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ECOLOGICAL RELATIONS BETWEEN THE HERRING AND THE PLANKTON OFF THE NORTH-EAST COAST OF ENGLAND

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CONTENTS

INTRODUCTION.

IN the years 1930 to 1934 investigations were carried out from the University College of Hull into the ecological relations between the herring and the plankton by the use of a specially designed instrument, the plankton indicator (Hardy, Henderson, Lucas and Fraser, 1936). The instrument (Text-fig. 1) was issued to the skippers of a number of herring drifters who used it in a standard manner (towing it for a mile on a given length of rope) to collect plankton at the place where they fished for herring. The samples of plankton, which were obtained on a gauze disc, were then wrapped up in calico, provided with a label giving the date, position and number of herring caught, preserved in a tin of formalin and eventually returned to the laboratory for examination. In this way just over 1400 records of herring catches were obtained with accompanying plankton samples for analysis. The statistical treatment of the data so obtained showed firstly that during the summer months when the herring were feeding there was on an average a positive correlation between the number of herring caught and the number of the copepod Calanus in the plankton, and secondly that throughout the year there was a negative correlation between the herring catches and the denser samples of phytoplankton. This led to the commercial application of the instrument as a guide to herring drifters in fishing.[1]

This investigation extended from the region of the Shetland Islands in the north to the East Anglian fishery in the south; and the most intensive sampling was made in the well-defined area of the Shields herring fishery, where 538 samples were taken during the three summers of 1931, 1932 and 1933 (Text-fig. 2). Due to limitations of time the analysis of the plankton samples for the years 1932 and 1933 was confined to total phytoplankton, the copepod *Calanus finmarchicus*, total Copepoda, the pteropod *Limacina retroversa*, and certain other zooplankton forms.

At Professor Hardy's suggestion, the author undertook a fuller examination of these plankton samples from the Shields area with two objects in view. Firstly to make a brief survey of the main changes in the plankton community in this

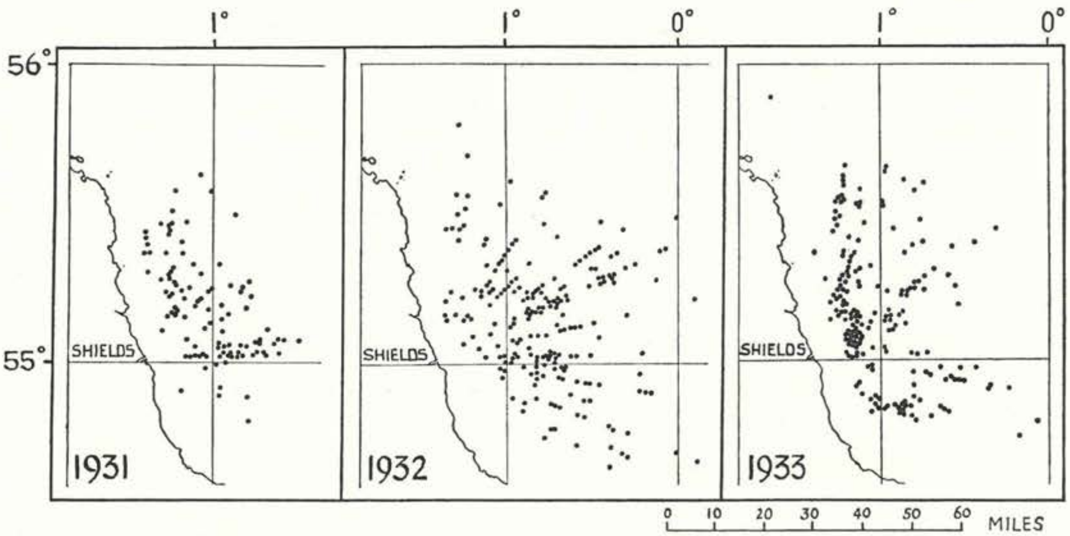
TEXT-FIG. 1.—The plankton indicator.

area during the period of the summer fishery, and secondly, and of more importance, to provide material to enable a comparison to be made between the nature of the plankton and the food taken by the herring during the same period as revealed by the investigations of Mr. Savage of the Ministry of Agriculture and Fisheries (Savage, 1937). Not only had Savage obtained his data from herring stomachs collected by fishermen working in the same fishery, but one of the drifters supplying him with samples in 1932, the S.D. *Violet and Rose*, was a vessel also taking part in the plankton indicator investigations. Savage himself (1926) made a detailed comparison of the Shields plankton with the food of the herring as found by Hardy (1924), and later he made a still more extensive study of the feeding of the herring in relation to the plankton (Savage, 1931). Both authors were much interested in the question as to whether the herring usually feeds by selecting only certain organisms from the plankton, or by taking whatever is present in the plankton at random. It seemed likely that a comparative study of the plankton indicator material and the food of the herring extending over several months in each of three years would be valuable as a contribution towards the solution of this

[1] Reports on its successful use by skippers have appeared in the trade papers (Balls, 1934; George, 1934).

important problem in the ecology of the herring, about which there still appeared some doubt.

It is with much pleasure that I express my most grateful thanks to Mr. Savage for his permission to use not only his published data, but his extracted individual results for the S.D. *Violet and Rose,* which he kindly placed at my disposal, to Mr. Lucas for kindly allowing me to incorporate the results of his 1931 plankton analysis, and to Professor Hardy for his valuable suggestions and criticisms. I should also thank Dr. Henderson, Mr. Rae and Mr. Macnae for their kind help in various ways.



TEXT-FIG. 2.—Charts showing the positions at which plankton indicator samples were taken by herring drifters in the Shields fishery in the summers of 1931, 1932 and 1933, from Lucas (1936).

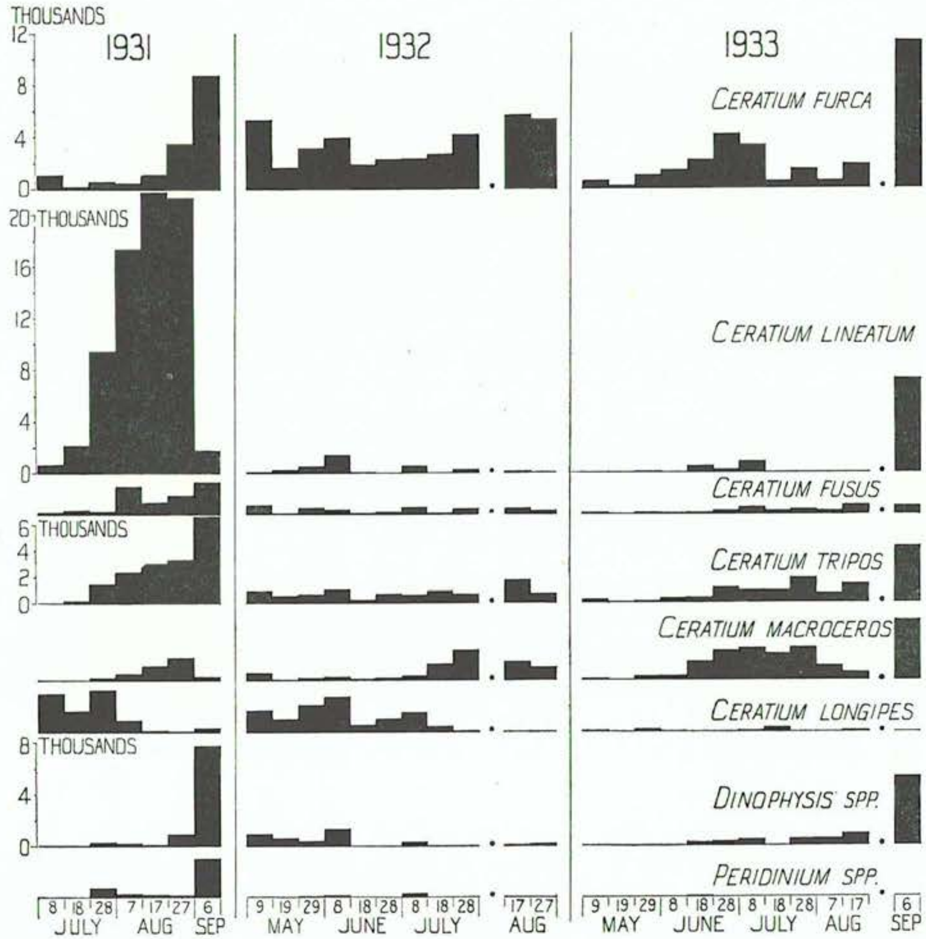
THE PLANKTON OF THE SHIELDS FISHING GROUNDS.

The plankton indicator, which is provided with diving planes like a paravane is so designed that it swims at a depth of between 7 and 10 metres when towed on the standard line provided—a depth approximately corresponding to that from which the herring are caught by the drift-nets. The summer herring fishery from Shields extends from the end of April to the beginning of September. The investigation did not begin until the end of June in 1931, but extended throughout the season in the years 1932 and 1933. The area considered in the present investigation is restricted to that which lies within a circle of 60 miles radius drawn with its centre at the mouth of the Tyne. All samples lying outside this area have been excluded. This, together with the fact that some of the samples used in the earlier investigation had been lost, reduced the total number of samples here considered to 430, distributed in time as follows :

1931, June 29th–September 8th	.	104 samples.
1932, May 5th–August 24th	.	184 ,,
1933, April 30th–September 1st	.	142 ,,

The distribution of the samples in space during the three seasons is shown in Text-fig. 2.

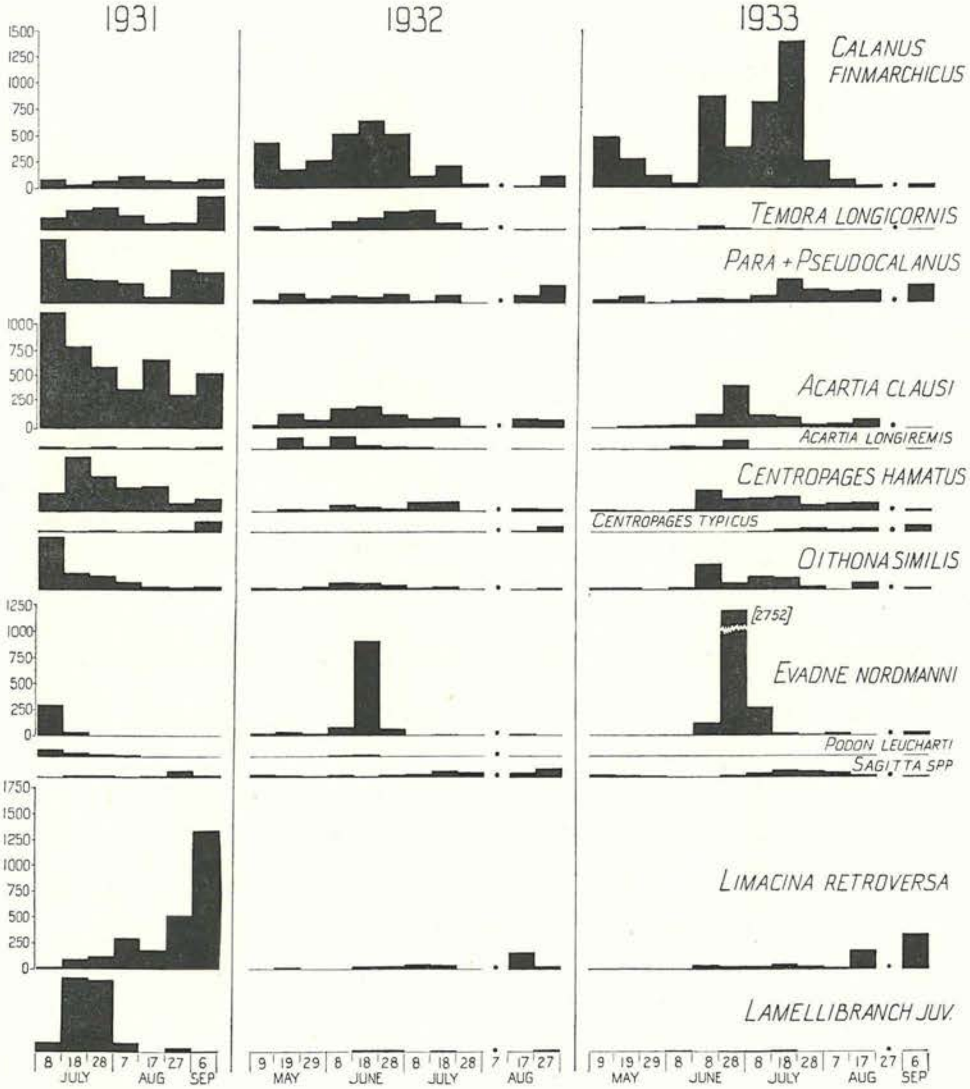
The samples were taken before the drifters shot their fleets of nets and thus were always taken at approximately the same time of the day, i.e. near sunset. This is important, for had the samples been taken at all times of the day and night,



TEXT-FIG. 3.—Histograms representing the average quantities of Dinoflagellates taken on plankton indicator discs in the Shields herring fishery during consecutive ten-day periods in the summers of 1931, 1932 and 1933. (The number of samples averaged in each period is shown in Text-fig. 6.) The dates given are those on which each ten-day period ended.

the varying vertical distribution of species showing vertical migrations would have greatly reduced the value of comparisons. This question has already been dealt with by Professor Hardy and Mr. Lucas (in Hardy, Henderson, Lucas and Fraser, 1936).

The method of collection on a gauze disc in an instrument towed at full speed and the wrapping up of the sample on the disc in calico in the preservative tin renders the condition of the plankton inferior to that collected by the tow-net. Whilst most organisms, including the crustaceans, are still identifiable, some of the more fragile ones such as medusae and Oikopleura have probably disintegrated



TEXT-FIG. 4.—Histograms representing the average quantities of the principal zooplankton forms taken on plankton indicator discs in the Shields herring fishery during consecutive ten-day periods in the summers of 1931, 1932 and 1933. (The number of samples averaged in each period is shown in Text-fig. 6.) The dates given are those on which each ten-day period ended.

and their absence from, or presence in small numbers in, the collection which has been stored for a long period after the original preliminary examination should not be regarded as significant. Against these limitations in method one must place the advantages of obtaining plankton samples from the actual vessels engaged in the fishery. Although from the standpoint of pure plankton research the samples may be incomplete, with the exception of Oikopleura they supply the information regarding the relative abundance in the plankton of all the organisms taken by the herring in this area and so supply the necessary material for a comparison.

On the re-examination of the 1932 and 1933 data it was not infrequently found that the total numbers for a group of organisms, e.g. Dinoflagellates, were less than those recorded by Mr. Lucas in his earlier analysis. Undoubtedly some loss, particularly in the Dinoflagellates but also in the Copepoda, must have occurred in the handling and re-handling of the material. Whenever the total in my analysis was less than that of Mr. Lucas his was taken and the numbers of the different constituent Dinoflagellate species found by me were increased by a proportionate amount to bring them up to the total as recorded by Mr. Lucas and so be comparable with his data for 1931. The same procedure was adopted with the Copepoda where there appeared to be obvious signs of loss.

The data from the analysis are presented as averages for ten-day periods throughout each season ; these periods were chosen to correspond exactly with the ten-day periods taken by Savage in his herring food examinations. In the graphic representations of the results the dates given throughout are those for the last day of each ten-day period.

Phytoplankton.

Diatoms are exceedingly scarce in the collections, since the samplings commenced after April, i.e. after the spring outburst of diatoms. The phytoplankton consists almost entirely of dinoflagellates of which species of Ceratium are most dominant ; *C. furca* (Ehrenberg) Dujardin, *C. lineatum* (Ehrenberg) Cleve, *C. tripos* (O. F. Müller) Nitzsch, *C. longipes* (Bailey) Gran, *C. fusus* (Ehrenberg) Dujardin, *C. macroceros* (Ehrenberg) Cleve and *C. horridum* Gran. Considerable variation in the abundance of these species was shown in the different years. Whilst we have no September samples for 1932, most species showed a maximum in September, 1933 (*C. furca*, *C. lineatum*, *C. tripos* and *C. macroceros*), and two species a maximum in September, 1931 (*C. furca* and *C. tripos*).

C. furca was generally more abundant in 1932 than in 1931 and 1933. *C. lineatum* was exceedingly rich in 1931 reaching its great maximum in August and became very scarce in the following two years, except for a smaller maximum in September of 1933. *C. fusus* was scanty throughout, but slightly more numerous in 1931 than in the other two years. *C. tripos* was also more abundant in 1931 than in the other years. *C. macroceros* was more abundant in 1933. *C. longipes* was extremely scarce in 1933, but was taken in moderate numbers in July, 1931, and from May–July, 1932. *C. horridum* was only taken occasionally. The relative abundance of the different species together with Dinophysis and Peridinium spp. in the different periods are shown in Text-fig. 3. Dinophysis showed a maximum in early September, and Peridinium spp. were extremely scarce except in September, 1931 ; the low numbers of these forms, however, compared with those of Ceratium should not be regarded as significant as they are more easily lost through the meshes of the gauze.

Zooplankton.

The Copepoda are the dominant animals in the samples, the following species being represented :

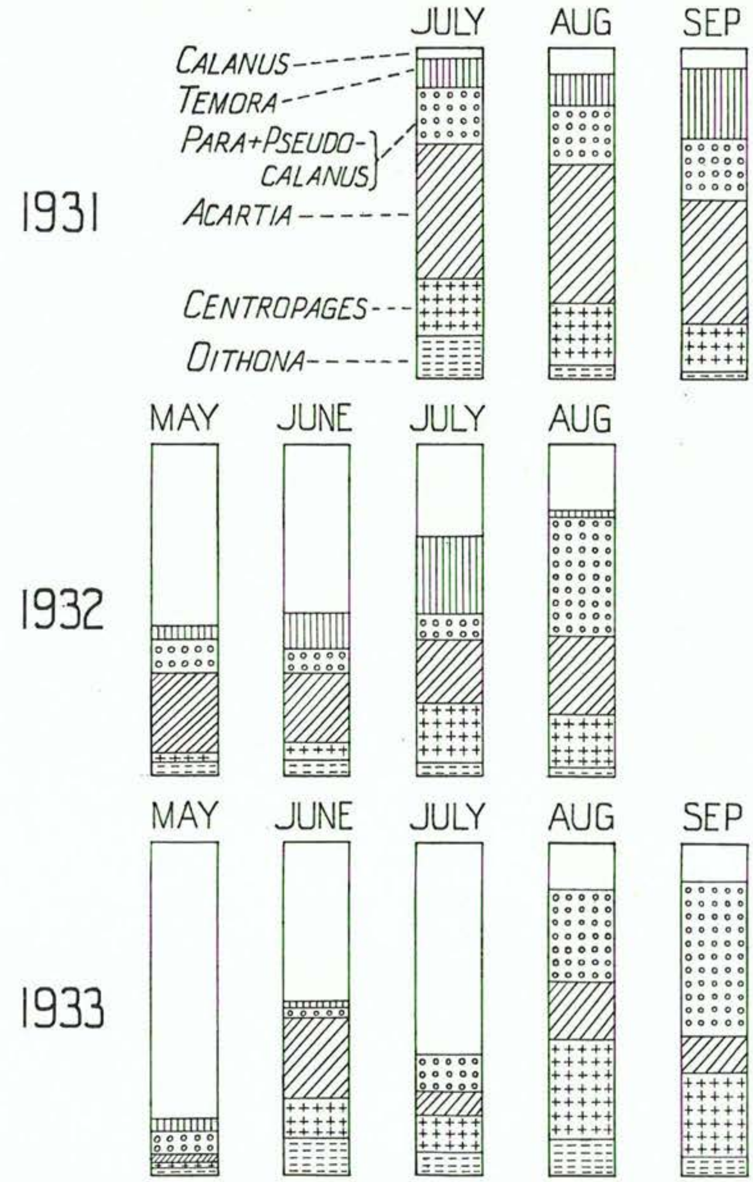
Calanus finmarchicus (Gunn).
Paracalanus parvus (Claus).
Pseudocalanus elongatus Boeck.
Temora longicornis (Müller).
Centropages hamatus (Lilljeb.).
Centropages typicus Kröyer.
Acartia clausi Giesbrecht.
Acartia longiremis (Lilljeb.).
Anomalocera pattersoni Templt.
Oithona similis Claus.

The relative abundance of the more important species in the different periods together with other zooplankton forms is shown in Text-fig. 4. *Calanus* greatly outnumbers the other copepods in 1932 and 1933, but was comparatively scarce in the later part of 1931 ; on the evidence of Savage's herring food investigations it would appear that *Calanus* must have been very abundant in the plankton in the earlier part of 1931 before our sampling commenced. The late persistence of the bulk of the Calanus in the Shields area in these years has been attributed by Lucas (1936) to the increasing inflow of northern Atlantic water into the North Sea year by year during this period. The other striking features of the Copepod distribution are the extreme scarcity of *Temora longicornis* in 1933 and the great abundance of *Acartia clausi* in 1931. The relative abundance of Temora in the latter part of 1931 at a time of scarcity of Calanus is of importance in relation to the herring, and will be further discussed in a subsequent section. In each year *Centropages typicus* occurred in smaller numbers than *C. hamatus*, and appeared later in the summer. *C. hamatus* was more abundant in 1931 than in the two following years. *Anomalocera pattersoni* is not shown in Text-fig. 4 ; it occurred in only very small numbers in August, 1931, and July, 1933. The relative proportions occupied by the different species within the total copepod population are shown as percentages of the totals for each month in the histograms in Text-fig. 5.

The Cladocera are represented by *Evadne nordmanni* Lovin and *Podon leuckarti* G. O. Sars. The occurrence of the latter in the samples was very rare indeed, and if present, its numbers were always very small. *Evadne nordmanni* occurred in large numbers, but only for a comparatively short period each year. Its maximum in 1932 occurred on June 17th, and in 1933 on June 22nd ; in 1931 no samples were obtained before July, but judging from Savage's herring food data it probably reached its maximum in that year in late June. (Jorgensen (1936) gives its maximum period as occurring mostly in June.)

Decapod larvae were very poorly represented in the samples.

The condition of the plankton on the indicator discs after long storage did not allow of specific identifications being made for Sagitta.



TEXT-FIG. 5.—Histograms showing the varying percentage proportions occupied by different Copepoda species within the total copepod population for different months as sampled by the plankton indicator in the Shields fishery.

The pteropod *Limacina retroversa* Flem. occurred in increasing numbers from August onwards in 1931, reaching its maximum on September 2nd; in the following two years it was present only in small numbers, but again being relatively more abundant at the end of the season.

Lamellibranch larvae were quite abundant in July, 1931, but extremely scarce in the following two years.

The small number of Oikopleura encountered in the samples (not shown in Text-fig. 4) should not be regarded as significant; whilst Savage (1926) has shown that they are more abundant in water layers deeper than that fished by the indicator, it is likely that these fragile organisms together with medusae have disintegrated in the process of sampling and storage.

Other Zooplankton forms: Amphipods, Mysids, Euphausiaceans, fish larvae and fish eggs were only occasionally encountered in the samples and their numbers were always very small.

Comparison of the Plankton with the Food of the Herring as Recorded by Savage (1937).

The question as to whether the herring feeds by selection, i.e. by a definite act of capture of certain favourite organisms or whether it feeds by swimming through the water and filtering out the plankton organisms encountered at random by the action of the gill-rakers was discussed by Hardy (1924). He reviews the opinions of former naturalists, some of which held one view and some the other, and upon the evidence of his own investigations comes to the conclusion that the herring feeds by a definite act of selection. Later Savage (1926) describes the plankton of the Shields herring grounds as found on a cruise made in July, 1922, and compares the results of the plankton analysis with the herring food recorded by Hardy. After discussing the occurrence of Calanus and Temora in the two sets of data (Temora at this time being predominant in both) he says: "It is noticeable that all the other species, which are of smaller size, were present in greater proportion in the plankton than in the food. Hardy states that the herring selects its food and these figures appear to confirm his conclusion." Bigelow (1926, p. 101), after discussing the menhaden, writes: "The herring and alewife, with coarser sieves, subsist chiefly on organisms with a longest dimension of at least 0·5 millimetre (copepods and larger animals), which they select individually, and not by swimming open-mouthed, as the menhaden does."[1]

In a subsequent paper, however, Savage (1931) makes a special study of the food of the herring in relation to the plankton obtained on a series of cruises to the Shields fishing area and writes as follows:

"Much has been written on the question as to whether herring feed by selection, or indiscriminately on anything which comes their way, but there is little unanimity amongst the different workers (see Hardy, 1924, p. 27). Our view is that selection of individuals takes place when the size and abundance of the latter make it worth while from the point of view of the labour and time involved in securing enough to satisfy the appetite. At other times, there is probably what might be called 'mass' selection, that is, the herring feeds *discriminately* on

[1] See also Battle, Hunstman and collaborators, 1936.

the mass of plankton in the water. Certain kinds of plankton, e.g. diatoms, coelenterates, *Phaeocystis*, etc., might be distasteful and cause the herring to move away in search of more palatable food.

" This is borne out by the results of the present work. Whenever a food species was at a maximum in the plankton, it was invariably present in the stomach in maximal numbers also, e.g. *Calanus*, *Temora*, *Oikopleura*, *Sagitta*. Hardy commented on the comparatively poor representation in the stomach contents of the smaller copepods such as *Pseudocalanus* and *Paracalanus*, which were numerous in the plankton, and considered that the herring probably do not trouble to take them so long as the larger species, *Calanus* and *Temora*, are abundant. In 1926 there were also many fewer of these small forms than the larger in the stomachs, while in the plankton collections they were much more abundant than *Calanus* and *Temora*. It must, however, be borne in mind that the estimates of the numbers in the plankton were in both cases based on collections with a net, the meshes of which were 60 to 1 linear inch. With such small meshes the smaller copepods would be caught in proportionately greater numbers than the larger ones ; an increase of mesh size results in a greater proportion of the larger species."

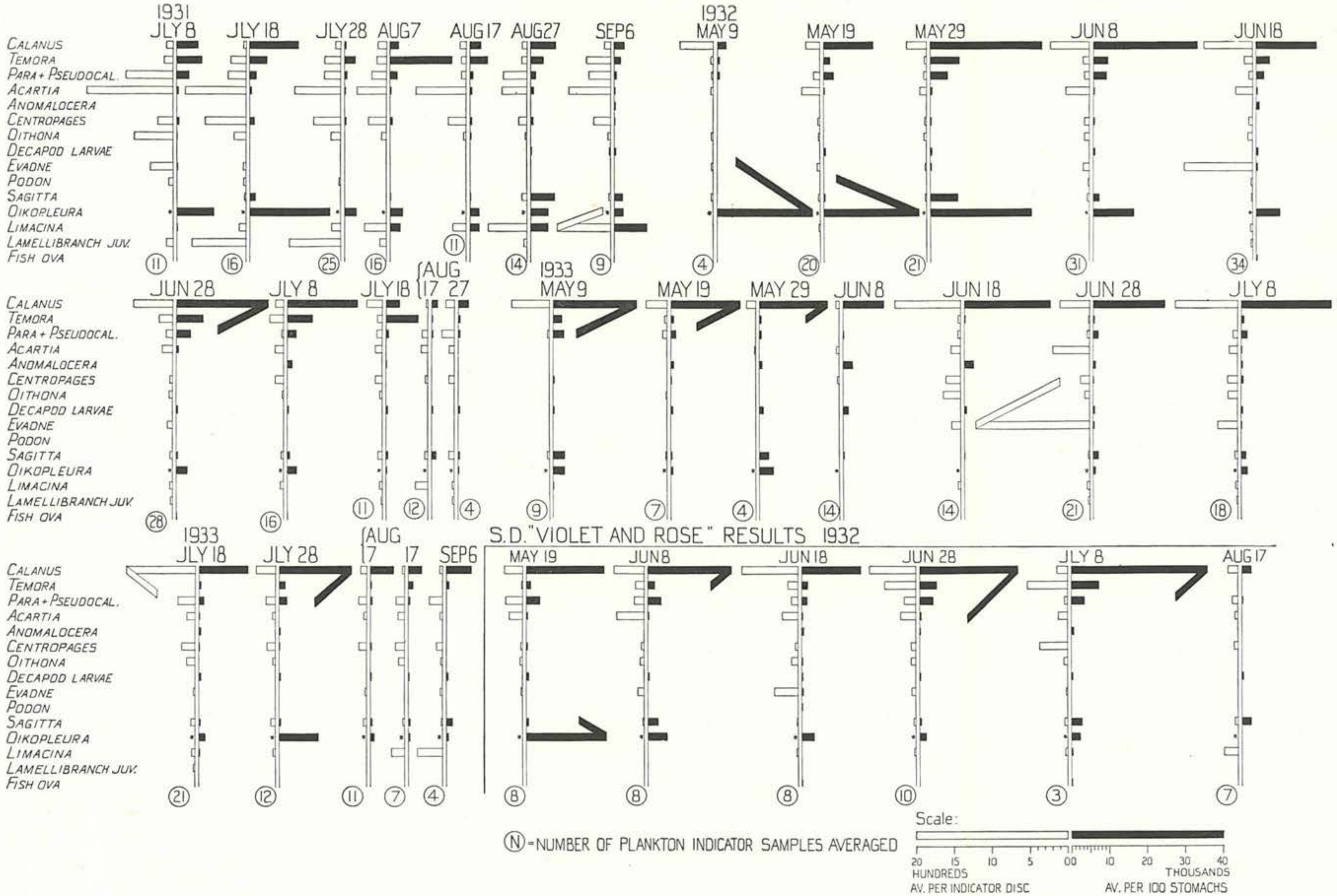
After giving examples of the marked differences found in the proportions of different species of copepods taken in nets of different mesh, i.e. the Hensen net with 60 meshes to 1 inch, and the Nansen net with 40 meshes to 1 inch, he concludes as follows :

" We cannot therefore say definitely that because a net made of a certain mesh catches more small copepods than large ones, that there are more of the former in the plankton than the latter, and that the herring is ignoring the most abundant copepods in its quest for food. In a way the herring can be considered as a catching machine in the same way as are plankton nets, and may lose some of the smaller elements of the food by way of the gill-rakers."

The gauze used for the plankton indicator discs has a mesh of 60 threads to the inch, i.e. the same as that of the Hensen net used in Mr. Savage's investigations, and Hardy (p. 154 in Hardy and collaborators, 1936) has shown that this does actually correspond approximately to the number of gill-rakers to the inch in the herring. Thus it would appear that Mr. Savage's fear that the plankton catch of a herring, if the herring is to be considered as a plankton sampling machine, could not be compared with the catch of a net of 60 threads to the inch, is removed.[1]

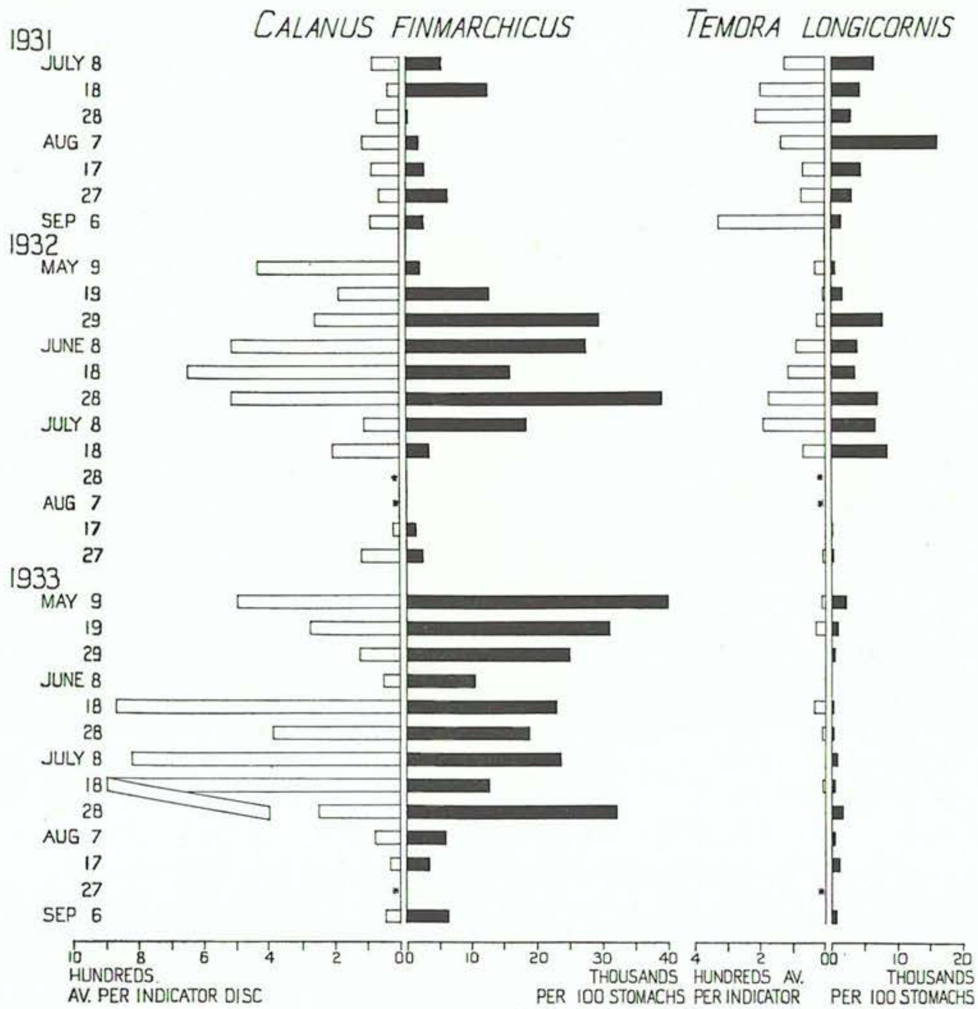
[1] Professor Hardy has recently made some counts of the number of gill-rakers per ½ inch in twelve herring of various lengths. The gills were cut out, laid flat and fully expanded, and the number counted per ½ inch along a line at right angles to the gill-rakers. There is some variation in the number ; in general, as would be expected, there are more per ½ inch in the smaller fish than in the larger. The average number is 31·5 per ½ inch, which compares closely with the meshes of the Hensen net and the plankton indicator gauze (30 per ½ inch). The numbers of gill-rakers were as follows :

Length of fish.	Gill-rakers per ½ inch.	Length of fish.	Gill-rakers per ½ inch.
22 cm.	32	24·5 cm.	30
22 ,,	36	25 ,,	26
22·5 ,,	34	27 ,,	26
23 ,,	35	27·5 ,,	29
23 ,,	35	27·5 ,,	32
23·5 ,,	35		
24 ,,	28	Average	31·5



TEXT-FIG. 6.—Comparative histograms arranged to show the relative abundance of plankton animals in samples taken by the indicator (open histograms) opposite those representing the relative abundance of the same species as found by Savage (1937) in the stomachs of herring caught during the same ten-day periods in the same fishery during 1931, 1932 and 1933. In addition to twenty-nine such periods there are shown six relating to data supplied by a single drifter, the *Violet and Rose*, in the summer of 1932. Plankton values for Oikopleura are omitted (see p. 243).

In Text-fig. 6 a series of comparative histograms are arranged to show the relative abundance of animals in the plankton as shown by the plankton indicator samples, side by side with histograms to show the relative abundance of organisms



TEXT-FIG. 7.—Histograms (open) representing the numbers of *Calanus finmarchicus* and *Temora longicornis* taken per average plankton indicator disc compared with others (blacked-in) representing the numbers of the same species as found by Savage (1937) per 100 herring stomachs during the same ten-day periods.

found by Savage in the stomachs of herring during each of the same 29 ten-day periods. Only those periods have been included for which there are more than four plankton samples ; the average number of samples per period is 15. The herring food is that found by Savage per 100 stomachs. The plankton histograms are left open and shown to the left; the herring food histograms are blacked in and shown to the right. In addition there are also shown at the bottom right-hand side of the figure similar comparisons, but for data supplied by a single drifter, the *Violet and Rose*, using the indicator at the same time as supplying Mr. Savage with samples of stomachs during six ten-day periods during 1932. He very kindly provided the latter data, which were not so separated in his published paper. We should clearly not expect there to be an exact agreement, or even always a general agreement, when the plankton samples may not have been taken in even approximately the same part of the area from which the fish were taken. We know how patchy the plankton may be in its distribution. Nevertheless, when considering all the 29 periods together, as well as the 6 more special *Violet and Rose* samples, we do see a number of striking features in the plankton and herring stomach comparisons.

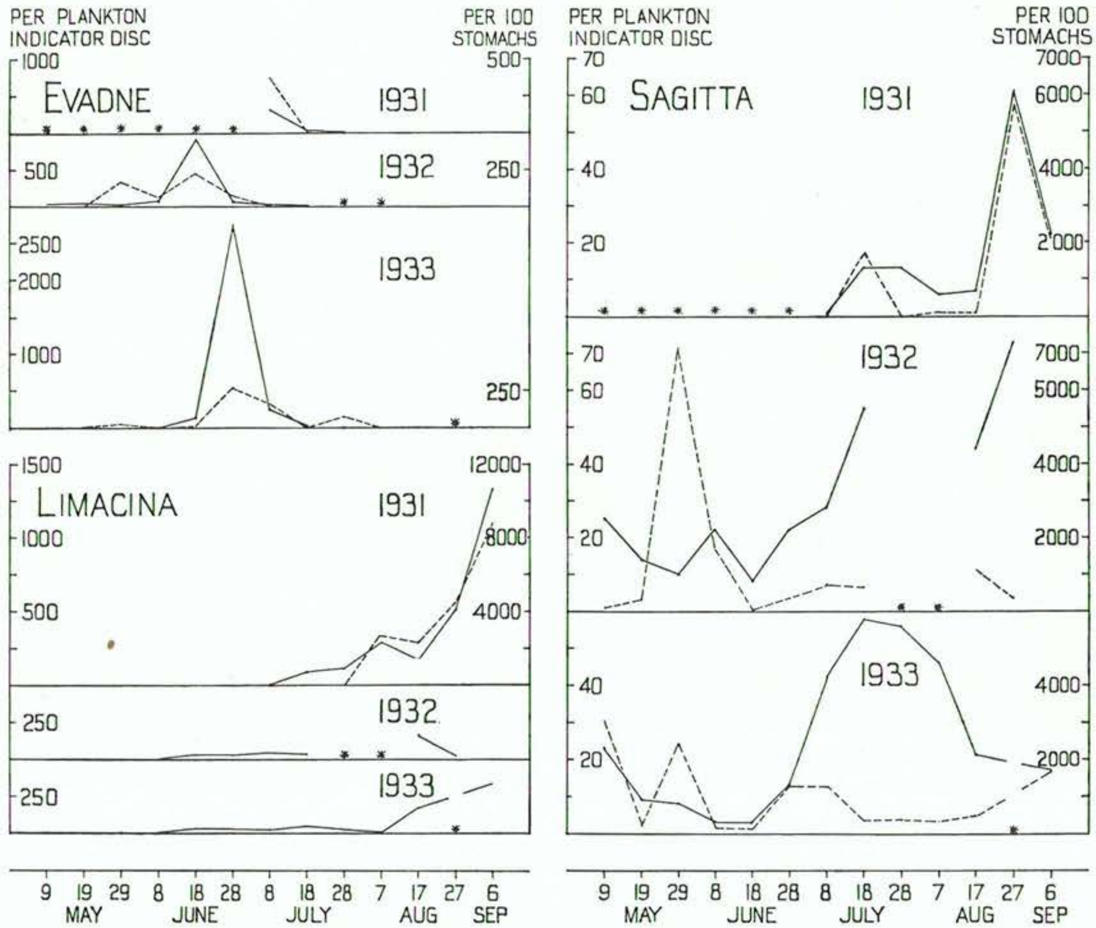
There is usually either a good correspondence between the proportions of Calanus in the herring stomachs and that in the plankton, or the proportion in the stomachs may be very much greater than that in the plankton. The same is generally true of Temora, but to a lesser extent. This correspondence between the number of Calanus and Temora in the plankton and stomachs is shown more clearly in the histograms devoted exclusively to these forms shown in Text-fig. 7 on a somewhat enlarged scale. When Temora is present in any quantity in the plankton it is taken by the herring; it was very scarce in 1933 in both the plankton and herring stomachs.

If Calanus and Temora were considered alone it might be said that there was little evidence of selection, but turning to the relative proportions of other organisms (i.e. in Text-fig. 6) we see a very different picture; Acartia, Oithona, Cladocera and Lamellibranch larvae are always present in larger proportions in the plankton than in the stomachs, and the same is true of Centropages except in two insignificant instances (periods ending May 9th and 19th, 1933). Frequently Centropages is present in the plankton in quite appreciable quantities, yet it is hardly ever present at all in the stomachs. The reverse is true of the larger copepod Anomalocera, which is frequently found in the stomachs but has only rarely been taken on the plankton indicator disc.[1] All these facts taken together strongly confirm the view that the herring does select the larger forms Calanus, Anomalocera and Temora by a definite act of capture, and tends to ignore the smaller forms. The fact that Oikopleura, whilst often an important element of the food, was not recorded in the plankton is not regarded as significant for the reasons given on p. 243.

Further valuable evidence is available from the data regarding the pteropod Limacina and the chaetognath Sagitta. The remarkable similarity in the increase

[1] It has been suggested by some authors that *Anomalocera patersoni* is almost entirely a surface form and, if this is so, the plankton indicator might have missed it entirely at a depth of 7–10 metres. Russell (1927), however, shows it may occur in fair numbers down to 10 metres and on one occasion had its maximum numbers at 20 metres.

in the number of Limacina in both the plankton and herring stomachs as the season advanced at the end of the 1931 fishery has been remarked upon by Lucas (1936) and Savage (1937). There is no such close agreement in 1932 or 1933. Curves of the abundance of Limacina in the plankton and the stomachs for the three



TEXT-FIG. 8.—Graphs comparing the numbers of Evadne, Limacina and Sagitta in the plankton as shown by the plankton indicator (continuous line) and in herring stomachs as found by Savage (1937) in the same ten-day periods (broken line) during 1931, 1932 and 1933. An asterisk indicates that no samples, or too few, were taken. The numbers of Limacina taken by the herring in 1932 and 1933 are too small to be shown as a graph on the scale adopted : the highest number being 92 in 1932 and 129 in 1933.

seasons are compared in Text-fig. 8. Now in the case of Sagitta, also shown in Text-fig. 8, we see just the same thing : a close correspondence in the latter part of the 1931 season, but not in the other two years, when, except for a short period in May there are distinctly higher proportions in the plankton than in the stomach contents. Whilst the number of Limacina in the plankton in 1932 and 1933 was very much less than in 1931, this is not true of Sagitta. The latter part of 1931 was marked by a singular scarcity of Calanus in the plankton, and it is difficult to escape the conclusion that the herring, when short of the food it usually prefers, turns to feed upon Limacina and Sagitta in larger numbers. It will be remembered that it was just in this period of 1931 that Lucas (1936) found that the positive herring-Calanus correlations for the Shields area broke down.

In Text-fig. 8 is also shown the relative abundance of the cladoceran Evadne in the plankton and stomachs. They are never taken in large numbers by the herring, but the peaks of abundance in the two series show a striking correspondence, although its maximal number in the stomachs is very small indeed in comparison with that in the plankton. It appears either that it may be taken in small numbers indiscriminately with the selected larger food elements just during its great maximum in June, or that only during this time of abundance is the herring likely to concern itself with them.

Summary.

1. 430 plankton samples which were taken by several herring drifters using the Hardy Plankton Indicator in the Shields fishing area during the summer seasons of 1931 to 1933 are analysed to show the main changes in the plankton during those seasons.

2. A comparison is made between the proportions of the different zooplankton organisms found in the plankton and the proportions of these recorded by Savage (1937) in the stomachs of herring obtained from drifters working in the same area and during the same time. The comparisons are made for 29 ten-day periods in the seasons 1931 to 1933, and in addition for 6 ten-day periods relating to a single drifter which obtained both plankton and stomach samples at the same time in 1932.

3. The comparisons in 2 provide evidence that the herring feeds by selecting certain organisms by individual acts of capture and not by swimming open-mouthed to strain out the plankton indiscriminately :

(*a*) Calanus and Temora in the stomachs either correspond fairly closely to the proportions in the plankton or they may be in very much higher proportions. The latter is always true regarding Anomalocera.

(*b*) Acartia, Oithona, Cladocera and Lamellibranch larvae are always in larger proportions in the plankton than in the stomachs ; this applies also to Centropages with two insignificant exceptions.

(*c*) There is a close correspondence between the numbers of Limacina and Sagitta in the plankton and stomachs in the latter half of the 1931 season, but not during 1932 and 1933, when the numbers in the stomachs were insignificant ; during the former period there was a great scarcity of Calanus in the plankton.

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