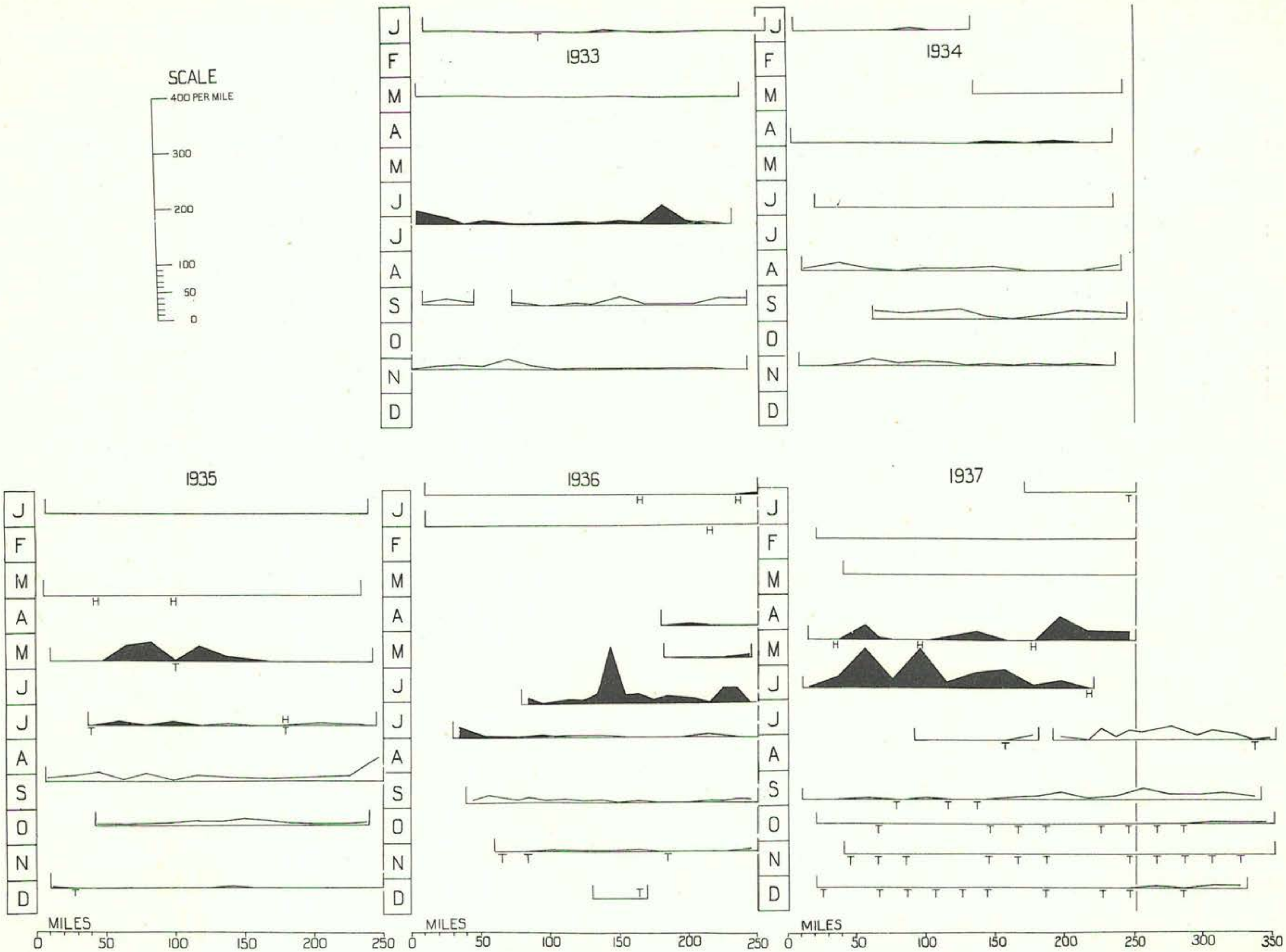


Records of **CENTROPAGES HAMATUS** *(blacked-in graphs) and* **C. TYPICUS** *(open line) on the* Rotterdam *line,* 1933 – 1937. *General arrangement as on Plates LXV and LXVI, but with time scale halved. Traces shown as 'H' and 'T' respectively.*

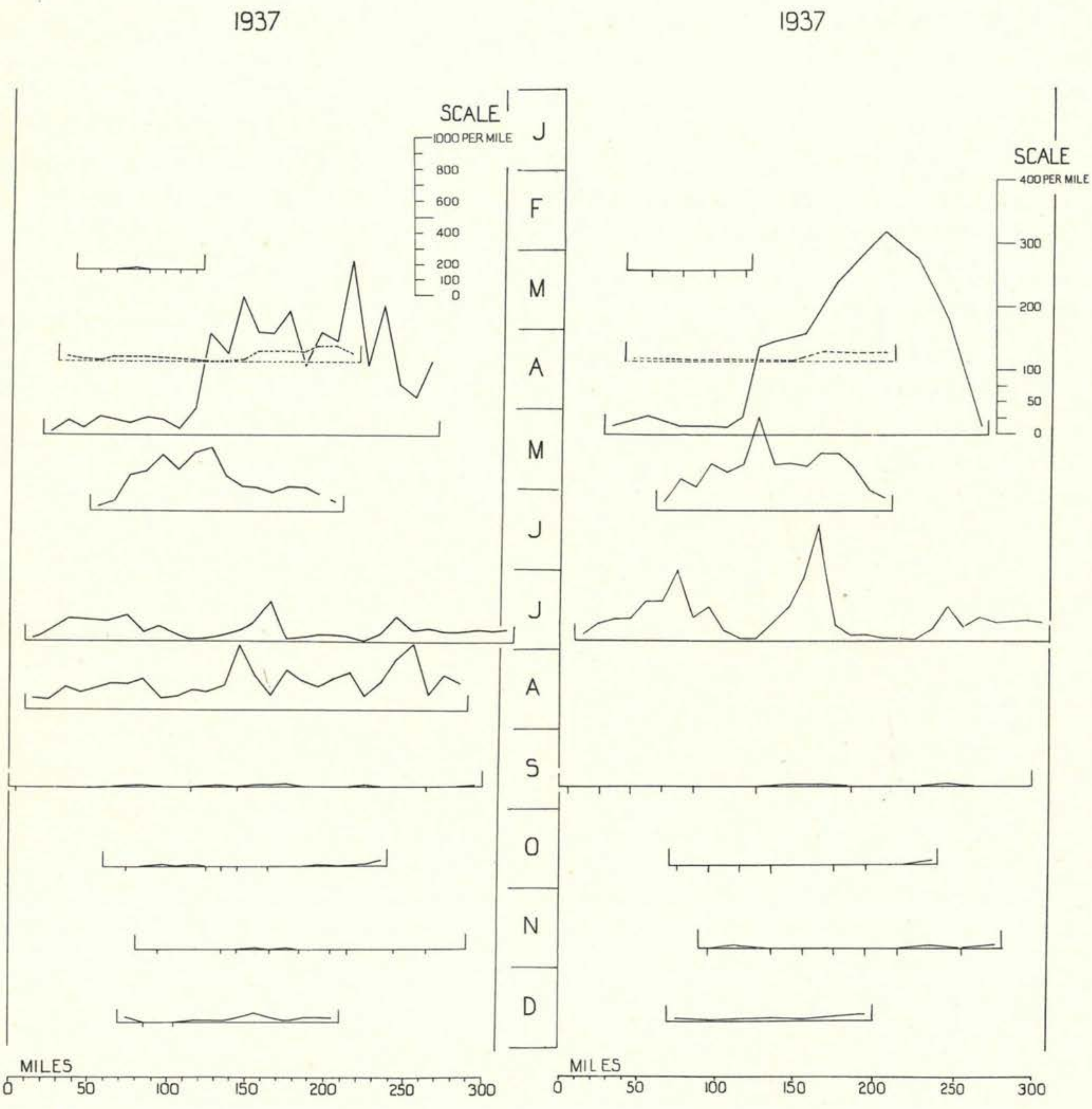


Records of **CENTROPAGES HAMATUS** *(blacked-in graphs) and* **C. TYPICUS** *(open line) on the* Bremen *line,* 1932—1937, *arranged as in Plates LXVII and LXVIII. Traces shown as 'H' and 'T' respectively. Scale as on Plate LXXXIX.*

PLATE XCI

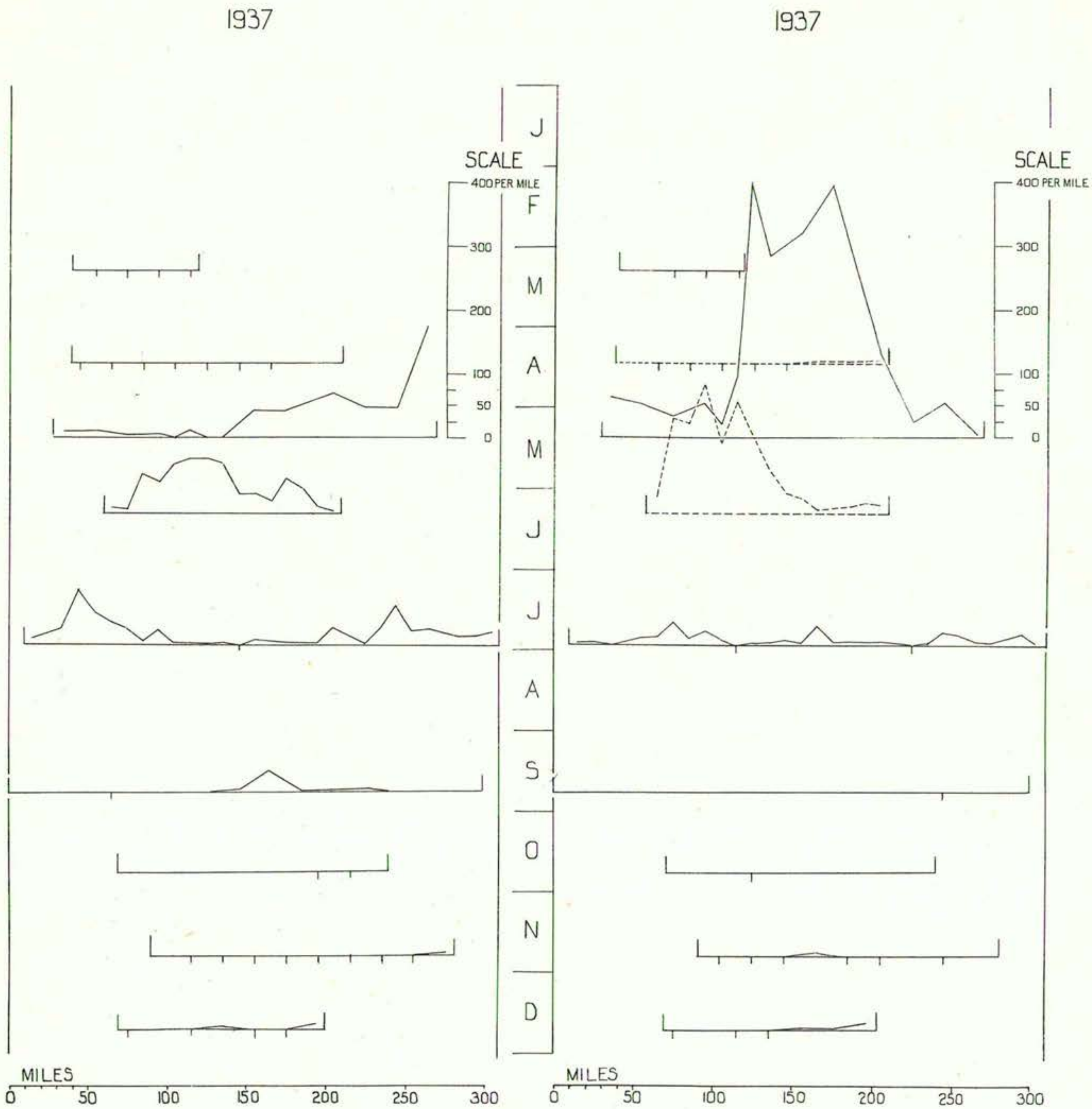


Records of **CENTROPAGES HAMATUS** *(blacked-in graphs) and* **C. TYPICUS** *(open line) on the Copenhagen line, 1933 – 1937, arranged as in Plates LXIX and LXX, but with time scale halved. Traces shown as 'H' and 'T' respectively.*



Records of **TOTAL COPEPODA** *(left) and* **PSEUDOCALANUS AND PARACALANUS COMBINED** *(right) on the* Esbjerg *line in* 1937. *General arrangement as described in Plate LXV, except that the vertical lines to left and right represent the positions of the* Sunk *and* Graadyb *lightvessels. Overlapping graphs may be shown in broken line for clarity.*

PLATE XCIII



Records of ***TEMORA LONGICORNIS*** *(left) and* ***ACARTIA*** *(right) on the* Esbjerg *line in* 1937. *General arrangements as described in Plate LXV except that the vertical lines to left and right represent the positions of the* Sunk *and* Graadyb *lightvessels. Overlapping graphs may be shown in broken line for clarity.*

PLATES XCIV–CXXV

MAPS SHOWING THE MONTHLY
DISTRIBUTION OF THE
TOTAL COPEPODA,
CENTROPAGES HAMATUS,
CENTROPAGES TYPICUS,
ISIAS CLAVIPES AND
CORYCAEUS ANGLICUS,
IN THE SOUTHERN NORTH SEA
JUNE 1932 TO DECEMBER 1937

PLATE XCIV

The following Explanation relates to
PLATES XCIV–CVI

This series of maps has been prepared to show the distribution of the ***TOTAL COPEPODA*** in the southern North Sea month by month from June 1932 to December 1937.

As on previous plates the estimated numbers per mile are shown as graphs above the base line and by short vertical strokes below.

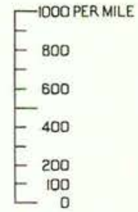
The date of each record is shown below its eastern end.

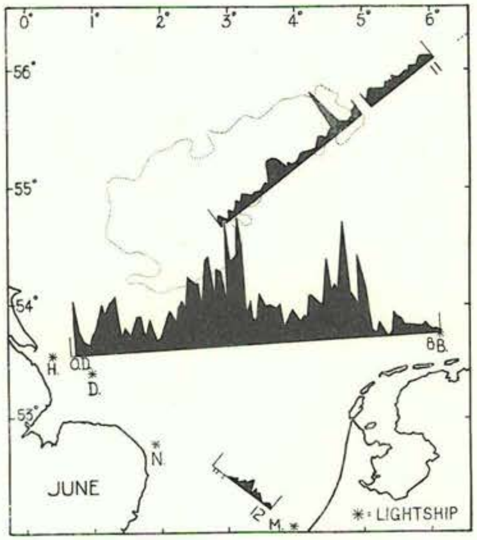
The letters H, OD, D, N, M and B indicate the positions of the HUMBER, OUTER DOWSING, EAST DUDGEON, NEWARP, MAAS and BORKUM lightvessels respectively.

The 20 fathom contour of the DOGGER BANK is marked by a faint dotted line.

The first records for June 1932 are shown in the map on the right.

Scale for Plates XCIV – CVI:





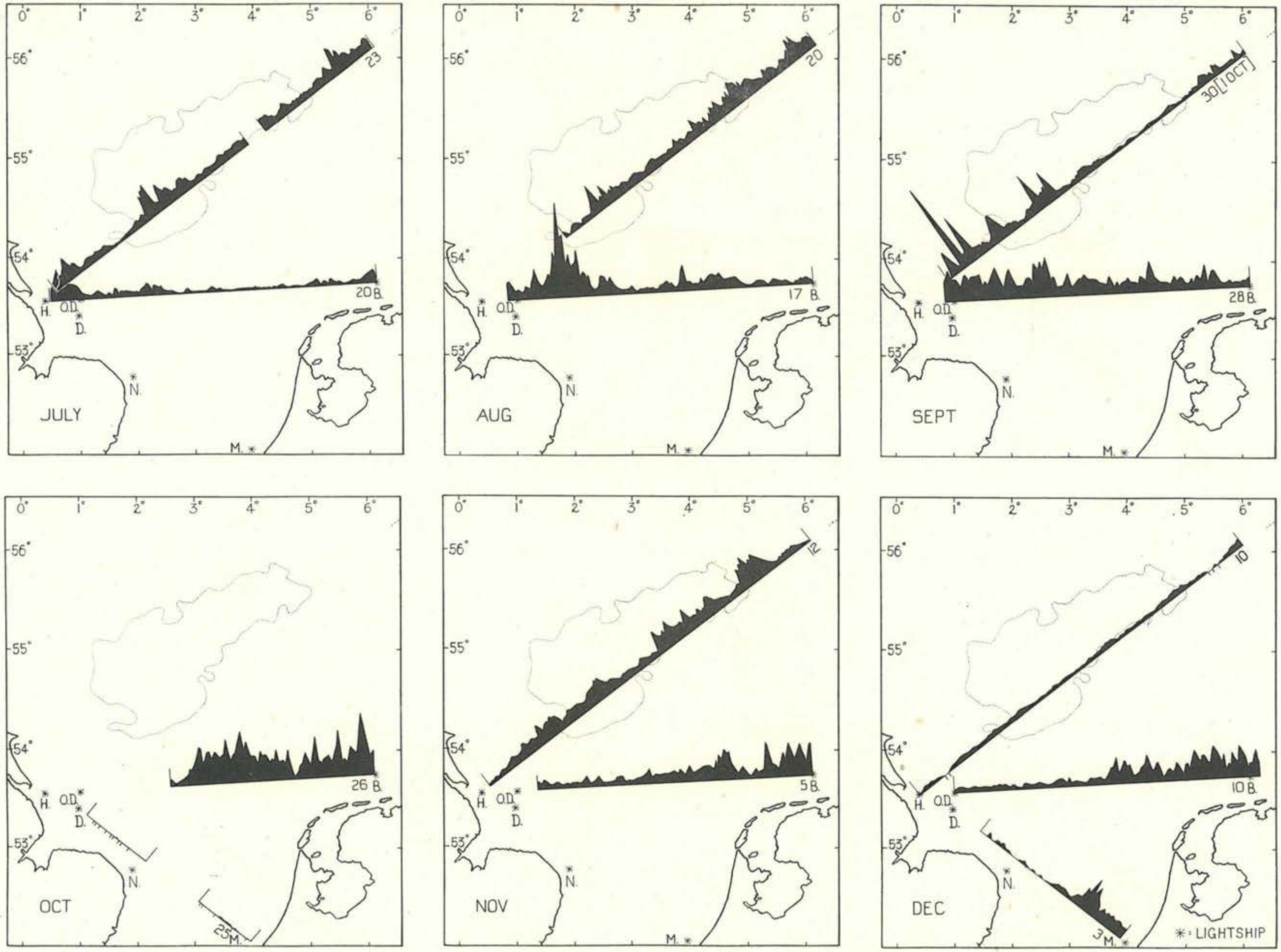
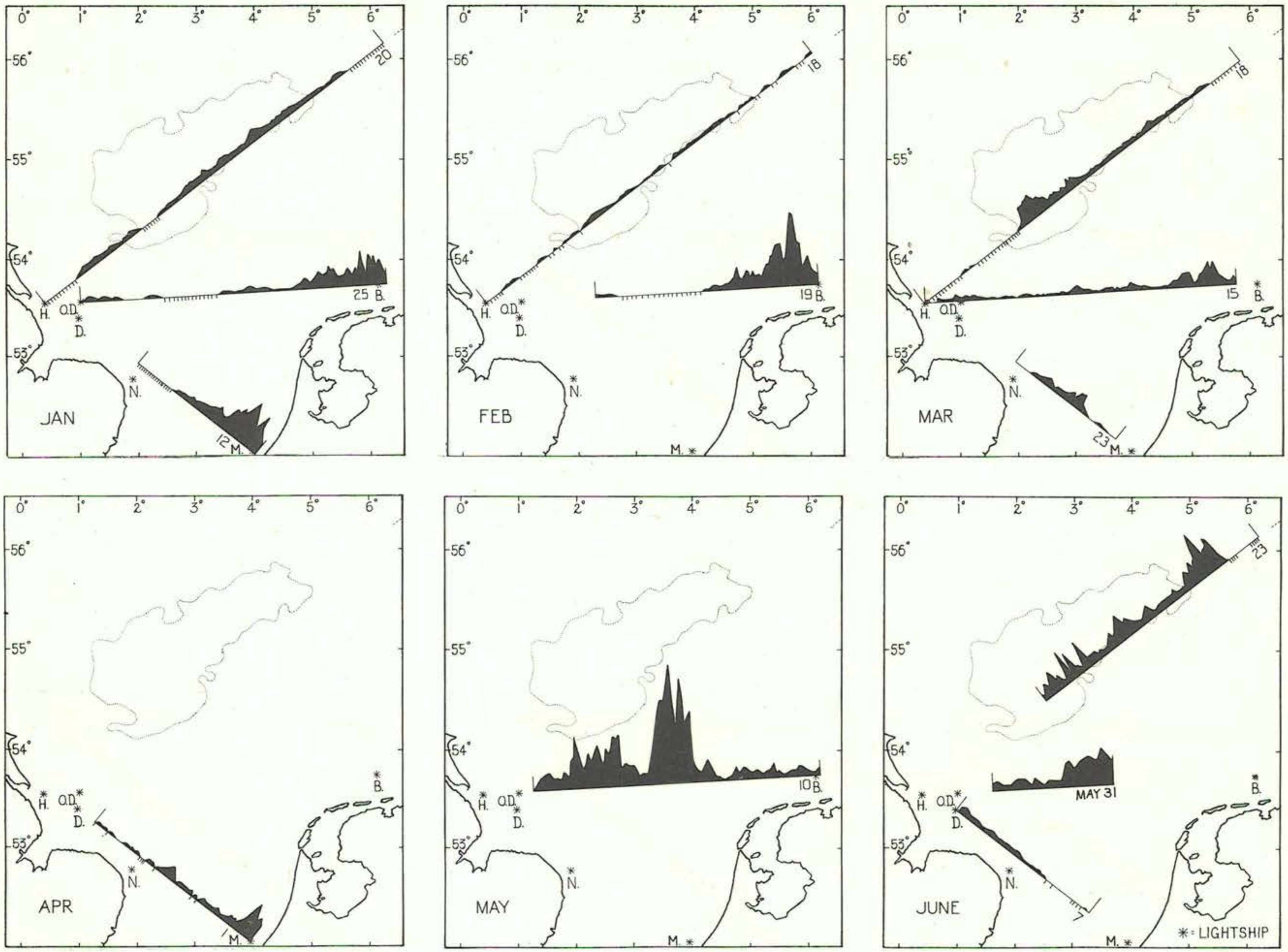


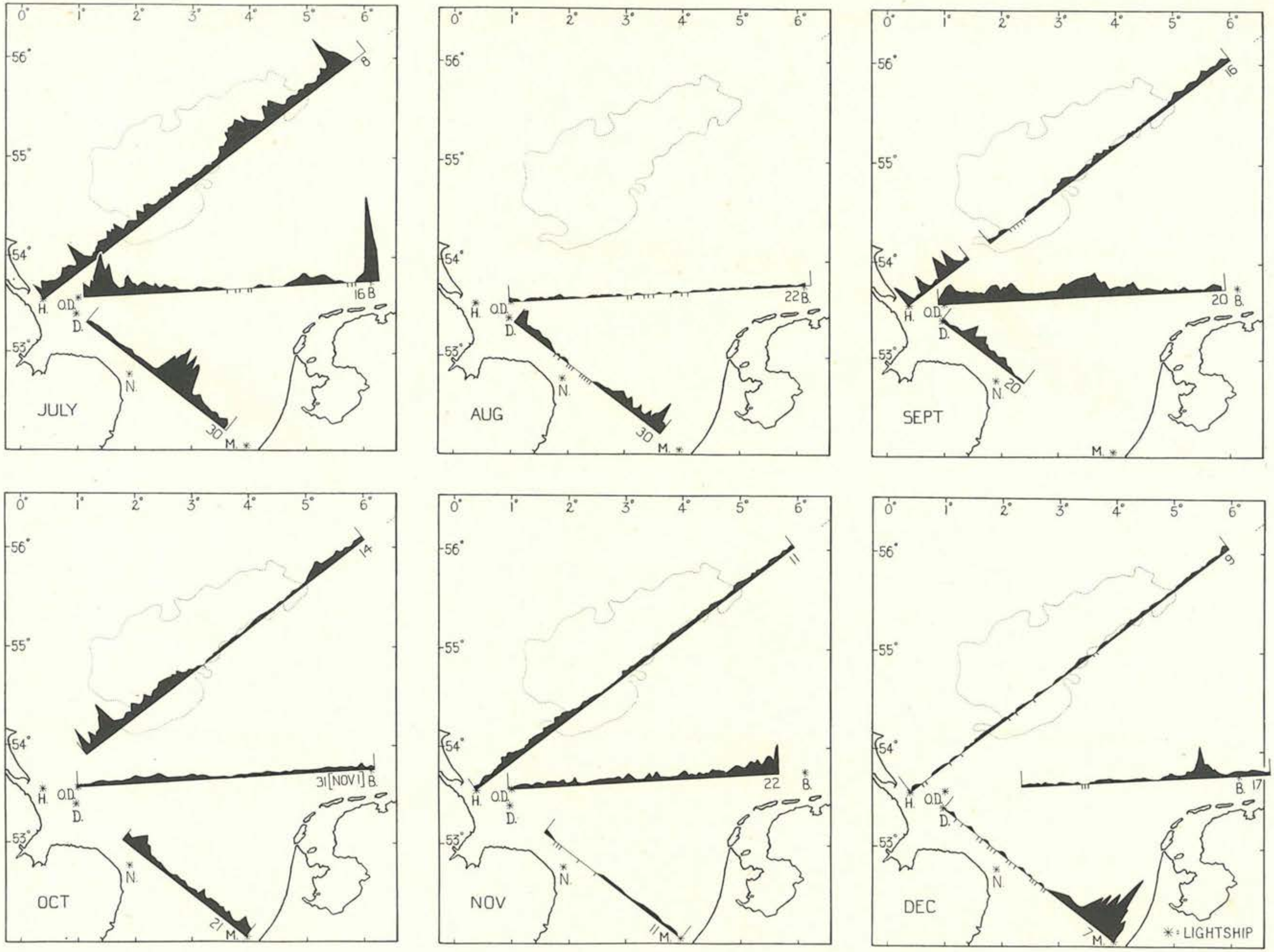
PLATE XCV

TOTAL COPEPODA, *July – December, 1932. For further explanation see Plate XCIV.*

PLATE XCVI



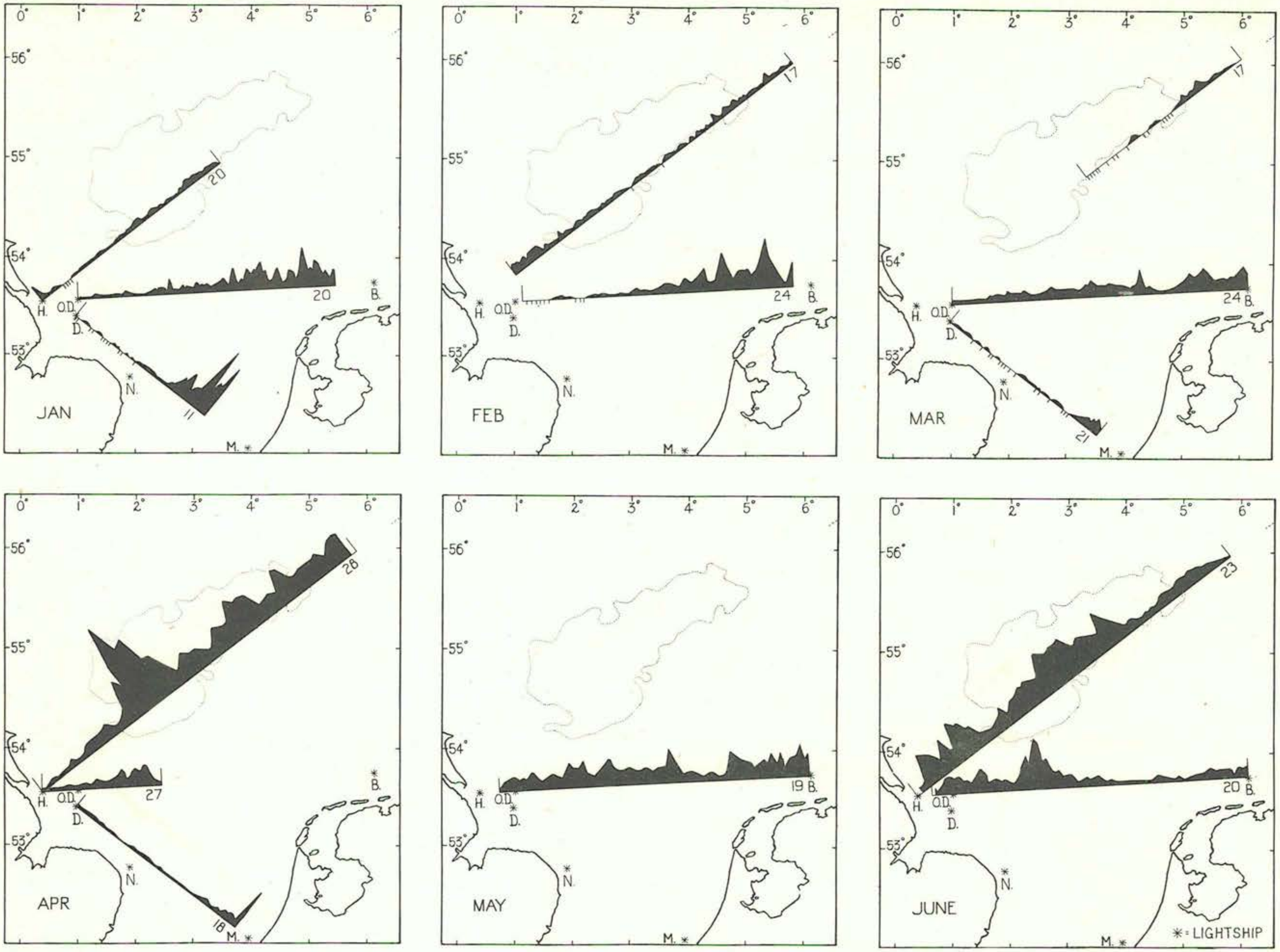
TOTAL COPEPODA, *January – June. 1933. For further explanation see Plate XCIV.*



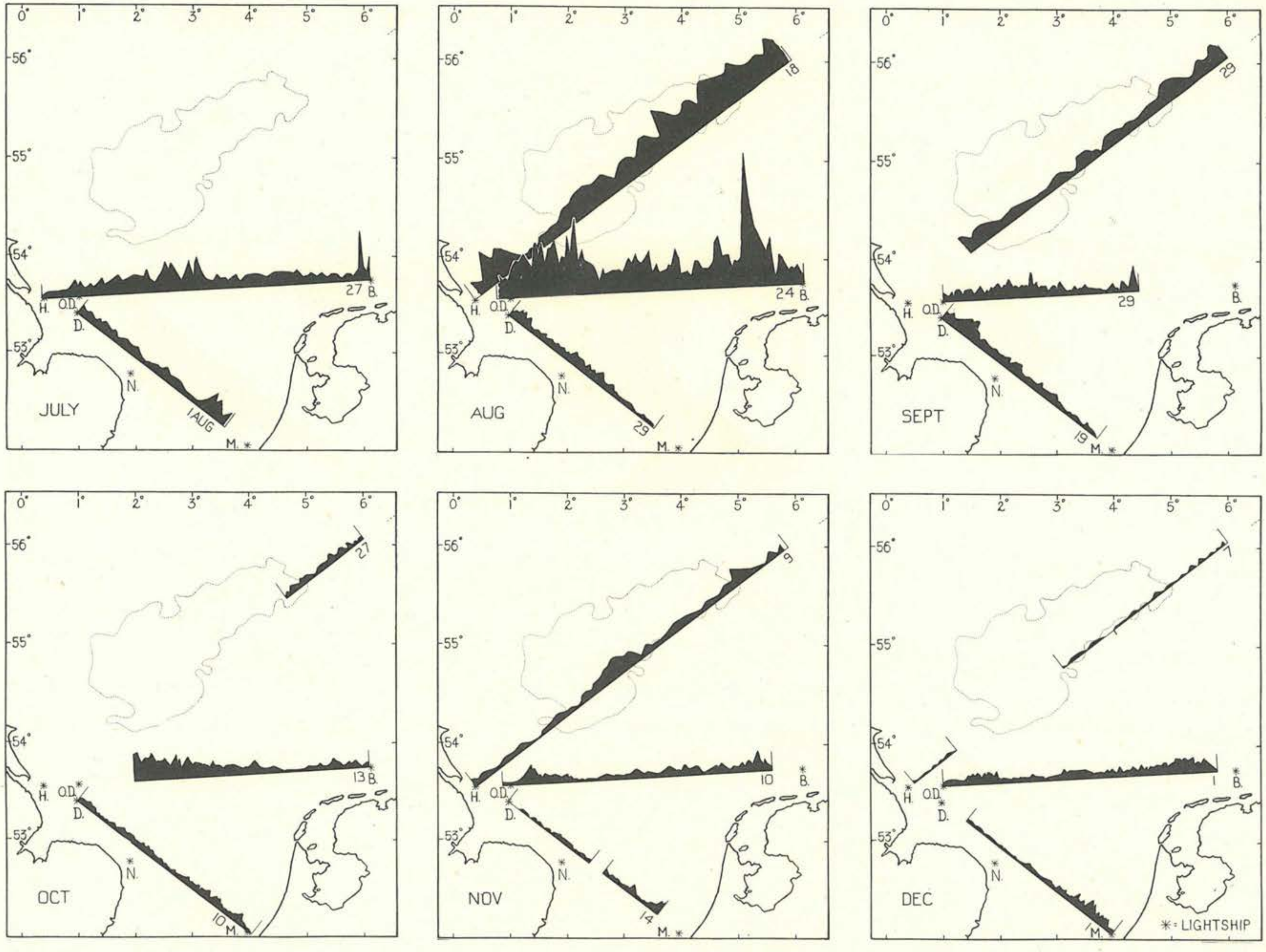
TOTAL COPEPODA. *July – December, 1933. For further explanation see Plate XCIV.*

PLATE XCVII

PLATE XCVIII



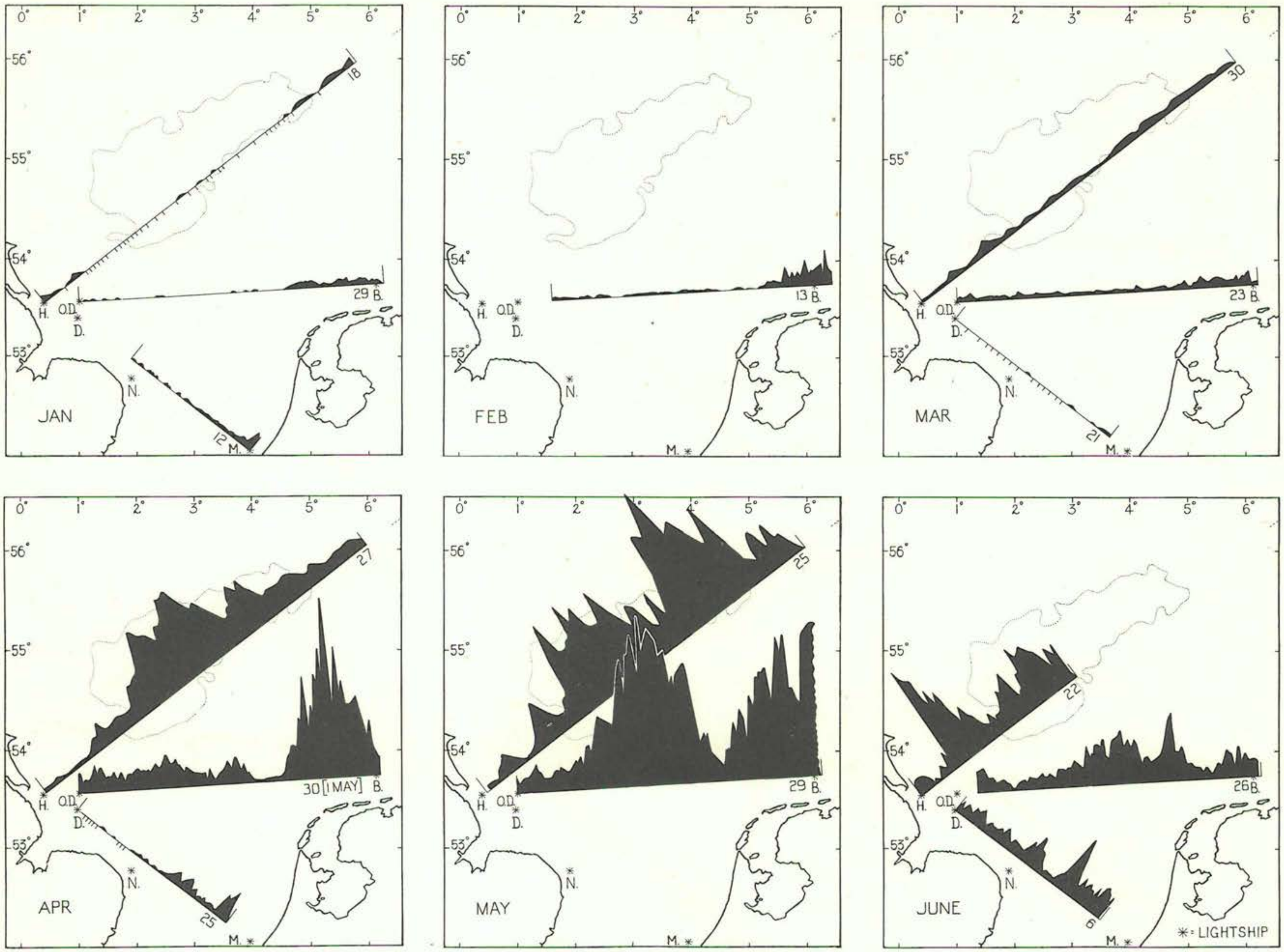
TOTAL COPEPODA. *January – June, 1934. For further explanation see Plate XCIV.*



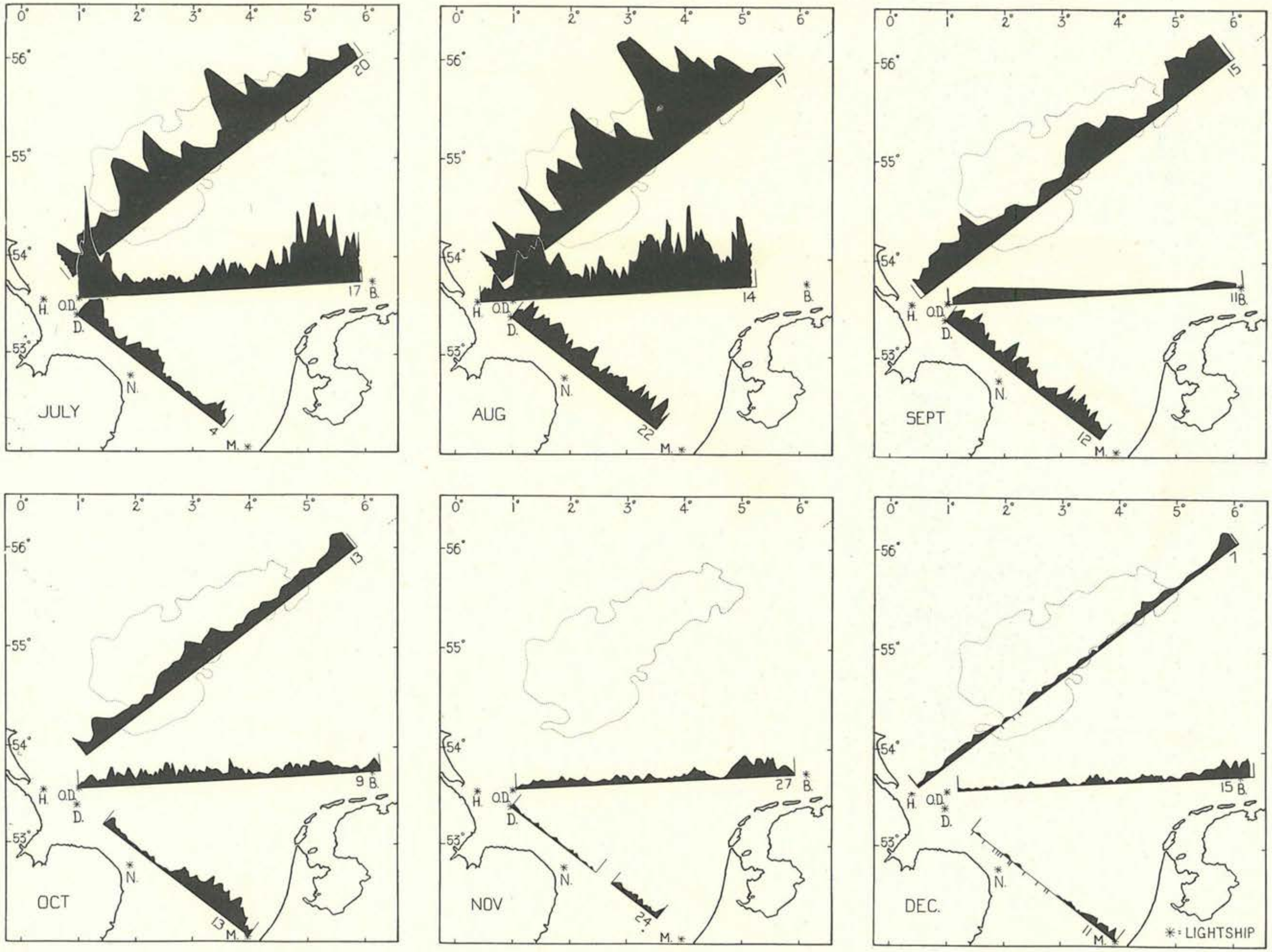
TOTAL COPEPODA, *July – December, 1934. For further explanation see Plate XCIV.*

PLATE XCIX

PLATE C

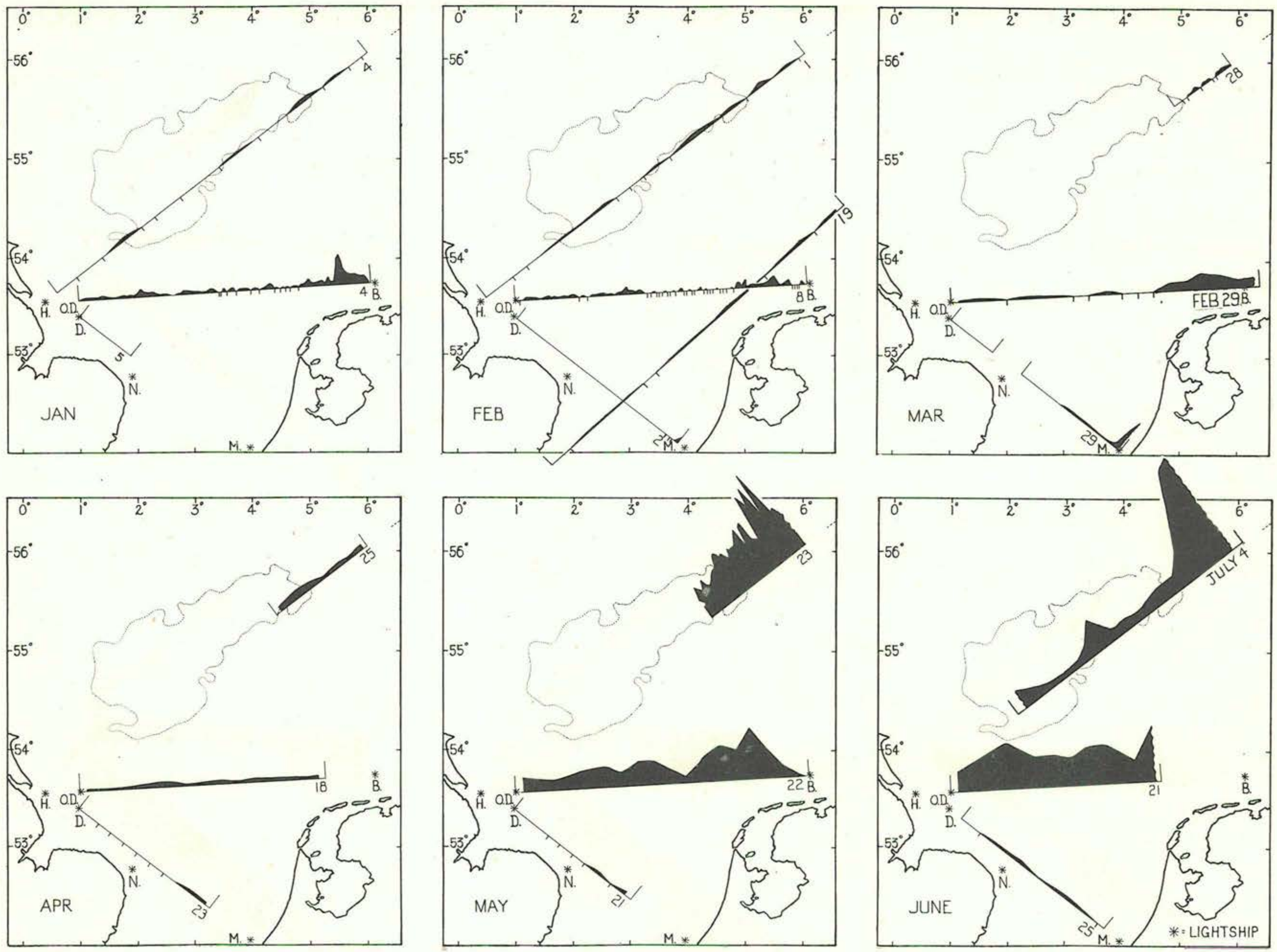


TOTAL COPEPODA, *January – June, 1935.* *For further explanation see Plate XCIV.*

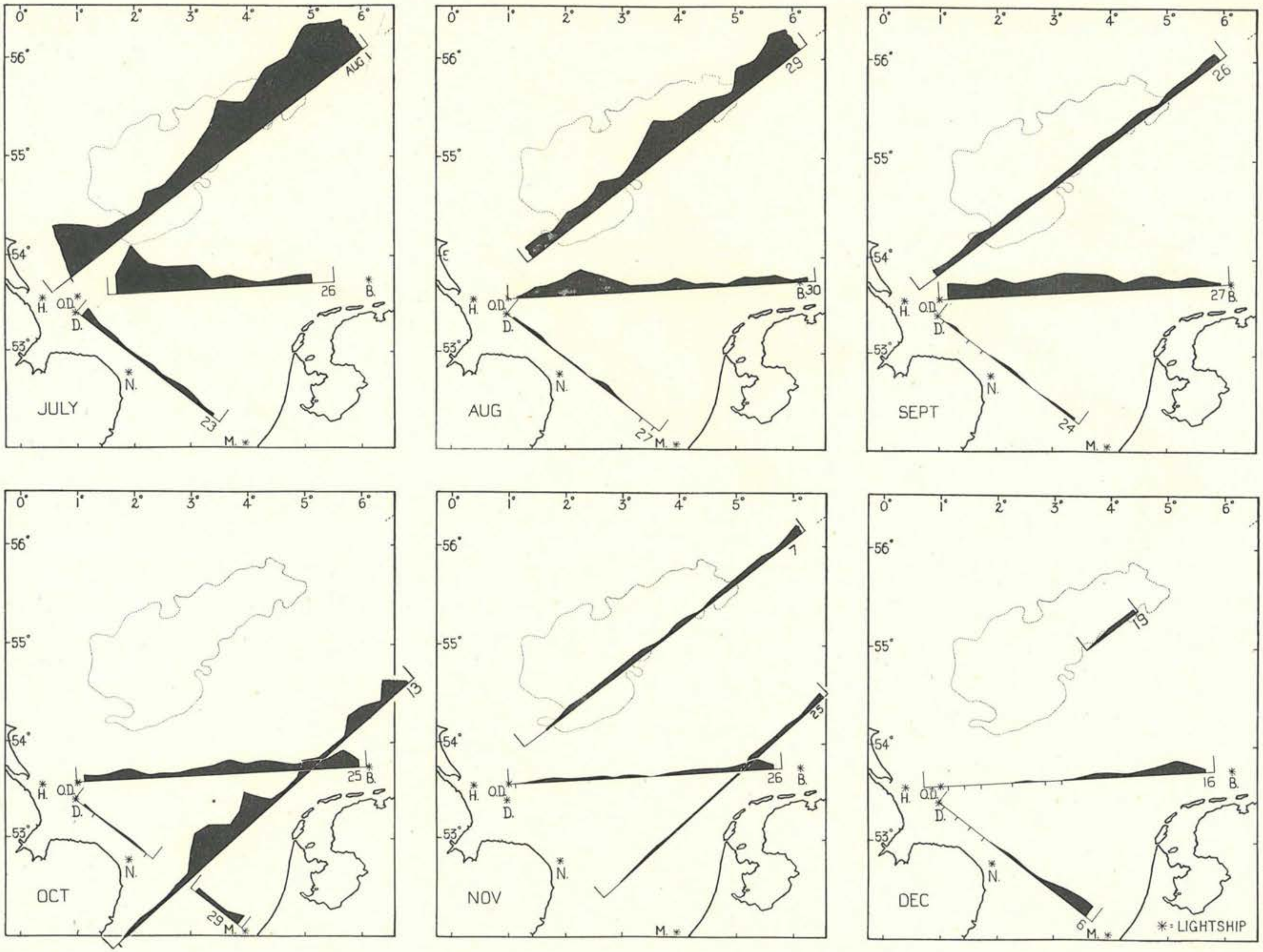


TOTAL COPEPODA. *July – December, 1935. For further explanation see Plate XCIV.*

PLATE CII



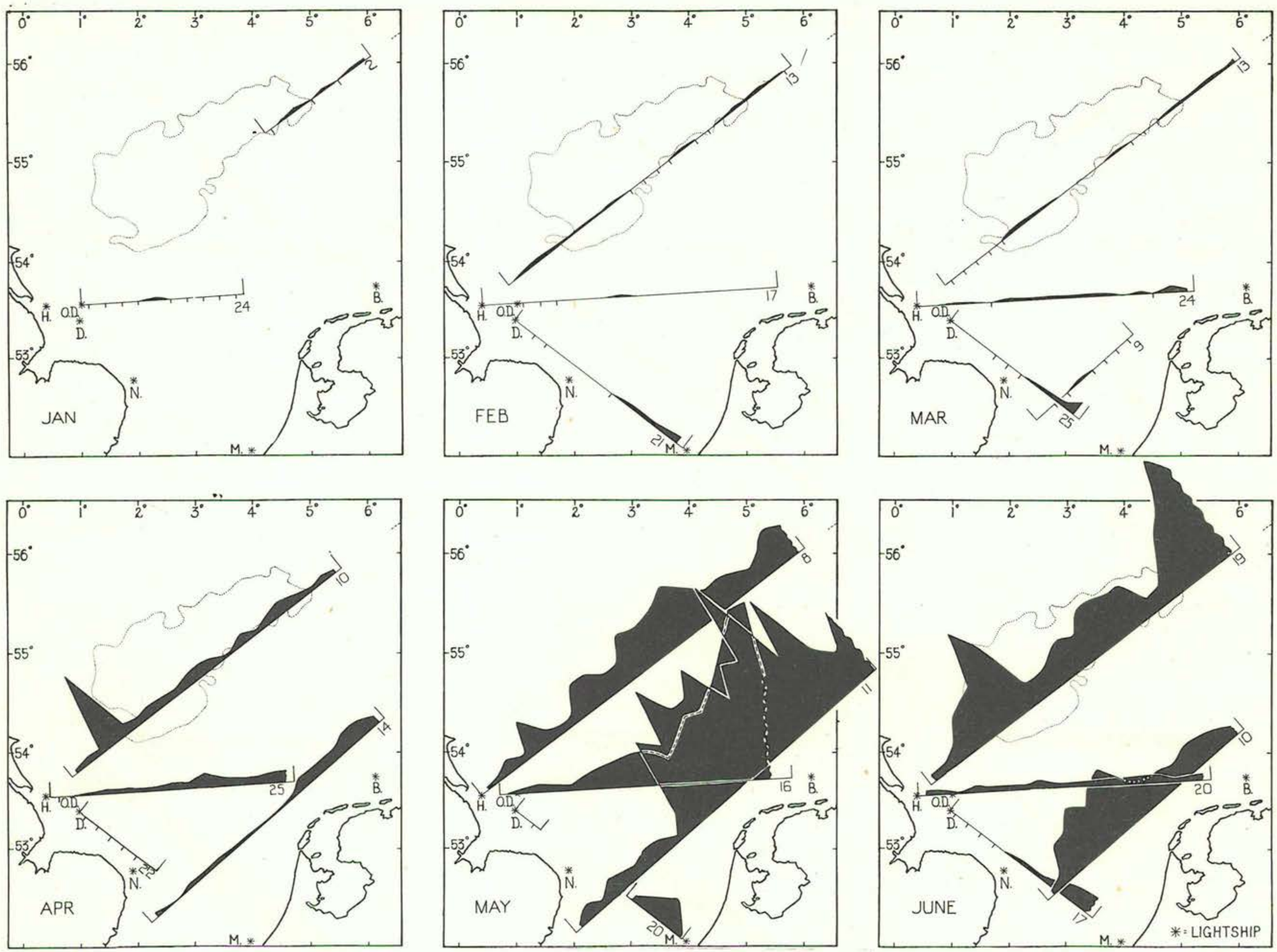
TOTAL COPEPODA, January – June, 1936. For further explanation see Plate XCIV.



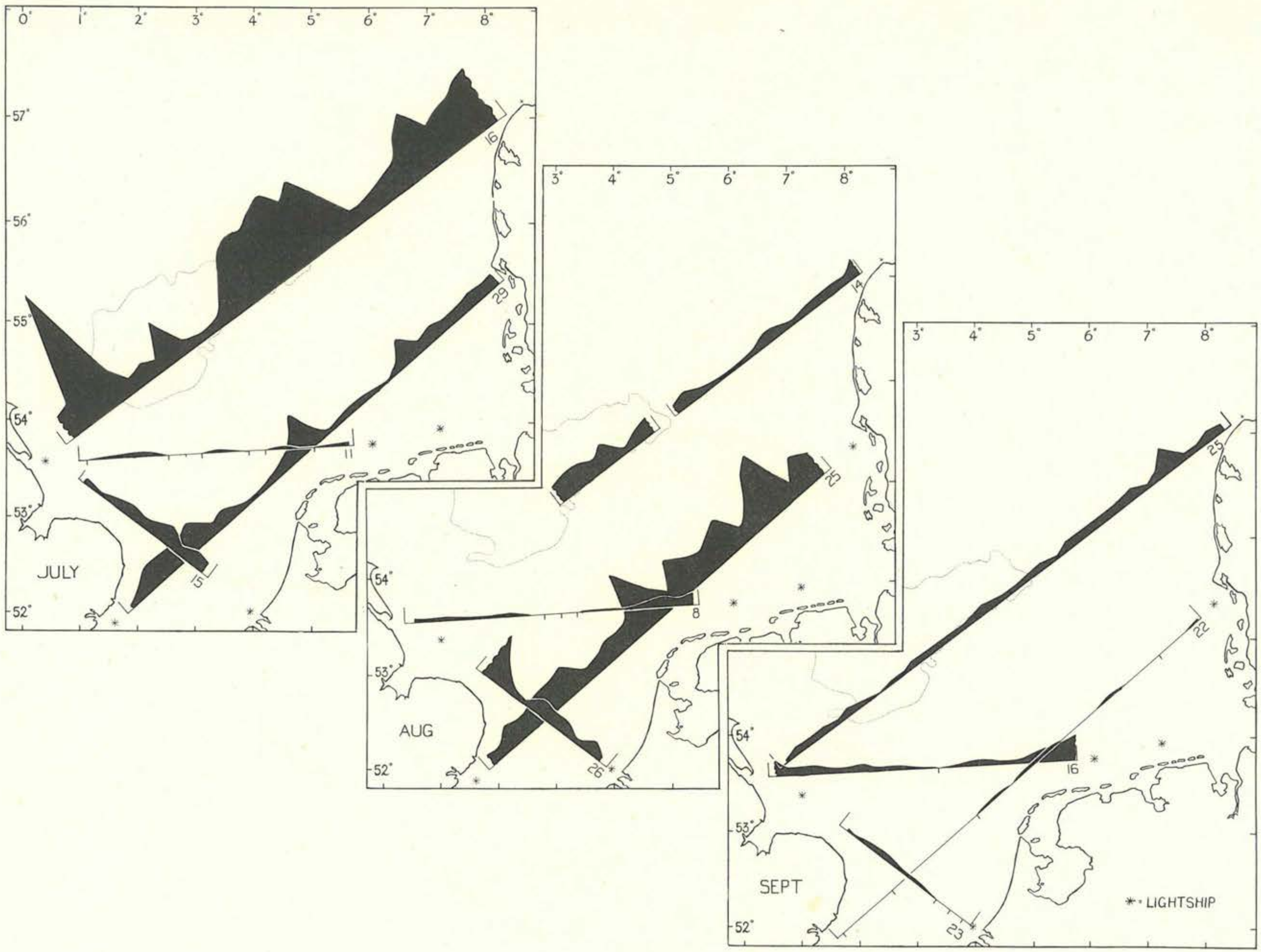
TOTAL COPEPODA, *July – December, 1936. For further explanation see Plate XCIV.*

PLATE CIII

PLATE CIV

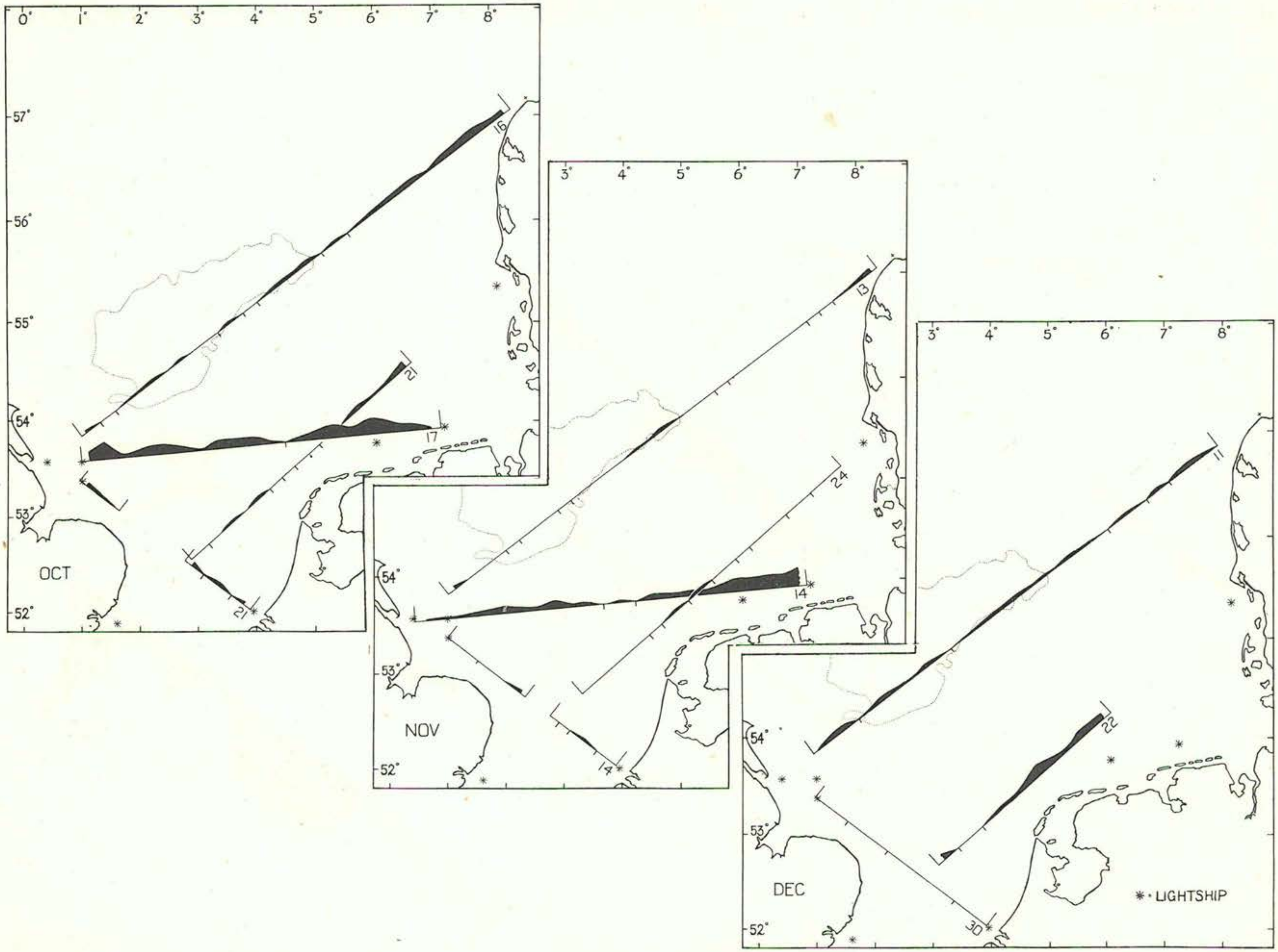


TOTAL COPEPODA, *January - June, 1937. For further explanation see Plate XCIV.*

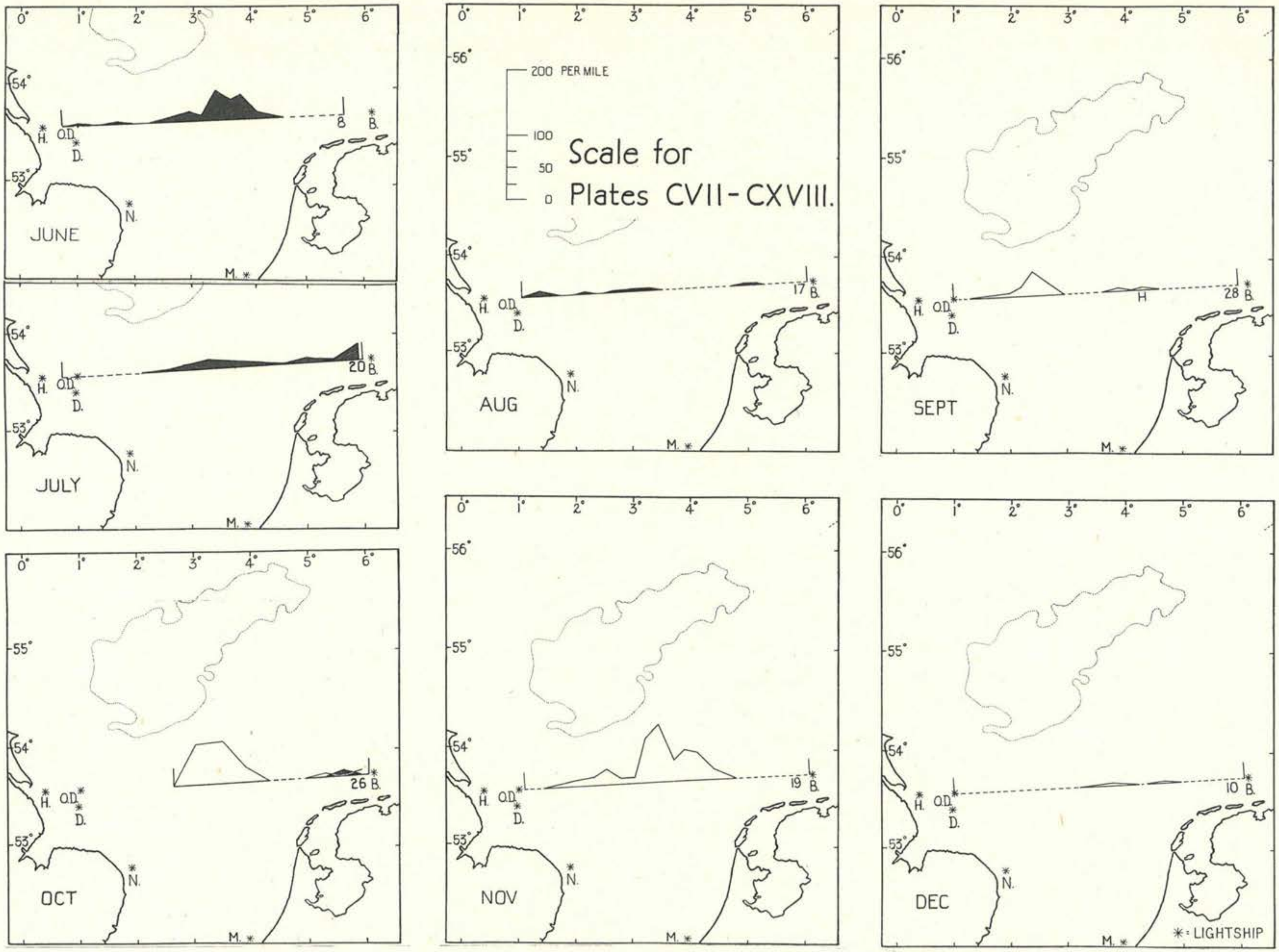


TOTAL COPEPODA, *July – September, 1937.* *For further explanation see Plate XCIV.*

PLATE CV



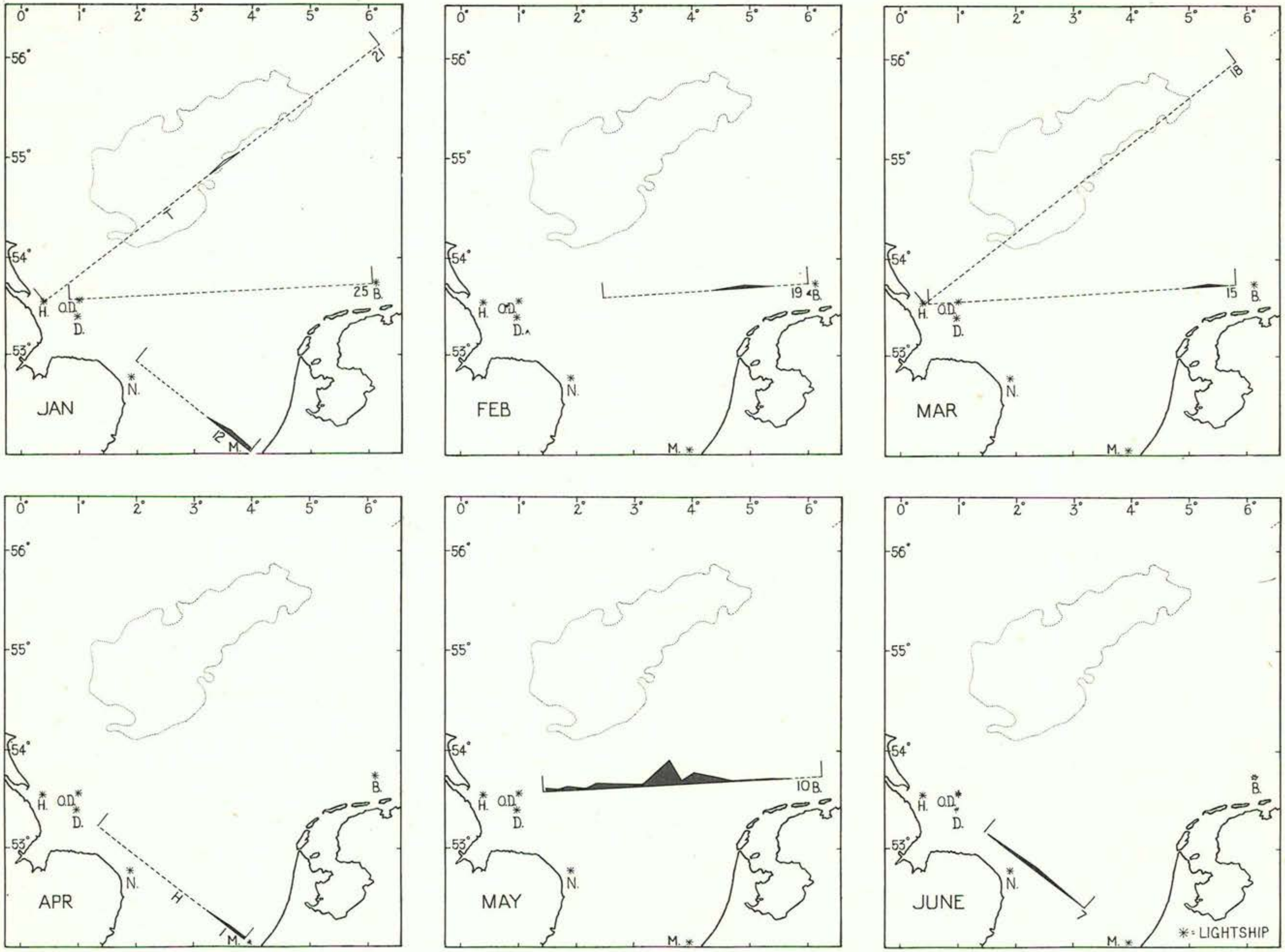
TOTAL COPEPODA, *October – December, 1937.* *For further explanation see Plate XCIV.*



CENTROPAGES HAMATUS *(blacked in graphs and 'H' for traces) and* ***C. TYPICUS*** *(open line) June – December, 1932. General arrangements as explained on Plate XCIV.*

PLATE CVII

PLATE CVIII



CENTROPAGES HAMATUS *(blacked-in graphs and 'H' for traces) and* ***C. TYPICUS*** *(open line and 'T' for traces) January - June, 1933. General arrangements as explained on Plate XCIV.*

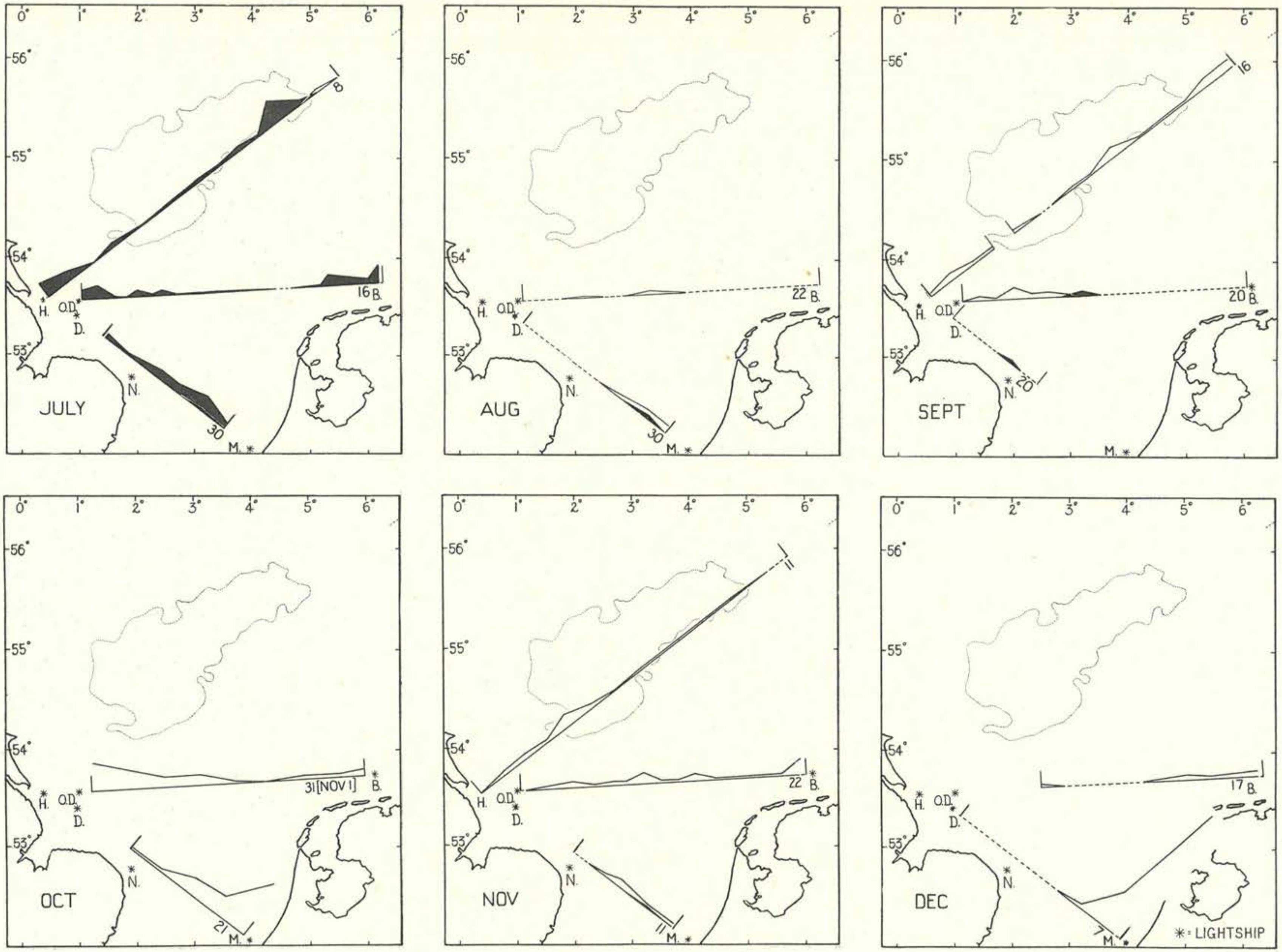
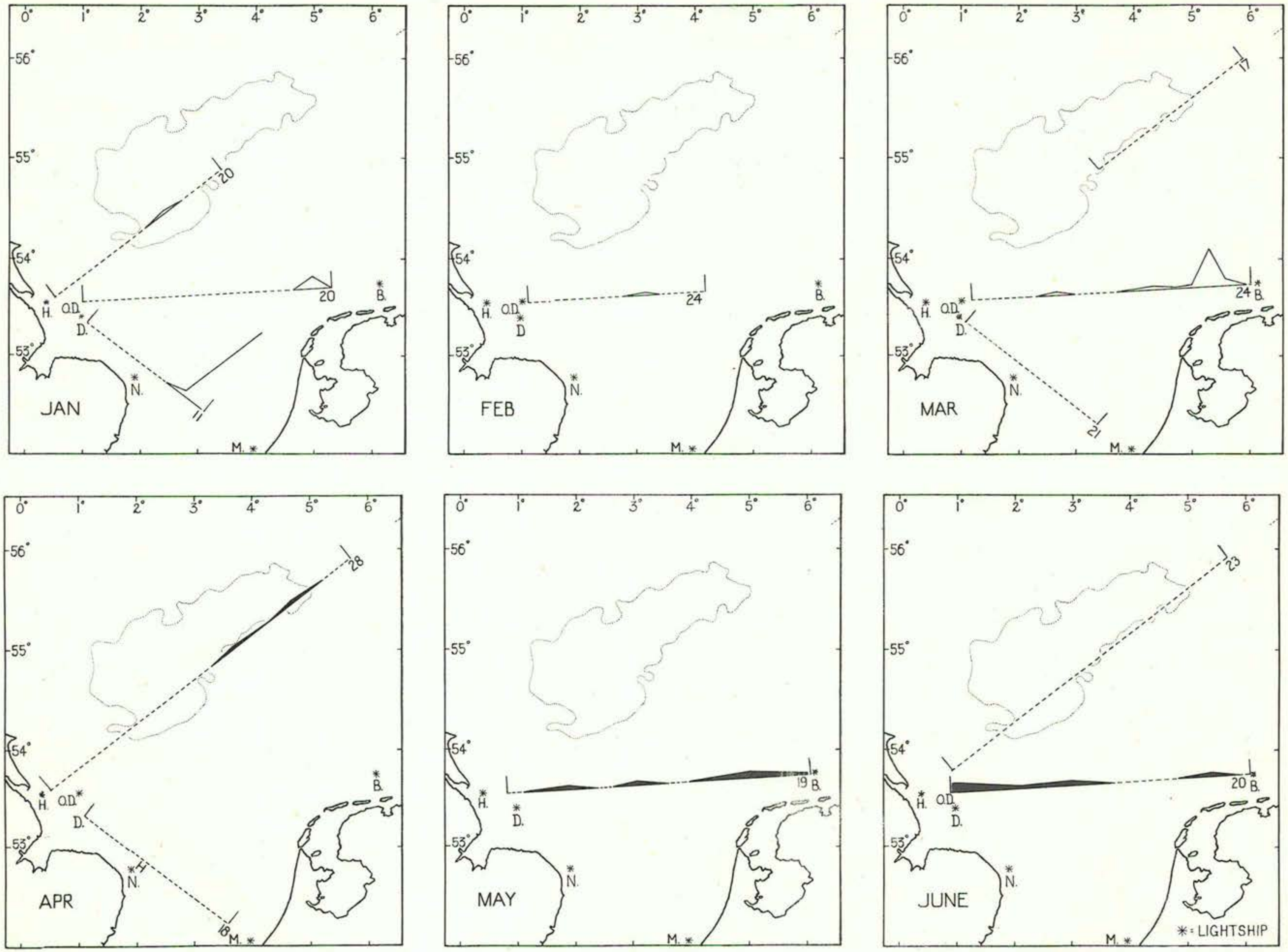


PLATE CIX

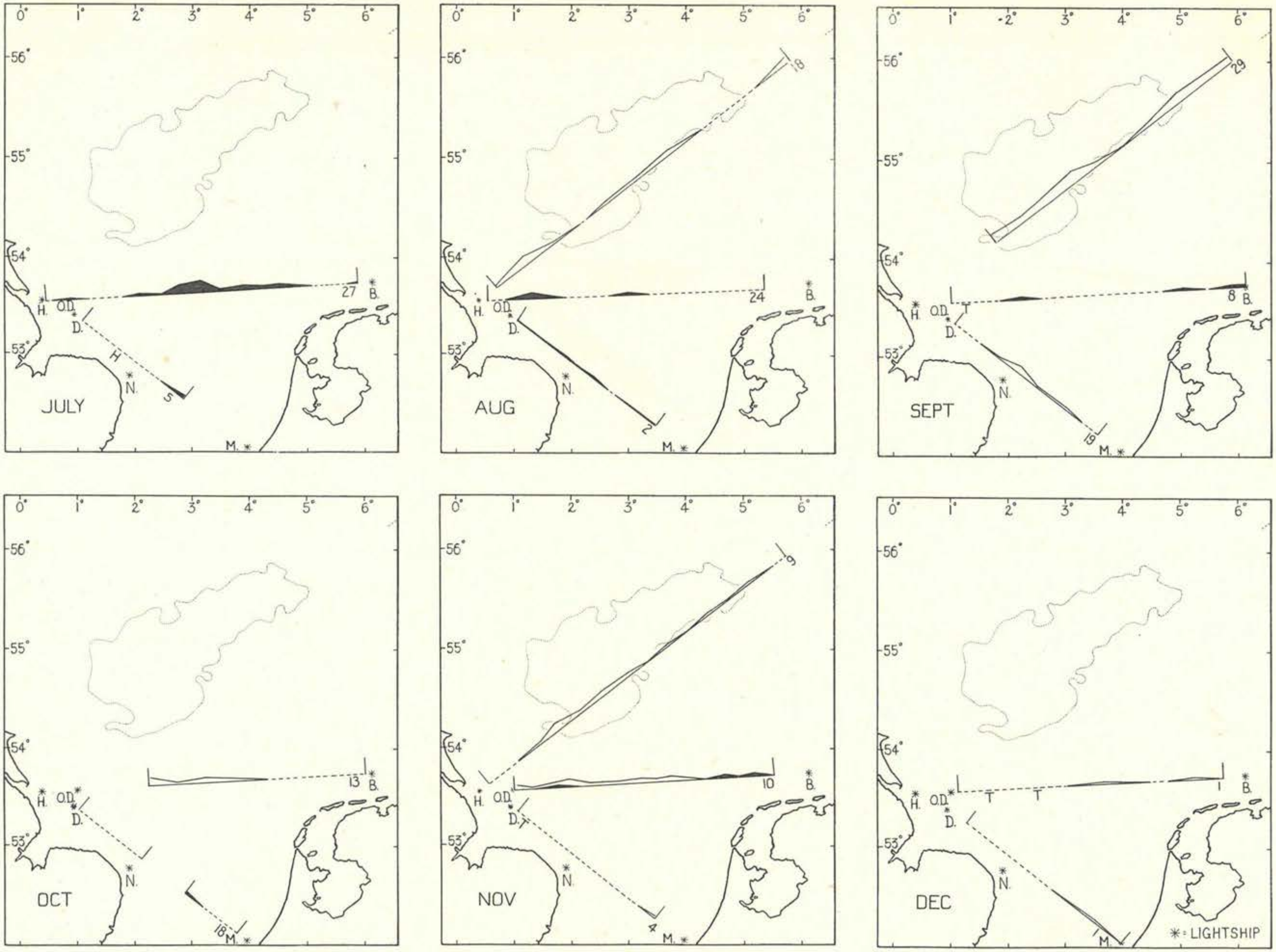
CENTROPAGES HAMATUS *(blacked-in graphs)* and ***C. TYPICUS*** *(open line)* July – December, 1933. *General arrangement as explained on Plate XCIV.*

PLATE CX



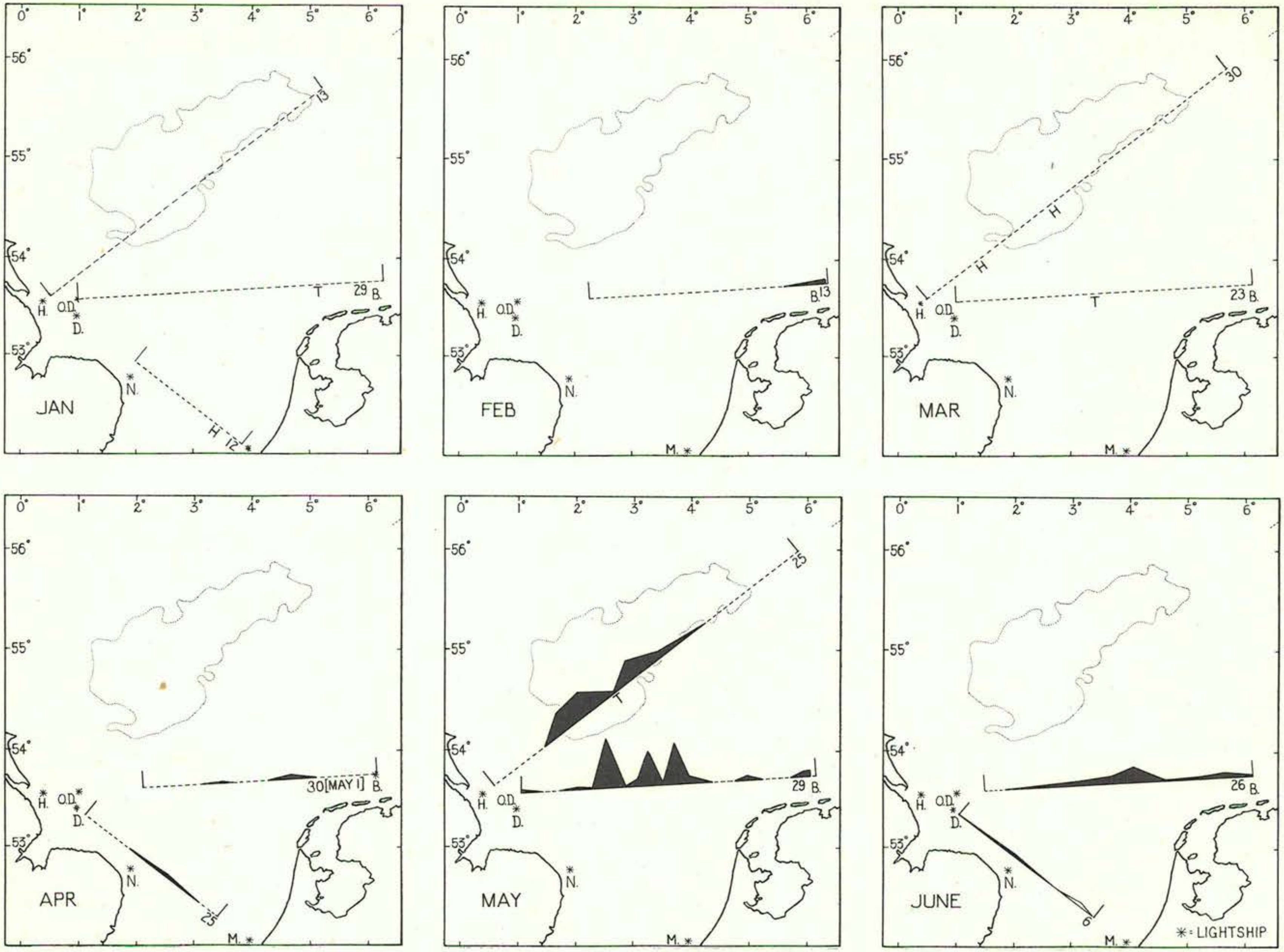
CENTROPAGES HAMATUS *(blacked-in graphs and 'H' for traces) and* **C. TYPICUS** *(open line) January—June,* 1934. *General arrangements as explained on Plate XCIV.*

PLATE CXI



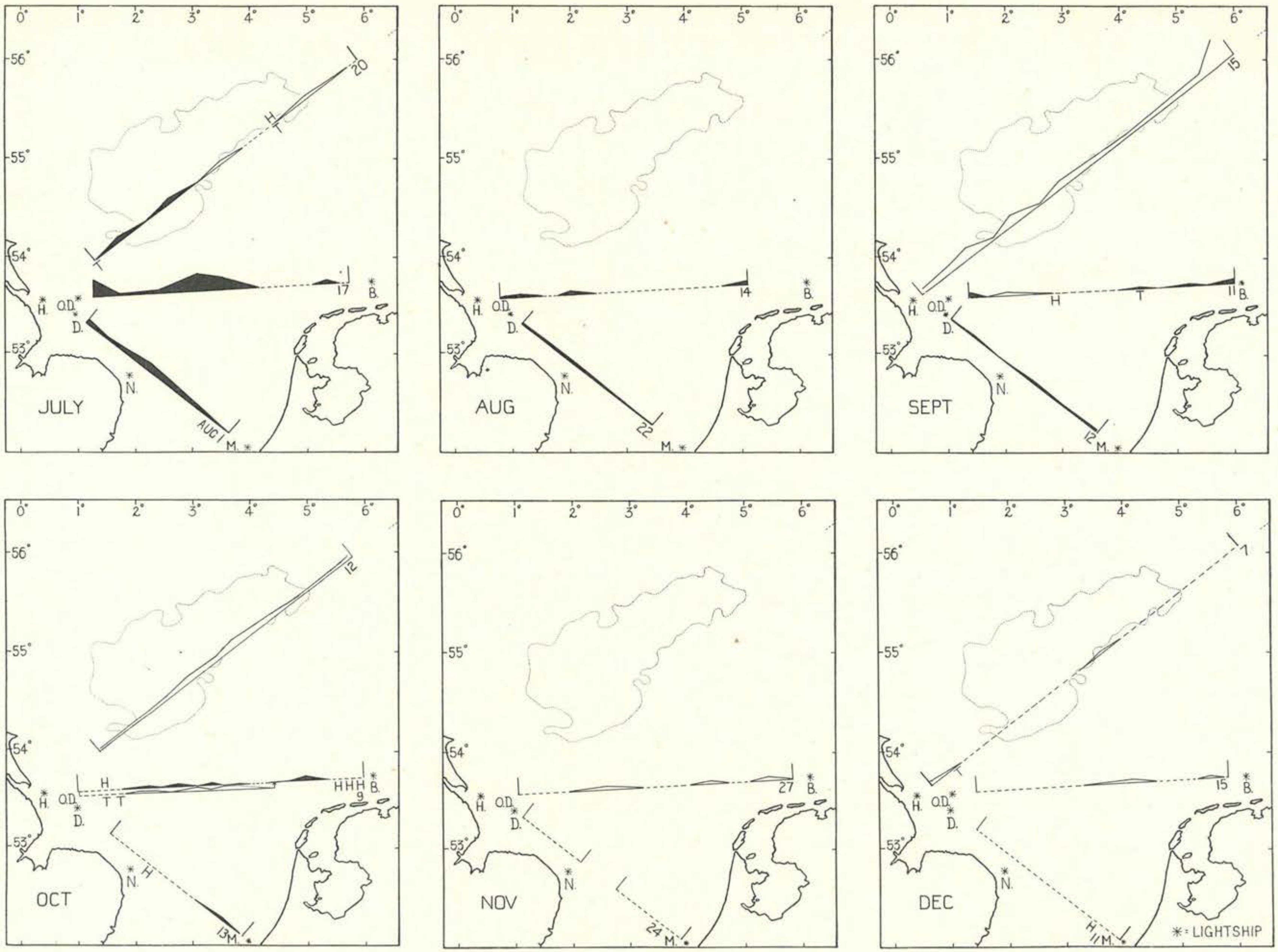
CENTROPAGES HAMATUS *(blacked-in graphs and 'H' for traces) and* ***C. TYPICUS*** *(open line and 'T' for traces) July – December, 1934. General arrangement as explained on Plate XCIV.*

PLATE CXII



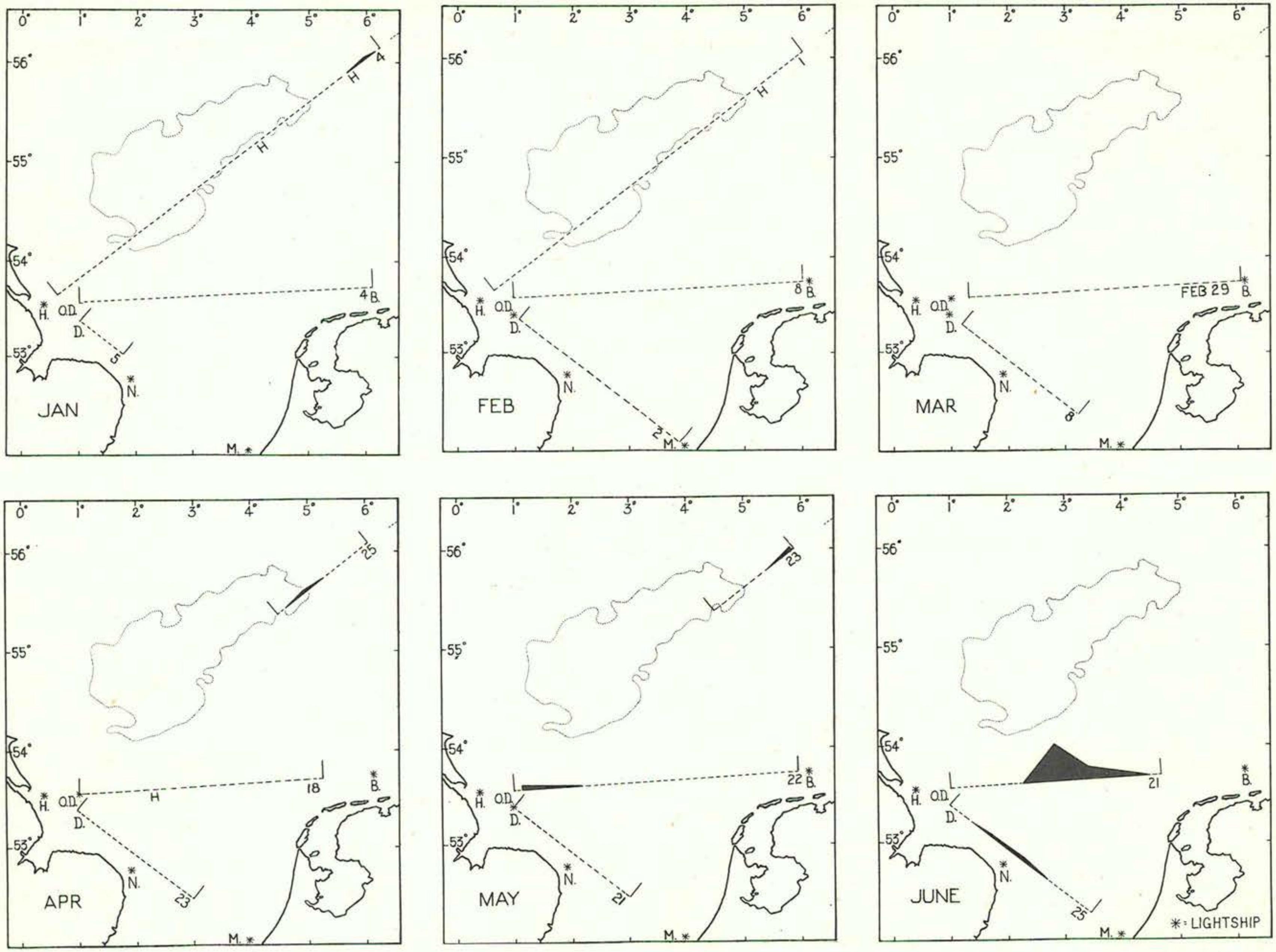
CENTROPAGES HAMATUS *(blacked-in graphs and 'H' for traces) and* ***C. TYPICUS*** *(open line and 'T' for traces) January – June, 1935.* *General arrangement as explained on Plate XCIV.*

PLATE CXIII



CENTROPAGES HAMATUS *(blacked-in graphs and 'H' for traces) and* ***C. TYPICUS*** *(open line and 'T' for traces) July – December,* 1935. *General arrangement as explained on Plate XCIV.*

PLATE CXIV



CENTROPAGES HAMATUS *(blacked-in graphs and 'H' for traces) and*
C. TYPICUS *(open line) January – June, 1936.* *General arrangement as explained on Plate XCIV.*

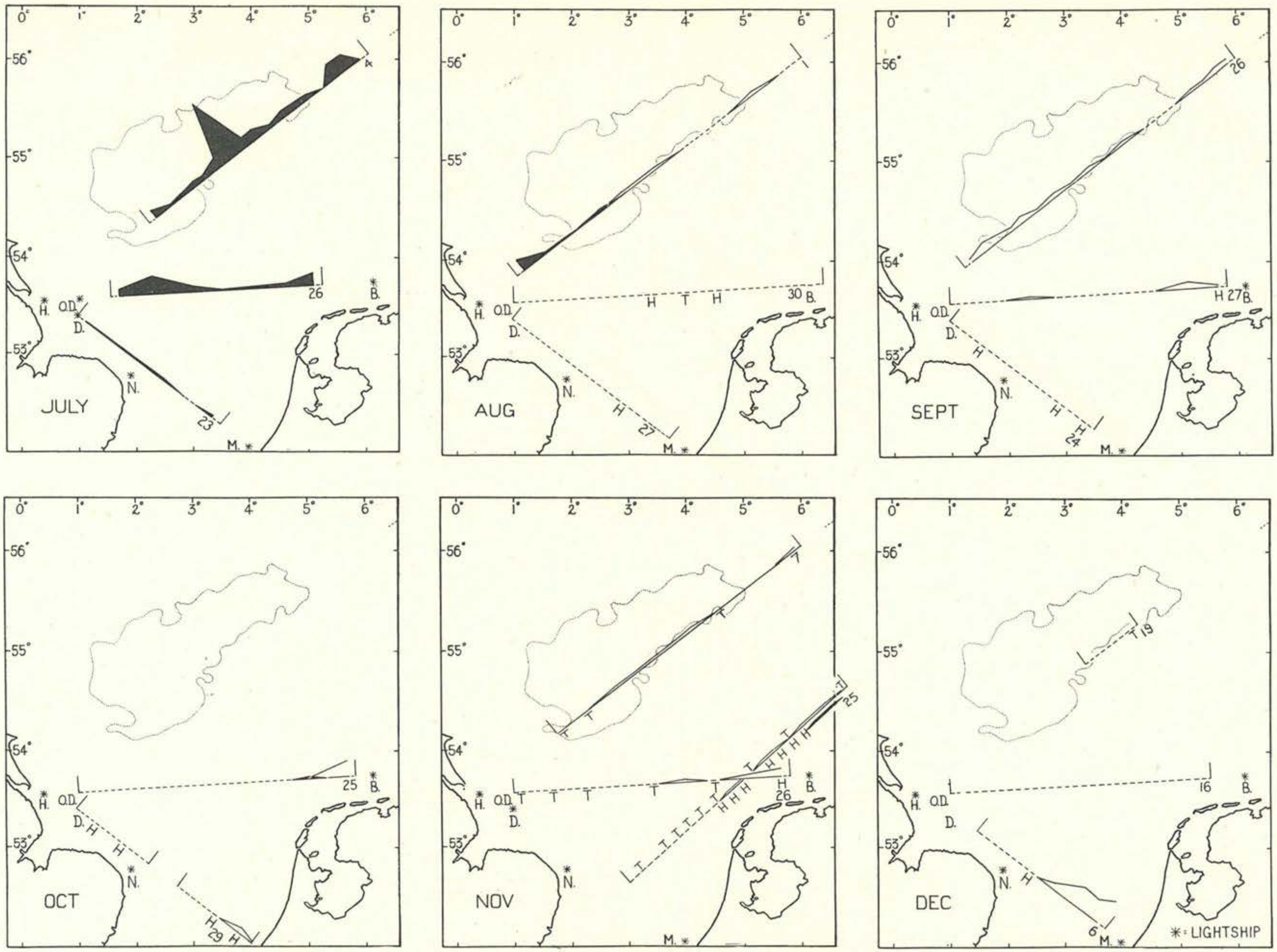
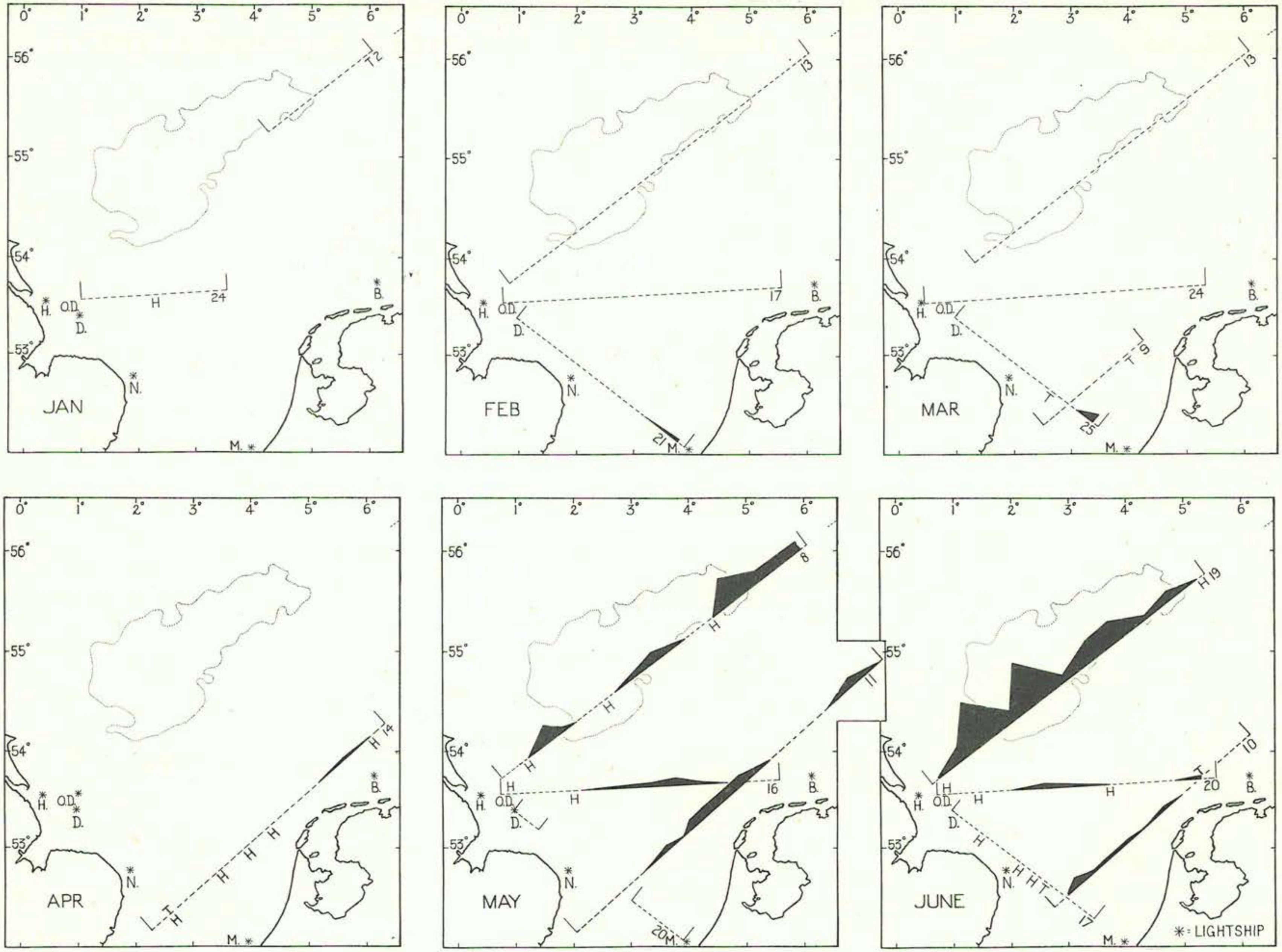


PLATE CXV

CENTROPAGES HAMATUS *(blacked-in graphs and 'H' for traces) and* ***C. TYPICUS*** *(open line and 'T' for traces) July–December, 1936.* *General arrangement as explained on Plate XCIV.*

PLATE CXVI



CENTROPAGES HAMATUS *(blacked-in graphs and 'H' for traces) and* ***C. TYPICUS*** *(open line and 'T' for traces) January–June,* 1937. *General arrangement as explained on Plate XCIV.*

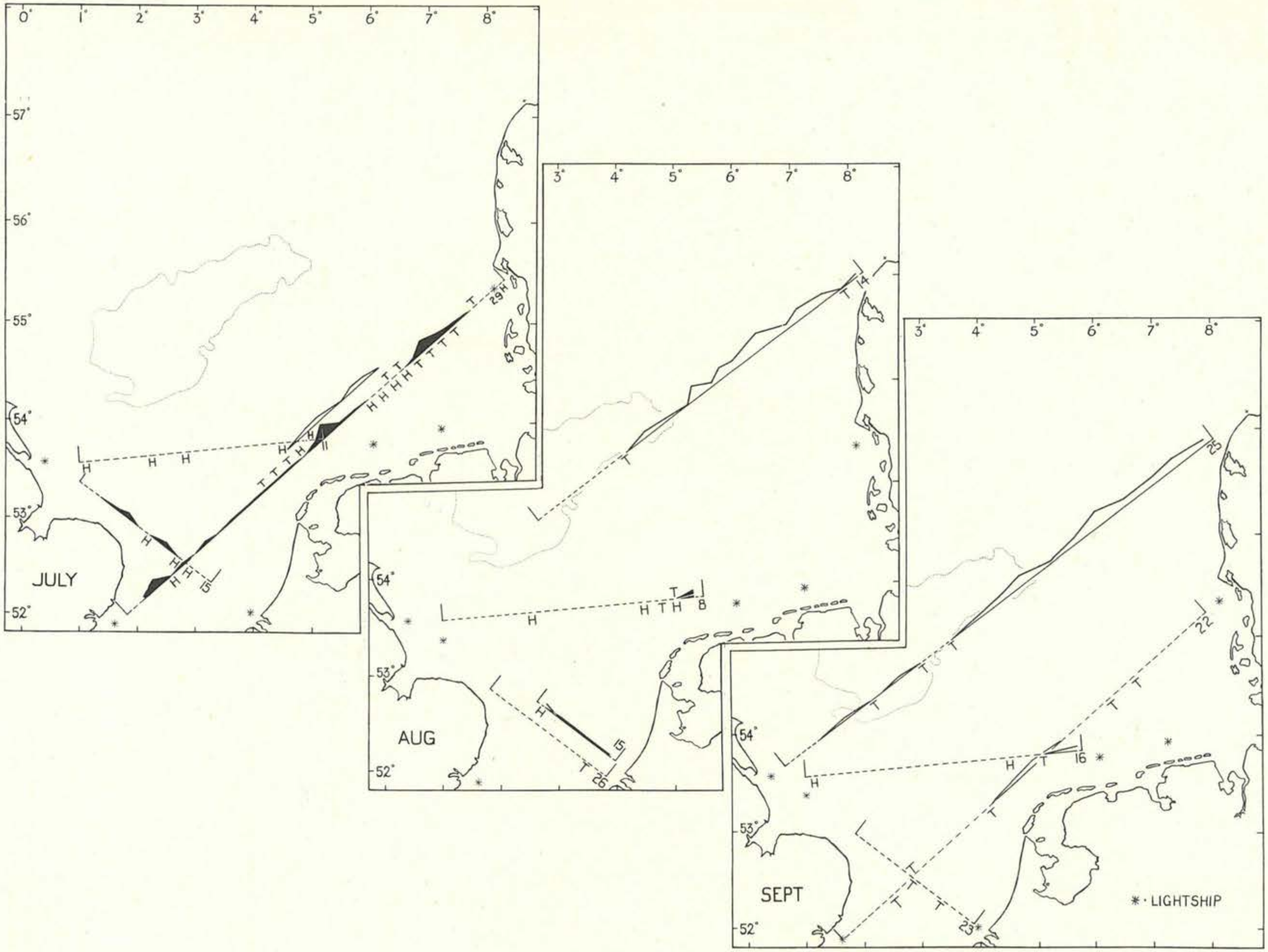
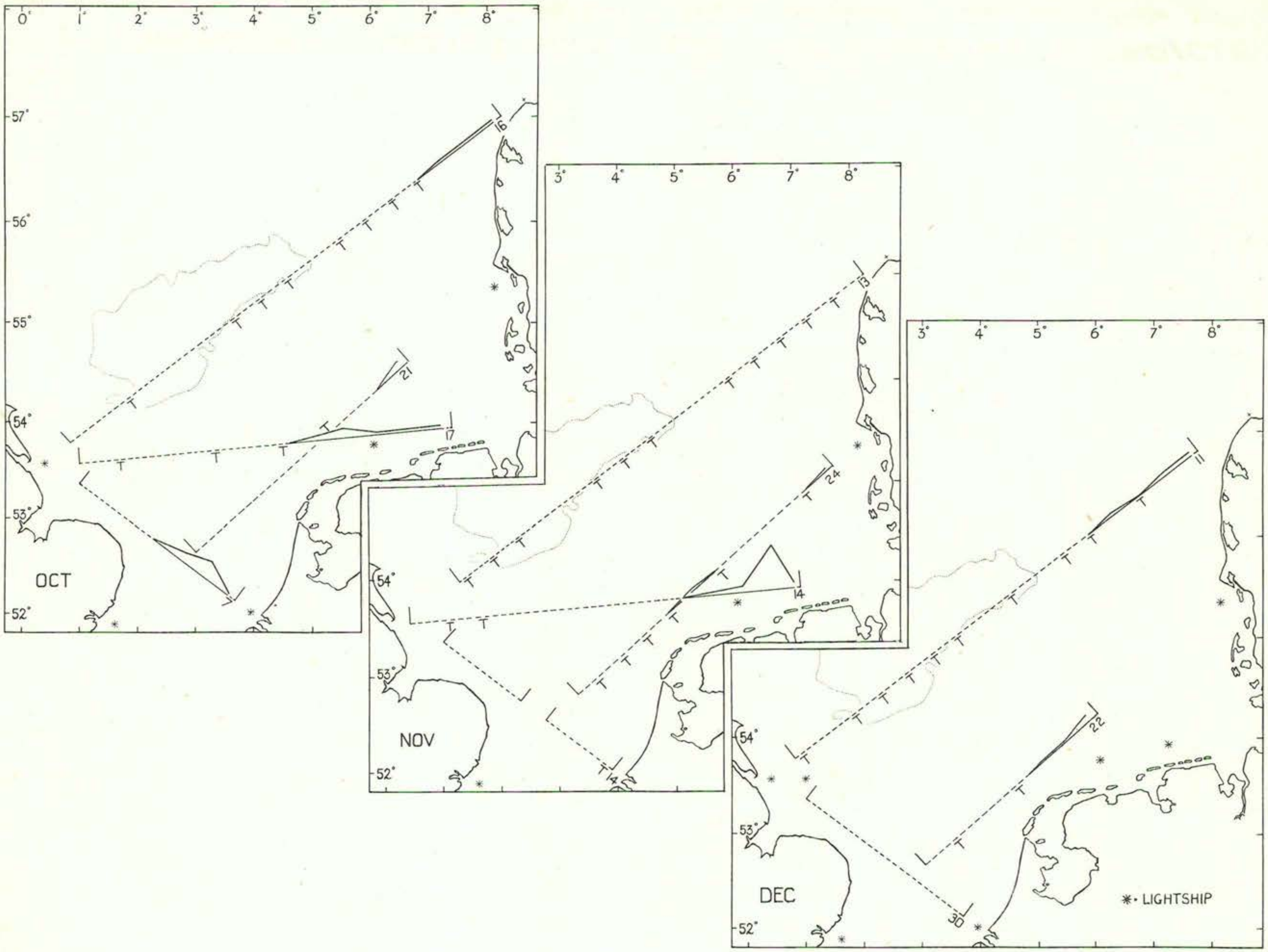


PLATE CXVII

CENTROPAGES HAMATUS *(blacked-in graphs and 'H' for traces) and* ***C. TYPICUS*** *(open line and 'T' for traces) July – September,* 1937. *General arrangement as explained on Plate XCIV.*

PLATE CXVIII



CENTROPAGES HAMATUS *(blacked-in graphs) and* ***C. TYPICUS*** *(open line and 'T' for traces) October-December, 1937. General arrangement as explained on Plate XCIV.*

Explanation of
PLATES CXIX-CXXV
showing the distribution of

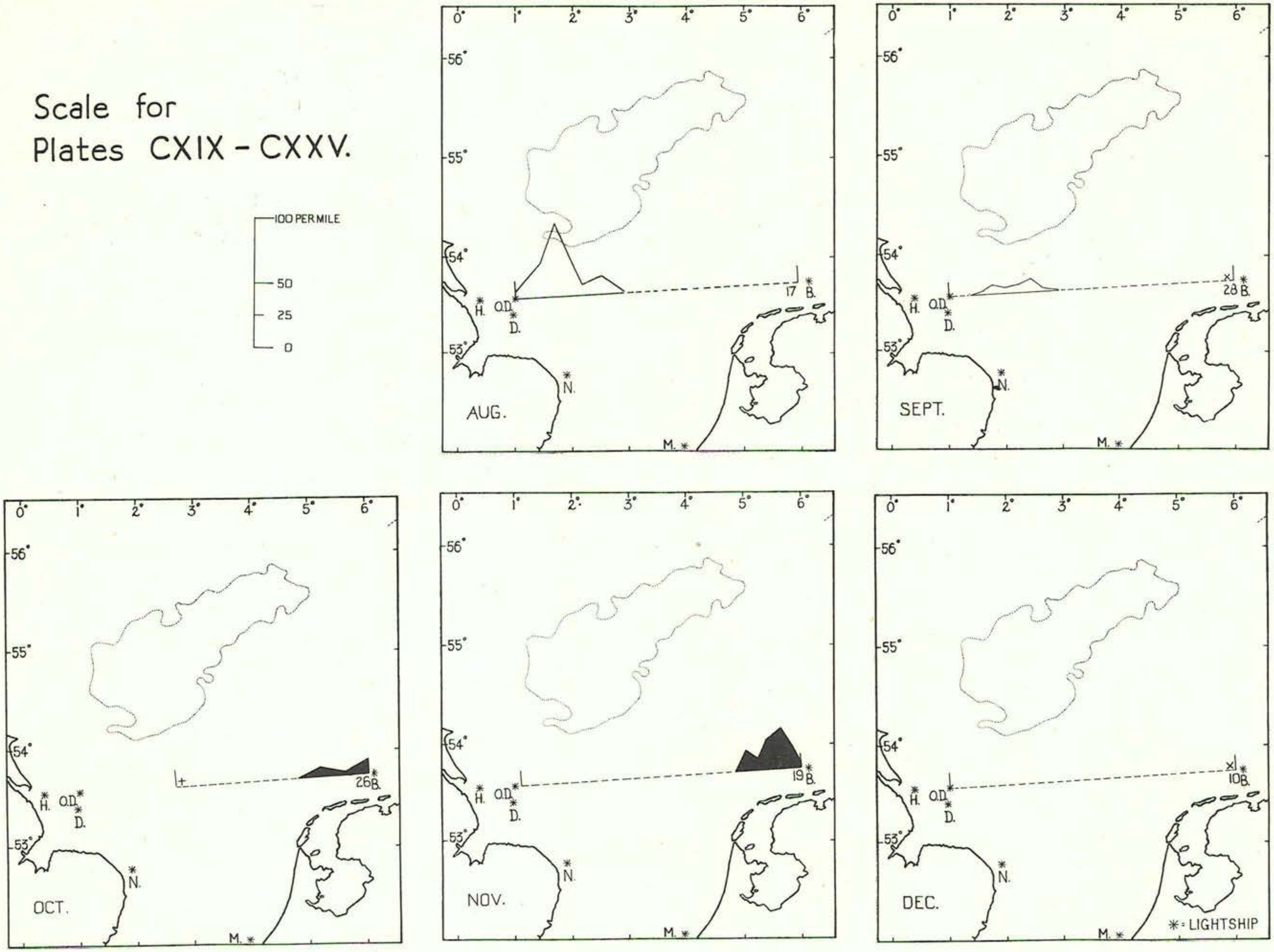
ISIAS CLAVIPES and ***CORYCAEUS ANGLICUS***

June 1932 — December 1937.

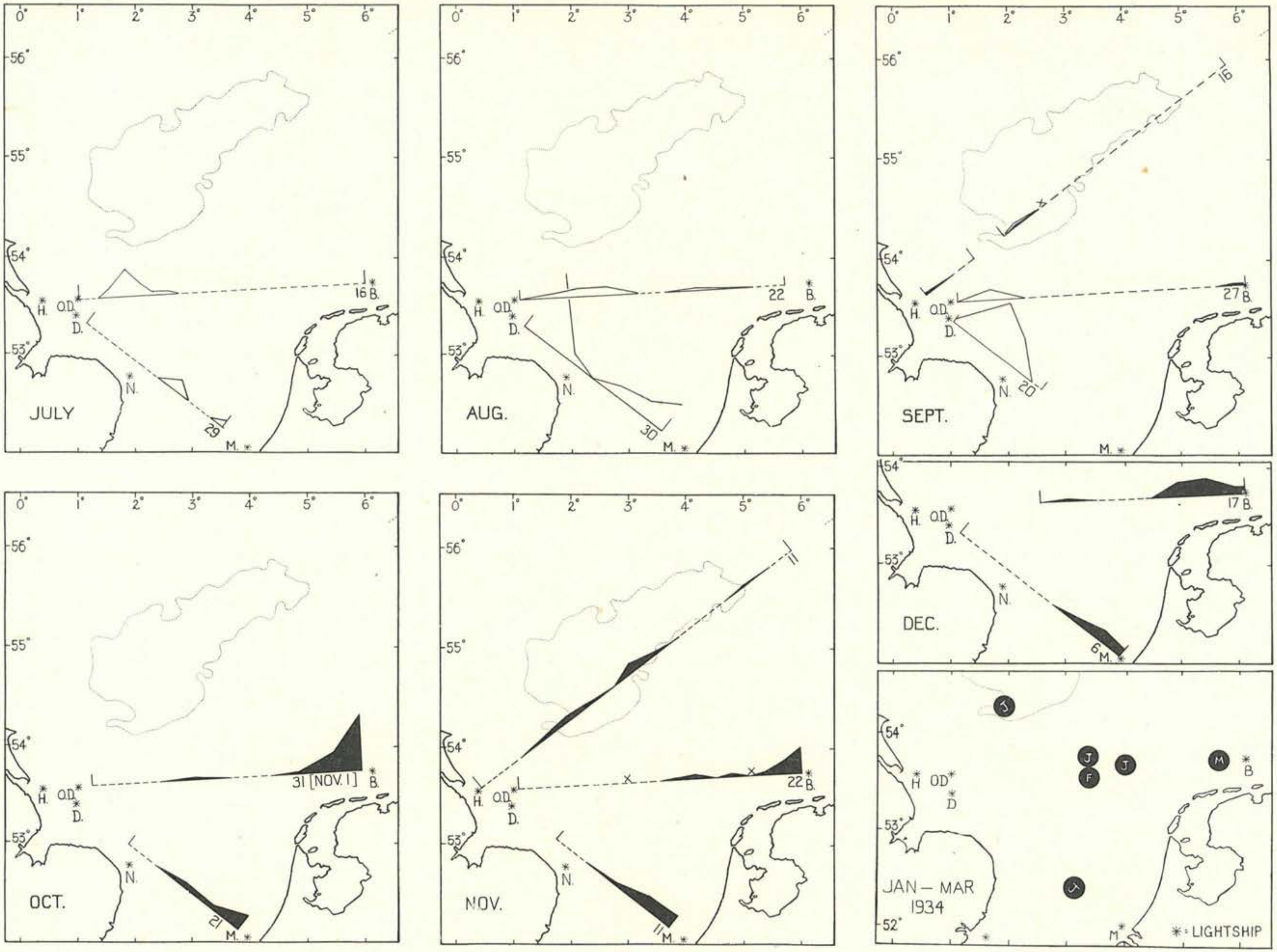
These species were usually only found in the latter part of the year. Charts for the earlier months have been omitted, but the records analysed, being the same as those for *CENTROPAGES*, are shown as on previous plates.

Occasionally *CORYCAEUS ANGLICUS* was recorded in January, February or March. Such traces are represented by black circles containing the initial letters of the months. They are placed in their correct position on the previous December chart, except on Plate CXX when an extra chart is inserted.

PLATE CXIX

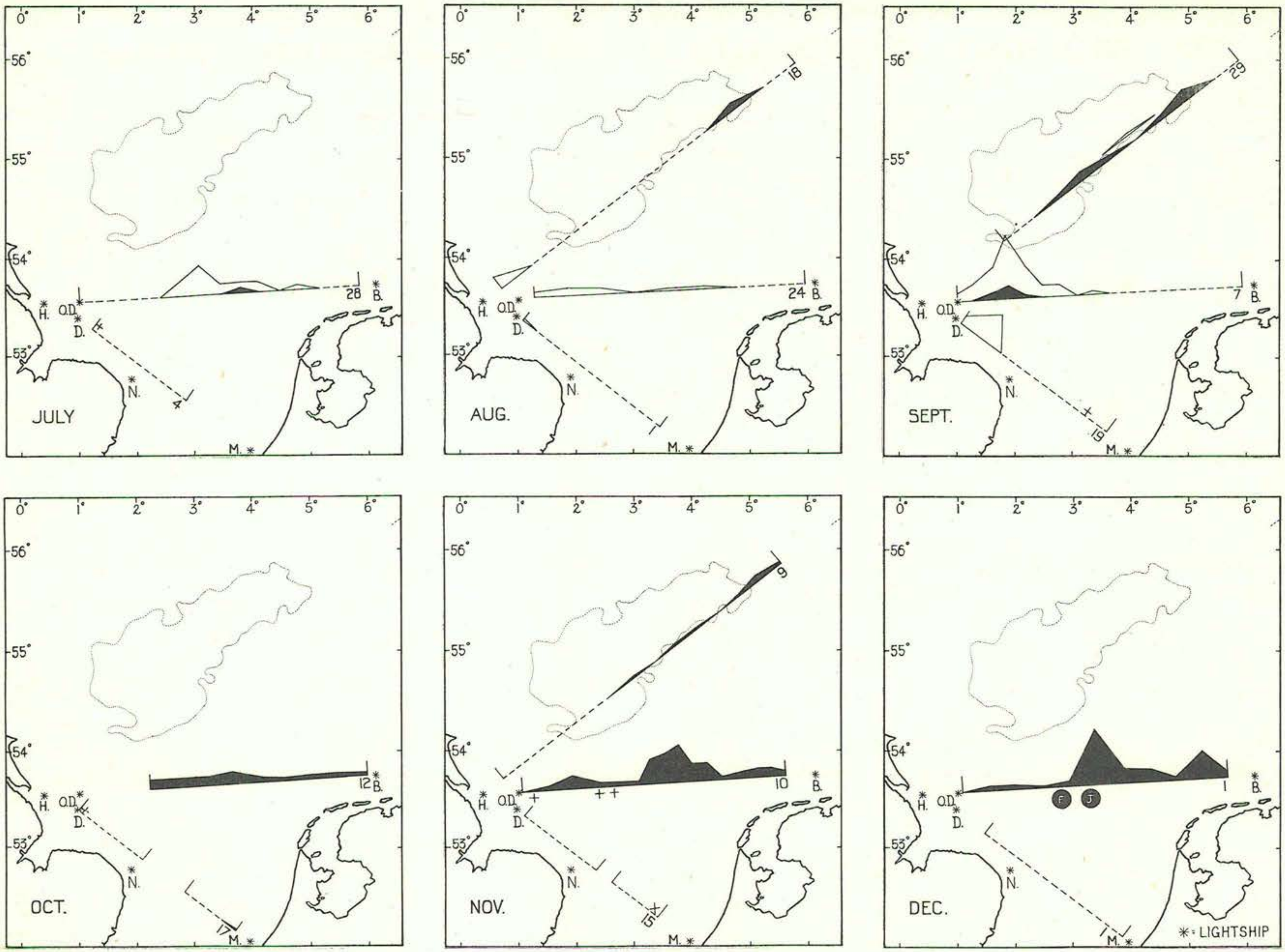


ISIAS CLAVIPES *(open line and + for traces) and* ***CORYCAEUS ANGLICUS*** *(blacked-in graph and × for traces)* 1932. *For further explanation see previous page.*

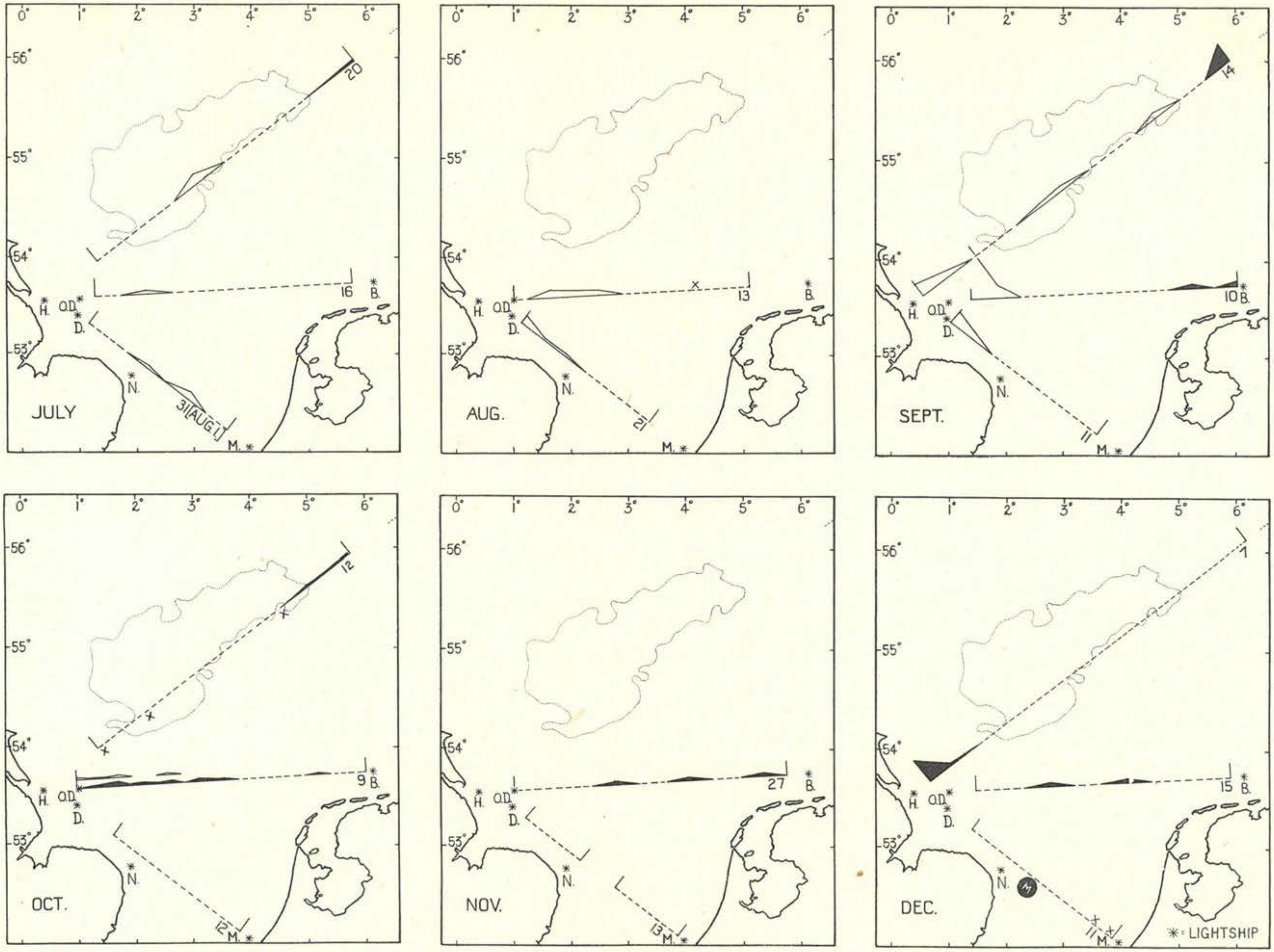


ISIAS CLAVIPES *(open line) and* ***CORYCAEUS ANGLICUS*** *(blacked-in graph and × for traces)* 1933. *For further explanation see page preceding Plate CXIX.*

PLATE CXX

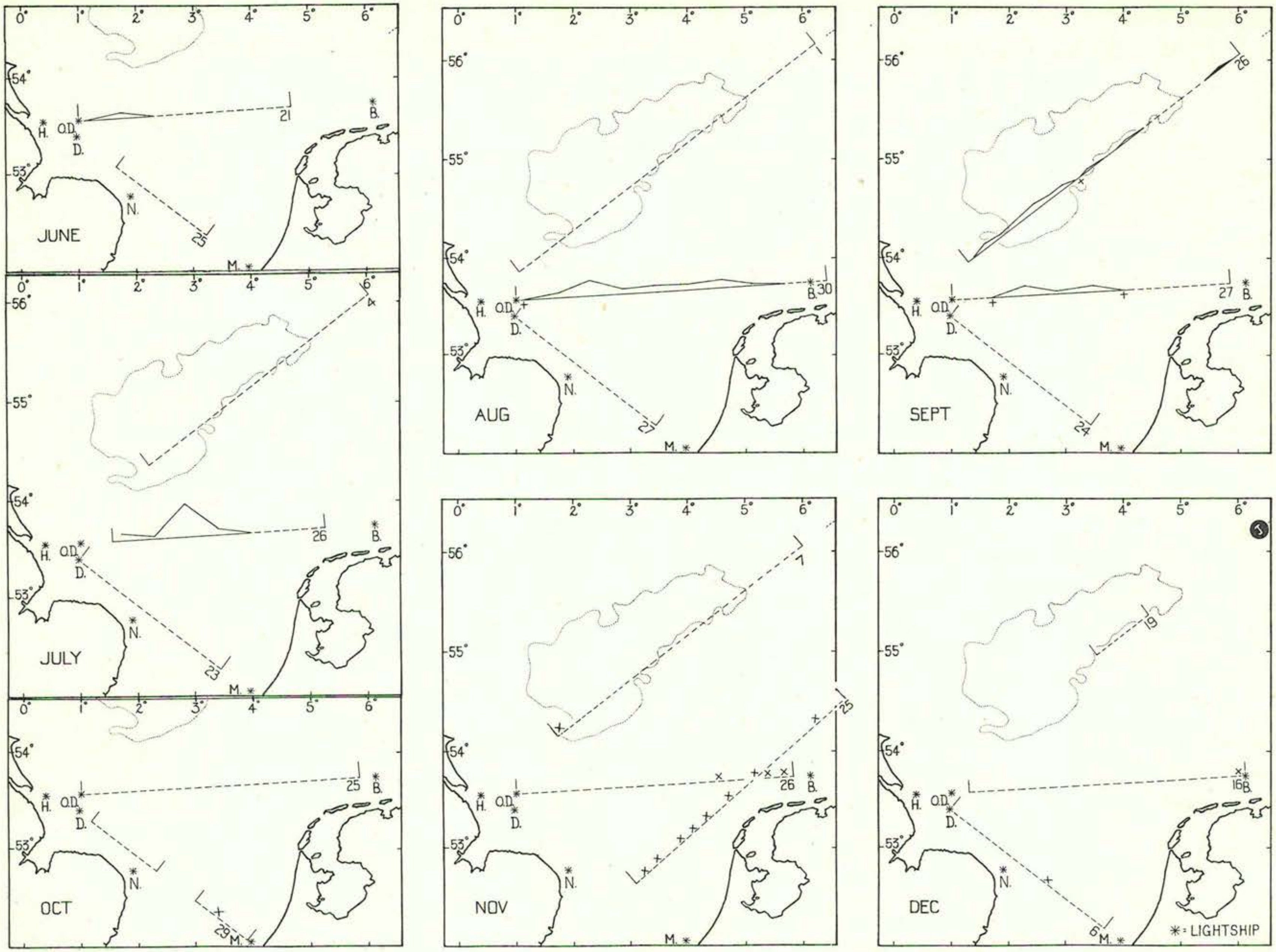


ISIAS CLAVIPES *(open line and + for traces) and* ***CORYCAEUS ANGLICUS*** *(blacked-in graph and × for traces)* 1934. *For further explanation see page preceding Plate CXIX.*

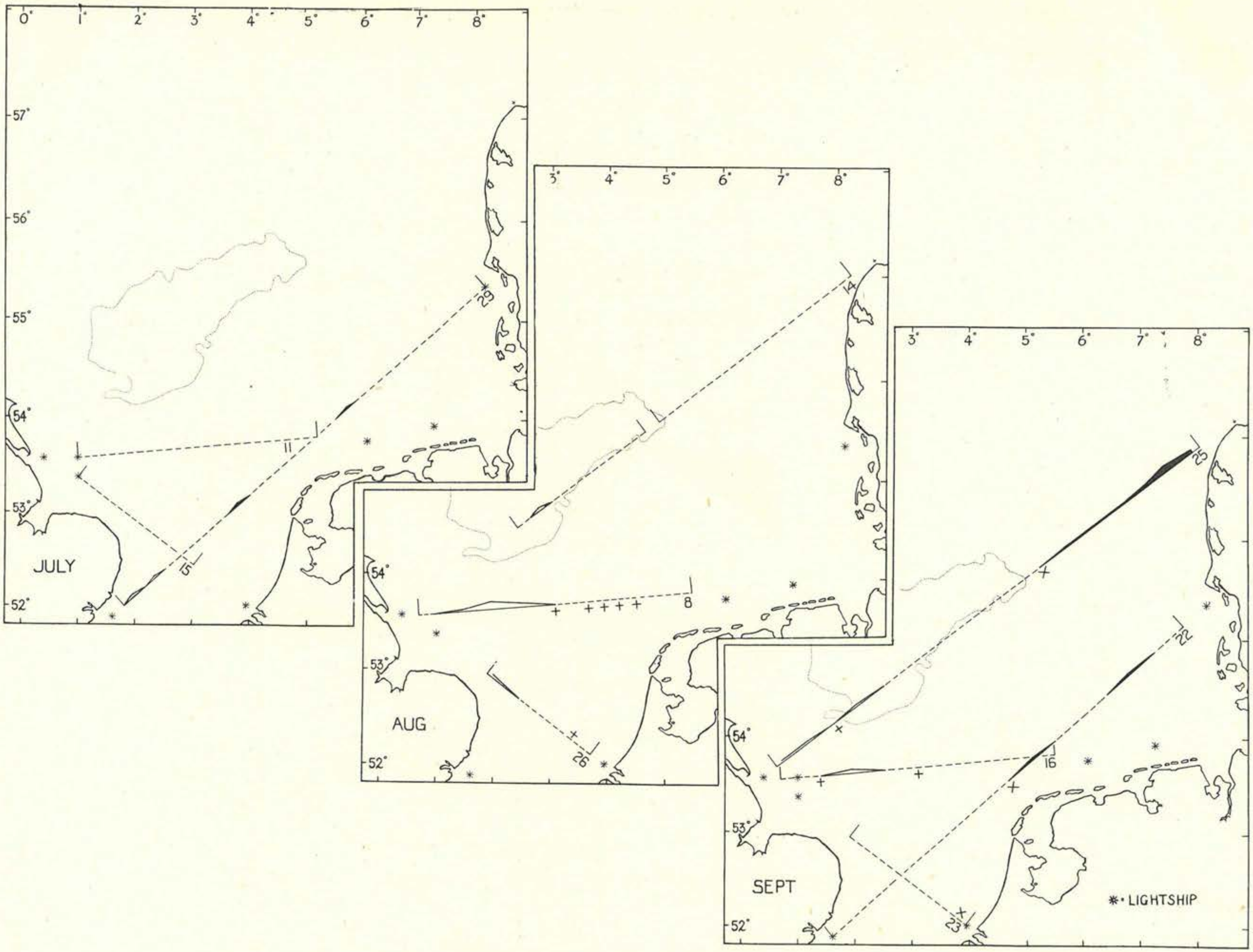


ISIAS CLAVIPES *(open line) and* ***CORYCAEUS ANGLICUS*** *(blacked-in graph and × for traces)* 1935. *For further explanation see page preceding Plate CXIX.*

PLATE CXXII



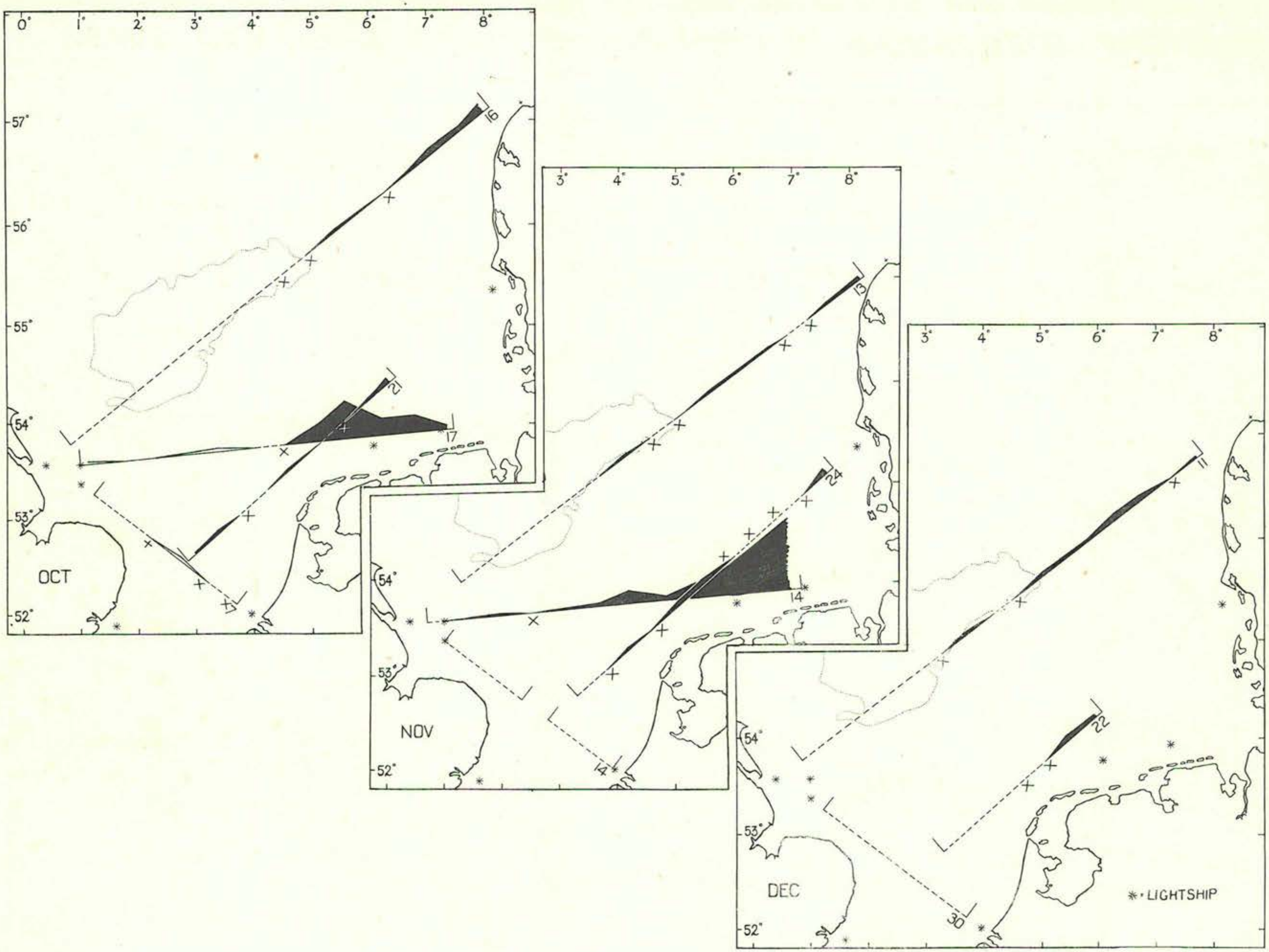
ISIAS CLAVIPES *(open line and + for traces) and* ***CORYCAEUS ANGLICUS*** *(blacked-in graph and X for traces)* 1936. *For further explanation see page preceding Plate CXIX.*



ISIAS CLAVIPES *(open line and + for traces) and* ***CORYCAEUS ANGLICUS*** *(blacked-in graph and × for traces)* 1937, *part I. For further explanation see page preceding Plate CXIX.*

PLATE CXXIV

PLATE CXXV



ISIAS CLAVIPES *(open line and + for traces) and* ***CORYCAEUS ANGLICUS***
(blacked-in graph and X for traces) 1937, *part II. For further explanation see page preceding Plate CXIX.*