

# ECOLOGICAL INVESTIGATIONS WITH THE CONTINUOUS PLANKTON RECORDER:

## THE PHYTOPLANKTON IN THE SOUTHERN NORTH SEA, 1932-37

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### INTRODUCTION: MATERIAL AND METHODS OF INVESTIGATION.

FOR reasons given in 'Bulletin' No. 1 it was necessary to postpone the publication of this report, which was originally intended to describe the

observations for 1932-35 only. Owing to the delay it became possible to include also the records for 1936-37, thus combining the whole of the data for the period when the survey was confined to the Southern North Sea, and forming a basis for the consideration of the more extended survey which began in 1938.

The material for 1932-35 consists of 60 continuous records of the phytoplankton at 10-metres' depth on the Bremen Line (between the Outer Dowsing Light-vessel and the Borkum Light-vessel), 38 on the Copenhagen Line (from the Humber Light-vessel for 250 miles towards the Hanstholm Light), and 41 on the Rotterdam Line (between the Dudgeon and the Maas Light-vessels). They were obtained between June, 1932, and December, 1935 (for further details, see List of Records, 'Bulletin' No. 2).<sup>1</sup> In addition there are also nine scattered records on a line from the Humber Light-vessel to the Pentland Firth, to which brief reference may be made, although they will not be dealt with in detail. In 1936-37, with a revised technique, we obtained similarly 41 records on the Bremen Line, 24 on the Copenhagen Line, and 32 on the Rotterdam Line, the first two lines being extended during 1937 to include certain coastal waters for a better definition of the limits of patches of plankton (from the Humber Light-vessel to the Norderney Light-vessel, and to the Hanstholm Lighthouse respectively). No records were obtained on the Pentland Firth line during 1936-37, but in the place of that service, arrangements were made to intensify the southern survey by the addition of a line between the Sunk and the Graadyb Light-vessels on a London-Esbjerg service, 15 records being obtained during the two years.

During this period we have aimed at obtaining at least one record on each line for each month, but occasionally this has been impossible owing, in various instances, mainly to mechanical defects in the recorder, bad weather, and to alterations in the sailing schedules of the steamships. On the other hand, in some months more than one record has been obtained on the Bremen and Rotterdam lines, particularly in the autumns of 1934 to 1937, when intensive programmes were deliberately arranged (in conjunction with the work of the Ministry of Agriculture and Fisheries Laboratory at Lowestoft) to provide information about the movements of patches of phytoplankton during the autumn herring fishery in the Southern Bight.

The mechanical principle of the plankton recorder is described in 'Bulletin' No. 1 and in greater detail in the 'Discovery Reports' (Hardy, 1936a). Briefly, the plankton is collected as a sandwich between two moving bands of silk netting (60 meshes to the inch), one of which is divided into 2-in. sections, each corresponding to a known distance through which the machine has been towed. In the 1932-35 records the machine has been towed  $1\frac{1}{2}$  to 2 miles whilst one section was passing across the water-tunnel, *i. e.* collecting plankton; in the later records we

<sup>1</sup> There are also two other Bremen records for September and October, 1931, and two Copenhagen records for January, 1932. These were preliminary records obtained whilst testing the early models of the present type of recorder and, owing to the large period separating them from the others, they will only be referred to occasionally in comparison with those months of the later years. The number of records here mentioned is more than that in 'Bulletin' No. 4; this is so because many of the records of the intensive autumn programmes were obtained and analysed for the phytoplankton only.

aimed at a mileage ratio of 5 miles per section (the more exact calculations of the individual mile per section ratios are shown for each record in the List, 'Bulletin' No. 2). After various periods of storage in the laboratory an analysis of the plankton on each section<sup>1</sup> has been made, and for the phytoplankton this at first comprised the examination of a number of microscope fields amounting to  $\frac{1}{150}$  of the area of the section. The resulting totals per section have been used in compiling the graphs for the earlier years; in the later years, however, when working at an approximate ratio of 5 miles per section, the method has been modified in order to provide standard estimations of organisms per mile in blocks of 10 miles. The silk has been examined in essentially the same manner, but the areas examined are smaller, and are adjusted according to the slightly varying ratios. The relative merits of these two methods will be discussed more fully in 'Bulletin' No. 4 and are referred to here on p. 86. The change also involved a change in the volume of the water passing through the machine (see p. 41 of 'Bulletin' No. 1).

After the counting process on the silk the plankton was scraped off (a process which has obviously involved some loss, most appreciable in the phytoplankton), and then preserved in tubes from which samples were drawn for checking purposes during the earlier years. Such analyses will be referred to as "tube analyses" in distinction from the "roll analyses". We have obtained, in addition, a relatively small portion of plankton from the formalin tank fluid in which the record was stored in the machine. This has been termed the "tank residue", and has on certain occasions provided evidence of material which has been missed on the roll, or, owing to the relatively better condition of the material, has allowed more detailed identifications to be made.

In the earlier part of the work we attempted to identify all the species of *Rhizosolenia* and *Biddulphia*, paying particular attention to *R. styliformis* and *B. sinensis*. Of the other diatoms usually only generic identifications were made, although in many instances these amounted to specific identifications with certainty. Estimates were also made of the numbers of Dinoflagellates as a whole, and of the volumes of *Phaeocystis*. In the later years it was possible to extend these a little, and in particular to separate from the rest of the Dinoflagellates the *Biceratia* (almost entirely *Ceratium furca*) and *C. fusus*. Other flagellates, etc., have been identified at various times, but they will not be dealt with in this preliminary work.

Planktologists used to more orthodox types of analysis and, in particular, systematists may think it unsatisfactory that specific identifications were not made throughout the work. There are reasons for this. At first the recorder was considered to be on its trial as a means of showing simply the changes in the broad features of the plankton. Also, only a minimum of time was available for analysis since the staff were largely occupied with another branch of the work—

<sup>1</sup> A few of the Copenhagen records have only been analysed on alternate sections. There is reason for believing that little loss in precision has resulted from this abbreviation (see also p. 84).

that of correlating the plankton with the changes of the herring fisheries by experimenting with the Plankton Indicator, this being regarded as an important preliminary to the survey (p. 6, 'Bulletin' No. 1). Thus the earlier results had to be treated in only the broadest way; whilst some of the diatoms were dealt with in detail, others were only estimated on a broad scale and the Dinoflagellates were considered only as a group. Yet again, as will be shown later, the analysis of the recorder material has presented many problems which are not encountered in other types of survey; we have had to make the choice between detailed work with a few samples and much more extensive work on a broader scale. Certain phytoplankton forms (fortunately already known to have great practical importance), *e.g.* *Rhizosolenia styliformis*, can be identified and counted with greater accuracy and ease than others, whilst many of the (usually smaller) forms are much more difficult to deal with in the conditions of the work, and have had to be dismissed more briefly for the sake of time economy. We must not, however, assume that such forms are of less importance than some better-known species, and we hope that later, due to reorganization of the work, we shall be able to investigate the ecology of a larger number in some detail. The results obtained in 1938 have shown that much more detailed work may be possible in some groups.<sup>1</sup>

#### THE LIMITATIONS OF THE METHOD.

In his introduction Professor Hardy has outlined certain of the limitations peculiar to this method of collection, and has assessed their demerits in comparison with the advantages which it provides. Here further consideration will be given to those concerning the phytoplankton. It must be clear that for a number of reasons, any machine designed to take continuous records over an appreciable area and for long periods must necessarily sacrifice some of the advantages obtained with more usual apparatus. These sacrifices seem to concern (1) the methods of collection, and (2) the methods of dealing with the large quantities of material collected. Taking the second factor first, it will be clear that it is impossible to examine the vast number of samples in the intensive manner which might otherwise be desirable and which is obtained in other branches of plankton sampling. Up to the end of 1935 some 25,000 miles of sea-water were sampled for the phytoplankton, in 1936 and 1937 another 20,000, and the new programme of work (see p. 168) aims at some 2500–3500 miles per month as a minimum, with more detailed surveys in particular seasons and areas. The 25,000 miles up to the end of 1935 represent some 15,000 sections of plankton for analysis, and to examine these sections for all the groups has only been possible by a more cursory method of examination than is customary. This has had the result that at least

<sup>1</sup> Gran, Hentschel and Russell (1936) have briefly discussed the problems of general plankton surveys and have made the point that it is not always possible to give that attention to detail which the specialist can give. In the later work we have made an attempt to come nearer to the requirements of their list in some of the groups, although certain modifications have necessarily to be made.

in some of the preliminary surveys, errors of enumeration and identification have appeared, as will be seen on p. 79. These errors have been corrected where possible (see also footnote on p. 116); elsewhere the unsatisfactory material has been discarded, or if used (as in some types of numerical error), it is only with qualifications regarding the validity. By reorganization of the work in the future we expect to be able to avoid a number of these errors, but there is little doubt that some peculiar difficulties in identification will remain a feature of this type of work.

The effects described may also be associated with the other type of disadvantage—that due to the method of collection. In order to obtain the maximum material of various types with the minimum of expense within the time available, it has been necessary to use throughout the work a standard mesh of silk and to tow the machine at a constant depth. The silk used on the recorder has 60 meshes to the inch, and thus is a grade which would not normally be used for phytoplankton. In this work, however, we have had to use a mesh, which would serve for the sampling of both the zooplankton and the phytoplankton, and an intermediate grade had to be adopted. Some idea of its catching power is given by the list in Table I of the types of diatoms which have been collected during this survey. For the area investigated this may be regarded as fairly representative, but some digression may be fitting here to discuss briefly the collection of phytoplankton by means of nets in its relation to the recorder work. Early attacks were made on the validity of samples collected by any system of nets (the arguments of Lohmann, amongst others, will be sufficient to recall these), and more recently Nielsen (1933 *et al.*) and Russell (1935) have emphasized their defects with particular reference to the nannoplankton and the microplankton respectively. The former even goes further, with some justice, to attack the validity of estimations following the use of the centrifuge. With reference to the present work, Nielsen has rightly pointed out that it is not possible to estimate the total production of the smaller phytoplankton forms by means of the silk mesh in use—that it is even doubtful whether one can obtain this for the larger forms—and this difficulty has been realized from the start. There is, in fact, a growing agreement that an estimation of total production can never be obtained by means of any mesh which could be constructed owing to (1) the small size of some of the important producers, and (2) the problems of filtration at the lower limits of mesh size. Yet it remains doubtful whether any of the critics would suggest that all the samples which have been obtained by the use of nets, etc., have been of no value, although from time to time it appears necessary to insist that the real value of such work can only be realized after more appreciation of its limitations.

Particularly does this apply to the results appearing in the recorder work. With this machine we can obtain widespread and almost simultaneous surveys over an important area, giving, we believe, after consideration of its limitations, important indications of the distribution of plankton forms. With regard to the phytoplankton, at least, we know that it cannot measure the *total productivity*.

But, on the other hand, we believe that with some of the larger forms (*R. styliiformis*, *B. sinensis*, and some of the *Ceratium* spp.) we can obtain records of their abundance

TABLE I.—*List of the Diatoms Recorded in the 1932-37 Survey.*

<i>Melosira Borreri</i> Greville.	<i>Biddulphia aurita</i> (Lyngb.).
<i>Paralia sulcata</i> (Ehr.).	„ <i>mobiliensis</i> (Bail.) Grun.
<i>Hyalodiscus steligier</i> Bailey.	„ <i>regia</i> M. Schultze.
<i>Coscinodiscus</i> spp.	„ <i>sinensis</i> Grev.
<i>Actinoptychus undulatus</i> (Bail.).	„ <i>granulata</i> Roper.
<i>Asteromphalus</i> spp.	„ <i>rhombus</i> (Ehr.) W. Sm.
<i>Thalassiosira Nordenskiöldii</i> Cleve.	„ <i>obtusa</i> Kützing.
„ <i>decipiens</i> (Grun.).	„ <i>favus</i> (Ehr.).
„ <i>gravida</i> Cleve.	„ <i>alternans</i> (Bail.)
„ <i>baltica</i> (Grun.).	„ Van Heurck.
<i>Coscinosira</i> spp.	„ <i>vesiculosa</i> (Ag.) Boyer.
<i>Lauderia</i> spp.	<i>Bellarochia malleus</i> (Brightw.) Van
<i>Schröderella</i> spp.	Heurck.
<i>Bacteriosira fragilis</i> Gran.	<i>Cerataulus</i> spp.
<i>Skeletonema costatum</i> (Greville).	<i>Cerataulina Bergonii</i> H. Pérag.
<i>Stephanopyxis turris</i> (Greville).	<i>Lithodesmium undulatum</i> Ehr.
<i>Detonula</i> spp.	<i>Ditylium Brightwelli</i> (West.).
<i>Dactyliosolen</i> spp.	<i>Eucampia zodiacus</i> Ehr.
<i>Leptocylindrus danicus</i> Cleve.	<i>Streptotheca thamensis</i> Shrubbs.
„ <i>minimus</i> Gran.	<i>Fragillaria</i> spp.
<i>Guinardia flaccida</i> Castr.	<i>Asterionella japonica</i> Cleve & Möller.
<i>Corethron criophyllum</i> Castr.	<i>Thalassiothrix longissima</i>
<i>Bacteriastrum hyalinum</i> Lauder.	Cleve & Grun.
<i>Rhizosolenia alata</i> Brightw.	„ <i>Nitzschioides</i> Grun.,
„ <i>delicatula</i> Cleve.	„ Van Heurck.
„ <i>faeröense</i> Ostenf.	<i>Grammatophora</i> spp.
„ <i>fragillima</i> Bergon.	<i>Lycmophora</i> spp.
„ <i>Stolterfothii</i> H. Pérag.	<i>Navicula</i> spp.
„ <i>robusta</i> Norman.	<i>Gyrosigma</i> spp.
„ <i>Shrubsolei</i> Cleve.	<i>Bacillaria paradoxa</i> Gmel.,
„ <i>setigera</i> Brightw.	„ Van Heurck.
„ <i>styliiformis</i> Brightw.	<i>Nitzschia closterium</i> (Ehr.).
„ <i>hebetata semispina</i>	„ <i>seriata</i> Cleve.
(Hensen).	<i>Nitzschia</i> spp.
<i>Chaetoceros</i> spp.	<i>Surirella</i> spp.

which will compare directly with those obtained by tow-nets, whilst other aspects of the work suggest that the methods may also yield important estimates of the varying production which cannot so easily be obtained by other methods. Further

we may say, as was said of the plankton indicator (Hardy, Henderson, Lucas and Fraser, 1936), that if it is possible by these methods to obtain useful correlations, these correlations and their applications will hold good in spite of any disadvantages due to the method. We hope to be able to show that the advantages of this type of survey are likely to outweigh the disadvantages.

It will be advisable to indicate in further detail the types of error which may arise by the use of the recorder method. It is clear that forms smaller than the mesh of the silk (*i. e.* most phytoplanktonts) will be lost to some extent. On the other hand, we find that the recorder does in fact collect from time to time most of the forms found in this area; the list of diatom species appearing in Table I will show how representative the collections are qualitatively. There seems little doubt that the smaller forms are only caught if present in fairly large numbers, when they adhere to the silk; they may also be caught because of the presence of numbers of another form which are effectively reducing the size of the mesh. Again, whilst it is not surprising that the larger forms may be caught in numbers sufficient to clog the silk and to colour it green, it is a fact also that the smaller ones may do this at times, even in relatively pure communities. From these considerations it follows that the presence of small numbers of many of the forms must be regarded only as evidence of their presence with its obvious but limited value, the greater numbers being regarded as evidence of patches of importance. We must realize also that when clogging has occurred—as in all collections obtained by means of nets—the numbers caught must be minimal; in other words the filtration will be more or less reduced.

Two other points remain to be considered regarding the position of the samples in space. These are (1) for the period dealt with here the limitation of the series of samples to relatively widely separated and divergent lines through a large area, and (2) the limitation of the samples to a fixed depth. Although the machine is a continuous recorder, it can only record along *lines* through the sea, and for reasons of economy these lines must be fairly widely spaced. This, whilst a necessity in the earlier stages of the work, is not a defect inherent in the method, and elsewhere an attempt will be made to show in the present work the relationship between the different lines, and how in the future more intensive recording can overcome the difficulties of discontinuity. The chief problem arises in the matter of tracing the identity of patches as they move along the lines from one record to the next, and also from one line to another. Whilst in many instances the configuration of the patch is helpful, further help can be obtained from consideration of the general constitution of the local phytoplankton complex. We are also exploring the problem of identity from the point of view of cell size taken by Wimpenny (1936) for the species of *Rhizosolenia*.

The limitation of sampling to one depth is more serious in the opinion of the writer, and can in the end only be answered satisfactorily by comparison of our findings with those obtained by other methods in an area at the same time. In the early stages of the work where economy has been essential, it must be remembered

that we have had to adopt a compromise in order to collect organisms of various habits with one machine at one time, and the depth of 10 metres was chosen for this purpose. This is obviously not the most suitable depth for all the forms which have been collected, and the various defects will be discussed in the appropriate sections. Reference to 'Bulletin' No. 1 (p. 50) will show that a new device is being considered which may to some extent solve the difficulty by fishing throughout a vertical plane of water; it will also be clear that if funds were available it could be solved by the use of more machines at the same time, or at very short intervals.

TABLE II.—Comparing Horizontal Hauls between 5 and 25 metres with Vertical Hauls at the Same Station (from Savage and Wimpenny, 1936). Values are given in units of one thousand cells. Figures in heavy type are for stations between 5 and 15 metres. The indices denote the number of samples when greater than one.

<i>R. styliformis</i>		<i>B. sinensis.</i>	
Horizontal net.	Vertical net.	Horizontal net.	Vertical net.
0 <sup>2</sup>	0	0 <sup>3</sup>	0
<b>0<sup>3</sup></b>	<b>0</b>	<b>0<sup>2</sup></b>	<b>0</b>
100	12	4	1
108	33	45	8
196	17	<b>76</b>	<b>0</b>
<b>300</b>	<b>26</b>	<b>215</b>	<b>8</b>
1550	102	1449	267
<b>8512</b>	<b>159</b>	1623	131
<b>17,850</b>	<b>420</b>	<b>4,830</b>	<b>352</b>
22,300	1,091	<b>6,000</b>	<b>137</b>
<b>26,324</b>	<b>420</b>	<b>10,950</b>	<b>376</b>
<b>27,000</b>	<b>796</b>	<b>42,300</b>	<b>1,417</b>
33,600	1,377	44,200	1,938

With regard to the phytoplankton, however, it will be realized that the depth of 10 metres is a significant one, being through a zone of active photosynthesis under normal conditions in the area. We may also consider that in the North Sea (and particularly in the Southern Bight), owing to the relatively shallow depth of water and the generally turbulent conditions, the distribution of the phytoplankton is less likely to vary markedly from layer to layer as it is in deep waters. Evidence on this point is to be found in the work of Savage and Wimpenny (1936) in this region during the years 1933–34. On pp. 52–59 (*loc. cit.*) they show graphs of the vertical distribution of the phytoplankton at different stations in a number of cruises, and it is evident that while the distribution may vary from time to time



(the densest zone may be in mid-water, at the surface or at the bottom), yet, in general, a record taken at a depth of 10 metres would on any one cruise have

TABLE III.—Comparing Mid-water Horizontal Hauls with the Means of Surface, Mid-water and Bottom Hauls at the Same Stations (from Savage and Wimpenny, 1936.) Values are given in units of one thousand cells. Figures in heavy type are for stations between 5 and 15 metres. The indices denote the number of samples when greater than one.

<i>R. styliformis.</i>		<i>B. sinensis.</i>	
Horizontal net.	Mean S.M.B.	Horizontal net.	Mean S.M.B.
0 <sup>24</sup>	0	0 <sup>3</sup>	0
<b>0<sup>9</sup></b>	<b>0</b>	<b>0<sup>2</sup></b>	<b>0</b>
0 <sup>2</sup>	+ to 1	0 <sup>5</sup>	+ to 1
<b>0<sup>4</sup></b>	<b>1 to 5</b>	+ to 7 <sup>12</sup>	+ to 7
+ to 6	+ to 3	<b>1 to 10<sup>7</sup></b>	<b>0 to 31</b>
+ to <b>10</b>	<b>1 to 31</b>	16 to 39 <sup>5</sup>	8 to 54
<b>30</b>	<b>20</b>	<b>10 to 38<sup>6</sup></b>	<b>13 to 34</b>
71	72	52 to 98 <sup>4</sup>	30 to 183
74	61	<b>75<sup>2</sup></b>	<b>100 to 170</b>
<b>74</b>	<b>64</b>	<b>105</b>	<b>101</b>
<b>105</b>	<b>67</b>	<b>107</b>	<b>74</b>
<b>413</b>	<b>198</b>	113	50
4,650	2,637	<b>150</b>	<b>164</b>
5,250	7,650	<b>189</b>	<b>242</b>
5,850	3,570	263	113
<b>6,075</b>	<b>9,975</b>	<b>267</b>	<b>90</b>
6,083	3,694	<b>375</b>	<b>208</b>
8,025	5,933	375	184
<b>12,750</b>	<b>9,967</b>	<b>450</b>	<b>165</b>
<b>14,250</b>	<b>8,058</b>	<b>600</b>	<b>555</b>
		<b>675</b>	<b>343</b>
		<b>720</b>	<b>845</b>
		725	1,599
		812	2,769
		1,260	2,113
		<b>1,590</b>	<b>606</b>
		<b>1,725</b>	<b>1,367</b>

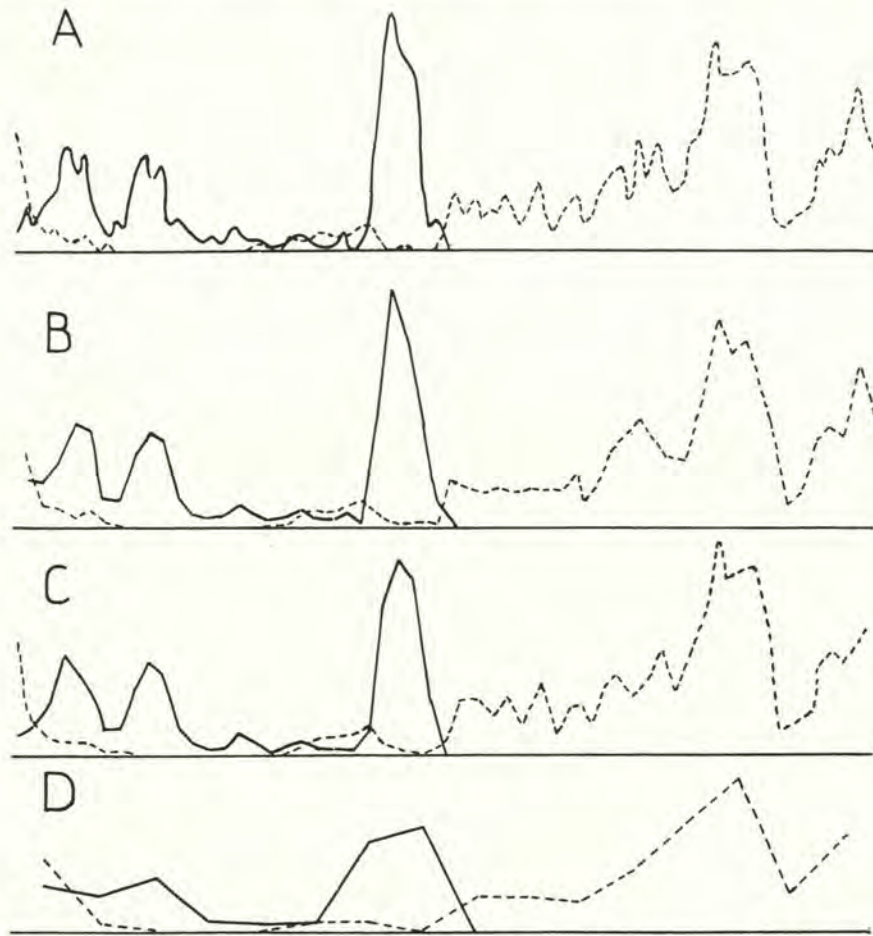
provided an adequate measure, for comparative purposes, of the production over the whole depth. Reference also to the paper by Savage and Hardy (1935) show comparable results for the same organisms and also for the flagellate *Phaeocystis*.

We can investigate this relationship in more detail by consideration of the actual findings of the numbers of *R. styliformis* and *B. sinensis* taken in mid-water horizontal hauls, and also in vertical hauls at the same stations (Savage and Wimpenny, 1936: tables xvi to xxxviii). In our Table II we have compared 16 mid-water hauls between 5 and 25 metres with the corresponding vertical ones.<sup>1</sup> Whilst there is not a perfect agreement in proportion between these pairs of figures—we could hardly expect it—yet the corresponding members of any pair are found to be of the same order in proportion to the other members of the pairs, suggesting that on a survey by means of horizontal hauls at these levels, the resulting idea of the distribution would have been similar to one obtained by means of vertical ones. There is further evidence to the same end, since Savage and Wimpenny's data also enable us to compare some 60 midwater horizontal hauls which were between 5 and 25 metres with the means of the series of surface, midwater and bottom hauls made together. This is shown in Table III and a similar degree of proportionality is shown, since the 5–25-metre hauls are clearly of the same order as the means of the three hauls and never are there any serious divergencies. It would seem reasonable that we should assume that the 5–25-metre hauls are fairly comparable with those samples obtained with the recorder, but an even closer approximation can be found from the figures in heavier type in these two tables, these being limited to hauls between 5 and 15 metres. The only differences in the proportions between these comparable hauls are no larger than the differences found by other workers when collecting pairs of samples simultaneously under as far as possible identical conditions (*e. g.* Herdman, 1923). The latter differences may be very large, and whilst due partly to defects in the methods of collection, they arise probably in extreme patchiness over small areas in the sea. They are undoubtedly larger than the errors from random sampling which are common to most methods of plankton analysis, and to which it is probable that many of the divergencies in Tables II and III may be due. For these various reasons, then, we feel justified in thinking that we are likely with horizontal hauls at 10 metres to be able to survey the phytoplankton with results comparable with those obtained by means of the orthodox vertical nets. The fact that phytoplankton taken appreciably below this level is more likely to be moribund than actively photosynthetic should add to the realism of the results, and the ability to make the samples in a continuous series should yet further increase their value.

Such findings tend to increase confidence in the recorder as a sampling instrument, but in many ways the final and most important test lies in checking the findings of one method against those of another which has other peculiar advantages and disadvantages—in this instance, sampling by means of vertical hauls with conical nets. We are able to do this within certain limits, by comparison of our records with the distribution of phytoplankton sampled by the Ministry of Fisheries' Research Ships *George Bligh* and *Onaway* at similar times and over a neighbouring

<sup>1</sup> In the course of abstracting from the original tables some slight alterations have been made, such as to provide standardized times (10-minute hauls for Table I and 5-minute hauls for Table II).

divergencies, thus emphasizing the "patchiness" which occurred at that time. Similar results would have been obtained by the use of a tow-net at (in this case) 16-mile intervals. The series of graphs shows that by starting at different points very different ideas would be obtained of the distribution of *Rhizosolenia* over a distance of 100 miles, and some would be quite erroneous.



TEXT-FIG. 1.—Graphs of *Rhizosolenia styliformis* (continuous line) and *Biddulphia sinensis* (broken line) recorded for the Bremen line on 2nd October, 1935: A, by plotting values for every section; B, by plotting values for every alternate section, i.e. 1st, 3rd, etc.; C, also for every alternate section, but 2nd, 4th, etc.; and D, the whole data arranged in units of ca. 10 miles each.

Along with the original detailed record in Text-fig. 1 (A) two other treatments have been adopted. In the first (graphs B and C) the two alternative groups of first, third, fifth, etc., and second, fourth, sixth, etc., sections have been plotted to show that by the omission of alternate sections there would in general be little loss of detail (see p. 75). In the second method (graph D) the whole data has been averaged in blocks of about 10 miles, and it is clear that here the only disadvantage

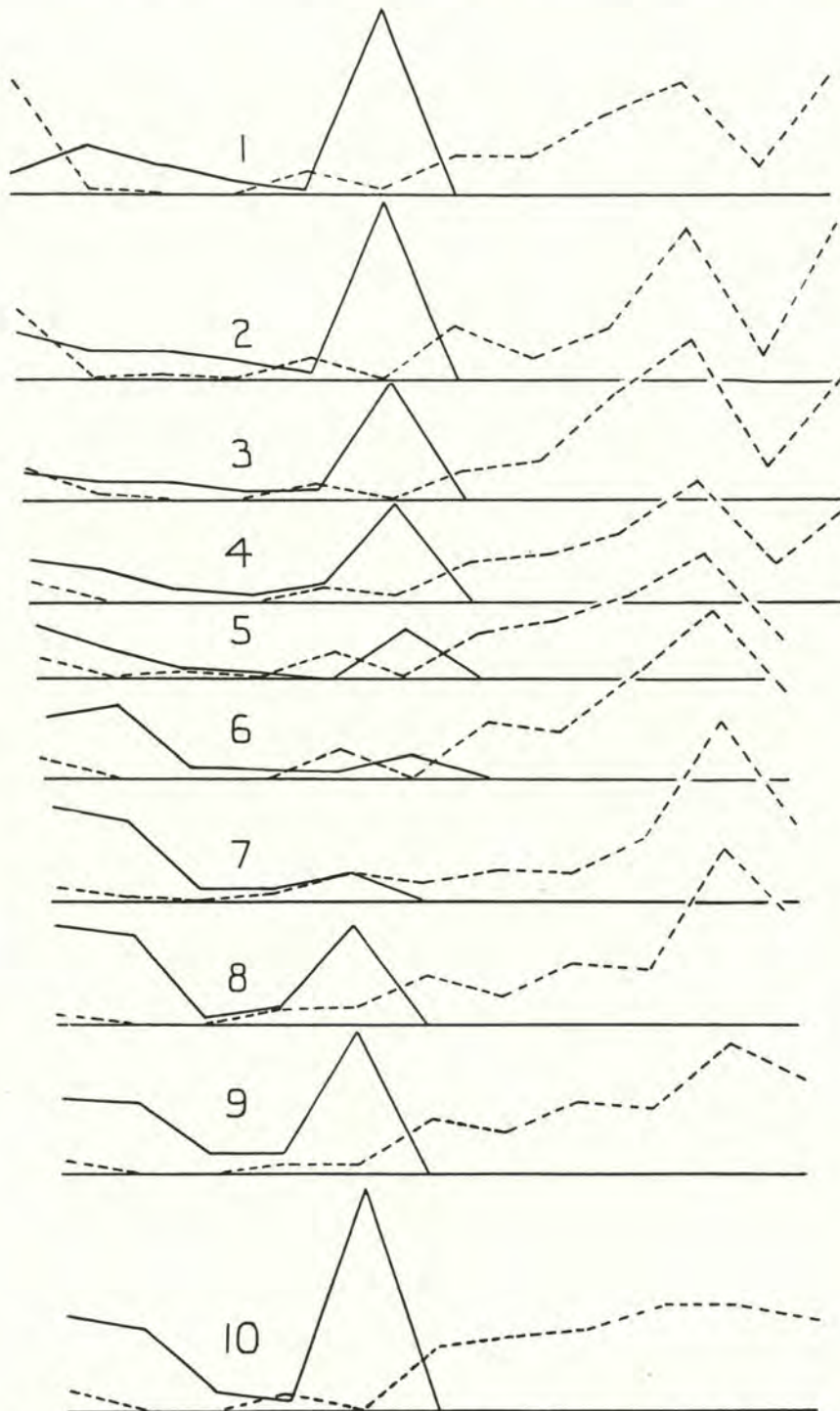
area. The limits to such checking are very definite unless deliberate tests are arranged (which so far has not been possible), and seldom have we had samples at the same time and place as those of the Ministry's ships, so that, in order to provide a reasonable number of comparisons, we have in some cases to consider data separated by as much as 14 days,<sup>1</sup> and including stations some miles distant from the recorder line. An idea of the relationship between results obtained by this method and during the usual plankton surveys can be obtained by comparison of our figures with those of Savage and Hardy (1935) and Savage and Wimpenny (1936), but it will be profitable to discuss one or two examples in more detail.

From a qualitative point of view the correspondence is very good, and rarely do the methods disagree in recording the presence or absence of either *B. sinensis* or *R. styliformis*, but whilst most of the comparisons from a quantitative point of view are proportionate, here and there are striking disagreements, particular examples occurring in November, 1933, and the period 22nd–29th October, 1935.<sup>2</sup> Of these the first may well be due to the large discrepancy in date (over ten days), but the second figure shows that towards the eastern end of the line when the recorder was collecting very little *Rhizosolenia*, within a reasonably short time a very large sample was obtained by means of vertical nets in almost exactly the same place. The result is that the recorder finding would undoubtedly suggest this diatom to be very scarce at the eastern side, while the more orthodox method (admittedly on the evidence of one station) leaves us with the impression that it is certainly not scarce, and possibly abundant.

In the final discussion some aspects of the patchiness of the phytoplankton are considered. Hardy (1936*b*) has already shown examples of the type of patchiness which the method of continuous recording has revealed, and the present survey shows more fully that whilst at times the phytoplankton may be fairly smoothly distributed, at other times there may be a very pronounced patchiness. Amongst many others, the Bremen line record for the 2nd October, 1935, is a good example, see Text-fig. 1 (A); the recorded distribution shows the bulk of the *B. sinensis* to be in the east, as *Rhizosolenia* is in the west, but the latter has a very striking patch near the middle of the record, and the former had a small but dense zone towards the western end. In Text-fig. 2 this graph has been analysed and treated in different ways. In the first derived graph the values for every tenth section have been plotted, and it is clear that by omitting some of the analyses in a regular manner it is possible to miss some of the essential features of the record. In the subsequent graphs the other nine sets of tenth sections are shown and, as might be expected, the results vary considerably. Some provide graphs differing little in essence from the complete one, but most of them show more or less serious

<sup>1</sup> Reference to Text fig. 17 will give some idea of how large a difference may be found in the distribution of the phytoplankton at 10 metres within a few days. The results of Savage and Wimpenny show similar changes within a short period of time.

<sup>2</sup> We should like to take this opportunity of thanking Mr. R. E. Savage and Mr. R. S. Wimpenny, of the Ministry of Agriculture and Fisheries, for their kindness in allowing us to see in advance some of their unpublished data for the distribution of *R. styliformis* and *B. sinensis* since 1934.



TEXT-FIG. 2.—The same record as in Text-fig. 1 (*R. styloformis* continuous line and *B. sinensis* broken line), but shown by plotting the values for every tenth section. The series of graphs 1 to 10 shows the differences obtained by starting to plot at the 1st, 2nd, 3rd . . . or 10th sections respectively.

is that due to the decrease in definition arising from the necessary "smoothing" (see also p. 90). It is impossible to treat this subject here in further detail, but the general findings have convinced us that when, in the extended survey, it became necessary to decrease the work of analysis, we should be justified in adopting a modification of this method, providing automatic "smoothing" by altering the mile per section ratio to one of 5 miles per section, and arranging the analyses to give estimates for blocks of 10 miles, or approximately two sections. The subject will be discussed more fully by Mr. Rae in 'Bulletin' No. 4.

It seems very probable that patchiness of this nature is partly the cause of such marked discrepancies as have been found between recorder findings and more usual methods. Marked patchiness may be found fairly frequently according to the recorder analyses (see p. 154), and it may be that the disagreement quoted above for the period 22nd-29th October, 1935, was due to the fact that the tow-net sample was taken in the middle of a small patch which had either moved off the line of the recorder in the fairly short period separating the two observations, or that at the very time that the line was sampled by the recorder there was nearby a dense patch which happened to be sampled by the other method.<sup>1</sup> From this it will be evident that here is implied a criticism of both methods. Many of the stations worked in the normal manner by means of a tow-net from a research ship are more than 25 miles apart, and it is clear that under such conditions significant patches may be missed and a false idea of the general distribution may be obtained; similarly the importance of a small patch may be exaggerated. On the other hand, whilst *along the line of the record* the recorder method gives a continuous sampling and so omits no patches, yet it may in a similar manner miss patches which are quite close to the line and similarly give a false impression. The results so far suggest that for some time the two methods must be regarded as complementary. We feel that the recorder surveys have opened up a new field of research by very speedy and economical methods, but it is clear that very much more value can be obtained from its findings when worked in conjunction with the older methods.

#### THE SIGNIFICANCE OF THE DATA.

We have felt it necessary to describe at some length the various disadvantages of this new method of research in order that a full realization of its limitations should be available from the beginning. Some of these may prove to be unavoidable in this type of work, whilst others have arisen as a result of the difficulties inherent in the earlier stages of a large scale survey when somewhat broad methods

<sup>1</sup> Further evidence on this point is, in fact, provided by the recorder material. Some days before the record referred to a dense but narrow patch appeared in this region (*cf.* the data for Text-fig. 1); this was apparently off the line when the next record was taken, presumably having moved a little, although it might well have been sampled within a very short distance from the recorder line. In the continuous series of records (see Text-figs. 3 and 4) this type of change often occurs and in practice our experience shows how extremely dangerous it may be to consider isolated samples, the actual on the contrary, being only appreciated as a dynamic condition.

had to be adopted. A few of these problems were overcome during the interim period 1936-37, and since the beginning of the extended survey of the whole of the North Sea, we have been able to overcome more of them. Throughout the work we are trying to bear in mind the limitations imposed by the method, and to present the data only in a form which is fully justified.

We shall consider here only the more precise data for *R. styliformis*, *B. sinensis*, the Dinoflagellates and Phaeocystis. The remarks will apply even more obviously to the other forms which will be more summarily presented, although in the future we hope to be able to present some of these forms with similar precision. All graphs are based upon the figures as actually found during analysis, and no attempt has been made to smooth out any irregularities in the curves (apart from the smoothing involved by the mechanical action of the machine, see 'Bulletin' No. 1, p. 36). It will be seen that most of the graphs are rather irregular and it is important to realize the significance of these irregularities—a feature which has been discussed from another point of view on p. 155. As is well known, the process of sub-sampling by any method during the process of analysis introduces a random error into the estimations. This is involved in the recorder work as a result of counting only random portions of the plankton on each section. In addition it is also well known that the distribution of the plankton in the sea may be such that even over a small area it is difficult to obtain samples of exactly similar constitution (amongst others, Herdman (1924) took samples from tow-nets towed from each quarter of the ship and obtained differences of a fairly high order between them). For these two reasons alone it is evident that we should not lay great stress on the smaller fluctuations in the graphs, some of which may undoubtedly be due to random errors of this sort and which together, there is reason to believe, may amount to as much as  $\pm 50\%$  of the true value. It is clear that only the larger fluctuations should be regarded as truly significant—perhaps we may include safely all those which show between consecutive sections differences of the order of  $\times 3$  and upwards. Yet this is not to say that smaller variations do not occur between the larger scale patchiness which is amply demonstrated by the recorder method (see p. 156 and Hardy, 1936*b*) and the very small spatial variations suggested by Herdman. We have good reason to believe that there will be significant patchiness over small distances of (say)  $\frac{1}{10}$ -1 mile, and it would be of interest to investigate these at some time by means of a recorder working with a very small mile per division ratio—say 20 divisions to 1 mile.

Again, on p. 79 we have referred to another aspect of the material. Samples will tend to be mainly minimal for the reasons discussed there, the smaller numbers of most organisms being necessarily low as the result of losses due to the size of the mesh, whilst the largest numbers may also be low from the effects of clogging. It is probable that at least in part the discrepancy in order between our findings and those of Savage and Wimpenny (1936) may have arisen in this way, and it should be realized that most of the denser patches should probably be denser still, and further, because of this, that the extent of the patches (spatially) may be

exaggerated—*i. e.* that patchiness may be even more pronounced than appears here (see also p. 156).

One thing remains which does not concern the peculiarities of this method. On p. 77 the point is made that the results from this or any other survey can only present an estimate of the "residual population" at any time—*i. e.* that "nett population" which remains from time to time after the effects of death from feeding of herbivores (or any other means) have occurred. This nett value should not be confused with the total production of any form or for any area, since this cannot directly be estimated by this method. Nor will the nett value necessarily give a *measure* of the total production or even the amount of food available for herbivores, as a simple hypothetical example should make clear. If we consider any form whose maximum rate of division is once per day, and minimum is once per 10 days (this should not be too extreme for some types of phytoplankton in different seasons), then although we might on sampling the water find an approximately similar quantity of the form throughout the year (the "nett" value), this clearly could not indicate a constant production since this might have varied markedly, yet, on the other hand, it would give no evidence regarding the amount of food which had been consumed, since we know from the hypothesis that this has varied from a yield of one unit per day per unit of catch to one unit in only ten days at different parts of the year. Certainly an example is not likely to arise in such a simplified form, but the possibilities of which this is an extreme case are such that we should be very wary of making deductions from the net stock regarding gross production, or of comparing productions at different times and in different areas; we need to know much more about the life of the phytoplankton themselves *and* of the biology of the forms which form their organic environment in the community. These matters are perhaps generally realized, but it seems seldom that they are made sufficiently clear.

Bearing these factors in mind we may say that the graphs which are shown in the following pages represent broad estimates of the minimal values of the "nett" residual stock of various forms from time to time along "lines" at 10-metre depth through the sea. It seems probable that only differences of the order of  $\times 3$  and upwards should be regarded as truly significant, although the whole series of samples should always be considered as a check on this. In considering them it must be realized that movements as well as growth processes can appreciably affect the distribution on any one line.

#### THE ARRANGEMENT OF THE DATA.

Whilst from one point of view the amount of plankton collected by the recorder is small, the method allows of the collection of enormous numbers of samples. In the period 1932–35 we have some 15,000 samples, each the equivalent (apart from bulk) of a horizontal net haul for a distance of  $1\frac{1}{2}$  to 2 miles, and in the last two years some 2000 10-mile samples, a total of some 45,000 miles recorded. These



have been taken over a small area at fairly regular intervals throughout  $5\frac{1}{2}$  years. The mere presentation of such data is a formidable task, and it might be done in several ways. It is necessary for economy to abbreviate this space as much as possible, and for this reason the data has been arranged mainly in a graphical manner, the text being reduced to notes emphasizing the more important and significant features of the graphs—points which will be referred to in later sections and papers—and the only tabular material consisting of abstractions from the primary data. There still remain two chief ways of grouping the material depending on the selection of routes or organisms as the basis of the arrangement. There are good reasons for the adoption of either of these, but on the whole it seems fitting to compromise and to discuss the data regarding each organism in turn, considering under these heads each of the lines, and subsequently attempting to relate them as a whole.

In an earlier section, discussing the relative validity of the material, we have found it advisable to divide this into two groups—the first to be dealt with in greater detail (*R. styliformis*, *B. sinensis*, total Dinoflagellates, *C. fusus*, etc., and Phaeocystis), and the remaining forms to be dismissed more briefly and according to the precision of the analyses. For the first group, of which the bulk of this paper will consist, the distribution of each form will be shown month by month by means of graphs, first on the Bremen Line, and then on the others in turn (the Bremen Line has provided the greater number of records, and so forms a basis to which the other data can be related, and it is suitably in the centre of the area), and then the results will be discussed for the whole area by reference to serial maps. In the third section of the paper various points arising from these data will be dealt with briefly, detailed discussion being deferred to later papers (by various members of the staff), in which different aspects of the  $5\frac{1}{2}$  years' results can be considered not only in relation to the phytoplankton, but in relation to the rest of the plankton and to specific marine problems. Whilst there are certain advantages in producing, as here, the results for several years in one paper, there are also disadvantages, the greatest of which concerns the delay in making known the data to other workers. Until now this has been unavoidable for a number of reasons, but from 1938 onwards we hope to be able to produce the data for each year as early as possible in the following year, and then, as the occasion provides, to produce general papers in which the various matters can be co-ordinated.

The graphs which have been used in presenting the data require some explanation, and since most of them will be arranged in a standard manner, much repetition may be avoided by outlining briefly here the methods which have been used. There are four main types for each organism of importance (*i. e.* of Group 1 above) on each line.

#### 1. *Annual Route-distributions*: Plates I to XXI.

Each line (Bremen, Copenhagen, etc.) has been designed to run normally between two termini (usually light-vessels); occasionally a record may be short,

owing to weather conditions or mechanical troubles (see List in 'Bulletin' No. 2), and sometimes they may be longer (in 1937 two of the routes, the Bremen and the Copenhagen, were deliberately extended), but in all records positions have been referred to these points as accurately as certain small limitations (outlined in 'Bulletin' No. 1) will allow. The numbers of each form per unit of distance have been graphed. In the first type of figure these graphs are arranged one above the other through each year according to the time-gaps between consecutive records. Thus we have in this arrangement an ordinate which can represent at the same time (*a*) a terminus for the line, (*b*) the passage of time, and (*c*) the quantity of plankton, whilst the abscissa represents distance from the termini. The data for each year have then been arranged consecutively, so that those for corresponding periods in different years may be compared as easily as possible. These graphs will form the basis for the description of the essential variations in position and of quantity of each form.

Whilst there have from time to time been changes in the aperture of the recorder (see 'Bulletin' No. 1, p. 43) and in the mile per section ratio, these figures are so arranged that the graphs shall be as nearly comparable as is possible. For 1932-35 the original analyses provided estimates of organisms per section, and from them could be obtained graphs showing numbers per section at intervals represented by the mile-per-section ratio. These cannot be exactly comparable *inter se*, but (see p. 74) the deviation from the average ratio (1.7 miles per section) rarely exceeds 10%, and this is insignificant compared with the much greater differences in quantity which have been found. The data for 1936-37, on the other hand, was analysed to provide immediately organisms per mile per 10-mile block; they are, of course, quite comparable *inter se*, and from now on this method will be adopted (see p. 86). By the simple process of modifying the scale for the 1932-35 data it is possible to make the whole sufficiently comparable for our purpose, so that within the limits specified all the graphs show approximately the numbers of organisms per mile, but whereas the earlier ones give observations for intervals usually less than 2 miles, all those for 1936-37 are automatically smoothed to provide 10-mile samples.

## 2. *Serial Charts*: Plates XXII to LXIV.

In order to co-ordinate the whole available data for each month, an alternative presentation has been adopted in which graphs obtained in the manner just described are traced on to charts of the area. It has not always been possible to show every record when more than one has been available on any line in one month and so representative ones have been chosen (*i. e.* those most nearly similar in date), and where it has been considered necessary, additional records are inserted on extra charts for comparison; elsewhere reference should be made to the graphs of Type 1. The charts are usually arranged so that six, representing half a year, appear on one page; the results for a whole year can be seen conveniently, and by

turning consecutive pages the different years can be compared. The maps will be used to form the basis of discussions of the phytoplankton as a whole, in relating our findings to other work in the area, and in relation to possible movements involved in the temporal changes in position. For reasons of economy and for comparison, two forms have been shown together on each set of maps.

After the introduction of the extension to the C-line and the new Esbjerg line in 1936-37, it was necessary to use a rather larger map. This has modified the arrangement a little and in the autumn of 1937 we have only been able to include three maps to the page.

It will be realized that in the graphs of Type 1 from which the charts have been derived the mileage scales have been similar throughout, whereas on the charts the mileage scale should normally be a varying one (the charts have been derived from Admiralty Chart No. 2339). Consequently the base-lines need to be distorted, or else some slight inaccuracy in the positions is involved in retaining a standard base-line. In this work it has been more convenient to have the base-lines strictly comparable, and since the errors have been usually very slight (particularly so considering the extensive reduction in reproduction), this method has been adopted.

### 3. *Annual Variations, e. g. Text-fig. 5.*

For each of the graphs of Type 1 it is possible to obtain a series of "totals" for the quantities of phytoplankton found on each of the series of records. It will be realized that the quantities so found cannot be anything other than minimal for reasons which have been discussed on p. 79, and they are best defined as those quantities found from the beginning to the end of a record at a given time. On the other hand, for each form the factors affecting the quantity will be similar, within certain limits, from time to time, and it is felt that the sums so obtained provide at least some measure of the quantities in the sea. Whilst a quantity, "a", which is (say) three times as great as another, "b", may not represent exactly a ratio in the sea of 3 : 1, yet we should be reasonably sure that the flora giving rise to the sample "a" was larger than that producing "b", and that a similar ratio of quantities on another occasion might represent similar ratios in the sea. The larger changes in these quantities which are found to occur are, moreover, of such an order that their significance is the greater for this reason. It is essential to realize that these are merely *changes* occurring over the line, and may arise from the processes of growth, death and physical movement.

Throughout the survey the totals used will only represent the quantities found between the termini which were in use at the beginning; the extensions to certain lines in 1937 have been excluded so that the figures shall be as strictly comparable as possible. There are, however, a number of short records for which totals clearly may be low, but which may have some value. Unless they should produce higher values than their neighbours, records of less than half of a line

have been omitted, and where more than 20% has been unrecorded the fact is indicated, and less reliance should be placed on such totals.

The resultant totals have been plotted against time to show annual variations in the records and variations between the different years. At times the quantities may be very greatly in excess of totals at other times when patches are small although, within their season, important, and for this reason two scales have been used to denote quantity: (a) the "normal" scale, covering the whole range and rising from the "true" base-line of the graph, and (b) a tenfold scale below the true base-line within which it is possible to see the variations due to small but possibly significant changes taking place when the form is not abundant. The general annual cycle should always be considered by reference above the true base, since the detailed changes taking place below this line are such that, on the normal scale, they would not be visible above it.

#### 4. *Maximal Quantities, e. g.* Text-fig. 6.

A further set of charts has been used to show the largest quantities of the various forms which have been found on any part of the line during each year and during the whole period of the survey. Over a long period they should provide a set of standards for comparison of conditions from time to time, and may also be used to show clearly the areas in which the various organisms are found to live.

Other graphs and data will be derived from the foregoing and will be described where necessary, as also will specific modifications of the general methods outlined above.

It remains to describe the scales denoting the numbers of organisms. For *Phaeocystis* and the total Dinoflagellates a simple linear scale has been used, but for the diatoms and individual species of the Dinoflagellates it has been more convenient to use a variable scale, which shall at once indicate the thin patches, which are relatively significant on occasions, and yet provide suitable limits to the heights of the graphs (see plates and figures for examples). For these forms the same type of scale has been used throughout.

#### THE DISTRIBUTION OF *Rhizosolenia styliformis* BRIGHTW.

The distribution will first be considered briefly on each route, as illustrated in the series of graphs of the quantities of this diatom recorded month by month and in each year. This series enables one to compare more easily the seasonal variations throughout the whole period. Then, by means of the monthly maps an attempt can be made to relate the records from the different lines, so that the general character of the annual distributions can be summarized. A description of the arrangement of these charts has just been given.

*The Bremen Line.*

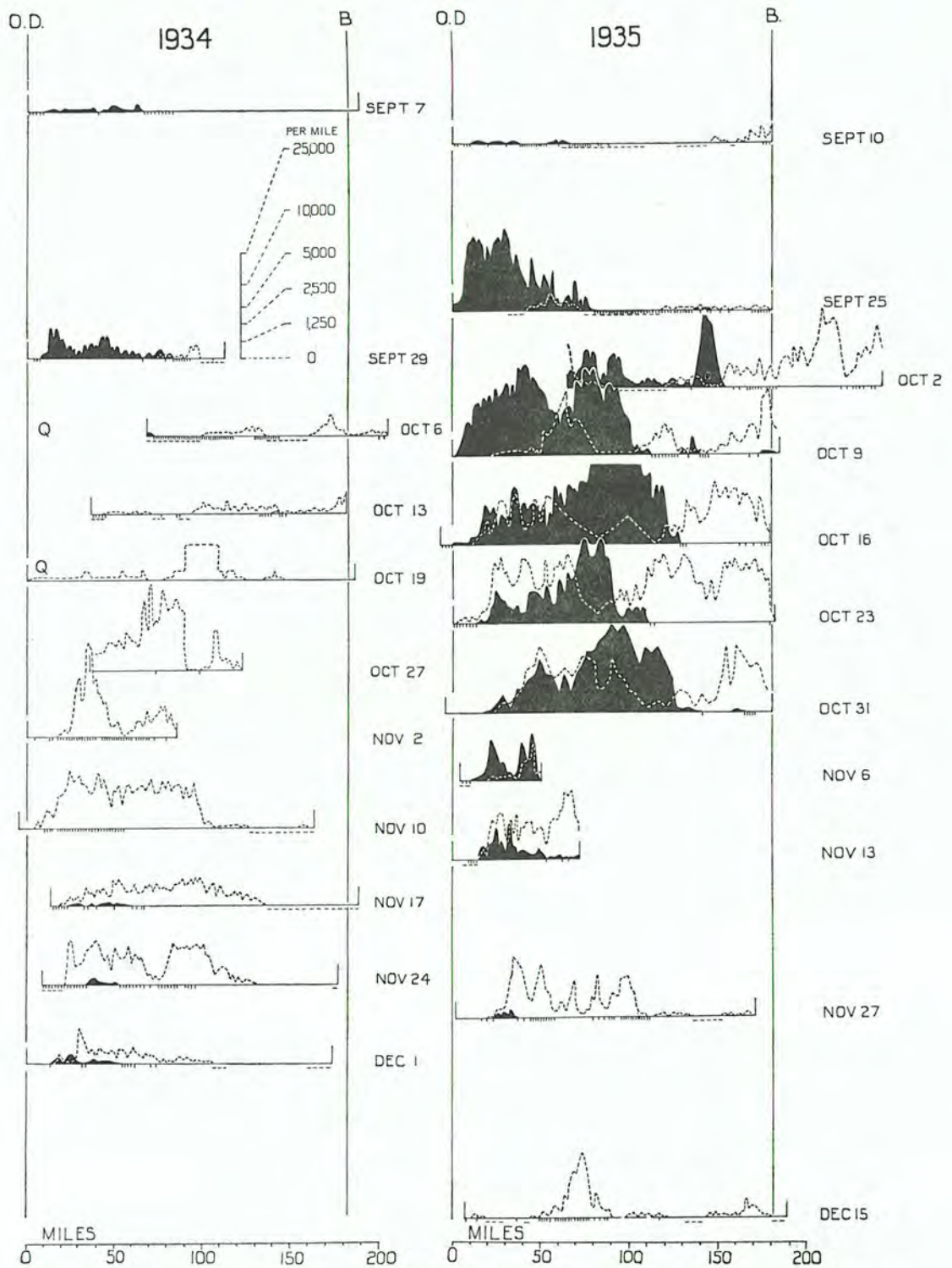
Representative monthly records for the period June, 1932, to December, 1937, have been arranged in Plates I and II, never more than two being shown for any month in order to prevent undue confusion of superimposed graphs. In the autumns of 1934-37 a more intensive programme was carried out, the records being shown graphically in Text-figs. 3 and 4 against an increased time scale. In both figures and plates the larger numbers of the diatom, forming well-marked concentrations, appear as blacked-in graphs above the line, whilst the smaller quantities, termed "traces", have been shown as small vertical strokes below the line. In the series of more detailed autumnal records (Text-figs. 3 and 4) it has been more convenient to combine the results with those for *B. sinensis*, the latter appearing as the broken-line graph and the traces being represented by horizontal strokes. Asterisks have been used to denote that the diatom was not seen during the silk-analysis. Occasionally (see List in 'Bulletin' No. 2) a record has been obtained which, although not as reliable as the others, has yet been thought to be of useful qualitative value; such records have been indicated by the symbol "Q".

Only the main features will receive comment here; others will be referred to later, and in future papers considering the results in relation to other factors.

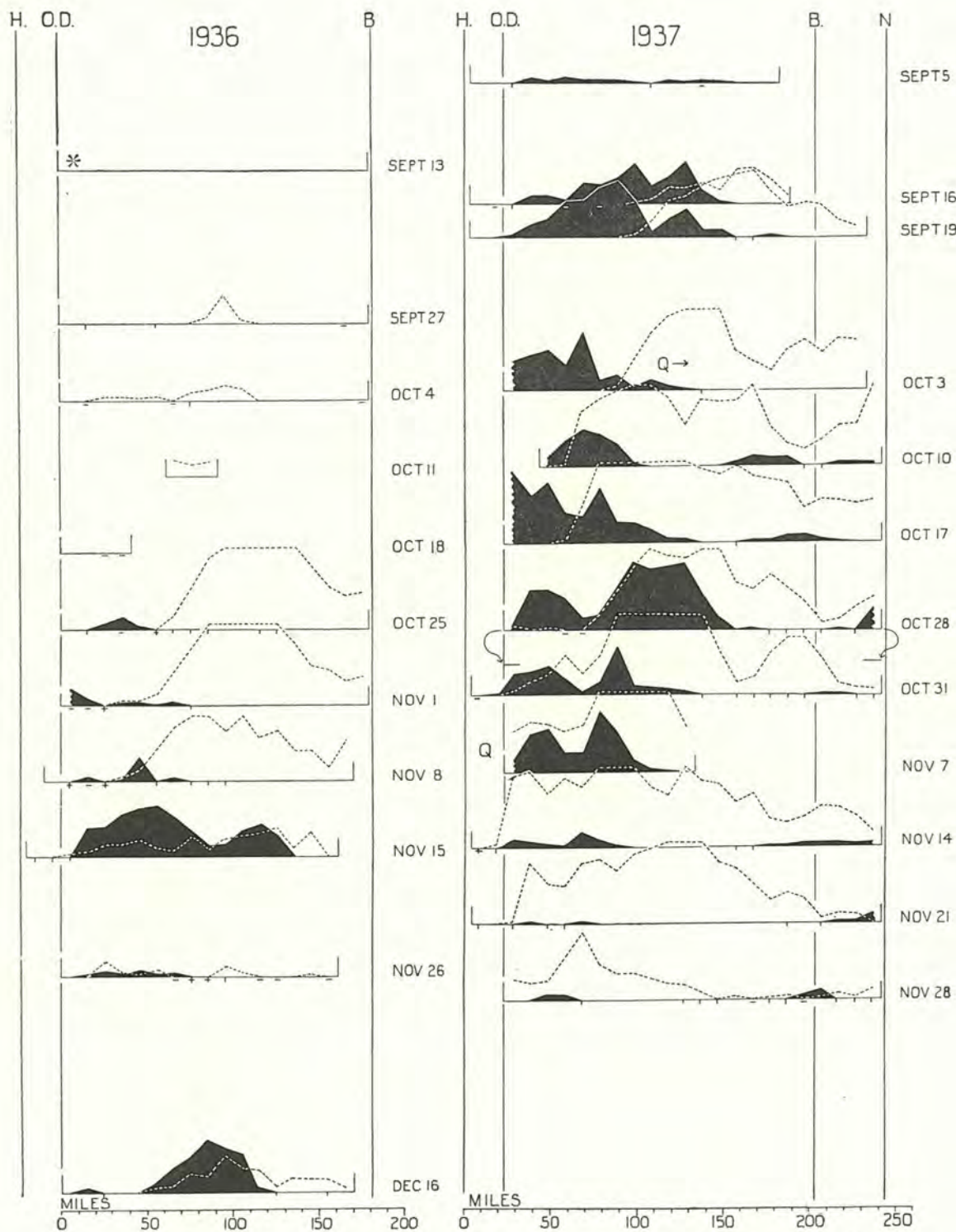
It is seen that the production is characterized by marked periodicity; patches are rarely observed in the months before August, but reach a maximum in September, October or November, and are normally small or absent in December. Within the main cycles there are annual variations. Whilst *Rhizosolenia* is generally scarce from January to June, in 1935 a patch occurred in early May, only to disappear again, except for traces, at the end of the month. More typically small patches have appeared in June and July, some disappearing before the onset of the autumn production, but others appearing to be connected with it.

The more significant differences have concerned the time of appearance, the duration and density of the autumnal concentrations, which have been considered to be so important in relation to the East Anglian herring fishery (Savage and Hardy, 1935, and Savage and Wimpenny, 1936). These are shown in some detail in the series of records in Text-figs. 3 and 4 for the years 1934-37, but for 1932 and 1933, when only monthly records were aimed at (and not always achieved), our knowledge is poorer. The lack of weekly records in these years has been unfortunate, and we realize that patches may have been missed as they passed across this route during the intervening periods, as the findings of Savage and Wimpenny (1936) suggest for 1933. Although the collection of weekly samples over a large area for very long periods is not likely to be feasible, we must realize that extensive changes may occur within one month; hence the necessity of recording at short intervals for certain purposes, which process should become less necessary as the number of recording lines can be increased.

Whilst in some years the general trend has led up to a maximum on this line

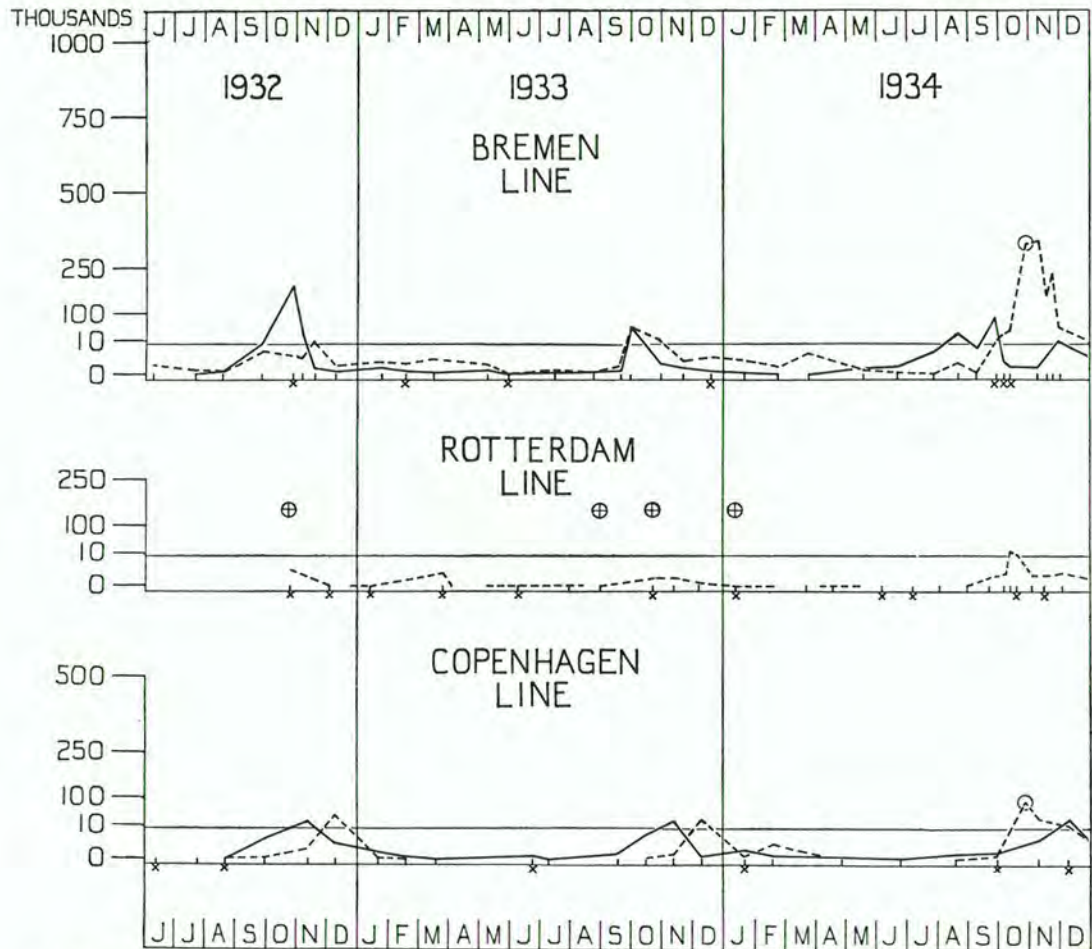


TEXT-FIG. 3.—Graphs of *Rhizosolenia styliformis* (blacked in) and *Biddulphia sinensis* (broken line) from records taken on the Bremen line during the autumns of 1934 and 1935. The vertical lines O.D. and B. indicate the positions of the Outer Dowsing and Borkum light vessels; they also represent a time scale from September to December against which each graph is placed in its appropriate position according to its date. Patches are shown above the base-lines (see scale above) and traces as small vertical or horizontal strokes below the line (*Rhizosolenia* and *Biddulphia* respectively). Data to the east of the sign "Q" may be mainly of qualitative value only. Records for the whole of the years are shown in Plates I, II, V and VI.



TEXT-FIG. 4.—Similar to Text-fig. 3 but for the autumns of 1936 and 1937. Here the graphs are smoothed by the data being treated in blocks of 10 miles. The scale is the same as that for Text-fig. 3. No traces were found on the record of 13th September marked \*. The additional vertical lines H and N represent the positions of the Humber and Norderney light vessels respectively.

followed by a more or less gradual disappearance, in 1934 and 1936 the trend was more irregular. The early patches of 1934 disappeared in October, others reappearing again in November, whilst in 1936 the maximum was much later than usual



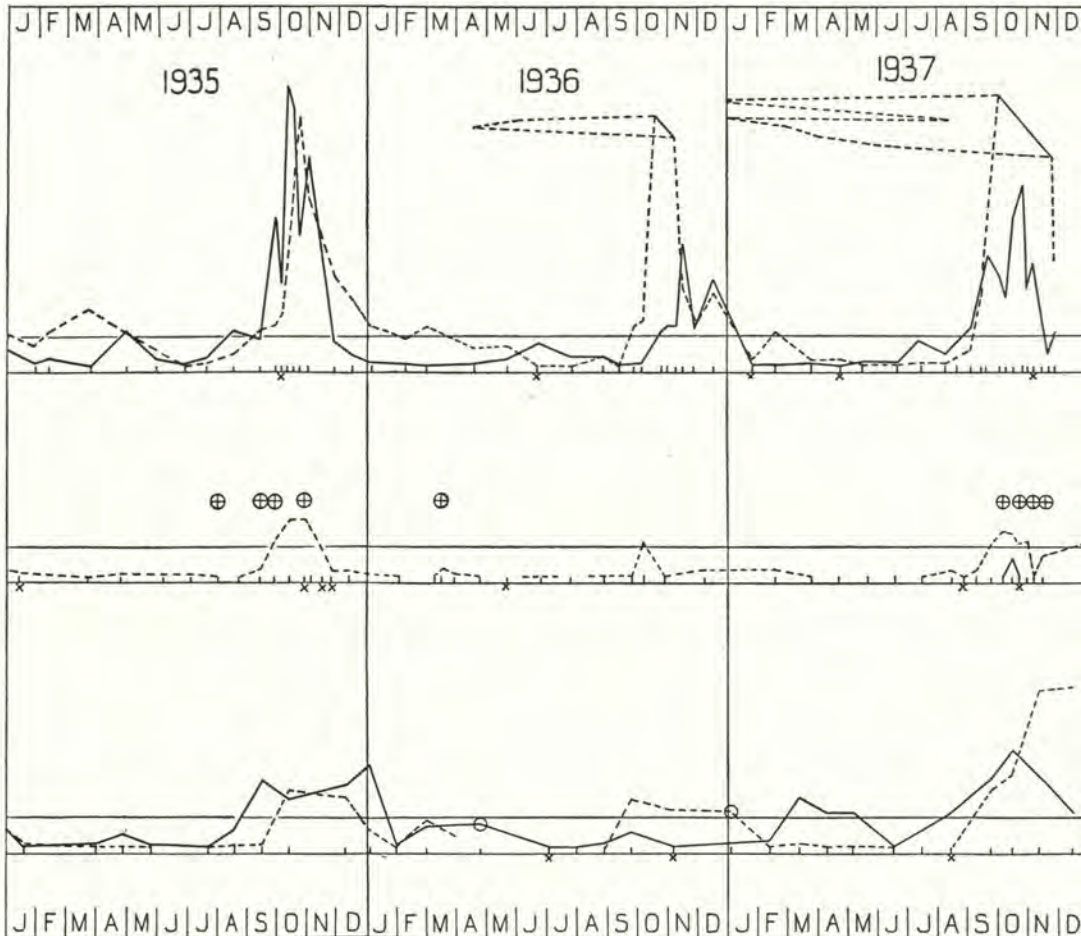
TEXT-FIG. 5.—Graphs showing the fluctuations in the total numbers of *Rhizosolenia styliformis* (continuous line) and *Biddulphia sinensis* (broken line) recorded between June, 1932, and December, 1937. The records for the Bremen line (between Outer Dowsing and Borkum light vessels), the Rotterdam line (between E. Dudgeon and Maas light vessels) and the Copenhagen line (from Humber light vessel for 250 miles towards the Hanstholm) are shown separately. Above and below are time scales in months: J., F., M., A., etc. Each point on a graph represents the total number of cells of the particular diatom found on one record; the exact positions of each record in relation to the time scale is shown as a small vertical line against the base-line of the graphs. The scale of numbers is in

and further irregularities occurred. The latter year was also noteworthy in the appearance of the densest of the series of patches in December, a month which in other years has only produced small patches or traces.

Text-fig. 5 shows the *total quantities* (see p. 91) found on each record during the period. The autumnal maximum is seen in each year and, as far as this material



will permit, we may obtain an idea of the annual variation; the quantities were the greatest in 1935, with 1937 similar but lower. We have already commented upon the scarcity of records in 1932-33, and the consequent risk of missing patches



thousands of cells per record; it should be noted that the vertical scale has been exaggerated below the 10,000 point in order to magnify the small but often significant changes which occur when these diatoms are scarcer. The true base-line, however, is also shown (i.e. just below point "10" on the scale). Records covering less than half the standard distance (see above) have been omitted unless where indicated as an open circle; records covering less than 80 per cent. are indicated by an  $\times$ . The few traces of *R. styliformis* on the Rotterdam line are indicated by a + sign within a circle. (The high peaks in the *Biddulphia* graph for 1936 and 1937 are shown folded over to the left for space economy.)

when they occur over the line; the findings of Savage and Wimpenny (1936) would suggest that we may have missed the densest period in 1933 and possibly in 1932 also. But in assessing the relative quantities we may also consider the time and space extents of the productions, and there is reason to think that we have sufficient records in these and the later years to decide that the *duration* of significant patches

over this line in 1932 and 1933 must have been much shorter than in the later years, and that any extensive occurrences did not exist for long.<sup>1</sup> This feature is clearly shown in the figures if we consider the extent of the autumn patches as they appear above the "true" base-line (see p. 92); the longer periods occurred in 1935 and 1937, whilst in addition we may note the unusually later production in 1936, with its rather smaller but still extensive patches.

Although occasionally no trace of it has been found, it has been seen in each of the twelve months, and only in February and April, 1937, in March of 1934 and 1935 and in June and July, 1932, has it not been recorded, although reference to the figures shows that occasionally a month has not been sampled. Sometimes cells were found in the Tank Residue which were not shown in Plates I and II.

#### *Copenhagen Line.*

All the records are shown in Plates III and IV, there rarely being more than one record in any month. As on the Bremen Line, there is a periodicity in numbers and variations between the different years. With the exception of a very dense patch in January, 1936, which we should associate with that of December, 1935, the period January-June is one of general scarcity; only in the spring of 1937 were more than isolated patches found. Autumnal patches occurred in October and November in 1932-34, and extended into December in 1934. In 1935 a small western patch in August was followed by large bimodal patches in September and October with smaller ones to the east. Although unfortunately we have no record for November, in December the diatom was still abundant, a large patch in the centre of the line suggesting a connection with that found in January, 1936. The records of 1936 were unfortunately few, the data for the western end of the line being particularly poor; only one small autumnal patch was found, in October. The most extensive quantities both in time and space were found in 1937, western patches appearing from July to December, together with varying quantities in the east and centre from September to December.

Text-fig. 5 shows the total quantities for this line, the autumnal maximum lasting the longest in 1935, although that of 1937 showed quantities nearly as great and generally more extensive. The only significant spring quantities were found in 1935-37, those of the last year being considerably the largest. In comparison with the Bremen Line we should note that the autumnal maxima here occurs later or persists until a later period in each year.

As on the Bremen Line, this diatom has been found in each of the twelve months, and, in fact, has only been absent in March, 1933 and 1934, June, 1932 and 1935, July, 1932 and 1933, August, 1932, and November, 1936.

<sup>1</sup> On the other hand, although the quantities in 1932 and 1933 were estimated on a broader basis than in the later years, we know them to have been greater than in 1934 (although less extensive in time and space), and colour estimations make it certain that they were much below the maximal densities of 1935-37.

*Rotterdam Line.*

Such traces as have been found on this line are shown in Plate IX, where they appear as vertical strokes, within circles, in distinction from the traces of *B. sinensis*. Where these coincide in 1936 and 1937 the vertical strokes representing *B. sinensis* have also been included in the circles. Traces have been mainly limited to odd broken cells and over the six years have been mainly found in the autumn; such as are referable to position have been in the west and centre. Most of them occurred in 1935 and 1937, in which year there was a very small patch (black in Plate IX) on the western half of the line in October. No signs were found in 1933 and 1936.

*Esbjerg Line.*

This line was introduced in 1936 in order to extend and to confirm the evidence from the older lines in this region; the graphs for 1937 are shown in Plate X. In 1936 only a few records were obtained and the autumn records revealed no signs of this form; whilst alone these few records would not provide adequate evidence of its scarcity, we may consider them in conjunction with its absence on the Rotterdam Line and general lower numbers on the Bremen and Copenhagen Lines in that year. The graphs for 1937 suggest that *R. styliformis* was still rather scarce on the line, but traces were found in May and traces and small patches at the north-eastern end of the line in the autumn; this increase compared with the previous year at the same time is paralleled on the other lines.

Since the data for this line is incomplete, it seems more suitable to defer the production of figures for total quantities (such as have been prepared for other lines) until a later paper, when similar data for a further period will be available. Meanwhile, apart from these few remarks, the chief value of the additional line will lie in the greater detail and co-ordination available in those of the serial maps to which these records apply (Plates XXII to XXXVI); they will be discussed further in relation to these.

*Distribution over the Area.*

Plates XXII to XXXVI show the distribution over the whole area by means of representative records for each month on such lines as were sampled in that month. Further details regarding these maps are given on p. 90, and here it remains merely to point out that readers should refer to the graphs discussed in the previous pages for such of the records as we have, for reasons of economy, been compelled to omit from the serial maps. The vertical lines used as ordinates in the graphs of Plates I to XXI represent also the positions of the light-vessels used as the normal termini or reference points in the charts and represented on them by various letters (see legends). For reasons of economy and purposes of comparison we have combined two species on the set of charts, and *R. styliformis* is here represented by the blacked-in graph and small vertical strokes below the base-lines.

Consideration of the data provided by these charts will perhaps make it more evident why I have considered it suitable to review first the findings on all the records for any one line, and only later to relate these in such manner as seems suitable. Two reasons contribute to this: (1) It has not been possible (and rarely will be) to obtain all records for one month even within one week (here we have been bound by sailing schedules and by accidents due to weather conditions and mechanical breakdowns), and so the charts cannot be comparable in the way in which we can compare the graphs already discussed; (2) having only data from discrete lines, the relations between them must be analysed with great care; the introduction in 1936 of a line which crosses two others helps in this process of relating the whole, and in later years we shall be able to go further than this, but the evidence for co-ordination must necessarily remain to a large extent circumstantial.

It will be of value to consider this question of relationship at this stage, and we may refer to Plates XXXIII to XXXV for data. Here are patches of *R. styliformis* and *B. sinensis* on most of the records, and we can consider the relations between them. Frequent reference to the different lines will be necessary in the discussion, and the letters B, C, E and R will be used to indicate the Bremen, Copenhagen, Esbjerg and Rotterdam lines respectively. In September and October there are patches of *Rhizosolenia* at the western ends of B and C, and although we cannot have proof, there seems good reason to think that they are different cross-sections through one patch at the edge of the Dogger Bank; this seems the more likely when we look at corresponding periods of other years and see (*e. g.* particularly in 1935) similar arrangements at the ends of the two lines, whilst the work of Savage and Hardy (1935) and Savage and Wimpenny (1936) has shown that such patches may occur frequently in such positions. Since this seems reasonably probable, it might be a working hypothesis that the smaller patches found in neighbouring places are also cross-sections through similar patches, but we must always bear in mind that there may be more than one patch in an area such as this, and at times there is good reason to believe so. The relationships between the patches of *B. sinensis* on B and R present similar problems, but even greater because of the greater distance between the lines in the region where *B. sinensis* is abundant on both; in 1937 particularly, it would be difficult to suggest any definite association if it were not for the presence of records on the E line, which enables us the more definitely to believe that in August, for example, there was no appreciable concentration of *Biddulphia* between lats. 52° and 54° N., whilst in September there probably was a patch extending over the E and R lines, a much larger one round the junction of B and R, and one or more to the north of these. Even with such data, which is about as good as we are able to provide for this survey, we must realize that there are appreciable uninvestigated areas each month, *e. g.* that between B, R and E, in which a large patch might lie unsampled. This means that deductions cannot always be made with reasonable probability, but on the other hand, it is sometimes possible to deduce from the

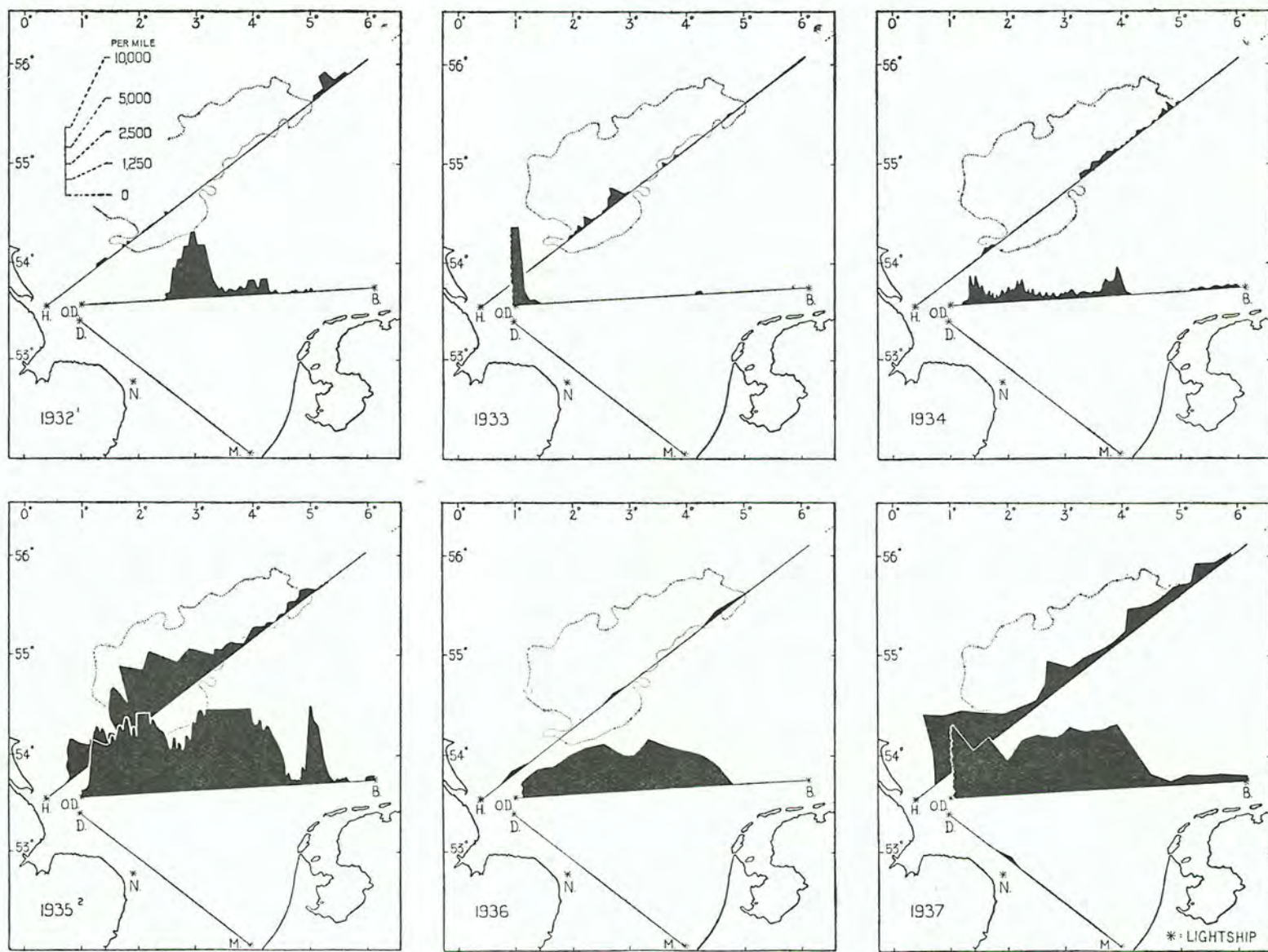
extra data in supplementary records (shown for this three months on Plate XXXV) the greater or lesser improbability that such further patches are in existence—the waters bearing patches are nearly always in movement, and the larger ones usually betray their presence by impinging on one or another line within the month.

This is a matter which must be discussed more fully when the phytoplankton and water movements are under consideration, but one cannot stress too strongly that the attempt to build up a two-dimensional picture from the strictly one-dimensional data available must be done with the greatest care when one species alone is under review, although in a review of the plankton as a whole the different ecological complexes will help to build up a more concrete picture.

At this stage it seems unnecessary to comment at length on the distribution as shown by these maps, which are expressly used so that they shall, as far as possible, speak for themselves and so avoid lengthy description. Details will be referred to in later sections, and future papers where particular points are concerned, though here we may review very briefly the general cycle as seen in the charts and draw attention to some matters of special interest. We may start for convenience in June, and from then to August we may note the appearance of traces and (usually later) patches generally towards the western end of B; in association (*i. e.* fairly close to B) there tend to be patches on C which are usually smaller. On the whole we may say the traces on B are a little more central in July than in June; in August they are rather more to the west again, and sometimes rather larger, but in 1935 and 1937 we may note also that the diatom has appeared in the region of the Heligoland Bight (also in July, 1934). With the exception of 1936, September shows an increase throughout, the bulk usually being in the west, with more or less extensive easterly components present in some years. Whilst the maximum is usually on B it may, as in 1935, be on C; in this month also we see the first traces on R.

In most years we find the maximum quantities in October,<sup>1</sup> but 1934 and 1936 are exceptions. The bulk of the production is in the west, but eastern growths are still evident, and in each year (except 1936) have by now appeared on C as well as on B. In 1935 and 1937 we should note that the main patches are bimodal, those for 1935 on B and C being suggestively similar. By the end of October the main or "primary" patch tends to be situated more towards the centre than in the early part of the month and in September. Again, with the exception of 1934 and 1936 there has been a reduction in numbers in November and a greater proportion of the total would appear to be typically on C; eastern traces on B are by now rarer. In 1934, however, there is a "return" of small patches (there being only traces in October), and in 1936 the first major growth is seen on B, only to decrease towards the end of the month and to appear denser still in

<sup>1</sup> The 1933 maximum according to us was found, in fact, on 27th September, but as we had another September record shortly before that, and there is no October record, this has been used as representative of October, and there is little doubt that the maximum was to be found in that month.

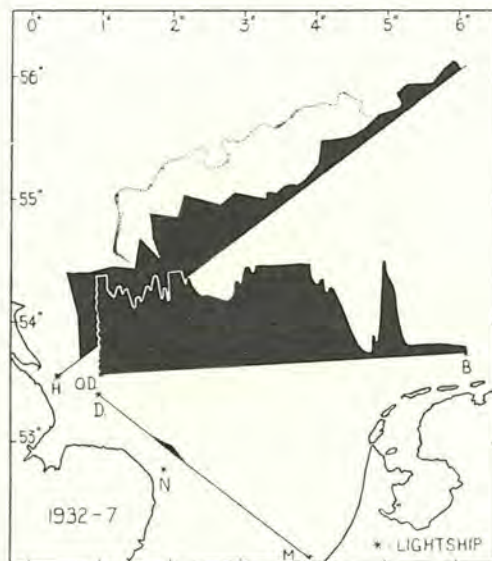


TEXT-FIG. 6.—Charts showing the maximal quantities of *Rhizosolenia styliformis* in numbers per mile (scale inset) recorded in each year at different points along the three lines.

<sup>1</sup> 1932 was incompletely sampled. <sup>2</sup> The data for January, 1936, have been included with those for 1935 (see text).

December; another December patch appeared on B in 1934, but there was a very marked reduction in all other years with the bulk of the form characteristically spread over C.

Typically from January to March there are only scattered traces on B and C, and for this reason the enormous patch on C in 1936 is the more striking (it provides the greatest density found on this line). There can be little doubt that this may strictly be considered as belonging to the previous autumn and winter development, and for this reason it has been included in the graph of maximal



TEXT-FIG. 6A.—Chart showing the maximal quantities of *R. styliformis* in numbers per mile recorded over the period June, 1932–December, 1937, at different points along the three lines. The separate year charts in Text-fig. 6 are here combined.

quantities for 1935 in order to prevent it from overweighting the maxima for 1936 on C (the actual date is 4th January). We may note also a dense patch on C in 1937. Such spring growth as is found usually occurs from April onwards and is scattered on B and C, small patches appearing in 1935–37 and disappearing by June.

Whilst the annual cycle of development shows essentially the same features each year, perhaps more striking are the differences which may occur. As pictured above, the general cycle is in broad agreement with and to some extent amplifies the findings which have been summarized by Ostenfeld (1931) from the early surveys of the International Council. One or two points, however, may be commented upon at this stage. The first concerns the almost permanent appearance of the form in this area compared with the general idea of its distribution in the past, since it has usually been considered to be a visitor in the North Sea, arriving

under the influence of currents. It is true that Ostenfeld (*loc. cit.*) points out that such incursions may give rise to subsequent local flowerings, but it has, in fact, usually been treated as though it were truly oceanic, and this is not necessarily in accord with the great flowerings which may be found so far south in the North Sea, and even less with its persistence there. From 1932 to 1937 we have obtained samples in 67 months, and it has only been absent from the rolls in 4 of these; in view of the very small samples taken by the recorder, this absence by no means proves that the form was ever entirely absent in the area. We can only come to the conclusion that, however much it may be under the *influence* of oceanic conditions, during this period at least, there must have been what we can only term an indigenous flora, and one persisting throughout very variable conditions of temperature and salinity. As far as they are available the results of Savage and Wimpenny (1936) for 1932 to 1934 show this also, whilst Savage and Hardy (1935) earlier suggested that the distribution for this form in 1924 gave ground "for believing that there are local flowerings" in this area. On the other hand it is not suggested that all the populations found have arisen in this area, and there may well have been a mixing of different "bodies" of the diatom from time to time.

Many of the variations from the general trend outlined above have been mentioned in discussing the data for the individual lines, but some others may more suitably be referred to here. Firstly, we may consider the evidence of the area as a whole regarding the quantities recorded. It seems probable that 1935 provided the greatest total bulk (*i. e.* allowing for extent of the patches in time and space), whilst 1937 was second. As far as these records go 1934 would appear to have provided the lowest maximal numbers, although the patches were more extensive than in 1932 and 1933. Whilst 1936 ultimately provided fairly large numbers on B, the numbers on C, as far as the records go, were quite low. These findings are shown diagrammatically in Text-figs. 6 and 6*a*, where the maximal quantities over all the lines are shown year by year. From this it would appear that there have been considerable changes between the years, and these not always in one direction, but a little further consideration to other factors will suggest that this is capable of some qualification.

Whilst the usual process, characteristic of each year, has led to the production of autumn patches which are usually at first most dense over the western end of B, and later may be denser over the centre and east of C, and which greatly outweigh the slight spring flora which may appear, we may further summarize the years as follows:

1932: Moderate numbers, mainly over the centre of B, and much lower ones over the eastern and western ends of C. General "movement"<sup>1</sup> north-easterly. Large numbers were evident on B only for a short time. The two records from 1931 suggested numbers to be even lower than in 1932.

<sup>1</sup> "Movement" here denotes general change in position.



- 1933 : Records incomplete in the middle of a significant part of the cycle, but the numbers were at least as high and probably higher than in 1932. The largest numbers on C were found in the centre, although we cannot say that they were absent in the west and east. Change in position was generally towards the east and north. Persistence over B can have been for little more than one month.
- 1934 : Numbers definitely lower than in 1932 and 1933, but patches were much more extensive on B, and although they fluctuated they persisted for a much longer time. Lower numbers were over the east and west of C, and the general "movement" was north-easterly.
- 1935 (including the January record on C in 1936) : The highest densities were obtained here on B and C, whilst extent in time and space were on the whole similar to 1937 and much greater than in any other year. Greatest densities appeared over the western ends of B and C, and as the season developed there was an undoubted anti-clockwise "movement".
- 1936 : Numbers lower on B and very low on C, no significant patches appearing until November, in contrast with the usually appreciable September patches in other years. The fluctuation on B is not dissimilar from the conditions in 1934. The bulk was found over the west and centre of B, and there was some movement in an easterly direction. Whilst small patches lasted from June to January, 1937, large patches were present only for a short time.
- 1937 : Densities approaching those of 1935 were attained, mainly over the western ends of B and C, although there were patches at their eastern ends. The only recorded patch on R was found. Large numbers were evident for a long period, and the general "movement" was undoubtedly towards the north and the east.

Two important points emerge from this summary. On the whole we should have to decide that there had been an increase in quantity from 1932 to 1935, although 1934 was in some respects peculiar. 1936 showed typically lower numbers during the maximal period of other years, whilst attaining moderate densities later on B, but 1937 showed some similarity to the general conditions of 1935 with rather lower densities. The second point concerns the north-easterly "movement" apparent in most years.

The significance of this general trend is discussed on p. 162 in relation to other forms found in this work and in other areas. From such results it should be possible over a long period to obtain a set of standards for comparison, and as a basis for general forecasting. The more detailed variations which have been found have their own more immediate value, and will be discussed from time to time in relation to other factors.

Text-figs. 6 and 6A showing the maximal quantities found over the lines bring out one or two other features. With rare exceptions we find that the patches

at the western end of the Bremen Line tend to end abruptly in the neighbourhood of the Outer Dowsing Light-vessel; the extensions of this line in 1937 have helped to delimit the edges of these patches more certainly, and there is reason to believe that this light-vessel forms a significant terminus, whilst there is some reason for considering the Borkum Light-vessel in the same manner. Similarly we can see that patches on C have never approached nearer than a point some 20 miles distant from the Humber Light-vessel, and that this was only obtained in 1935-37. These points, combined with the sparse occurrences on R, provide for the period a fairly distinct western boundary for productions of this diatom. Eastern limits are by no means precise, but clearly the greatest numbers are usually in the west.

Co-ordination between these results and those of other workers at the same time in the area—principally Savage and Wimpenny (1936) in 1933 and 1934—will be dealt with in detail in a later paper on the general survey in relation to hydrological conditions and movements in the area. We may state that, on the whole, comparison of these results with those of Savage and Hardy (1935) and Savage and Wimpenny (1936) shows no serious divergence, although there are certain discrepancies which must and, we believe, can be resolved. When the limitations of the two methods have been allowed for it is possible not only to see confirmation between the results, but also to see how the methods can be complementary one to the other in various ways.

One more point remains to be discussed. In this and similar sections dealing with the distribution and changes in numbers of the various species, it would be desirable to make some estimate of the rates of growth and general development of any form, since the present material provides the first survey over a large area within relatively short time intervals. The problem, however, is a complicated one. Reference to Text-fig. 5 will give a good idea of the total numbers found over the lines from time to time, but it will be clear that this is very different from the required estimate of growth and development for a number of reasons. We have to bear in mind the features peculiar to the recorder method: (1) Even in the case of a large form such as *R. styliformis*, the numbers are almost certainly less than those in the sampled water; (2) we know that necessarily the recorder does not always pass through the densest areas of any patch; and (3) we have yet to prove continuity from patch to patch between consecutive records and adjacent lines. Again, on more theoretical grounds, and as already explained on p. 88, results such as these, however they may be obtained, only give what may be termed the "residual population" at any time. Any increase or decrease found between consecutive surveys only shows the net change in number after some period in which death and loss have occurred due to a variety of reasons, perhaps feeding by herbivorous plankton being the most obvious. Whilst of some value, in that at any moment this estimate of the residual population more or less exactly forms a basis on which to speculate upon the future available source of production (*e. g.* the available food supply for some herbivore), it seems clear that until we know very much more regarding the life of any basic producer and that of its fellows in

the community, the values of a series of "residual populations" may give a very limited idea of the sequence of production variations. Until we know that it is most unlikely, or even impossible, for the appropriate herbivores to affect seriously the stock of any diatom during its most productive stage, we can never avoid this criticism. At present we have no definite knowledge whatever regarding the relations between the "residual stock" and the actual production for any diatom. Our knowledge could not be appreciably improved by means of more intensive investigations, and for any mixed population contemporary analysis of the relevant chemical salts will not necessarily provide the information; nor yet the analysis of the numbers of dividing cells, since these analyses can have but momentary value, being dependent upon the immediate conditions of the environment. A number of factors are playing their parts in this matter, and for its elucidation we need to investigate some characteristic of the stock in which the effects of these factors are at a minimum. It seems possible that such a characteristic may be that of cell diameter, which has recently been investigated by Wimpenny (1936) from another point of view. This is not likely to be affected by the depredations of herbivores, and so long as we are able to take a random sample of the population, results from its measurements will not be so affected by the peculiar effects due to the collecting appliance (clogging and filtration problems). The possible effects of the physical and chemical environment should be reasonably easy to ascertain, and may not be extensive. Subject to these possible effects being shown to be inconsiderable or *adequately measurable*, it would seem that the gradual reduction in size of the diameter of the cells in any self-contained stock of diatoms may bear a relation to the number of divisions undergone by the majority of that stock; by the continuous measurement of this value we may be able to obtain a better conception of the varying rate of division and consequently of the "production" of the stock than by any other method yet attempted. Furthermore, as Wimpenny has pointed out, by means of these measurements we are able to ascertain more certainly the relationship of patches some distance apart in time or space. Garstang (1938), in his review of Wimpenny's analysis, criticizes the chief use to which the latter has applied his data, and in emphasizing their application to the problems of the life-history of patches, he points out also the peculiar suitability of the recorder material in this respect. Measurement of samples of phytoplankton collected during the earlier part of the survey has been in progress now for some time, and meanwhile measurements are being made of the contemporary material, bearing in mind the different uses to which they may be applied. The results already show that the growth cycle can only be followed (as was also implied by Garstang) by consideration of the whole area of the North Sea, and that even then we may not be able to trace all the inter-relations of the different "bodies" of diatoms.

THE DISTRIBUTION OF *Biddulphia sinensis* OSTENF.

The general arrangement of the graphs is similar to that adopted for *Rhizosolenia*, the broad annual cycles being shown in Plates V to X (the patches appearing as blacked-in graphs above the base-line and traces as small vertical strokes below that line), whilst the details of the autumn programmes on the Bremen Line are shown on an extended time scale in Text-figs. 3 and 4 in association with the records of *R. styliiformis*. Since two organisms are shown in these last figures, it has been necessary to show the patches of *B. sinensis* as broken-line graphs above the line, and its traces as small horizontal strokes below the line. The general course of the description will be similar to that adopted for *R. styliiformis*.

*Bremen Line.*

Again it is evident that in each year there has been a cycle of relatively small spring growth and a very much more extensive autumnal production (Pls. V and VI). In June and July it has been usual to find only traces, although a small patch appeared in July, 1937. August has shown small eastern patches in the last four years which are the forerunners of the larger ones typical of the autumn, although in the first two years these did not appear until September. The densest concentrations have usually been found in October, although the greatest extension has sometimes occurred in November. In general the December patches have been smaller, although quite significant in 1934-36. Although there is this general similarity, there has been a marked difference in the spatial arrangement; the small patches of 1932 were mainly eastern, those of 1933 more central and those of 1934-37 generally much more widespread, usually appearing first in the east, with rather later central patches extending more or less to the west (particularly in 1935 and 1937), and then in a more central position in December.

Before dealing with the winter and spring developments we should note the following points: (1) the progressive westerly extension of the diatom throughout the period until in 1937, when the greatest production both in quantity and extent was attained, the dense zones of the diatom came nearer than in any other year to the Outer Dowsing Light-vessel; and (2) the very widespread productions in 1935 and 1937.

The patches and traces found in January are probably most correctly to be associated with those of the previous Decembers; although usually thin, we may note the greater numbers in 1936. In February and March there have usually been more extensive traces, together with eastern patches, the outstanding example being that in March, 1935. In April and May again the numbers have been lower, but patches have been found in the east and rather more generally in the west. These various patches show definitely that there is what may be termed a spring growth on this line, but we should note that not always has this been distinctly separated from the preceding autumnal developments.

The diatom has been found in each of the twelve months on this line, although apparently absent in June of 1932 and 1935-37, and in July, 1934.

Text-fig. 5 shows the total quantities on this line and serves to underline the steady increase from 1932 to 1937 (it seems possible that we may extend this to include 1931, since the two autumnal records which we then obtained, whilst in some ways unsatisfactory, showed much lower values than at similar times in 1932). Whilst in each year the autumn numbers always have exceeded those for the spring, there is a suggestion that the large spring growth of 1935 may have exceeded autumnal ones of some other years, *e.g.* 1931-33, although we must remember, as with *R. styliformis*, that the smaller number of records in the autumn series for these years may well involve the loss of important evidence; on the other hand, the time and space extensions tend to confirm the general low numbers in 1932 and 1933. In comparison with *R. styliformis* we may note that the present form tends to produce a maximum a little later in the autumn, and that this is seldom quite distinct from a smaller spring production which is usually rather early. On the whole it is rather more of a winter form, although it is scarce in the middle of the winter.

#### *Copenhagen Line.*

The distribution is shown in Plates VII and VIII. It will be most convenient to begin the description in September, for whilst there have been traces and very small patches in the first three months, from April to August inclusive there have been only a few traces found in 5 records out of 25. Again the autumn is the period of maximum numbers, and the annual cycles are broadly similar in leading up to the appearance of eastern patches towards the end of the year, but there are also interesting differences. In 1932 and 1933 patches do not appear until December, whereas from 1934-37 eastern patches were found as early as the end of September, and persisted until the end of the year, or even longer. Again, whereas in 1932 and 1934-36 the western limits of these patches were some 220 miles from the Humber Light-vessel, that in 1933 was only some 150 miles away. Similarly, whilst the first patch in 1937 was situated as usual, the western edge became progressively more westerly until in December it was only some 80 miles from the Humber Light-vessel, although other patches extended eastwards of this up to the Hanstholm. We may note also the traces and occasional very small patches near the Humber at this time in earlier years.

From the condition found in December of each year it seems logical to consider the numbers found in the east in the earlier months as being related to those of the previous autumns, this being most clearly shown in January both of 1936 and 1937, and perhaps reflected in the February and March records of 1934. The widespread traces at the end of February in 1936 are unusual.

The differences between the annual autumnal patches may be seen from another aspect in Text-fig. 5 and, with the possible exceptions of 1934 and 1936,

we are led to conclude that there has not been a spring maximum over this line, the autumn development being the characteristic one each year. Owing to its density and extension in space this attained a maximum in 1937, the totals increasing more or less steadily each year, although 1936 provided lower densities whilst persisting longer than in the earlier years.

*Rotterdam Line.*

The distribution is shown in Plate IX, and we see that but for a small patch in March, 1933, the patches are almost entirely limited to the autumn, although traces have been found at other times and mainly in the east. The major productions each year have been found in October, decreasing in November according to our records, with usually little more than traces being found in December. We may note, however, September patches in 1935 and 1937, and a relatively strong December one in 1937. Only in 1933, 1935 and 1937 were any appreciable western growths found. Perhaps we should note the bimodal patches found in 1935, central patches being joined to eastern ones, and the less obvious signs of such an arrangement in 1933 and 1934. Only one record showed a patch in the autumn of 1936, and it may be significant that this was more central than easterly.

The total quantities are seen in Text-fig. 5; the importance of the autumn patches is underlined, as also the greater productions of 1935 and 1937, 1936 resembling 1934 to some extent and the earlier years being probably even lower. As on the Bremen Line there are some signs of a spring growth. Unfortunately, we were unable to obtain records in February and May of the earlier years, but these were sampled in 1936-37, the only traces appearing in February, 1937. No signs were found in March of 1934, 1935 or 1937, April, 1936-37, June and July, 1934, 1936 and 1937, and August, 1933, 1934, 1935 and 1937.<sup>1</sup>

*Esbjerg Line.*

This line was introduced in 1936 in order to extend the observations from the older lines; the graphs for 1937 are shown in Plate X. In the first year only a few records were obtained, and the data seems only relevant in association with those of other lines. The more complete year, 1937, shows a fair development of *B. sinensis* in the autumn, and although the maxima were in the north-east, patches were to be found along the line down to its terminus near the Sunk Light-vessel. The graphs for 1936 show that patches may occur in January and February also, whilst that for October showed a particularly large patch near the Sunk Light-vessel. There may thus be a spring maximum on this line, but the bulk would appear to be found in the autumn as on the others.

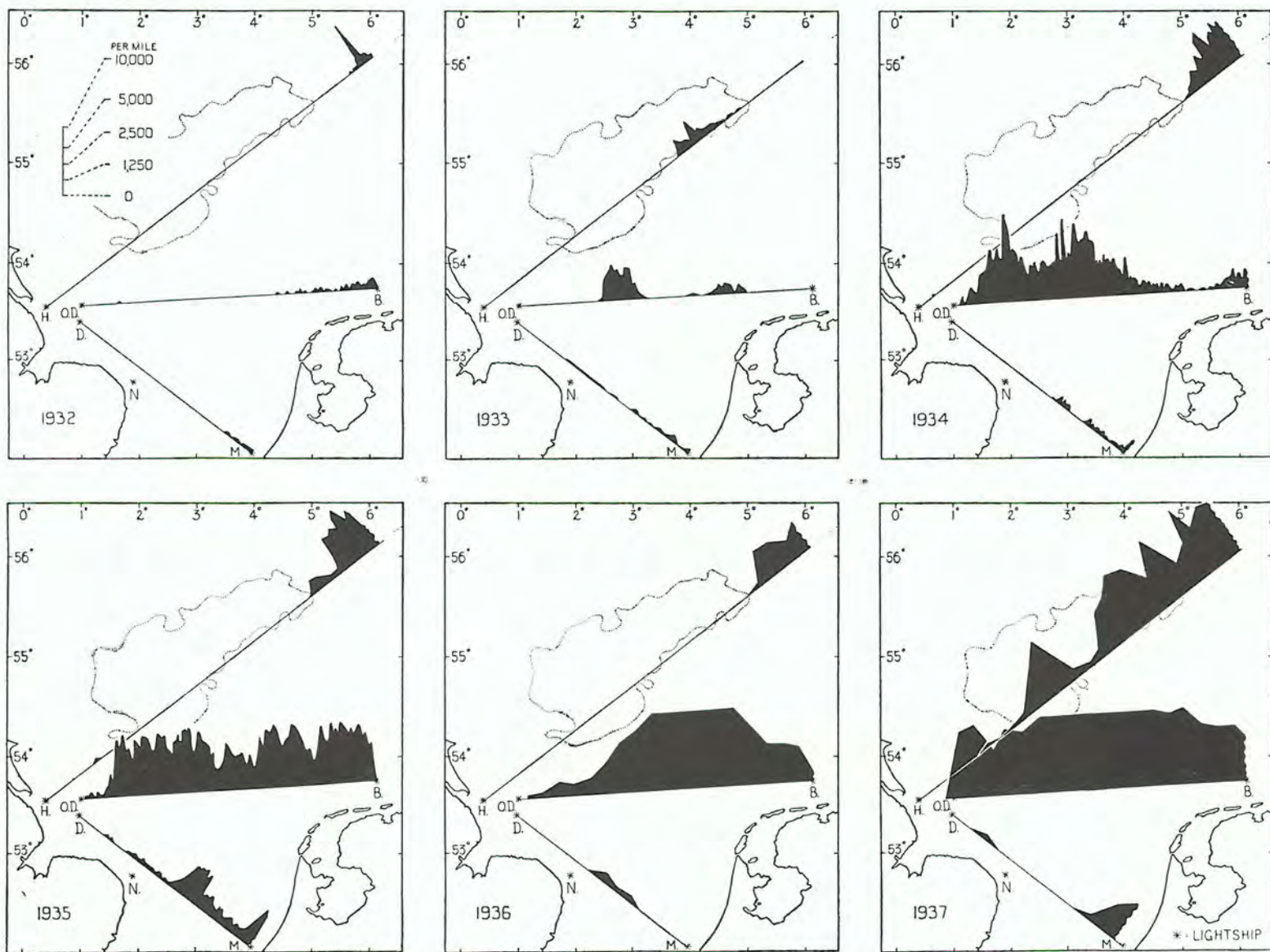
<sup>1</sup> In association with the results from this line, we may say that data from Plankton Indicator discs kindly taken for us by Prof. Gilson, showed appreciable numbers of *B. sinensis* over the eastern side of the Dover Straits in September, 1937.

*Distribution over the Area.*

The records are arranged in cartographical form in Plates XXII to XXXVI, along with those for *R. styliformis*, *B. sinensis* appearing as the broken line (patches) and its traces as horizontal strokes below the base-line. It is evident that we can trace a broadly similar annual cycle each year and the following features seem typical, although there are the usual variations; we may, for convenience, begin the description in July when only a few (mainly eastern) traces have been found. There has usually been little further development in August, but the location of a large patch in 1937 on the new line renders it possible that there may in other years have been patches in the region of the Heligoland Bight; this tends to be supported by the appearance in September of typical patches over the eastern half of B (these were more towards the centre in 1933, 1934 and 1936). We note at this time also the first patches on C and R, the latter (in 1937) in close association with one found at the southern end of the new line. Maximal densities have usually been attained in October, and while patches are still evident in the east in some years, either they have extended centrally, or others have appeared to the west of the former on the Bremen and Rotterdam lines (examples are 1937 and 1935 respectively). The month of November has usually shown some decrease, although generally not so marked as in *R. styliformis*; typically there has also been a further extension to the west on B, and in both October and November small patches and traces have been found at the western end of C in some years. The double patches seen in October are hardly perceptible in November. In every year December has shown evidence of a further decrease on the southern lines and typically the bulk has been found on C, some years providing an increase in that month or even the first patches then. On the whole there has also been a trend away from the western end of B.

Such small patches and traces as have been found in January continue the conditions found in December, being situated a little more to the east in some cases, but evidently as residues of the former months. February and March have sometimes shown an increase, usually at the eastern ends of the lines (or in the centre of the Esbjerg Line); on the other hand, April, May and June have shown progressive decreases in numbers, and the main patches have been at the western end of B (see also Fig. 5).

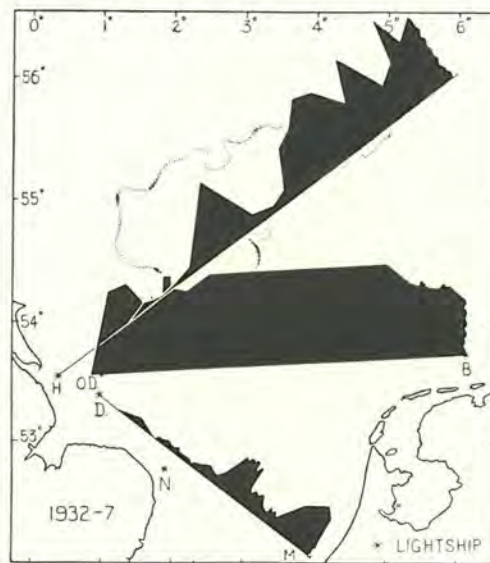
The general distribution of this form and the contrasts shown between it and *R. styliformis* are in general conformation with the findings of the surveys organized by the International Council (Ostenfeld, 1931), although the great extensions towards the west in some years may be more recent features. Ostenfeld (1908) has described the earlier findings of *Biddulphia* in these waters, and the growth which took place between 1903, when it was first found, and 1907; records obtained since then (Savage and Hardy, 1935, and Savage and Wimpenny, 1936), whilst obtained at irregular intervals and apparently with no object of investigating this particular phenomenon, do suggest that in recent years it had increased, and the



TEXT-FIG. 7.—Charts showing the maximal quantities of *Biddulphia sinensis* in numbers per mile (scale inset) recorded in each year at different points along the three lines. Note that 1932 was incompletely sampled.



records we have available from 1931-37 suggest that the increase in density and the extension in space had not then stopped. This type of swing in the balance of the community will be discussed more fully at a later stage, but here it is interesting to note that the nearly related forms *B. regia*, *B. mobiliensis* and *B. granulata* (the first two of which used to be considered important in the area) have never in our records attained anything like the great densities of *B. sinensis*. It is interesting to note that the annual cycle as found by us is on the whole so similar to the course of events found by Ostenfeld: "it has found . . . places suited to it in certain areas from which every year in late autumn (September-November) it



TEXT-FIG. 7A.—Chart showing the maximal quantities of *Biddulphia sinensis* in numbers per mile recorded over the period June, 1932-December, 1937, at different points along the three lines. The separate year charts in Text-fig. 7 are here combined.

shoots up and spreads out with the currents"; he quotes the Elbe, the Skagerrak and the Belgian coast as such places. We also found the spring maximum to originate in the same region, although the patches of the later spring months were over to the west.

Whilst considering the general distribution we may refer to Text-figs. 7 and 7a, showing the maxima throughout the period, and note the quite striking overall occurrence. We saw that with *R. styliformis* there was generally a marked discrepancy between the numbers found at the western ends of B and R, there rarely being even traces on R, although the numbers on nearby C were seldom so different from those on B. With *B. sinensis* we find that the discrepancy applies to both R and C, there seldom being any patches at the western ends of these lines, although neither is far from B where it was abundant; whilst numbers may be large over the greater part of B, they are rarely found other than at the eastern

ends of R and C. The conditions which can account for such a distribution and the variations which are found (*e. g.* on C in 1937) may well prove to be significant.

We have said that there are variations between the different years, and the most striking of these is probably the gradually increasing quantity found on the records from 1932 (or 1931 ?) to 1937, but the gradual increase is not shown on every line and we can best describe the individual years as follows :

- 1932 : Rather small eastern patches found first on B and R, and not until December on C. There is some easterly extension on B during the autumn.
- 1933 : In the autumn there were larger and more central patches on B followed by scattered patches on R, and one, in December, towards the centre on C. Such "movement" as was evident in the autumn was from centre to east on B. Small patches appeared on B and R in March.
- 1934 : Autumn patches first appeared on B, spreading from the centre nearly to the west, eastern patches appearing at the same time. The first significant patches on C and R were in October and in the east ; they lasted until December on C. After the extension towards the west there was a slight easterly "movement" at the end of the year. Small patches were on the east and west of B in the spring.
- 1935 : The autumn patches first appeared on B in the east and centre, with later ones spreading nearly to the west. A double patch was on R in October, whilst one in the east persisted on C from October to the end of the year, at which time an easterly trend was observed on B. The largest spring patches appeared this year in the east and west on B.
- 1936 : The first autumn growth appeared in the centre of B in September, later extending to the east and somewhat to the west, but less than in 1935. At the same time an eastern patch appeared on C and persisted after the end of the year (January, 1937), but as we have seen, only one small patch appeared on R. Although there is no evident easterly "movement" on B at the end of the year we should note the decrease in November and December. There was a fair patch towards the eastern end of B in January and February (on the Esbjerg Line).
- 1937 : The densest growths were found on B in the autumn of this year, first appearing in the east in August (*i. e.* on the Esbjerg Line) and then extending towards the centre of the line, and ultimately further to the west than previously had been attained. Large patches appeared on C in September and, unlike other years, they also extended to the west during the next three months, whilst on R the most westerly patch of the period was found, and eastern patches extended from September to December. There was some recession towards the east on B near the end of the year. There was apparently no spring production of any size.

There are a number of points in these differences which enable us to qualify the general statement of a trend over the period, and as with *R. styliformis*, we should rather regard it as a trend from 1932 (or 1931 ?) towards 1937, in which 1936 and to some extent 1934 show retrogressive or peculiar features. Amongst these are the less westerly extension on B in 1936 and the low numbers found on R, whilst others can be inferred from the summaries above and from the diagrams. This will be discussed further on p. 162 and in relation to other subjects.

As with the previous form, the general changes over the years 1931-34 agree broadly with those found by Savage and Hardy (1935) and Savage and Wimpenny (1936), and whilst there are certain discrepancies at first sight (in addition to those involved in the different methods), the more continuous records obtained by the recorder make it possible to resolve these to a large extent (see a later paper, in which these results will be assessed as a whole in relation to the hydrology and movements in the area).

Two other matters may be dealt with briefly here. As we have pointed out on p. 88, it would be desirable to have some better measure of the general annual growth than is provided by Text-fig. 5. For reasons discussed there this can only give a very approximate estimate of the changes in the "residual" population, and the picture may not be closely related to the actual growth and death-rates of any form. It seems possible that with certain qualifications the continuous measurement of cell sizes might provide for this form (as for many other diatoms) a more useful measure of the varying growth than has yet been obtained, and this work is being started.

The other matter concerns the almost persistent occurrence of this diatom in some parts of the area. Out of the 67 consecutive months in which the area was investigated (1932-37) *Biddulphia* has only been missed on 7 occasions (never in 1935, and three times in 1936), and the small samples which are obtained in any one place suggest strongly that it may still have been present on some of these. Such findings are not so surprising for *B. sinensis* as they were for *R. styliformis*, since the former, during the period from its first finding in these waters in 1903, appears so to have increased that it has become a truly indigenous form. On the other hand, few other diatoms have been found by us to be so persistent in our samples, and whilst some of them must necessarily be ruled out of comparison owing to their very small size (they may only be caught when very abundant), there are others having a sufficiently similar size to have approximately the same chance of being caught. These findings lend weight to the conclusion of Ostenfeld (1913), that whilst *R. styliformis* "is . . . the most important of all plankton diatoms", yet *B. sinensis* "has been one of the dominant forms of the plankton" in this area, although it is important to remember that both have been subjected to more intensive analysis than has been usual for other forms.

## THE DISTRIBUTION OF THE OTHER DIATOMS.

As already explained, the concentration in the early years of the survey upon the economically important diatoms *Rhizosolenia styliformis* and *Biddulphia sinensis* (together with the Dinoflagellates and Phaeocystis) led, in the limited time available, to a much more cursory treatment of the remaining diatoms. This material in consequence has its definite limitations, and cannot be treated in the same manner as the forms just mentioned. Nevertheless provided its limitations are fully realized and accepted, it is felt that it may profitably be used in presenting a picture of the main phytoplankton changes in the area over the period under review, and in addition will be useful as a basis for comparison with the more detailed phytoplankton work in the extended survey undertaken since 1938.

These limitations must be carefully stated. It has been found by checking that the method of analysis adopted in the early years led to some errors in enumeration and identification. These have been corrected, whenever possible<sup>1</sup>; elsewhere the material may have been discarded, or if used (as in some types of numerical error), it is only with qualifications regarding the validity. This means that the negative evidence on some occasions will be misleading; the omission of some material will have given a false impression of the absence or scarcity of a species. Further, in the more cursory treatment of the remaining diatoms, the determinations have in many cases been carried only to the genus, or in some cases two or more species have been treated together as a subgeneric group. The latter step has been taken in some instances where specific identification has been doubtful. Unfortunate as these points undoubtedly are, it is felt that the data, with these qualifications kept in mind, are of significance and worth recording.

The occurrence of the different diatoms has been summarized in the following way: The records have been subdivided into blocks each of about 20 miles' distance; in 1936 and 1937 these have been exactly 20 miles, but in the earlier years blocks of ten sections have been taken, and these will each represent a distance varying between 15 and 25 miles according to the varying ratio of 1.5 to 2.5 miles per section (the actual ratio for each record will be found in the Record List in 'Bulletin' No. 2). The quantities within these blocks have been averaged to provide values for diatoms per mile per block. These values are then assessed on a broad scale of "traces", "thin patches" and "major patches"; the second category is on an average some ten times the density of the first, and the third category ten (or more) times the second. There are reasons to believe that the addition of a

<sup>1</sup> We have been able to check certain of the errors. In 'Bulletin' No. 4 Mr. Rae will describe how, in at least one record for each route per month, an analysis has been made of every fifth or tenth tube for specific identification of the Copepoda, etc. At the same time the phytoplankton content of the tubes was analysed. From these estimates we obtain a random estimate of certain types of error, but whilst in many instances these can be detected, they cannot always be corrected. The tubes contain only the plankton which could be scraped off the silk, and so they usually contain only a part of the plankton which was originally caught. The chief types of error involved would appear to be (1) low estimations of some forms in the presence of others, and (2) mistakes of identity under the conditions of dense scum or in dense patches of diatoms.

TABLE IV.—Showing the Periods of Occurrence of some of the Rarer Diatoms over each Line (C, B and R) during the Survey. The numbers 2–7 denote the years (1932–1937) in which they were found to occur during the different months.

		Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
<i>Biddulphia rhombus</i>	C	..	..	..	6	..	5	3, 7	5	6	7	..	..
	B	3, 5, 6	5	3–5	4	3, 4	4, 5, 7	4, 7	5, 7	2, 4, 5	2, 4, 5, 7	5–7	4
	R	..	7	..	5, 6	6, 7	5, 7	5, 7	4–7	5–7	3–7	5, 7	3
<i>Cerataulina</i>	C	6	7	5, 7	5, 7	7	4, 5	6, 7	7	5	5	..	4, 7
	B	..	6	6, 7	4, 6	..	..	..	..	..	5, 7	6	6
	R	..	7	7	..	..	..	..	7	..	6	7	..
<i>Rhizosolenia fragillima</i>	C	..	..	..	6	6	..	7	6	..	..	..	5, 7
	B	..	7	..	..	5	..	..	6	3, 4, 6	5, 6	5, 6	..
	R	..	7	6	5	7	..	..	..	7	7	..	..
<i>Bacteriastrium</i>	C	..	..	..	..	..	..	..	5, 7	7	7	..	..
	B	..	..	..	..	..	..	..	6	5–7	7	..	..
	R	..	..	..	..	6	..	6	7	7	6	..	..
<i>Biddulphia alternans</i>	C	..	..	..	..	..	..	..	..	7	7	7	..
	B	..	..	7	..	..	..	..	4	5, 7	5, 7	6, 7	..
	R	..	..	..	..	..	..	..	7	5–7	6, 7	..	..
<i>Streptotheca</i>	C	..	..	..	..	..	..	..	..	..	..	..	7
	B	..	..	6	..	..	..	..	..	7	7	6	..
	R	..	7	..	..	..	..	..	..	..	..	7	..
<i>Hyalodiscus</i>	C	..	..	..	..	..	..	..	..	..	7	7	7
	B	..	..	..	..	..	..	..	..	7	7	7	..
	R	..	..	..	..	..	..	..	7	..	6	..	..





further "very dense" grade would have been desirable, but certain aspects of the earlier work make it impossible to provide comparative data for such a grade. The third density may be taken to indicate all the most important patches, but those of intermediate value need to be variously assessed accordingly to the size, etc., of the cells concerned, although for all the larger forms these also should indicate significant patches. The "traces" have only their limited value as indications.

DIATOMS	LINE	1932						1933						1934																	
		J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N
EUCAMPIA ZOOIACUS	C	○	○	○	○	—	○	○	○	○	○	—	○	○	○	—	○	⊕	○	⊕	○	○	⊕	○	—	○	○	○	○	○	○
	R	○	○	○	○	○	○	○	○	○	○	○	—	○	○	○	○	○	○	○	⊕	○	○	⊕	⊕	○	○	○	○	○	⊕
NAVICULA SPP. ETC.	C	○	⊕	○	⊕	—	⊕	⊕	⊕	⊕	○	—	○	⊕	—	○	○	○	○	●	○	⊕	⊕	○	—	○	○	○	○	○	⊕
	R	⊕	⊕	⊕	○	○	⊕	⊕	⊕	⊕	⊕	—	⊕	⊕	⊕	○	⊕	⊕	○	⊕	⊕	⊕	⊕	○	⊕	⊕	⊕	⊕	⊕	⊕	○
ASTERIONELLA JAPONICA	C	○	○	○	○	—	○	○	○	○	○	—	○	○	○	—	○	○	⊕	○	○	⊕	○	●	—	○	○	○	○	○	○
	R	○	○	○	○	○	○	○	⊕	⊕	⊕	—	○	○	○	○	○	○	⊕	⊕	○	⊕	○	○	○	⊕	○	○	○	○	○
THALASSIOTHRIX NITSCHIOIDES	C	○	○	○	○	—	○	○	○	○	○	—	○	○	○	—	⊕	⊕	⊕	⊕	⊕	⊕	○	●	—	○	○	○	○	○	○
	R	○	○	○	○	○	○	○	⊕	⊕	⊕	—	⊕	○	○	○	○	○	⊕	⊕	○	⊕	○	⊕	●	⊕	○	⊕	⊕	⊕	⊕
GYROSIGMA SPP.	C	○	○	○	○	—	○	○	○	○	○	—	○	○	⊕	—	⊕	○	○	○	○	○	○	○	—	⊕	○	⊕	○	○	○
	R	⊕	○	○	○	⊕	○	○	⊕	○	⊕	—	○	○	○	○	○	⊕	○	○	○	⊕	○	○	○	⊕	○	○	○	○	○
BACILLARIA PARADOXA	C	○	○	⊕	○	—	○	○	○	○	○	—	○	○	—	○	○	○	○	○	○	○	○	○	—	○	○	○	○	○	○
	R	○	○	○	○	○	○	○	○	○	○	—	⊕	○	○	○	○	○	○	○	○	⊕	⊕	○	⊕	⊕	○	○	○	○	⊕
NITZSCHIA SPP.	C	○	○	○	⊕	—	○	○	⊕	○	○	—	○	○	—	○	○	○	○	⊕	○	○	○	⊕	—	⊕	○	○	○	○	○
	R	⊕	○	○	○	○	⊕	○	⊕	○	○	—	⊕	○	○	○	○	○	○	○	○	○	○	○	⊕	⊕	○	○	○	○	⊕

TEXT-FIG. 8A.—Continuation of Text-fig. 8.

Text-figs. 8 and 9 provide a graphical representation of the variations in the occurrence of the more important species during this survey; the presence or absence of patches of the different grades, as revealed by these records, is shown month by month on each line. Some of the scarcer forms appear in Table IV in an abbreviated manner. In view of the extent of the material it is impossible to show all the occurrences of each form, and description will be limited to a series of short notes outlining the general distribution during the survey, variations and unusual features, and occasional comparisons with the findings of the International Council within this area. Graphical representation of the spatial distribution will be limited to a series of charts, Plates XXXVII-XLIV, showing the main phytoplankton complexes which have been recorded during the survey; except for one or two forms these will show the major and intermediate patches mentioned above for each species. These charts are more diagrammatic than the others of this



kind, and certain slight differences in arrangement are due to this as are slight differences between these maps and Text-figs. 8 and 9. No extensions outside the original area have been used. From the charts it should be possible to see the main trend of events, and its variations, for each form, and to follow the distributions of different species in relation to those of others. In order to follow the whole phytoplankton cycle they should be considered in conjunction with the charts of Rhizosolenia, etc.

1935												1936												1937												
J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	
⊕	-	○	●	●	○	○	⊕	⊕	⊕	-	⊕	⊕	⊕	⊕	●	⊕	-	○	⊕	●	-	●	○	○	⊕	⊕	●	●	○	○	⊕	⊕	○	⊕	⊕	
○	○	○	⊕	●	○	⊕	○	○	⊕	⊕	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	⊕	○	○	○	⊕	○	○	○	
○	-	○	⊕	-	○	○	○	○	⊕	○	○	○	○	○	○	○	○	○	○	○	○	○	-	○	-	○	⊕	○	⊕	○	○	○	⊕	○	○	○
⊕	-	●	⊕	⊕	○	○	○	○	○	-	⊕	○	⊕	⊕	⊕	⊕	-	○	○	○	-	⊕	○	○	⊕	⊕	⊕	⊕	○	○	○	○	⊕	⊕	○	
○	⊕	●	○	●	○	○	○	○	○	○	⊕	⊕	⊕	●	⊕	⊕	○	○	○	⊕	○	⊕	⊕	○	○	○	○	○	○	○	○	○	⊕	⊕	⊕	
○	-	○	⊕	○	⊕	○	○	○	○	○	○	○	⊕	●	⊕	○	○	○	○	○	○	○	-	○	-	○	⊕	○	⊕	○	○	○	○	○	○	○
○	-	○	○	-	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	
○	-	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	
⊕	-	○	⊕	⊕	○	⊕	⊕	⊕	⊕	-	○	○	○	○	⊕	⊕	-	⊕	⊕	-	○	○	○	⊕	⊕	●	●	●	⊕	○	○	⊕	○	⊕	⊕	
○	○	○	○	⊕	⊕	⊕	⊕	⊕	⊕	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	
○	-	○	⊕	-	⊕	⊕	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	-	⊕	⊕	○	⊕	○	○	○	⊕	○	○	○	
○	-	○	○	-	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	
○	-	○	○	-	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	
○	-	○	○	-	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	
○	-	○	○	-	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	
○	-	○	○	-	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	
○	-	○	○	-	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	
○	-	○	○	-	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	
○	-	○	○	-	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	

TEXT-FIG. 8A continued.

A striking feature of the results of this phytoplankton survey over the period under review is the tendency for a greater number of species to figure more prominently as the survey progressed, and even to attain their maxima during the last year. We were much disturbed as to whether this result could be due to an improvement in our technique as the survey progressed, and not to an actual change in nature. There is no doubt that our methods and our knowledge of the material have improved, but whilst this may to some extent have contributed to this effect, we have evidence that this has not been a major factor in the problem. This tendency was becoming very evident in 1935, and in order to obtain some check on it we examined the numbers of different forms present in the "tube analyses" (p. 75), and whilst we know that these are necessarily minimal, we found that generally the forms appeared in those tubes in the same order and in proportions similar to those which had already been found from analysis on the rolls. Whilst

these last had been spread over a number of years and had been made by a number of workers, the tube analyses have been done within a short time, in chance order and all by the same person (Mr. K. M. Rae). This alone suggested that the changes were really significant. Again, the doubts were applied only to some forms which were small or easily damaged in storage, but we still found that some others to which these doubts were not applicable had also increased (*cf.* also the much more striking increases of *C. fusus* on the Rotterdam Line over this period, and the evident increases of *R. styliiformis* and *B. sinensis*). Moreover, certain forms had either decreased during the period or had shown irregular variations and, in view of the whole series of factors, we have been led to conclude that whilst there may well have been improvements in the technique (particularly that involved in the decreasing time-lag between recording and analysis) which have led to relatively higher values in later years, yet the results show changes which have significance, the precise values not being obtainable (as, indeed, applies to other estimates based upon filtration, p. 77). A discussion of the significance of this increase in the phytoplankton during the course of the survey is reserved for consideration in the more general conclusions and will be found on p. 162.<sup>1</sup>

Brief notes will now be given regarding all the more important forms encountered, and these will include an indication of the tendencies of the different species to occur in association with other forms or to live in relatively "pure" communities. The recorder method provides useful material for such ecological correlations and the subject will be more fully dealt with in a later paper. The general identification and classification has been based on Lebour (1930).

*Paralia sulcata* (Ehr.).

This has been very widespread in time and space, being found in each of the twelve months, although seldom plentiful: the largest numbers were found in the autumn. As a whole it has had a very coastal distribution, rarely being found in the central parts of the lines, but as might be expected, being commonest in the presence of patches of debris, which are abundant at times in the waters of the southern North Sea. It has definitely been most common on line B, and rarest on C. Since this is a chain form and seldom more than a few chains are seen, only its presence has been considered as evidence, and no patches are dealt with.

*Coscinodiscus* spp. (C in Plates XXXVII–XLIV.)

As a whole the genus has been found in each of the twelve months, except in 1933 and 1936 when it was entirely missing in June. Patches (except one on the extension of the C line in September, 1937) have always been found in the spring, and have been dominantly *C. concinnus*. They occurred on line B in 1933 and 1934 and on C in 1934–36, mainly in the east and centre.

This is one of the few genera not having a maximum in 1937, and with the exception of the patch to the east of the usual terminus on C in September (not *C. concinnus*) there were no patches this year. It rarely attained great numbers.

<sup>1</sup> Further evidence that this increase was an actual one in nature, and not entirely due to an improvement in technique, appears in the results for 1938–39 when a marked decrease was observed in many forms: see the addendum note on p. 168.

*Thalassiosira* spp. etc. (TH in Plates XXXVII–XLIV.)

Owing to the difficulty of identification on the roll when large numbers are present, we have found it better to combine the *Thalassiosira* spp. with *Coscinosira* spp. and *Lauderia* spp. In this area the dominant one has been *Thalassiosira* (*Th. Nordenskioldii* and *gravidia*). Whilst very common at times they have never been recorded in August, being most abundant on lines B and C in the spring. Patches have occurred on all parts of the lines, but there are irregularities, *e. g.* on R, where no appreciable numbers were found until 1936 (east), whilst in 1937 they extended up to the East Dudgeon Light-vessel. On C we may note the unusually extensive patches in 1935 and 1937 (March), and on B in March, 1937. No patches were found on line C in 1936 or on B in 1935, and as a whole they were by far the commonest on all lines in 1937, in association with *Chaetoceros* spp., *Thalassiothrix nitzschioides*, *Asterionella japonica* and others in various combinations.

*Skeletonema costatum* Greville. (S in Plates XXXVII–XLIV.)

Since this form may not be found in representative numbers owing to its small size, and probably only the major patches are strictly comparable, we have limited consideration to these. It has rarely been seen from July to December, and only in 1936 and 1937 has it appeared on line R. The only patches appeared in April, 1934, on C, and March, 1937, on C and B; all were at the western ends of these lines. Its common associates have been *Chaetoceros* spp., *Thalassiosira* spp. etc., *Thalassiothrix nitzschioides* and *Asterionella japonica*.

The absence of an autumn secondary maximum may be of interest in view of the suggestion of Ostenfeld (1913) that this usually occurred in his data.

*Leptocylindrus danicus* Cleve. (L in Plates XXXVII–XLIV.)

This has been absent in February, June and December, and rare in January; it did not appear on line R until 1936–37. The greatest numbers were found in 1935 (particularly on B in April and May), but patches also occurred on C and B in 1937. In addition to *L. danicus* some very small cells were included which were probably *L. minimus* Gran.

*Guinardia flaccida* Castr. (G in Plates XXXVII–XLIV.)

The only patches were found in 1937 at either end of line C in July and at the western end of B; it has been very rare on line R. This is another form which is rather easily damaged and may have been missed on occasion, as some of the analyses of "tank residues" have suggested. A tendency to live in somewhat deeper waters than other forms may cause it to be rarer in our records than might be expected. It has been found throughout the year, but only once in February.

*Bacteriastrum* spp. (BTM in Plates XXXVII–XLIV.)

Although it would be impossible to vouch for all specific identifications in view of the peculiar difficulties of this work, the periodical confirmation and peculiar distribution of these diatoms make it reasonably certain that *B. hyalinum* Lauder (of Lebour, p. 83) is the one concerned; no certain specimens of *B. delicatulum* Cleve have been seen. Patches have been limited to the period 1935–37, occurring in August, September and October at the eastern ends of lines B and R; in addition one was found on R in May, 1936, and another outside the usual area (*i. e.* the extension of C) in September, 1937. It is probable that these, along with some associated forms, may form useful indicators of hydrological conditions in the southern area, and we may note that it was remarkably scarce in the early years.

*Rhizosolenia alata* Brightw. and *R. hebetata semispina* (Hensen). (R in Plates XXXVII–XLIV.)

It has been considered necessary to combine these forms to avoid the use of possibly erroneous data due to some confusion in the earlier years, and from time to time in very dense numbers of a mixed population. It seems probable that rarely, if ever, have cells of *R. hebetata hiemalis* Gran been seen in these records. The two species (*R. alata* and *R. h. semispina*) have been broadly separable in 1936–37.

As a whole they have been rare on line R (no patches), most of the patches being found in the spring and autumn on B and C, the greater number in 1936 and 1937; on the whole they have been rather more autumnal on B than C. As might be imagined, this heterogeneous group has had a widespread distribution, tending on the whole to appear over the central area

DIATOMS	LINE	1936												1937											
		J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
RHIZOSOLENIA ALATA	C	⊕	○	⊕	○	⊕	—	⊙	⊙	○	—	⊕	⊕	⊕	⊕	⊙	⊙	⊕	⊕	⊙	⊙	⊕	⊕	⊙	⊙
	B	○	○	○	⊕	○	○	⊕	⊙	⊕	⊙	⊙	⊙	⊕	○	⊕	○	⊕	⊙	⊙	⊕	⊕	⊕	⊕	—
	R	○	○	○	○	○	○	○	○	○	⊕	—	○	—	○	○	○	○	○	○	⊕	⊕	⊕	⊕	○
RHIZOSOLENIA SEMISPINA	C	⊙	⊙	⊕	⊙	⊕	—	○	⊙	○	—	○	○	○	○	⊙	⊕	⊕	⊕	⊕	⊙	⊙	⊕	○	○
	B	○	○	○	⊕	⊕	○	⊕	⊙	⊕	○	⊕	○	○	○	⊕	⊕	⊙	⊕	○	⊕	⊙	⊙	○	—
	R	○	○	○	○	⊕	○	○	○	⊕	○	⊕	—	○	—	○	○	○	○	⊕	○	○	⊕	○	○
HYALOCOAETES	C	○	⊕	⊕	⊙	○	—	⊙	⊙	⊙	—	○	○	⊙	⊙	⊙	⊙	○	○	⊙	⊙	⊙	⊙	⊙	⊙
	B	⊕	⊕	⊙	⊙	⊙	⊕	⊙	⊙	⊕	⊙	⊙	⊙	⊙	⊕	⊙	⊙	⊙	⊕	○	⊙	⊙	⊙	⊙	—
	R	○	○	⊙	⊕	○	○	○	○	⊕	⊙	—	○	—	⊕	○	○	○	⊙	○	⊙	⊙	⊙	⊕	○
PHAEOCERIDS	C	○	⊙	⊕	⊙	○	—	○	○	○	—	○	○	○	○	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙
	B	⊕	○	⊕	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊕	⊕	⊕	⊙	⊙	⊙	⊙	⊕	⊙	⊙	⊙	○
	R	○	○	⊕	○	⊕	○	⊕	○	⊕	○	—	○	—	⊙	⊙	○	○	⊕	⊕	⊙	⊙	⊙	⊕	—

TEXT-FIG. 9.—Arrangement similar to Text-figs. 8 and 8A but for *Rhizosolenia alata* and *R. h. semispina*, the Hyalochaetes and the Phaeocerids for the years 1936 and 1937. For explanation see legend to Text-fig. 8.

of C and to be spread over B. The more detailed results for 1936 and 1937 show that *R. h. semispina*, although appearing in the autumn, was more typically a spring form (particularly in 1936), whilst *R. alata* was commonest in the late summer and the autumn. This is also borne out by the less reliable information for the earlier years (particularly on C), and is in general agreement with the findings of other workers (*cf.* Ostenfeld, 1913). Whilst forming "pure" communities of one or the other form (usually one is considerably dominant, even if they are present together), they have also often been found mixed with large numbers of Chaetocerids, and *Thalassiosira*.

A note regarding *R. alata* may be added. Both the forma *gracillima* and the forma *typica* have been common in these records. The forma *indica* has generally been very scarce, but was unusually abundant at the eastern end of line C in the autumn of 1937.

*R. Stolterfothii* H. Pérag. (RT in Plates XXXVII–XLIV.)

Whilst occasionally a significant patch may have been missed in the earlier years, this form being among the more difficult to deal with after some period of preservation on the rolls, there can hardly be any doubt that it was most abundant in 1936, and that 1937 was probably next to that year in abundance. It has been found only once in February, patches being most common in the early summer and sometimes in the autumn. They were found on line R in 1935 and 1937 only, the greatest numbers appearing on B from 1934 onwards, and on C from 1935

onwards. Patches were found at the western ends of C and B, and at the eastern end of B and R, *i. e.* a typical coastal distribution. They have not generally been mixed with large numbers of other forms.

*R. Shrubsolei* Cleve. (RB in Plates XXXVII–XLIV.)

It has appeared in all months, although not in February until 1937. With the exception of one on line B in December, 1933, there were no significant patches until 1935, after which they mainly appeared in the spring, early summer and the autumn. It has been most common on B (particularly in 1936), but was also abundant on R in 1935 and on C in 1935 and 1937. The patches have been mainly spread over the B line, the centre and western third of C and the eastern end of R. On the whole it has tended to be most abundant when other forms were scarcer.

Other species of *Rhizosolenia*.

*R. fragillima* Bergen, *R. delicatula* Cleve, *R. Faeröense* Ostenf. and *R. setigera* Brightw. have all been found from time to time, mainly on lines B and R, and at the western end of C. Perhaps of greater interest was the recording of *R. robusta* Norman on two records for B in October, 1936.

*Chaetoceros* spp. (CH in Plates XXXVII–XLIV.)

We have found it necessary to deal only with the genus, although in 1936 and 1937 it has been subdivided into *Hyalochaetes* and *Phaeocerids*, of the latter group *Ch. borealis* Bailey being the most prominent in this work.

As might be expected they have had a wide distribution as a group, being found in every month, but never on line R in December. The quantities found on B in 1936 and particularly 1937, and on R and C in 1937, were very much greater than in any of the earlier years, there being, *e. g.*, at least an intermediate patch on C in every month of 1937. Most of the larger patches were found in spring, but some occurred in the autumn. Although widespread in space, most patches have appeared towards the ends of C (*i. e.* near the edges of the Dogger Bank), widespread over B and at the eastern end of R. We should note the exceptionally extensive productions in 1937 on C in March and April, and on B in March, June and October: they were also extensive on R in April and May, 1936. In addition there is the unusual appearance of a patch at the western end of line R in September, 1937, this being an area which is usually devoid of diatom patches.

Although they very often appear in great numbers alone, they have been frequently mixed with large numbers of *Thalassiosira*, *Thalassiothrix nitzschioides*, *Asterionella japonica*, *Rhizosolenia alata* and *h. semispina* and other forms in varying proportions.

*Biddulphia aurita* (Lyngb.) (BA in Plates XXXVII–XLIV.)

Although this is a small form, the major patches have usually been so dense that it is unlikely that any important ones can have been missed. It has had a very limited distribution in time, *viz.* February and March, 1933–37, January, 1933, 1935 and 1937, April, 1935–37, May, 1933–35, August, 1932, October and September, 1933, November, 1935, and December, 1932 and 1933. In view of other features of this survey, it may prove interesting that all the more unusual occurrences have been in the earlier years, the later appearances being limited to February, March and April, *i. e.* the months in which patches have been most common. The years 1936 and 1937 had the most extensive productions, although 1933 produced by far the densest patch. All have been limited to the eastern ends of lines B and R, and the western ends of B and C. Although often dominant, it has commonly been found with *Asterionella japonica* and some other early spring forms.

*B. regia* M. Schultze, *B. mobiliensis* (Bail.) Gran in Van Heurck, and *B. granulata* Roper. (BR in Plates XXXVII–XLIV.)

The three species have been grouped together for this survey, but it should be quite possible to separate them in the future, thus providing more information regarding their little-known relationships and distribution. There is no doubt, however, that most of the significant patches have been restricted to the former two species and mainly to *B. regia*. As a whole they have been seen in every month and were undoubtedly most widespread in 1937, 1933 being second and having the denser patches; there were no patches in 1934. No patches were found on line C, and on B and R almost all were restricted to the east, and were limited to the spring and the autumn.

*B. rhombus* (Ehr.). (BRH in Plates XXXVII–XLIV.)

This has been found most frequently on line B, less often on R, and rarely on C. The occurrence has been mainly autumnal; 1934 and 1935 were probably the dominant years on B, with 1937 on R. It has been scarce on the whole.

*B. alternans* (Bail.) Van Heurck. (BT in Plates XXXVII–XLIV.)

This has been very scarce until the autumns of the years 1935–37, there being only one earlier observation. Mainly it has appeared near the eastern ends of lines B, C and R. The only patch occurred on B in September 1937.

Other species of *Biddulphia*.

In addition to those mentioned above, *B. obtusata* Kutzing, *B. favus* (Ehr.), *B. vesiculosa* (Ag.) Boyer, and *B. arctica* (Brightw.) Boyer have all been found. They were mainly on R in 1935, although *B. favus* was found on B from 1934–36.

*Bellarochea malleus* Van Heurck. (B in Plates XXXVII–XLIV.)

Because this is a chain form rarely showing less than ten cells at once, it has been thought most suitable to consider only the major patches. These have occurred mainly on line B, less often on R: only rarely have traces been found on C. Whilst it has been found in all months on B, it appeared only in the autumn on C and R. The distribution has been definitely coastal, mainly at the eastern ends of B and R, spreading centrally on occasion. We may note the unusual occurrence of a patch to the west of the centre of R in September, 1937. 1935 was the maximal year on B and 1937 on R, the former providing much the greatest extension and numbers. Patches were absent in 1932 and 1936. Generally it has not been associated with the other forms reviewed in this section.

*Cerataulina Bergonii* H. Pérac.

Although no significant patches have been recorded, this form has been seen fairly often in the later years (particularly on line C), and generally in the spring and autumn. Owing to its fragile nature the apparent absence of this species in 1932 and 1933 should not be given too much weight; in these years the rolls were stored for a considerable time before analysis.

*Ditylium Brightwelli* (West). (D in Plates XXXVII–XLIV.)

This has been found at times in the midst of dense patches of *Biddulphia sinensis*, and in these conditions it is possible that some of the lower values may be too low, but it is unlikely that any appreciable patches have been missed and, in fact, the only ones to be recorded were in the spring and autumn of 1937, near the centre of line B. The traces have also tended to appear at these seasons. It has been scarce on line R and very scarce on C.

*Eucampia zoodiacus* Ehr. (U in Plates XXXVII-XLIV.)

This has had an interesting time distribution since no patches were found until 1935, when they appeared on all three lines. It was definitely maximal in 1936 and scarcer again in 1937, and was limited to the northern lines in these years. With the exception of the one patch in July, 1935, it has been scarce on line R, being entirely absent in 1933 and 1934 and nearly so in 1936. Some patches appeared in the spring, but most have been in the autumn, the only July findings being in 1935. They have been most evident at the eastern and western ends of B and C, and the eastern end of R. The unusually dense production in the autumn of 1936 will be referred to again in relation to other features of the survey.

*Asterionella japonica* Hassal. (A in Plates XXXVII-XLIV.)

We have found this diatom throughout the year, although only once in July (on line R in 1935). It has been most abundant on B (1936-37), and least on R, being absent in 1933 and only once seen in 1934, although it was abundant in 1937. Patches were mainly limited to the spring in the early years, but appeared in the spring and autumn in the later ones, the spring patches always being the denser. Generally they have been found over the western ends of B and C, and even over the western half of R in 1936 and 1937. Fairly often they have been mixed with large numbers of *Thalassiosira*, *Chaetoceros*, *Thalassiothrix* and *Navicula* species.

## Thalassiothrix species. (TX in Plates XXXVII-XLIV.)

Whilst it is safer to limit this group to the genus, it does in fact consist mainly of *Thx. nitzschioides* Gran, and only small numbers of *Thx. longissima* Cleve and Gran have been seen over the eastern half of line C (e. g. autumn, 1937). *Thx. Frauenfeldii* (Gran) Cleve and Gran has not been recorded, although the separation of this from the first presents well-known difficulties. At least it is certain that it must have been relatively rare.

The group has been found at all times of the year and patches on each line from 1934 onwards, mainly in the spring, but also in the autumn. On line C they were most abundant in 1937 with 1934 second; highest numbers were attained on B in 1936 and 1937 and on R in 1934 and 1937. The patches have been commonest over the ends of the lines although none have been found over the western ends of R. Unusually extensive patches appeared in 1935 on C, and in 1937 on B and C in March. It has seldom been found "pure", but usually with *Chaetoceros*, *Thalassiosira* and *Asterionella* species.

## "Naviculoids". (N in Plates XXXVII-XLIV.)

Under this very wide head are included a number of *Naviculas* and *Fragillarias*, and occasional other small chain forms which have presented great difficulties for identification on the recorder rolls. However, there is some order in the distribution, and the observations for the whole may have application with the rest of this data. They have been present at all times of the year and patches have appeared on all lines, but only on C in 1933 and 1935, on B in 1935-37, and on R in 1936-37. They have been mainly found in the spring, and have appeared exclusively at the western ends of B and C, but at both ends of R. (The only occurrence at the western end of R was in June, 1937.) Whilst sometimes "pure", they have usually been mixed with *Thalassiosira* and *Asterionella* species.

## Gyrosigma species.

This includes all the sigmoid diatoms (mainly limited to a few types commonly found along with *Paralia*, etc.). They have been found on all lines and in all months, but generally more abundantly in 1935-37, the only patch appearing in 1937 on the extension of C past the old terminus.

*Bacillaria paradoxa* Gmel., Van Heurck. (BCA in Plates XXXVII–XLIV.)

No patches were found until 1936, and 1937 had by far the greater number, most of them appearing in the spring and the autumn; it has been found in all other months excepting January (but only once in December). It has been very scarce on line C and most abundant on R, where most of the patches appeared over the eastern half, as did also the few on B. The most extensive production has been in March, 1937, on R, and it has most usually been found along with *Thalassiothrix nitzschioides*.

*Nitzschia* species.

These are very small diatoms and, since the most usual species, *N. closterium* Ehr., is not a chain form, it clearly cannot be caught in anything like representative numbers by our silk, although under certain conditions it can be very plentiful, the presence of *Phaeocystis* being the most striking. Thus, whilst our records show it to have been present in most months and on all lines, its chief abundance has been in the spring, when *Phaeocystis* is also abundant. For this reason it would be dangerous to discuss variations, since they are here more evidently affected by possible arbitrary conditions than in any other form (the general scarcity of other forms in the presence of dense *Phaeocystis* suggests that this is not likely to play a large part in disturbing their apparent distribution).

It is difficult to decide whether the *Phaeocystis* acts as a very fine filter or whether there is an association between these forms (*e. g.* see Gran, 1902). Ostenfeld (1931) did not find any form other than *N. seriata* to be of sufficient importance to be included in his résumé under the criteria there adopted, thus implying that *Nitzschia* as a whole had been much rarer than *Phaeocystis*, which is included; on the other hand, it has been seen in apparently very close association. It must be remembered that *Phaeocystis* might act as an efficient filter when using tow-nets, as well as with the recorder, and that the apparent association might merely be due to this factor. The point is of interest and worth investigation in the future, but meanwhile we can record that it is not always found in the presence of *Phaeocystis*, and that sometimes moderate numbers may appear in its absence (or relative scarcity). Even on the same record (*e. g.* on line R in June, 1932) at one end *Nitzschia* may be very abundant and at the other very scarce in comparison. As a result of such distributions it became apparent that at times the *Phaeocystis* "jelly" may owe much of its coloration to the presence of the diatom (or has developed it in association), and in some rolls where few or no *Nitzschia* have been present the flagellate has appeared as an almost colourless jelly.

In the presence of *Phaeocystis* the usual form is found to be *N. closterium* (Ehr.), generally in a very slender variety (at times so slender as almost to suggest the possibility of another species); there may, at times, be relatively enormous numbers. In the normal way no attempt has been made to estimate the numbers, since they are considered to be unduly arbitrary, but the numbers have sometimes been so great that an estimate has been attempted of one of the thicker patches, and this suggested a density of some 500,000,000 cells per cubic metre, or 500 cells per c.c. Any such calculation must be considered minimal because (1) it was assumed that the maximum volume of water has flowed through the machine, and this is unlikely in view of the clogging of the silk by *Phaeocystis*; (2) possibly not until the *Phaeocystis* has attained a certain density would it begin to filter the diatoms; (3) the calculation had necessarily to be made from the observed volume which is itself minimal for reason (1) above; and (4) there would be a loss as the result of scraping off the plankton prior to measurement. Clearly, at times the actual density of this form must be very great—much greater than is usually considered possible outside such waters as those of Loch Striven or Kiel.

*N. closterium* is almost as often recorded on line C as on B and R, although on the first line *Phaeocystis* is very scarce; it thus appears to be commoner in the open waters of this area than has usually been thought. Other species have been found, of which *N. seriata* has



probably been the commonest, and although it has never been abundant, it was probably most evident in 1937, whereas if we consider only the areas of denser Phaeocystis, it is probable that *N. closterium* was most abundant in the earlier years.

Other species.

*Corethron criophyllum* Castr. has been seen on lines B and R in 1932 and 1933. *Streptotheca thamensis* Shrubbs. on B, C and R in the autumns of 1936 and 1937; similarly *Hyalodiscus steliger* Bailey. *Melosira Borreri* Greville and *Stephanopyxis turris* Greville have both occurred, the former most in the earlier years and the latter probably more abundant in the later years. Other species which have occurred from time to time will be seen in the representative list on p. 78.

#### *General Annual Distribution and Variations.*

We may now consider the general cycle of diatom production throughout the year. The records of the intermediate and major patches are shown in Plates XXXVII-XLIV, which should enable one to have in view the main seasonal developments in these waters.

Reference to the maps and the general Record List in 'Bulletin' No. 2 will show that from time to time a record is absent on one line or another, and it is clear that such omissions may seriously disturb annual comparisons, either for individual species or for the general distribution for the area. Such omissions have probably been most serious during the months of February and May (*e. g.* on R) during the earlier years and probably contribute towards the relative sparsity of those years, yet we should note that on such records as are available for these periods there is a similar scarcity. Similarly the spring months were not too well sampled on line C. Further, it must be remembered that the recorder will normally record only the denser patches of phytoplankton, and that as a result it is often possible to obtain records showing no patches and which are almost entirely blank. It must not be thought that such records really indicate that no phytoplankton was present (even of the species which are usually caught by the machine); they merely indicate the relative scarcity of the phytoplankton.

As elsewhere in this paper, it will be assumed that the charts will speak for themselves, and the notes will be limited to emphasizing points which are considered of significance and which will be referred to in later papers.

#### *January and February:*

The records are generally thin, but we may note the persistence into January, 1936, of patches of *Rhizosolenia* (*alata* and *h. semispina*), which are almost certainly derived from similar patches in December, 1935 (*cf.* also *R. styliformis*: this form, together with *B. sinensis*, may also "carry over" from the previous year.) In February, 1937, there is a western patch of *Biddulphia aurita*, etc., which will be seen to anticipate the typical formations of March; similarly an *Asterionella-Navicula* patch near the Maas appears to be an early development.

*March :*

It is clear that the growths in the earlier years appear to have been slighter than in 1935-37, and this appearance is reinforced by the associated differences of flora and distribution. The typical growths in the earlier years were eastern, whilst those of 1935-37 were more in the west: whilst *Coscinodiscus* and *Biddulphia regia* were important in 1933 and 1934, the significant forms in 1935-37 were Naviculoids, *Asterionella*, *Thalassiosira*, *Biddulphia aurita* (also present in 1933, but in the east), and *Thalassiothrix*, with *Skeletonema* in 1936 and 1937 and *Chaetoceros* in 1937. Amongst the later years we may note the much more widespread patches on lines B and C in 1935 and 1937, and the central patch on R in 1937.

It will be remembered that patches of *B. sinensis* are not uncommon in this month.

*April :*

Such differences are found again in April, when the general numbers tend to be rather lower. In 1934 a patch appears which should be related to those found typically in March, whilst from 1935 onwards several forms (*Rhizosolenia Shrubsolei*, *R. Stolterfothii* and *Eucampia*) appear which are more typical of later months. In 1937 we may note the absence of *Coscinodiscus* and, as in February and March, the unusual extensions of *Bacillaria* along the Dutch coast.

*May :*

*Chaetoceros*, which was probably the dominant form in April, is very widespread again in May, commonly in association with *Rhizosolenia (alata and h. semispina)* in 1933, 1934 and 1936. *R. Shrubsolei* and *R. Stolterfothii* are common, and we may note the presence of *Eucampia* in 1935, 1936 and 1937. The omission of several important records in May renders comparisons difficult, but in view of some other observations we should note the presence of central patches on line R in 1936 and 1937.

Reference to plates XXII to XXXVI will show also that patches of *R. styliformis* and *B. sinensis* are found in these months.

*June :*

Numbers are very much lower on the whole, although there are still extensive growths in 1937. There were no patches in 1932 and 1933, and very few in 1934, whilst another difference is seen in the unusual appearance of patches at the western end of line R in 1937. We may note again the persistence of small patches of *Bacillaria* throughout May and June scattered in the Dutch coastal waters: otherwise *Chaetocerids* and *Rhizosolenia* spp. were the typical forms.

*July :*

Once again the early years are blank, and in 1935 patches were very few. The dominant forms are *Rhizosolenia* species, as in June, but we may note also the presence of *Eucampia* in 1935 and *Guinardia* in 1937. In this month and sometimes in June we may note the small patches of *R. styliformis* which usually extend into August and appear to be forerunners of the autumn patches.

*August :*

Only *Rhizosolenia alata* and *h. semispina* were found up to 1935, other species appearing in 1936 and 1937, amongst which we see *Bacteriastrum* in both years, the persistence of *Guinardia* and the first appearance of *Bellarochia* in 1937. In the last year *Bacillaria* shows a general increase, whilst in some years we find the first of the autumnal patches of *B. sinensis*.

*September :*

*Bellarochia* is a typical form, and is the only one in the earlier years. We should note its absence in 1936 and the unusually large development of *Eucampia* in that year. There is also an unusually strong growth, mainly of *Asterionella* and including *Bellarochia*, over the western half of line R in 1937.

In this and the next two months we must bear in mind the large patches of *R. styliformis* and *B. sinensis* which may appear. They also were generally more abundant in 1935-37, and it may be significant that there appeared to be some reciprocal relation between the numbers of the first and those of *Eucampia*. Whilst both were abundant in those years, in 1936 *R. styliformis* was scarcer on the whole and very late in appearance, whilst *Eucampia* was most abundant in that year, and in September and October was plentiful in the area usually occupied by *Rhizosolenia*.

*October :*

Apart from *Rhizosolenia styliformis* and *Biddulphia sinensis* there were practically no patches in the first three years, but many forms show small patches in 1935-37. The *Rhizosolenia* spp. persist, together with *Bacteriastrum* and *Eucampia*, whilst there are signs of further growth of *Thalassiothrix* and *B. regia*.

*November and December :*

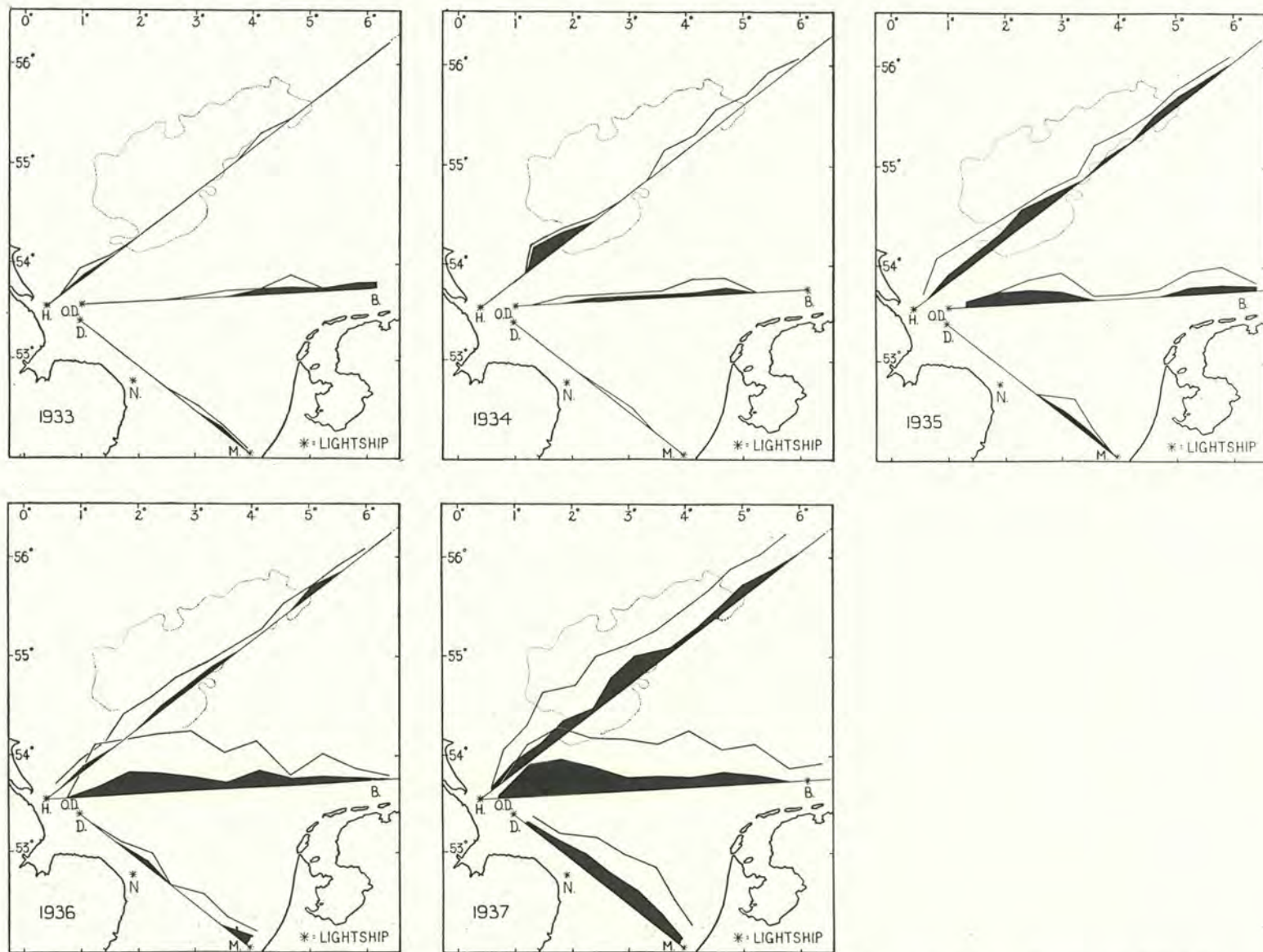
Again the characteristic difference lies in the smaller numbers of the earlier years. *Rhizosolenia* and *Thalassiothrix* are typical species, but we should perhaps note the rather early growth of *Naviculoids* and *B. aurita* in December, 1933. *R. styliformis* and *B. sinensis* are now decreasing and generally situated more to the north-east, but they may well persist into the next year.

*General.*

It will be seen that there are certain trends common to all the years to a greater or lesser extent. These include the production of spring patches, based on *B. aurita*, *Asterionella*, *Naviculoids*, *Thalassiothrix* and *Thalassiosira*, and leading up to a dominantly *Chaetocerid* complex. This is followed by extensive productions of *Rhizosolenia* spp. in the late spring, smaller numbers throughout the summer and further development in the early autumn in association with, or followed by, secondary maxima of certain of the spring forms, and the appearances of other forms, such as *Bellarochia*, *Bacteriastrium*, *B. sinensis* and *R. styliformis*, which are normally only found in the autumn as large patches. On this basic theme, which is essentially in agreement with the findings of earlier workers, there are large numbers of variations in the annual cycles, and it is by means of these that we should ultimately be able to characterize the different years, relating the differences to hydrological features and to variations in the commercial fisheries. Such characters have been the variable appearance of patches of *Coscinodiscus*, the extensive production of *Bacillaria* along the Dutch coast in 1937, the unusually high production of *Eucampia* in the autumn of 1936 in association with the much lower production of some other forms at the same time. In addition we may note the more extensive productions in the later years, and in particular the apparently unusual (within these records) production of patches in 1936 and 1937 over the generally barren area between the Dudgeon and the Newarp Light-vessels. These last features are summarized in Text-fig. 10, showing the overall numbers of patches<sup>1</sup> over the different parts of each line for each year from 1933-37. These figures present only the most tentative assessment of the overall numbers, based upon the number of occasions in each year that patches of different diatoms have been recorded in different parts of the area. No allowance is made for the varying size of the forms, nor can we allow for the occasions when a region has not been adequately sampled at a time when large patches may have been present (*e. g.* the spring of 1936 on the C line). Apart from the obvious difference of the total quantities there are quite striking differences in position: during the first years the diatoms tended to appear more at the edges of the Dogger Bank, whereas in 1936 and 1937 they have been more widespread and even central. On B line there has been an increasing development of westerly patches with the passage of time, and on R, as we have seen, a similarly-marked westerly progression has occurred.

In general there is a contrast between the years 1932-34 and 1935-37, the early years and the last being extremes in many examples, yet, although there is this difference, it is not progressive in all respects, and in many features 1936, for example, tends to be somewhat retrogressive, whilst 1935 and 1937 are more similar. Also the year 1934 is perhaps less like the later ones than is 1933. Many of the characteristics seen in reviewing these forms may remind the reader of those found in discussing the diatoms, *R. styliformis* and *B. sinensis* and to be seen in the

<sup>1</sup> *i.e.* of patches of diatoms other than *R. styliformis* and *B. sinensis*.



TEXT-FIG. 10.—Charts showing the broad indications of the varying productions of the diatoms other than *Rhizosolenia styliformis* and *Biddulphia sinensis* during each of the years 1933 to 1937. The occurrence of medium patches is indicated by the continuous open line and major patches by the blacked-in line. For further explanation see text.

Dinoflagellates and Phaeocystis, and there seems little doubt (see later) that such common differences are to be related with significant changes which can be shown for the current systems of the area during this period.

#### DINOFLLAGELLATES.

For the first few years the Dinoflagellates (practically all Ceratia) were necessarily treated as a whole group; later it became possible to subdivide them. Not all the records of 1935 were so treated, but with one or two exceptions in the early part of 1936, when the group was scarce in the plankton, the data for 1936-37 has been. From 1938 onwards a more detailed treatment is being adopted. In order to maintain continuity over the whole period distribution graphs and serial charts have been presented for the whole group, and much of the discussion must necessarily refer to these as the only consistent data. When using the graphs one should remember that they have not been plotted on the same vertical scale as that adopted for the rest of the phytoplankton. Comparison of Plates XVII and XVIII (in which some totals for 1935 are shown on the new scale), with Plates XI and XII (the standard graphs for totals on the usual scale) will show the relationship between the results from the two methods. That for the whole group emphasizes the maximum, whilst the variable scale used for the species emphasizes the smaller patches by exaggerating their scales relatively, although the maxima are still clearly shown.

#### *Bremen Line :*

The distribution is shown in Plates XI and XII along with that for Phaeocystis, the Dinoflagellate graphs being blacked in. The arrangement of these graphs is similar to that of those already seen with the exception that the asterisks here denote the absence of patches, since traces are usually so common that they have not been shown. In January, February and March the numbers are usually low, but we may note small easterly patches in 1934 and 1936, and more central ones in 1937. The first significant patches have usually appeared in April and early May, the numbers increasing rapidly to a maximum in May or June. The greatest numbers have been mainly central in 1932-34 and 1936, more westerly in 1935, and mainly eastern in 1937, although more or less appreciable growths have been found elsewhere in all these years. Later development has varied, there sometimes being a decline after the maximum, followed by a recovery, although this was not evident in 1933 and 1936, and was less marked in 1935. In general the patches composing this second maximum have been over the eastern end of the line, and in 1935, a typically western year in general, these patches were close to the Borkum Light-vessel, and included one of the densest recorded on the line.

The limitation of most of the 1935 patches to the west seems worthy of note, the highest numbers on this line appearing in a similar position from the end of

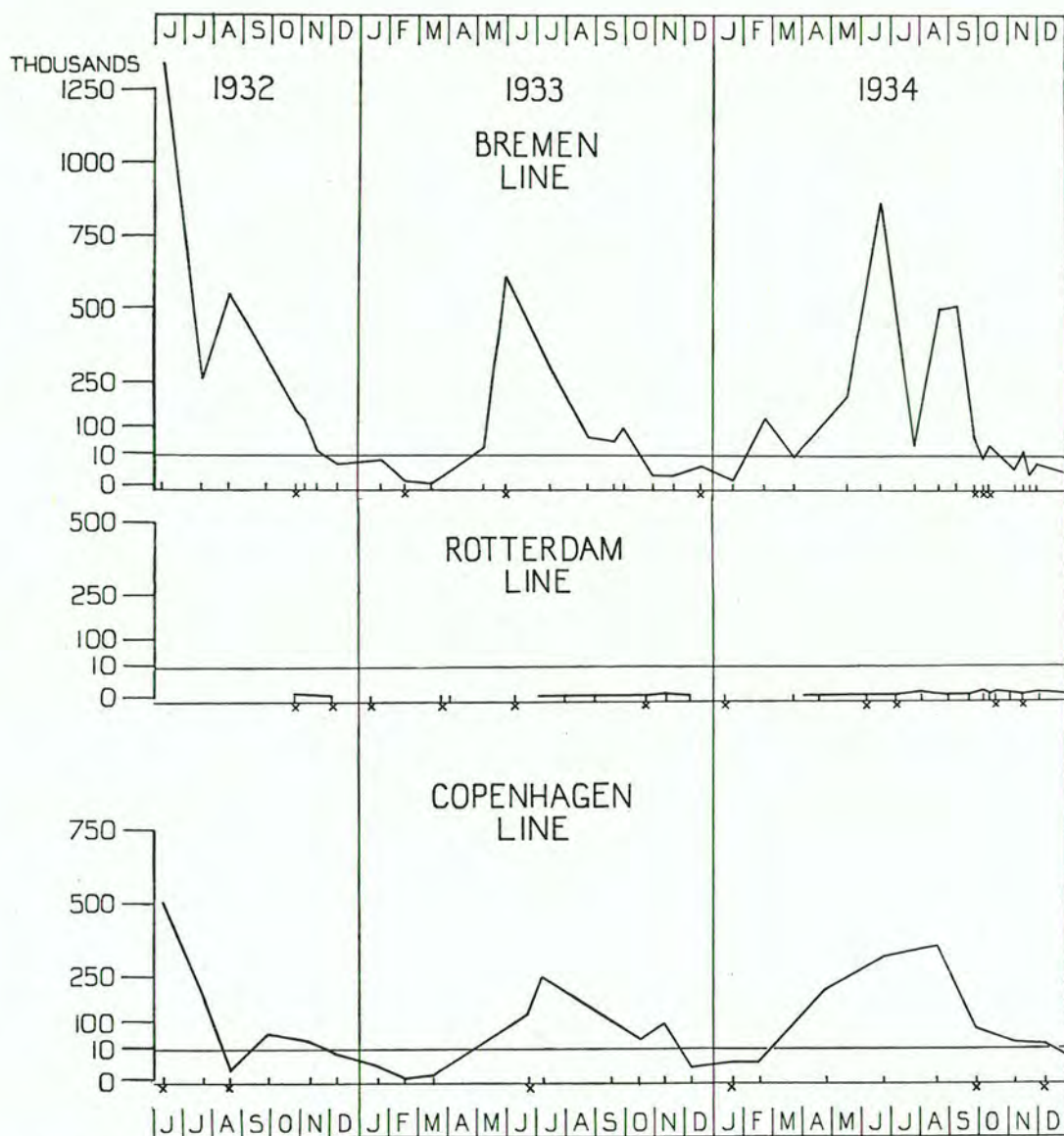
April to mid-August, after which they rapidly declined. In 1937 the main patches were confined to the east, and unusually large numbers were found in that year.

Quantitative variations may be seen more clearly in summary form in Text-fig. II. In distinction from the diatoms there is a less evident increase in quantity over the period of the survey; although the numbers in 1937 were very high, those for the partly sampled year 1932 must have been nearly as high and possibly higher. The year 1933 presented the lowest concentrations. This diagram also brings out the seasonal variations already noted, and we see that except in 1933 and 1936 the graphs show two modes: this is a reflection of the early autumn decrease and recovery already noted being most marked in 1934 and 1937, and less so in 1932 and 1935. We may also draw attention to the very slight peak at the end of September in the 1933 graph. It is proposed to refer to the two modes as the "Primary", being the earlier and larger, and the "Secondary"; reference back to the annual graphs will show that the secondary peak has been due mainly to an increase in the easterly components of the patches (in 1937 there was the exceptional large westerly patch at this time also).

#### *Copenhagen Line :*

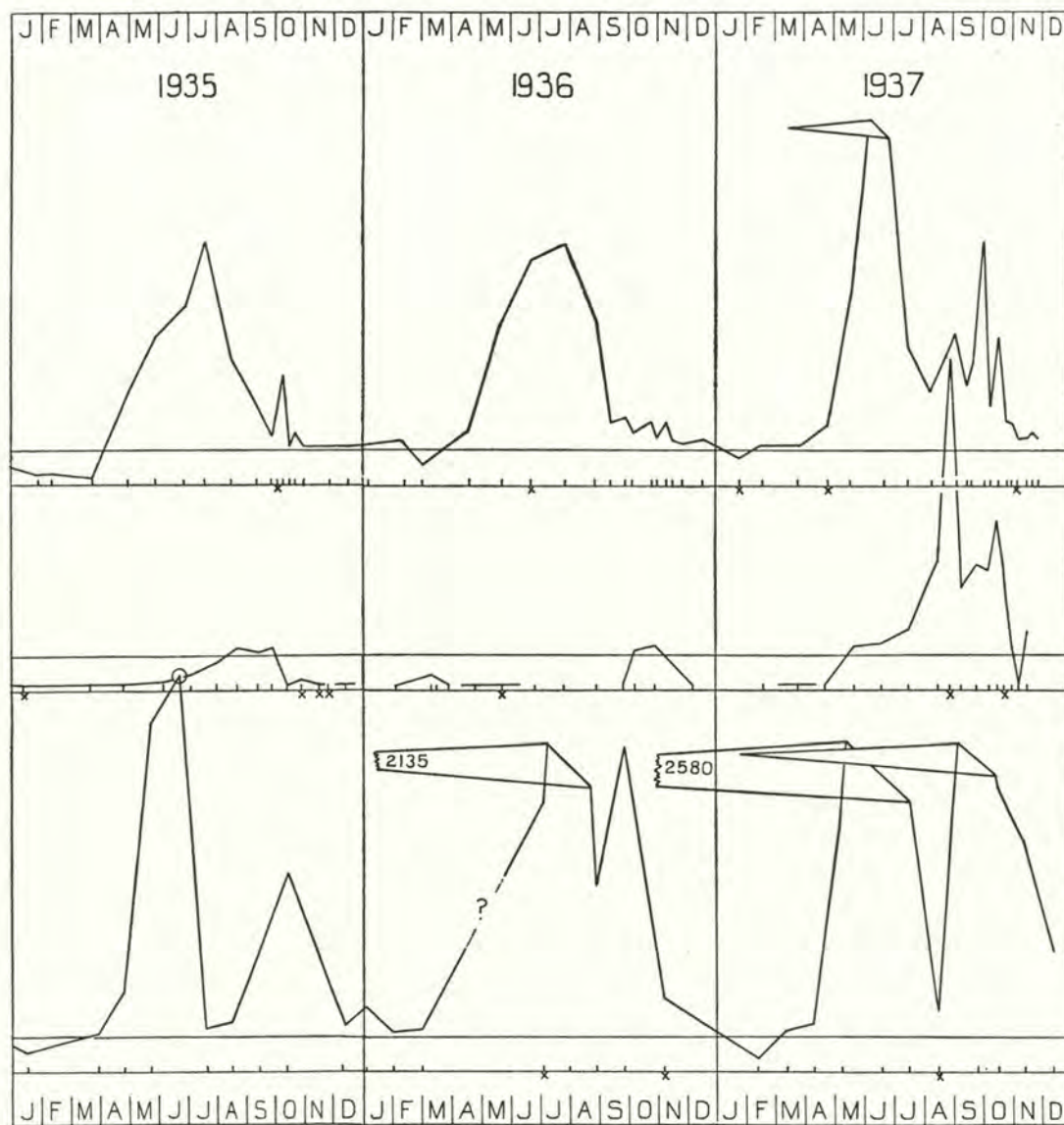
The distribution is shown in Plates XIII and XIV. As on the Bremen Line, the numbers were very low in January, February and March, but such records as we have for April showed an increase. This continued in May, leading to maximal numbers in June or July. Again in some years this has been followed by a decline and subsequent recovery (clearly shown in 1935-37), but in other years only a decline. In October, November and December the numbers have always been lower again, although in 1937 they were relatively very high for this period.

In this main development towards a summer maximum the annual cycles have been reasonably similar, but differences may be seen, both in the numbers found and in the spatial arrangement. From 1932-37 there has been an increasing tendency for the records to be dominated by patches at the eastern or western ends of the line (*i. e.* near the old termini for this line, although in 1937 we also recorded large patches to the east of the old terminus). The year 1935 was interesting in presenting some rather regular features. At the end of March there were small eastern and western patches and, as far as our records go, such patches (particularly the western ones) are found within a small area from record to record. Although there was no western patch in April, well-defined traces were present, and a small patch in May is followed by a dense one in June, small ones in July and August, denser again in September, and smaller ones in October and December. The eastern ones are not so regular, but the series as a whole makes it necessary to recall a rather similar persistence of patches and traces of *R. styliformis* on the Bremen Line over a similar period. If such regularity is not so apparent in 1936 and 1937, yet the terminal patches are even more obvious, the western ones being dominant in 1936 and the eastern ones in 1937.



TEXT-FIG. 11.—Graphs showing the fluctuations in the total numbers of Dinoflagellates recorded between June, 1932, and December, 1937. The records for the Bremen line (between Outer Dowsing and Borkum light vessels), the Rotterdam line (between E. Dudgeon and Maas light vessels) and the Copenhagen line (from Humber light vessel for 250 miles towards the Hanstholm) are shown separately. Above and below are time scales in months: J., F., M., A., etc. Each point on a graph represents the total number of Dinoflagellates found on one record: the exact position of each record in relation to the time scale is shown as a small vertical line against the base line of the graphs. The scale of numbers is in thousands per record, with an exaggerated lower end below the true base-line, as in Text-fig. 5. Records covering less than half the standard distance (see above) have been omitted unless where indicated, as an open circle; records covering less than 80% are indicated by an x.





TEXT-FIG. 11 (continued).—(The very high peaks in 1936 and 1937 are shown folded over to the left for space economy.)

The general arrangement and some annual variations are emphasized in Text-figs. 12 and 12a, showing the maximal quantities from year to year. The varying weight of the easterly and westerly components is brought out (we must allow here for occasions when one or other end of the line has not been sampled), and also that of the more or less marked central one (often due to patches at the

I, 3.

end of the year). The overall graph for the period shows how the greatest numbers have been found in the east and the west.

Unlike the Bremen Line there was, on the whole, a progressive increase in numbers over the six years. In some years there was a marked fall in numbers and a later increase in the early autumn, as is more clearly shown in Text-fig. 11, giving the total numbers on the line month by month. In 1935-37 we have the best examples, the secondary modes being very small in 1932 and 1933, and, if present, only appearing as a slight inflection in the general downward slope in 1934; the dip in 1936 was appreciably less than in 1935 or 1937. The fact that these bimodal tendencies should appear in Bremen records and in Copenhagen records suggests that they may have real significance. The progressive increase in numbers is shown to begin probably in 1933 (there is little doubt that the poorly sampled 1932 should have produced much larger quantities than 1933), and it extended to 1937.

*Rotterdam Line :*

The distribution is shown in Plate XV (continuous line), a characteristic being the usually low numbers compared with those of the previous lines. The low numbers of 1932-36 (and particularly 1932-34) are the more pronounced in view of the relatively very large numbers found in 1937. Whilst patches were almost absent in 1932-34, the numbers were relatively quite high in 1935, and patches were found on several records. In 1936 they were lower again, only one patch being found.

Dinoflagellates have been found on all parts of this line, but larger numbers have occurred in the eastern sector. Although occurring all the year round, they have been more numerous in the summer and early autumn. In 1935 the patches were limited to the eastern side of the line. In 1937 they spread well over to the west, beginning in May with a small easterly patch; larger ones in June and July were in the centre, followed by still larger patches from August to October, which were at first eastern and then bimodal (east and centre), the bulk lying near the Maas Light-vessel. Only a smallish patch was found in November and only traces in December.

The differences between the six years appears most definitely in Text-fig. 11, if we consider that part of the graph lying above the true base-line (see p. 92). The quantities in 1932-34 were so small that they would not have been visible above the true base although they appear here on an exaggerated scale below it. In contrast 1935 and 1936 appear above the line (1936 being lower than 1935) whilst for all the shortness of this line the year 1937 provides a graph comparable with those of B, C and H. The relatively enormous increase found should indicate a change of fundamental importance during the period, and this is emphasized by the recording of numbers similar to those of 1937 in 1938.<sup>1</sup>

<sup>1</sup> See, however, Addendum on p. 168.

*Esbjerg Line :*

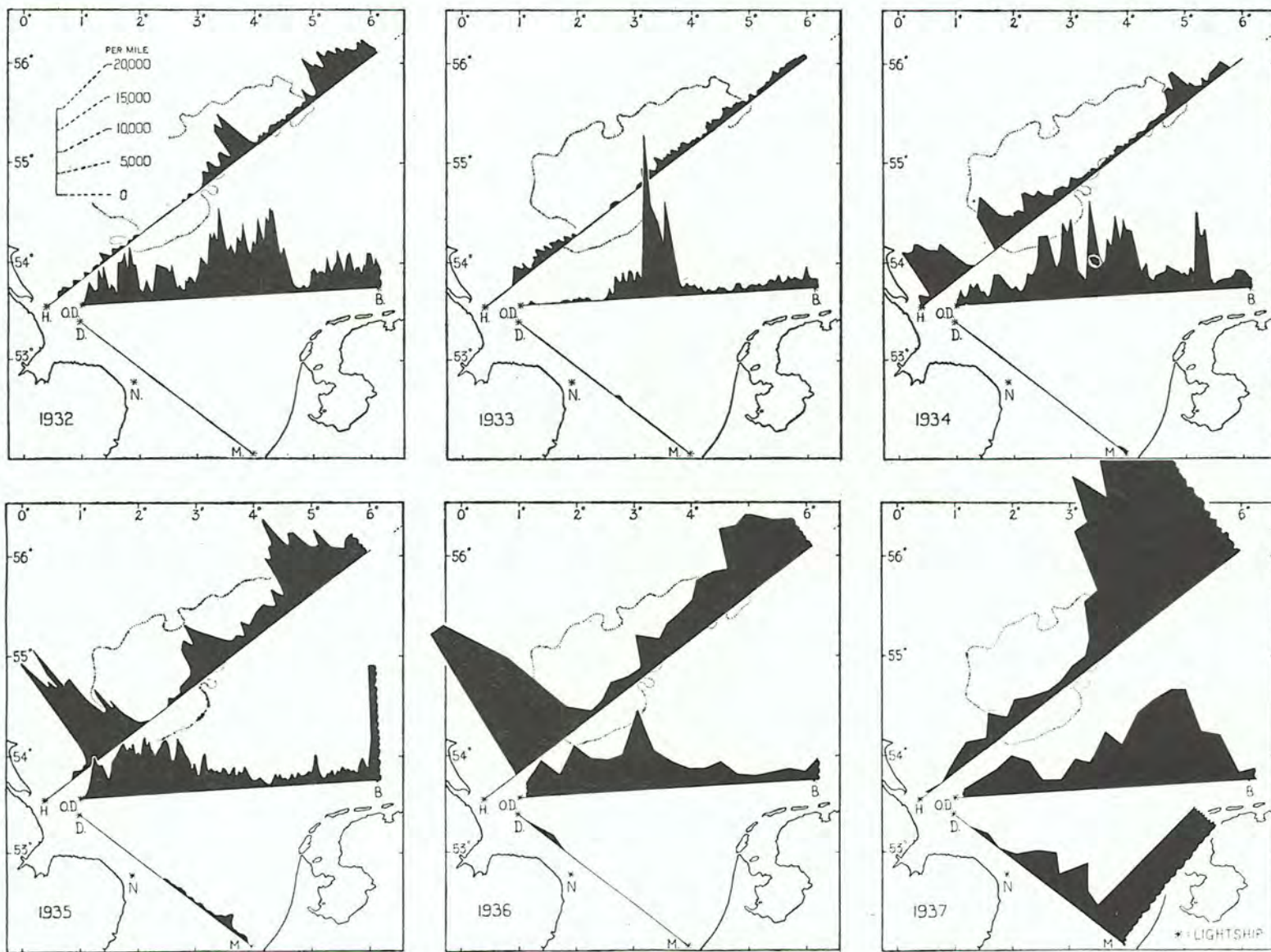
The data on the whole show a cycle similar to those already seen, there being a summer and early autumnal maximum. In 1937, the only year adequately sampled, the bulk of the Dinoflagellates were found to the east of the centre, although patches extended almost to the Sunk Light-vessel (Plate X). We may note also the particularly dense patch near Graadyb at the end of July.

*Distribution over the Area.*

The serial charts for the Dinoflagellates are shown in Plates XLV to LVII, the graphs being blacked-in in contrast to those of Phaeocystis in broken line.

In March and April the first small patches usually appear each year and are typically at the eastern and western ends of B and C, being perhaps most evident in the east. Thereafter there is a great increase in numbers until June, and the main trend of events has taken three main courses during the period ; in 1932-34 and in 1936, whilst there are still greater or lesser eastern and western components (mainly on C), the bulk has been found on the centre of B and there were appreciable central patches on C, although no patches were found on R. In 1935 and 1937 one or other of the eastern or western components dominates the picture, primarily the western in 1935 and the eastern in 1937, whilst in the latter year also the first patch on R was found, in the east. During July there is generally a decrease in numbers (in August in 1936), whilst in the following months there has been a more or less marked recovery in 1932, 1934, 1935 and 1937, particularly in 1937 if we include under the head of "recovery" the enormous increase on R at that time. During the month of July the characteristic distribution of the years was generally maintained, although in 1936 we can note the dominance of the terminal components on C. Later the numbers tend to decrease (the month varying according to the year), and by October the bulk tends to be in the east on one or more lines in each year, although at different times we can note the appearance of patches near the Humber (also on R in 1936 and 1937). In contrast to the only other significant patch on R—October, 1936, in the west—the eastern growths in 1935 and particularly in 1937 form important deviations from the "normal" as seen during the period. In November and December patches are generally low and scattered, but progressively larger and more abundant during the period. Those of January and February, which seem logically to be connected with the previous years' growths, are fewer and scattered, February probably providing the termination of the cycle for these forms as a whole.

The deviations are here perhaps even wider than in the previous forms discussed, and this may well be due in part to the heterogeneity of the group. Some have been necessarily pointed out in reviewing the course of the annual cycles, and other details must be left until they may be referred to in relation to other factors, but in Text-figs. 12 and 12a some of the differences are emphasized graphically. Text-fig. 12a shows the maximal numbers found on all parts of the lines during



TEXT-FIG. 12.—Charts showing the maximal quantities of Dinoflagellates in numbers per mile (scale inset) recorded in each year at different points along the three lines. Note that 1932 was incompletely sampled.

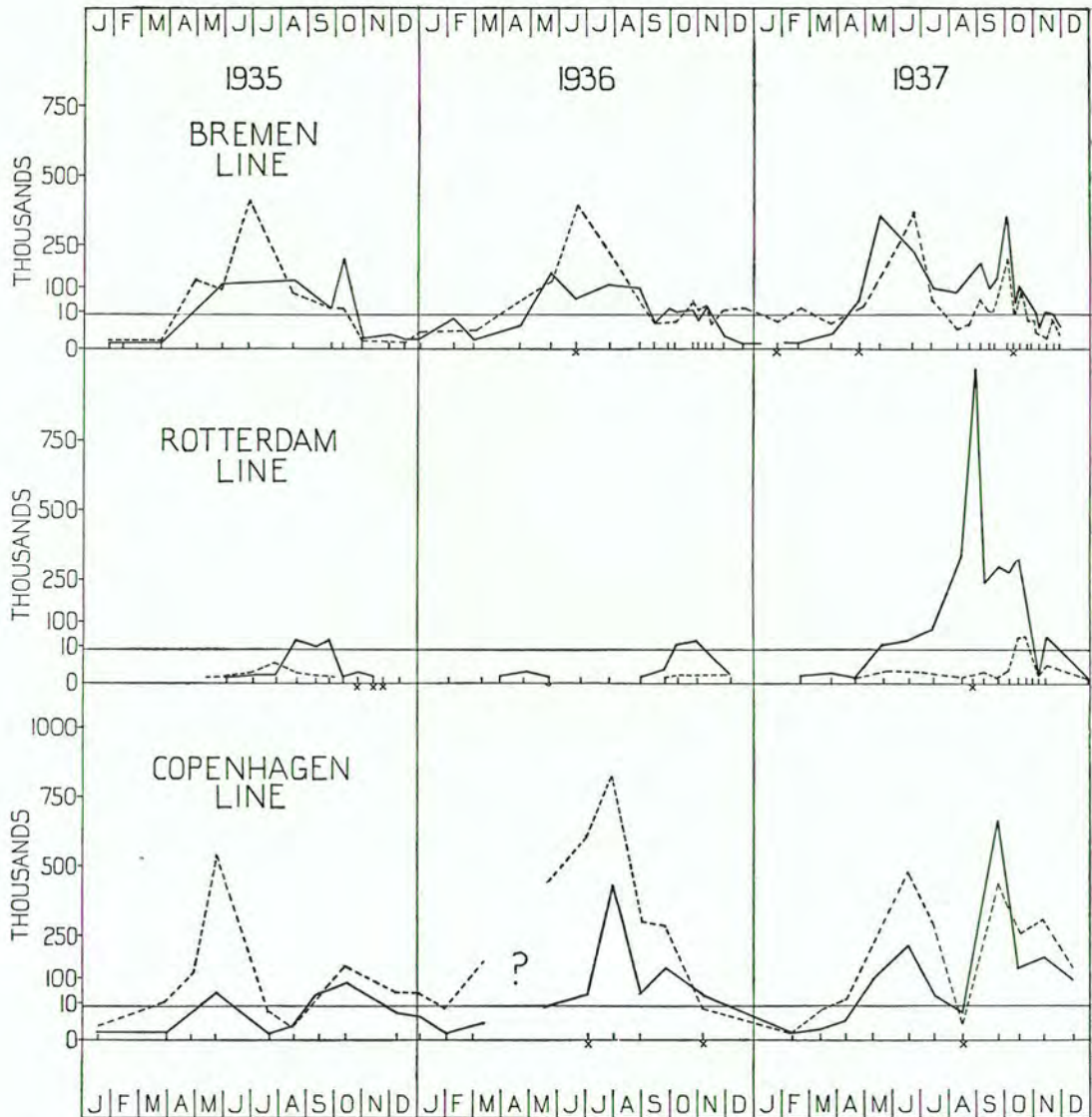
the whole period, and the regions of "maximal" numbers have been over the east of B, C and R, the centre of B and over the west of C. In other words the greatest quantities have been at the edges of the Dogger Bank (to the west, the east and the south) and along the Dutch coasts. Large patches have been rather scarcer in the centre of the Copenhagen Line, over the western half of B and, except in 1937, generally over the Southern Bight. The several years have shown a varying emphasis on these areas which should provide standards for comparison with other forms and other periods.



TEXT-FIG. 12A.—Charts showing the maximal quantities of Dinoflagellates in numbers per mile recorded over the period June, 1932–December, 1937, at different points along the three lines. The separate year charts in Text-fig. 12 are here combined.

#### *Ceratium furca* and *C. fusus*.

In view of the suggestions and findings of Gran (1902, 1912) and others (*e. g.* in contemporary literature, Frost, 1938) regarding the biology of the Dinoflagellates and their relations with the physical and chemical conditions of the water, it seems unfortunate that in the more recent investigations they should have been relatively neglected (see, however, Frost, *loc. cit.*); for our part we must regret that it was not possible to separate from the beginning the different species, at least those of the *Ceratia*, although from 1938 we are undertaking this separation in some detail, and we hope in the future to be able to extend it to include varieties of the most variable "species". It is felt that the methods of the recorder are essentially suitable for investigations into specific variation (providing information regarding



TEXT-FIG. 13.—Graphs showing the fluctuations in the total numbers of *Ceratium furca* (broken line) and *C. fusus* (continuous line) taken on recorder lines between January, 1935, and December, 1937. The records for the Bremen line (between Outer Dowsing and Borkum light vessels), the Rotterdam line (between E. Dudgeon and Maas light vessels) and the Copenhagen line (from Humber light vessel for 250 miles towards the Hanstholm) are shown separately. Above and below are time scales in months: J., F., M., A., etc. Each point on the graph represents the total number of the particular species found on one record: the exact position of each record in relation to the time scale is shown as a small vertical line against the base-line of the graphs. The scale of numbers is in thousands per record, with an exaggerated lower end below the true base-line, as in Text-fig. 5. Records covering less than half the standard distance (see above) have been omitted: those covering less than 80% are indicated by an x.

gradual changes in association with the environment), and we hope to be able to make this a feature of the work, since Gran (*loc. cit.*), in particular, has suggested how these may be useful as guides to important differences in water masses—in fact as “indicators”.

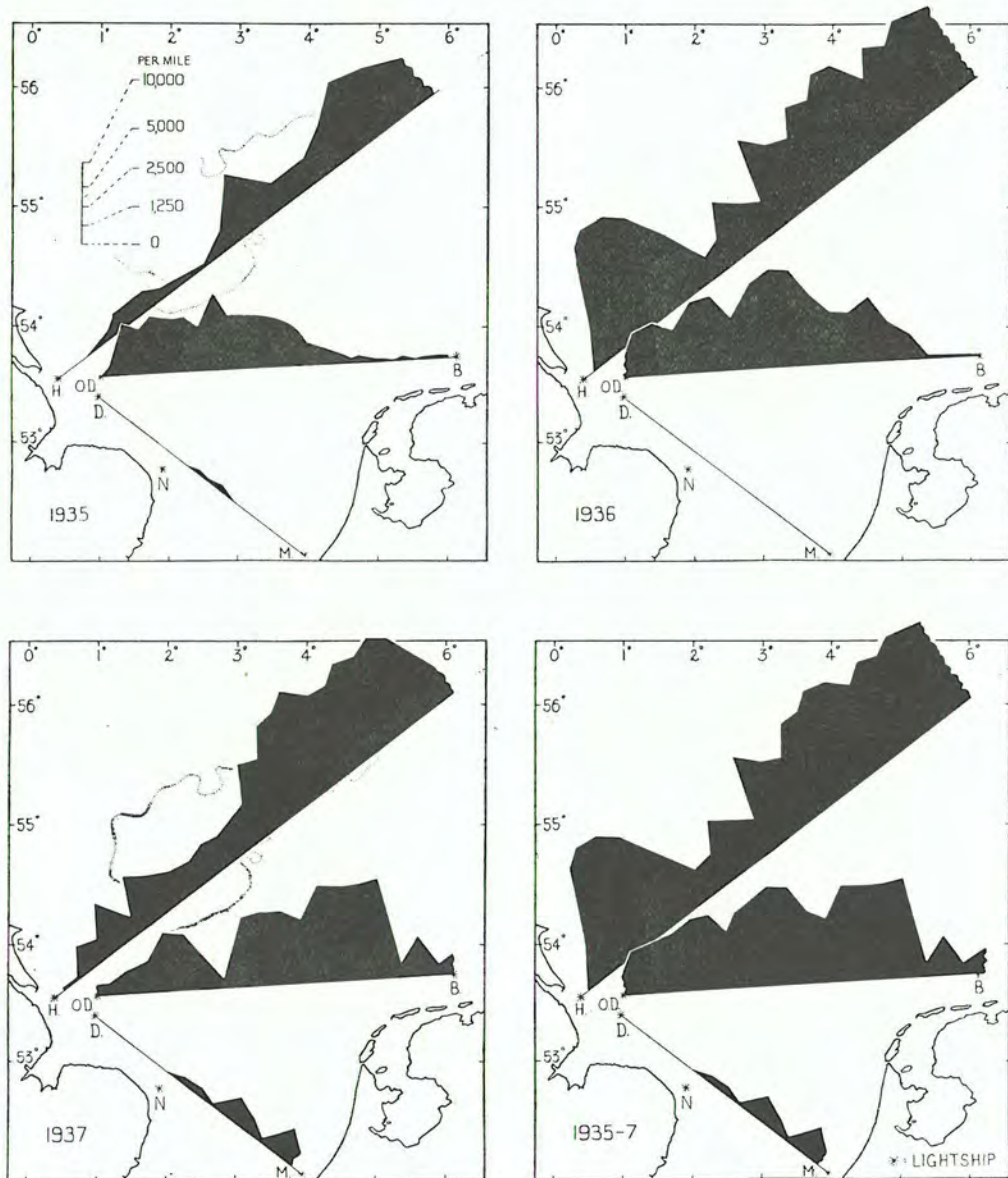
Partly in 1934 and 1935, but mainly in 1936–37, we arranged to separate from the rest the Biceratia and *C. fusus*, the former being almost limited to *C. furca* (*C. lineatum*, *C. minutum* and the biceratioid forms of *C. tripos* being scarce in our samples for this area). The Dinophysids and the non-ceratioid Peridiniidae were also usually scarce. It is felt that little of value would arise from a discussion of the heterogeneous group of other Ceratia, etc., so description will be limited to *C. fusus* and what we propose to term for convenience the *C. furca* group.

On p. 75 we have referred to the analysis of silk scrapings (tube analyses), and from 1932–35 these have given some data, supplemented by notes, regarding the dominant species. This is inadequate for a full description or for graphical purposes, but the chief implications may quickly be summarized. In support it should be said that as far as we had comparable analyses on the roll during 1935 the suggestions from the tube analyses were in general borne out. The 1932 data suggest that on B the proportion of *C. fusus* increased towards the end of the year, and that this form was particularly evident in the eastern patches of the later months. In 1933 it seems to be scarcer, and may only have been significant in the eastern patch of late September on B; the heterogeneous group of other Dinoflagellates was perhaps more numerous this year than in 1932. The small eastern patch of February, 1934, consisted mainly of *C. fusus*, and throughout this year the form was most evident in the east on B, particularly the “secondary” maximum showing higher proportions; it appears to have been more abundant than in 1933, and probably there was a higher proportion of the *C. furca* group than in the earlier years. There seems little doubt that in these years we can say that the earlier patches contained a smaller proportion of *C. fusus* than the later ones. On C, on the other hand, there was no such variation as far as this evidence goes, although there was a suggestion that *C. fusus* was scarce in 1933, compared with 1932 and 1934. The general scarcity of the group on R makes it unnecessary to comment on the species. From 1935 there is more detailed evidence, and we may discuss it in the usual manner in relation to 1936–37.

#### *Bremen Line :*

The western patches in May, 1935 (Plates XVII and XVIII) contained a high proportion of the *C. furca* group, a condition persisting until August, when *C. fusus* had become more abundant; the western component thereafter diminished in proportion to the others. On the other hand, eastern patches showed a high proportion of *C. fusus* from May, when they first became significant, until October, culminating in one of the densest patches of the year and consisting almost entirely of *fusus*. The general trend is not dissimilar from that deduced for the earlier

years, and in particular we see that the secondary maxima have been due to increases in the numbers of *C. fusus*.

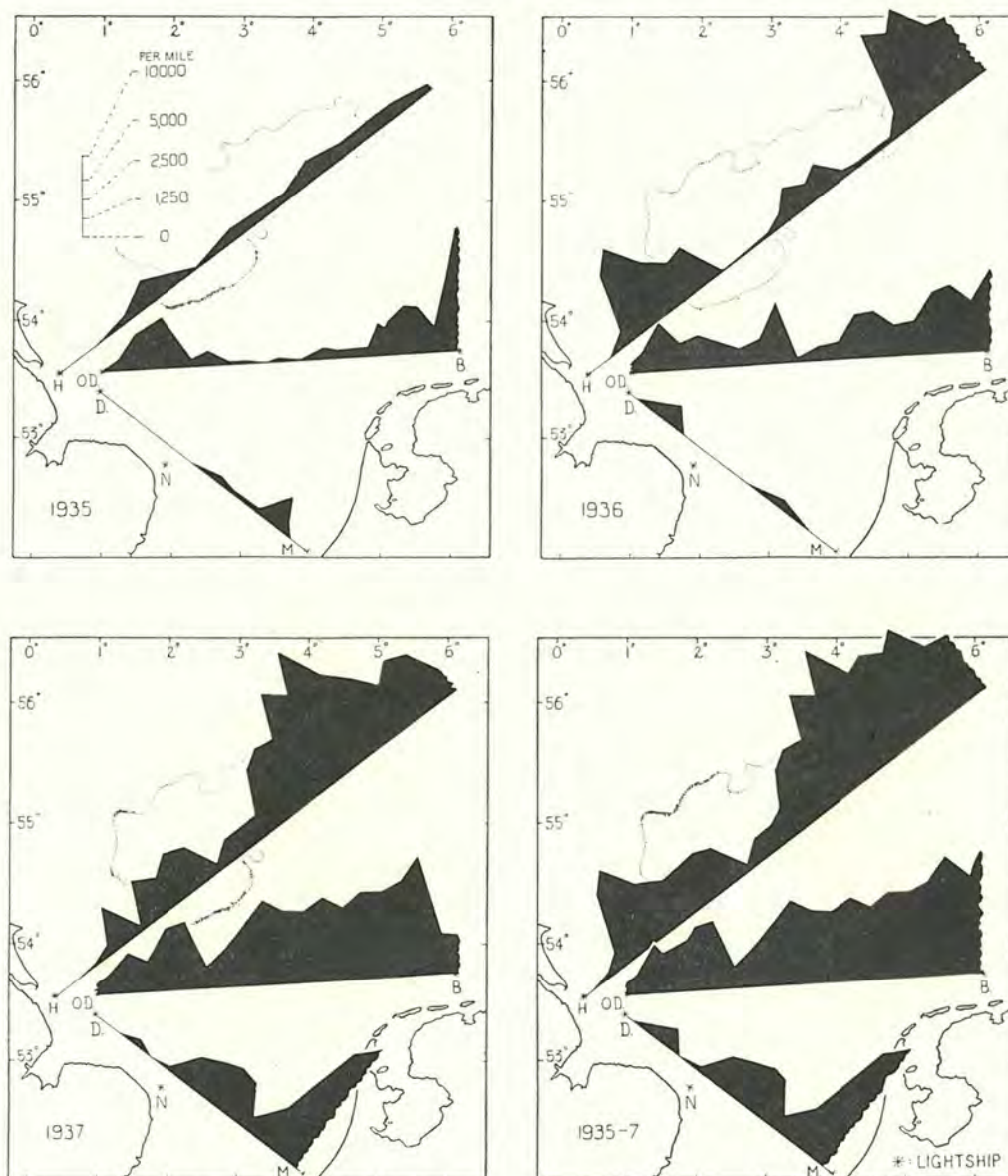


TEXT-FIG. 14.—Charts showing the maximal quantities of *Ceratium furca* in numbers per mile (scale inset) recorded in each of the years 1935, 1936 and 1937, at different points along the three lines together with a chart combining the three years.

In 1936 a somewhat similar sequence occurred, but the summer patches were central. The *furca* group was dominant over *C. fusus* in these, but we should note an eastern patch of *fusus* in May, and its relative abundance in the east from



August, or earlier, although there were no distinct primary and secondary maxima this year. In 1937 the whole *Dinoflagellate* complex was more easterly, and



TEXT-FIG. 15.—Charts showing the maximal quantities of *Ceratium fusus* in numbers per mile (scale inset) recorded in each of the years 1935, 1936 and 1937 at different points along the three lines together with a chart combining the three years.

this is necessarily reflected in the distribution of these forms: usually the dominant one is *C. fusus*, and it is probable that these two facts are associated. In no previous year has *fuscus* been so abundant in the early part of the year, but whilst this was

unusual, it still played a similar part in the autumn and dominated the patches of the east, giving rise to a definite secondary maximum.

Although detailed analyses are not available, reference to Plate XI shows that there could have been no important easterly patches of *C. fusus* in the spring of 1933 since the whole group was scarce there; from 1934 onwards these have been increasingly important. Again, its importance could only have been slight in the autumn of 1933, and it was relatively slight in the autumn of 1936. On the whole it probably increased in numbers from 1933 onwards (appearing to be relatively scarce even in that year of low values), and the maximum was undoubtedly in 1937. For 1935-37 some of these features are shown graphically in Text-fig. 13, and we can see how the relative proportions of the furca group and *C. fusus* may be reversed during each season. There seems good reason to believe that such a change occurred from 1932-34 also. In Text-figs. 14 and 15 the maxima are shown for these forms and the relationships are seen also in their spatial aspect, the furca group being dominant each year over the western sector and *C. fusus* over the eastern one. Necessarily a feature for each form includes a tendency to be relatively more abundant towards the east during the three years, perhaps emphasizing the trend noticed for the whole group.

#### *Copenhagen Line :*

We have already seen that the greatest Dinoflagellate productions on this line appear at the eastern and the western ends with variable patches in the centre. *C. fusus* (Plate XX) takes part in the formation of each of these, but as far as our records go (incomplete in the west in 1936, but supported by some detailed evidence in 1934), it plays no large part in the west until July or later, although being variably important in the east from April onwards, when the first appreciable patches appeared (*cf.* also the Bremen Line). On the other hand the furca group (Plate XIX), whilst contributing to the formation of both types of patch, is proportionately more abundant in the early part of the year, *C. fusus* increasing numerically at both ends towards the end of the year, and sometimes in the centre. It is not, however, necessarily dominant at this time, as we found it to be on B.

In these respects the three years 1935-37 have been sufficiently similar to be described together; a somewhat similar course seems to have been followed in 1932-33 as far as the evidence goes. Differences concern the varying quantities and the primary and secondary maxima. We have suggested that *C. fusus* was scarce in 1933 on this line and probably more abundant in 1934. The year 1935 was perhaps similar, but numbers were higher in 1936, and higher still in 1937, as we see in Text-fig. 13. On the other hand, the furca group probably increased from 1933 onwards until 1936 and then was lower in 1937 (considering only that part of the line between the old termini). The remaining group of Dinoflagellates was definitely most abundant in 1937, increasing steadily from 1935 (and probably 1933). On p. 138 we saw that 1932-34 were low years as a whole, and showed a rather weak trough between the primary and secondary maxima, whilst 1935-37

were all increasingly denser and had more marked troughs, 1936 having the weakest trough. On B, *C. fusus* contributed mainly to the secondary maximum, but here we see that *furca* and *fuscus* both contribute largely, although the proportion of *fuscus* may be greater. Text-figs. 14 and 15 show the maxima over this line; over all there is little difference between the distributions of the two forms, but the *furca* group tends to weigh a little more heavily in the west (the difference is mainly seasonal and not so clearly reflected in space as on B).

*Rotterdam Line :*

This line may quickly be dismissed (Plate XVI). Although not fully analysed, the tube analyses and notes make it clear that in 1935 the relatively large production was due mainly to *C. fusus*, although the more central (and earlier) patches contained more of the *furca* group. In 1936 totals were lower again, *furca* was rare and the only patches were made up mainly of *fuscus*.<sup>1</sup> Until 1937 no patches had been seen before the early autumn, but in this year from May until the dense patches of September and October *C. fusus* was definitely dominant (almost pure patches being common) and only small patches of the *furca* group were to be found in September and October. Throughout the period *Eucratia* were remarkably scarce, although one or two patches appeared in the autumn of 1937.

*Esbjerg Line :*

The only complete series on this line was in 1937 (Plate XXI), and as far as these records are concerned, *C. fusus* was undoubtedly the dominant form, particularly at the southern end of the line. It thus shows general agreement with the other lines, as will be seen in the serial charts.

*Distribution over the Area.*

This is shown for 1935-37 in Plates LVIII to LXIV. It is not possible to give serial charts for the earlier years, but the general picture shown by the notes and tube analyses suggested the appearance at the eastern end of B of patches more or less dominated by *C. furca* in the early autumn of each year, information about the earlier months being less certain. From January to March, in the later years, *C. fusus* is the dominant form, small patches occurring in the east and west of B and C. The total numbers increase considerably in April, the *furca* group dominating sometimes (1935 and 1936) and *C. fusus* at others (1937). Somewhat similar conditions persisted into May, June and July, eastern patches on the C Line in these and earlier years often spreading to the west and consisting mainly of the *furca* group, as also the western patches. On the other hand, *C. fusus* has been relatively more abundant in the east and may even be dominant. Subsequently there has been the usual decrease, and this was followed in 1935<sup>2</sup> and 1937

<sup>1</sup> More "patches" are shown here than in Plate XV (total Dinoflagellates); this is due to the difference between the scales, that for Plate XVI exaggerating small patches.

<sup>2</sup> The patches of Dinoflagellates on B in September and October (Plate LIX, dotted line) consisted almost entirely of *C. fusus*.

by secondary maxima composed largely of *C. fusus*; whilst this was not so clear in 1936 (no sign on B or C), the patch of *fuscus* on the new E line in October (actually overlapping B) suggests that a small increase might actually have been missed then on B. Meanwhile the proportions generally of the furca group have been decreasing and those of *fuscus* increasing, quite appreciable patches appearing near the Humber on both B and C and even on R. The greater numbers, however, have been mainly in the east, this being particularly marked in 1937, and in the unusual numbers found over the eastern part of R in that year. As in the whole group, the distribution in November and December is very irregular, the furca group perhaps dominant on the whole, but we may note a large patch of *fuscus* on the new E line in December, 1937.

The general picture, then, shows the dominance of the furca group in the west, its preliminary importance in the east and subsequent decrease in favour of *fuscus*, together with the temporary appearance of the latter in the west in July, August or September. With these changes are associated the primary and secondary maxima. The annual variations are evident in Text-figs. 14 and 15 (maximal numbers), and have already been touched upon in various aspects. A particularly striking feature concerns the tendency of the furca group not only to be most abundant in the west, but to be relatively more abundant at the edges of patches which may be primarily *fuscus*, and apparently well separated from primarily furca patches.

This picture is in general accord with that of Jorgensen (1910) reviewing the distribution of the Ceratia during the years 1902-08. He found both forms to be common in the North Sea, entering from the North between Shetland and Norway; *C. furca* is suggested to have an autumnal maximum in the area and *C. fusus* one in late autumn, but as far as our material goes we have to conclude that furca had a summer maximum and that *fuscus* has relatively smaller numbers in the summer, its true maximum probably extending into the early autumn. Whilst the former is said to be rarer in the English Channel (and consequently rarely enters the North Sea from there) the latter is more common and, according to Jorgensen (p. 217), "kann aber anscheinend in gewissen Jahren durch reichliche Vermehrung der Art in der südwestlichen Nordsee den Bestand der Nordsee wesentlich vergrössern". It is possible that the findings on the Rotterdam and the Esbjerg Lines may be taken as related to the variable pressure of Channel water, but this is a complex matter, and must be deferred for discussion in a subsequent paper. However this may be, the remarkable variations in the stock of *C. fusus* in the Southern Bight should indicate changes during the period in which 1935 and to a much greater extent 1937, differ from the other years.

It is on the basis of these preliminary results that we feel that more detailed study of the Ceratia may provide useful evidence of long-period changes, and also suitable indications of differences between water masses. Gran (1902, 1912) has stressed the latter aspect, although not in reference to these particular species, whilst Frost (1938) has presented some evidence from Newfoundland waters

regarding six species and the associated water temperatures. Of these *C. fusus* is suggested to have a strong Atlantic water preference, although as the contrasts are between Atlantic and Arctic water in that area, such a preference need not be applicable to the present region. *C. macroceros* and *C. tripos* are found generally to indicate warmer conditions than those for *C. fusus*, and *C. longipes* colder conditions. If correlations of this type can be established and extended during the coming survey it may be that, with limitations, phytoplankton results could be extensively used to supplement hydrological evidence obtained by other means. Such correlations could provide broad indications of marked differences, whilst the material just reviewed for *C. fusus* and the furca group suggests that more subtle differences might be determined by detailed reference to their very closely associated distribution (the changing proportions of the two species at the edges of patches is referred to here).<sup>1</sup>

#### PHAEOCYSTIS.

The analysis of this form has presented peculiar problems in this work. The pressure which it undergoes whilst on the large spool of the recorder results in the colonies becoming quite coalesced and inseparable, appearing as a more or less homogeneous jelly containing a variable proportion of algal cells (and, of course, other forms if present). This has prevented any certain specific identification, although it is probable that by far the greater part, if not all, of the Phaeocystis has consisted of *P. globosa*. A secondary difficulty has been that of distinguishing the thin film of Phaeocystis when catches are low from other common scums and films which also may contain similar but unidentifiable algal cells. Further, it has only been possible to estimate the quantities of Phaeocystis by measurement of the volume after scraping off the silk and settling for periods in standard tubes. This last is clearly unsatisfactory in many ways, of which the most important may be that there is some inevitable (and perhaps variable) loss due to the scraping process, and that this will be a larger percentage when the quantities are low. Further, it is not possible to separate Phaeocystis from the other organisms in the samples, and so the values are necessarily inclusive of the volumes of these. Since it is not often that other organisms are abundant in the presence of dense patches of the flagellate this weighting is less serious than it might be. The most serious effect of these disadvantages arises when volumes are low—that is, the time when identification is most doubtful. In view of this we have set a lower limit, and only patches attaining this limit have been included, even for the sake of consistency, excluding some undoubted patches which only attain values below this figure. All forms of collecting apparatus have a threshold value below which they will not indicate satisfactory forms which are still definitely present. With the recorder this threshold is higher than with most of the more usual samplers,

<sup>1</sup> The results for 1938-39 already suggest that this may not be too optimistic a view.

and in the case of *Phaeocystis* it has been felt that in order to avoid the more doubtful samples it would be quite justifiable to raise this limit slightly.

The values obtained in this way form the basis of the distribution graphs and, as a result of this particular method, it has been possible in some respects to retain more consistency throughout the survey than holds for the diatoms. The chief difference concerns the process of recording in longer units (10-mile blocks) during the last two years. The adoption of the threshold volume leads to the inclusion of samples having lower volumes *per mile* in 1936 and 1937 than in 1932-35, and so apparently more extensive patches may be the result. Another effect of this alteration has led to the type of smoothing referred to elsewhere. Dense patches of small area which would have appeared as such in the earlier years cannot appear so in 1936 and 1937 (*e. g.* a patch providing a volume of 20 c.c. and extending over 2 miles would have been recorded as such in the earlier part of the survey, but in later years must appear as 20 c.c. over not less than 10 miles—a definitive 10 c.c. per mile for 2 miles, as against an apparent 2 c.c. per mile for 10 miles). It is clear that the data have gone through an averaging process, and we must guard against this in assessing the relative productions.

#### *Bremen Line :*

The distribution is shown in Plates XI and XII with that of the Dinoflagellates, *Phaeocystis* being indicated by the broken line. The major patches have been most common in May and June, although a few large ones and some smaller ones have appeared at other times. In this and some other respects there have been similarities between the years, but there are also well-marked differences. On the whole there has been a tendency for much of the development to take place in the east, but this can only be described as the major region in 1932, 1933 and 1937, there being a strong central and even some western growth in 1934-35 and a mainly western element in 1936. There have also been variations in dates of appearance, although as yet these do not seem to call for particular comment. Owing to the problems concerning small quantities, which may yet be appreciable in total quantity over an area, the usual graphs of record totals will not be shown, but there are significant differences, the years 1933-34 and 1937 being probably years of larger production than 1935 and 1936. This difference may be seen in Text-figs. 16 and 16a, where the maximal quantities found on all parts of the line have been plotted for each year.

#### *Rotterdam Line :*

The distribution is seen in Plate XV (broken line). As on the Bremen Line the maximal patches have been found in the spring, and there have been no significant growths during the whole of this survey outside the period March-August. The maxima have usually been found over the eastern half or third of the line.

and in 1932-34 they were limited to this, but whilst in 1935-37 the patches each year began in that region, by June they had spread over to the western coast, the densest areas in the last two years having changed from east to west. There do not seem to have been any striking variations in quantity with the possible exception of the year 1934, in which there was no growth before May (and possibly June), and when only very small quantities were found after the incompletely sampled month of June; this was also the only year in which samples were obtained in August. The general annual distribution is shown in Text-figs. 16 and 16a.

*Copenhagen Line :*

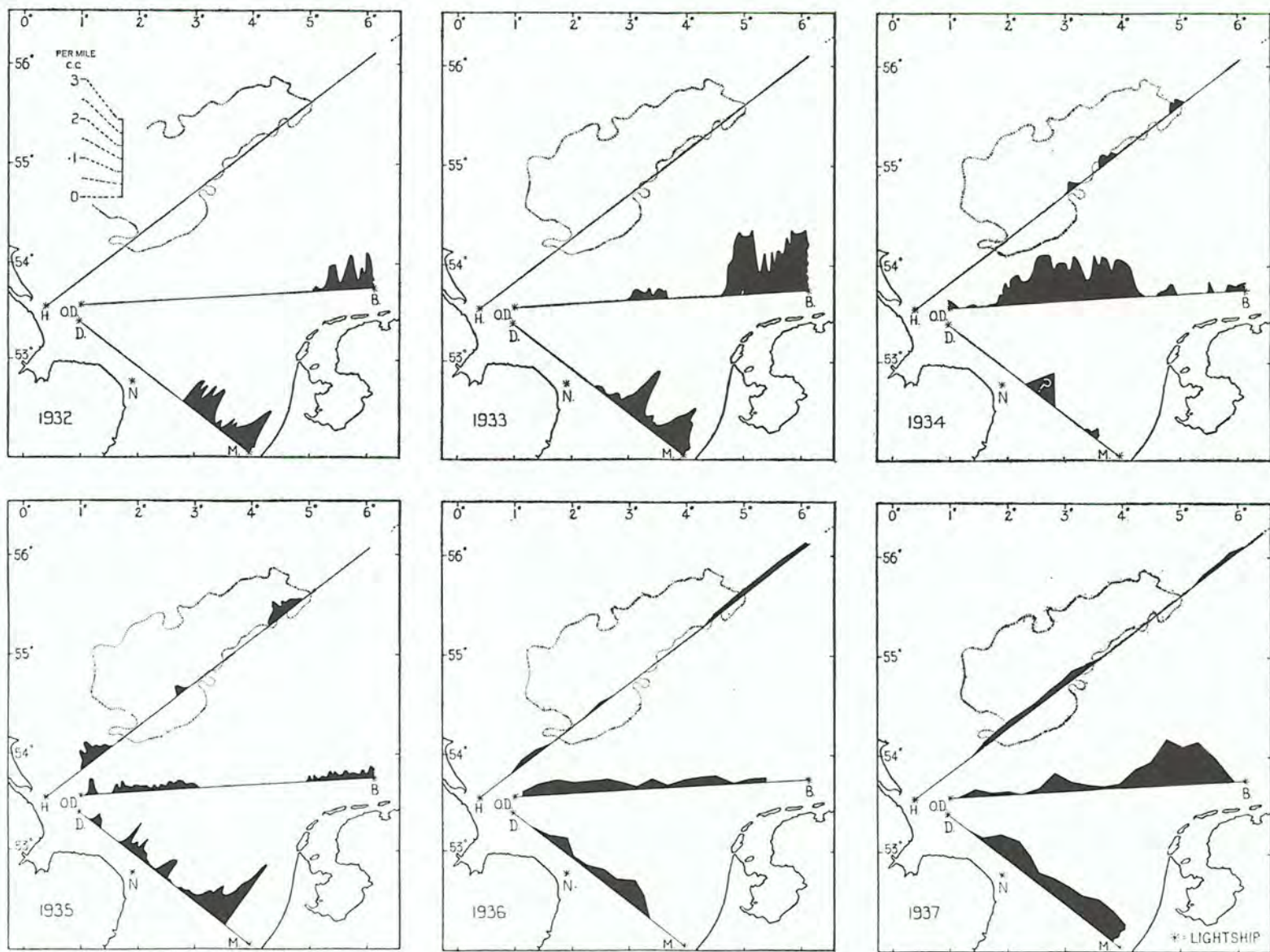
The distribution is shown in Plates XIII and XIV (broken line). No patches were found in 1932 and 1933, and only very small ones in March, April and December, 1934 (the latter is the only occurrence we have for that month). They have been more extensive in the later years (April-July in 1935, at least June and July in 1936, and April-June and August-September in 1937), but even then the densities and extensions in space have been much below those found on lines B and R. Undoubtedly the greatest quantity was found in 1937 (even allowing for the possible distortions caused by the inclusion of smaller amounts per mile).

*Esbjerg Line :*

No records were obtained in 1936 after March, and no Phaeocystis was found. The results for 1937 appear in Plate X; it was widespread in May and June, and small patches occurred at the end of July.

*Distribution over the Area.*

This is seen in Plates XLV to LVII along with that for the Total Dinoflagellates (Phaeocystis shown by the broken line). Whilst these charts reinforce the general conclusions that the greatest bulk has been found in the east, the exceptions are similarly obvious and can easily be compared on the different lines. In particular it now becomes clear that each year (except 1934) eastern patches are among the first to appear, and that later there has been a variable tendency for patches to appear centrally or in the west and the north. The latter may never have occurred in 1932 (we have no information before June, when patches were definitely over the eastern ends of B and R), and in 1933 there was only a slight central extension over B and R in June, the last samples being found in the east again. Both central and northern (C) patches were found in 1934, and in contrast to the previous years patches extended up to the Outer Dowsing Light. The westerly elements dominated on the whole in 1935 and 1936, but although they were still evident in 1937 the strong eastern patch on B is a dominant feature.

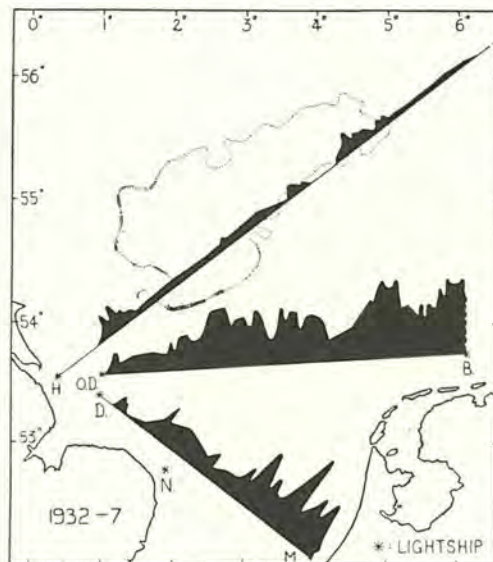


TEXT-FIG. 16.—Charts showing the maximal quantities of Phaeocystis in volumes of c.c. per mile (scale inset) recorded in each year at different points along the three lines. Note that 1932 was incompletely sampled. The “patch” on the R. line in 1934 (labelled “?”) may have extended further to the East.



Northerly patches were found in all these three years, and in the last even extend up to September.

As with the other forms, the differences may be at least as evident as the similarities. For spatial distribution both are summarized in Text-figs. 16 and 16a, showing the maximal annual distributions along each line; they present a general estimate of the quantitative variation over the whole area, and it is evident that we can broadly distinguish the years 1932-34 and 1937 as being dense years, and 1935-36 as being less dense. Other differences concern the general time distributions; although the dense patches have commonly occurred in the



TEXT-FIG. 16A.—Charts showing the maximal quantities of Phaeocystis in volumes of c.c. per mile recorded on the period June, 1932-December, 1937, at different points along the three lines. The separate year charts in Text-fig. 16 are here combined.

spring there have also been small ones in the late summer and autumn, the most extensive being those found in September on C in 1937. Both the spring and the autumn patches are in agreement with the findings of previous surveys in these waters (*cf.* Ostenfeld for a résumé, and Savage and Hardy, 1935, with Savage and Wimpenny, 1936, for some detailed surveys; also Wulff, 1934). The last two of these papers provide actual data for comparison with our records, and in such instances there has been a substantial agreement between results from the two methods, although at times small patches have been found, *e. g.* in the region of the Copenhagen Line and in the south in the autumn, for which we can show little or no data in Plates XLV to LVII. It seems clear that such differences must be due to the very much higher threshold value of the recorder, the quantities at these times being below the lower limits which can be attained.

## GENERAL DISCUSSION.

Professor Hardy has outlined in 'Bulletin' No. 1 the plan on which we are hoping to produce the results of this and the extended surveys. The object is to further the understanding of the North Sea as a whole while relating our conclusions to the broad problems of the fisheries, ecology and meteorology. Although it is convenient to produce the bulk of the data in the rather water-tight compartments of phytoplankton, Copepoda, etc., which we have adopted, it will be necessary later to assess these in relation to the entire plankton community, as far as is possible, and so discussion in this paper will only be brief, and must be limited to outlining some of the more obvious conclusions from the phytoplankton data alone.

*Patchiness in the Phytoplankton.*

Since early in the history of pelagic ecology there has been discussion regarding the regularity of distribution of life in both the oceans and in more coastal waters. Some of the evidence has recently been reviewed by Hardy (1936*b*), who has demonstrated clearly that the oceanic plankton may at times be very patchy. Hensen's hypothesis of even distribution, at any rate in regard to coastal waters, has been more or less rejected for a long time but, although irregularity has been recognized, its existence has not been fully acted upon, and investigation still proceeds, to some extent perforce, *as if* distribution were largely regular (biologically and physically). With the finances available it would rarely be feasible for research ships regularly to cover large proportions of even the North Sea, and yet to take samples less than some 30 to 50 miles apart; the more intensive one survey may be, the longer the time likely to elapse before another may be undertaken. As a result there is a tendency to take samples in order to ascertain variation over the area, and then to assume regular distribution between the stations for the purpose of producing contour lines and a resultant picture of the distribution.

Interpolation, and even occasional extrapolation, are adopted in the process of contouring, and it is important to realize the limitations of the methods, and to have some information concerning the probability that the assumed distribution between a pair or more of stations will be sufficiently like the real one. Workers on a small scale have at times found considerable differences between adjacent stations, Herdman (1923), for instance, finding much greater variation between the catches of similar nets (towed at the same time on either side of the ship) than could have been caused by the errors of random sampling in analysis. Hardy and Gunther (1935) and Hardy (1936*b*) found similar variations between consecutive samples in Antarctic waters, whilst almost any record taken during the period of abundance of any form during this survey shows similar or more pronounced irregularity, varying according to the conditions. The records may thus provide

a means of comparing theoretical distributions with certain actual conditions in the sea—a process which may not only be applicable to immediate pelagic problems, but which could, with suitable arrangements, provide the very necessary checks upon certain principles generally assumed to apply to population studies.

In considering patchiness a word is necessary regarding the accuracy of recorder analyses. It has been explained that the graphs have been produced without any smoothing of irregularities (apart from the automatic action of the recorder discussed in 'Bulletin' No. 1); the immediate data from the analyses have been used and, as in any other process involving subsampling, there are probable errors which arise from that process. Such possible variations must discount to a large extent the smaller irregularities found in the graphs, but apart from these there remain much more significant variations which we may truly describe as showing "patchiness". Typical are the dense and extensive patches of *R. styliformis* in the autumn, those of *B. sinensis*, and the large patches of Dinoflagellates; in addition there are the smaller but still dense patches of these and other forms which occur from time to time (*e. g.* the eastern patch of *R. styliformis* in October, 1935, on the B line, and the patch of Dinoflagellates at the western end of the C line at the same time). Of these, the former would undoubtedly be revealed by the usual methods of plankton survey (as the patches of *Rhizosolenia* and *Biddulphia* have been found), but the latter would not so likely be found, since their small extent places them within the usual distance separating adjacent stations on a survey. Similarly, although the more extensive patches would probably be found, it is less likely that their boundaries would be determined with any precision and, as we may see from a large number of *Rhizosolenia* patches, either or both of their boundaries may be very abrupt. It is this type of abrupt rise and fall in the population which is the important feature of patchiness. I have discussed at some length on p. 83 the relation between a continuous series of samples obtained with the recorder and the impression received from graphs of every tenth sample, by reference to an actual record including such sharp variations. It was seen that a very different picture might be found if samples were even as little as 15 miles apart, and clearly there is greater chance of being misled when the distances are larger. The series of examples shown in Text-figs. 1 and 2 will also demonstrate that no usual system of interpolation could have deduced the real conditions from some of the possible alternatives when the samples were more than a minimal distance apart.

There should be little need to stress the importance of such variations; they suggest sharp changes in the hydrological conditions in most instances, and would be of even greater interest if this were not the explanation. This being so, there seems reason to qualify to some extent the picture produced by contouring between a set of scattered observations. The individual samples have their own undoubted value, but the contours may provide a picture (even apart from the unjustifiable process of extrapolation) which may be ambiguous or even erroneous. The recorder surveys demonstrate the existence and extent of such variations, and there can

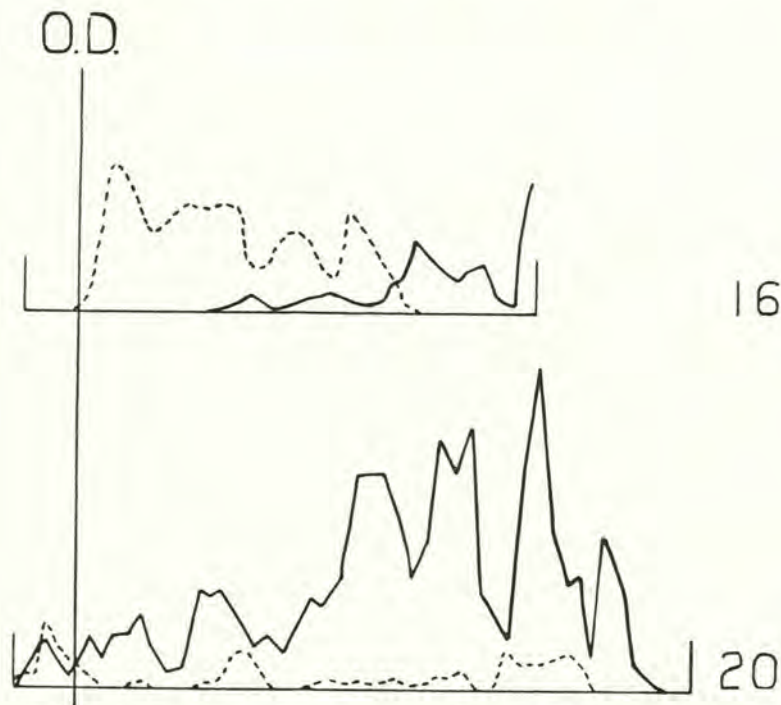
be little doubt that at least some of the divergences between these results and others at the same time in the area have arisen from such factors.

It is unlikely that the limit of patchiness is shown in the graphs: in 'Bulletin' No. 1 Professor Hardy has discussed the "smoothing" action of the recorder, through which there is no doubt that the more abrupt changes have been levelled to some extent. Mechanical "clogging", which has undoubtedly taken place when the plankton was very abundant, will have had a similar effect. The former process will be more effective in the graphs for the years 1936-37, when the treatment of the data in blocks of 10 miles must have masked any of the particularly high peaks which might have occurred. Comparison of these with those for 1932-35 will show that, although sometimes higher numbers were found in the later years, yet during these years no patches appeared similar to that of the Dinoflagellates in 1934, for example; similarly the autumnal patches of *R. styliformis* have not in these years shown such abrupt changes near the Outer Dowsing Light-vessel as were a feature of 1932-35. These changes often occurred within less than ten miles, and on the new system would be more or less smoothed and the slope of the graph would become more gradual. In changing the method we realized that some sacrifice of precision must be made for the purposes of spatial extension, *but the results still are continuous records*, taking in all the data, although giving "smoothed" values at greater intervals.

In the forms which have been more fully discussed in this report the smaller dense patches have usually been at least some 10 miles in extent, and the rapid changes at the edges of patches have often occupied some 3 or 4 miles, but Herdman has referred to patchiness over smaller distances than this, and it is not of purely academic interest to wonder what are the lower limits of patchiness. Whilst our data shows that often the edges of patches may occupy the space of a few miles, at times this has been much less, and during the earlier part of the survey we have often noticed the abrupt change on the recorder silk as occupying only a fraction of the section—and so presumably occurring within a distance of not more than one mile and probably less. For certain purposes there would appear to be good reason for investigating further the details of patch boundaries by means of a recorder working at a ratio of, say, ten sections per mile, or even more. In this general connection we may note that Helland Hansen (1910) saw reasons to believe that the usual distance between hydrological stations was by no means satisfactory, and often misleading, for the important purposes of determining the edges of different water masses, and his earlier work, together with the recent results from the Bergen school (*e. g.* Eggvin, 1937) provide ample justification for such a view. Such results, together with information regarding the plankton, point strongly to the necessity of obtaining hydrological data at much closer intervals if certain types of "water change" are to be adequately understood.

Helland Hansen and also Herdman likewise postulated the probability of sharp changes in time, both providing some evidence of this. The close association between certain changes in space and time in pelagic ecology has already been

stressed elsewhere (Lucas, 1936 and 1938), and there is little doubt that some of their examples concerned temporal changes which, seen from another aspect, would have appeared as spatial variation. It is clear that certain changes observable in the sea at intervals of a week or less might also be seen during one day by an observer moving from place "a" to take samples at "b", which, under the influence of currents, will be due to replace "a" within a few days. On the other hand, there will undoubtedly be other changes due to the growth or death of the



TEXT-FIG. 17.—Graphs of total Dinoflagellates (continuous line) and Phaeocystis (broken line) for the Bremen line on 16th and 20th June, 1934, showing changes of distribution in this short period. The former record was incomplete at its eastern end. The vertical line marked O.D. denotes the position of the Outer Dowsing light vessel. The scale is proportionately as that in Plate XI, which also shows the second graph; this actually extended further to the east than is shown in this figure.

plankton or to physical mixing of the water, which cannot be seen in both ways. However this may be, there are undoubtedly marked changes in time in these records as well as changes in space. A particular one is shown here in Text-fig. 17, the interval between these two records being sufficiently small to render the two records confusing when superimposed in their correct places in the compound graph for 1934. The Dinoflagellates are seen to have increased very much during the four days, and the Phaeocystis patch has almost entirely disappeared. Other examples will be seen in the various graphs, and will at once illustrate the rapidity with which the picture may be changed during a short interval, and also some defects

in both the present and the more usual methods of survey. In so far as such changes are temporo-spatial, then the type of patchiness which the recorder reveals along its line of travel may, along another axis, be the cause of rapid change in that picture; on the other hand, when these changes are more truly temporal the orthodox methods suffer in that their surveys are necessarily at relatively large intervals of time. (For example, the appearance of primary and secondary peaks in the Dinoflagellate maxima in this area reveals a type of temporal change, not over a very short period, which would not be likely to be revealed by the customary quarterly surveys.) Such considerations should also weigh heavily in assessing the evidence of larger surveys, in which necessarily an appreciable time-lag occurs between the first and the last station. Particularly if the stations are not taken in consecutive spatial order, temporal changes may produce great deviations from actuality between adjacent stations. Except for very good reasons an attempt should be made in all such surveys to obtain *adjacent* stations with the least possible delay, and even then due allowance should be made, as Kunne has pointed out (1937), for the time interval between the first and the last. Such changes emphasize the essentially dynamic nature of pelagic ecology (perhaps seen more clearly than in terrestrial ecology), and, in particular, the danger of drawing conclusions too extensively from the values of isolated surveys for certain comparative purposes.

Usually we find that there are one, two or three major patches on the combined graphs for any one month; this in itself may be a feature of interest, but it suggests another aspect of patchiness which may in the future be worthy of investigation. With the data available it should be possible to obtain correlations between the density and extent of patches and, in the case of some which seem to be annual features in this area (*e. g.* the annual patches of *Rhizosolenia*), such measurements should give standards of variation from year to year. Rather similar statistical investigation of patches should over a long period provide information for determining under what circumstances interpolation might be justified. Except in so far as some broad characters of patches in different years have been used here, such an intensive investigation of patchiness must be reserved for a later paper which can assess the subject for other planktons as well. Here we can merely insist on the reality of patchiness for all forms (see also 'Bulletin' No. 4) which have been dealt with, and its importance in plankton ecology. Later also it may be possible to devote some discussion to the causes of patchiness. Some will immediately suggest themselves—the natural growth from a "seeding" in a suitable locality, physical processes such as have been suggested by a number of writers (the suggestions of Helland Hansen would have application here), available supplies of food salts, etc.—but in addition there are biological effects which have been suggested to be important in the formation of aggregations of organisms (Allee, 1931 and 1934, and Lucas, 1938). Continuous records may throw further light on these matters.

*Inter-relationships in the Phytoplankton.*

When the recorder surveys were begun it was hoped that the method would provide a suitable means for attacking broad problems of ecology on a large scale, as well as problems of more immediate importance. One of the more interesting problems in the sea, as elsewhere, concerns the relationships between the organisms themselves in so far as, for the purpose of analysis, we try to distinguish such organic relationships from the "organism-environment" complex in the widest sense (see Lucas, 1938). The continuous records provide a series of correlations between "isolates" of this complex, and although these have not been investigated in detail as yet, certain correlations may be pointed out which will illustrate some possibilities of such work. Here it will not be possible to attempt a separation or analysis between the different factors—this could only be done satisfactorily by reference to detailed hydrological evidence in conjunction with the evidence to be produced in later Bulletins—and only general indications of positive or negative correlations will be made.

Reference to Plates I to X and Text-figs. 3 and 4 remind one that *R. styliformis* and *B. sinensis*, although occurring in the same season, are only for a short time during their annual cycle found together in appreciable numbers. Patches may often be side by side, but only during the Octobers of some years has typical "mixing" taken place; from these and other findings in this area there is very good reason to believe that this mixing is the result of a physical process as distinct from a "growing together". It is clear that immediately we are face to face with the problem of the causation of such correlations, and the type of problem illustrated here—how far the usual separation of these forms in space is due to any direct relationships between them, or to more physical factors, how far they are at times brought into association by physical factors and what reciprocal effects may result, if any—are ones to which continuous records may provide a partial solution.

If now the graphs of Phaeocystis and the Dinoflagellates are considered we shall again notice negative association as the rule. However, although Phaeocystis and the diatoms referred to above are seldom associated, there may be associations between Phaeocystis and the other diatoms, as also between these and the Dinoflagellates, which can be seen by comparison of Plates XXXVII to XLIV and XLV to LVII. On p. 148 I have referred to the association between *C. fusus* and *C. furca* (the latter often being relatively more abundant on the western edges of patches of the former), and have suggested that this association might arise from slight hydrological differences, but we must also bear in mind that this might also appear from some more biological relationship between the two. Careful comparison between the graphs for *R. styliformis* and *C. fusus* will show from time to time a somewhat similar correlation between these, and there are numerous other examples concerning the different groups of the phytoplankton. Whether these

features are the result of hydrological influence or of more specific inter-relationships, they are features which may likely repay further investigation in the phytoplankton and in the other groups.

These have all been relationships in space, but as has long been observed, there are time sequences in the production of different forms (*e. g.* spring diatoms, Phaeocystis, Dinoflagellates, summer diatoms and the autumnal forms such as *R. styliformis* and *B. sinensis*), and these present another aspect of inter-relationship which may not be unconnected with the former, and will form the subject of future investigation.

#### *Movements in the Area.*

In spite of certain limitations in this method of survey it has still been possible to obtain more or less detailed information about the movements of the larger patches of phytoplankton at certain times of the year, and particularly in the autumns since 1933, when on some of the lines fortnightly and weekly samples have been taken. The introduction in 1936 of the E line, which crosses both R and B, has further aided in such work, as also did the extension of B and C in the latter half of 1937. Apart from the obvious benefits of increasing the number of the lines, much greater aid can be obtained from those which intersect others or run in other directions. The extension of the survey in 1938, in addition to providing merely more data, has already shown that a network of lines should enable this side of the work to develop further.

Savage and Hardy (1935) referred to the complementary evidence to be obtained from both records and tow-net samples, and from these they suggested an overall north-easterly drift of the Rhizosolenia complex in 1932 round the southern edge of the Dogger Bank. Somewhat similar movements have been found by us in later years when the greater number of records made more detailed deductions possible. The general trend suggests the now familiar appearance of patches of *R. styliformis* in the region of the south-west patch, their growth and more or less gradual movement in that region and, mainly later, an apparent drift to the north and east. Associated with this we have found the patches of *B. sinensis* appearing variously in the south and east of the area (Flemish coast, Dutch Islands and German Bight), developing, and also appearing to move north and north-eastwards, the bulk of both forms being usually found later over the centre and eastern parts of line C respectively. There are striking detailed differences from time to time, and without attempting to justify the suggested connections between the patches, reference to Plates XXII to XXXVI may support some of these. Often we see *B. sinensis* appearing earlier on B and R than on C, and it is suggested that the later patches on the latter may be in part due to a northerly movement. Typically these patches have been more than 200 miles from the Humber Light-vessel, but in 1933 the patch was only some 150 miles distant, and in 1937 patches extended very much closer still. Whilst they may have been of the same type,



movements at these times in 1933 and 1937 must have differed from those of other years, and it may be also significant of variation in the current systems that such patches appeared on C in December in 1932-33, but in September or October from 1934-37. Similarly there was a more marked segregation of the patches of *R. styliformis* and *B. sinensis* from 1932-34, whilst from 1935-37 fairly extensive mixing occurred at some stage of their autumnal development. Perhaps in association with this we can think of the progressive approximation of the western edge of the Biddulphia patch to the Outer Dowsing Light-vessel from 1932 to 1937 (with the exception of 1936, which showed some recession). Numbers of other differences will show that, for all the general similarities, the conditions of each year are quite peculiarly determined, and although such analyses are most easy in the autumn, similar deviations can be made out for other parts of the year.

It will be seen how the movements of patches of *C. fusus*, *e. g.* in 1937, must have differed from those of other years. Similarly the variations in the annual distributions of certain forms must indicate important variations in movement; we may recall, for example, the generally central position of the Dinoflagellates in 1932-34, their westerly position in 1935, and the eastern one in 1937, whilst the apparent stability of conditions in 1935 (the maintenance of patches of various forms in similar places for long periods) further distinguishes it from some of the others.

Knowledge regarding the movements in the North Sea has gradually advanced, the earlier work of Fulton and Böhnecke (to mention only two) being extended by the more detailed surveys of Tait and Carruthers. Even now the picture tends too much to be a static one, as both writers have emphasized, although in this particular area the continuous current measurements at certain light-vessels (*e. g.* Carruthers, 1935) are gradually building up a set of standards and temporary deviations from them which are valuable in understanding more fully the generalized picture now available. It is, we hope, with a full appreciation of the limitations of the present work that it is suggested that a series of continuous records of the plankton may also give data which, apart from its intrinsic value for ecology, may help to supplement the hydrological and hydrographical information which is being produced. Cleve, who first tried to follow the movements of the plankton, was shown to be wrong in many of his premises, but more recently there has been a return to a modified version of Cleve's ideas in which more attention has been paid to the life-histories and habits of the "indicators" (*e. g.* Russell, 1935). Whilst in some ways the macroplankton species are more valuable as indicators (see, *e. g.*, Russell, 1936, and Kunne, 1937), it is felt that a satisfactory method of following the life-histories of major phytoplankton "bodies" (*i. e.* characteristic long-lived patches such as those of *R. styliformis* in 1935 and 1937, *C. fusus* in 1937, and such complexes of other diatoms which have been found to persist for some period) may have a similar value. On the other hand, the very variability of the phytoplankton species can, if the necessary limitations be allowed for, be used to distinguish between different water masses and to delimit their boundaries with precision.

Even at this stage of the recorder survey there is evidence that it may provide such a method, and as the surveys develop more precise data may be produced.

This subject can more satisfactorily be reviewed in reference to the data for various other groups of plankton, and will later be dealt with in a paper by Mr. K. M. Rae and the present writer, dealing with the whole of the material for 1932-37 in relation to hydrological conditions.

In association with water movements we may also consider the phytoplankton in relation to the floor of the sea. Its importance to the benthic fauna and ultimately to the commercial fishes makes this the more important, and this side of the work will also be reviewed later. Here brief reference may be made to the significance of the patches of phytoplankton found so regularly over the south-west edge of the Dogger Bank, and particularly to the variations which they undergo. Other centres are apparent, whilst certain areas are more often barren, although at times a more extensive flora is found over them (*e. g.* the western end of the Rotterdam Line). These features and their variations are not likely to be without their effect on the bottom fauna and the stocks of fish.

#### *Annual Variations in the Area.*

The general trend of development of the various forms has been reviewed separately in the preceding pages. The cycle as a whole is a familiar one, although we believe that the method of continuous recording has helped to make some details clearer and, in various ways, may extend the application of such data. Yet throughout this work one of the more interesting features has been the persistent occurrence of variations upon the central theme and their association with other changes. The determination of the main lines of annual cycles formed one of the chief objectives of the International Council's programme from 1902-08, and their investigations revealed some good and bad years for different forms, the period 1904-05 being an example. More recently the year 1921 and certain years during the period under review have also attracted attention.

Variations have been found in the occurrence of all the more abundant forms which we have been able to deal with, and they have concerned spatial distribution, apparent movements, temporal occurrence and size of maximum, etc. Clearly the methods are not ideal, and some of the apparent variations may be misleading. In the relatively short lives of some of the diatom patches, the omission of a record in any month may seriously affect the picture of its cycle, whilst within the usual period of one month between two records very extensive changes may occur in the distribution of any form. But equally clearly these are criticisms which apply, perhaps even more seriously, to some other forms of survey. We have to make such use as we can of the methods available, and when certain allowances have been made for such inherent defects in the methods, there still remain very significant changes of which there seems little doubt. An example has been raised on an

earlier page regarding the occurrence of *R. styliformis* and *B. sinensis* during the earlier years of the survey. The larger gaps between the records in the autumn of 1932 and 1933 make it fairly certain that important information has been lost, and so the quantities found may be below the possible maximum, either in numbers per mile or in the extent of the patches. Nevertheless the series of records in the later years make it equally certain that large patches occurred over a longer period in these years than in 1932-33. Whether or not the actual densities attained were greater, the patches are likely to have had a more extensive influence on the area covered by the recorder lines.

By analysing the available evidence and the variable factors in the ways indicated, it is possible to reduce the apparent variations to such as should be truly significant. By no means are all the variations in the same direction, but a number of them are suggestive of a general inter-relationship and these will be reviewed briefly here :

(1) As far as our evidence goes the size and persistence of the autumnal patches of *R. styliformis* increased up to 1935, decreased in 1936, and increased again, although not to the level of 1935, in 1937. There is no doubt that the maximal density of 1934 was much less than in 1932 and 1933 ; the density in 1932 was probably lower than in 1933 and October records in 1931 suggested it to be even scarcer then. Patches were very late in 1936, and we should note the unusual occurrence of large patches in the Januaries of 1936 and 1937.

(2) Somewhat similarly the size and persistence of patches of *B. sinensis* increased up to 1935, decreased in 1936, and were even more extensive in 1937. The numbers were very low in 1932, and October records in 1931 suggest it to have been still scarcer. As with *Rhizosolenia*, this form was unusually late in 1936. Another aspect of the temporal changes is seen in the change of date of the first appearances of patches on the Copenhagen Line ; this was in September or October in 1934-37, but not until December in 1932 and 1933. In general, the quantitative changes were reflected on B, C and R, but a further point of interest has been the continuous approach of patches towards the Outer Dowsing Light-vessel until the western edge of patches in 1937 almost reached it.

(3) Overall the Dinoflagellates have been most abundant in the last three years ; this was most apparent on lines C and R, the appreciable patches of 1935 and the relatively enormous ones of 1937 on the latter line being striking features. Of the individual species we may note that the numbers of *C. fusus*, which were generally low up to 1935, increased greatly during the later period. A trend is also seen in the occurrence of " primary " and " secondary " maxima (see p. 139). These did not appear on C from 1932-34, but they were evident on B in 1932 and 1934, and were more marked still on both lines in 1935 and 1937. They were indistinct in 1936. In addition we may remember that whereas the Dinoflagellates were mainly central from 1932-34 and in 1936, they were more prominent in the west in 1935, and in the east in 1937.

(4) We can broadly distinguish the years 1932, 1933 and 1937 as providing

denser patches of *Phaeocystis* and 1934–36 as less dense on the whole, 1935 showing perhaps as the poorest. Again, in the earlier years the growths were largely limited to lines B and R in the spring, whilst 1935–37 showed increased growths on C, and in 1937 these extended into September. Whereas the early patches were mainly eastern, there were central ones in 1934, and in 1935–36 there were relatively well-developed ones in the west also. In 1937 eastern patches were again a feature.

(5) Whilst the trends mentioned above are in many respects the most reliable, those shown by the other diatoms are equally interesting and often parallel those mentioned. Overall there has been an increase in numbers since 1932, and culminating usually in 1937, although in some respects 1934 and 1936 showed themselves as being outside this trend. Some discussion has been given (p. 122) to the possibility that this effect might be due in part to improvements in the technique, but it was found that in general it must reflect a genuine increase in numbers. The increase, although large, is no larger than some others which have been observed, and is relatively less than that of the enormous changes in the numbers of *C. fusus* which were found on R, and about which no similar doubts can be expressed.

Although this increase is shown by many forms it does not appear in all, but has been most typical of *Asterionella*, *Bacillaria*, *Thalassiosira*, *Rhizosolenia alata* and *R. semispina* and the *Chaetocerids*. On the other hand, some forms have had maxima or secondary maxima in other years, e. g. *Biddulphia regia* (1933), *B. aurita* (1933 and 1936), *Eucampia* (1936), *Naviculoids* (1935), *Thalassiothrix* (1934), *Coscinodiscus* (1934) and *Rhizosolenia Stolterfothii* (1936). In association with the main trend we may note that during the period central patches on line C have become more common, and that there has been an increasing westerly element in the patches on B; the last directs attention also to the unusual occurrence of patches over the generally barren area of the Rotterdam Line between the Dudgeon and the Newarp Light-vessels in the later years.

In review we may say that broadly there has been a progression towards greater numbers during the period under survey, although there are details qualifying this trend. In some respects a contrast can be seen between the period 1932–34 and 1935–37, but in others 1934 and 1936 may be thought to deviate from this tendency. Not all the characters have shown an increase, and those that did were not necessarily minimal in 1932, but may have had a minimum (or a maximum) in 1933. Similarly others have shown such signs of regression in 1937 (e. g. *Phaeocystis*) as to suggest some features of the earlier years.<sup>1</sup>

The occurrence of such a series of changes in the phytoplankton would seem to indicate some related fundamental changes in the area. Immediately one thinks of hydrological changes (cf. a similar comparison for the years 1931–33, Lucas, 1936), and there is reason to believe that these have been associated, but before considering this it will be instructive to compare these findings with those

<sup>1</sup> See also Addendum, p. 168.

of other plankton surveys. Since 1930 Russell (*e. g.* 1935, 1937, 1938) has analysed the proportions of *S. elegans* and *S. setosa* in the waters off Plymouth and has found a marked change in the constitution of the plankton; precise values are as follows (derived from Kemp, 1938):

	1930.	1931.	1932.	1933.	1934.	1935.	1936.	1937.
% <i>S. elegans</i>	94.1	16.7	6.2	4.7	3.5	3.6	39.7	3.8
Numbers in thousands	86.1	19.6	7.3	5.5	3.3	1.7	9.5	0.9
% <i>S. setosa</i>	5.9	83.3	93.8	95.3	96.5	96.4	60.3	96.2
Numbers in thousands	5.4	97.7	111.0	111.9	91.2	46.5	14.5	25.2

Although only one has been stressed by Russell, there appear to be two significant features in this table. Firstly the numbers and percentage of *S. elegans* have been unusually low since 1930–31, although the numbers, and particularly the percentage, were higher again in 1936. Secondly the high numbers of *S. setosa*, attained in 1931 as *S. elegans* decreased, persisted only up to 1934, a decrease following in 1935, a minimum in 1936, and a slight increase again in 1937. In association Russell observed the numbers of several other animals (*Muggiea*, *Cosmetira*, pelagic tunicates, etc.), and found that they showed similar changes over the period. Even more important were the changes in the numbers of all young fish, which decreased tremendously from 1930 to 1937 (Russell, 1938, fig. 2). Summer spawning larvae decreased steadily from 1930–35, and then increased slightly, whilst those spawned in the spring only decreased markedly in 1935 and remained low in 1937. Russell was led to suggest that "some factor adverse to all species of fish indiscriminately" must be in operation and, showing that this was not likely to be due to the effects of commercial fishing, he put forward the suggestion that it might be in association with the parallel decrease in the phosphate content of the Channel waters (see also Cooper, 1938).

A number of these features were gathered together by Dr. Kemp at the British Association Meeting in 1938, where, in addition, he showed how the herring catches at Plymouth had decreased from 1934–35, and the percentage of young from 1931–32 (Kemp, 1938).

It seems that here are some parallels to the events which have been recorded in the North Sea. Russell (1936) has previously commented on the possible association between the decrease of *S. elegans* off Plymouth, and the increase of *R. styliformis* over the Dogger Bank as found by Savage and Hardy (1935) and Savage and Wimpenny (1936) over the period up to 1934. Whilst our findings are not in exact agreement with the latter, they also tend to confirm this suggestion and enable it to be extended; it was not until 1936 that we noted a decrease in the general abundance of *Rhizosolenia*. In this year *S. elegans* was relatively more abundant, but it was scarcer again in 1937, when we found also larger numbers

of *R. styliformis* over the Dogger Bank. Russell has suggested that "the two populations of *Sagitta* swing to and fro off Plymouth according to the strength of flow of the Atlantic water into the North Sea from the north", and in view of what is known of such inflows in recent years it seems not unreasonable to support this view, and to suggest that the progressive increase of phytoplankton in this area is a reflection of northern pressure, and possibly arises from an *increase* of phosphates in the area. In this connection it is important to note that Cooper (1938), in discussing the changes of winter phosphate maxima at the station E1, has calculated that the production of phytoplankton in that region changed during 1933-34 to give much lower values in 1935-37, a condition almost the reverse of that found in our area.

The Reports of the Fishery Board for Scotland (1931-38) record observations of the effects of Atlantic pressure upon the northern North Sea and, as is now well known, this has shown important changes during the last few years. Briefly, there was a steady increase in Atlantic pressure from 1931 (or even 1930) until 1934 at least, this being shown by increasing temperatures and salinities (Tait, 1936). The maximum effects were attained fairly early in the year and numbers of exotic forms have been found from time to time, such as doliolids, which were also found in 1933 as far south as the latitude of Aberdeen (Lucas, 1933). Latterly there are signs that the effects are decreasing; the maximum effects have been attained progressively later in the year, and in 1937 "the inflow of Atlantic water into the northern North Sea . . . appears to have been weaker than for at least five years", although salinities were still above the average (Report for 1937). In association the occurrence of a large number of exotic forms in various waters during the period 1932-34 has been recorded by Stephen (1938), along with variations in annual broods during that time.

The possible relation of these trends to those already mentioned is evident; they are clearly in some respects parallel, and it seems reasonable to look to broad changes over a wider area as the "causes" of changes in more restricted regions such as the southern North Sea. It has been suggested by Carruthers (1935) that the flow of water past the Varne Light-vessel may be the result of a buffer action between pressure from the north and that from the English Channel, which is in accord with Russell's suggestion concerning the possible relation between biological features of Plymouth waters and those of the North Sea. It is already clear that certain parallels can also be drawn between the hydrological conditions of the Varne area and the variations which we have observed in the phytoplankton cycles; the discussion of these is reserved for a later paper dealing with relations between the whole plankton and the hydrology of these waters. Whilst it is too early yet to draw more definite conclusions, it seems likely that the changes which have been observed in the phytoplankton are at least in part related to the changes observed in the northern North Sea and to probably connected events in the Varne region. If such a relationship can be maintained, then the general increase in the phytoplankton during the period may well have been the result of an increase

in the phosphate content of these waters (*cf.* also the important conclusions of Graham, 1938) arising from the unusual water movements which have been occurring both within this area and also further north, just as in the Plymouth area the reduction in Atlantic influence appears to have led to decreased phosphates, decreased phytoplankton, and an abnormal decrease in the numbers of fish larvae.

The implications of such a possibility are obvious, but it would be dangerous to speculate further at this stage, although it is hoped that some of these lines may be followed up. Meanwhile it is interesting that cycles of events with some features in common should be observed in several places in the course of different types of work. Dr. Kemp (1938), referring to the recently projected western Atlantic survey, has pointed out that this "will lose much of its value if we are unable to obtain comparable data in our own waters". We hope that the extended recorder programme—and in particular the new Atlantic route from Pentland to the Faeroes—will not only provide data linking together events within the North Sea, but may help to link these with processes occurring further afield.

#### SUMMARY.

1. The changes in the composition and distribution of the plankton of the Southern North Sea have been investigated month by month from June, 1932, to December, 1937; the present report deals with the phytoplankton. The survey was carried out by the continuous plankton recorder, towed at a standard depth of 10 metres, by ships on regular steamship lines across the North Sea from Hull towards the Skagerrak, to Bremen and to Rotterdam, and later between London and Esbjerg.

2. The material and methods are described, together with a discussion on the validity of this type of survey and some comparison of its results with those obtained by other methods (pp. 76–86).

3. Particular attention has been paid to *Rhizosolenia styliiformis* (pp. 92–107), *Biddulphia sinensis* (pp. 108–115), Phaeocystis (pp. 149–153), and the Dinoflagellates (pp. 134–149); of these the first three are known to be of particular importance in relation to the herring fisheries. More generalized data are available for the principal diatoms other than *R. styliiformis* and *B. sinensis* (pp. 116–134).

4. The main part of the work is an ecological study of the phytoplankton changes in time and space over the 5½ years. Each year is marked by some distinct variations in the abundance and the times of increase, maximum numbers and decline as recorded in the different forms. These variations in the annual cycles are compared on the different lines by a series of graphs arranged against a time scale of months, a set for each year being placed side by side (Plates I–XXI). More detailed studies by more frequent records were made in the autumns of 1934, 1935, 1936 and 1937 (*cf.* Figs. 3 and 4). The changes in spatial distribution are

shown by a series of monthly maps arranged in a similar manner for each year (Plates XXII–LXIV). These intensive studies of the changes in time and space are also intended to form the basis for correlations with other features in the general ecology of the area (*e. g.* the zooplankton, hydrology, meteorology and fisheries) to be made in later publications.

5. Whilst each form has shown its own peculiar features, a trend towards a general increase in the phytoplankton as a whole has been observed during the period, although the years 1934 and 1936 have in some respects shown deviations and regressive features, and not all organisms have revealed the same trend. The possible relation of this gradual trend to other events observed in recent years in these and neighbouring waters is discussed (pp. 162–167).

6. The application of these results to the study of patchiness (pp. 154–158), inter-relationships in the plankton (pp. 159–160) and to water movements (pp. 160–162) is briefly discussed.

#### ADDENDUM.

Since the beginning of 1938 the recorder programme has been extended to cover the whole of the North Sea and, in 1939, to include a line between Scotland and the Faroes (see 'Bulletin' No. 1). The results of the extensions are now (1940) in preparation for the press, but it may be of use to record here that during this period a number of the forms in the Southern North Sea have shown a marked tendency to return to numbers not so dissimilar from those of the earlier years. This makes it the more likely that the whole series of records has concerned a significant cycle of events in these waters, although the onset of the war may prevent conclusive demonstrations of this.

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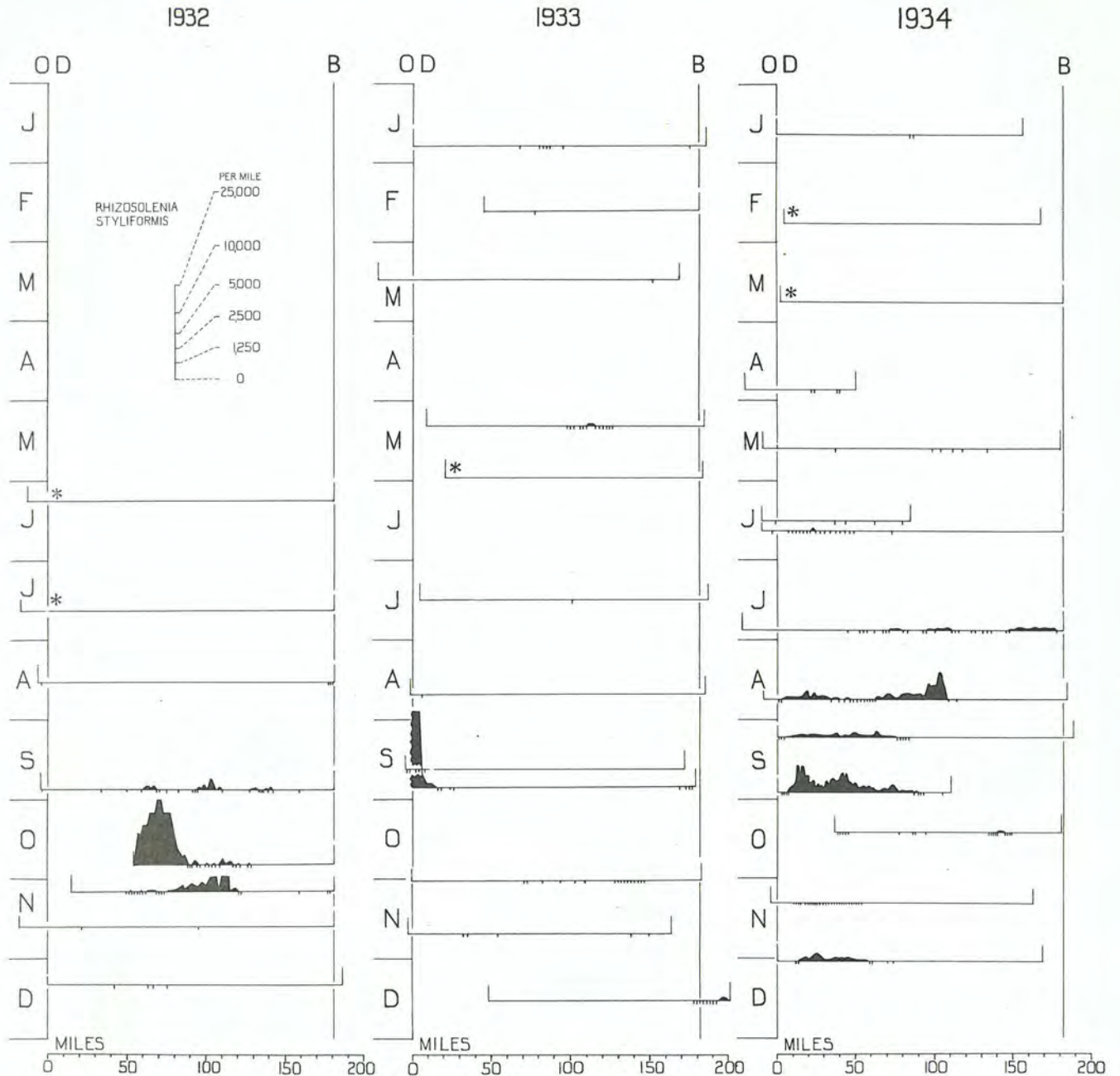
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# PLATES I - XXI

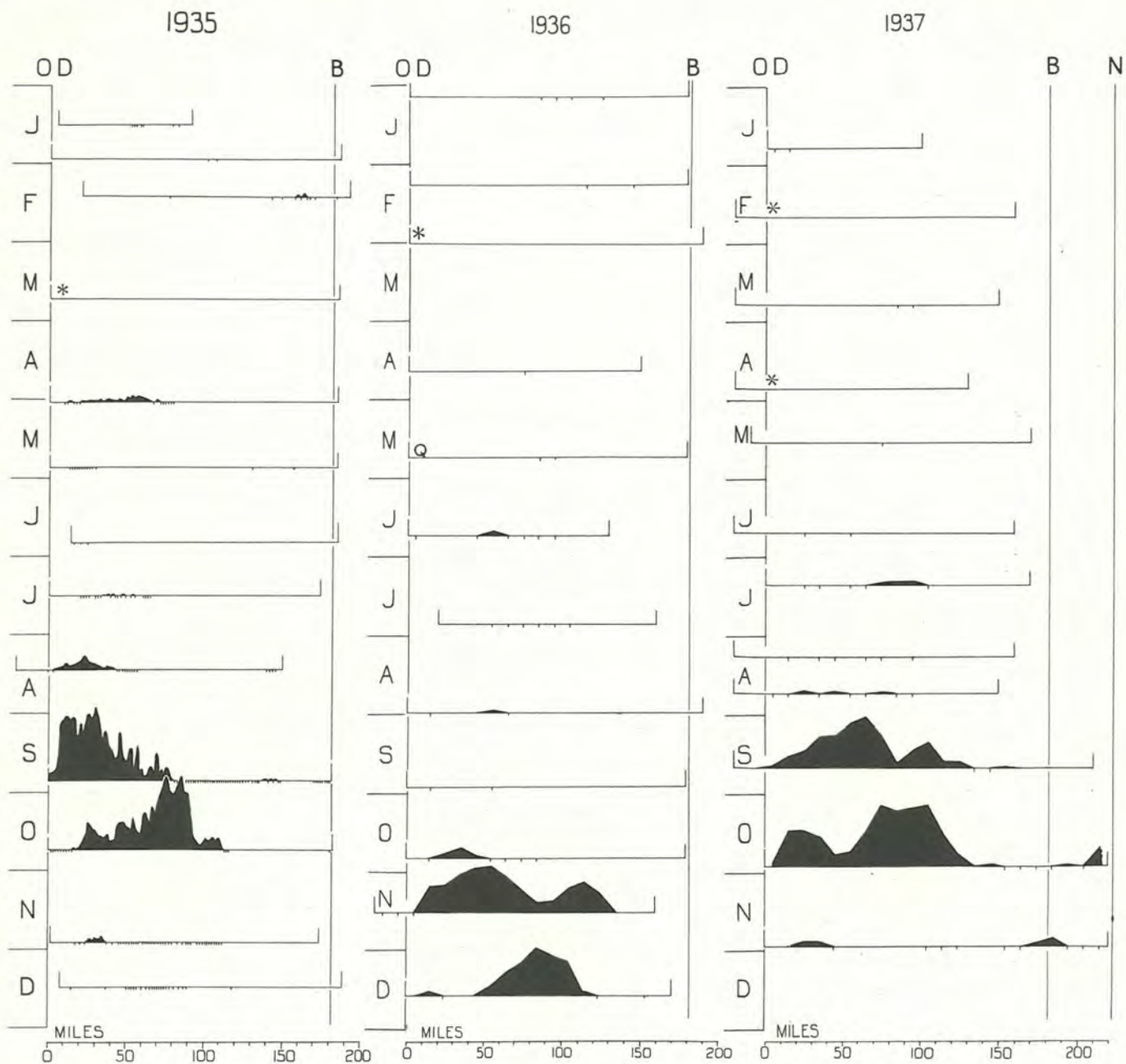
SERIAL GRAPHS COMPARING  
THE VARYING QUANTITIES OF  
THE PRINCIPAL PHYTOPLANKTON  
FORMS YEAR BY YEAR ON THE  
DIFFERENT RECORDER LINES IN  
THE SOUTHERN NORTH SEA  
JUNE 1932 TO DECEMBER 1937

# PLATE I

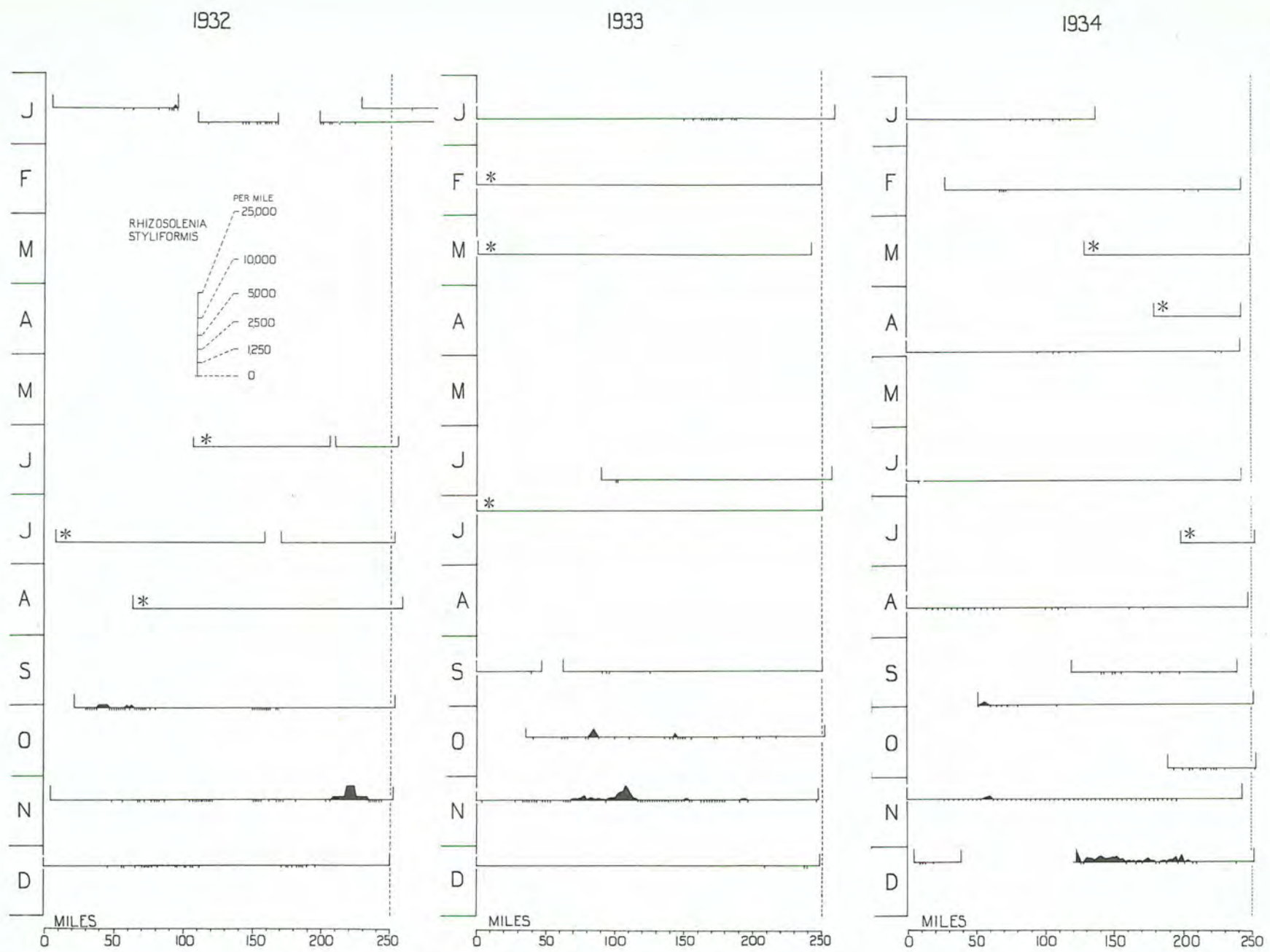


Records of **RHIZOSOLENIA STYLIFORMIS** on the Bremen line, 1932-1934, each placed in its position of date against a vertical scale of months indicated by the letters J, F, M, etc., in each year. The vertical lines under the letters OD and B represent the positions of the Outer Dowsing and Borkum lightvessels. Patches are shown above the base lines and traces as small vertical strokes below them. No traces were found on the records marked with an \*. Additional records in the autumn of 1934 are shown in text-figure 3.

# PLATE II



Records of **RHIZOLENIA STYLIFORMIS** on the Bremen line, 1935-1937, arranged as explained on Plate I. The vertical line under the letter N represents the position of the Norderney lightvessel. The record marked 'Q' is of qualitative value only. Additional records in the autumn of each year are shown in text-figures 3 and 4.

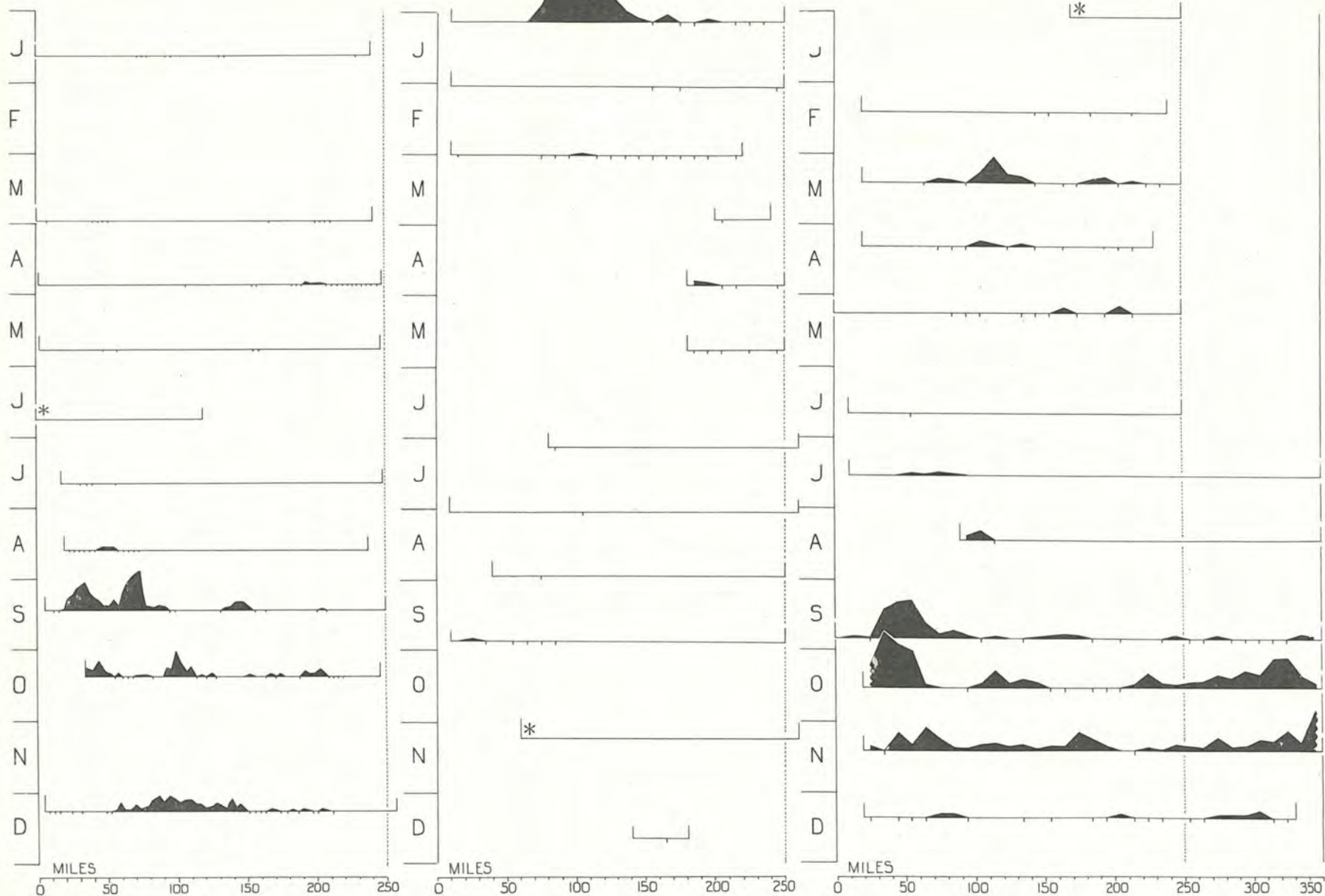


Records of **RHIZOSOLENIA STYLIFORMIS** on the Copenhagen line, 1932-1934, arranged as explained on Plate I except that the vertical line on the left represents the position of the Humber lightvessel and the broken vertical line on the right marks the position of a point 250 miles from the lightvessel.

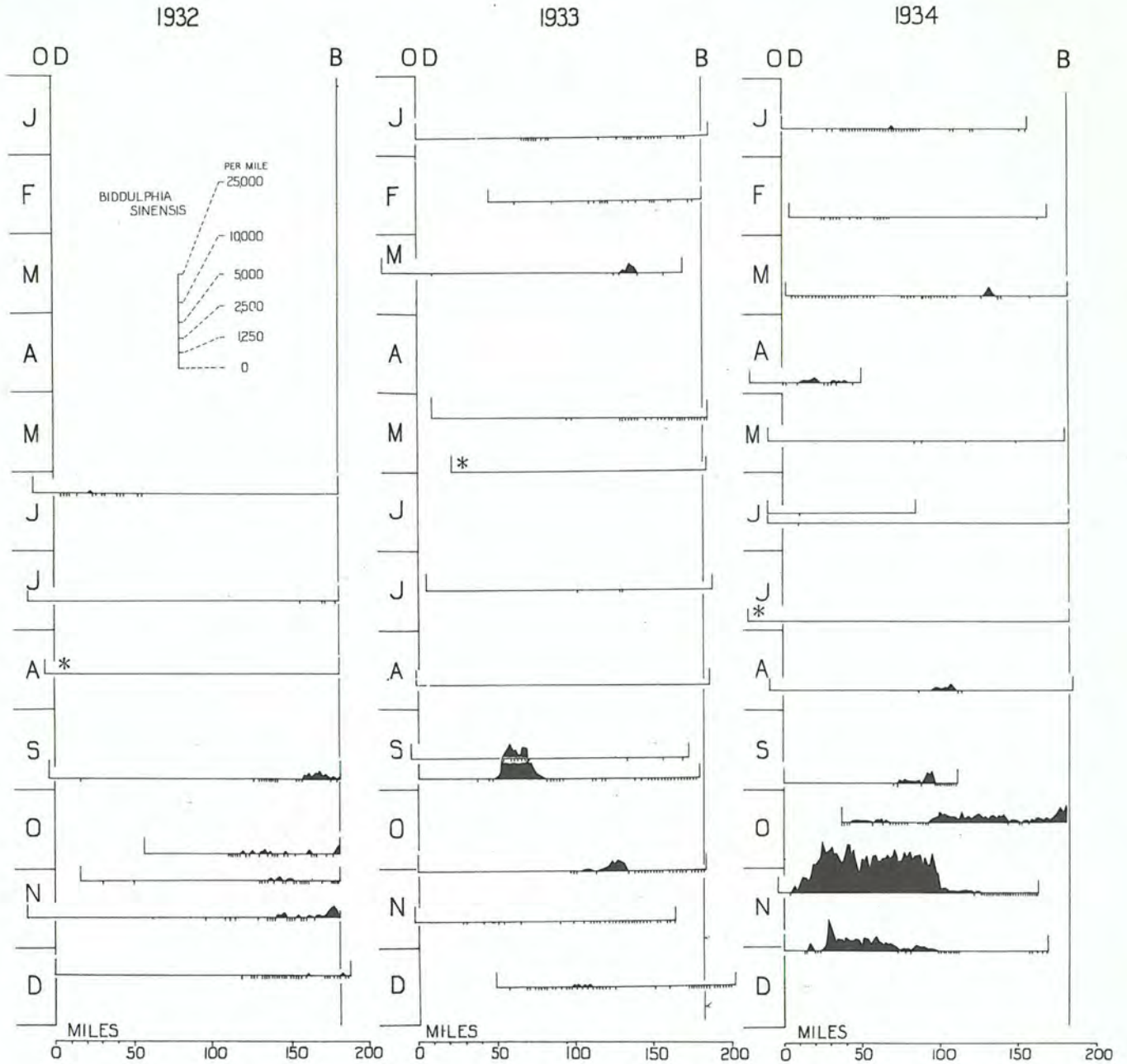
1935

1936

1937



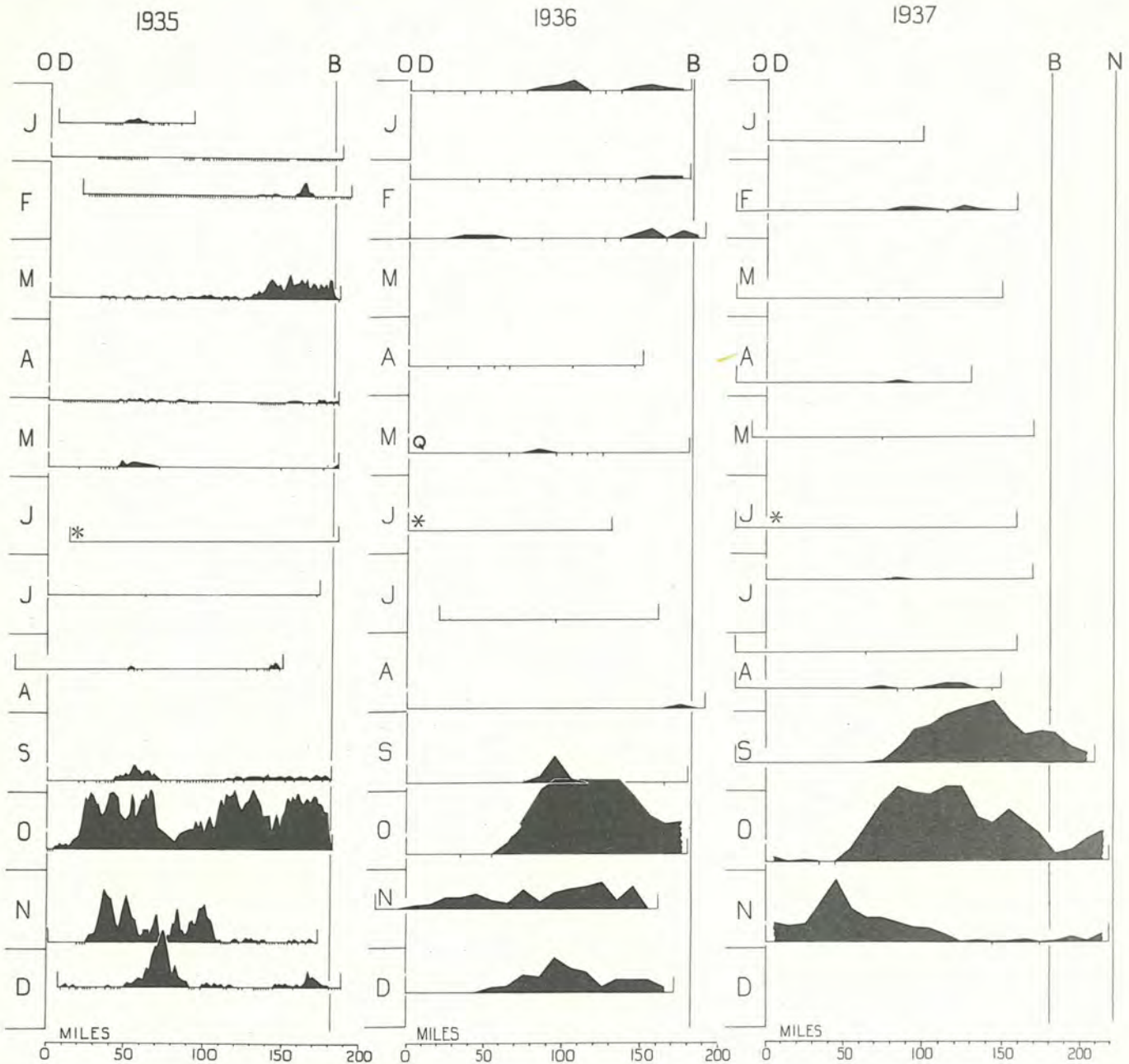
# PLATE V



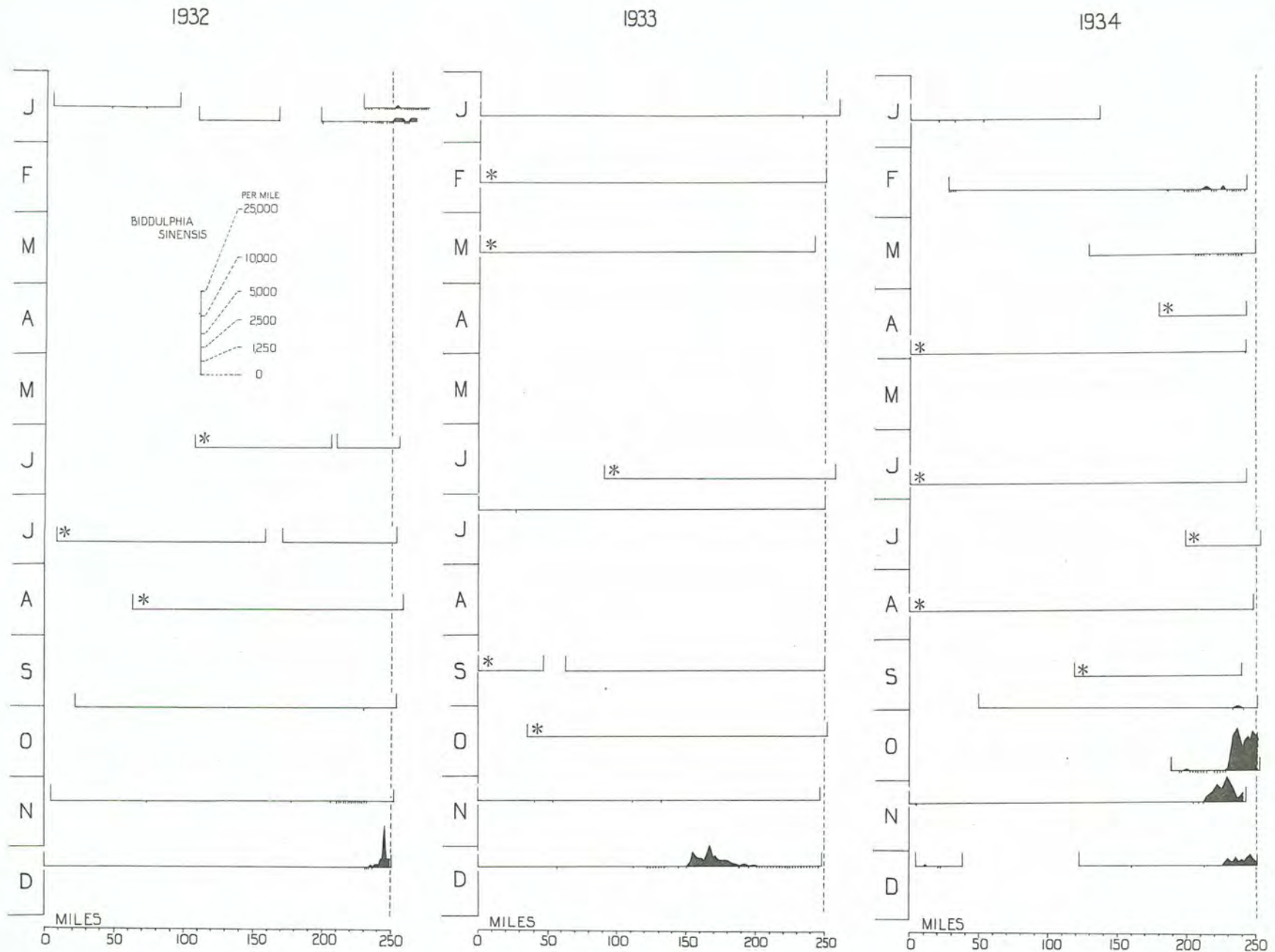
Records of *BIDDULPHIA SINENSIS* on the Bremen line, 1932-1934, arranged as explained on Plate I. Additional records in the autumn of 1934 are shown in text-figure 3.



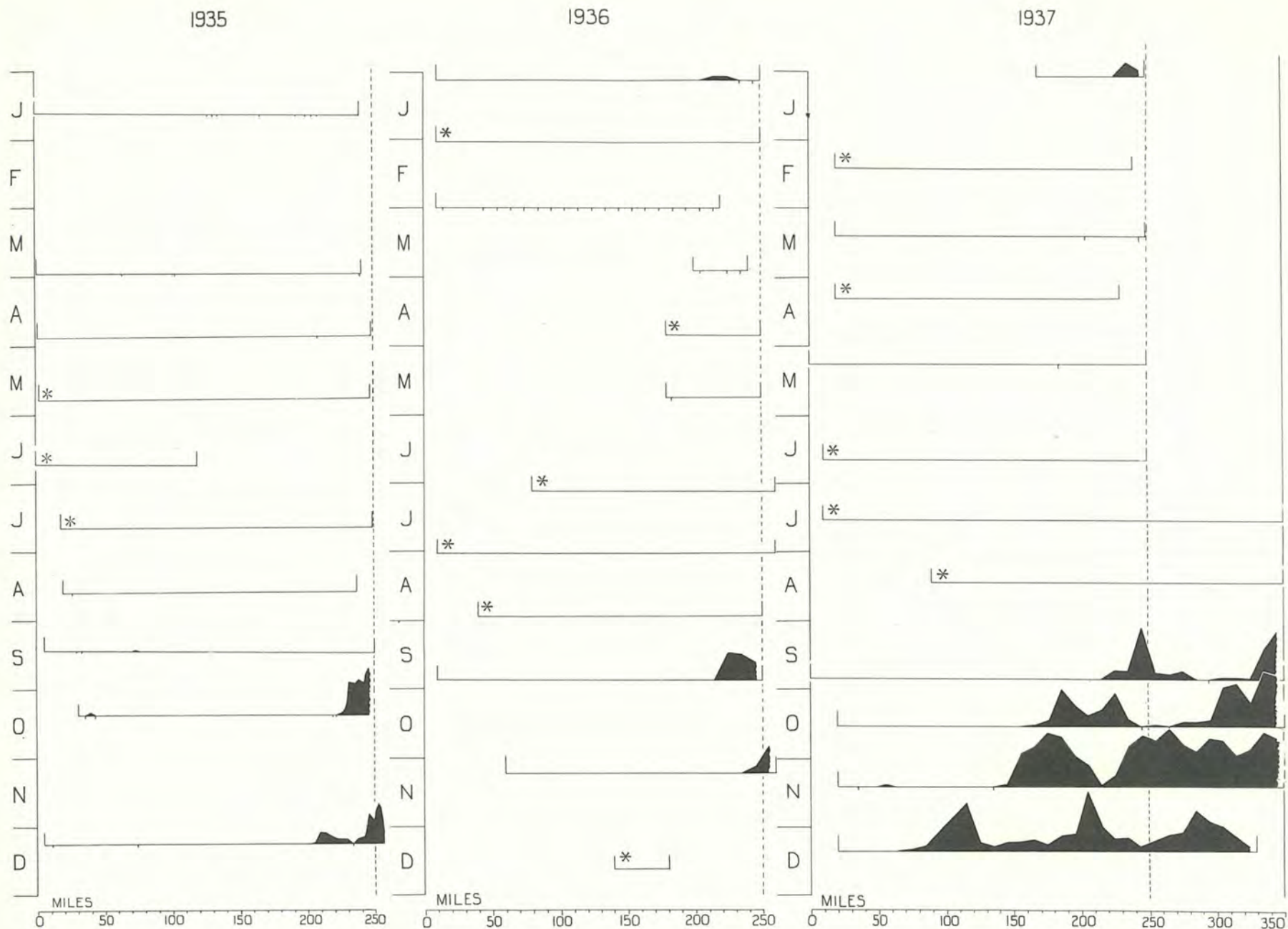
# PLATE VI



Records of *BIDDULPHIA SINENSIS* on the Bremen line, 1935-1937, arranged as explained on Plates I and II. Additional records in the autumn of each year are shown in text-figures 3 and 4.

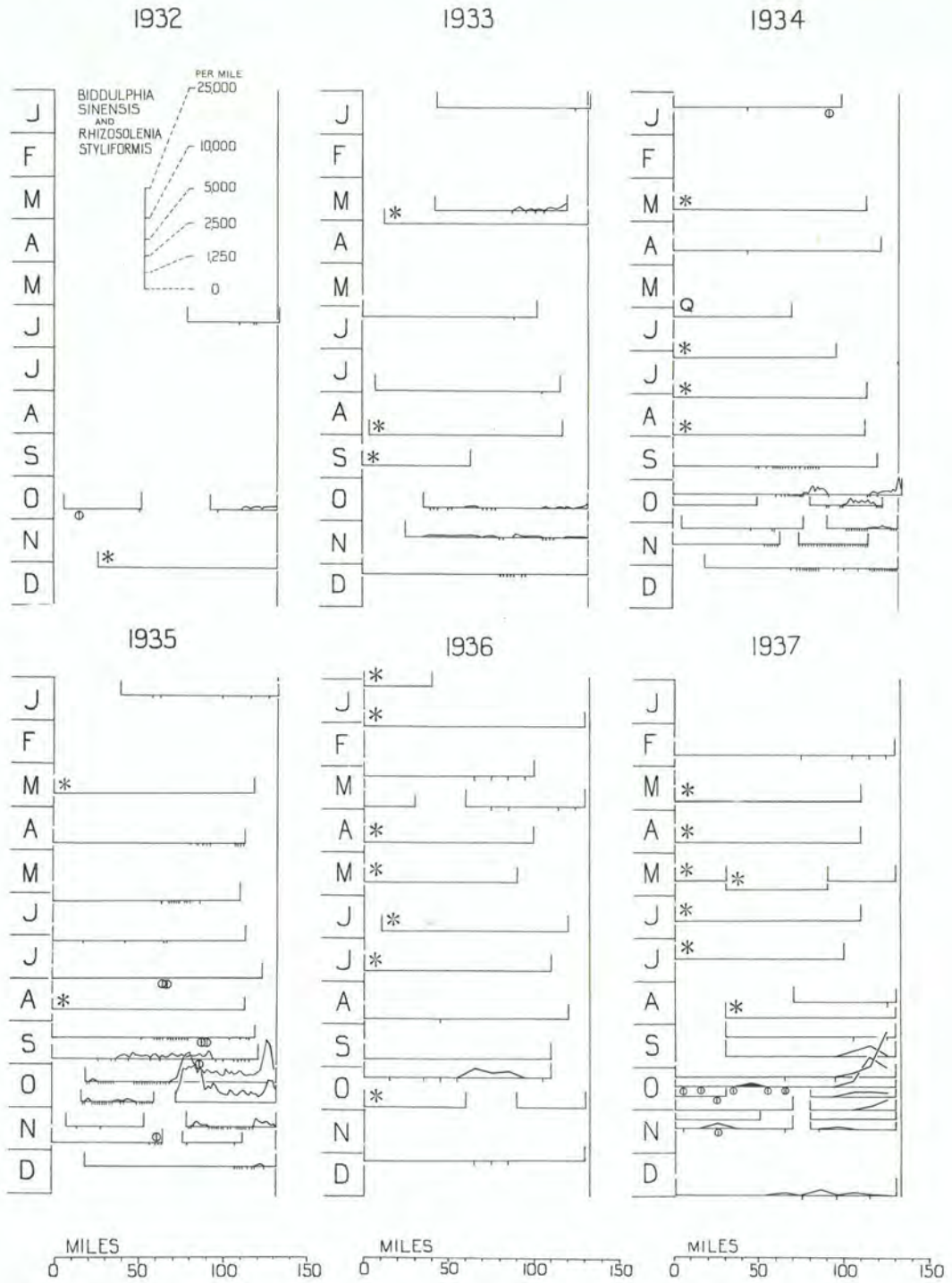


Records of *BIDDULPHIA SINENSIS* on the Copenhagen line, 1932-1934, arranged as explained on Plate III.



Records of *BIDDULPHIA SINENSIS* on the Copenhagen line, 1935-1937, arranged as explained on Plate III.

# PLATE IX

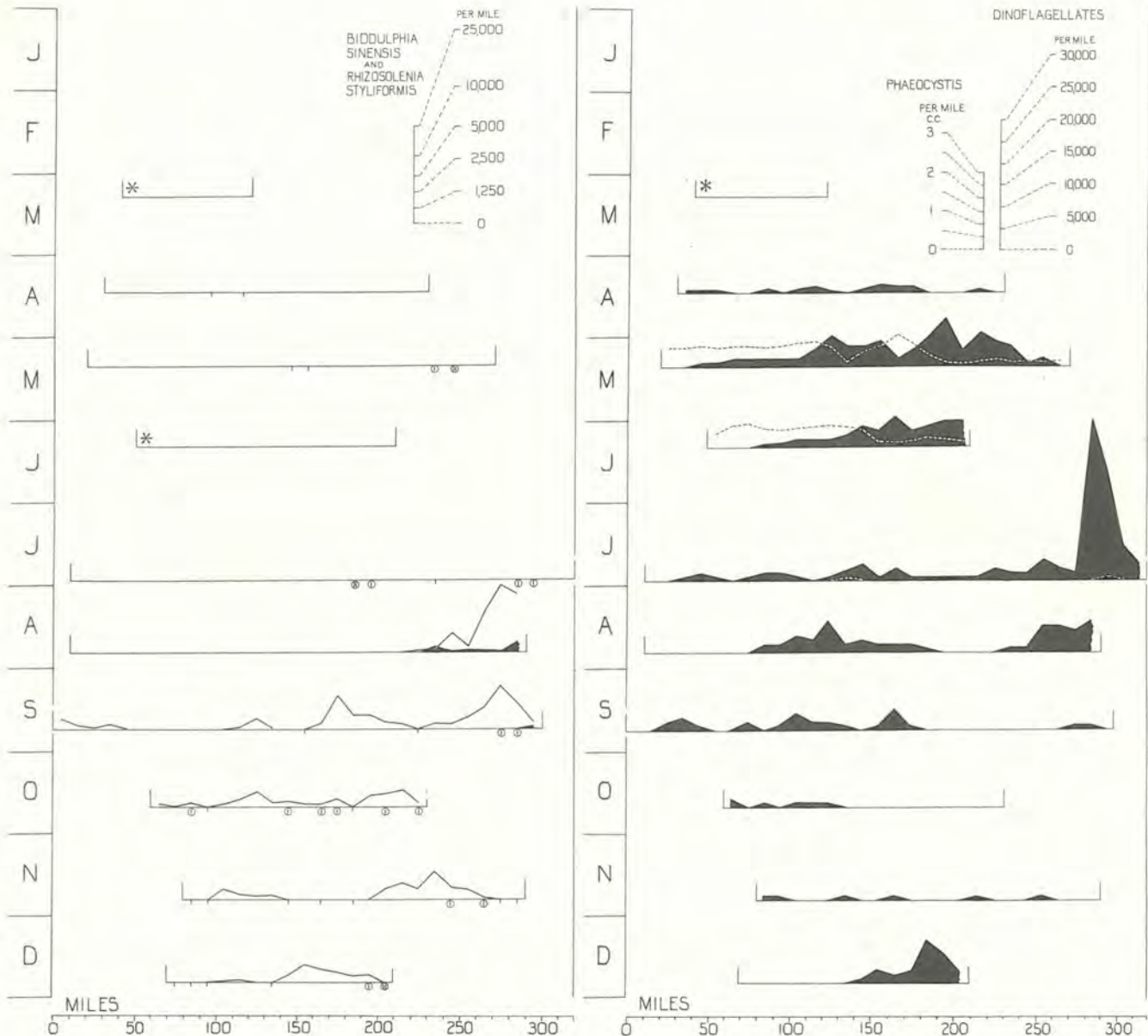


Records of **BIDDULPHIA SINENSIS** and **RHIZOSOLENIA STYLIFORMIS** on the Rotterdam line, 1932-1937. General arrangement as explained on Plate I except that the vertical lines to right and left represent the positions of the East Dudgeon and Maas lightvessels. Patches of *B. SINENSIS* shown as open line graphs and traces as vertical strokes below the base lines; *R. STYLIFORMIS* as blacked in graph (only one patch) and vertical strokes in circles below the base lines. When there are two strokes within one circle both forms are present as traces.

# PLATE X

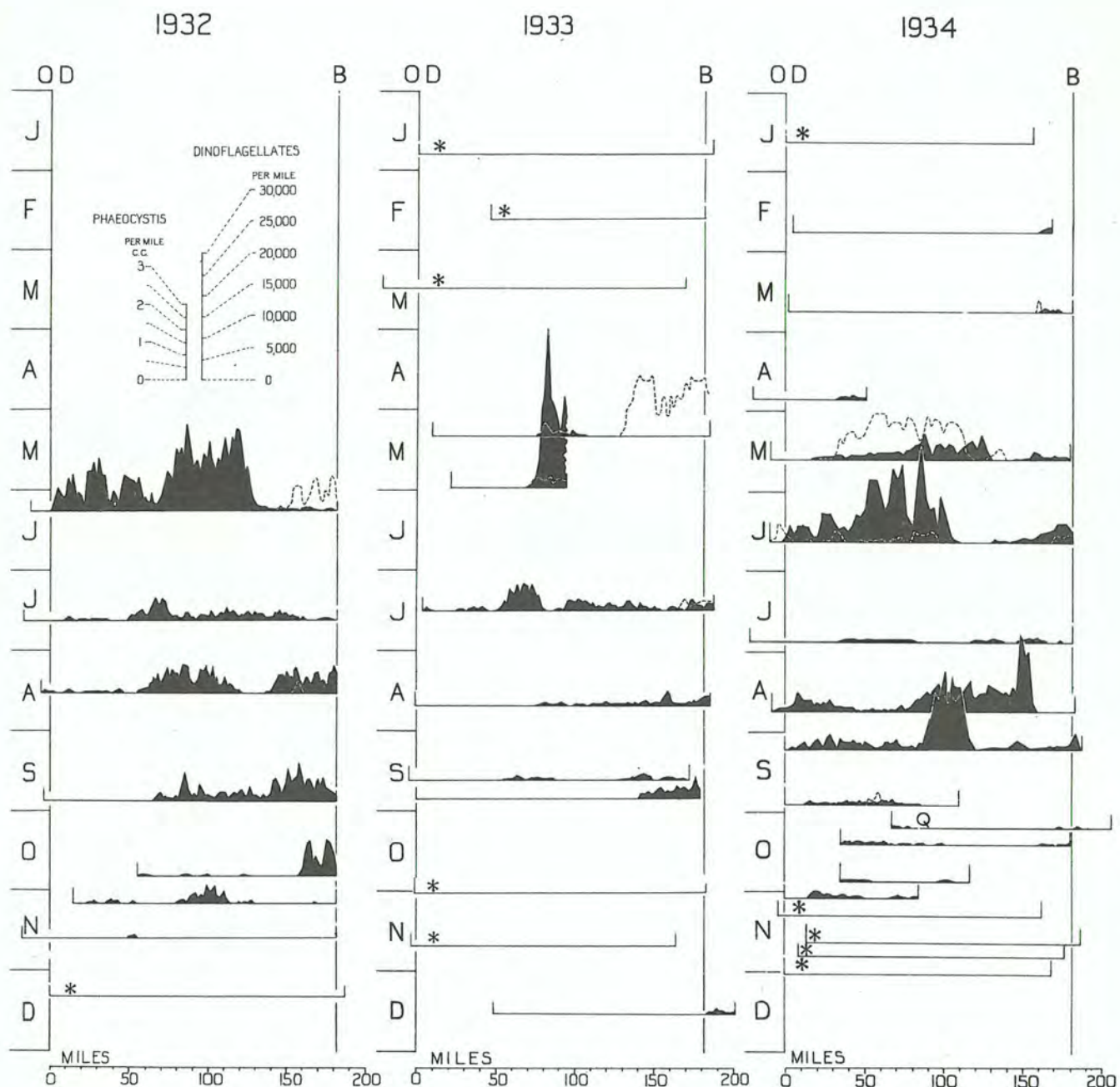
1937

1937



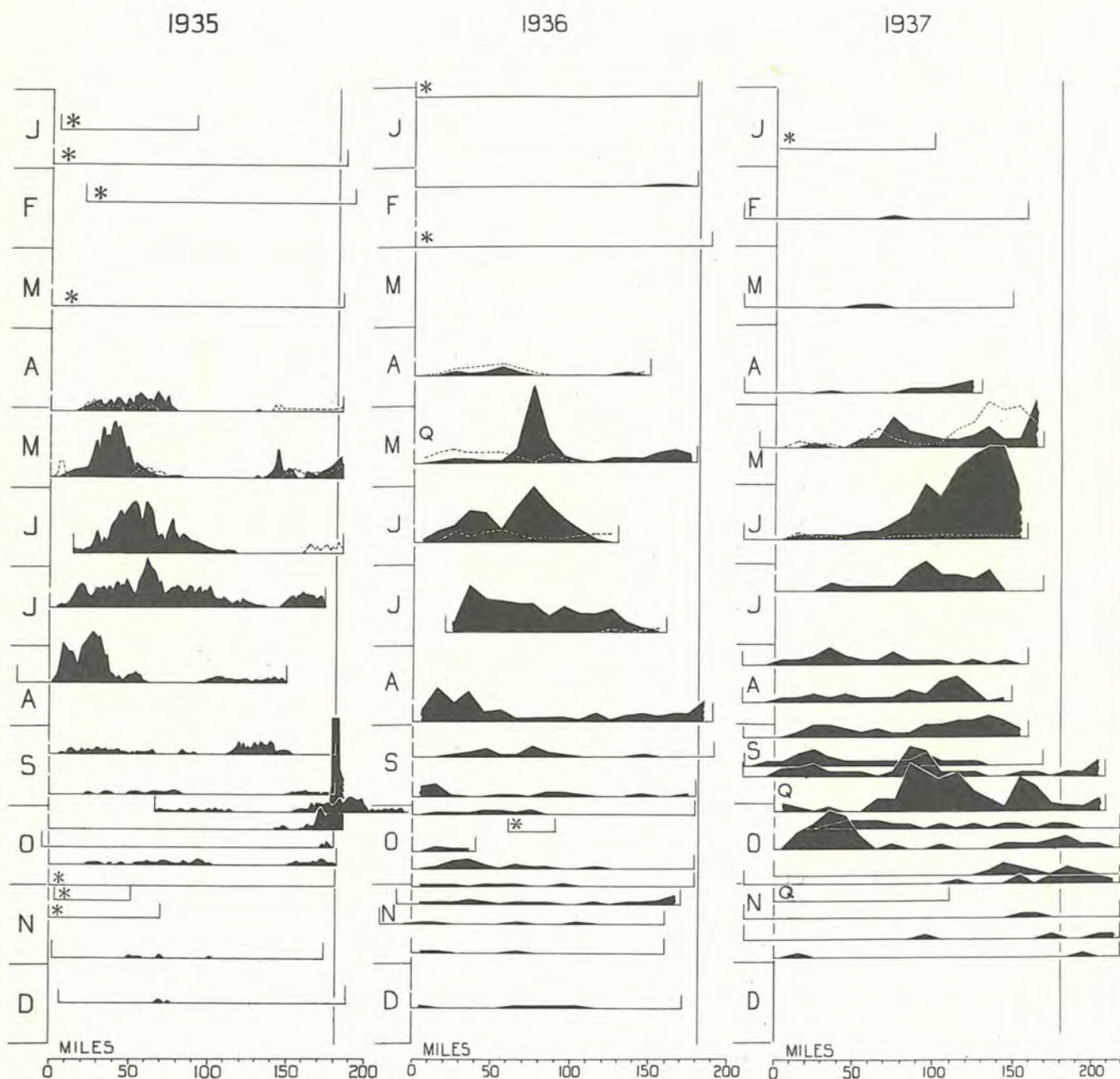
Records of **BIDDULPHIA SINENSIS** and **RHIZOSOLENIA STYLIFORMIS** (left) and **DINOFLAGELLATES** and **PHAEOCYSTIS** (right) on the Esbjerg line in 1937. General arrangement as explained on Plate I except that the vertical lines to the right and left represent the positions of the Sunk and Graadyb lightvessels. **B. SINENSIS** shown as open line graphs, **R. STYLIFORMIS** and **DINOFLAGELLATES** as blacked-in graphs and **PHAEOCYSTIS** as broken line graphs. Traces of **B. SINENSIS** and **R. STYLIFORMIS** shown below the base lines as in Plate IX.

# PLATE XI



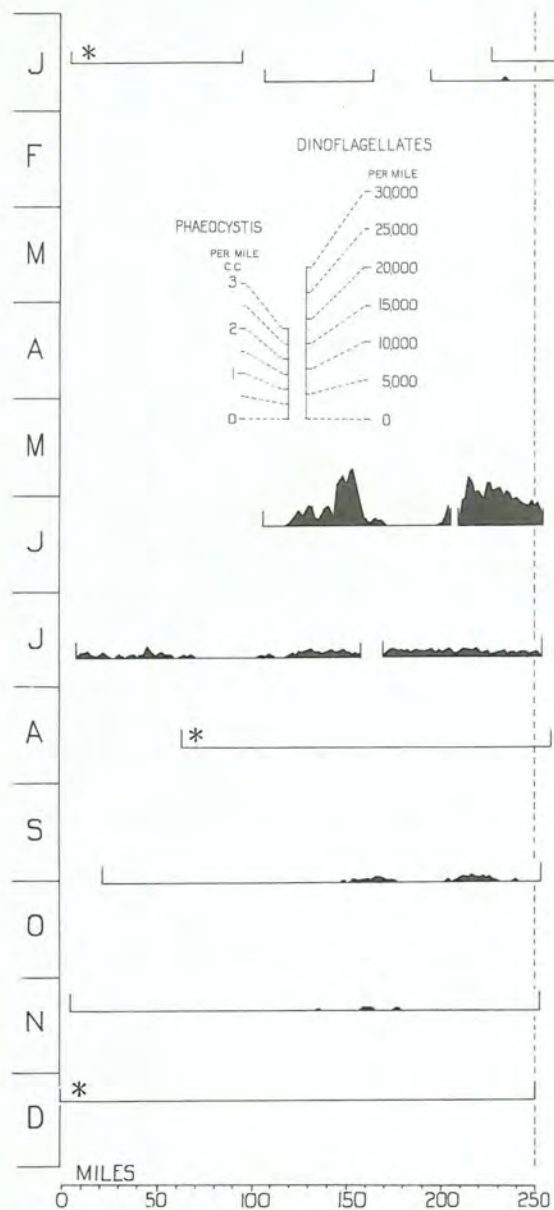
Records of **DINOFLAGELLATES** (blacked-in graph) and **PHAEOCYSTIS** (broken line) on the Bremen line, 1932-1934, arranged as explained on Plates I and II.

# PLATE XII

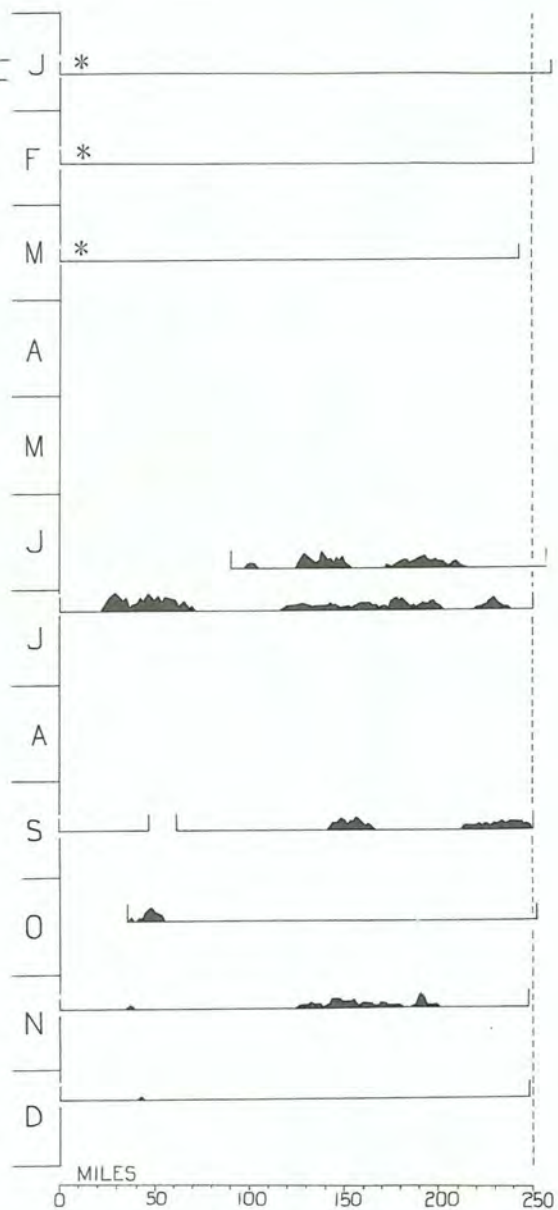


Records of **DINOFLAGELLATES** (blacked-in graph) and **PHAEOCYSTIS** (broken line) on the Bremen line, 1935-1937; arrangement and scale as on Plate XI.

1932



1933



1934

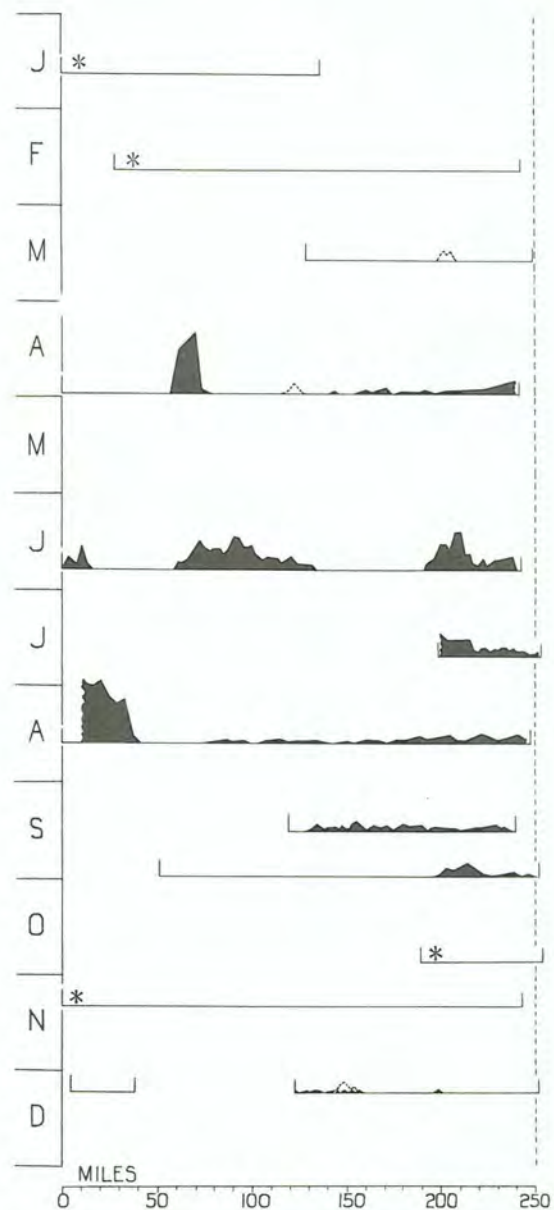


PLATE XIII

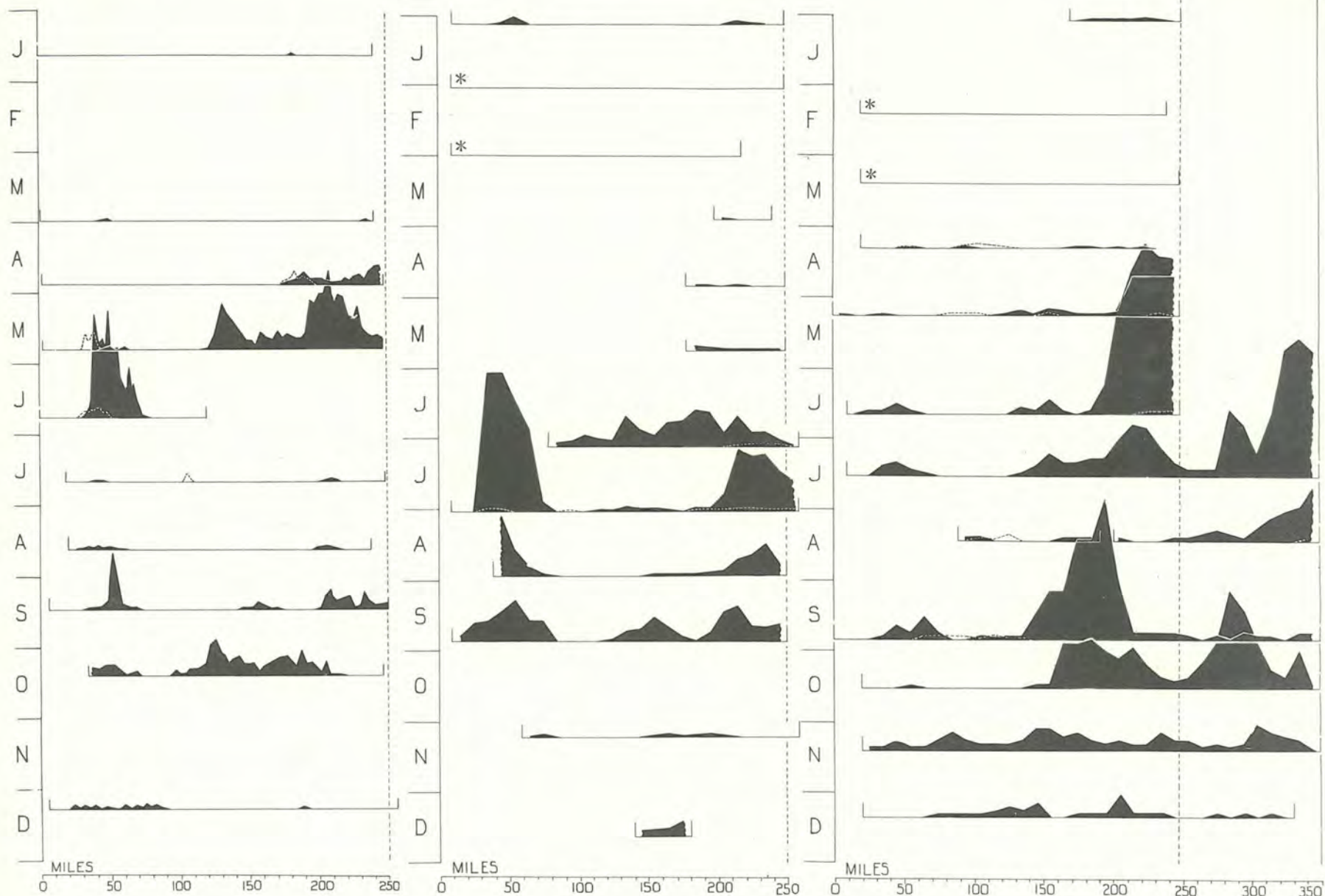
Records of **DINOFLAGELLATES** (blacked-in graph) and **PHAEOCYSTIS** (broken line) on the Copenhagen line, 1932-1934, arranged as explained on Plate III.



1935

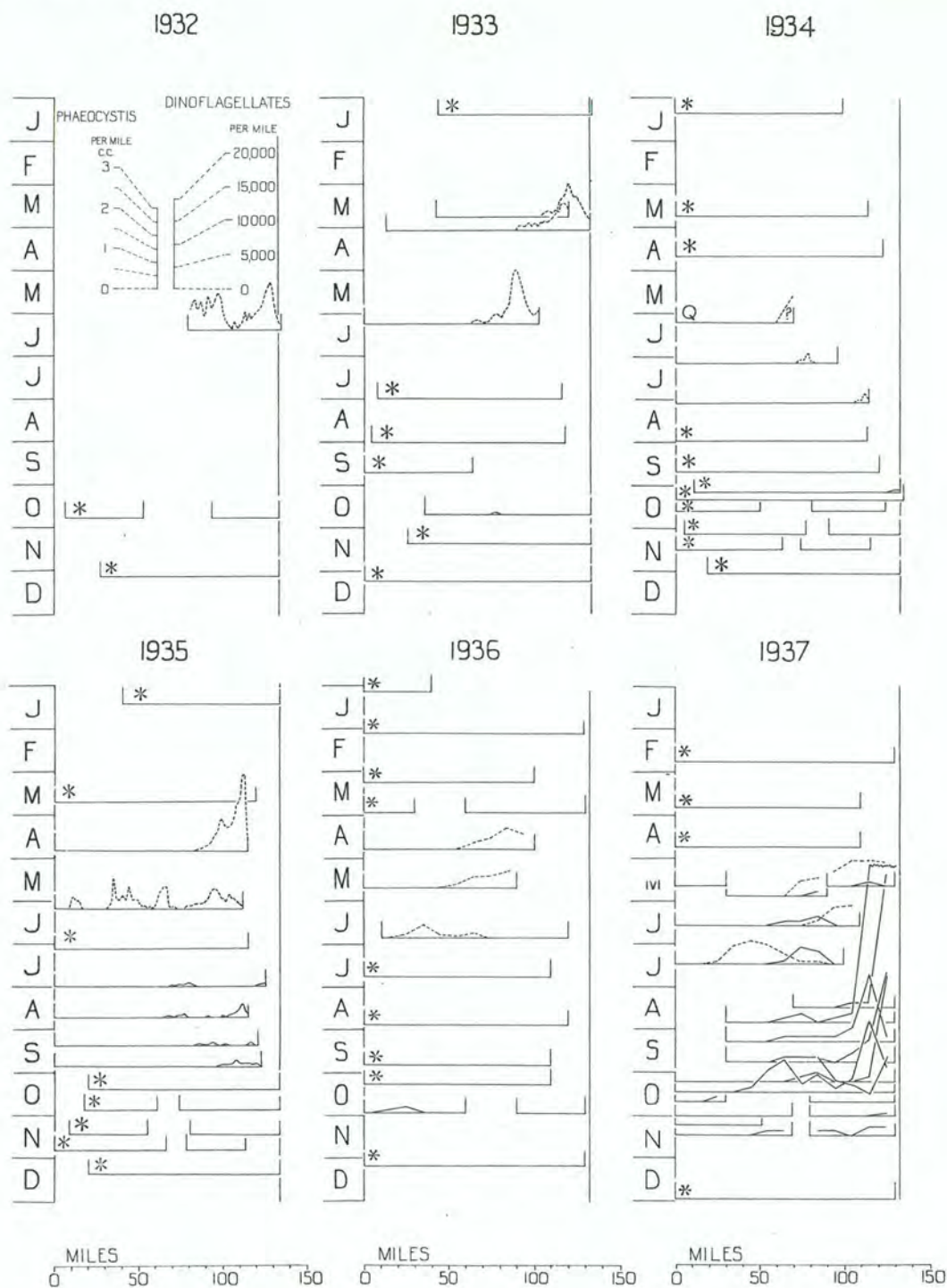
1936

1937



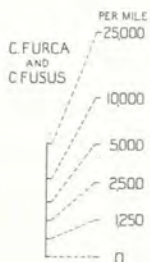
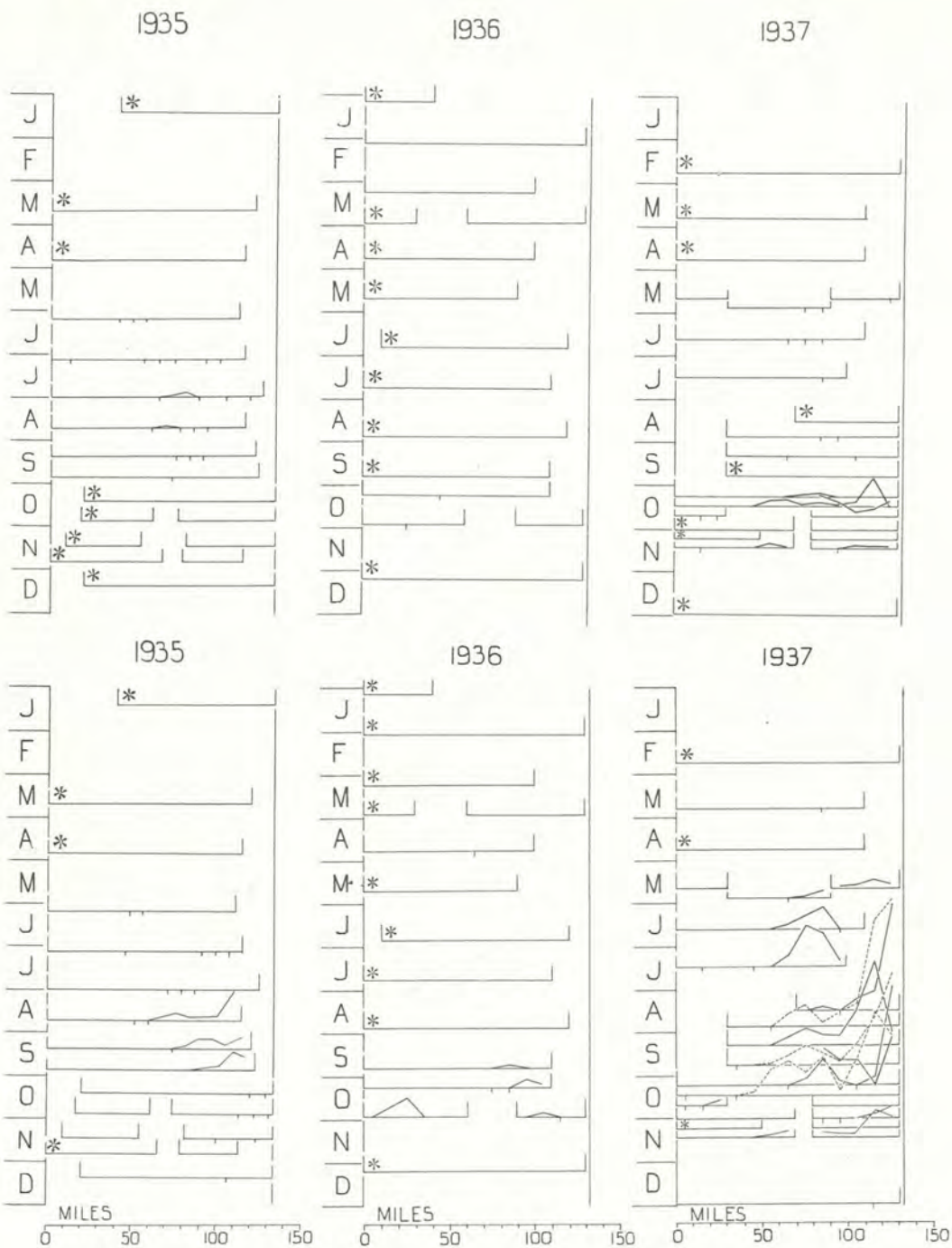
Records of **DINOFLAGELLATES** (blacked-in graph) and **PHAEOCYSTIS** (broken line) on the Copenhagen line, 1935-1937; arrangements and scale as on Plate XIII.

# PLATE XV



Records of **DINOFLAGELLATES** (continuous line) and **PHAEOCYSTIS** (broken line) on the Rotterdam line, 1932-1937, arranged as explained on Plate IX. 'Q' indicates a record of qualitative value only.

# PLATE XVI



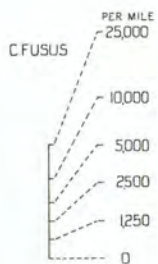
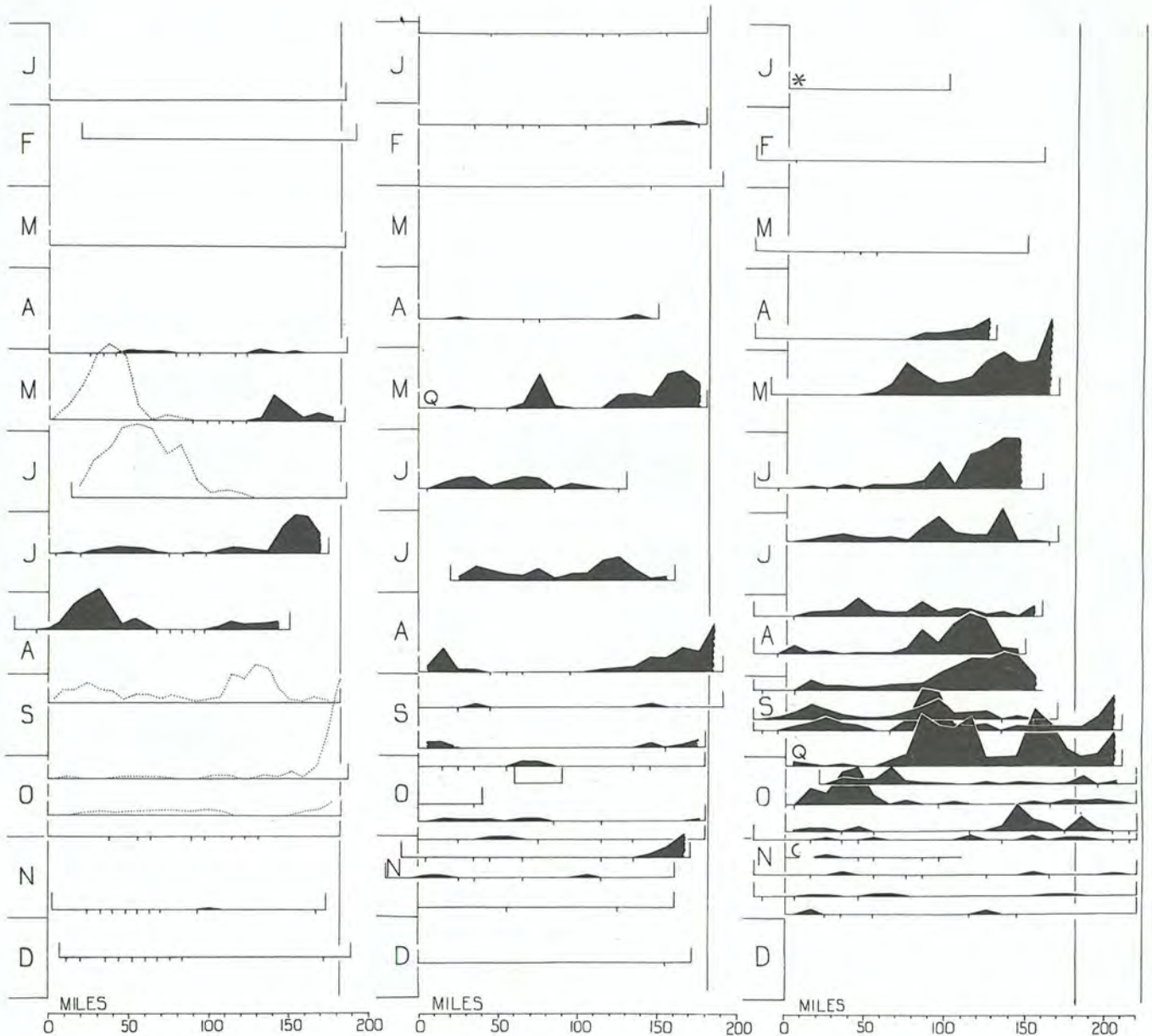
Records of **CERATIUM FURCA** (above) and **C. FUSUS** (below) on the Rotterdam line, 1935-1937, arranged as explained on Plate IX. The scale is the same as that on Plate XVII. For the sake of clarity alternate continuous and broken lines have been used for **C. FUSUS** in the autumn of 1937.

# PLATE XVII

1935

1936

1937



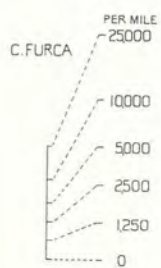
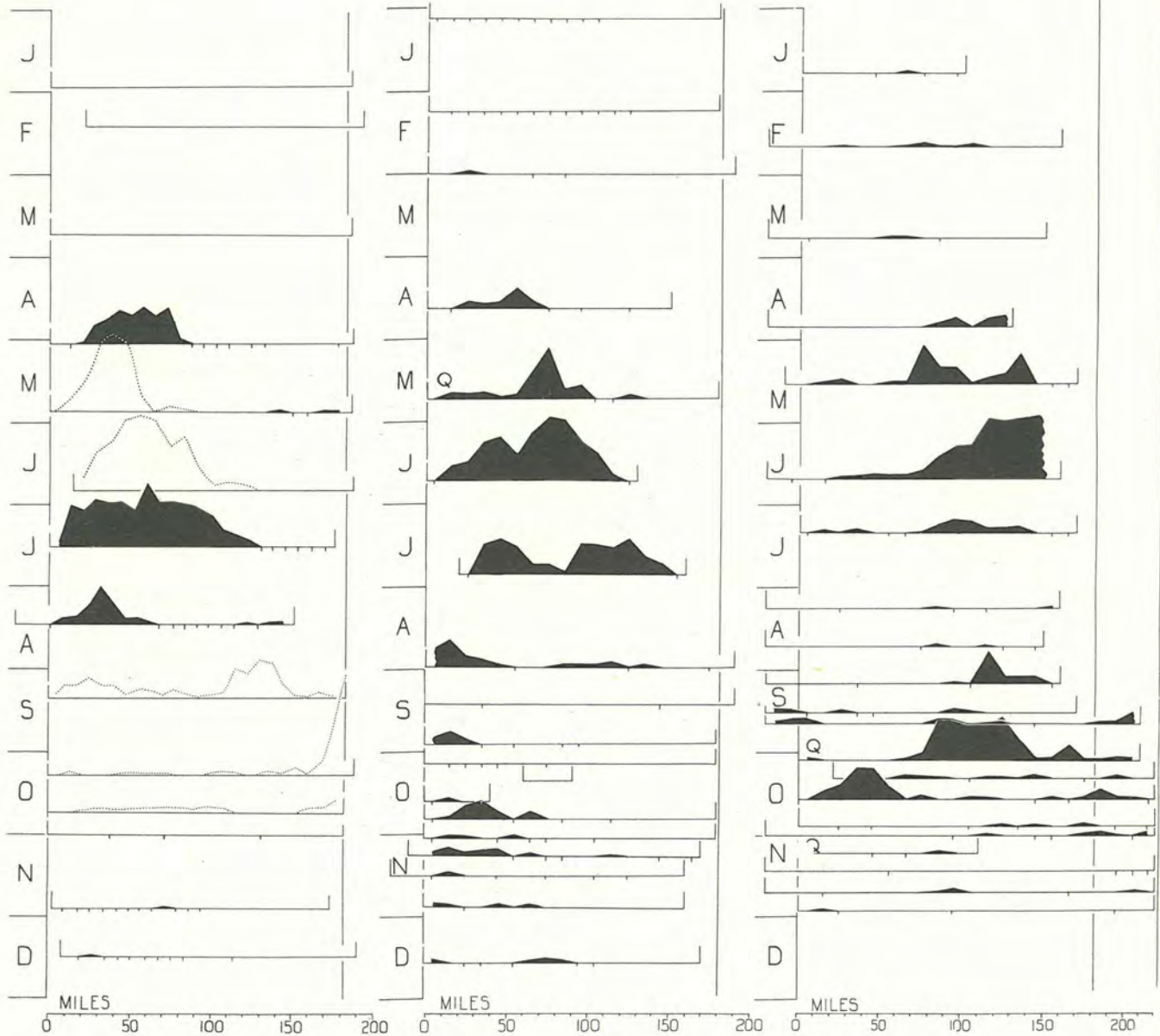
Records of **CERATIUM FURCA** (blacked-in) on the Bremen line, 1935-1937, arranged as explained on Plates I and II. On a few occasions in 1935, when no detailed analysis was made, the corresponding graphs of Total Dinoflagellates have been provided in dotted line.

# PLATE XVIII

1935

1936

1937



**FURCA**  
 Records of **CERATIUM FUSUS** (blacked-in) on the Bremen line,  
 1935-1937, arranged as explained on Plate XVII.

1935

1936

1937

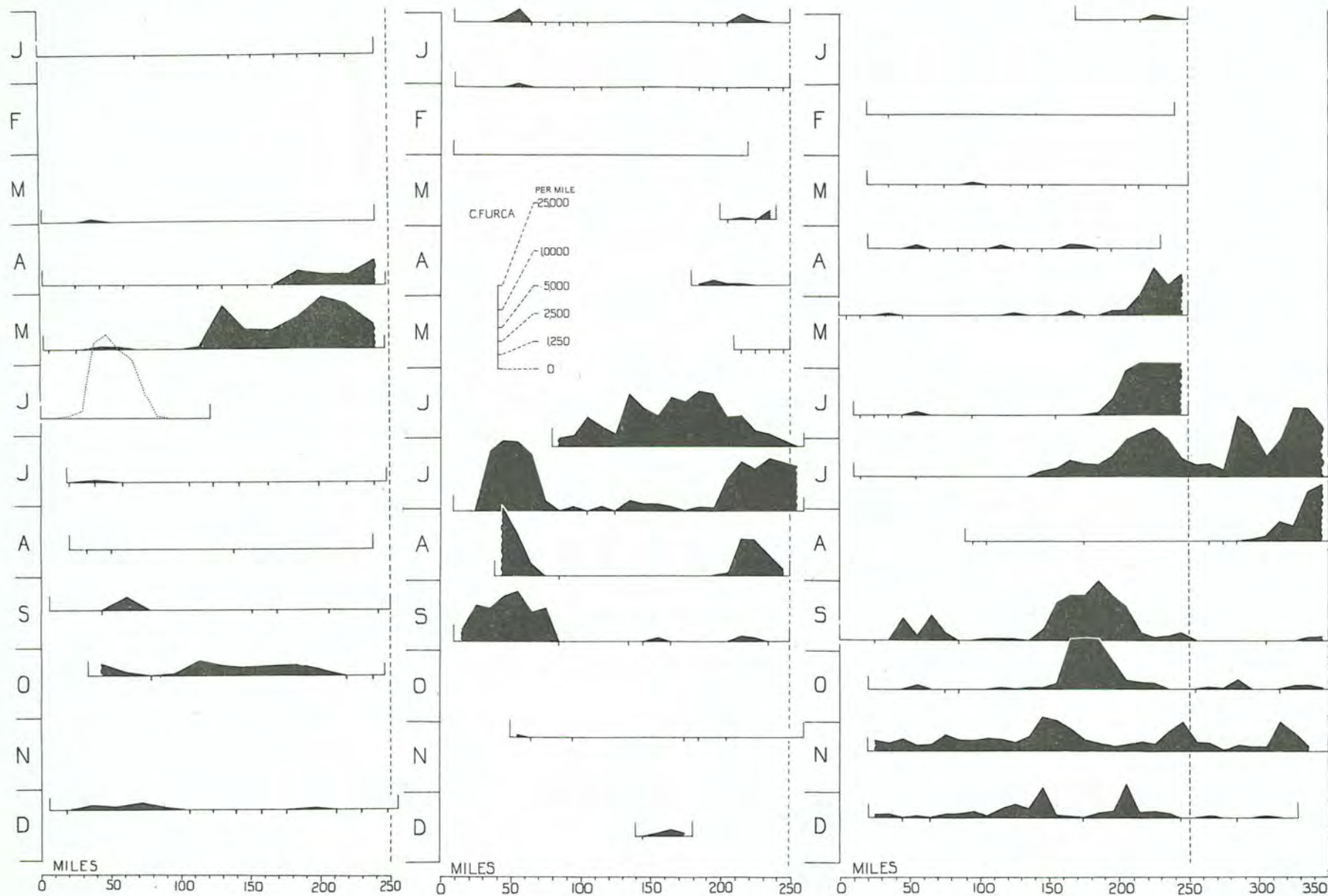


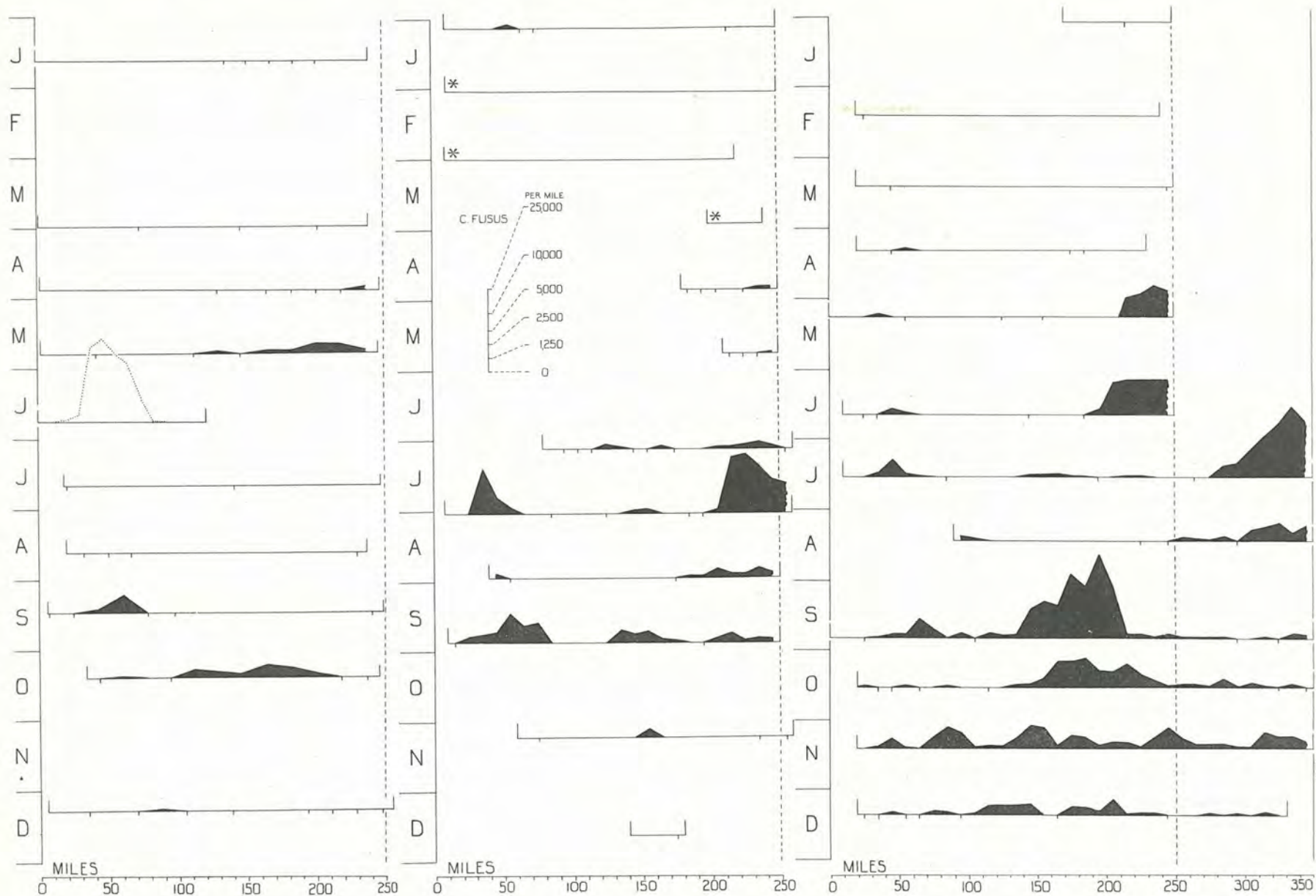
PLATE XIX

Records of **CERATIUM FURCA** (blacked-in) on the Copenhagen line, 1935-1937, arranged as explained on Plate XVII, except that the vertical lines on the left represent the position of the Humber lightvessel.

1935

1936

1937

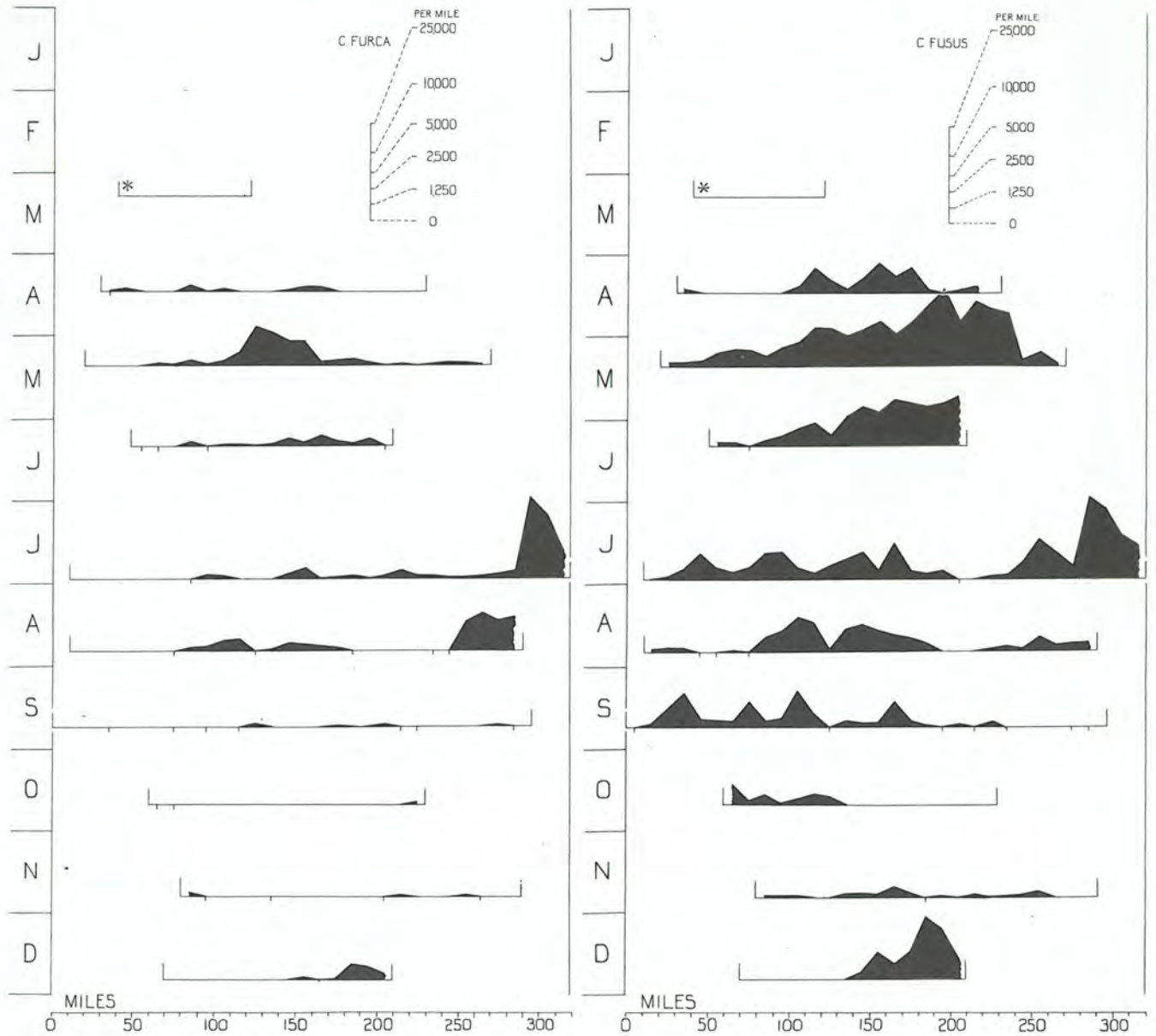


Records of *CERATIUM FUSUS* (blacked-in) on the Copenhagen line, 1935-1937, arranged as explained on Plate XVII, except that the vertical lines on the left represent the position of the Humber lightvessel.

# PLATE XXI

1937

1937



Records of **CERATIUM FURCA** (left) and **C. FUSUS** (right) on the Esbjerg line, 1937, arranged as explained on Plate XVII, except that the vertical lines on the left represent the position of the Sunk lightvessel.



# PLATES XXII-LXIV

MAPS SHOWING THE MONTHLY  
DISTRIBUTION OF THE  
PHYTOPLANKTON IN THE  
SOUTHERN NORTH SEA  
JUNE 1932 TO DECEMBER 1937

## The following Explanation relates to PLATES XXII—XXXVI

This series of maps has been prepared to show the distribution of *RHIZOLENIA STYLIFORMIS* and *BIDDULPHIA SINENSIS* in the southern North Sea month by month from June 1932 to December 1937. Usually only one representative record is shown in each month for each line, but more have been obtained in the autumns of the later years; some of these have been included in the standard series, but others for 1935-1937 are shown in additional maps at the end of the series on Plates XXXV and XXXVI. A few remaining graphs not shown will be found in text-figures 3 and 4.

*RHIZOLENIA STYLIFORMIS* is shown as a blacked-in graph or vertical strokes below the base lines (traces).

*BIDDULPHIA SINENSIS* is shown as a broken line graph or horizontal strokes below the base lines (traces).

The date of each record is shown at the eastern end of each line.

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

The position of the 20 fathom contour of the DOGGER BANK has been indicated by a faint dotted line.

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

Scale for  
Plates XXII—XXXVI :

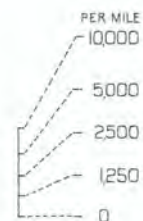
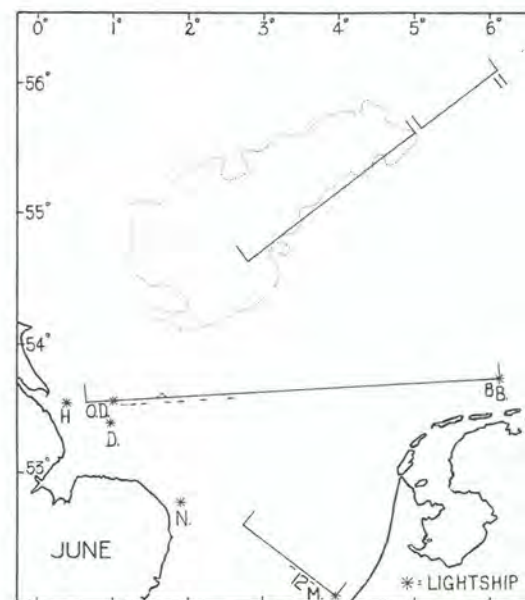
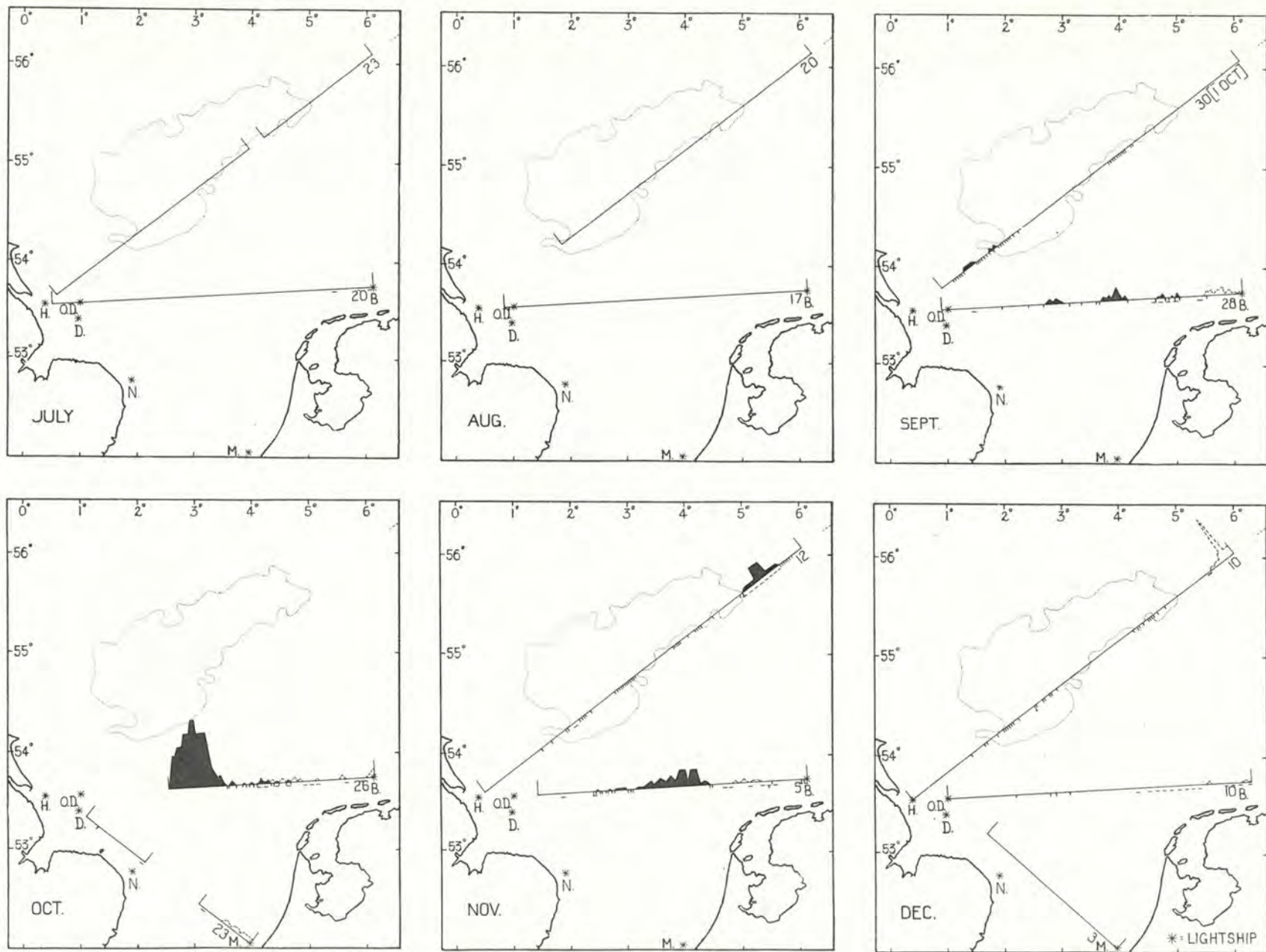
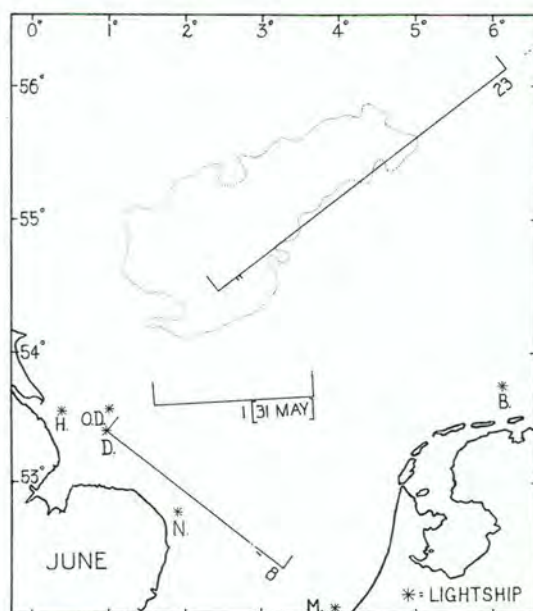
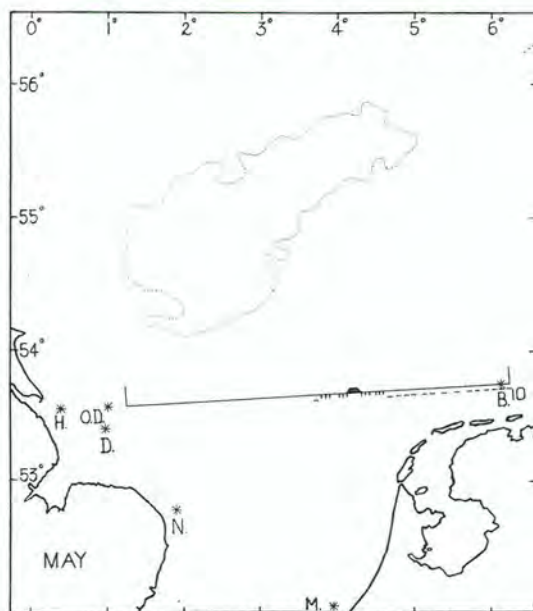
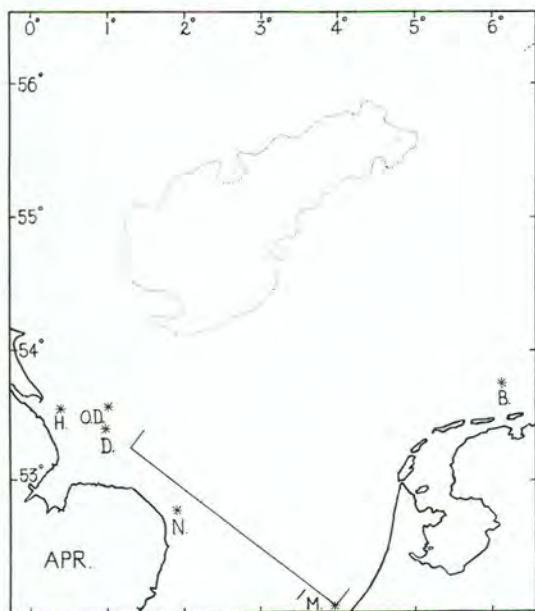
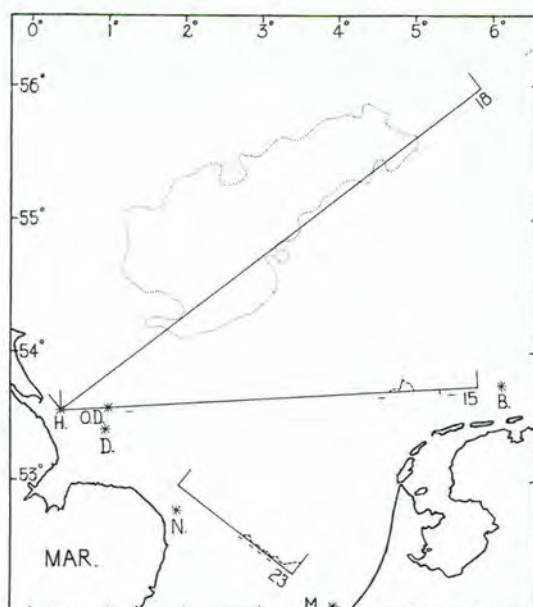
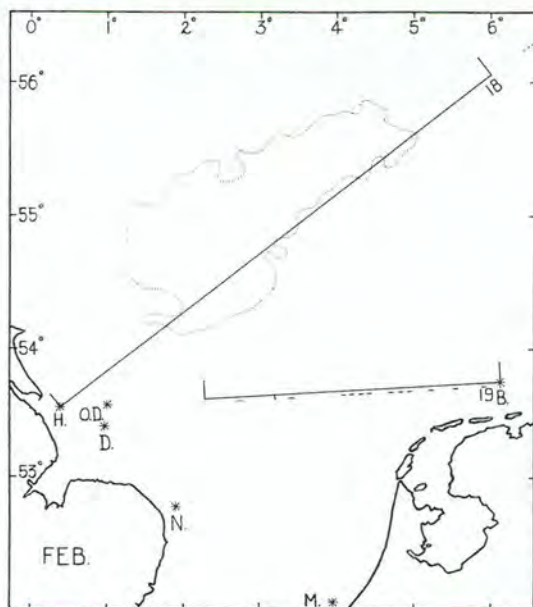
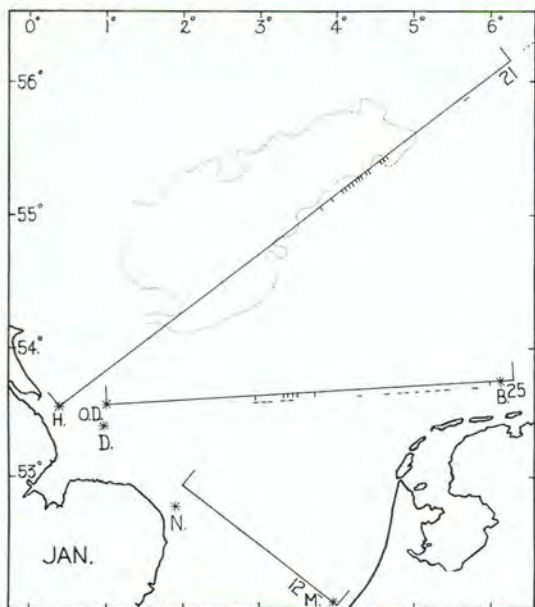


PLATE XXII

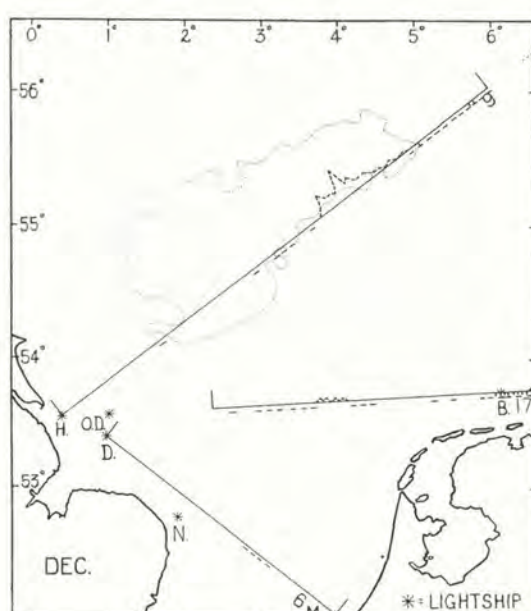
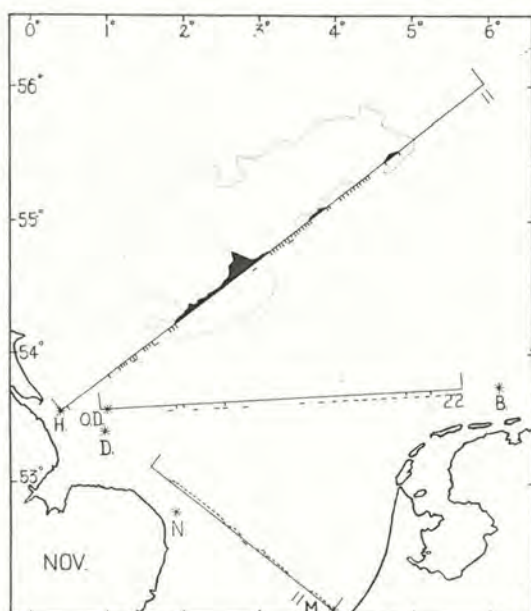
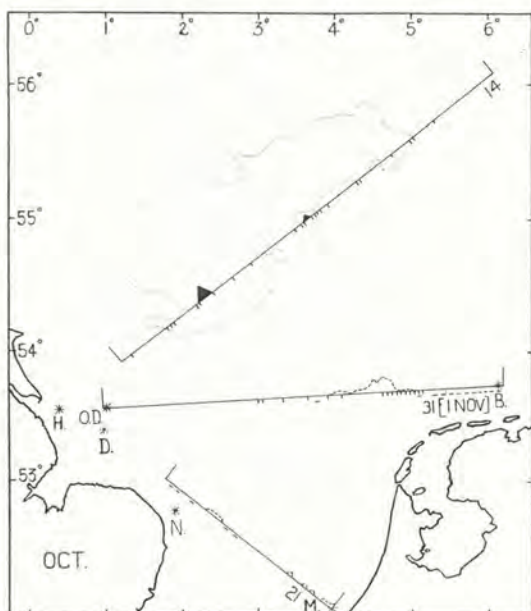
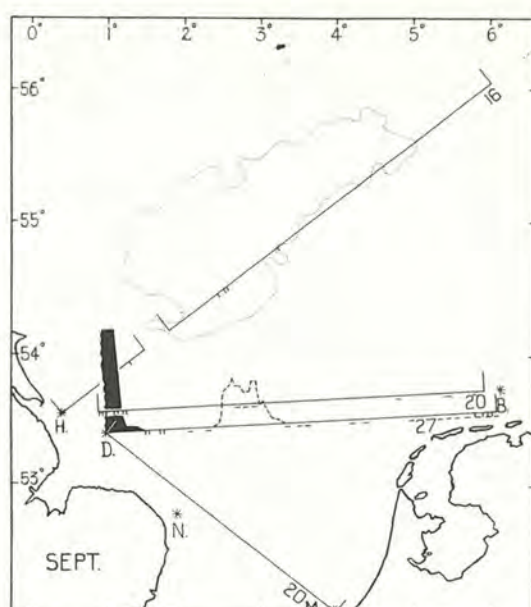
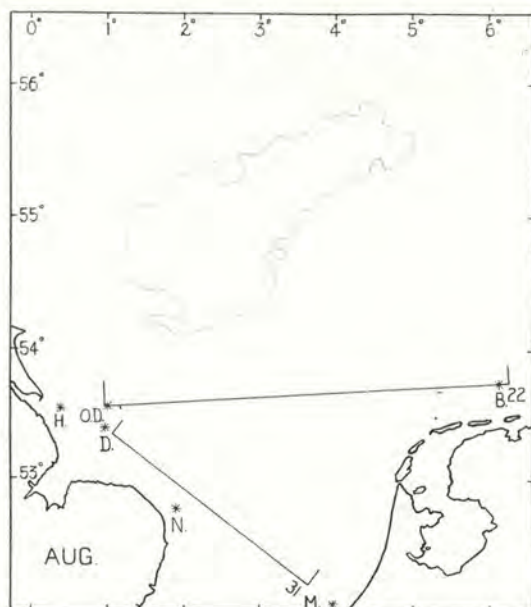
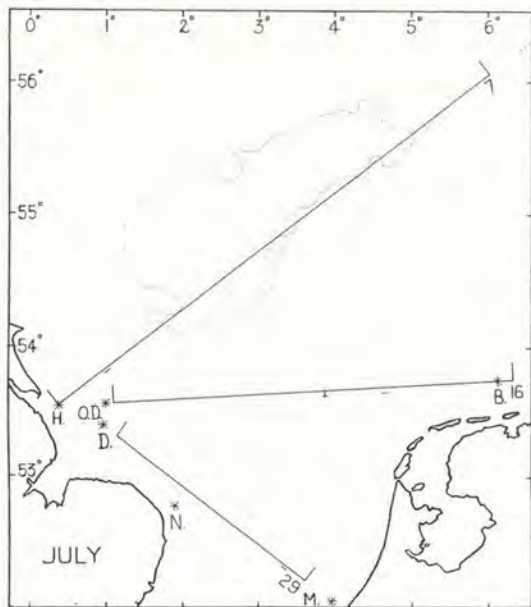




**RHIZOSOLENIA STYLIFORMIS** (blacked-in graph) and **BIDDULPHIA SINENSIS** (broken line), 1932, for further explanation see Plate XXII.

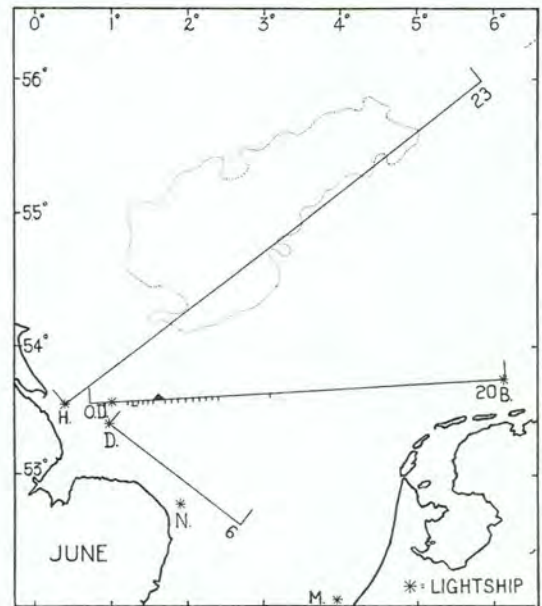
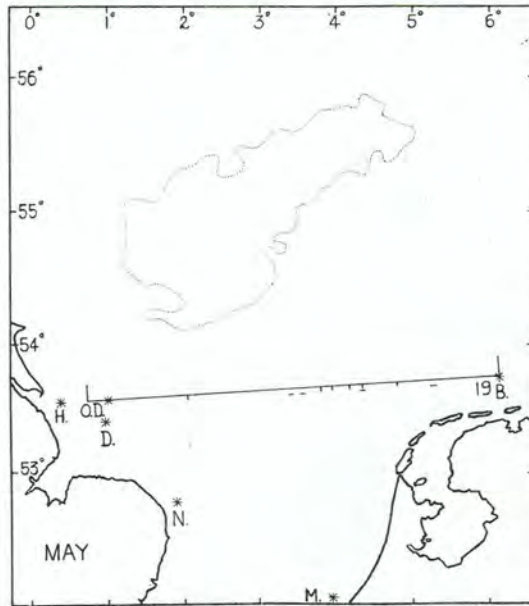
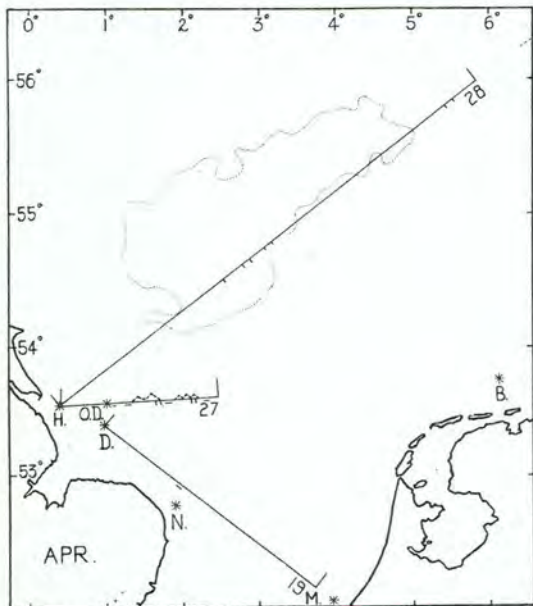
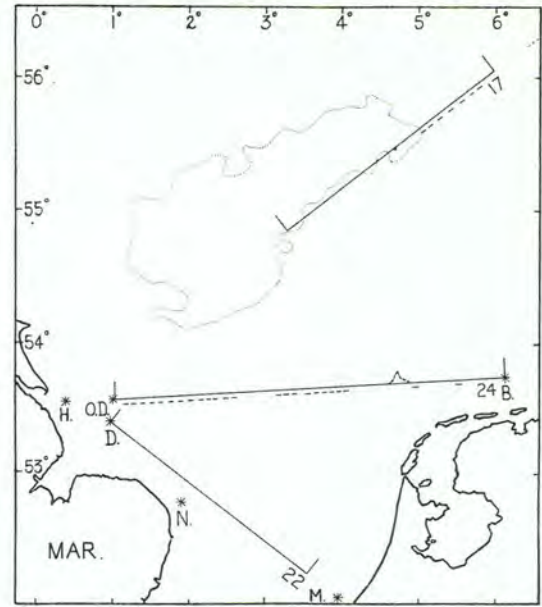
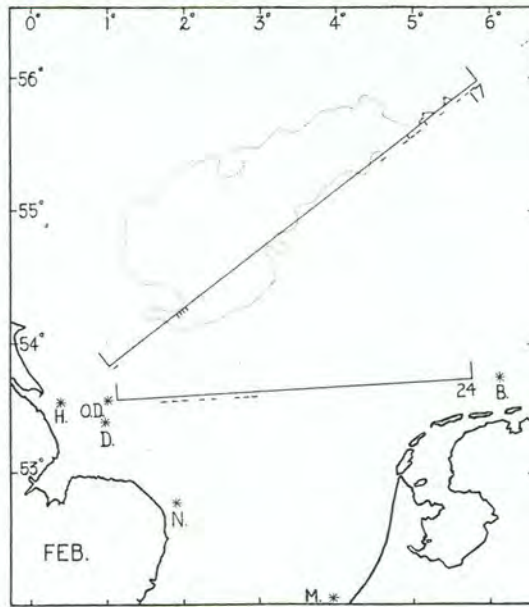
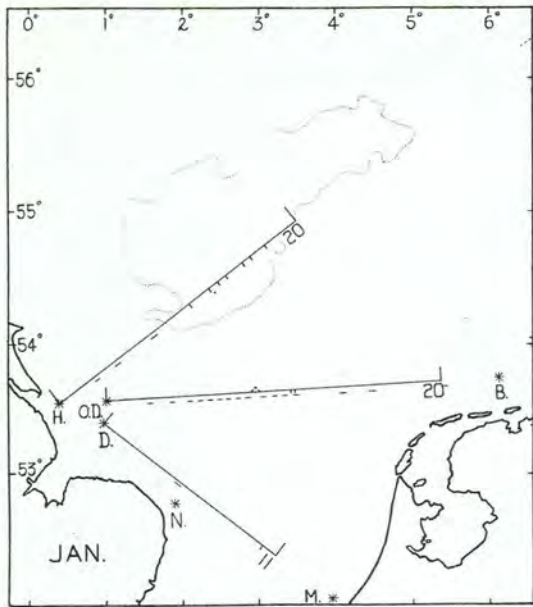


**RHIZOSOLENIA STYLIFORMIS** (blackened-in graph) and **BIDDULPHIA SINENSIS** (broken line), 1933, for further explanation see Plate XXII.

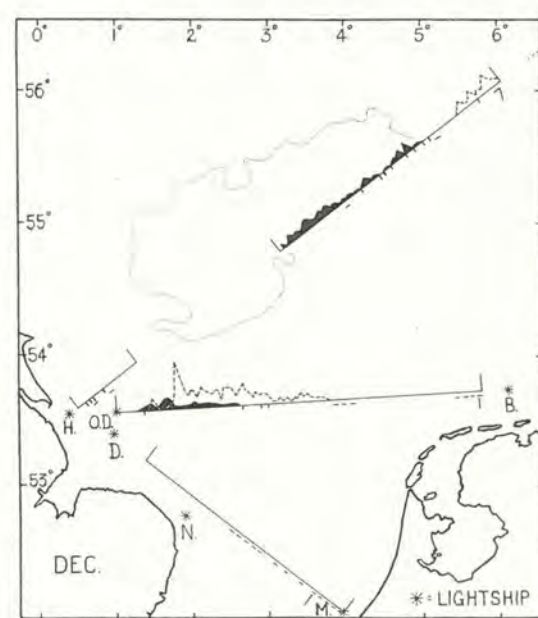
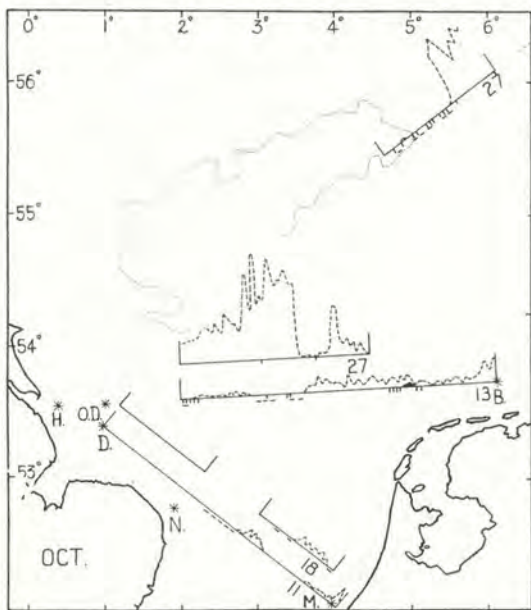
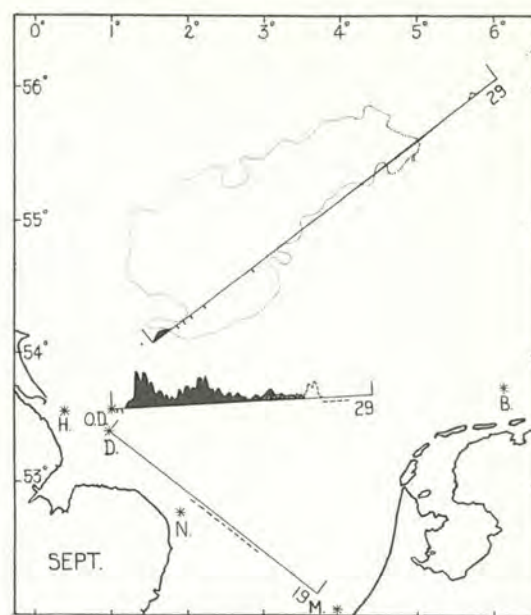
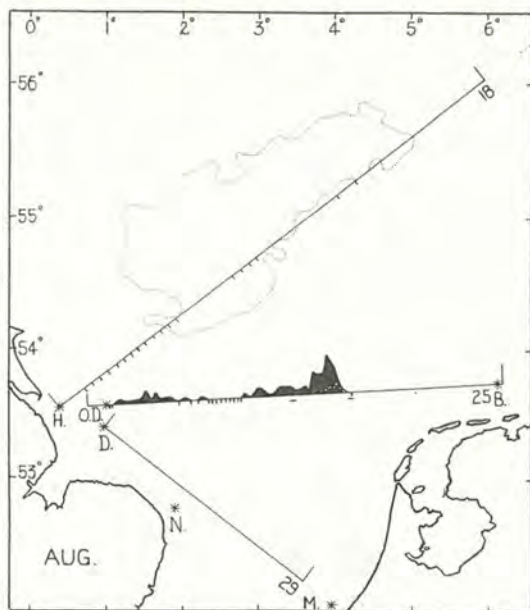
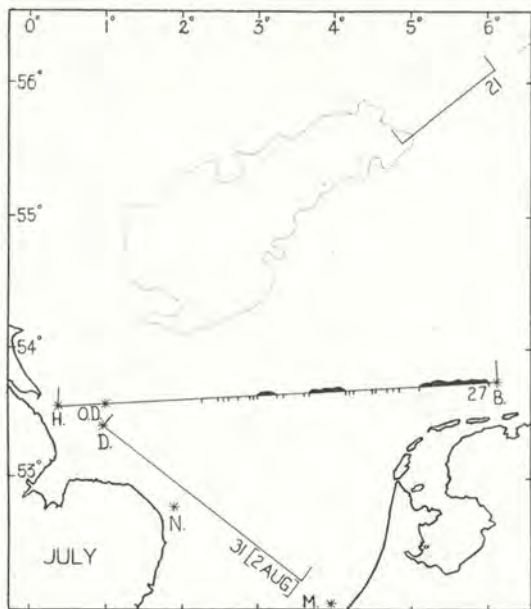


\* = LIGHTSHIP

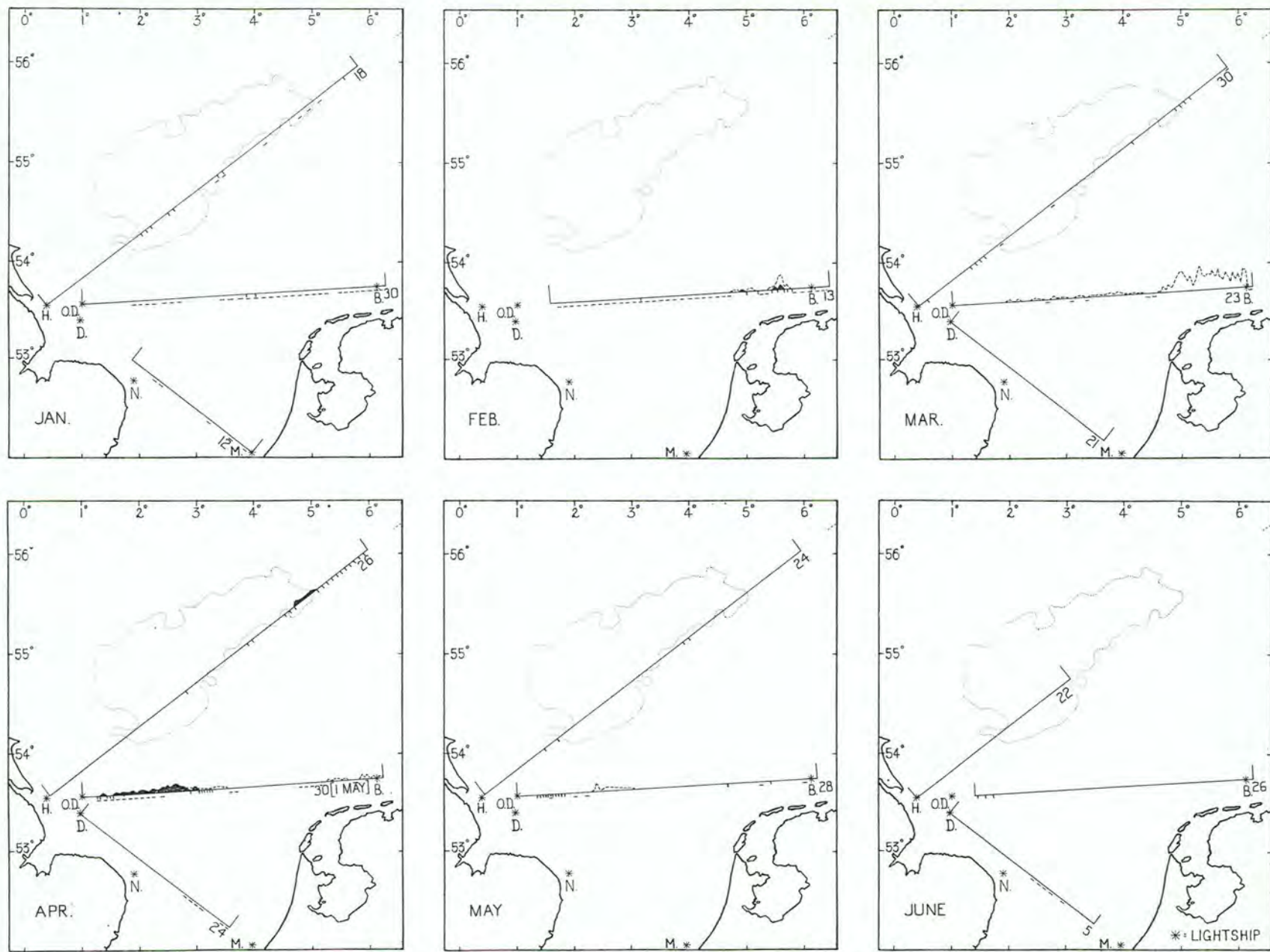
**RHIZOSOLENIA STYLIFORMIS** (blacked-in group) and **BIDDULPHIA SINENSIS** (broken line), 1933, for further explanation see Plate XXII.



**RHIZOSOLENIA STYLIFORMIS** (blacked-in graph) and **BIDDULPHIA SINENSIS** (broken line), 1934, for further explanation see Plate XXII.

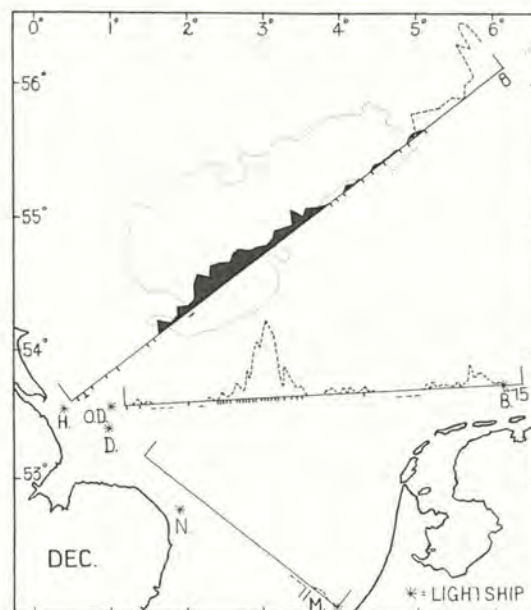
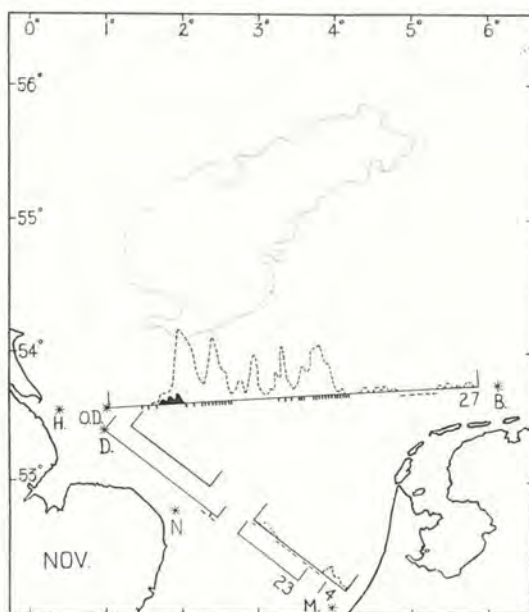
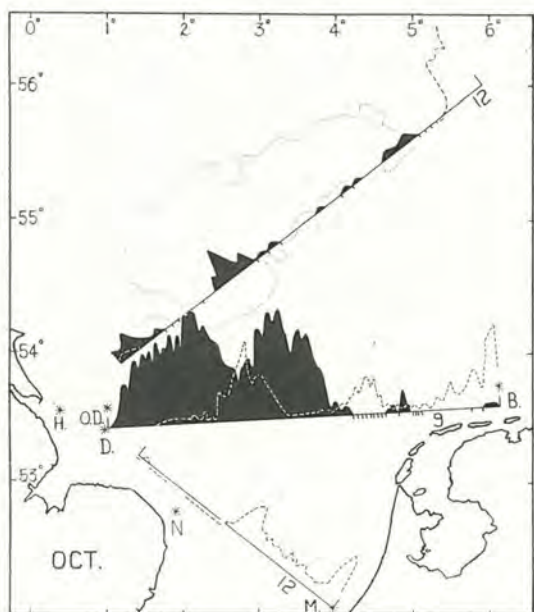
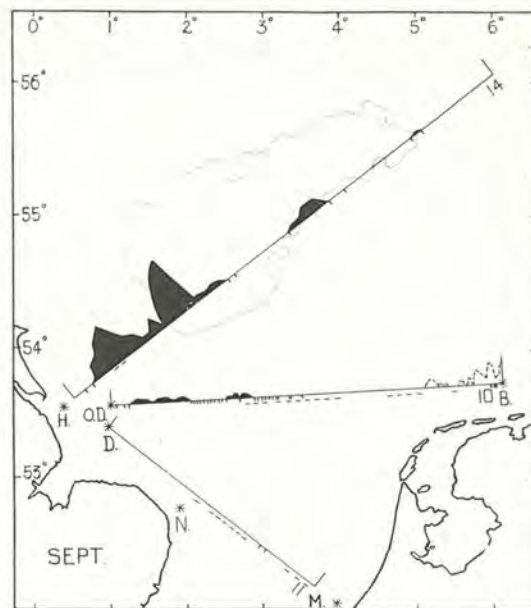
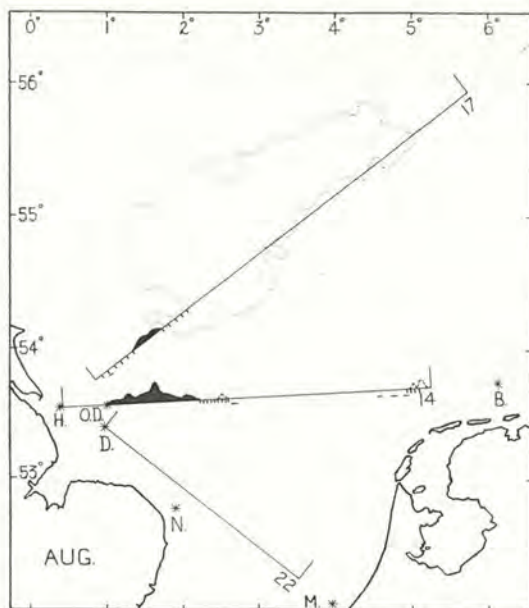
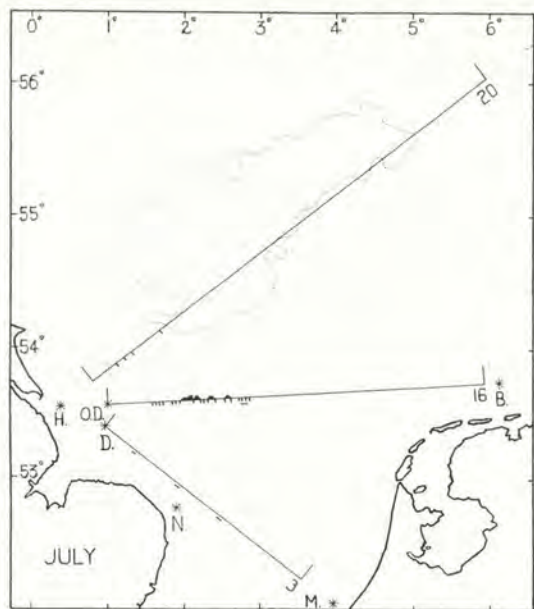


**RHIZOSOLENIA STYLIFORMIS** (blacked-in graph) and **BIDDULPHIA SINENSIS** (broken line), 1934, for further explanation see Plate XXII.

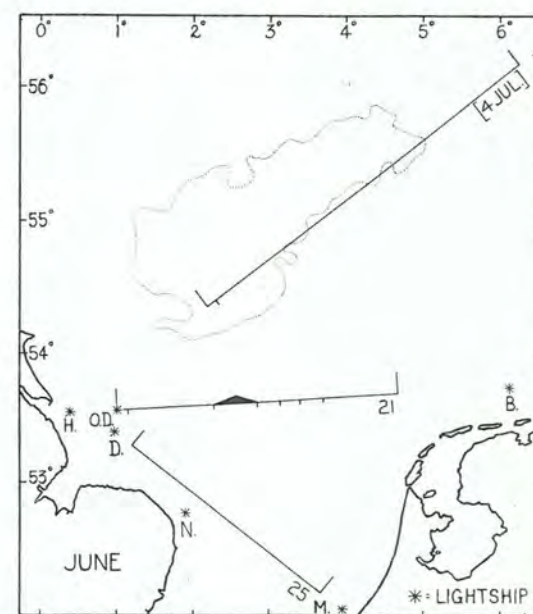
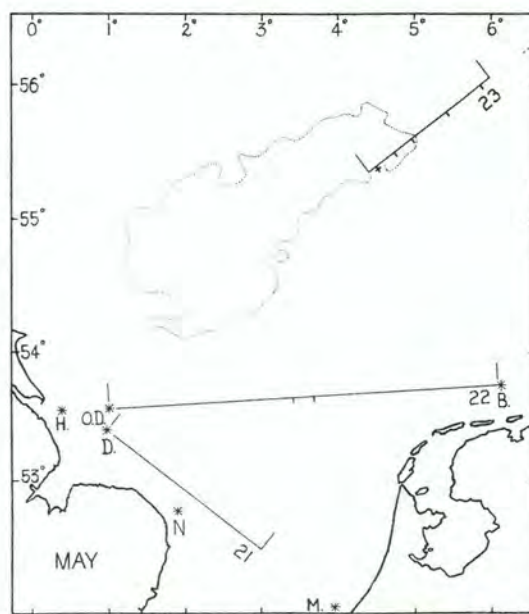
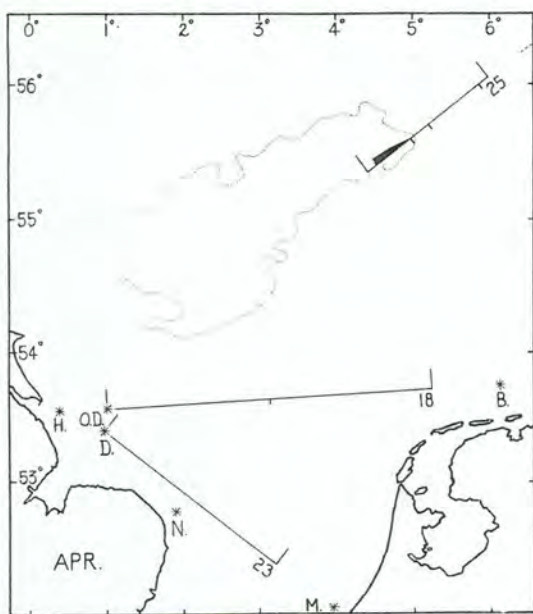
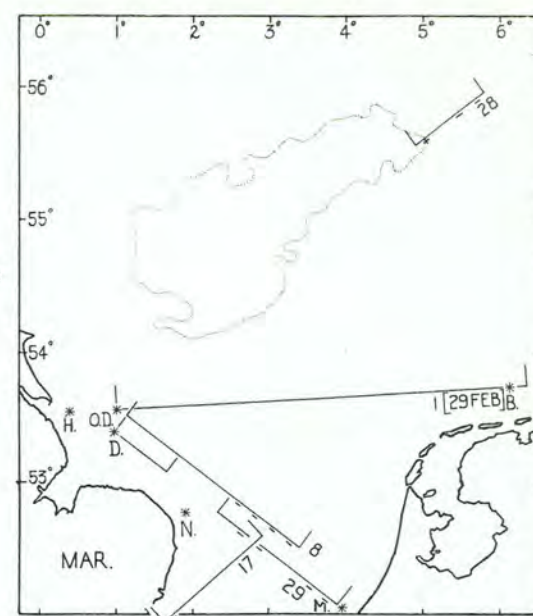
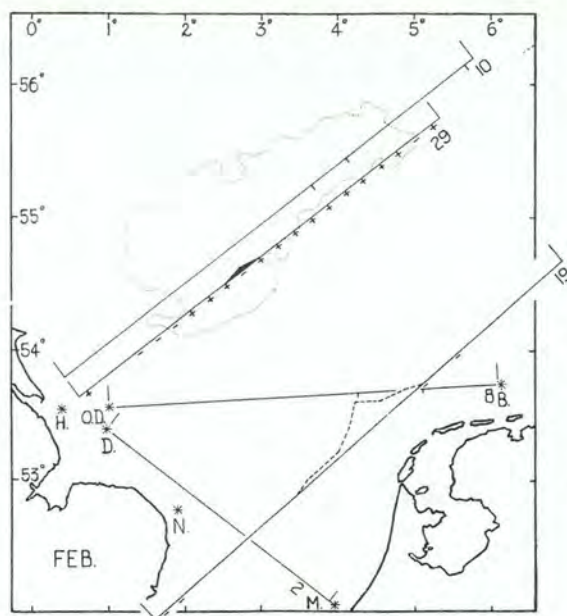
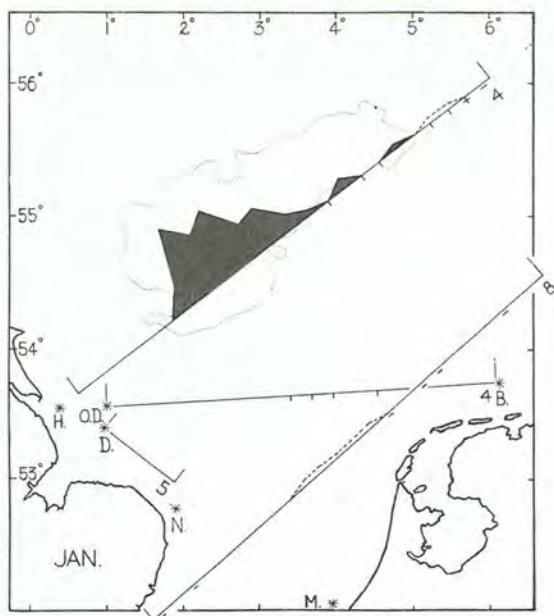


**RHIZOSOLENIA STYLIFORMIS** (blacked-in graph) and **BIDDULPHIA SINENSIS** (broken line), 1935, for further explanation see Plate XXII.

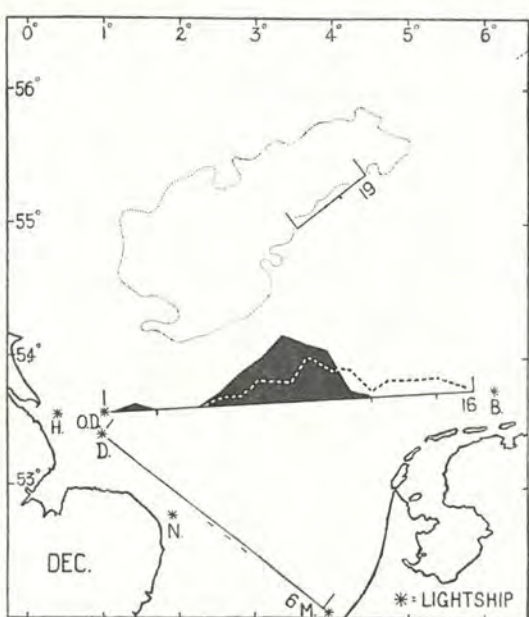
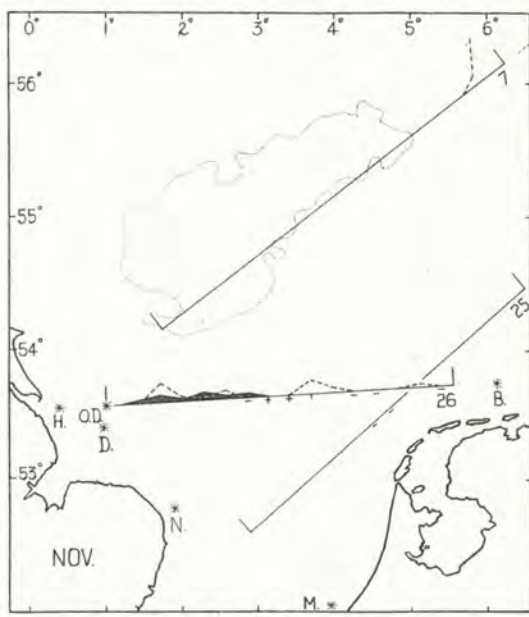
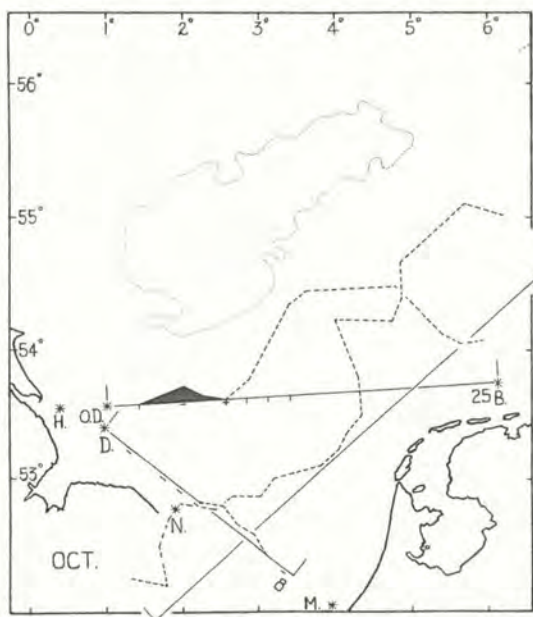
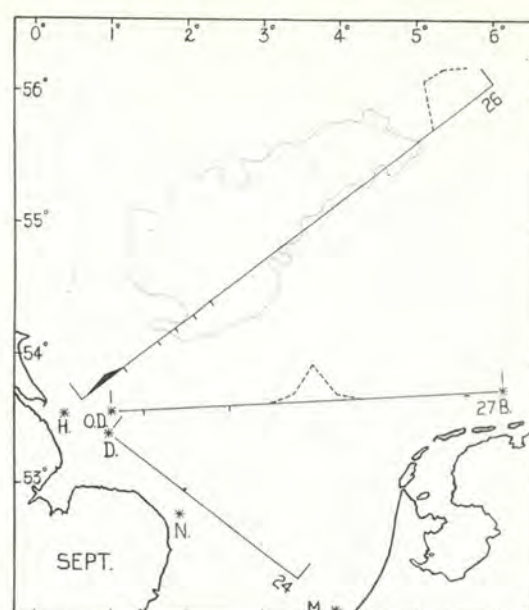
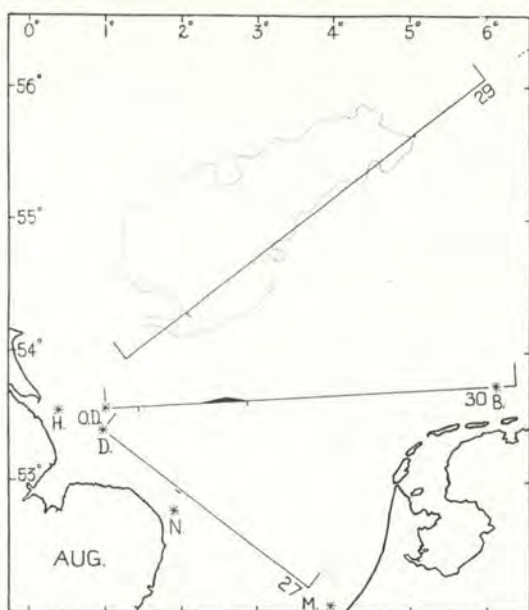
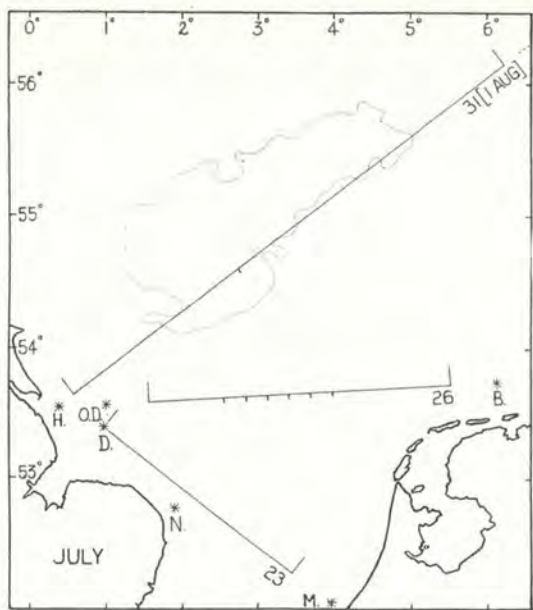




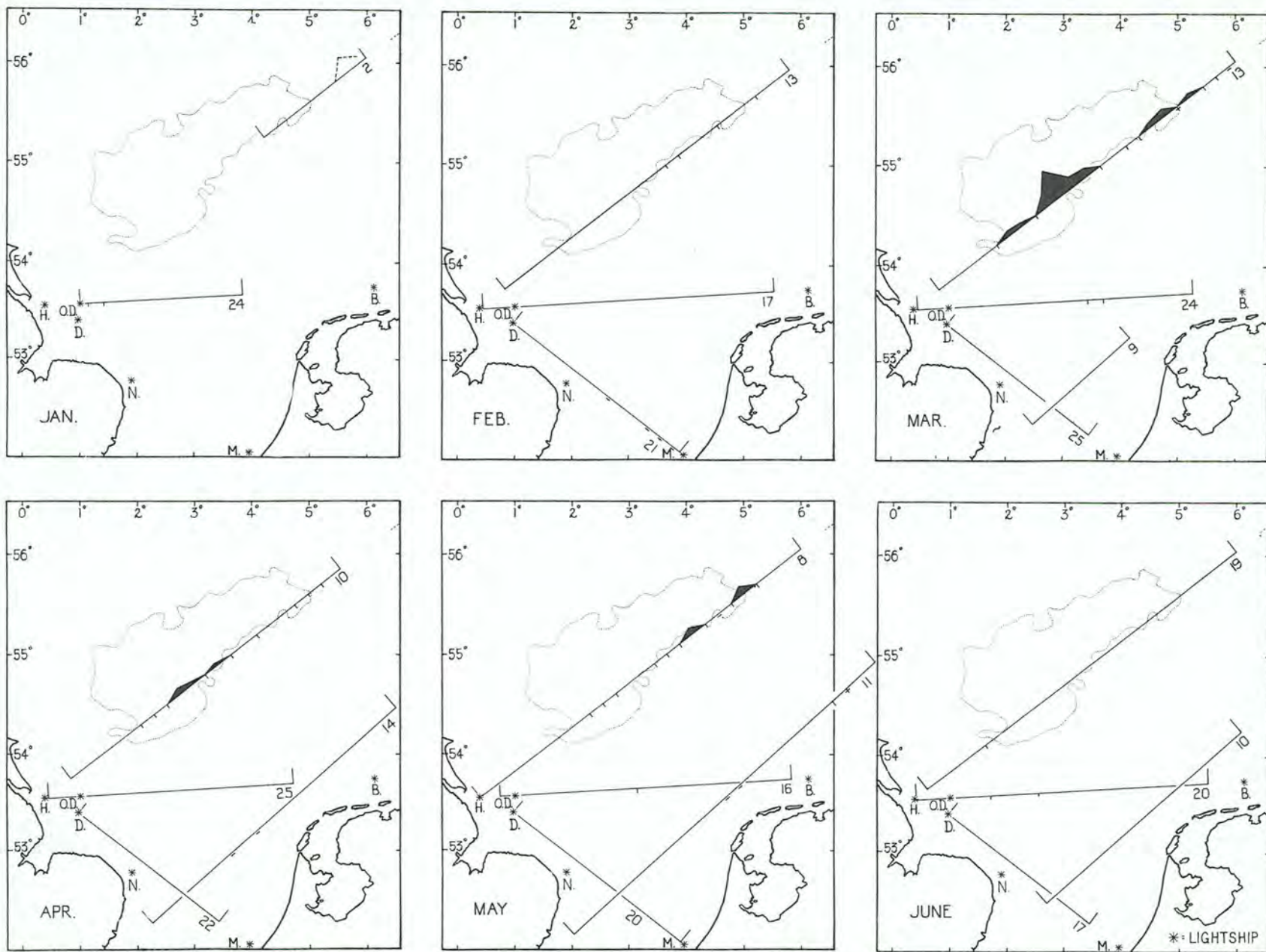
**RHIZOSOLENIA STYLIFORMIS** (blacked-in graph) and **BIDDULPHIA SINENSIS** (broken line), 1935, for further explanation see Plate XXII. See also Plate XXXVI for supplementary maps.



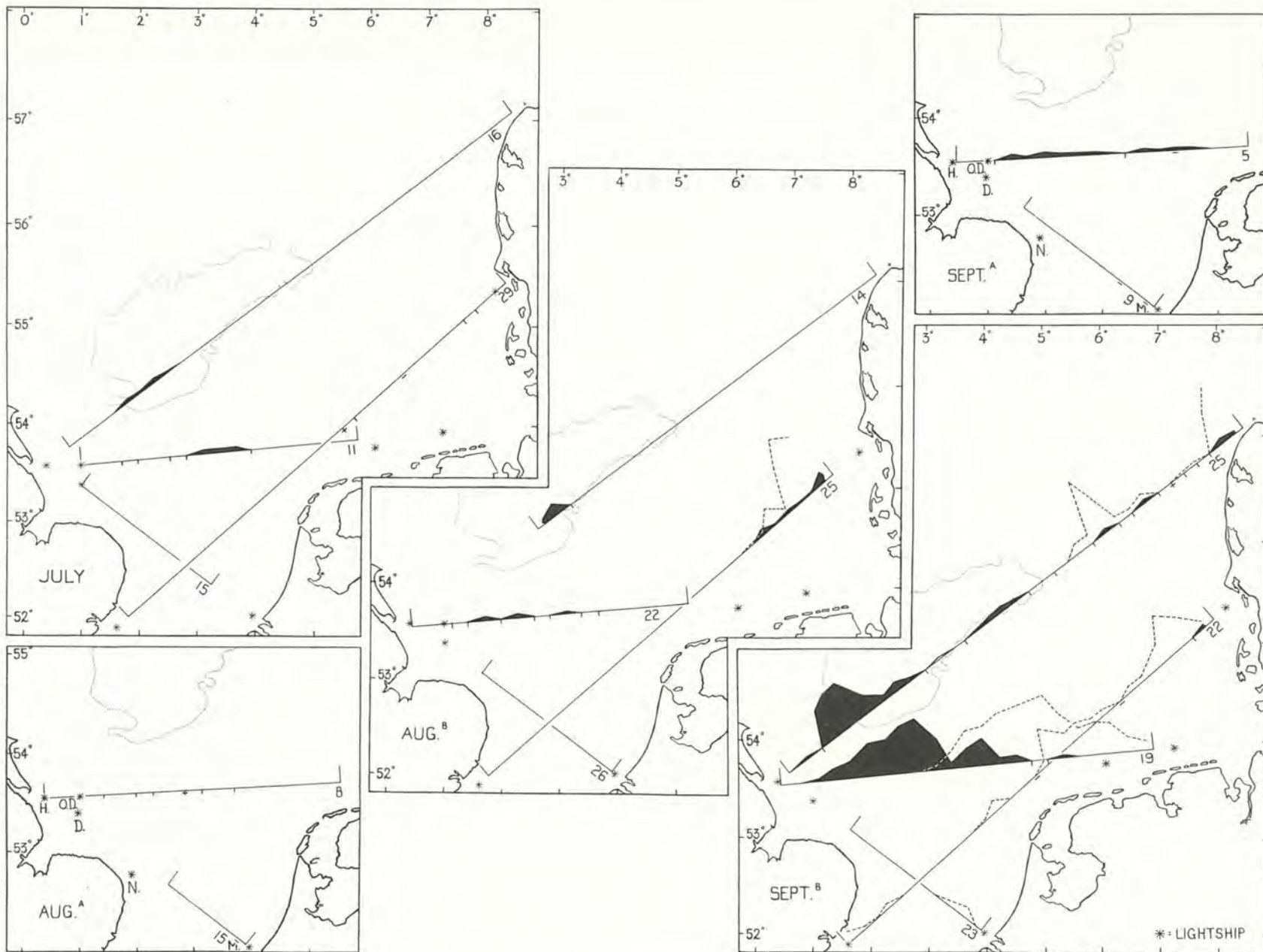
**RHIZOSOLENIA STYLIFORMIS** (black-in graph) and **BIDDULPHIA SINENSIS** (broken line), 1936, for further explanation see Plate XXII.



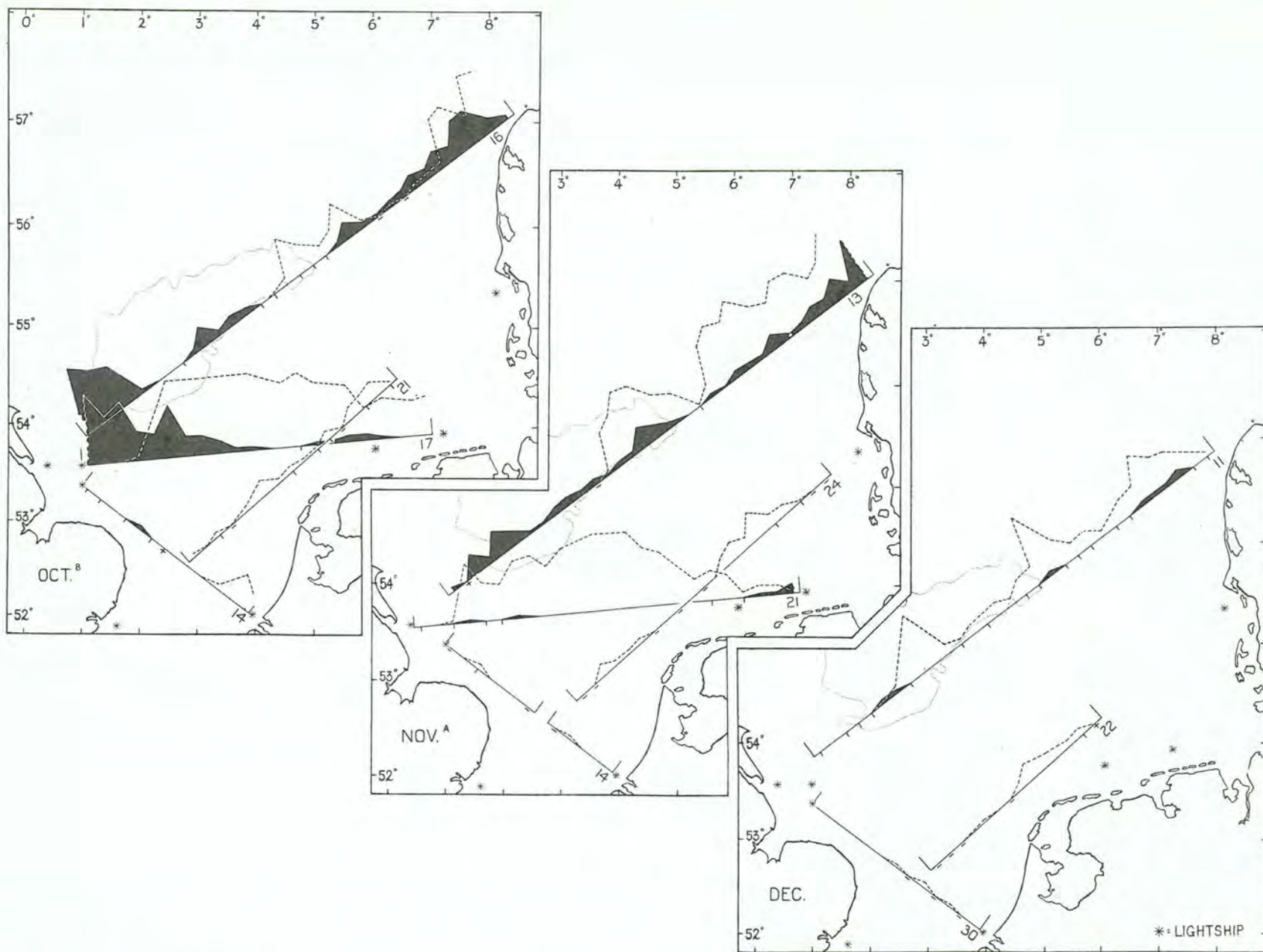
**RHIZOLENIA STYLIFORMIS** (blacked-in graph) and **BIDDULPHIA SINENSIS** (broken line), 1936, for further explanation see Plate XXII. See also Plate XXXVI for supplementary maps.



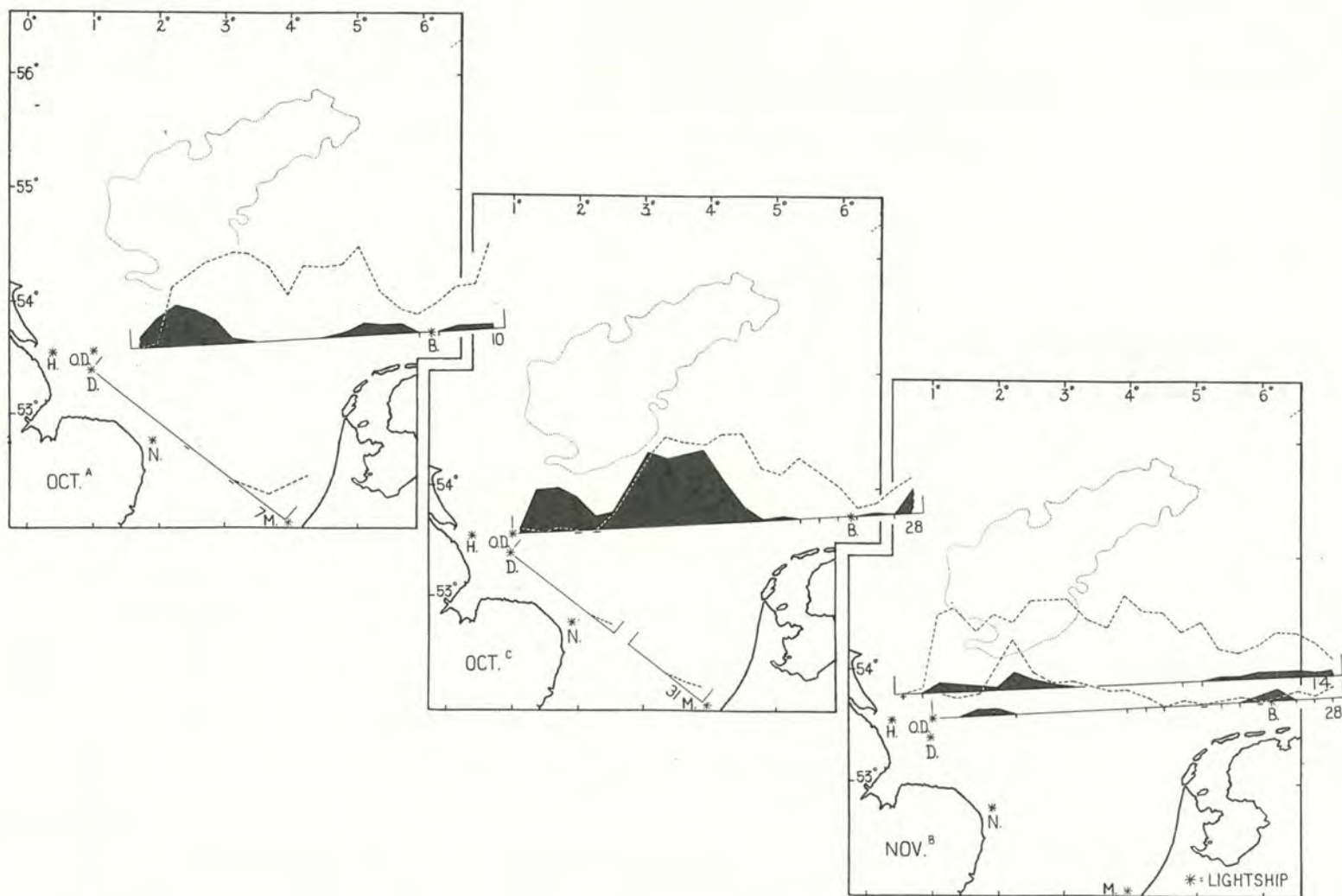
**RHIZOSOLENIA STYLIFORMIS** (blacked-in graph) and **BIDDULPHIA SINENSIS** (broken line), 1937, for further explanation see Plate XXII.



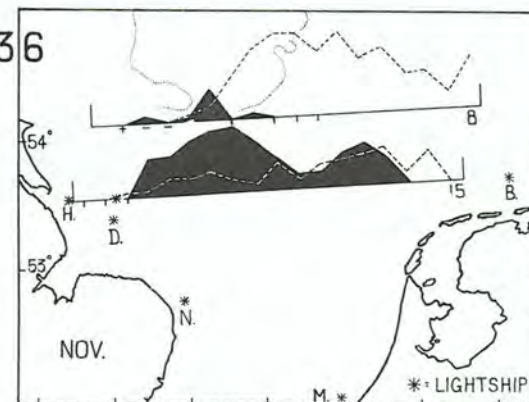
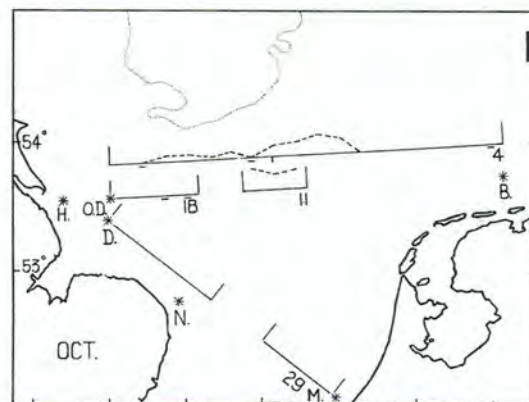
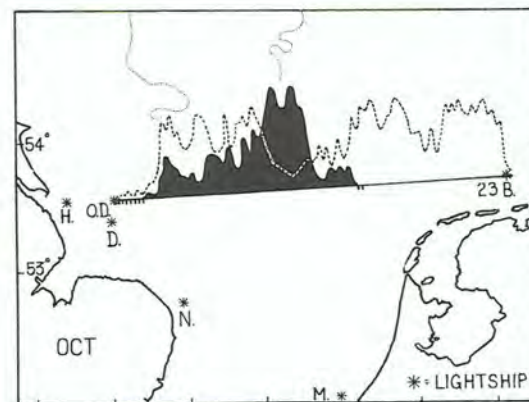
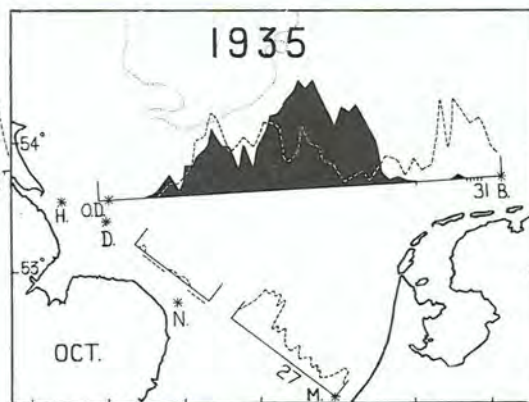
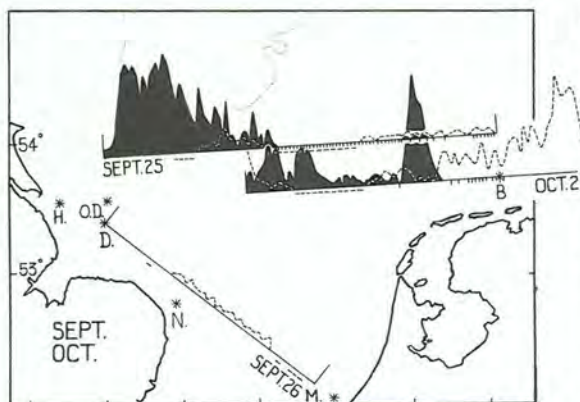
**RHIZOSOLENIA STYLIFORMIS** (blacked-in graph) and **BIDDULPHIA SINENSIS** (broken line), 1937, and continued on Plates XXXIV and XXXV, for further explanation see Plate XXII.



**RHIZOSOLENIA STYLIFORMIS** (blacked-in graph) and **BIDDULPHIA SINENSIS** (broken line), 1937 continued, for further explanation see Plate XXII.



**RHIZOSOLENIA STYLIFORMIS** (blacked-in graph) and **BIDDULPHIA SINENSIS** (broken line), 1937 maps supplementary to Plate XXXIV.



**RHIZOSOLENIA STYLIFORMIS** (blacked-in graph) and **BIDDULPHIA SINENSIS** (broken line), maps supplementary to Plates XXIX (1935) and XXXI (1936).



## Explanation of PLATES XXXVII—XLIV

showing the distribution of patches of **OTHER DIATOMS**,  
i.e., other than *RHIZOSOLENIA STYLIFORMIS* and *BIDDULPHIA*  
*SINENSIS*, during the period June 1932 to December 1937.

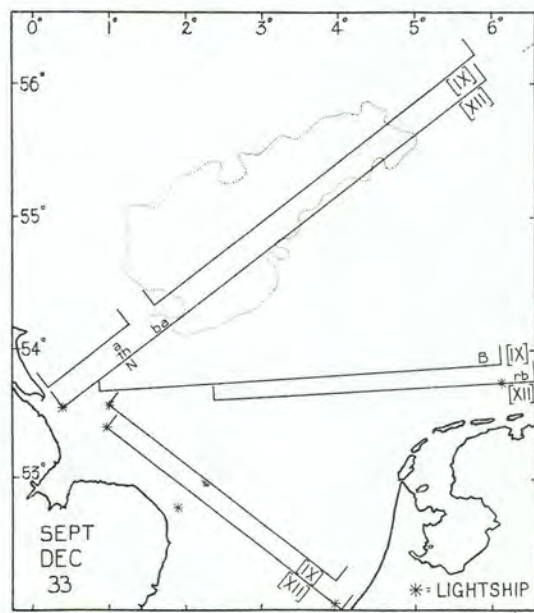
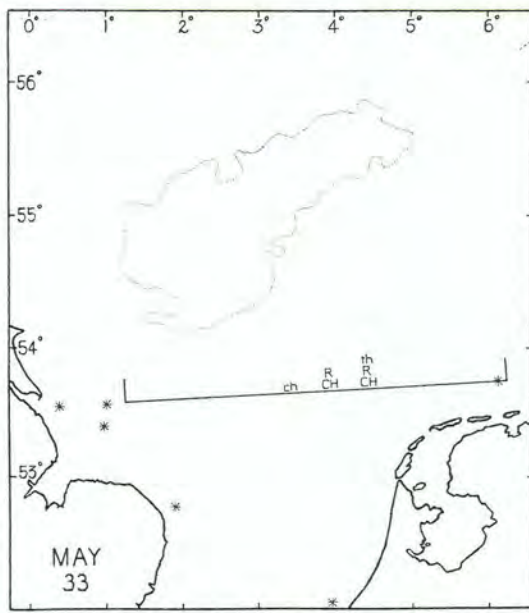
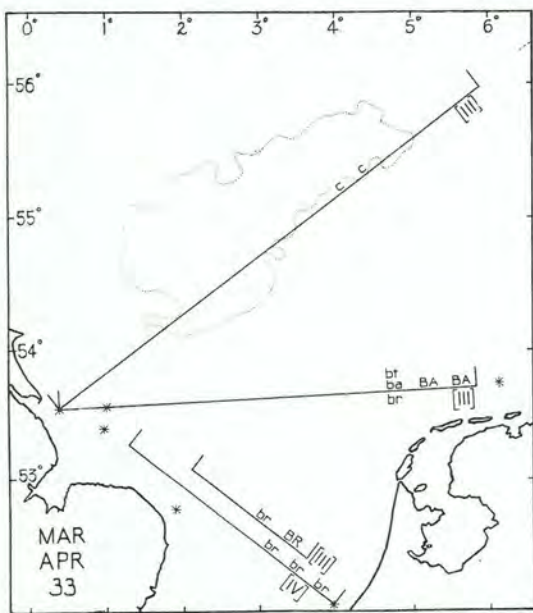
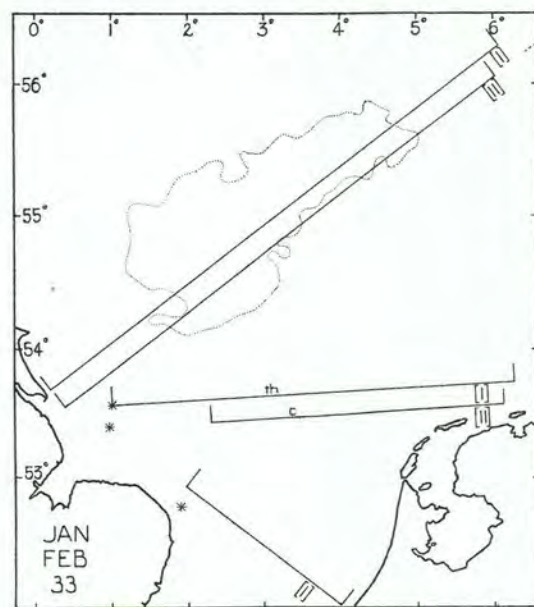
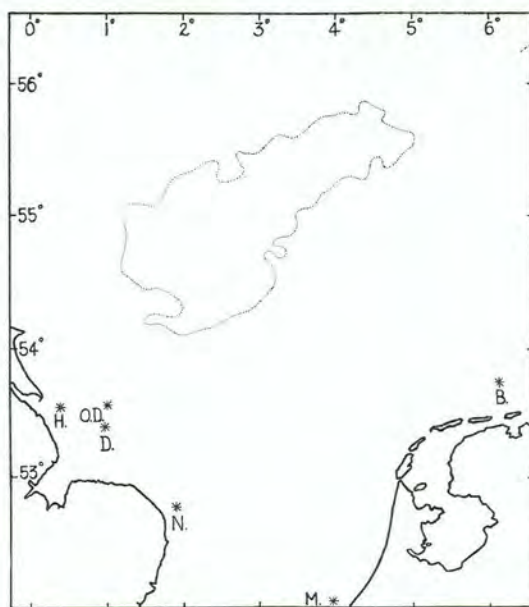
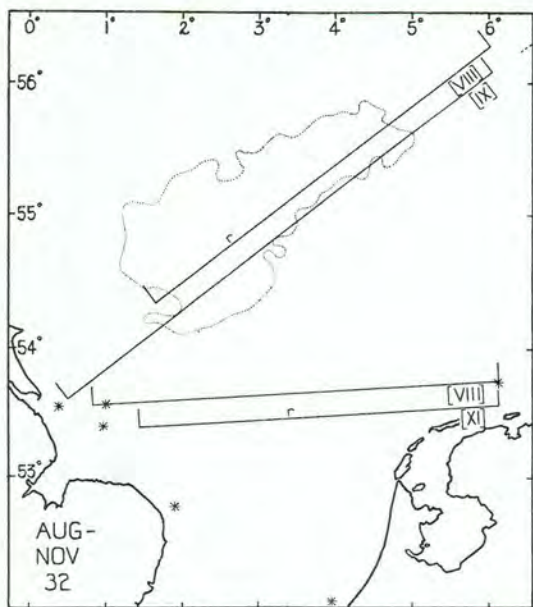
The lines have been divided into blocks of *ca.* 20 miles each and the presence of a patch or patches is denoted by the use of various letters signifying the different diatoms (see below).

Only one comprehensive record will be shown for any month in which there has been more than one. For the later years the observations for all the months have been shown, but for space economy, only those months which provided patches have been shown for the earlier years (reference to previous plates will indicate which lines were sampled in any month not shown).

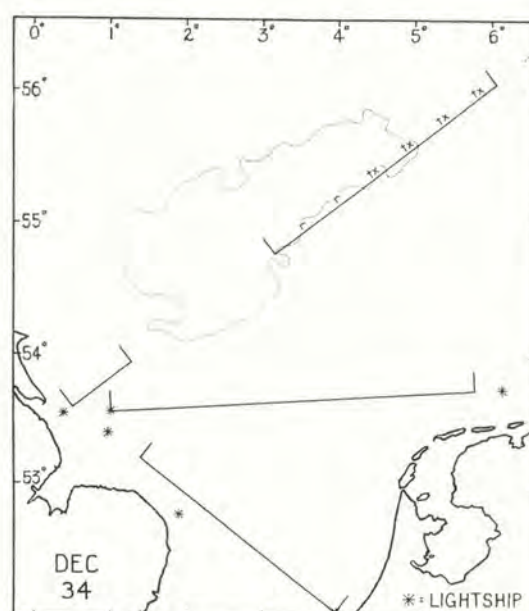
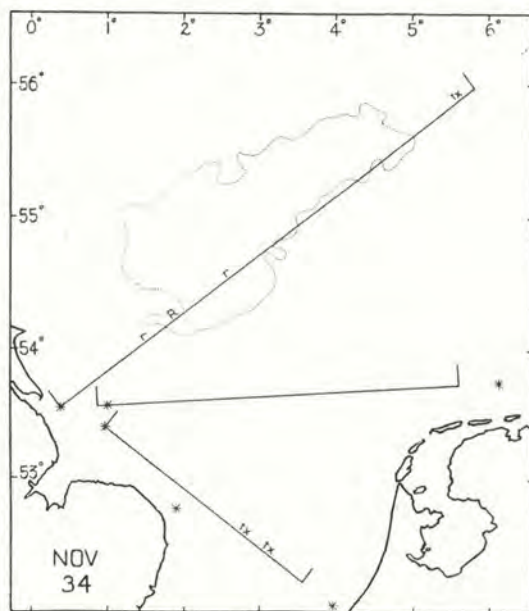
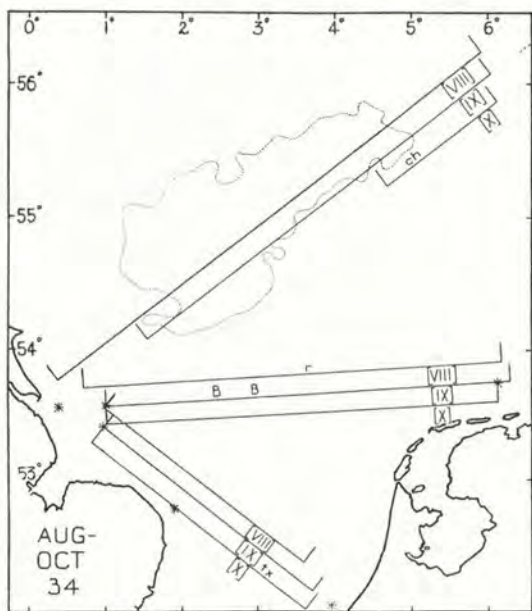
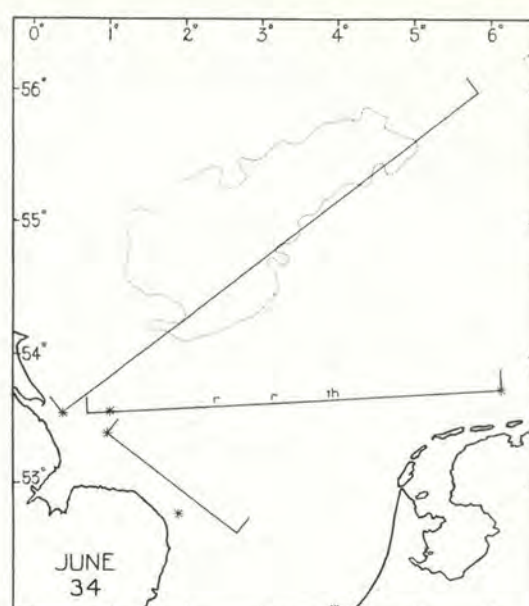
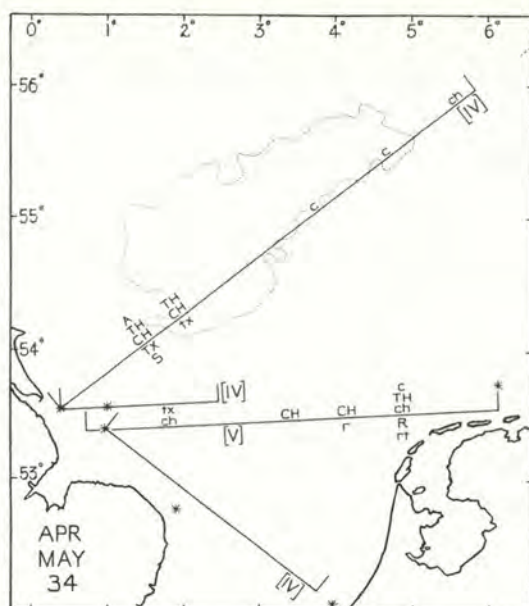
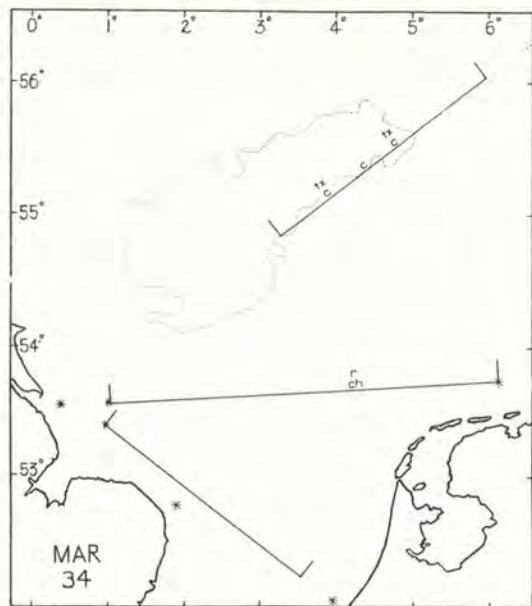
The following symbols are used for the different forms, capital letters indicating major patches and small letters intermediate patches (see text) :

A, a,	ASTERIONELLA	G, g,	GUINARDIA FLACCIDA
*B,	BELLAROCHIA	L, l,	LEPTOCYLINDRUS
	MALLEUS	N, n,	NAVICULA (etc.)
BA, ba,	BIDDULPHIA AURITA	R, r,	RHIZOSOLENIA
BCA, bca,	BACILLARIA		ALATA and SEMISPINA
	PARADOXA	RB, rb,	RH. SHRUBSOLEI
BR, br,	BIDDULPHIA	RT, rt,	RH. STOLTERFOTHII
	REGIA (etc.)	*S,	SKELETONEMA
BRH. brh,	BIDDULPHIA		COSTATUM
	RHOMBUS	Th, th,	THALASSIOSIRA
BTM, btm,	BACTERIASTRUM		(etc.)
Ĉ, c,	COSCINODISCUS	TX, tx,	THALASSIOTHRIX
CH, ch,	CHAETOCEROS	U, u,	EUCAMPIA
D, d,	DYTILIUM		ZODIACUS
	BRIGHTWELLI		

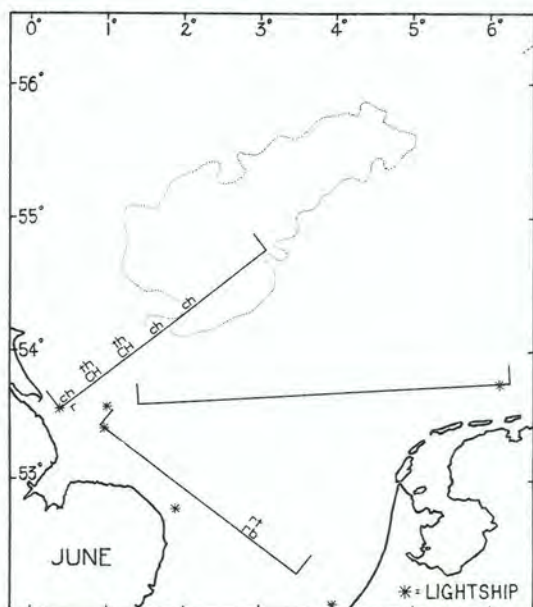
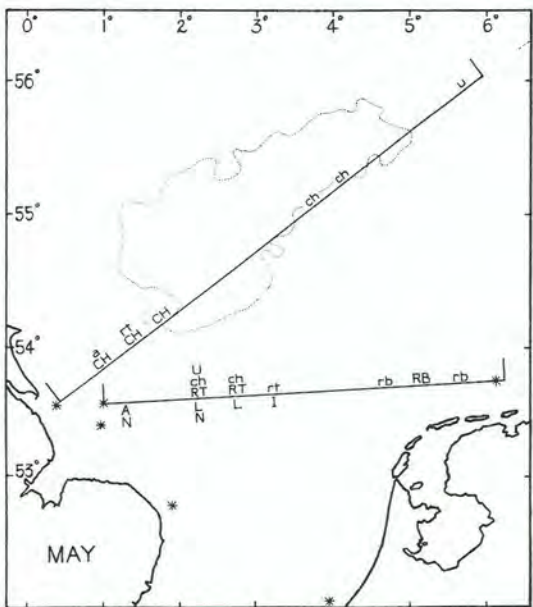
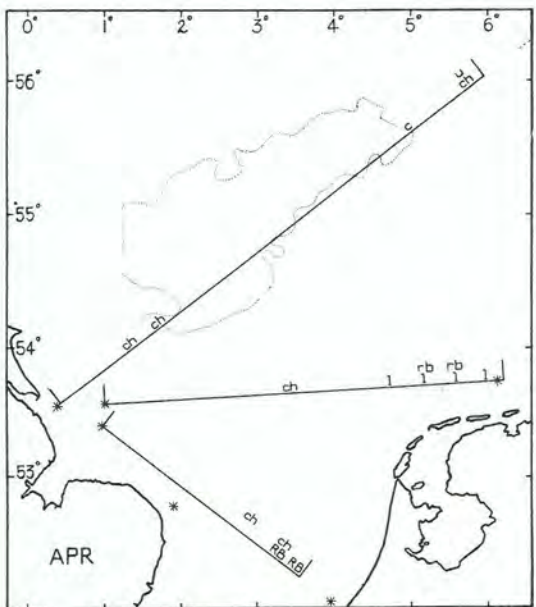
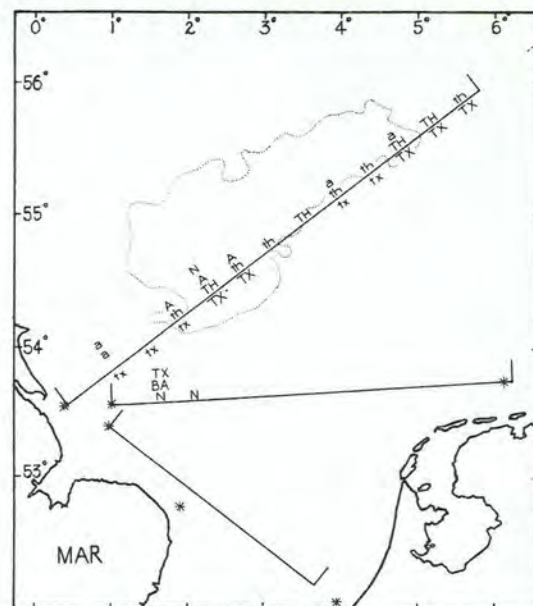
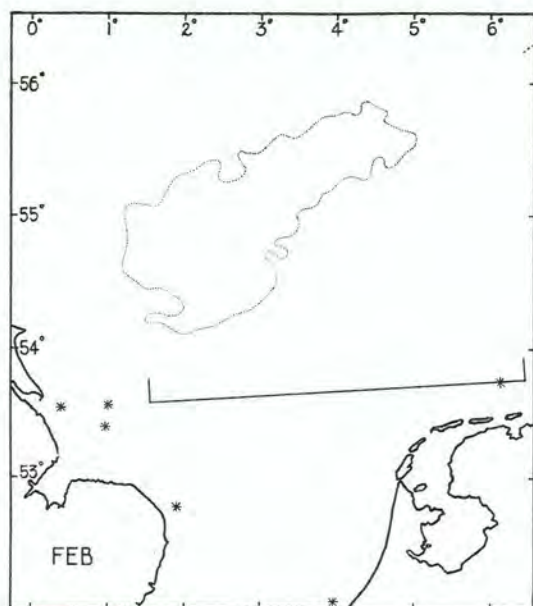
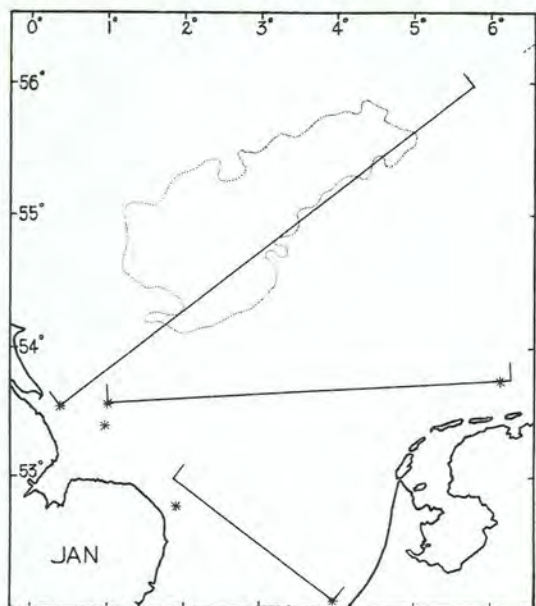
\*Intermediate patches of BELLAROCHIA or SKELETONEMA have  
not been shown (see text).



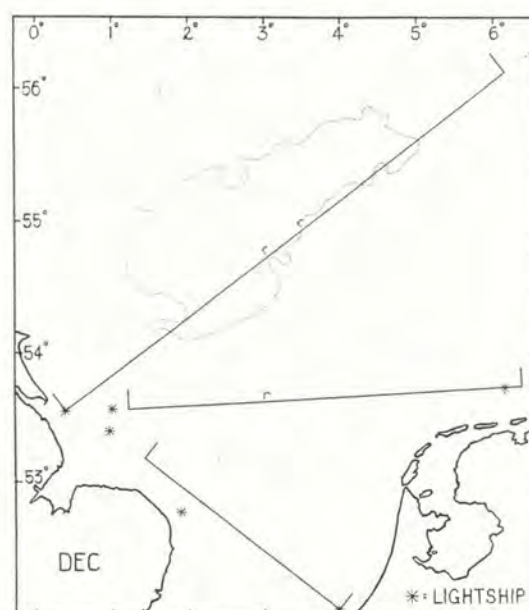
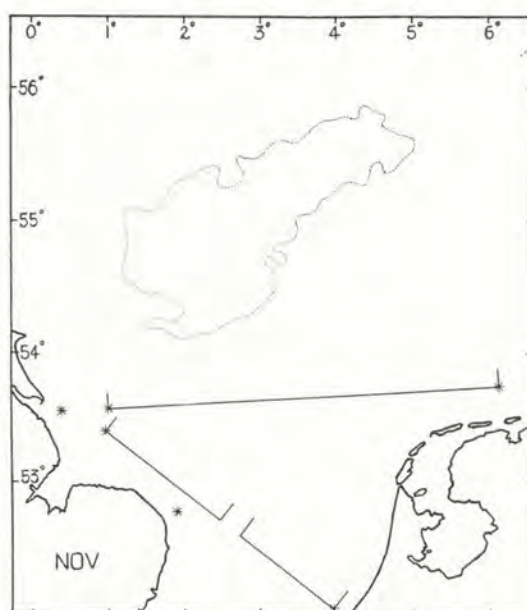
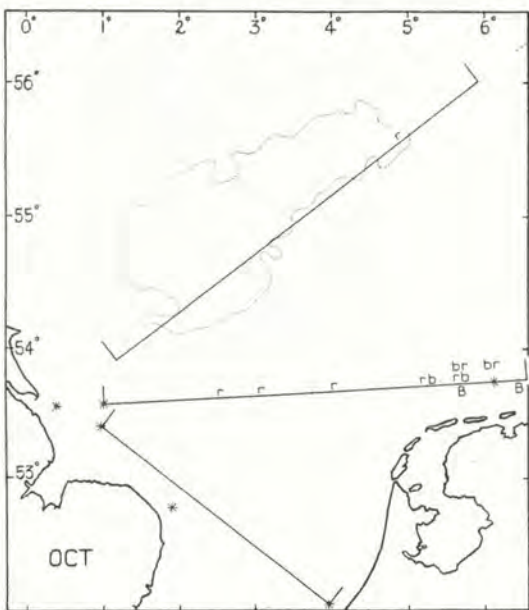
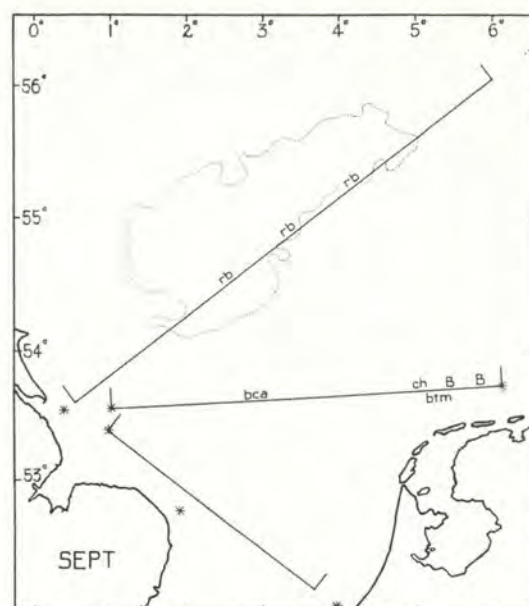
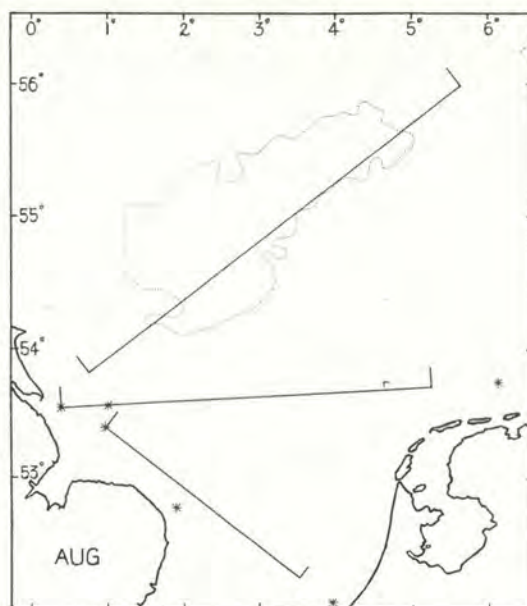
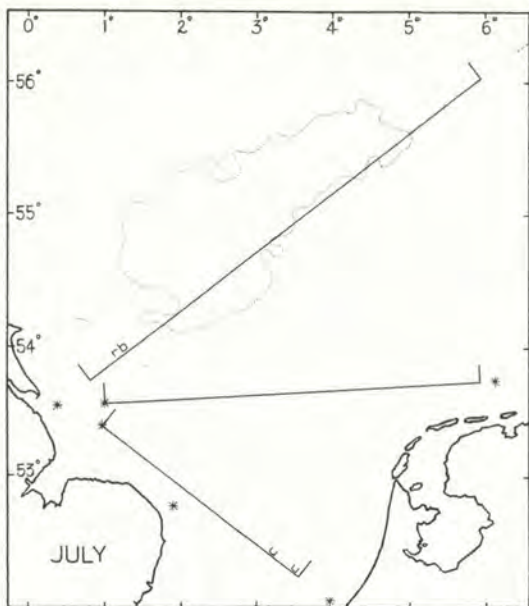
'OTHER' DIATOM patches, 1932 and 1933, see explanation on preceding page.



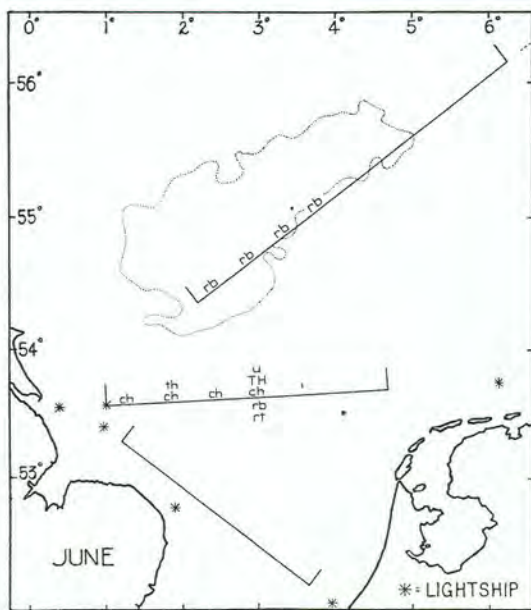
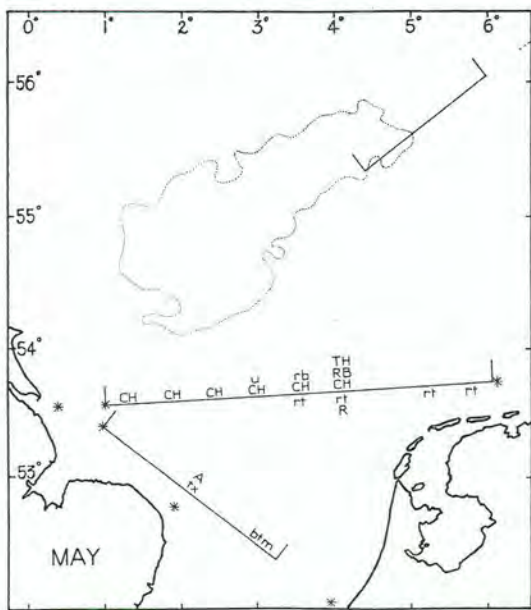
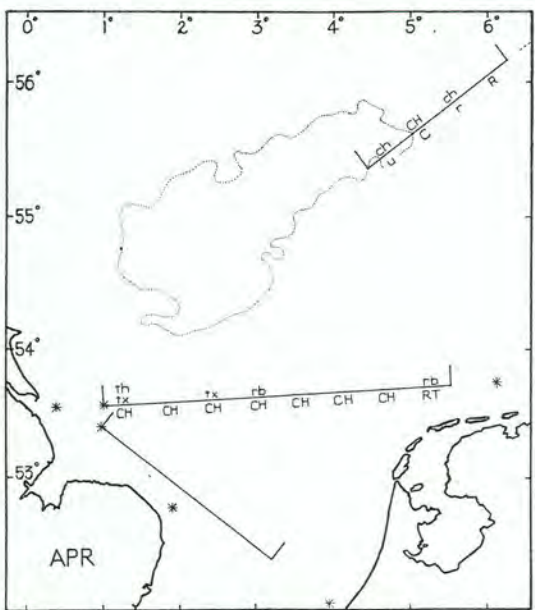
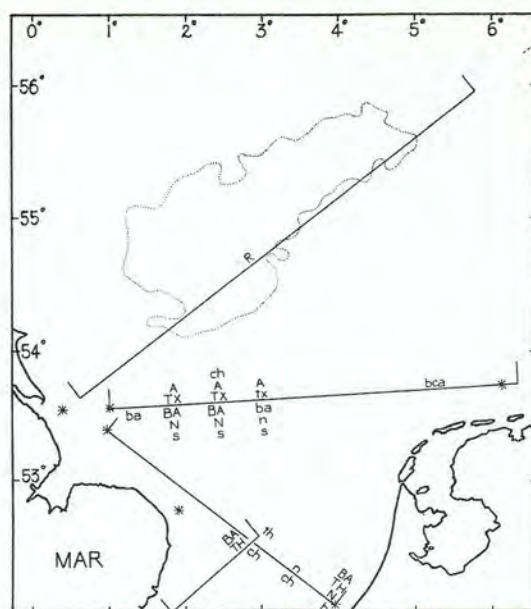
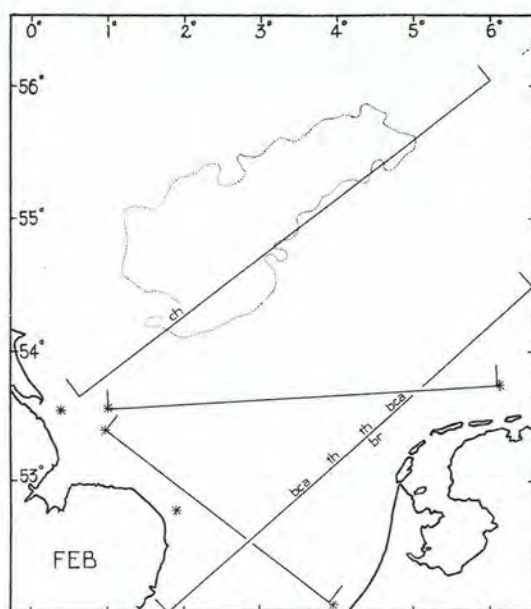
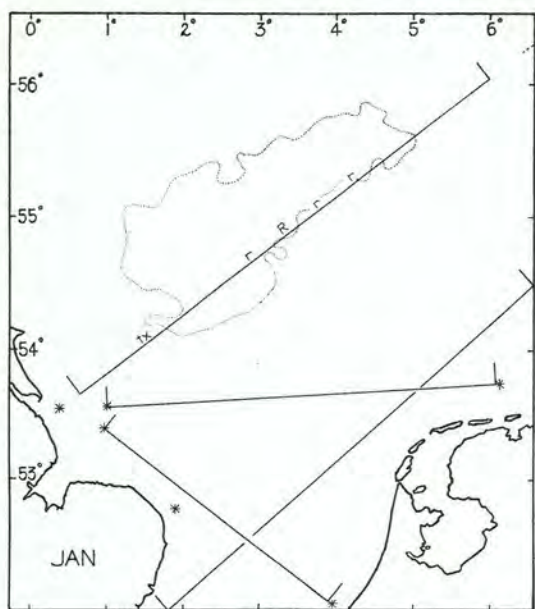
'OTHER' DIATOM patches, 1934, see explanation preceding Plate XXXVII.



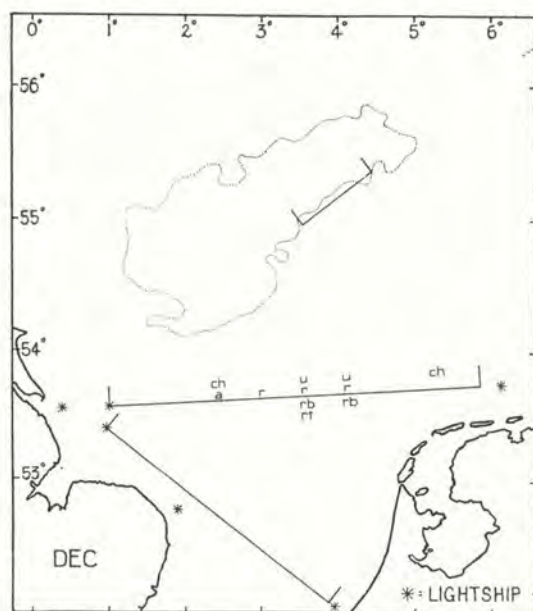
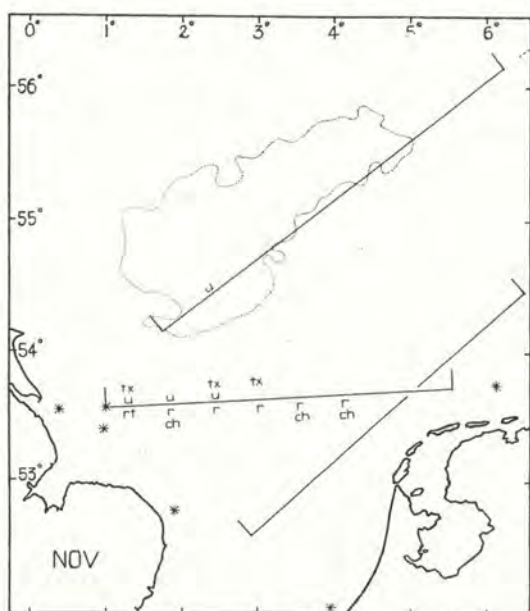
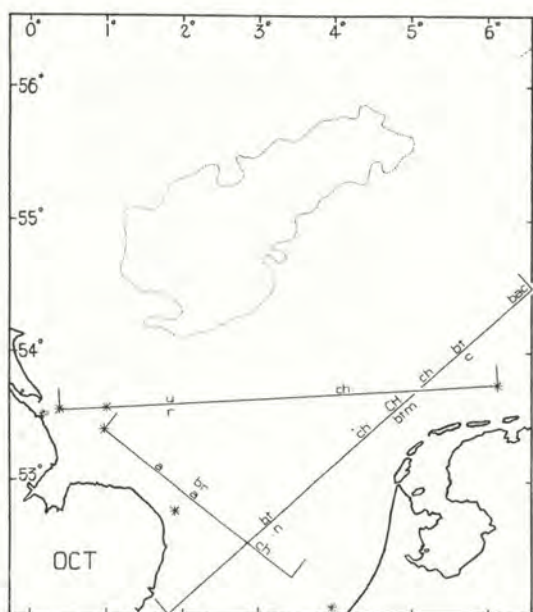
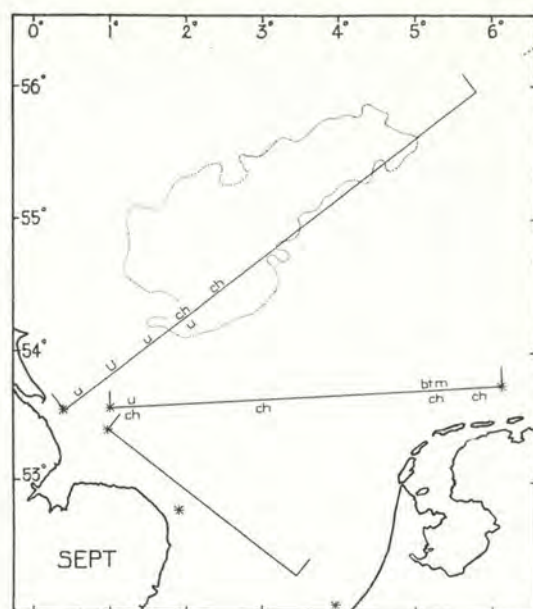
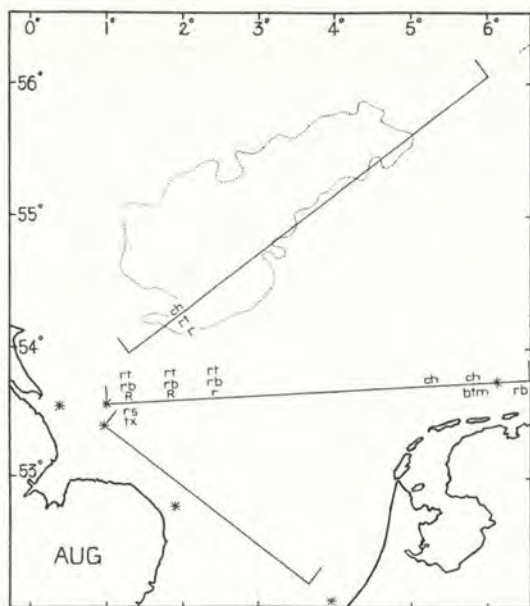
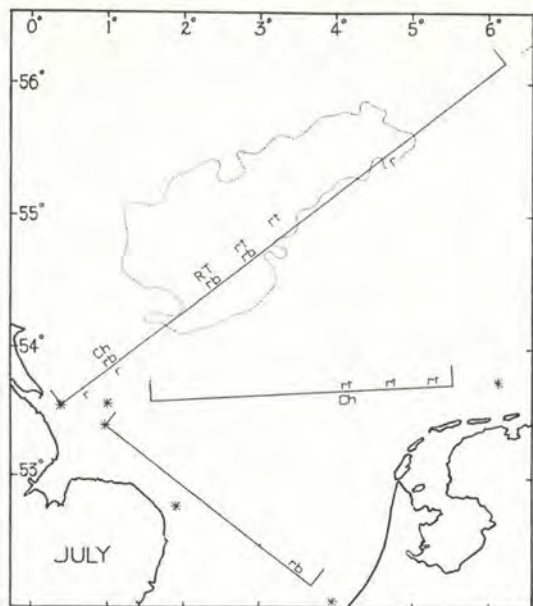
'OTHER' DIATOM patches, 1935, see explanation preceding Plate XXXVII.



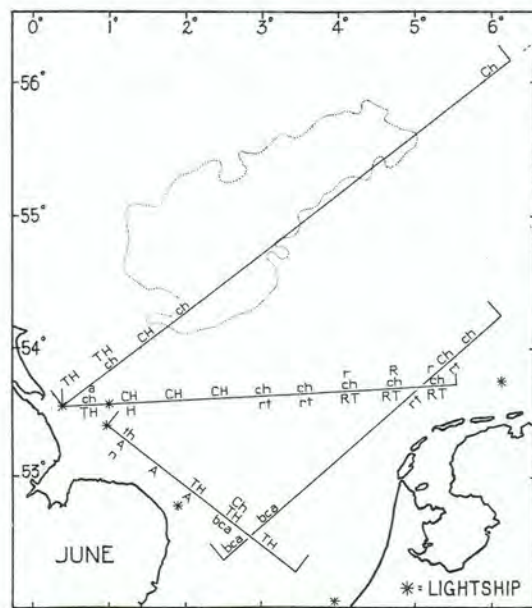
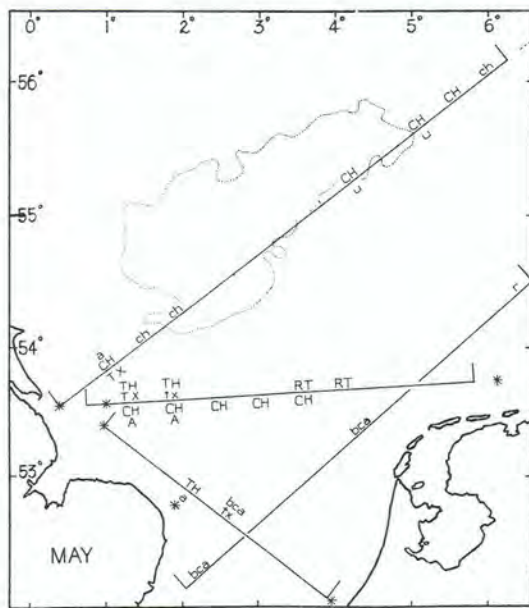
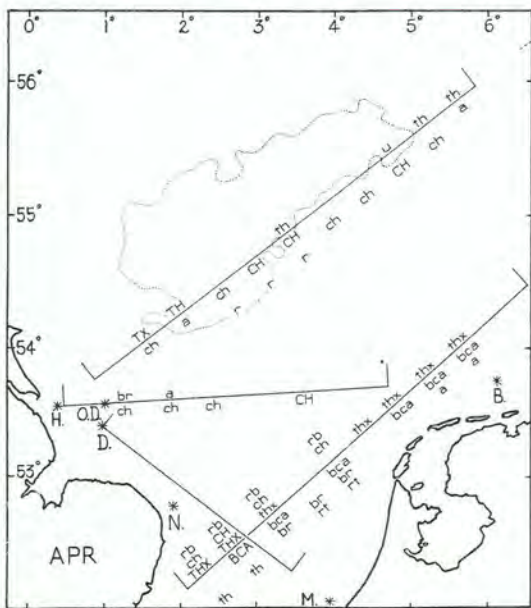
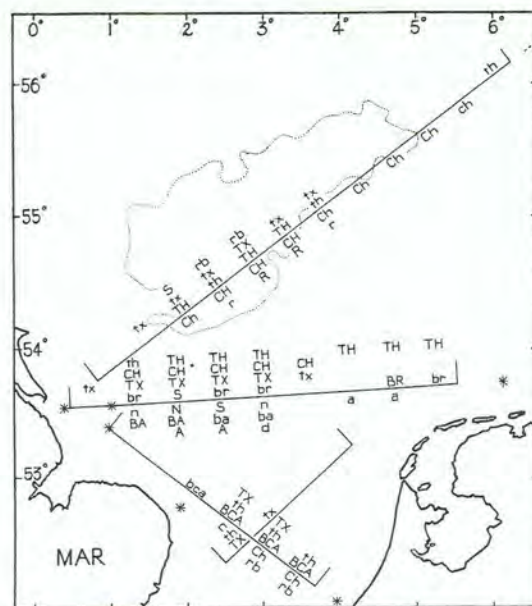
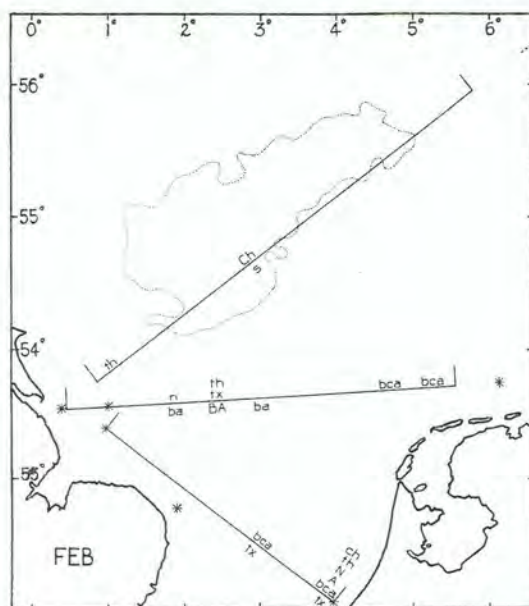
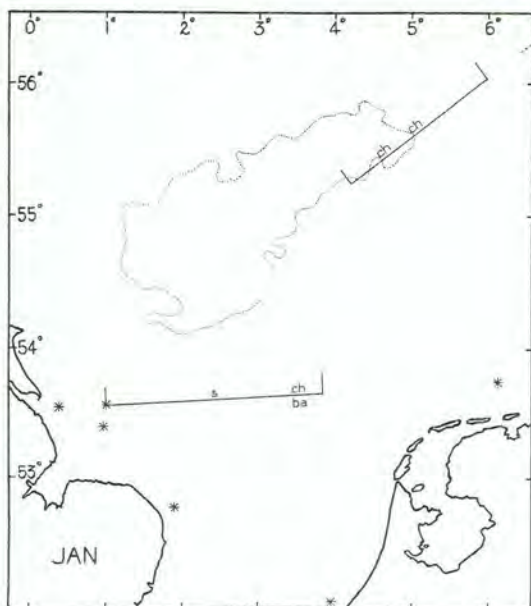
'OTHER' DIATOM patches, 1935, see explanation preceding Plate XXXVII.



'OTHER' DIATOM patches, 1936, see explanation preceding Plate XXXVII.

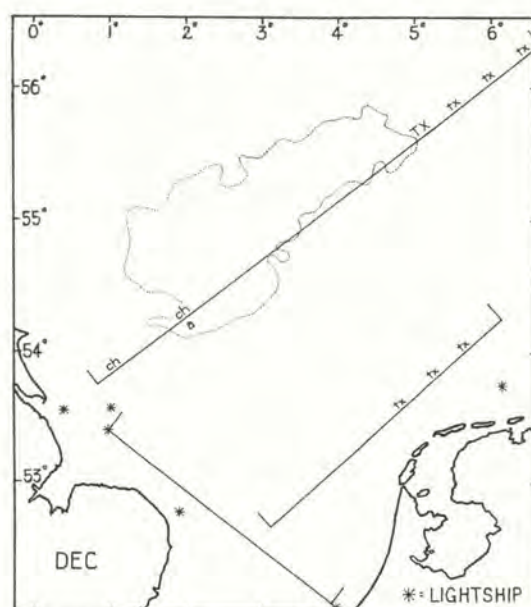
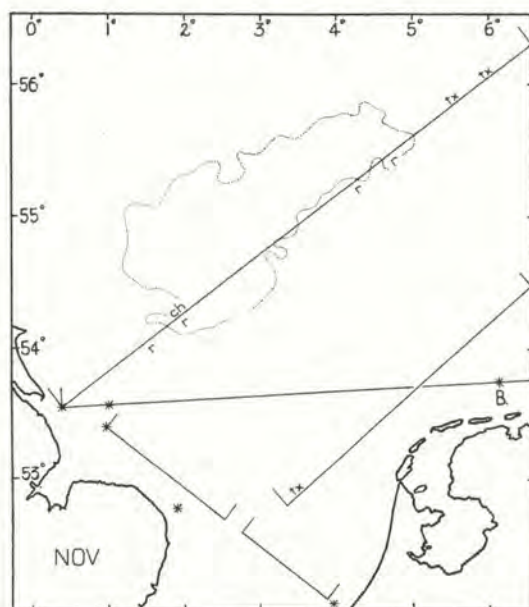
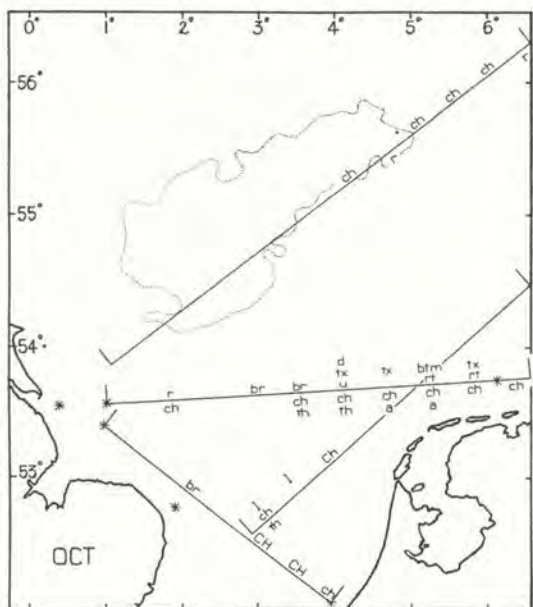
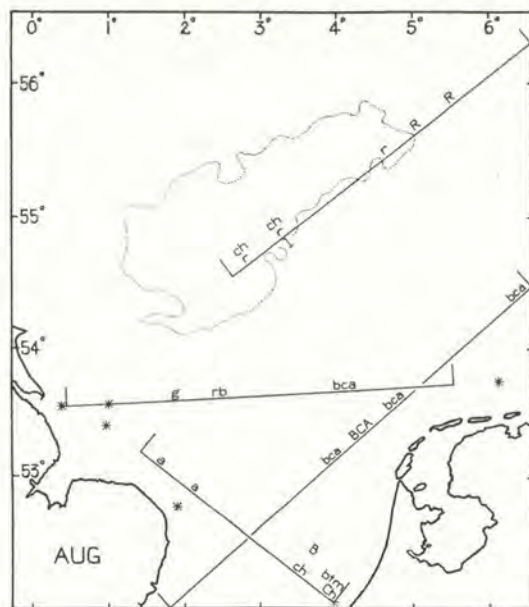
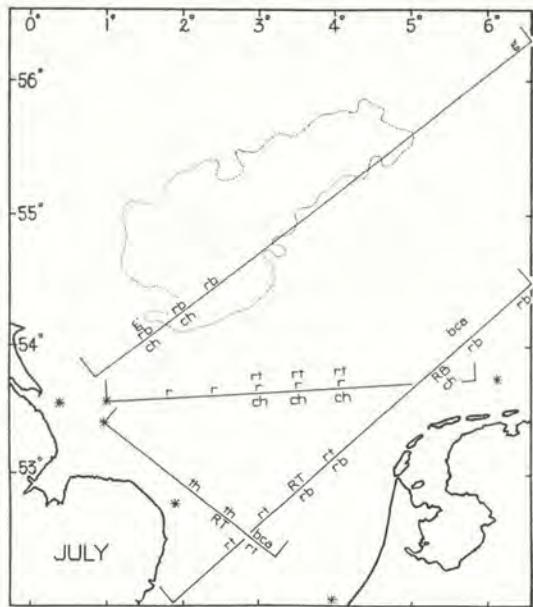


'OTHER' DIATOM patches, 1936, see explanation preceding Plate XXXVII.



'OTHER' DIATOM patches, 1937, see explanation preceding Plate XXXVII.





'OTHER' DIATOM patches, 1937, see explanation preceding Plate XXXVII.

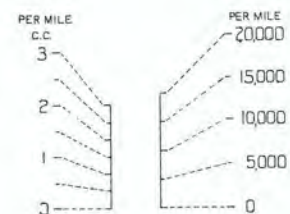
The following Explanation applies to  
**PLATES XLV—LVII**

This series of maps has been prepared to show the distribution of the **DINOFLAGELLATES** and **PHAEOCYSTIS** in the southern North Sea month by month from June 1932 to December 1937. When more than one record have been obtained on one line in any month they have been included where possible ; others omitted will be found on Plates XI, XII and XV and text-figure 17.

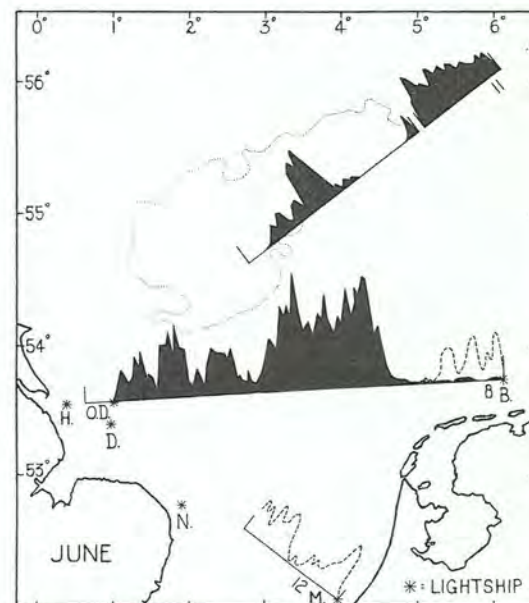
The **DINOFLAGELLATES** are shown as blacked-in graphs and **PHAEOCYSTIS** as broken line graphs. Other details as explained on Plate XXII.

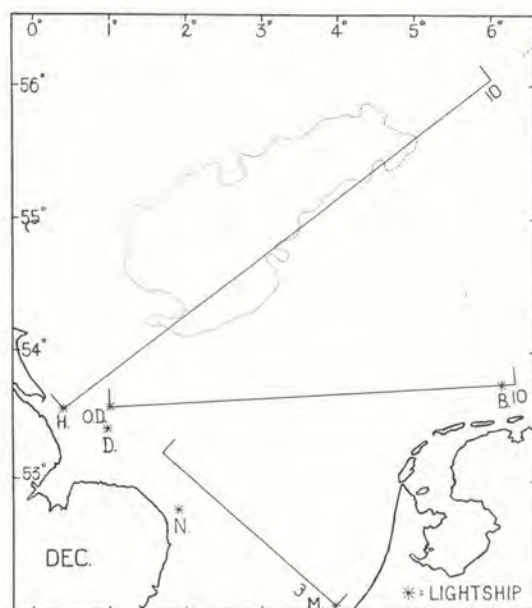
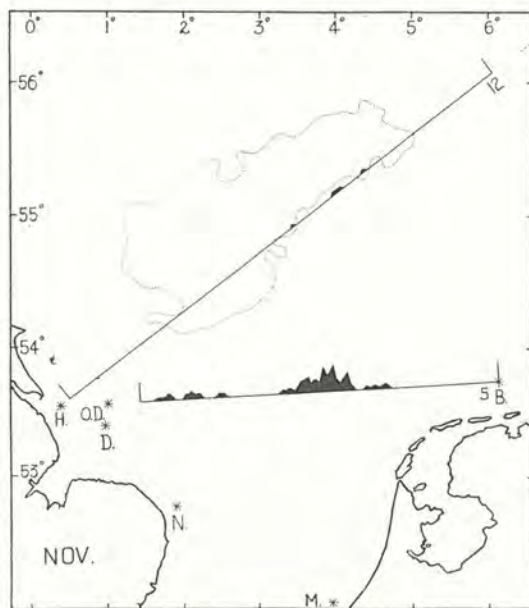
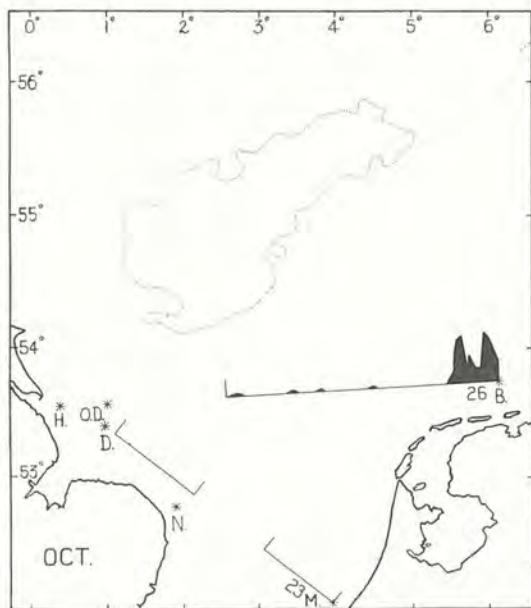
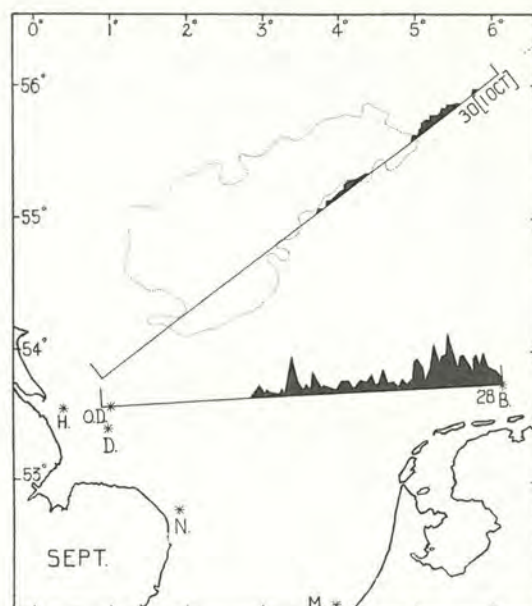
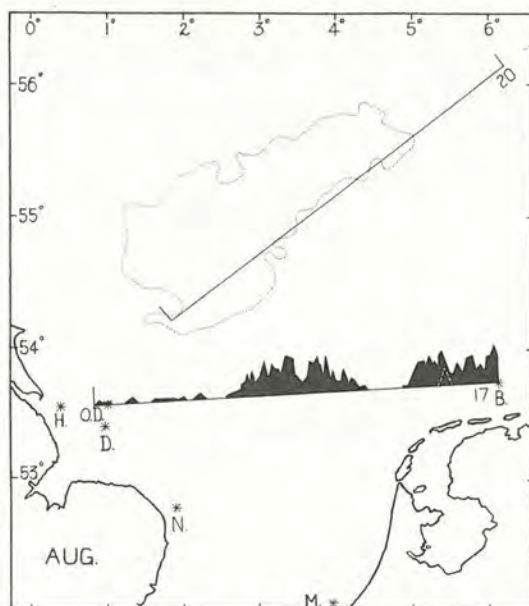
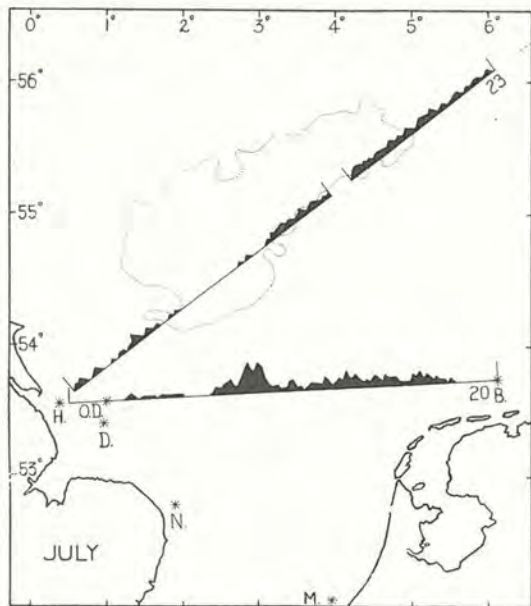
The first records, for June 1932, are shown in the map on the right.

Scale for  
 Plates XLV—LVII :

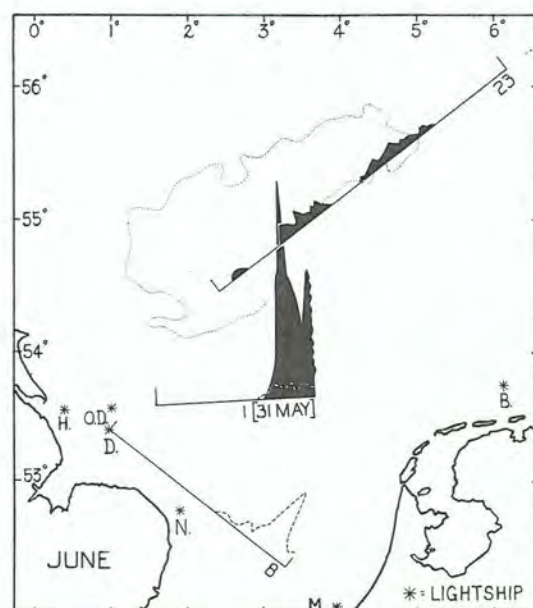
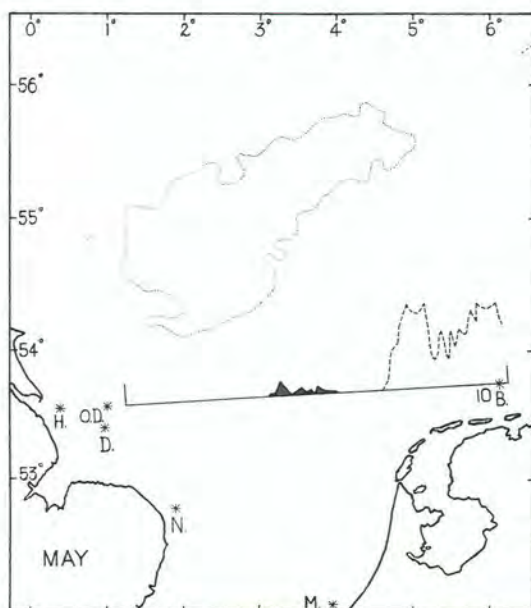
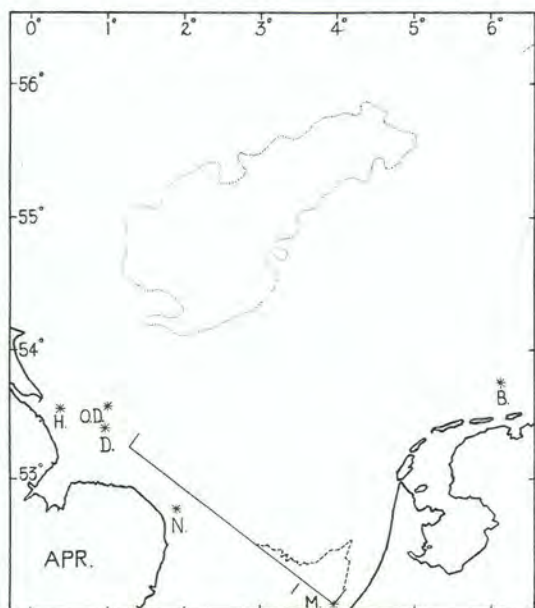
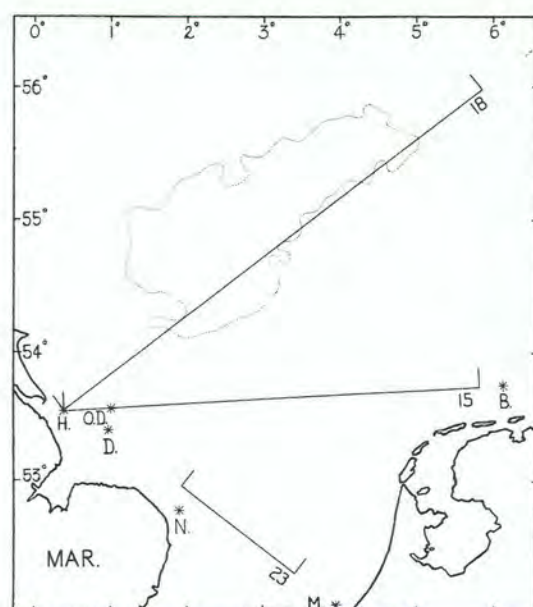
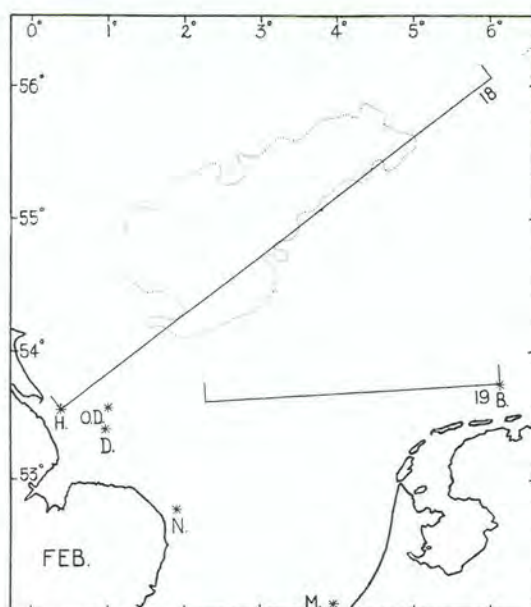
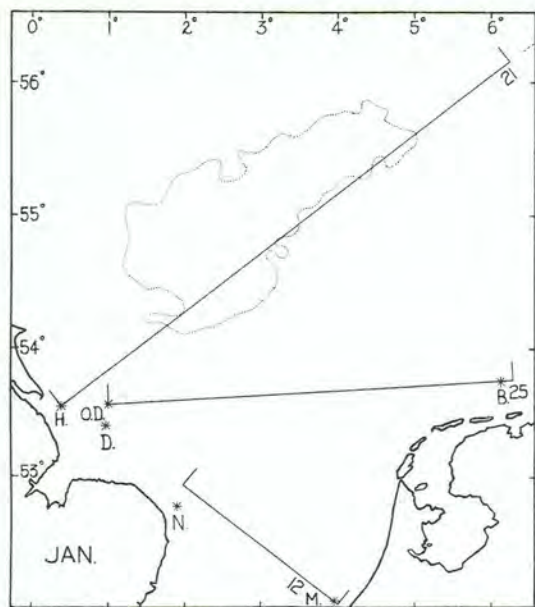


**PLATE XLV**

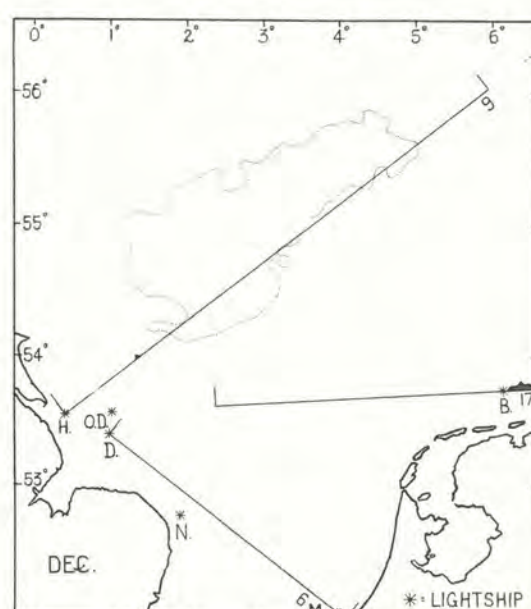
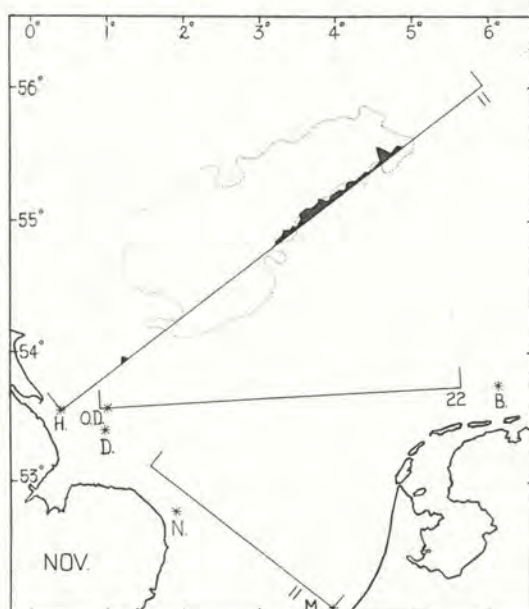
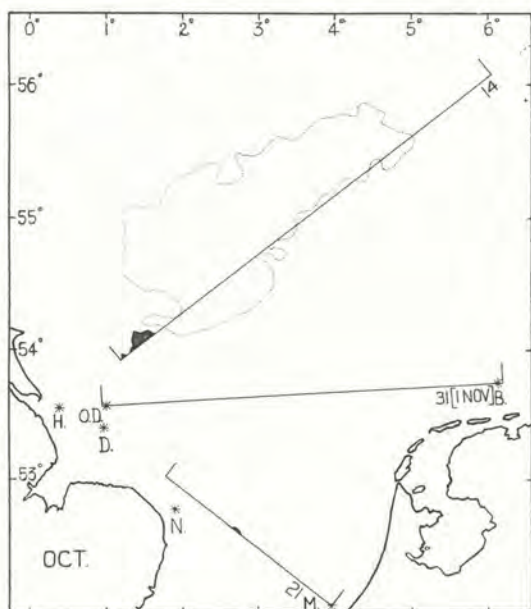
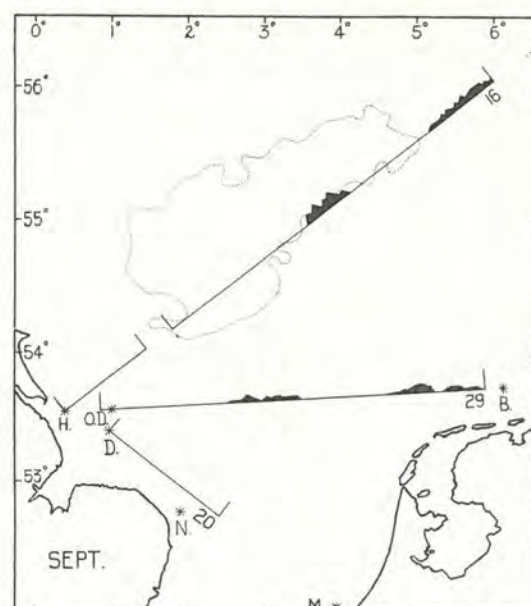
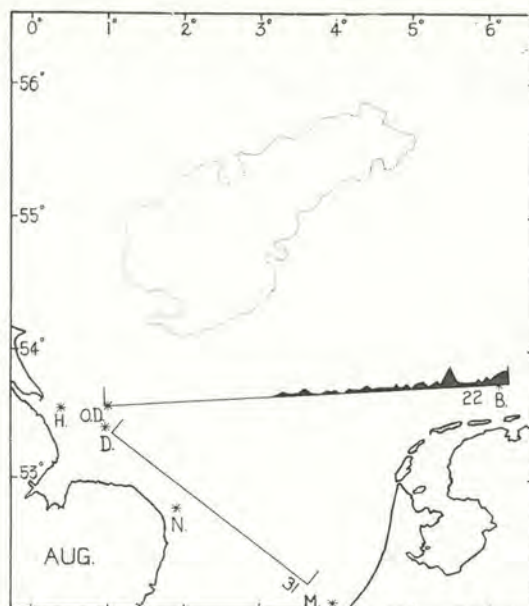
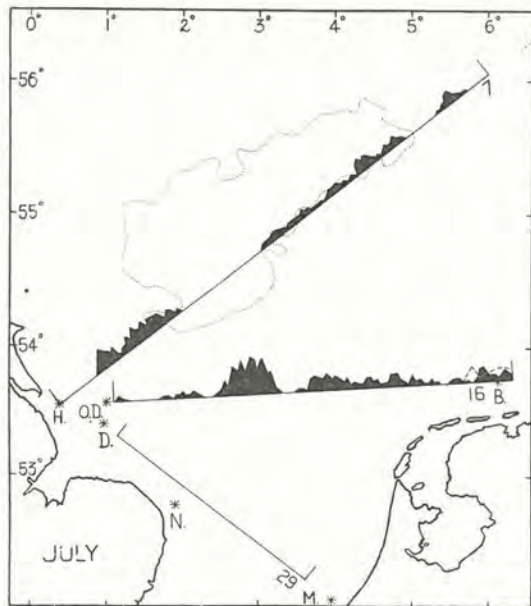




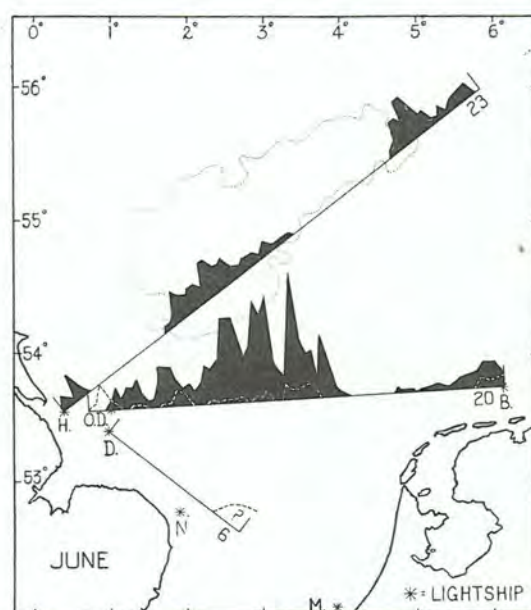
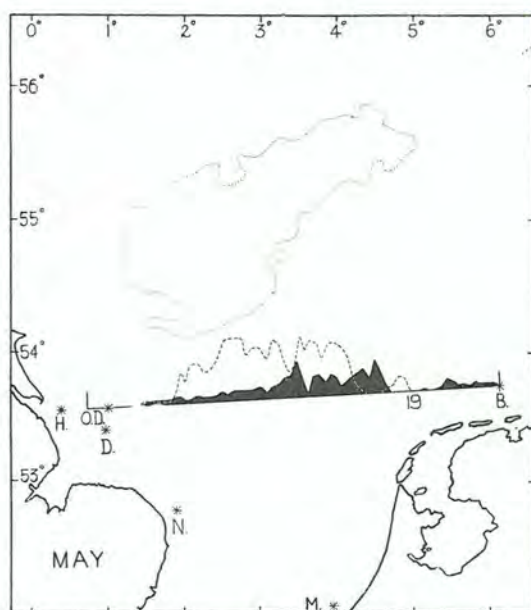
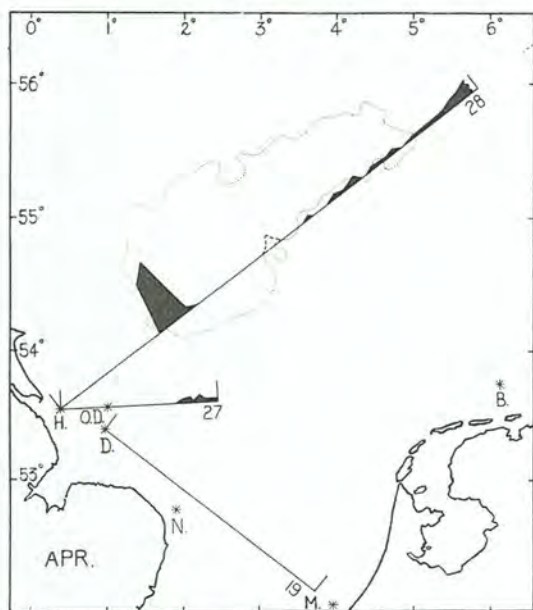
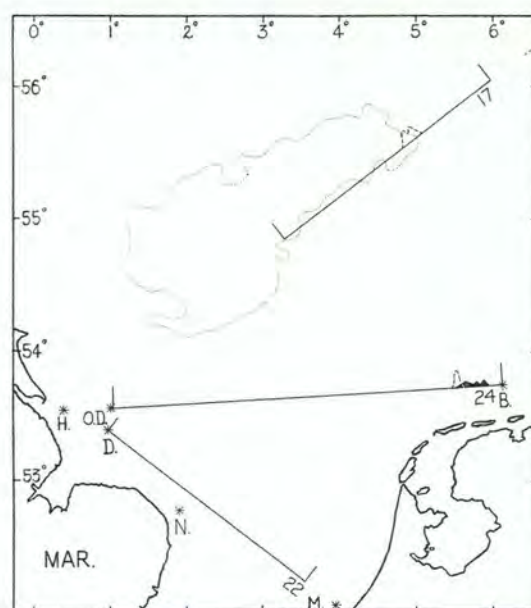
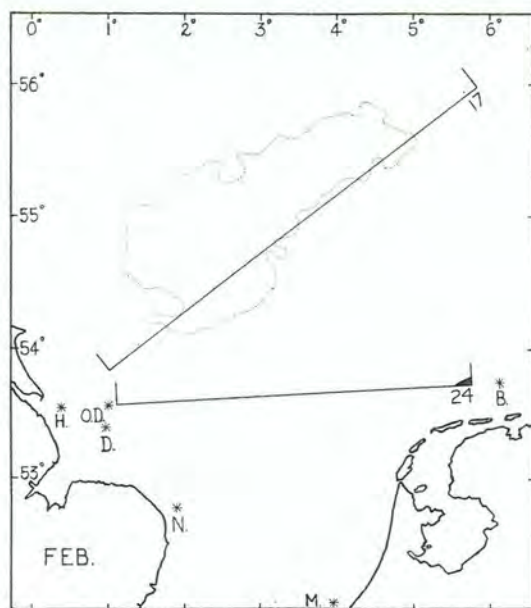
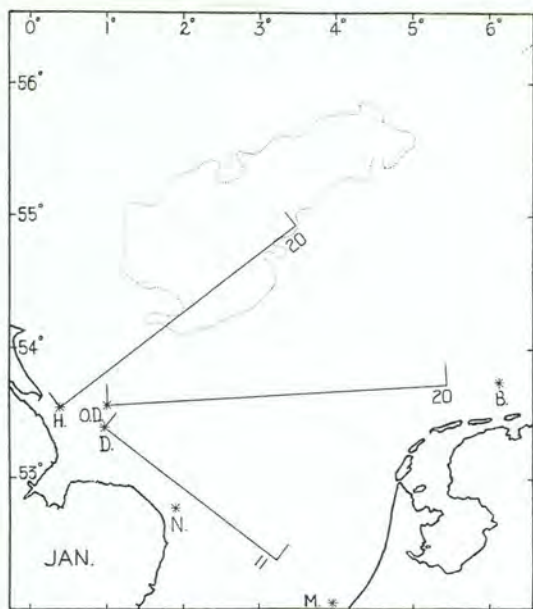
**DINOFLAGELLATES** (blacked-in graph) and **PHAEOCYSTIS** (broken line), 1932, see explanation on Plate XLV.



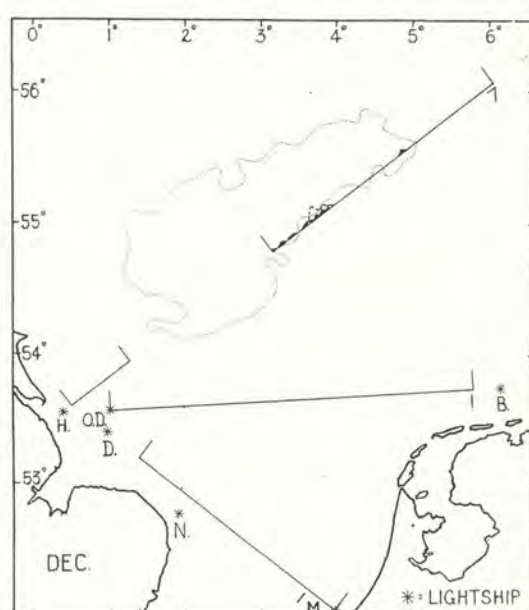
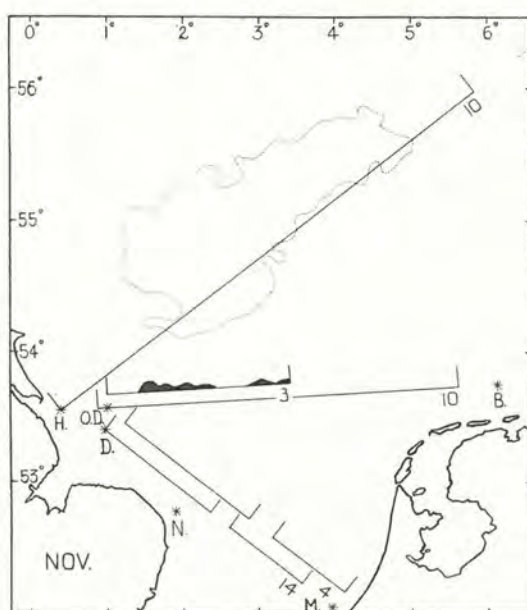
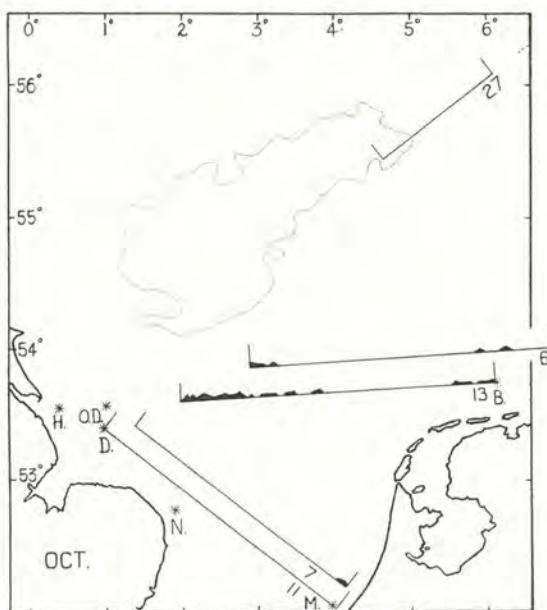
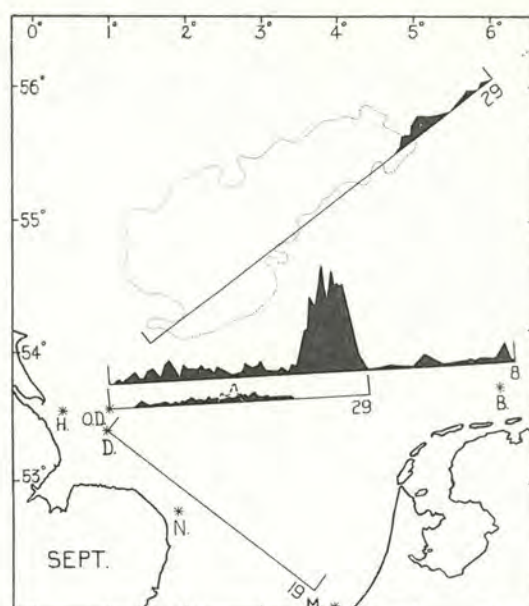
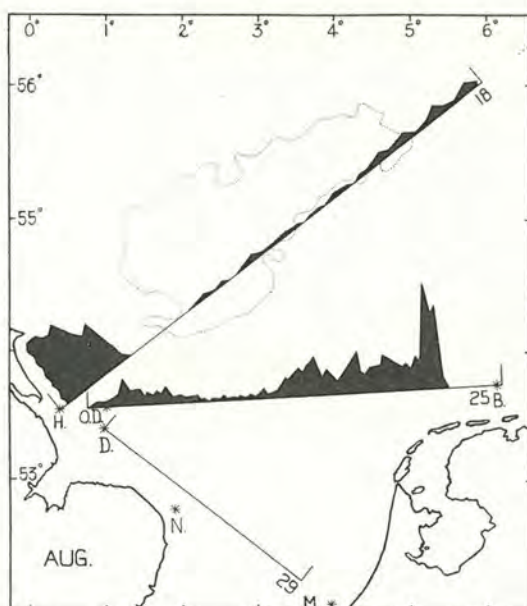
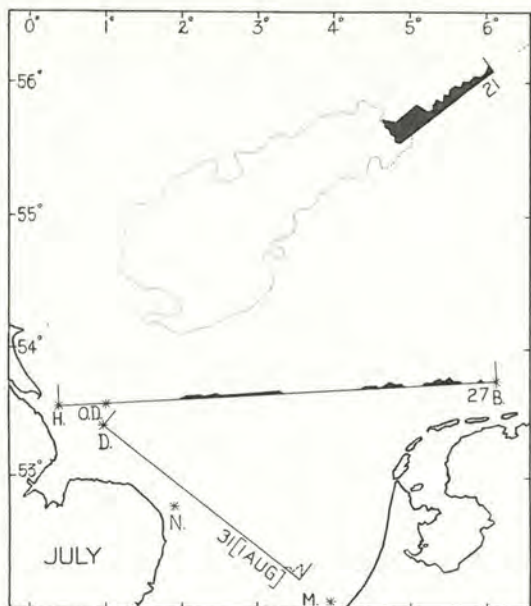
**DINOFLAGELLATES** (blacked-in graph) and **PHAEOCYSTIS** (broken line), 1933, see explanation on Plate XLV.



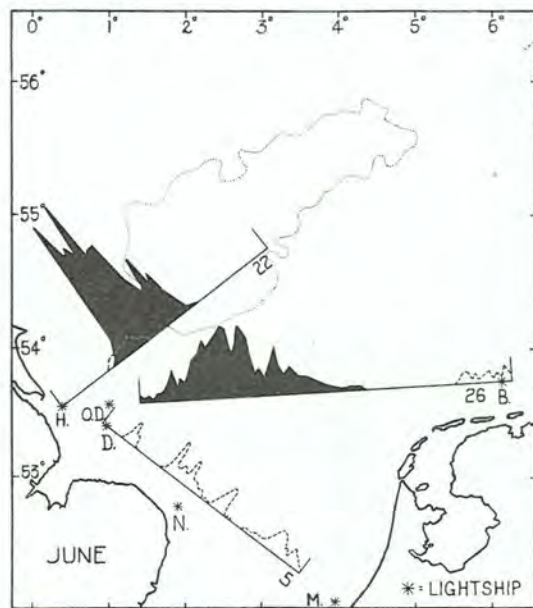
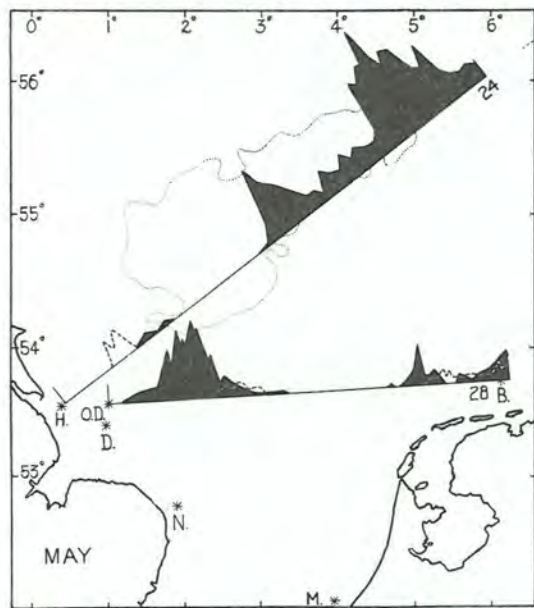
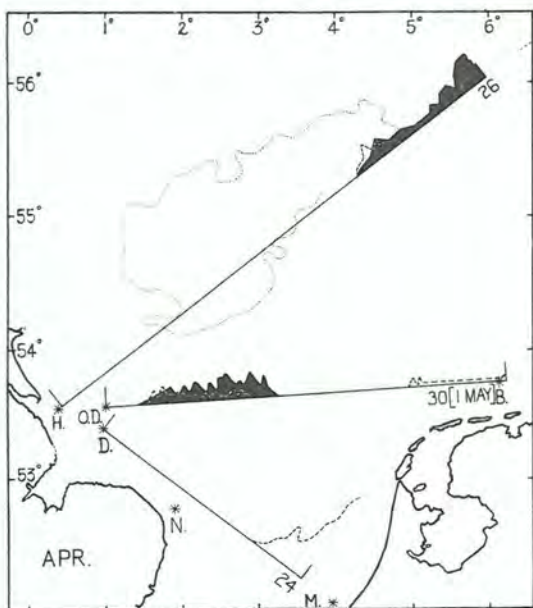
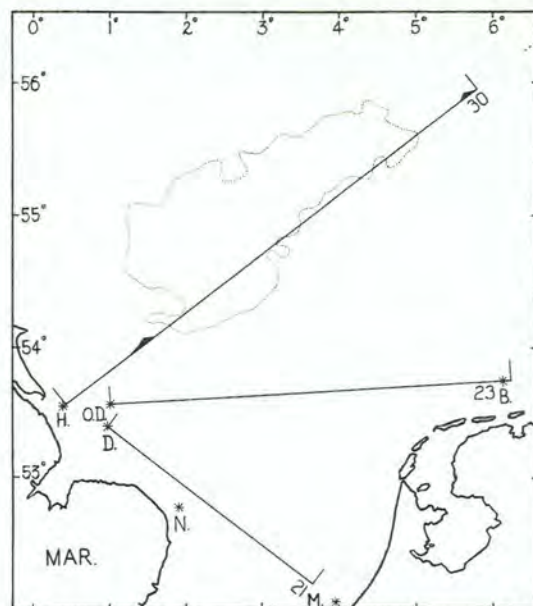
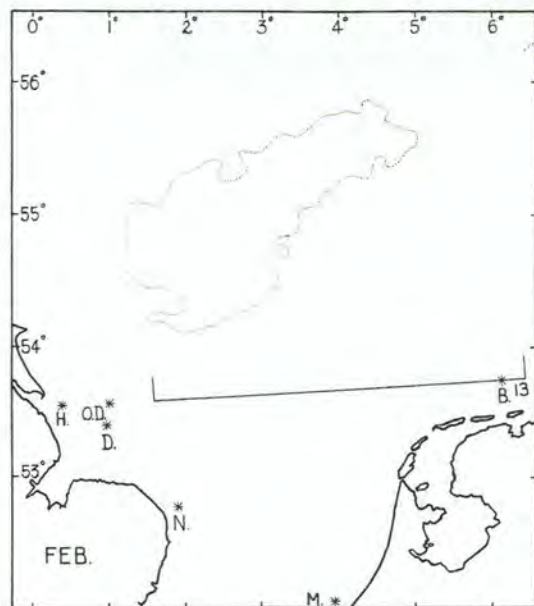
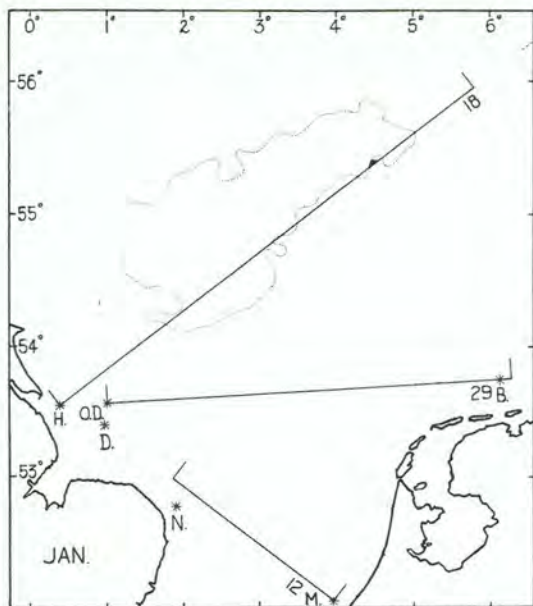
**DINOFLAGELLATES** (blacked-in graph) and **PHAEOCYSTIS** (broken line), 1933, see explanation on Plate XLV.



**DINOFLAGELLATES** (blacked-in graph) and **PHAEOCYSTIS** (broken line), 1934, see explanation on Plate XLV.

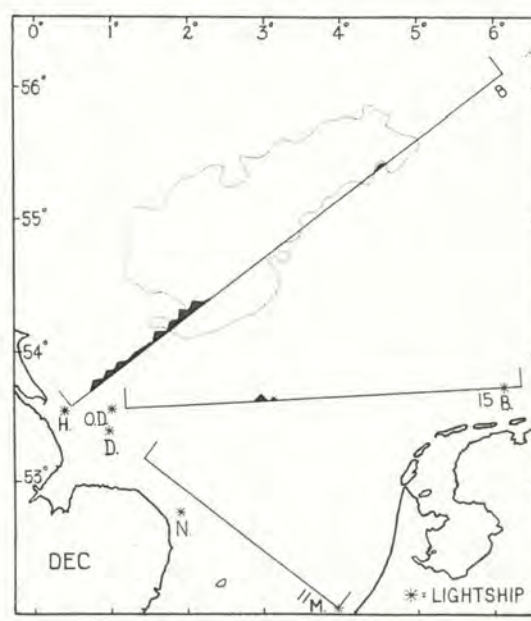
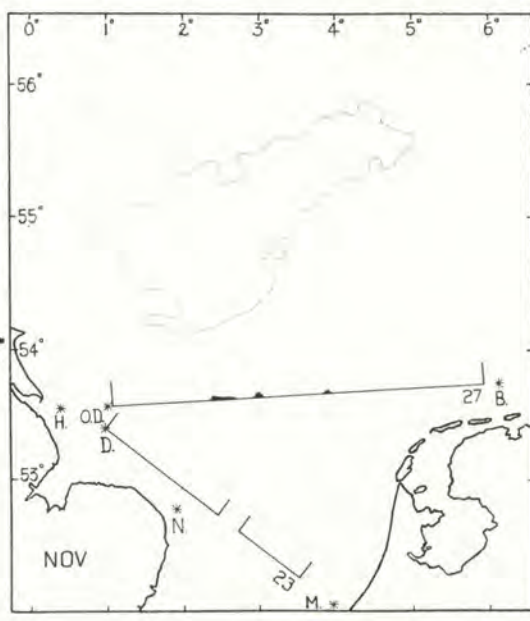
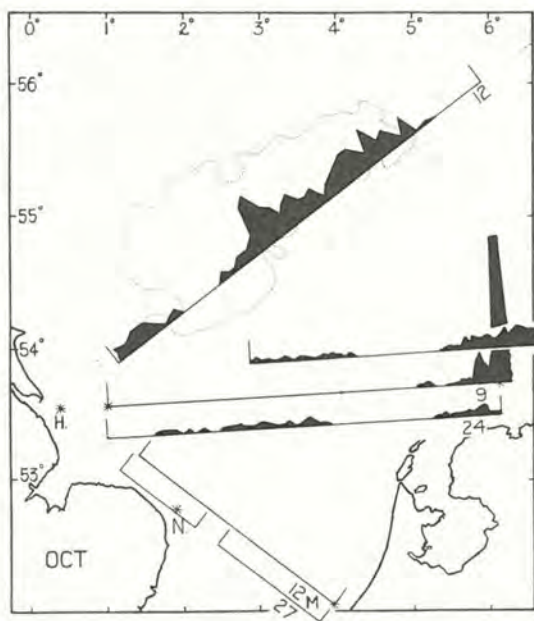
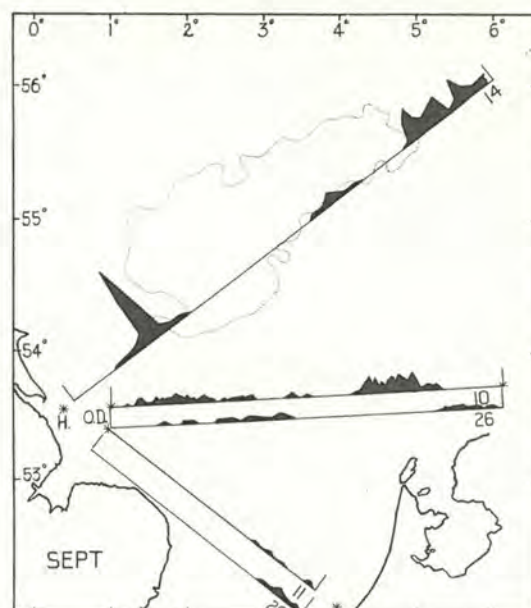
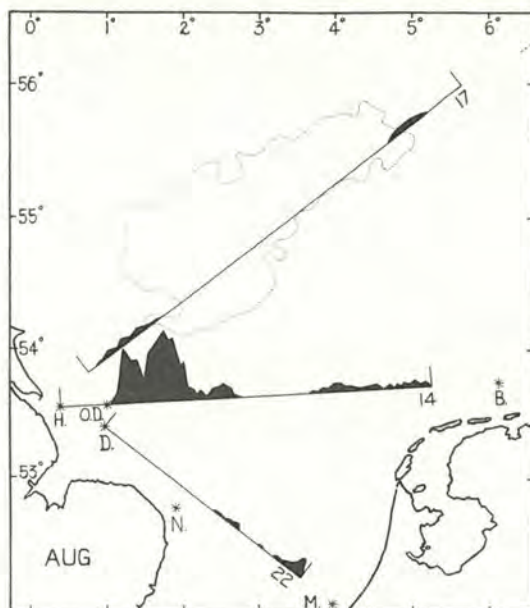
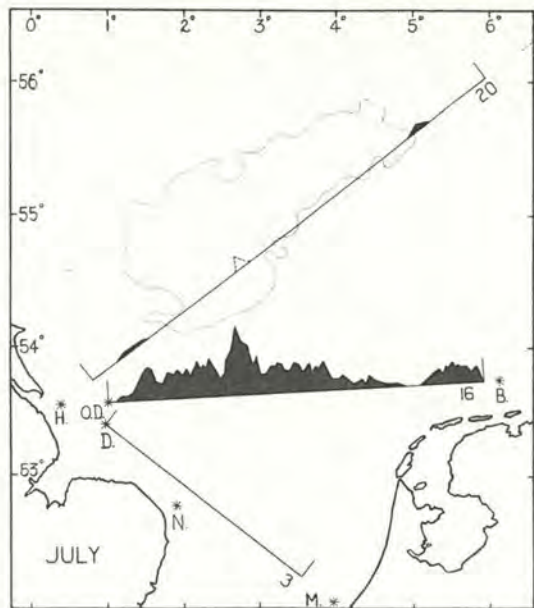


**DINOFLAGELLATES** (blacked-in graph) and **PHAEOCYSTIS** (broken line), 1934, see explanation on Plate XLV.

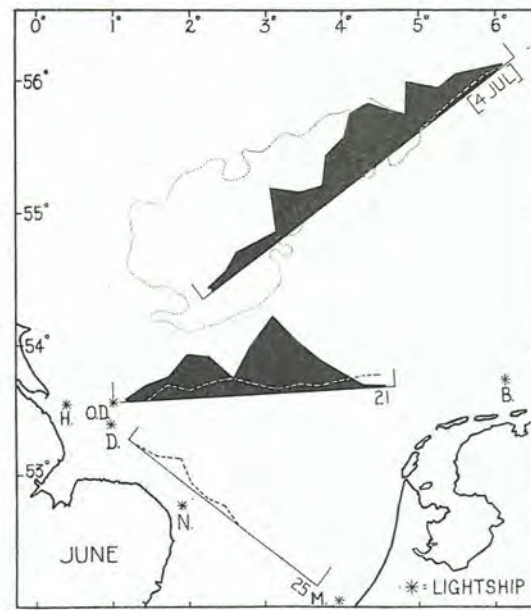
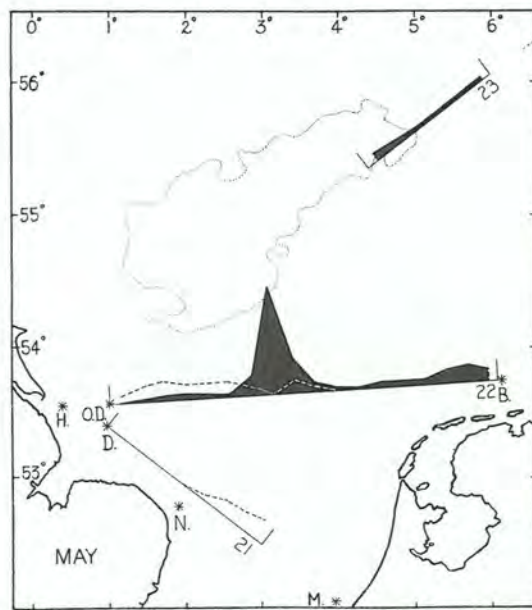
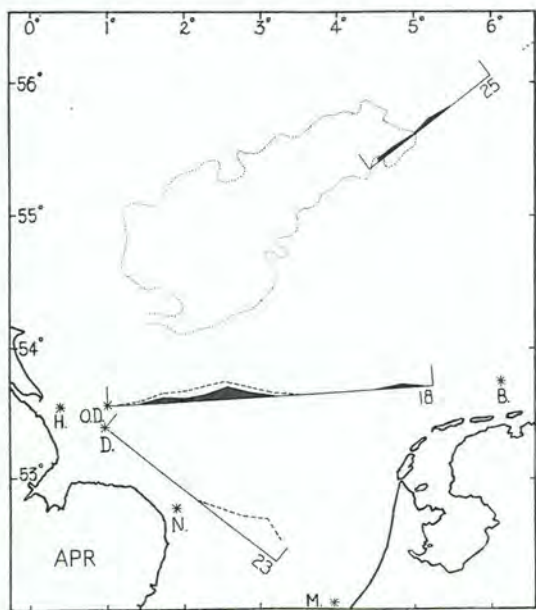
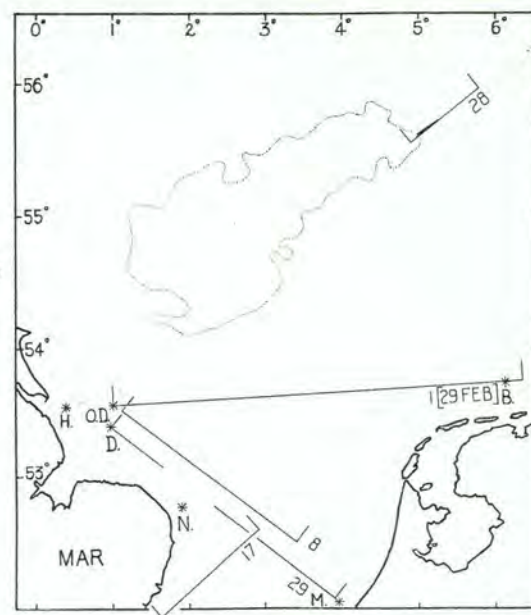
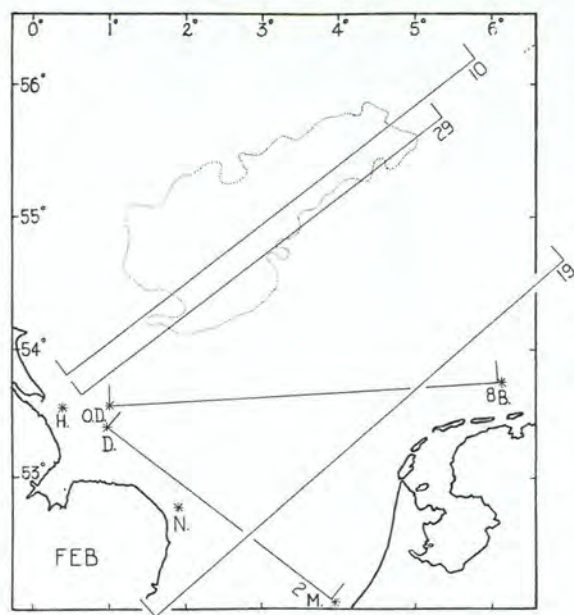
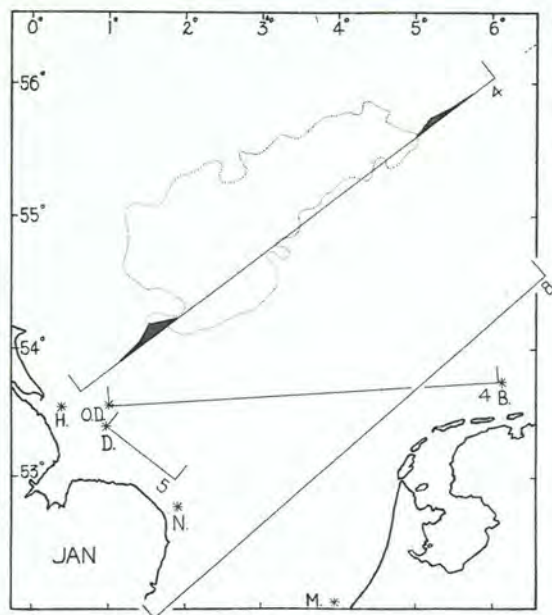


**DINOFLAGELLATES** (blacked-in graph) and **PHAEOCYSTIS** (broken line), 1935, see explanation on Plate XLV.

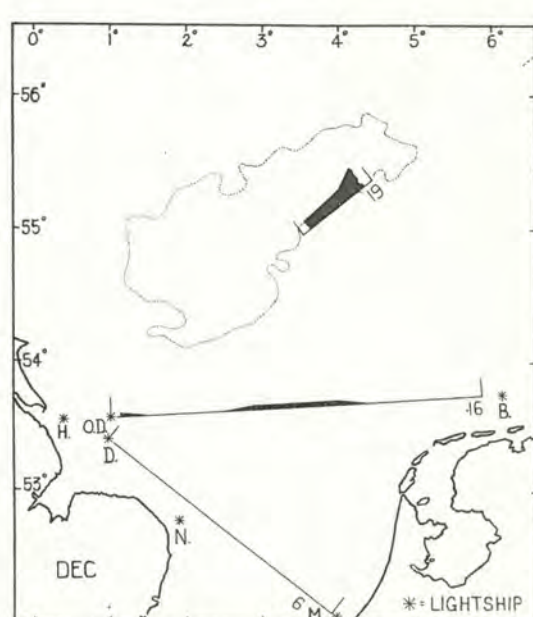
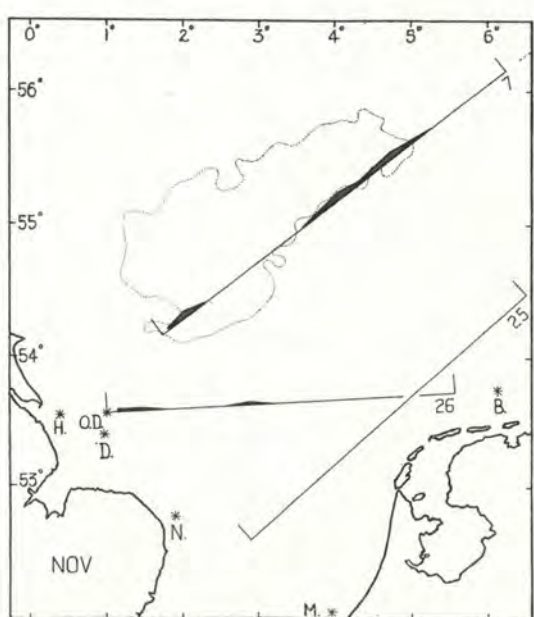
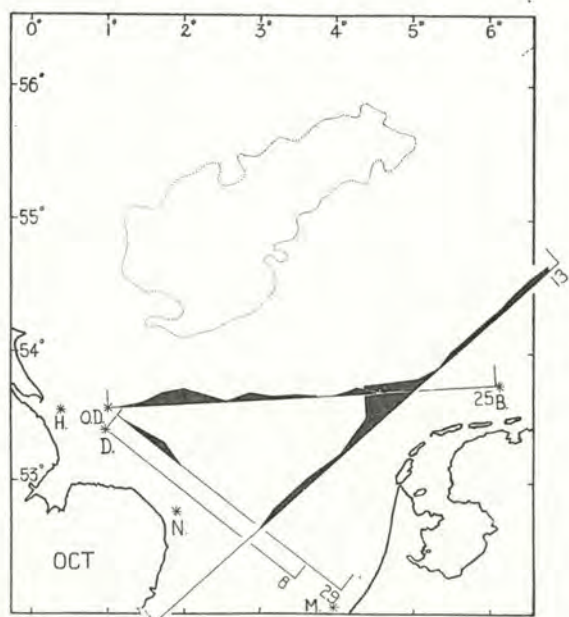
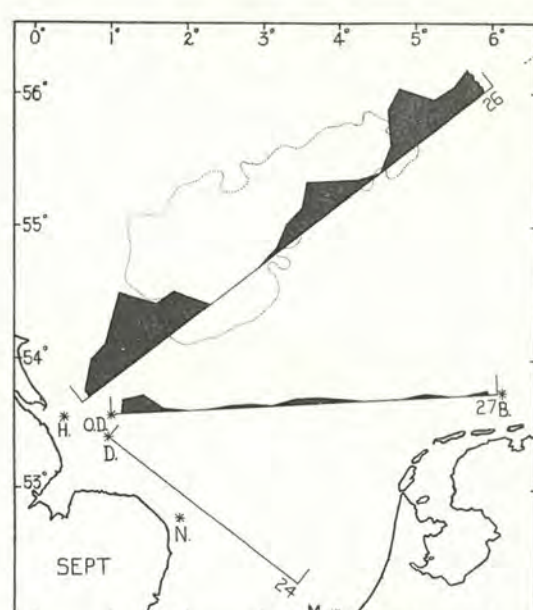
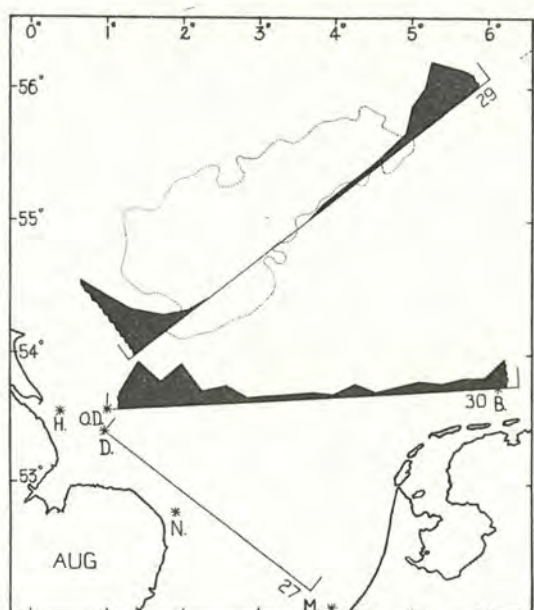
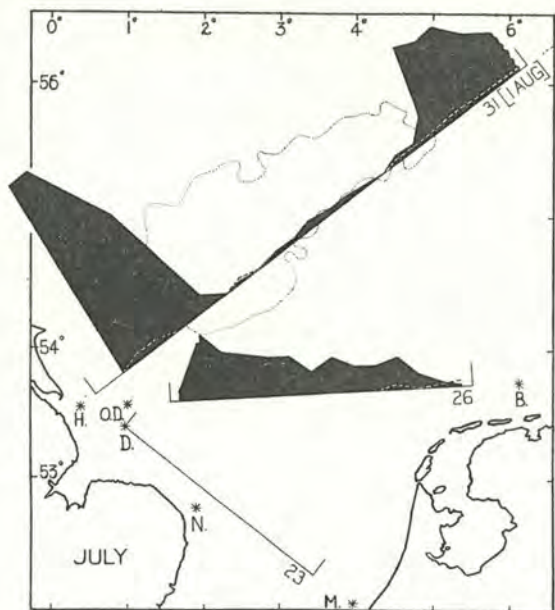




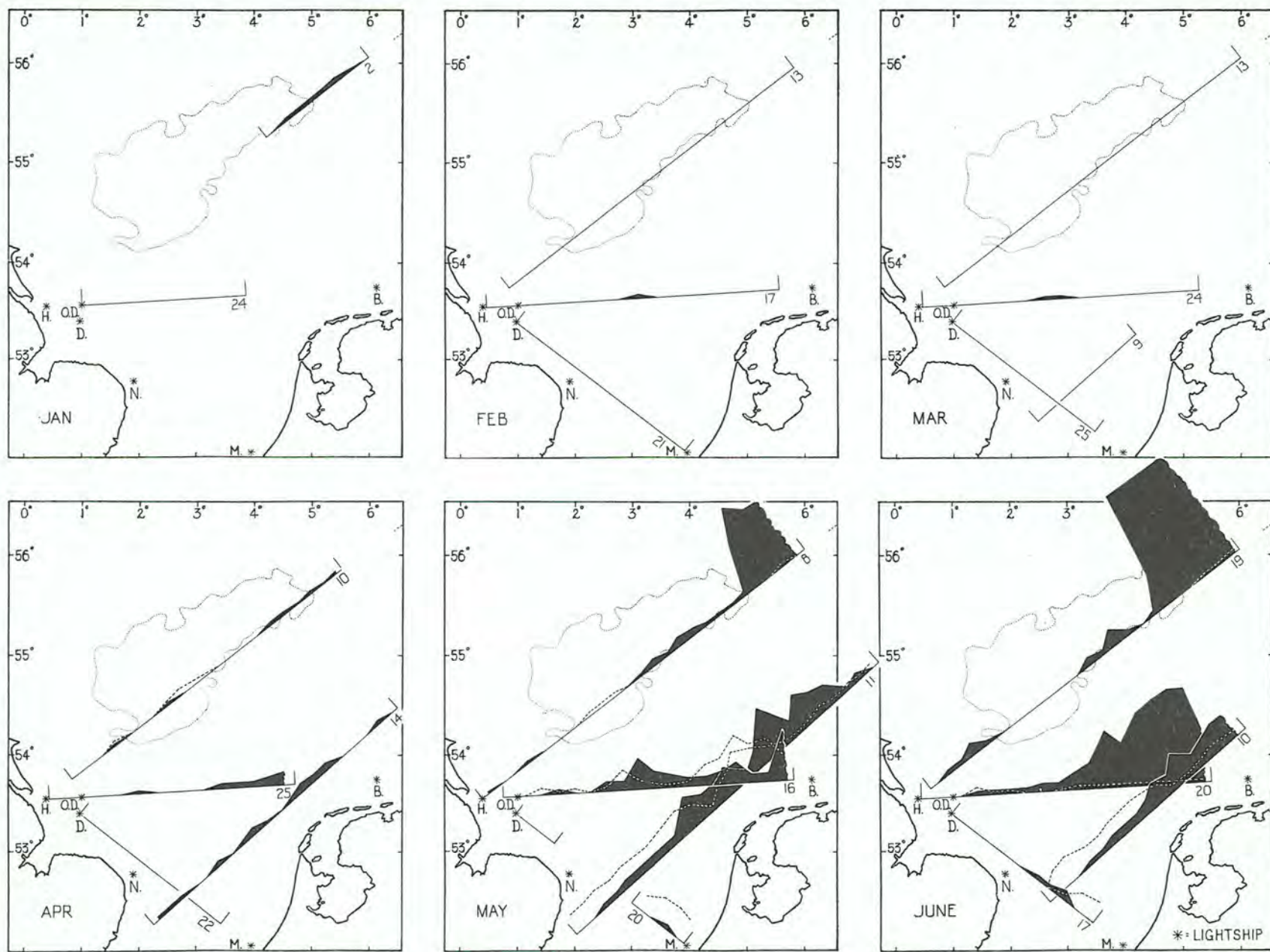
**DINOFLAGELLATES** (blacked-in graph) and **PHAEOCYSTIS** (broken line), 1935, see explanation on Plate XLV.



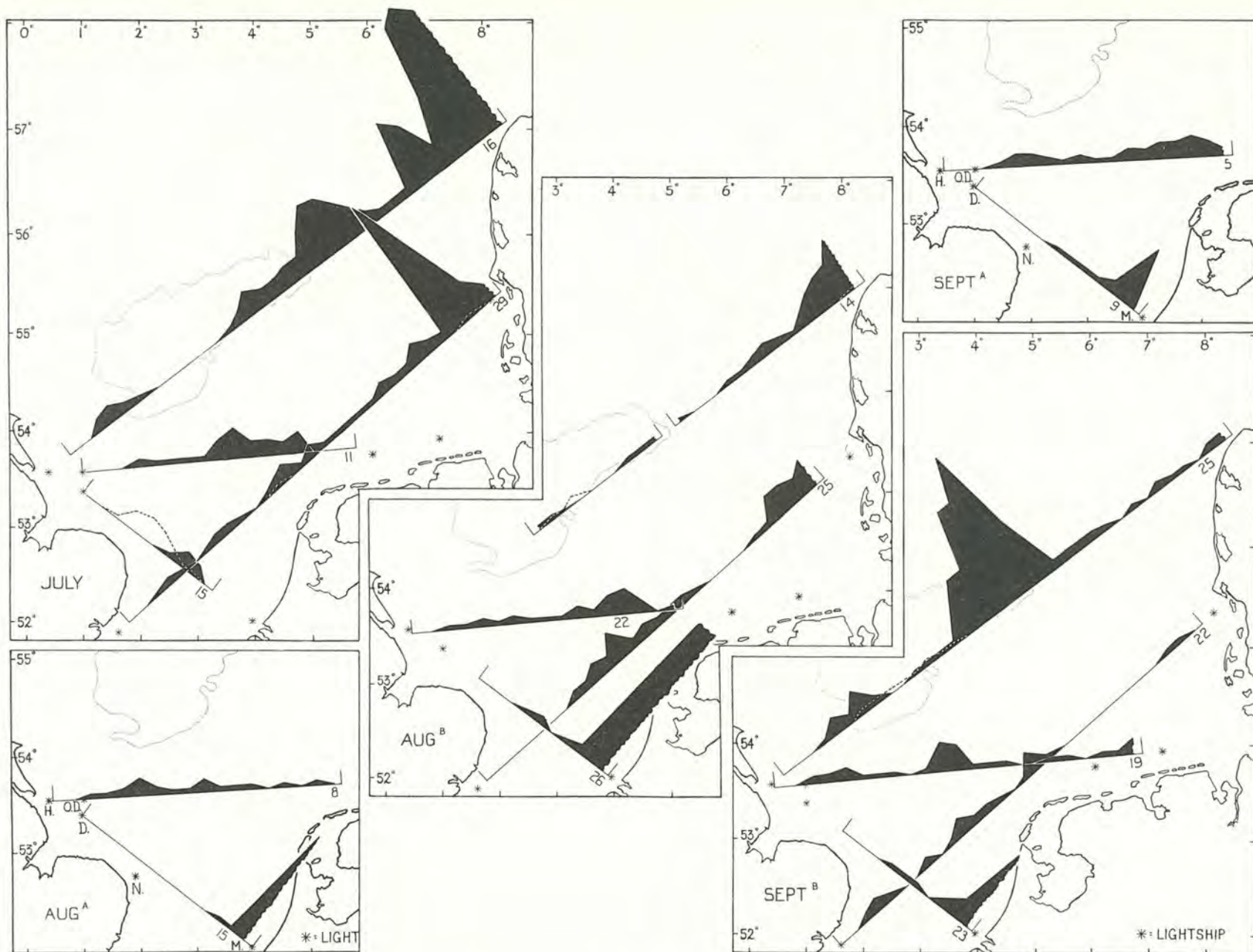
**DINOFLAGELLATES** (black-ed-in graph) and **PHAEOCYSTIS** (broken line), 1936, see explanation on Plate XLV.



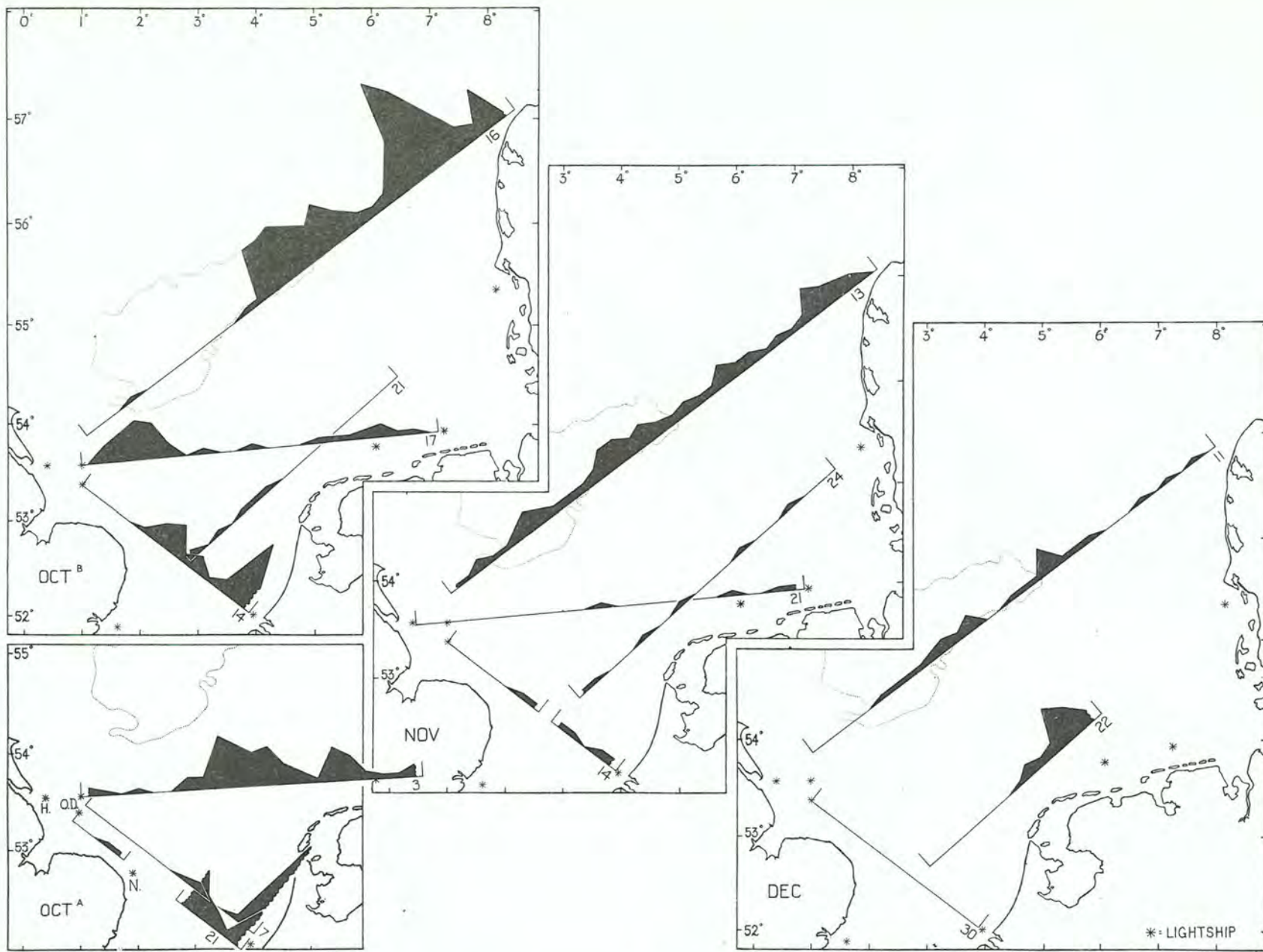
**DINOFLAGELLATES** (black-in graph) and **PHAEOCYSTIS** (broken line), 1936, see explanation on Plate XLV.



**DINOFLAGELLATES** (blacked-in graph) and **PHAEOCYSTIS** (broken line), 1937, see explanation on Plate XLV.



**DINOFLAGELLATES** (black-in graph) and **PHAEOCYSTIS** (broken line), 1937, and continued on Plate LVII, see explanation on Plate XLV.



*DINOFLAGELLATES* (black-ed-in graph) and *PHAEOCYSTIS* (broken line), 1937 continued, see explanation on Plate XLV.

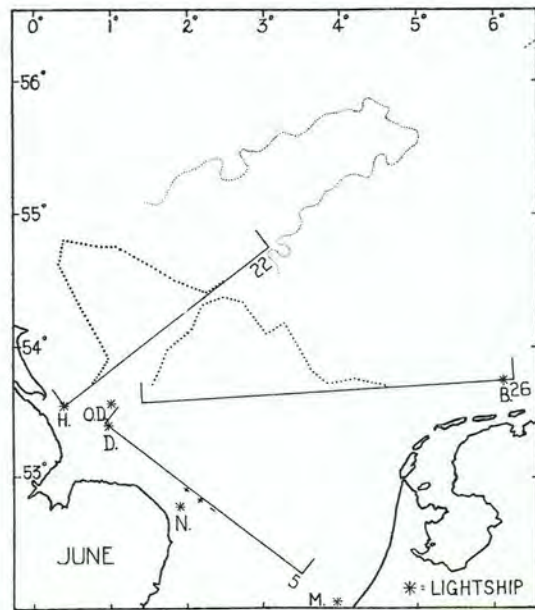
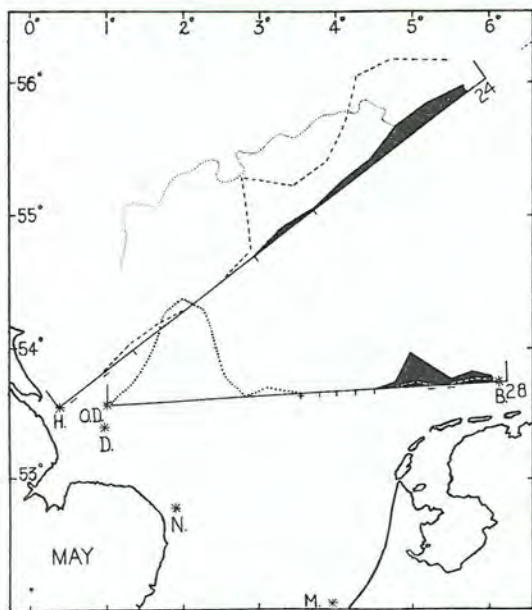
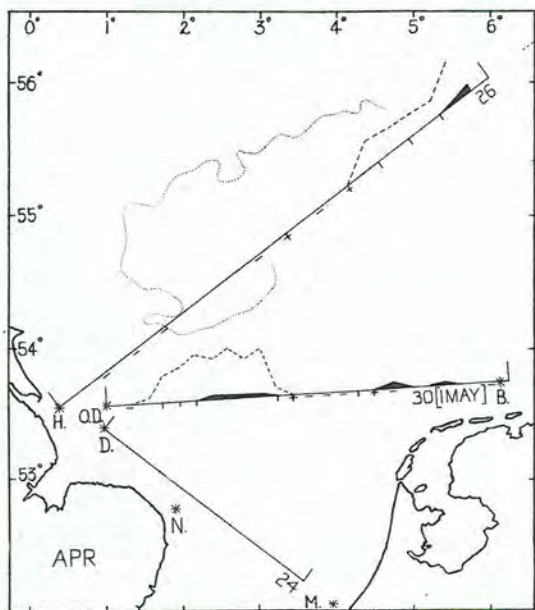
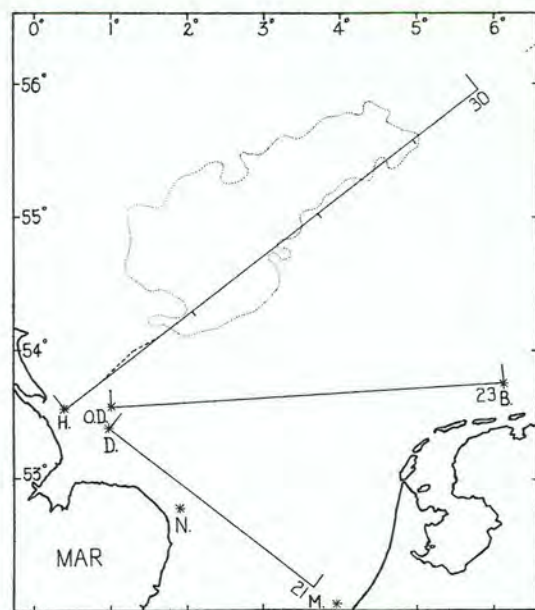
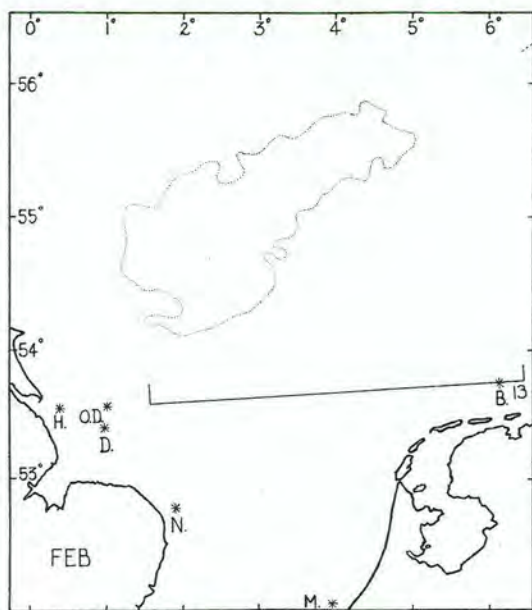
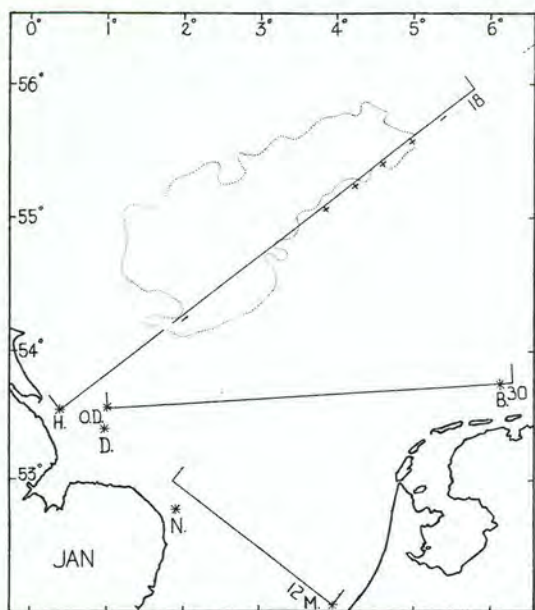
Explanation of  
PLATES LVIII—LXIV

showing the distribution of *CERATIUM FURCA* and  
*C. FUSUS* in the southern North Sea month by month  
during the years 1935-1937.

When more than one record have been obtained on one line in any month they have been included where possible; others omitted will be found on Plates XVI—XVIII.

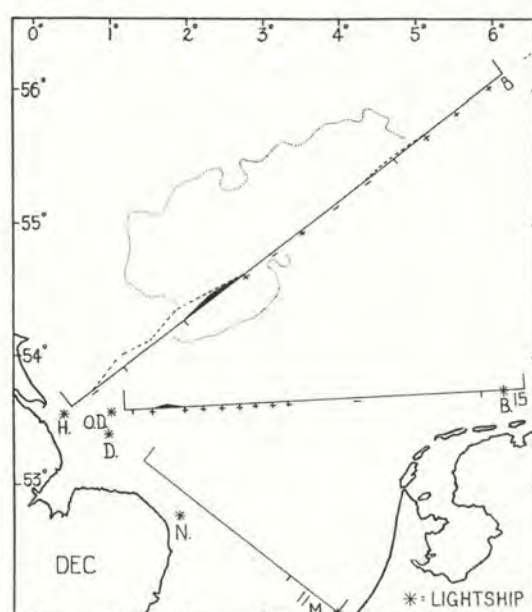
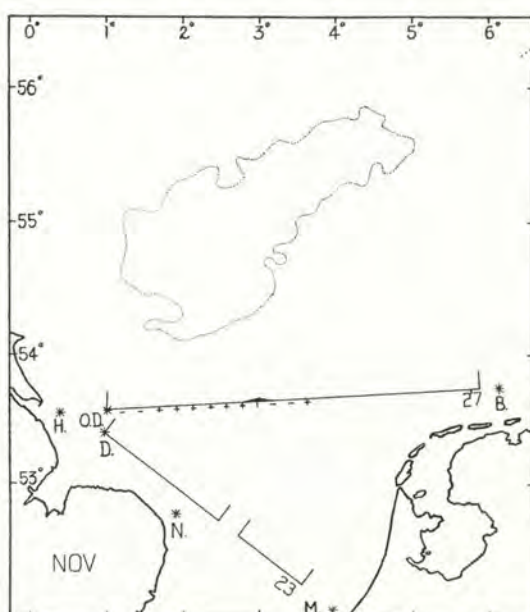
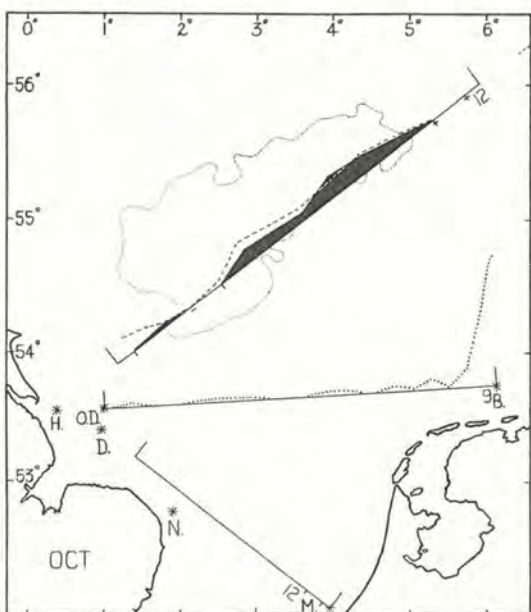
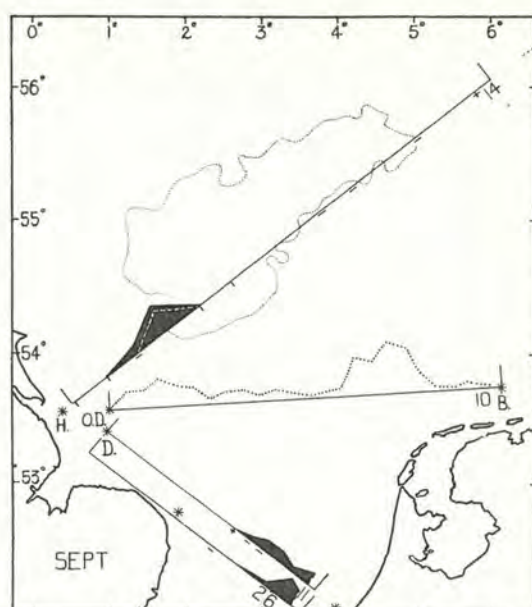
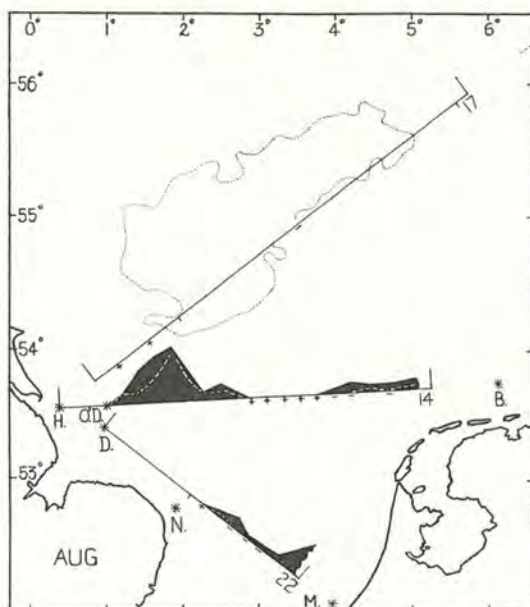
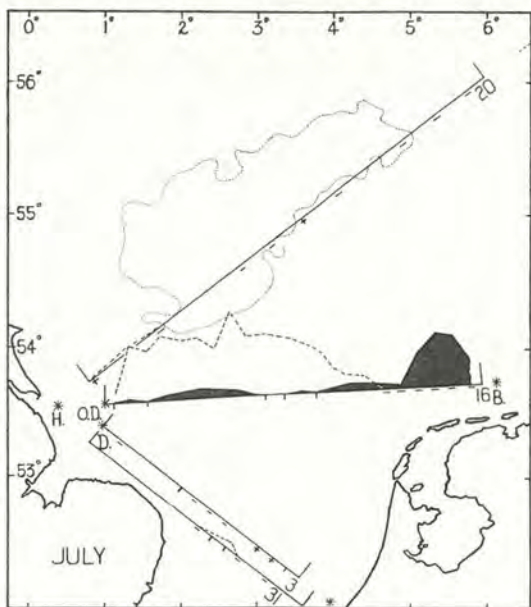
*CERATIUM FURCA* is shown as broken line and *C. FUSUS* as blacked-in graphs. On a few occasions in 1935, when no detailed analysis was made, the corresponding graphs for TOTAL DINOFLAGELLATES have been provided in dotted line.

Other details of maps as explained on Plate XXII.

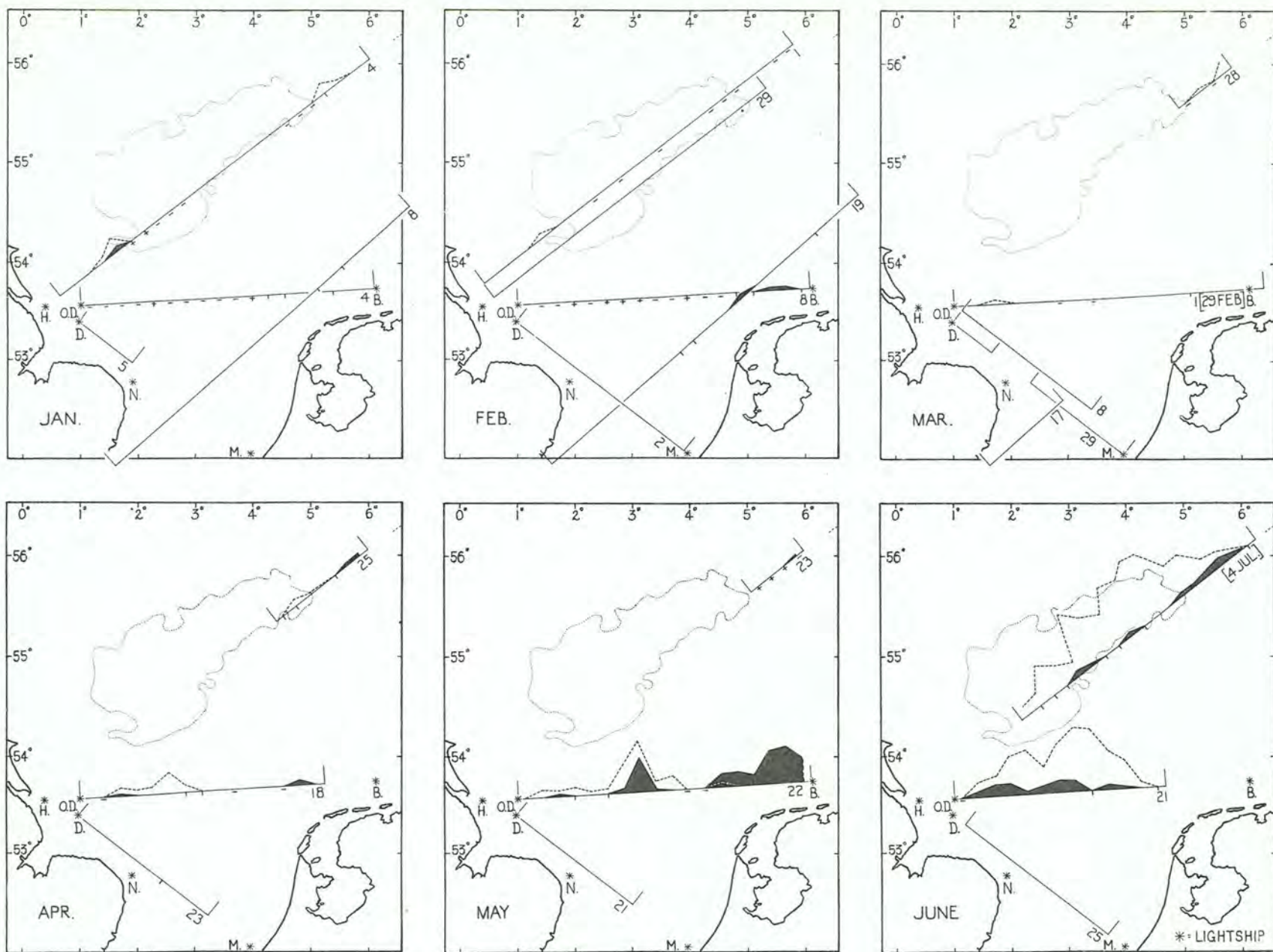


**CERATIUM FURCA** (broken line) and **C. FUSUS** (blacked-in graph), 1935, see explanation on previous page.

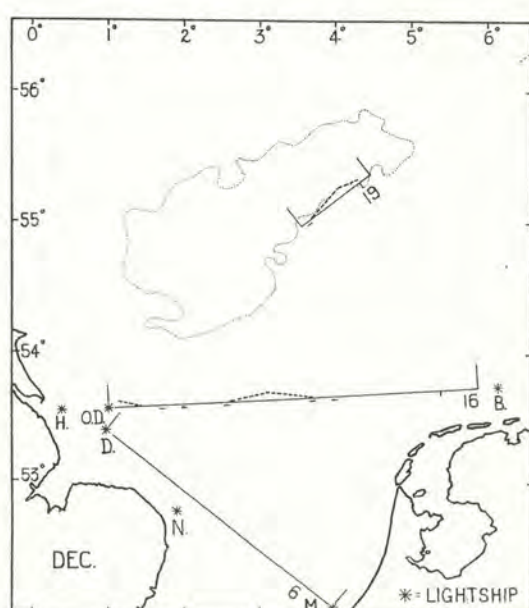
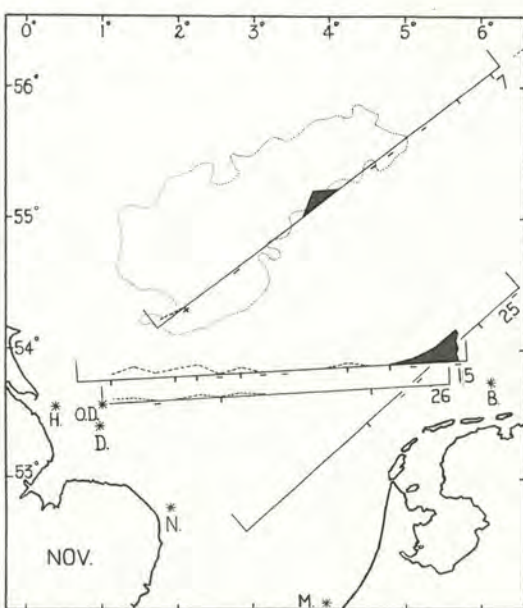
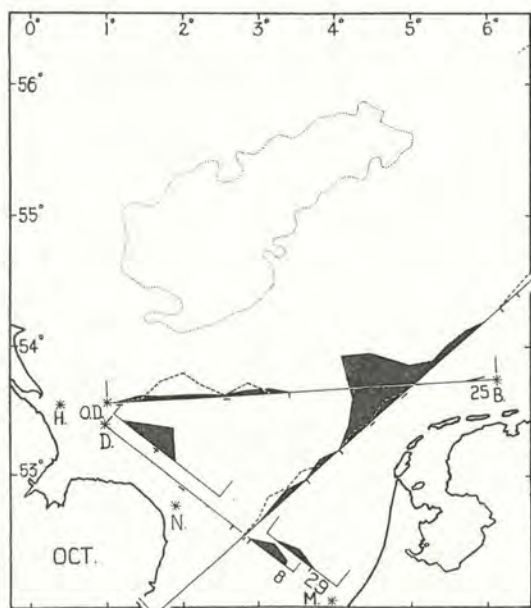
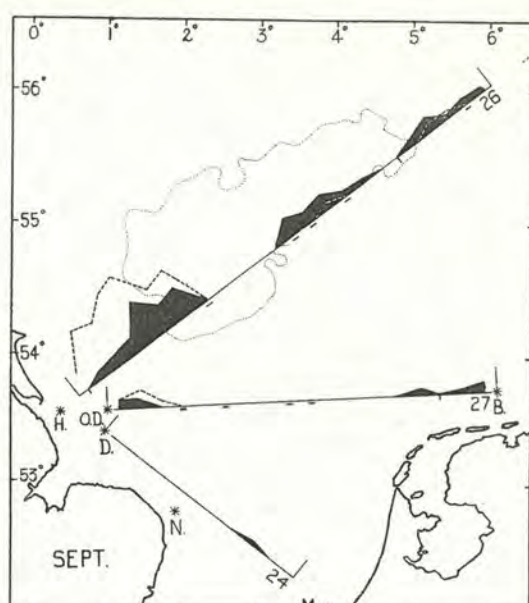
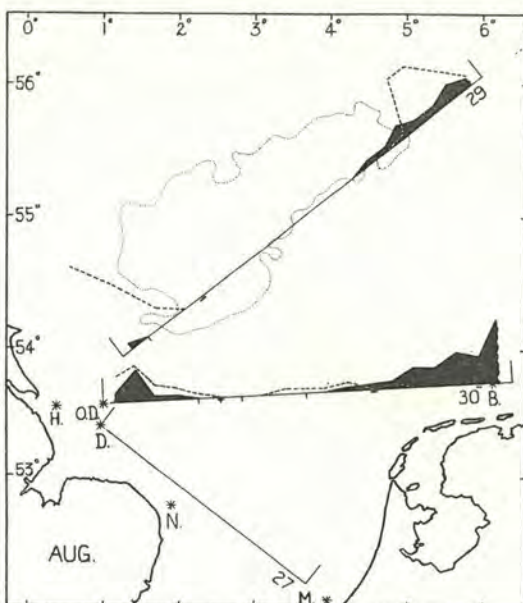
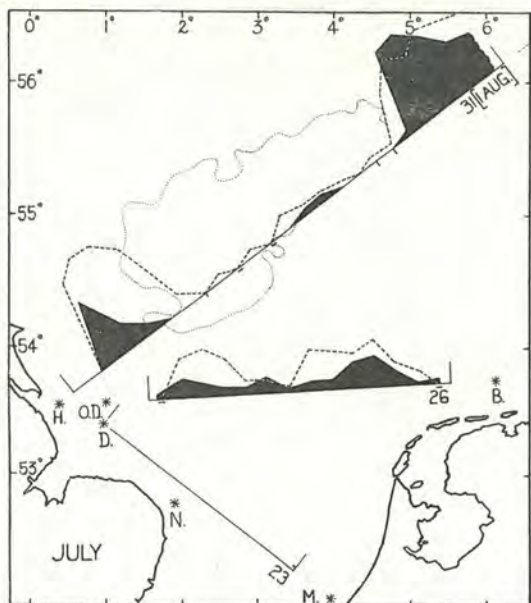




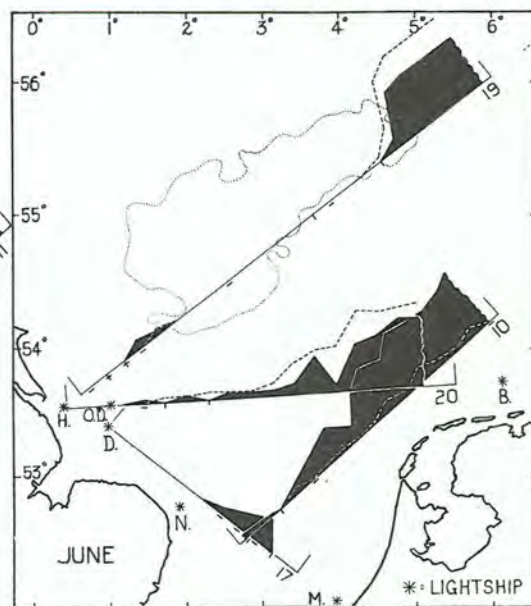
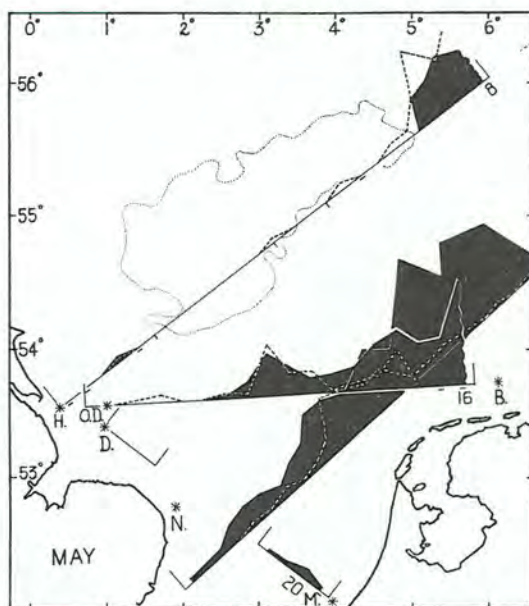
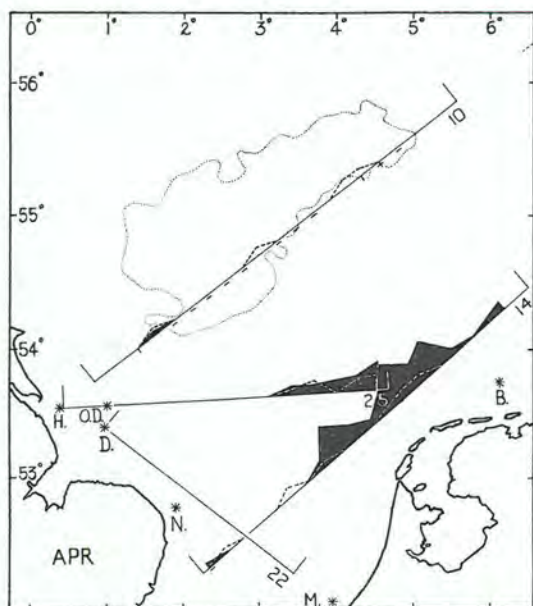
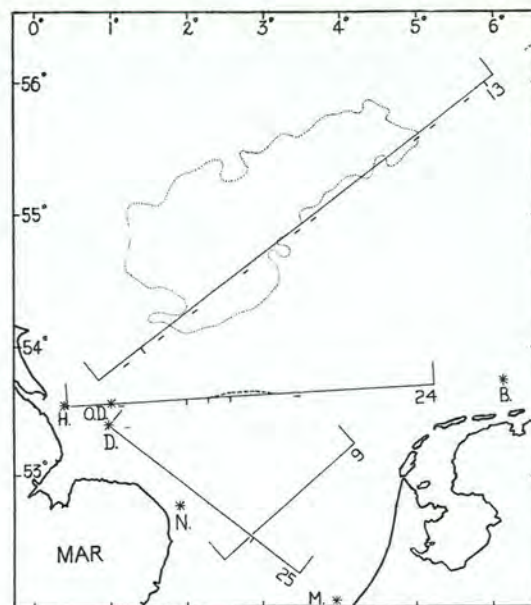
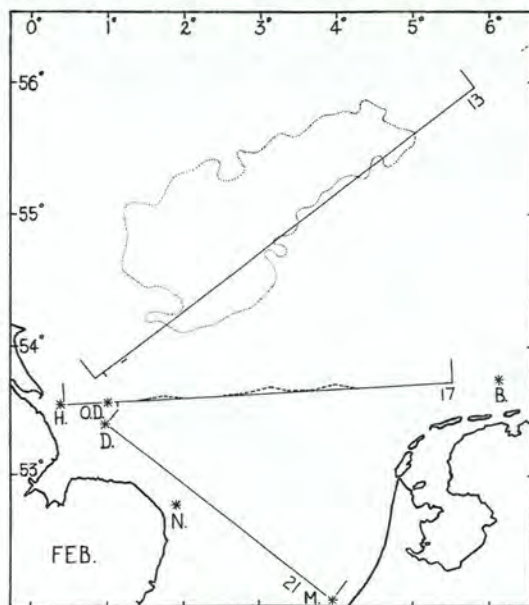
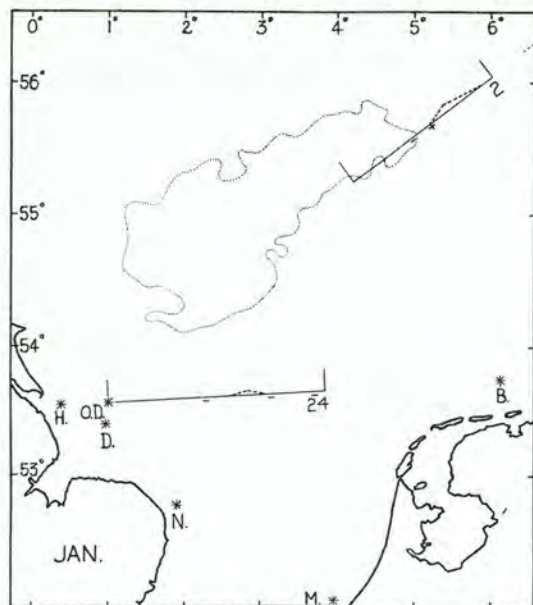
**CERATIUM FURCA** (broken line) and **C. FUSUS** (blacked-in graph), 1935, see explanation preceding Plate LVIII.



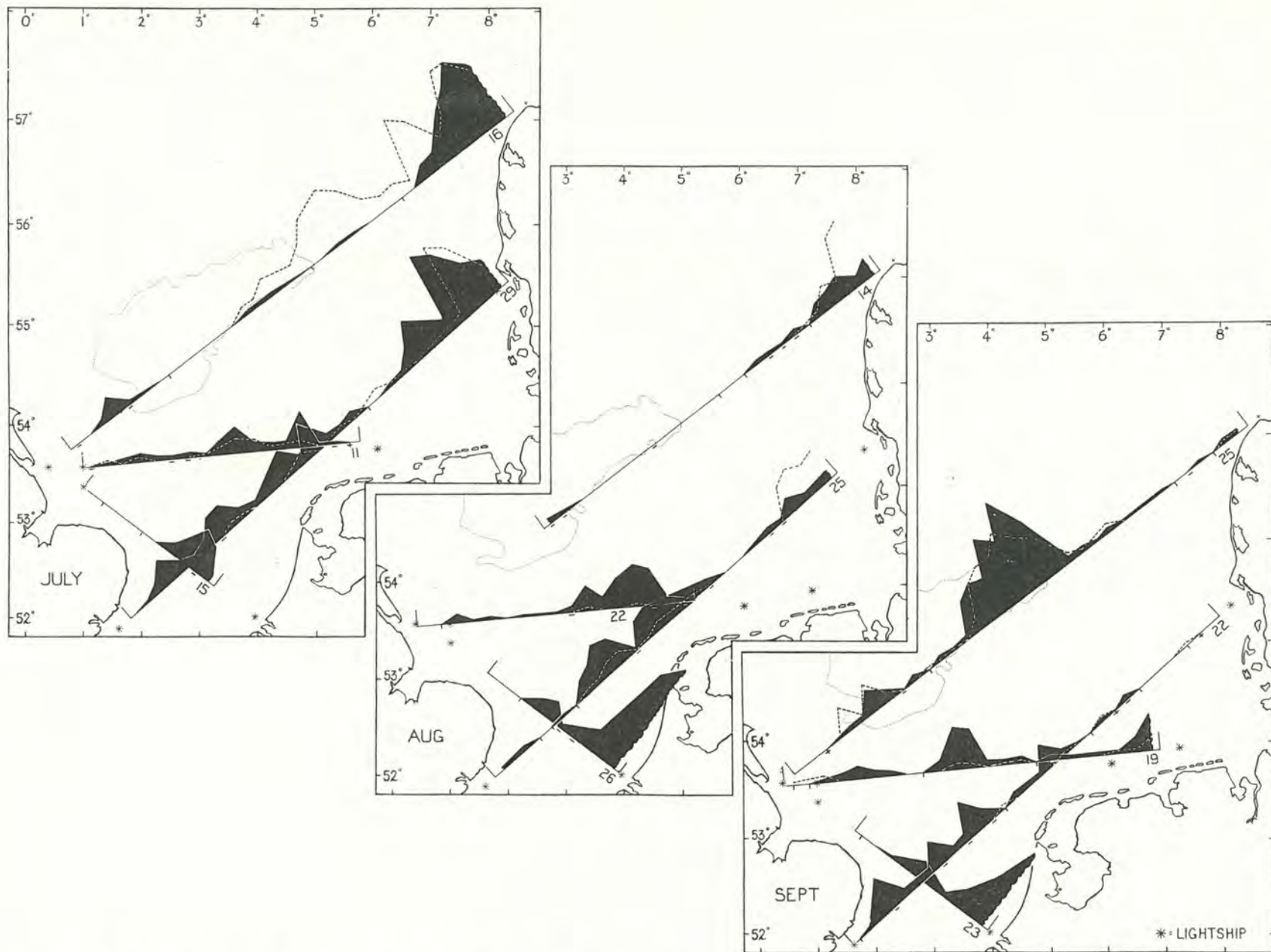
**CERATIUM FURCA** (broken line) and **C. FUSUS** (blacked-in graph), 1936, see explanation preceding Plate LVIII.



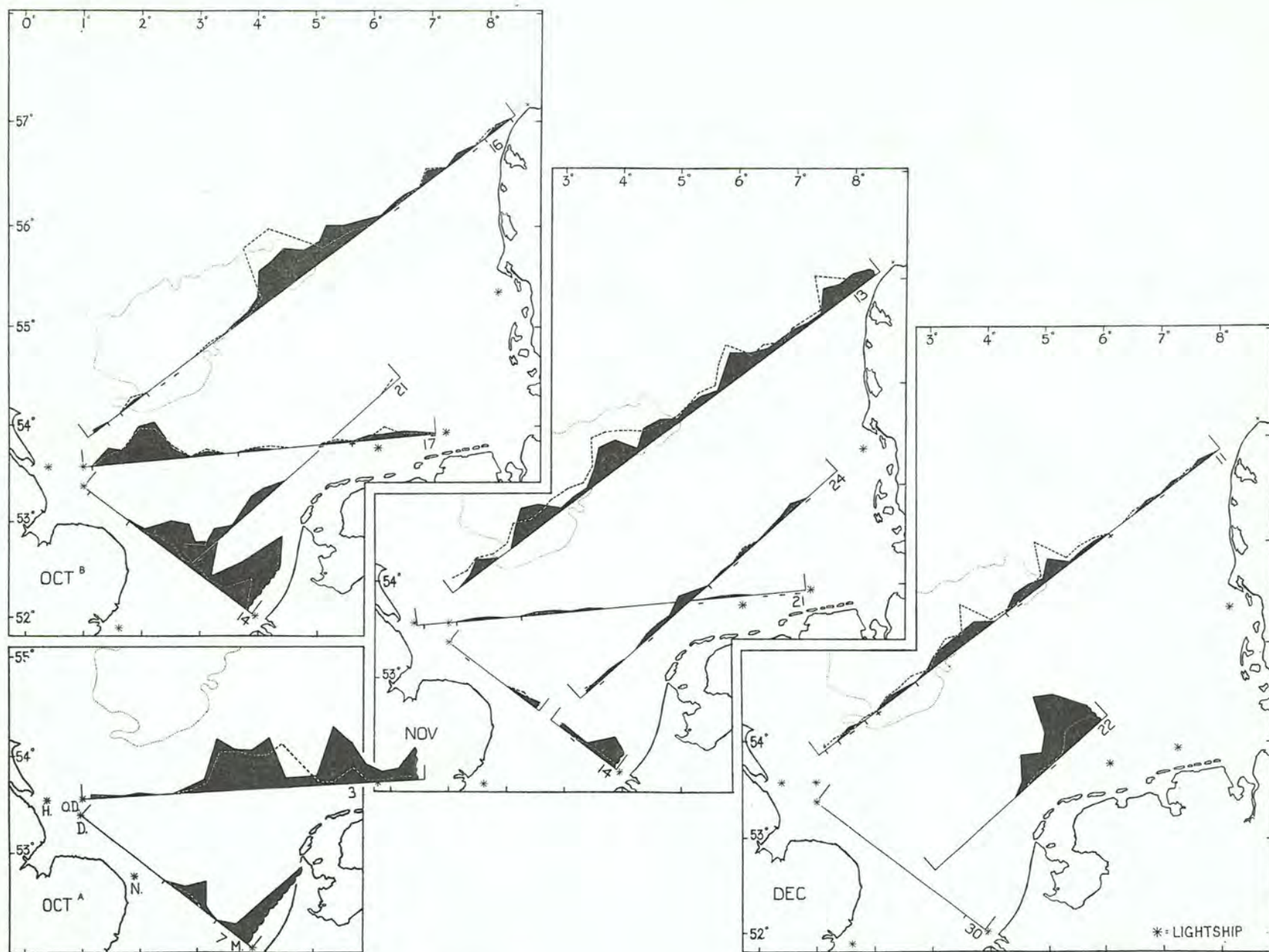
**CERATIUM FURCA** (broken line) and **C. FUSUS** (blacked-in graph), 1936, see explanation preceding Plate LVIII.



**CERATIUM FURCA** (broken line) and **C. FUSUS** (blacked-in graph), 1937, see explanation preceding Plate LVIII.



**CERATIUM FURCA** (broken line) and **C. FUSUS** (blacked-in graph), 1937, and continued on Plate LXIV, see explanation preceding Plate LVIII.



**CERATIUM FURCA** (broken line) and **C. FUSUS** (blacked-in graph), 1937 continued, see explanation preceding Plate LVIII.