On the Biology of *Calanus finmarchicus*. I. Reproduction and Seasonal Distribution in the Clyde Sea-Area during 1932.

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With 4 Figures in the Text and Plates I and II.

CONTENTS.

INTRODUCTION.

THE problems concerned with the breeding of *Calanus finmarchicus* have been dealt with by numerous workers, mainly during the last twenty years. Taken as a whole the results show remarkable uniformity if the differences in methods of sampling and in the geographical regions over which the work has been spread, are taken into account.

The two points which stand out on reviewing this work are firstly, that breeding occurs in spring and summer and secondly, that during the winter the species is represented by its fourth and fifth copepodite stages, chiefly the latter (Farran, 1927, p. 142).

Work in the Clyde Sea-Area was undertaken to discover to what extent this area was in agreement with other regions of northern temperate waters and to obtain more detailed information on the number of breeding periods, the time taken for development, and other related facts. This work was an extension of the programme carried out by Marshall and Orr in 1931 (Ann. Rep. Scot. Mar. Biol. Assoc., 1930–31).

This area with its semi-enclosed lochs appears to be particularly suitable for such work since it is separated from the waters of the Irish Sea and the Atlantic by a comparatively shallow platform. Unfortunately, little is known about the currents entering the Clyde Sea-Area, but those drift-bottle experiments which have been carried out by Cunningham (1907) of the Irish Fisheries Board lend support to the view that no deep-water currents enter the area. (Other drift-bottle experiments affecting this area have dealt only with surface drift.) The lochs of this area are, in most cases, still more completely cut off from outside waters by bars (Mill, 1889–91 ; Marshall and Orr, 1927) of shallow depth across their mouths.

It is felt that movements of surface waters will not affect the population to any great extent and will in any case be dependent upon weather conditions.

It seems certain then, especially in the lochs, that any changes in the numbers of Calanus will be due to factors operating within the locality.

Stations and Methods.

Four stations were selected within the area for investigation and comparison (see Map, Text-Figure 1). Station I was situated over the deepest part of the channel between the south end of Bute (Garroch Head) and the Little Cumbrae. This station had an average depth of 113 metres, and was taken as typical of the open waters of the Clyde Sea-Area. Station II was in the channel which runs in a north-westerly direction between Arran and Bute, ending in a "deep" of about 200 metres at the mouth of Loch Fyne. The average depth of this station, which was midway between the north of Arran (The Cock of Arran) and Inchmarnock, was 151 metres. Station II, also, was assumed to be typical of the open waters of this region and acted as a check upon Station I.

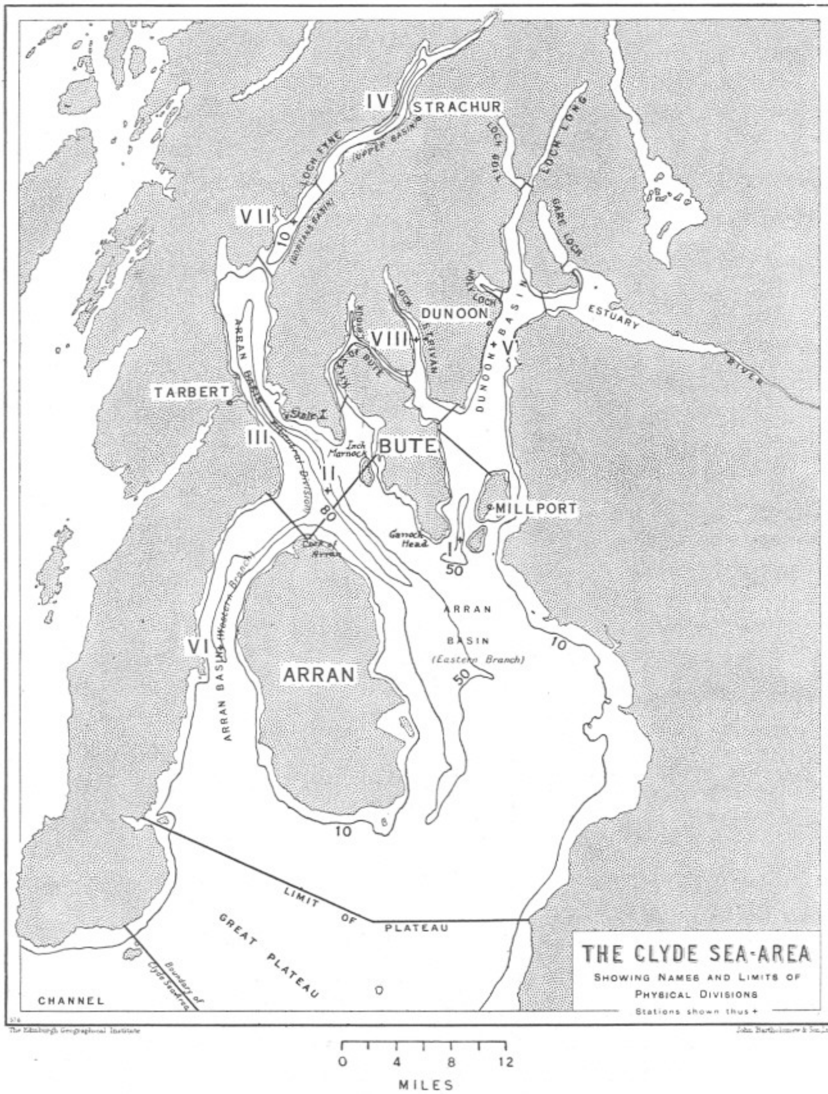
Station III was situated in the vicinity of the "deep" at the mouth of Loch Fyne, off Skate Island. The catches from this station were not counted, but rough observations were made to check the possibility of the loch forming a breeding ground whence Calanus might spread to the rest of the area, since it was known from previous work in this area that Calanus was abundant there at times when it was very scarce elsewhere.

Station IV was nine or ten miles from the head of Loch Fyne, in the deepest part of the loch, off Strachur. Upper Loch Fyne is separated from the rest of the area by two bars which divide the loch into three basins, Strachur being in the innermost. The average depth of the hauls was 130 metres.

It was hoped that these stations would give a comparison between the loch and the open waters, and that some light might be thrown on the reason for the large numbers of Calanus present here when they were scarce elsewhere.

Three other stations were selected, one off Dunoon (Station V), a second in the Kilbrennan Sound (Station VI), and the third about half-way up Loch Fyne in the middle, or Gortan's Basin (Station VII), and these were visited and hauls taken at quarterly intervals to provide a further check upon the validity of the regular stations.

Vertical hauls were taken at each of the stations with a modified form of the Standard Net described by Ostenfeld and Jespersen (1924). The



Text-Fig. 1.—Map of the Clyde Sea-Area showing positions of Stations. Depth contours are shown for 10, 50, and 80 fathoms.

cylindrical part of the net was made of canvas instead of netting and the conical part of fine-meshed bolting-silk (77 strands in 1 cm.). An ordinary townet bucket was used. A hand winch was used for hauling the net, the rate at first being kept as nearly as possible to half a metre per second, which approximates to that given by Ostenfeld and Jespersen. Later, as the meshes of the net became smaller with use, allowance was made for the reduced filtration and more time was taken for hauling.

The first hauls were taken on September 3rd, 1931, and continued at approximately fortnightly intervals until September 5th, 1932, a final haul being made on October 30th. At Station I extra hauls were taken when possible from March to June, making the intervals between hauls approximately a week. At the time of taking each haul notes were made of the depth of the haul, time of day, and of the time taken to haul the net from the bottom to the surface (Table I). The condition of sea and sky, and approximate force and direction of the wind were also noted.

Each station was visited at approximately the same time of day throughout the year. In a few cases, owing to weather conditions or other factors, this was not possible.

The catches were preserved in 5% formalin at the time of taking and later sorted and counted in the laboratory. For counting, Russell's modification of Bogorov's counting tray was used and found very satisfactory. A description of this tray will be found in the Scientific Reports of the Great Barrier Reef Expedition, Vol. II, 2, 1931, p. 24. My thanks are due to Mr. F. S. Russell for procuring this tray for me.

All stages from ovum to adult were counted. It was considered that a count of 1,000 would give a representative sample of the number of different stages present in the catch. In some cases this necessitated taking an aliquot sample of the catch for counting. When this was done the method described by Russell (1925, p. 776) was used. Since the apparatus in use was not identical with that described by him, the method was checked by dividing a catch into ten parts and counting each. The error in sampling was found to be similar to that obtained by Russell (p. 775).

Before examining the results of this work there are one or two points to be borne in mind.

Allowance must be made for the error incurred in using single vertical hauls as the means of obtaining the catches. It has been shown by Gardiner (1931, p. 457) that in 145 hauls, two may be taken which will deviate from the mean by as much as 90% and that occasionally even greater deviation may be expected. He states, however, that variation in the speed of hauling and in the time of day at which the hauls are made does not cause appreciable errors and the conclusion is reached that "the main cause of variation in the size of the catch" is probably due to "lack of uniformity in the distribution of the organisms themselves" (p. 467).

In the course of this investigation over 130 hauls were made of which over 100 were counted and the possibility of "freak" hauls occurring must be taken into consideration. To safeguard as far as possible against the occurrence of such "freak" hauls Gardiner suggests that 5 hauls as a minimum should be taken at each station, since 4 out of 5 will probably confine the deviation to under 40% and "give a value which for all practical purposes may be considered the true one." As he points out this requires much time.

Another factor to be considered is the difficulty of identifying the different nauplius stages and of separating these and the ova from those of other copepods without taking too much time. In most cases this separation could only be done by means of measurements, which must always be approximate owing to the variation in size of the individuals of each particular stage. The ova and nauplii of Pseudocalanus closely resemble those of Calanus and even the difference in size is not marked thus early in the life history. The figures for the nauplii, therefore, must not be regarded as being as accurate as those for the copepodites.

The initial difficulty of identification of the nauplii of Calanus was overcome with the assistance of Dr. M. V. Lebour, to whom I am indebted for sending me specimens of such nauplii from the English Channel.

Variations in the depth from time to time at different stations has not been regarded as important and no allowance has been made for such variation.

It is with pleasure that I take this opportunity of expressing my thanks to my colleagues, Miss S. M. Marshall and Mr. A. P. Orr, for much practical assistance from time to time.

Results.

In the charts, Plates I and II, will be seen the variation in the population of Calanus in this area from September, 1931, to September, 1932. The results obtained from each of the three stations counted are shown, expressed as total numbers in Plate I and as percentage composition in Plate II. Details of catches at all stations will be found in Tables II, III, IV, and V.

Owing to the considerable variation in total numbers it was impossible in Plate I to represent the individual stages separately throughout, so the Calanus were divided into four groups, ova, nauplii, copepodite stages, and adults. In the case of the percentage chart it was found necessary to group only the nauplii (I–VI) and the copepodite Stages I–III, each of the others being given individual representation.

On examining the total numbers curve for Station I (Garroch Head) it will be seen that numbers were low in September and decreased further through the autumn and early winter and it was not until the end of March that an increase occurred. This was of short duration. Numbers then increased suddenly at the end of April and through May, thereafter falling away steadily to reach a constant level in August. A final haul taken at the end of October showed little change.

Turning now to the percentage chart (Plate II) for this station it will be seen that Stage V copepodites formed the bulk of the catch through the autumn and early winter. During October and November ova, nauplii, and young copepodites formed a large percentage, but were very small in actual numbers and not sufficient to make any marked increase in total numbers. At the end of December the Stage V copepodites began to moult into adults, the maximum percentage of males being attained at the beginning of February, the largest actual number having occurred a fortnight earlier. Females attained their maximum number and percentage on February 22nd.

As will be seen from Table II the ova and nauplii found in January were relatively unimportant though representing a fair proportion on the percentage chart. There were no ova or nauplii on February 8th, but on 22nd 84 ova were found, representing 57% of the catch, females amounting to 37%. From this time onwards there followed a regular sequence of ova, nauplii, copepodites, and adults.

The adults which had moulted from the autumn-winter stock of Stage V copepodites died out early in March to be replaced shortly after by their own offspring which, liberated as ova soon after February 8th, appeared as adults soon after March 7th. Through April and May these in turn produced ova which began to reach maturity in May and June. From the middle of May until the end of June this second brood liberated eggs which grew to maturity, the later ones remaining as Stage V copepodites. Further successive small broods of ova in July and August added to the number of Stages IV and V copepodites which were to carry the stock over the autumn and early winter.

Total numbers at Station II (Cock of Arran) in September, 1931, were over 2,000, i.e. higher than those of Station I, and maintained a fairly high average (over 3,000) until the end of November, by which time a considerable and real fall off in numbers was observable, 1,000 being reached on only one occasion after that time until breeding had started in the spring.

On May 2nd numbers increased to over 40,000 from having been under 500 on April 18th, to be followed by as sudden a fall to below 4,000 a fortnight later. From this date numbers showed a gradual fall to the end of June, followed by a gradual rise to the end of September, maintaining an average of just over 2,000 for the period. The average had fallen to under 1,000 by the end of October.

It will be seen from Plate II that, as at Station I, through the autumn and early winter nearly 90% of the Calanus present were Stage V copepodites with a small percentage of Stage IV and a very few adults. Moulting of these Stage V copepodites started at the same time as at Station I, both males and females attaining their greatest numbers on February 8th.

Ova appeared shortly after January 25th and from February 8th until 22nd increased rapidly in number, falling off again to March 7th. These ova appeared as adults from March 7th until early in May. On April 18th an increase in the number of ova was again noticeable which was followed by the extraordinary increase of May 2nd, when over 34,000 ova and about 5,000 nauplii were estimated to be present. These as quickly disappeared, leaving only about 900 ova, 1,300 nauplii, and 1,500 copepodites.

For the next two months the number of ova was fairly constant, but the number of nauplii and copepodites fell off so that in the latter half of June a third noticeable increase is represented in the percentage chart for this station. Through July and August the number of Stage V copepodites moulting into adults decreased, resulting in an increase in the number of copepodites to form, as at Station I, the autumn-winter stock.

At Station IV (Strachur) the numbers of Calanus (mainly Stage V copepodites) averaged 10,000 for the first six weeks of this investigation. They then fell away steadily from November to March, by which time the survivors had all become adults, which as at Stations I and II first appeared at the end of December and attained maximum numbers on February 8th ; the males far outnumbered the females all the time (see Table IV).

It is impossible to follow the sequence of events at Stations V, VI, and VII, where hauls were taken only quarterly. The figures for these stations, however (Table V), show no striking disagreement with those for other stations at the times when these hauls were taken, except that in winter numbers were usually much lower.

Discussion.

The most striking features in the chart showing total numbers (Plate I) are : firstly, a fairly high number of Calanus present at the beginning of the autumn, gradually falling away to a minimal value, well under 500 in every case, at the time when reproduction is starting in the spring ; secondly, the coincidence of large catches from the two stations in open waters (I and II) on May 2nd ; thirdly, the disappearance of this sudden increase ; and fourthly, the smaller number of Calanus present in September, 1932, compared with the same time in the previous year.

Noticeable features of the percentage chart (Plate II) are the homogeneity of the Calanus population during the autumn and winter at two stations in particular (II and IV) ; the appearance of three successive and well marked breeding periods at all three stations, coincident at I and II and the first slightly delayed and overlapping the second at Station IV; and the accumulation of copepodites of Stages IV and V, particularly the latter, at all stations after the middle of July.

This minimum, occurring towards the end of winter, seems to be of general occurrence and has been found by several investigators working on Calanus. Farran (1927, p. 142) investigating the same problem off the south-west coast of Ireland found a minimum in March. Ruud (1929, p. 78) studying the copepod population off the coast of Norway also found the number of Calanus to be at a minimal value in March and the recent work of Sömme (1933, p. 32) confirms this. At Station I in this area Calanus were very scarce from November to the beginning of March. At Station II low numbers were recorded from January until March, the actual minimum falling early in the latter month; but at Station IV numbers did not reach low values until the beginning of March and the minimum was delayed until April, by which time numbers were increasing at the other stations.

The low numbers found by Sömme at the end of March are ascribed to a definite migration of Calanus towards the surface early in March, after which they were carried away by surface currents. This can scarcely be the cause in the Clyde Sea-Area since it has been shown that currents can play little part in such an enclosed area. Moreover, any outward migration from Loch Fyne would have been detected at Stations II and III as explained below.

Natural mortality, possibly directly connected with food supply, will account for the steady decrease in numbers through the course of the winter leaving comparatively few females to produce the first brood which is, consequently, small in numbers compared with later broods.

Farran (1927, p. 137) found that in January males were more abundant than females and that in the following month females were in excess. This was apparent at Stations I and II though numbers were low; at Station IV males were more numerous than females right through this period, and it was not until April 18th, when the new brood had developed, that females noticeably outnumbered males.

The result, then, of this gradual moulting of the autumn-winter stock of Stage V copepodites was the production of a brood of ova, small in numbers compared with later broods, which gave rise to a new brood of adults, mainly females. These appeared through March and April (see Plate II). It was these adults which produced the extraordinary increase at Stations I and II at the beginning of May, to which reference will be made later.

We must here take into consideration the probable life of a single

Calanus ; the time taken for the development of the ovum to the adult ; and the probable number of ova produced by one female.

From an inspection of the percentage chart (Plate II) and Table III showing numbers throughout the year at Station II, it will be seen that by March 7th males, females, and Stage V copepodites of the autumn-winter stock have disappeared completely from the catch, their places being taken by younger stages which they have themselves produced. This clearly indicates that all the fifth copepodites of the autumn-winter stock moult or die at this time and that those which reach maturity, having spawned, die also. Gran (Paulsen, 1906) and Damas (1905) concluded that the individuals normally died after breeding.

This limits the life of a Calanus to one year, but in all probability it is much less. On examining the column of numbers for females for Station I (Table II) it will be seen that from December 29th to February 22nd they increase from 1 to 55, falling away rapidly to 1 at March 7th. This is followed by a sudden increase to 62 by March 21st, rising gradually to 99 on April 18th and falling away again a fortnight later to 47. This is, in turn, followed by a sudden increase to 104, rising to 757 on May 23rd and falling with fluctuations to 15 on June 13th. Once more this is followed by a sudden rise to 205 on June 27th with a fall to the end of July and a sudden drop thence to August 8th, after which the numbers remain steadily low. A similar state of affairs is observable at the two other stations.

The conclusion is that though the adult life of the females from the autumn-winter stock may be nine weeks, for succeeding broods it is not more than 6 or 7 weeks.

The results from Station I (Plate II) show that from March 7th until 21st females increased rapidly (1 on 7th to 62 on 21st), corresponding with the increase in the number of ova from February 8th to 22nd (0 on 8th to 84 on 22nd). This indicates a maximum period of 28 days for the development of the ova to adults at this time of year. The ova and nauplii present before February 8th were insignificant in number and may be neglected.

Subsequent experimental work carried out in the laboratory (jointly with Miss S. M. Marshall) confirmed the view that four weeks was the maximum time required for the ova to reach maturity.

Calanus of different stages were kept each in a separate beaker, the sea-water of which was changed daily and the Calanus examined. The temperature was kept as close as possible to that of the sea at the time (June, July, and August), by standing the beakers in shallow tanks through which sea-water was circulating. It was assumed that each Calanus would find sufficient food for its daily requirements in 250 c.c. of sea-water. Each specimen was kept until it had moulted at least twice so that the interval between each successive stage in its development could be fixed. Females were kept and the time noted from the shedding of the ova to the appearance of nauplii. It was difficult to distinguish the different nauplii while living, so the time taken to pass through the nauplius stages was taken from the shedding of the ova to the appearance of the first copepodite. The minimum time was eleven days. Each of the successive moults up to Stage V occurred at minimal intervals of 3 days, and the shortest interval between the Stage V copepodite and the adult was 4 days. It will be seen that when the shortest intervals are added together 27 days are required for the complete development from the egg to the adult.

Ruud (1929) found that in the Norwegian Sea Calanus took about 3 months for its entire development. Lebour (1916) states: "Nauplii first appeared between the 17th and 24th of April, and on May 19th Stage V was taken from the jar, having taken certainly less than two months to grow from the egg to this stage." This shows close agreement with the results obtained in this region, and it must be remembered that the slower development in the Norwegian Sea is probably correlated with a lower temperature.

We have now two and a half months as the probable life of a single Calanus during the active breeding periods of spring and summer; one month in which to reach maturity and six weeks of adult life. But the Calanus produced towards the end of the breeding season will live through the autumn and winter until early the next spring, with a life of 5 or 6 months.

There seems to be no record of the number of ova produced by one female Calanus, neither has it been possible to obtain this information experimentally. Referring to the figures in Tables II, III, and IV and correlating the number of females on any particular date with the number of eggs on the same date we find a variation of from 1 to 120 eggs per female. It is probable that the number of eggs liberated by any one female is from 60 to 70, with larger numbers occurring occasionally. It seems possible, also, from observations on the copepod *Euchæta norvegica* (as yet unpublished) that each female can produce more than one brood of ova.

Reference has been made to the striking increase in the number of Calanus which was found on May 2nd. On this date at both outside stations (I and II) extraordinarily large catches of Calanus were obtained,

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EXPLANATION OF PLATES.

PLATE I.—Chart showing the changes in total numbers and composition of the population of *Calanus finmarchicus* at three positions in the Clyde Sea-Area for one year.

PLATE II.—Chart showing the changes in the percentage composition of the population of *Calanus finmarchicus* at three positions in the Clyde Sea-Area for one year.

PLATE I.

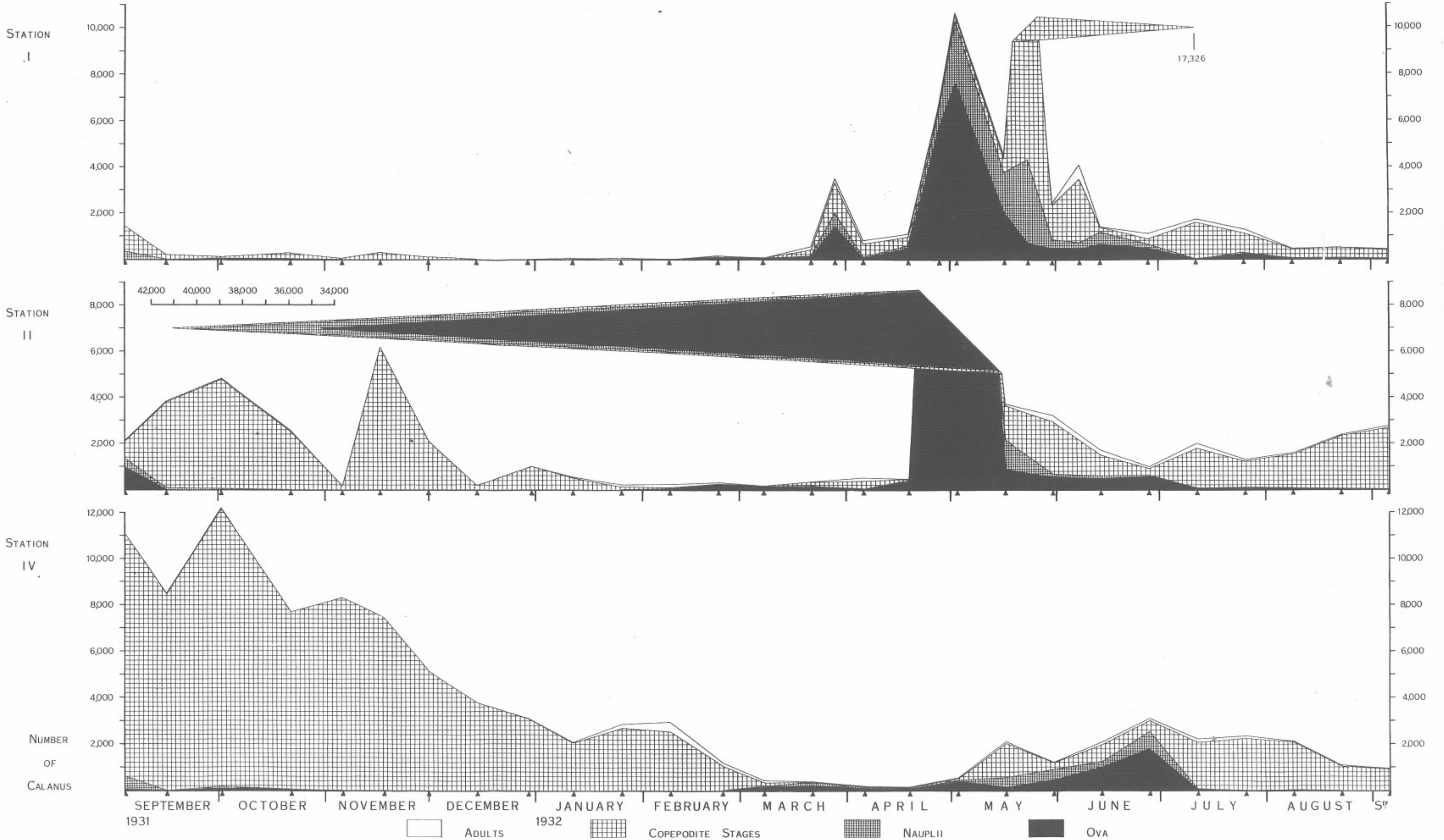
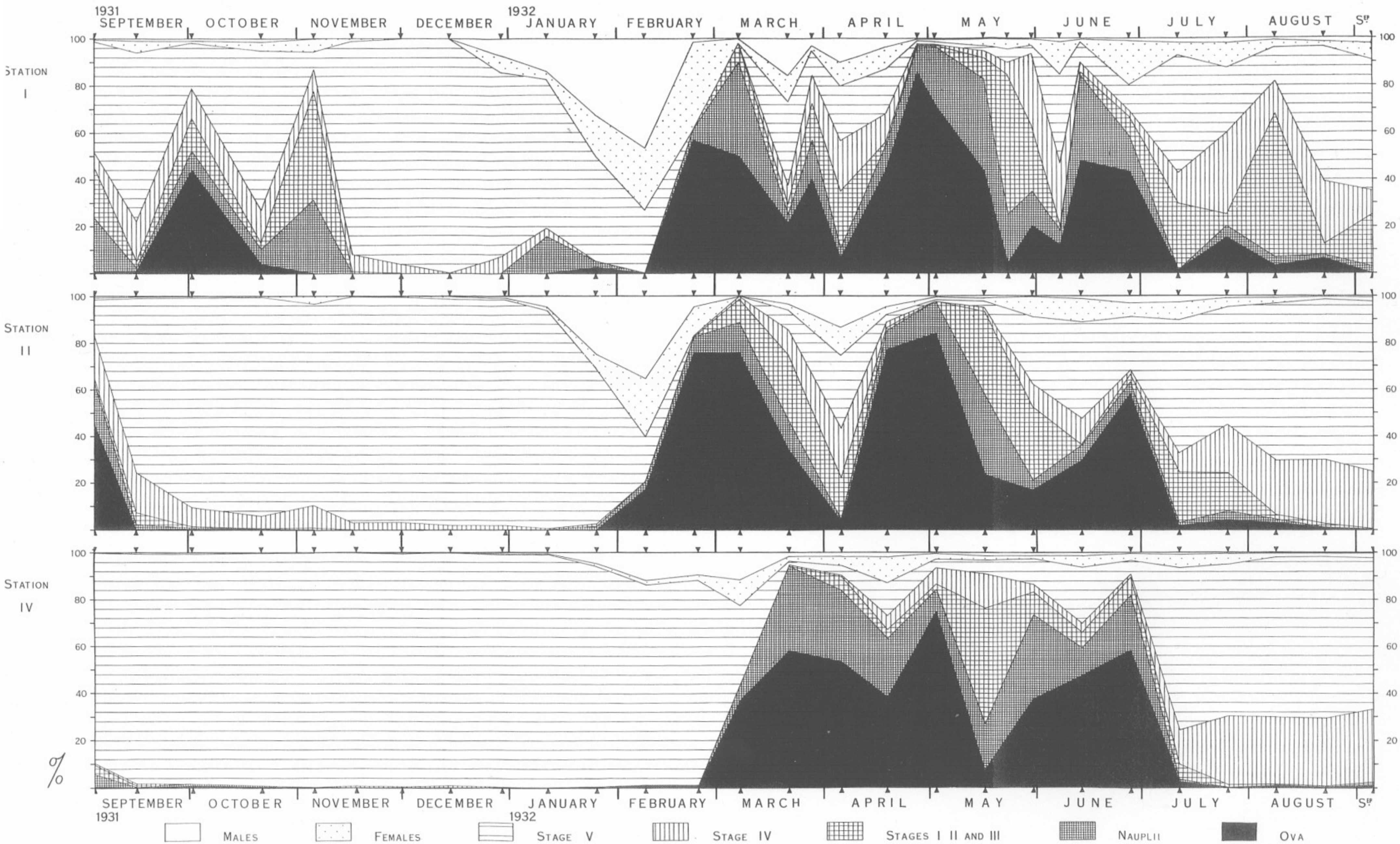

STATION I
10,000
8,000
6,000
4,000
2,000
17,326
STATION II
8,000
6,000
4,000
2,000
42,000 40,000 38,000 36,000 34,000
STATION IV
12,000
10,000
8,000
6,000
4,000
2,000
NUMBER OF CALANUS
SEPTEMBER 1931
OCTOBER
NOVEMBER
DECEMBER
JANUARY 1932
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
S^R
ADULTS
COPEPODITE STAGES
NAUPLII
OVA

PLATE II.


1931
SEPTEMBER
OCTOBER
NOVEMBER
DECEMBER
1932
JANUARY
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEP
STATION I
STATION II
STATION IV
100
80
60
40
20
%
SEPTEMBER
1931
OCTOBER
NOVEMBER
DECEMBER
JANUARY
1932
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEP
MALES
FEMALES
STAGE V
STAGE IV
STAGES I II AND III
NAUPLII
OVA

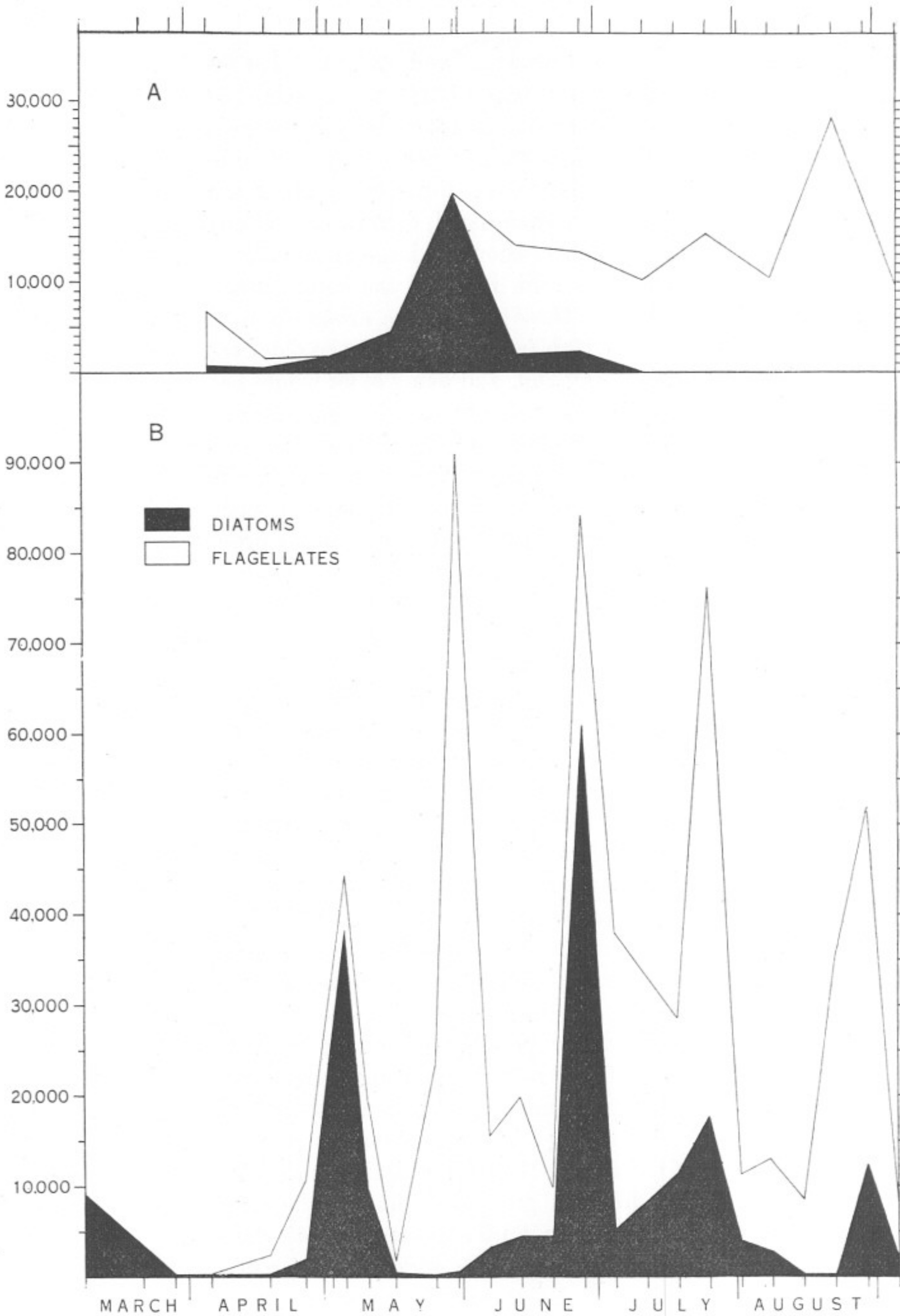
numbering over 10,000 at Station I and over 41,000 at Station II. Three weeks later another large catch (17,326) was obtained at Station I. In the first two cases this was due to a very large increase in the number of ova (with a ratio of not more than 70 per female) and an increased number of nauplii derived from these ova. Copepodite stages and adults, though present in numbers larger than usual, formed only a small percentage of the catch. On the second occasion of a large catch (May 23rd at Station I) copepodite stages formed the mass of the catch, Stages I, II and III being most abundant. These must have arisen from the ova liberated between May 2nd and 16th (about 9th) and the older copepodites would have been ova about May 2nd, and being older would have suffered more from natural mortality, the rate of which is high (p. 89).

Taking into account the length of life of the ovum as such and the time passed by Calanus in its nauplius stages, it is possible to say that, with one exception, at no time in the year were more copepodites found than could have been produced from the ova or nauplii present the requisite length of time before. The following hypothetical case may make this clear. If 10,000 ova were present on a certain date and 20,000 Stage II copepodites were found a fortnight later it might be argued that so many copepodites could not arise from so few ova and that, therefore, immigration must have occurred from some other locality where reproduction was in progress. It must be remembered, however, that whereas the ova remain as such for not more than 24 hours (Grobben, 1881) the copepodites remain in each stage for 3 days, and the effect will be an accumulation of copepodites. These will, of course, be subject to mortality.

The one exception referred to above occurred at Station I on May 16th when too few nauplii were present to produce the copepodites of May 23rd. This catch will have to be accepted as a "freak," since the number of ova present early in May was ample to produce the copepodites of 23rd.

At both stations the enormous increase found on May 2nd was of a temporary nature and died away as quickly as it had risen. This points to a very large mortality possibly correlated with the food supply. Farran (1927, p. 139) found reproduction was occurring generally in April and May, at which time numbers rose to ten times what they had been a few months before. Bigelow (1926, p. 168) records similar sudden increases in the number of Calanus in the Gulf of Maine during May.

Whereas Farran found a gradual decline in the numbers of Calanus subsequent to the increase in April and May, at both stations at which the decline occurred in this area it was sudden. Reference to the work of Marshall and Orr (1927, 1930) will show that the number of diatoms present during the spring increase of 1928 was over 5,000 cells per c.c. for some time and was over 12,500 cells per c.c. for a few days. Similar numbers were found in 1926 and 1927.



Text-Fig. 2.—Chart showing numbers of diatoms and of flagellates in 20 c.c. samples from the surface, A at Strachur and B at Keppel, from March until September, 1932. Other micro-organisms were negligible.

Text-Figure 2 shows the variation in the number of diatoms and in other microplankton at Keppel and at Strachur from March to September, 1932. I am indebted to Miss S. M. Marshall for the information expressed in this figure. It will be seen that though diatoms were spasmodically abundant during the spring and summer, on the whole numbers did not once reach those attained by the phytoplankton in the course of an ordinary spring increase and were, on the average, low for the whole season. The highest value reached at Keppel in 1932 was 3,000 cells per c.c. in June, and the spring increase figures were only 2,000 cells per c.c. It is possible, therefore, that under normal conditions the decline would have been as gradual as that found by Farran, and that the number present in the autumn of 1932 would have been similar to that of 1931.

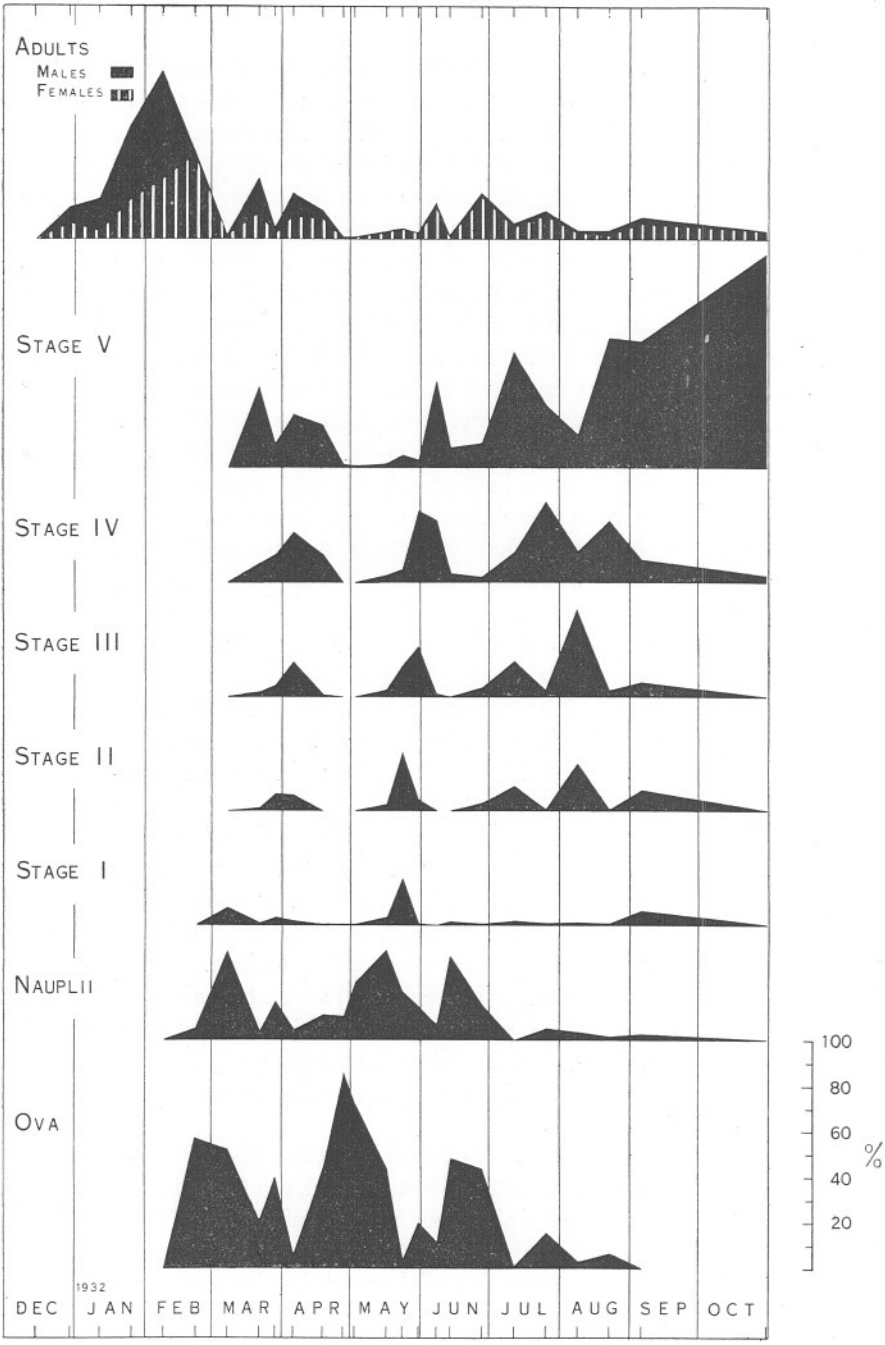
At Strachur (Station IV) diatoms were even less abundant (Text-Figure 2, A) and the Calanus in September, 1932, numbered about 1,000 compared with 10,000 in September of the previous year.

It has already been seen that as autumn approaches development is arrested and the Calanus remain as Stage V copepodites, mixed with a number of Stage IV and a very few adults.

The next point which arises is the appearance of three well defined breeding periods on the percentage composition chart (Plate II). This becomes more marked if the percentage composition of the catch during the reproductive season is separated into different stages and each is graphed individually (Text-Figures 3 and 4 ; in these figures certain details present in the chart, Plate II, which would only tend to confuse the issue, have been left out.) Here is plainly marked the succession of stages from ovum to adult in three successive breeding periods followed by the subsidiary ones at the end of the summer. This is not so obvious at Station IV where the results are confused by the large initial lag and a subsequent overlapping of the first two breeding periods.

The results from Station II (Text-Figure 4) suggest an almost diagrammatic accuracy. Each maximum of females is followed by a maximum of ova, and this maximum can be followed through each stage to adults, which attain their maximum at a month after the maximum of ova, and so on through the summer.

The difficulty which arises is to explain why there should be such a long interval between any maximum of females and the following maximum of ova, the latter actually coinciding with a minimum of females. It appears that the Calanus, having moulted into adults, require from three weeks to one month for maturation of the reproductive organs and for the transference of the spermatophores to the females, and that meanwhile they are subject to a high rate of mortality so that by the time that sexual maturity is reached comparatively few females remain. Thus the egg peak would coincide with the female minimum. The number of



TEXT-FIG. 3.—Diagram illustrating the succession of breeding periods at Station I (Garroch Head). Copepodite Stages IV and V occurring prior to February 22nd and ova and nauplii prior to February 8th have been omitted.

females then rises again a month later when these ova have completed their development.

This explanation appears satisfactory in its general application. If, however, we examine the curve for Station I (Plate II and Text-Figure 3) we find a number of inconsistencies with this hypothesis. Firstly, a secondary peak of ova is present at the end of the first breeding period. If this were the result of an almost immediate liberation of ova from these females which reached maturity on March 21st, it would leave only one week for the maturation of the reproductive organs and fertilisation of the females. This would appear to be too short, and, moreover, would result in continuous breeding throughout the reproductive season and a more or less constant representation of all stages throughout this period.

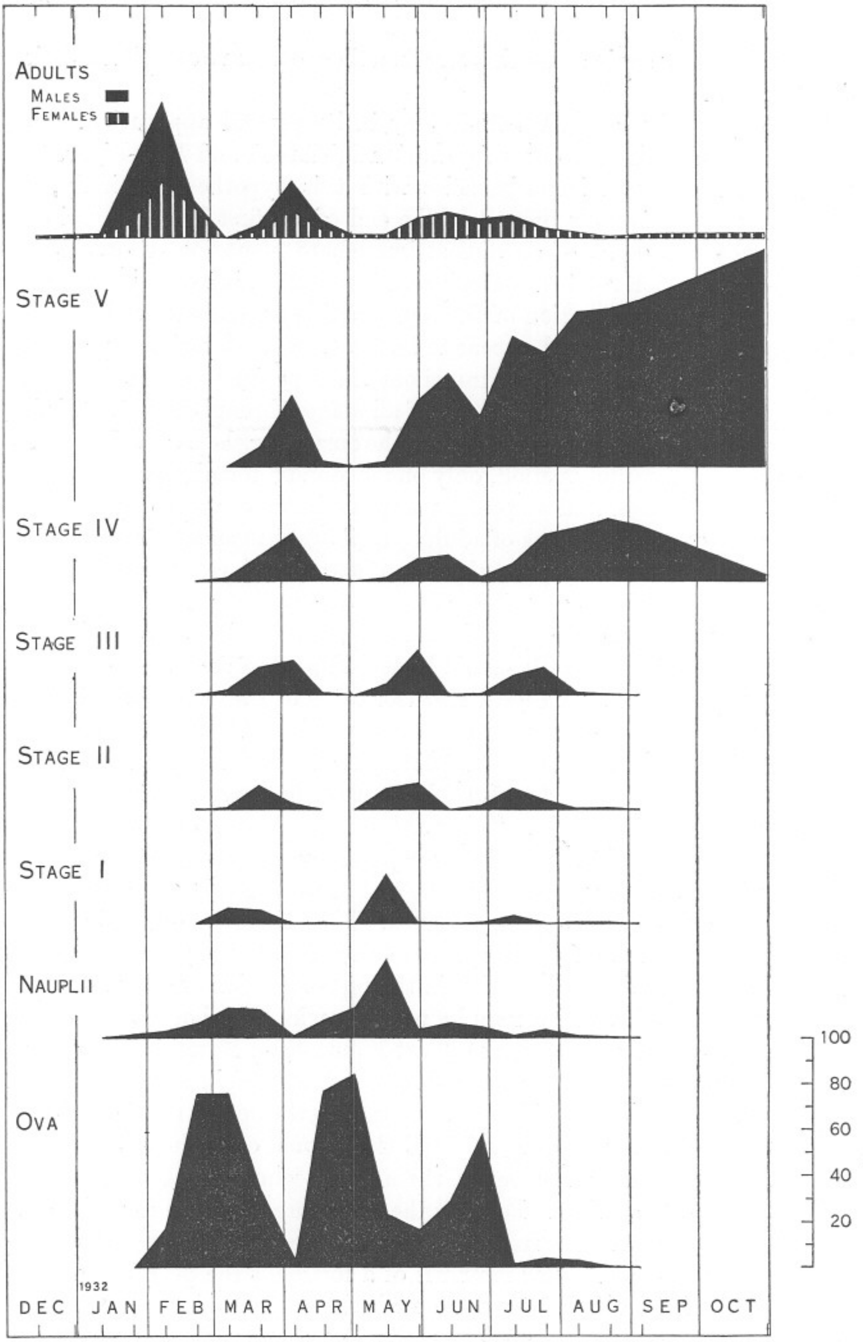
Though two peaks are thus present in the curves for the ova and nauplii during the first breeding period, only one is found a fortnight later in the Stage II copepodites, and a second reappears in the Stage V copepodites and adults. The second peak of adults (April 5th) has undoubtedly arisen from the ova of March 7th, and the ova of March 28th receive no distinct representation on these curves after Stage I copepodites ; neither do they appear to affect the curve for adults at all, these being at a minimum when the eggs of March 28th should be reaching adult stage.

From Table II it would appear that this catch of March 28th was in the nature of a "freak"—owing to the net passing through a swarm of Calanus—since, from March 7th until April 18th (neglecting March 28th), total numbers rose from 52 to 1,086 by more or less regular intervals of a few hundred each fortnight. This catch on March 28th contained 3,488 specimens and may be regarded as exceptionally and unexpectedly large.

A similar effect was produced at the end of the second breeding period (May 30th) when a minor peak occurred. It is, however, of less importance since it does not affect the curves of any of the other stages and may be regarded as a minor fluctuation in the representation of the ova.

A further question which may be raised is why ova should be present to so large an extent at Station II (Text-Figure 4) on March 21st if adults had died out by 7th and the new brood did not begin spawning until April 5th. From Table III it will be seen that the actual number of ova present on this date was only 117, and these could easily have been produced by two or three females of the autumn-winter stock which were still surviving at this time. Possibly they were producing a second brood.

It will have been seen from the Text-Figures and Plates that when catches are taken at regular intervals of a fortnight the period of reproduction can be divided into three main breeding periods, February–March, April–May, and June–July with a fourth subsidiary one early in August and that this can be applied in general to all stations. The main variations are in the number of subsidiary late summer broods at each



TEXT-FIG. 4.—Diagram illustrating the succession of breeding periods at Station II (Cock of Arran). Copepodite Stages IV and V occurring prior to March 7th, and ova and nauplii prior to February 8th have been omitted.

station (more numerous at Station I and of less importance at Station IV), and an overlapping of the first two breeding periods at Station IV owing to a lag in the starting of reproduction at this station. The cause of this has not yet been determined.

Comparison of the station inside the loch with those of the open waters showed that Calanus was still quite abundant in the early winter at Strachur when numbers outside had fallen to minimal values. This, however, was only a lag in the dying off of this population, since numbers in the loch were reduced to similar low values at a later date. Although Calanus at Station I was scarce by the middle of December it was not until late in March that it became scarce at Station IV. This lag was followed by a delay in the starting of reproduction, the first brood of eggs not appearing until the end of February, a fortnight after reproduction had begun at the stations in open waters.

Furthermore it can be stated that the enclosed waters of the loch do not form a breeding ground whence Calanus spreads to outside waters. If this had been the case evidence of such migration would have been found in the quarterly catches from Station VII and in the fortnightly catches from Station III. Those from the latter obviously followed those of Station II, and it has already been pointed out that both these stations are geographically similar.

Without more knowledge of the factors which control the development of the autumn-winter Calanus it is difficult to say why this lag occurred. That temperature is not directly concerned is fairly certain. It remains for future work to discover the actual cause.

It will have been seen that the results from this area confirm and elaborate the suggestions made by Farran (1911, p. 85) and Russell (1928, p. 444) on the course of the life cycle in Calanus.

It has been pointed out by Russell (1928, p. 434) that at certain times of the year Calanus may be found swarming at the surface during the day, even though it be a clear day with bright sunshine. This has been observed on several occasions in the Clyde Sea-Area. From March until June, and again later on, hauls at Stations I and II were divided at the 30-metre line, the object being to simplify counting by confining the diatoms to one part of the catch.

As it happened in this year diatoms were seldom rich enough to cause any difficulty of this nature. It will be noticed, however, from Tables II and III that at Station I on May 16th and at Station II on June 13th, more males, females, Stages V and IV copepodites were found in the upper 30 metres than below, a reversal of the usual condition. On both these occasions young stages and ova remained more abundant above the 30-metre line.

This will be discussed in a paper dealing with the vertical distribution of Calanus in this area.

SUMMARY.

1. Fortnightly samples were taken with a fine-meshed net in single vertical hauls at different positions in the Clyde Sea-Area.

2. Each stage of Calanus present, from ovum to adult, was counted, and charts were constructed expressing these results for one year as total numbers and as percentage composition.

3. Calanus passes the autumn and early winter mainly in its Stage V copepodite form.

4. In general, total numbers were high in September, 1931, and fell steadily to a minimum in March ; in Loch Fyne the minimum occurred in April.

5. A sudden increase was observed in May and numbers rose to maximal values ; the decline also was sudden.

6. Reproduction began in February and three plainly marked breeding periods were observed between February and July.

7. The time taken by the egg in developing into the adult was four weeks.

8. The total life of a Calanus during the summer was estimated to be about two and a half months ; in winter it is five to six months.

9. In Loch Fyne a noticeable lag occurred during the winter and early spring.

10. The number of Calanus present in the autumn of 1932 was considerably less than at the same time in 1931. This may have been due to a shortage of food.

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TABLE I.

Date.	Station I.			Station II.			Station IV.		
	Time of Day. a.m.	Depth in Metres.	Time of Haul. m. s.	Time of Day. a.m.	Depth in Metres.	Time of Haul. m. s.	Time of Day. p.m.	Depth in Metres.	Time of Haul. m. s.
3/9/31	10.00	120	—	11.30	100	—	5.20	138	—
15/9/31	9.45	105	3 20	11.25	140	4 00	5.15	130	4 30
1/10/31	9.45	110	3 35	11.30	140	3 50	4.30	150	3 50
21/10/31	9.45	120	*4 15	11.15	135	4 15	5.00	130	4 30
5/11/31	10.35	115	3 45	noon	112	3 35	4.50	132	4 20
16/11/31	10.30	109	3 40	11.40	165	4 50			
17/11/31							8.27 (a.m.)	136	4 15
30/11/31	9.15	110	3 45	10.50	155	4 50	4.15	130	4 50
14/12/31	9.26	110	4 05	11.15	154	4 20	4.32	131	5 ca.
30/12/31	9.05	113	3 45	10.10	160	5 30	5.10	128	3 40
11/1/32	9.50	120	4 00	11.30	155	3 50	4.15	129	4 15
25/1/32	9.10	120	4 00	10.30	165	5 30	3.50	134	4 05
8/2/32	9.50	110	*3 50	11.10	170	5 45	4.45	130	4 15
22/2/32	9.05	109	3 45	10.15	153	5 30			
23/2/32							8.00 (a.m.)	—	4 40
7/3/32	9.15	110	(a)3 05 (b)1 00	10.55	154	(a)4 50 (b)1 00	4.20	128	4 10
21/3/32	10.20	115	(a)3 00 (b)1 00	11.00	161	(a)6 45 (b)1 27	4.30	126	4 45
28/3/32	9.30	110	(a)4 03 (b)1 00						
5/4/32	9.15	109	(a)3 20 (b)1 00	11.15	162	(a)5 10 (b)1 00	5.00	131	4 45
18/4/32	8.20	110	(a)3 05 (b)1 00	9.55	116	(a)3 15 (b)1 00	3.10	131	4 35
27/4/32	8.50	115	(a)3 40 (b)1 25						
2/5/32	9.29	114	(a)3 05 (b)0 56	11.00	157	(a)4 25 (b)0 55	4.42	130	4 15
16/5/32	8.15	113	(a)3 45 (b)1 05	9.50	145	(a)4 35 (b)1 05	3.05	130	5 05
23/5/32	11.00	119	(a)3 45 (b)1 03						
30/5/32	8.20	110	(a)3 00 (b)1 00	9.45	166	(a)5 35 (b)1 00	6.30	130	5 15
7/6/32	9.00	118	(a)3 40 (b)1 05						
13/6/32	8.25	115	†4 30	9.55	159	(a)4 30 (b)1 00	3.15	131	5 25
27/6/32	10.20	112	4 55	12.10 (p.m.)	158	7 40	5.25	124	4 30
11/7/32	8.20	113	4 15	10.15	152	5 35	3.50	130	4 45
25/7/32	8.20	115	(a)3 15 (b)1 02	10.10	165	(a)4 55 (b)1 00	3.05	130	4 40
8/8/32	8.20	115	(a)3 10 (b)1 00	10.15	163	(a)4 15 (b)1 00	3.30	135	4 30
22/8/32	8.25	112	3 55	9.55	158	5 45	7.15	130	4 30
5/9/32	8.50	110	4 20	10.15	165	6 50	4.05	130	4 45
30/10/32	9.15	117	3 25	11.00	144	4 50	4.15	122	3 55

APPENDIX.

	Station V.				Station VI.				Station VII.			
					p.m.				a.m.			
13/11/31	11.05 (a.m.)	92	2	50								
16/11/31					2.00	145	3	40				
17/11/31									10.25	60	1	45
22/2/32					12.20	125	3	35				
23/2/32									10.05	51	1	40
25/2/32	3.35 (p.m.)	89	3	30								
30/5/32					noon	117	(a)3 (b)1	25 00	p.m. 4.50	59	2	00
3/6/32	9.40 (a.m.)	90	(a)2 (b)1	25 00								
22/8/32					12.30	128	4	58	5.30	62	2	30
29/8/32	3.00 (p.m.)	88	3	20								

* Indicates that the haul was not vertical owing to state of the weather.
† Indicates that the closing apparatus failed to work and haul was not divided.

TAB

STAT

Date.		Ova.	I.	II.	Nauplii. III.	IV.	V.	VI.
3-9-31	No.	10	30	110	60	30	20	80
	%	*·7*	*2·1*	*7·6*	*4·2*	*2·1*	*1·4*	*5·5*
15-9-31	No.	1	–	–	1	2	–	–
	%	*·5*	–	–	*·5*	*1·0*	–	–
1-10-31	No.	50	2	1	3	3	–	–
	%	*44·2*	*1·8*	*·9*	*2·7*	*2·7*	–	–
21-10-31	No.	12	11	2	6	–	–	–
	%	*4·0*	*3·7*	*·7*	*2·0*	–	–	–
5-11-31	No.	–	1	–	5	6	2	3
	%	–	*1·9*	–	*9·3*	*11·1*	*3·7*	*5·6*
16-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
30-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
14-12-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
29-12-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
11-1-32	No.	–	2	–	7	–	–	–
	%	–	*3·5*	–	*12·1*	–	–	–
25-1-32	No.	1	–	–	1	–	–	–
	%	*2·5*	–	–	*2·5*	–	–	–
8-2-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
22-2-32	No.	84	4	–	2	1	–	–
	%	*56·8*	*2·7*	–	*1·4*	*·7*	–	–
7-3-32	No. (1)	8 } 27	– } 3	–	– } 5	2 } 5	– } 2	2 } 5
	(2)	19	3	–	5	3	2	3
	%	*51·9*	*5·8*	–	*9·6*	*9·6*	*3·8*	*9·6*
21-3-32	No. (1)	70 } 116	10 } 11	–	– } 2	– } 2	– } 1	– } 4
	(2)	46	1	–	2	2	1	4
	%	*21·0*	*2·0*	–	*·4*	*·4*	*·2*	*·7*
28-3-32	No. (1)	250 } 1400	30 } 160	– } 185	10 } 140	5 } 40	– } 25	5 } 35
	(2)	1150	130	185	130	35	25	30
	%	*40·1*	*4·6*	*5·3*	*4·0*	*1·1*	*·7*	*1·0*
5-4-32	No. (1)	30 } 49	15 } 17	– } 1	– } 5	5 } 8	– } 2	– } 3
	(2)	19	2	1	5	3	2	3
	%	*6·0*	*2·1*	*·1*	*·6*	*1·0*	*·2*	*·4*
18-4-32	No. (1)	60 } 480	5 } 30	– } 35	– } 45	– } 5	– } 5	–
	(2)	420	25	35	45	5	5	–
	%	*44·1*	*2·8*	*3·2*	*4·1*	*·5*	*·5*	–
27-4-32	No. (1)	138 } 5708	90 } 450	– } 200	– } 20	– } 20	– } 10	1 } 21
	(2)	5570	360	200	20	20	10	20
	%	*85·3*	*6·7*	*3·0*	*·3*	*·3*	*·1*	*·3*
2-5-32	No. (1)	14 } 7649	15 } 1800	– } 475	– } 215	1 } 101	– } 30	– } 55
	(2)	7635	1785	475	215	100	30	55
	%	*71·8*	*16·9*	*4·5*	*2·0*	*·9*	*·3*	*·5*
16-5-32	No. (1)	64 } 1984	4 } 424	10 } 640	7 } 377	3 } 203	1 } 41	2 } 92
	(2)	1920	420	630	370	200	40	90
	%	*43·7*	*9·3*	*14·1*	*8·3*	*4·5*	*·9*	*2·0*
23-5-32	No. (1)	340 } 700	150 } 210	90 } 130	960 } 1170	790 } 930	560 } 670	450 } 520
	(2)	360	60	40	210	140	110	70
	%	*4·0*	*1·2*	*·7*	*6·8*	*5·4*	*3·9*	*3·0*
30-5-32	No. (1)	370 } 488	324 } 337	2 } 11	4 } 5	–	–	–
	(2)	118	13	9	1	–	–	–
	%	*20·2*	*13·9*	*·5*	*·2*	–	–	–
7-6-32	No. (1)	95 } 465	75 } 175	– } 25	– } 30	– } 20	– } 5	–
	(2)	370	100	25	30	20	5	–
	%	*11·4*	*4·3*	*·6*	*·7*	*·5*	*·1*	–
13-6-32	No.	670	270	60	90	70	20	–
	%	*47·9*	*19·3*	*4·3*	*6·4*	*5·0*	*1·4*	–
27-6-32	No.	475	80	20	15	20	15	15
	%	*43·4*	*7·3*	*1·8*	*1·4*	*1·8*	*1·4*	*1·4*
11-7-32	No.	20	–	–	–	–	–	–
	%	*1·2*	–	–	–	–	–	–
25-7-32	No. (1)	10 } 195	– } 15	– } 10	5 } 35	–	–	–
	(2)	185	15	10	30	–	–	–
	%	*15·4*	*1·2*	*·8*	*2·8*	–	–	–
8-8-32	No. (1)	9 } 15	– } 1	– } 2	– } 7	– } 2	– } 2	– } 3
	(2)	6	1	2	7	2	2	3
	%	*3·2*	*·2*	*·4*	*1·5*	*·4*	*·4*	*·6*
22-8-32	No.	33	2	1	–	–	1	3
	%	*6·5*	*·4*	*·2*	–	–	*·2*	*·6*
5-9-32	No.	–	–	–	–	–	–	11
	%	–	–	–	–	–	–	*2·7*
30-10-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–

LE II.

ION I.

Copepodites. I.	II.	III.	IV.	V	Adults. ♀	♂	Total.
95 *6·6*	127 *8 8*	79 *5·5*	103 *7·0*	677 *47·0*	13 *·9*	7 *·5*	1441 *99·9*
– –	1 *·5*	5 *2·5*	35 *17·2*	147 *72·1*	10 *4·9*	2 *1·0*	204 *100·2*
1 *·9*	11 *9·7*	4 *3·5*	14 *12·4*	22 *19·5*	1 *·9*	1 *·9*	113 *100·1*
– –	1 *·3*	7 *2·4*	41 *13·8*	203 *68·1*	11 *3·7*	4 *1·3*	298 *100·0*
5 *9·3*	4 *7·4*	16 *29·7*	5 *9·3*	4 *7·4*	3 *5·6*	– –	54 *100·3*
– –	– –	2 *·7*	22 *7·4*	272 *91·0*	3 *1·0*	– –	299 *100·1*
– –	– –	– –	3 *3·7*	77 *96·3*	– –	– –	80 *100·0*
– –	– –	– –	– –	4 *100·0*	– –	– –	4 *100·0*
– –	– –	– –	1 *7·1*	11 *78·6*	1 *7·1*	1 *7·1*	14 *99·9*
– –	– –	– –	2 *3·5*	37 *63·6*	2 *3·5*	8 *13·8*	58 *100·0*
– –	– –	– –	– –	18 *45·0*	7 *17·5*	13 *32·5*	40 *100·0*
– –	– –	– –	– –	4 *26·7*	4 *26·7*	7 *46·7*	15 *100·1*
– –	– –	– –	– –	– –	55 *37·2*	2 *1·4*	148 *100·2*
2, 2 } 4 *7·7*	– – –	– – –	– – –	– – –	1, – } 1 *1·9*	– – –	15, 37 } 52 *99·9*
–, 5 } 5 *·9*	6, 2 } 8 *1·5*	9, 2 } 11 *2·0*	44, 1 } 45 *8·2*	192, 2 } 194 *35·5*	59, 3 } 62 *11·4*	82, 3 } 85 *15·6*	472, 74 } 546 *99·8*
–, 121 } 121 *3·5*	3, 254 } 257 *7·4*	73, 95 } 168 *4·8*	393, 25 } 418 *12·0*	352, 12 } 364 *10·4*	74, 1 } 75 *2·2*	98, 2 } 100 *2·9*	1293, 2195 } 3488 *100·0*
1, 14 } 15 *1·9*	1, 54 } 55 *6·8*	5, 123 } 128 *15·7*	60, 117 } 177 *21·8*	135, 56 } 191 *23·5*	75, 6 } 81 *10·0*	57, 24 } 81 *10·0*	384, 429 } 813 *100·1*
–, 3 } 3 *·3*	– – –	6, 3 } 9 *·8*	120, 11 } 131 *12·0*	185, 21 } 206 *19·0*	95, 4 } 99 *9·1*	37, 2 } 39 *3·6*	508, 579 } 1087 *100·0*
4, 30 } 34 *·5*	2, 10 } 12 *·2*	– – –	16, – } 16 *·2*	95, 8 } 103 *1·5*	46, 1 } 47 *·7*	16, – } 16 *·2*	408, 6249 } 6657 *99·3*
–, 55 } 55 *·5*	1, 15 } 16 *·2*	–, 1 } 1 –	6, 1 } 7 *·1*	112, 17 } 129 *1·2*	92, 12 } 104 *1·0*	19, 5 } 24 *·2*	260, 10401 } 10661 *100·1*
3, 146 } 149 *3·3*	–, 125 } 125 *2·8*	2, 125 } 127 *2·8*	11, 126 } 137 *3·0*	22, 68 } 90 *2·0*	36, 105 } 141 *3·1*	4, 7 } 11 *·2*	169, 4372 } 4541 *100·0*
2490, 1040 } 3530 *20·4*	3360, 1060 } 4420 *25·5*	1840, 520 } 2360 *13·6*	770, 143 } 913 *5·3*	890, 86 } 976 *5·6*	730, 27 } 757 *4·4*	40, – } 40 *·2*	13460, 3866 } 17326 *100·0*
2, 5 } 7 *·3*	32, 94 } 126 *5·2*	332, 200 } 532 *22·0*	634, 118 } 752 *31·1*	58, 30 } 88 *3·6*	42, 22 } 64 *2·6*	8, – } 8 *·3*	1808, 610 } 2418 *99·9*
–, 5 } 5 *·1*	5, 5 } 10 *·2*	40, 15 } 55 *1·3*	1035, 89 } 1124 *26·9*	1515, 37 } 1552 *38·0*	560, 3 } 563 *13·8*	65, – } 65 *1·6*	3390, 704 } 4094 *99·5*
20 *1·4*	– –	– –	53 *3·8*	125 *8·9*	15 *1·1*	5 *·4*	1398 *99·9*
8 *·7*	39 *3·6*	43 *3·9*	28 *2·6*	120 *11·0*	205 *18·7*	12 *1·1*	1095 *100·1*
32 *1·9*	183 *10·8*	264 *15·6*	219 *13·0*	852 *50·4*	92 *5·4*	28 *1·7*	1690 *100·0*
10, – } 10 *·8*	15, – } 15 *1·2*	37, 1 } 38 *3·0*	430, 11 } 441 *34·8*	342, 9 } 351 *27·7*	129, 5 } 134 *10·6*	24, – } 24 *1·9*	1002, 266 } 1268 *100·2*
1, 6 } 7 *1·5*	76, 23 } 99 *21·2*	171, 9 } 180 *38·4*	59, 5 } 64 *13·7*	63, 4 } 67 *14·3*	13, 2 } 15 *3·2*	4, – } 4 *·9*	396, 72 } 468 *99·9*
6 *1·2*	2 *·4*	15 *3·0*	135 *26·8*	287 *56·9*	10 *2·0*	9 *1·8*	504 *100·0*
26 *6·3*	38 *9·2*	27 *6·6*	42 *10·2*	228 *55·5*	29 *7·0*	10 *2·4*	411 *99·9*
– –	– –	– –	11 *3·1*	329 *93·5*	12 *3·4*	– –	352 *100·0*

TAB

STAT

Date.		Ova.	I.	II.	Nauplii. III.	IV.	V.	VI.
3-9-31	No.	970	–	–	380	–	–	–
	%	45·5	–	–	17·8	–	–	–
15-9-31	No.	–	–	–	79	2	–	1
	%	–	–	–	2·1	·1	–	–
1-10-31	No.	25	–	–	25	–	–	–
	%	·5	–	–	·5	–	–	–
21-10-31	No.	3	–	3	3	–	–	–
	%	·1	–	·1	·1	–	–	–
5-11-31	No.	–	–	–	–	–	–	–
		–	–	–	–	–	–	–
16-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
30-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
14-12-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
30-12-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
11-1-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
25-1-32	No.	–	1	–	2	–	–	–
	%	–	·5	–	1·0	–	–	–
8-2-32	No.	41	6	–	1	–	–	–
	%	17·6	2·6	–	·4	–	–	–
22-2-32	No.	231	8	–	8	1	1	2
	%	76·0	2·6	–	2·6	·4	·4	·7
7-3-32	No. (1)	–	–	–	–	–	–	–
	(2)	119 } 119	4 } 4	4 } 4	4 } 4	5 } 5	1 } 1	·3 } 3
	%	75·8	2·6	2·6	2·6	3·2	·6	1·9
21-3-32	No. (1)	–	–	–	–	–	–	–
	(2)	117 } 117	10 } 10	9 } 9	11 } 11	4 } 4	4 } 4	5 } 5
	%	34·0	2·9	2·6	3·2	1·2	1·2	1·5
5-4-32	No. (1)	4	–	–		–		
	(2)	13 } 17	3 } 3	1 } 1	–	1 } 1	–	–
	%	3·4	·6	·2	–	·2	–	–
18-4-32	No. (1)	33	3	–	–	–	–	–
	(2)	313 } 346	15 } 18	12 } 12	3 } 3	2 } 2	1 } 1	–
	%	77·2	4·0	2·7	·7	·5	·2	–
2-5-32	No. (1)	22	13	1	–	–	–	–
	(2)	34600 } 34622	3920 } 3933	1240 } 1241	190 } 190	70 } 70	50 } 50	50 } 50
	%	84·3	9·6	3·0	·5	·2	·1	·1
16-5-32	No. (1)	506	148	76	92	44	20	28
	(2)	370 } 876	90 } 238	250 } 326	180 } 272	90 } 134	130 } 150	140 } 168
	%	23·6	6·4	8·8	7·3	3·6	4·0	4·5
30-5-32	No. (1)	370	57	–	–			
	(2)	177 } 547	33 } 90	30 } 30	13 } 13	–	–	–
	%	16·9	2·8	·9	·4	–	–	–
13-6-32	No. (1)	178	66	2	–	–	–	–
	(2)	320 } 498	22 } 88	10 } 12	6 } 6	1 } 1	1 } 1	–
	%	29·5	5·2	·7	·4	·1	·1	–
27-6-32	No.	582	32	6	4	–	–	8
	%	58·4	3·2	·6	·4	–	–	·8
11-7-32	No.	31	1	1	7	6	6	6
	%	1·6	–	–	·4	·3	·3	·3
25-7-32	No. (1)	13	3	–	1			
	(2)	40 } 53	16 } 19	12 } 12	16 } 17	–	–	–
	%	4·1	1·5	·9	1·3	–	–	–
8-8-32	No. (1)	19	2	–	–	–		–
	(2)	27 } 46	6 } 8	3 } 3	8 } 8	1 } 1	–	2 } 2
	%	2·9	·5	·2	·5	–	–	·1
22-8-32	No.	14	2	2	2	–	–	–
	%	·6	·1	·1	·1	–	–	–
5-9-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
30-10-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–

LE III

ION II

		Copepodites.			Adults.		
I.	II.	III.	IV.	V.	♀	♂	Total.
–	3	32	387	334	19	10	2135
–	·1	1·6	18·1	15·6	·9	·5	100·1
–	19	179	660	2876	19	8	3843
–	·5	4·7	17·2	74·9	·5	·2	100·2
–	–	20	395	4320	20	5	4810
–	–	·4	8·2	89·9	·4	·1	100·1
–	–	–	135	2398	10	–	2552
–	–	–	5·3	94·0	·4	–	100·0
–	–	1	15	134	5	–	155
–	–	·7	9·7	86·5	3·2	–	100·1
–	–	–	190	5975	10	–	6175
–	–	–	3·1	96·8	·2	–	100·1
–	–	–	64	2038	4	2	2108
–	–	–	3·0	96·7	·2	·1	100·0
–	–	–	3	176	2	–	181
–	–	–	1·7	97·2	1·1	–	100·0
–	–	–	18	968	6	9	1001
–	–	–	1·8	96·8	·6	·9	100·1
–	–	–	3	506	8	25	542
–	–	–	·5	93·5	1·5	4·6	100·1
–	–	–	2	137	13	51	206
–	–	–	1·0	66·5	6·3	24·8	100·1
–	–	–	–	45	58	82	233
–	–	–	–	19·3	24·9	35·2	100·0
–	–	–	–	2	39	12	304
–	–	–	–	·7	12·8	3·9	100·1
–	–	3	2	–	–	–	5
11 } 11	1 } 1	– } 3	– } 2	–	–	–	152 } 157
7·0	·6	1·9	1·3	–	–	–	100·1
–	–	6	24	27	9	12	78
20 } 20	36 } 36	35 } 41	13 } 37	2 } 29	– } 9	– } 12	266 } 344
5·8	10·5	11·9	10·8	8·4	2·6	3·5	100·1
	–	1	19	102	55	59	240
–	14 } 14	75 } 76	87 } 106	55 } 157	6 } 61	7 } 66	262 } 502
–	2·8	15·1	21·1	31·3	12·1	13·1	99·9
–		–	3	4	11	11	65
2 } 2	–	4 } 4	8 } 11	10 } 14	4 } 15	9 } 20	383 } 448
·5	–	·9	2·5	3·1	3·3	4·5	100·1
–	–	–	3	219	520	98	876
17 } 17	17 } 17	15 } 15	1 } 4	7 } 226	32 } 552	20 } 118	40229 } 41105
–	–	–	–	·6	1·3	·3	100·0
54	90	52	30	96	41	23	1400
750 } 804	240 } 330	119 } 171	33 } 63	3 } 99	8 } 49	6 } 29	2309 } 3709
21·7	8·9	4·6	1·7	2·7	1·3	·8	99·9
–	–	10	97	897	280	3	1714
10 } 10	380 } 380	617 } 627	223 } 320	33 } 930	3 } 283	– } 3	1519 } 3233
·3	11·7	19·4	9·9	28·8	8·8	·1	100·0
–		–	19	251	17	1	534
1 } 1	–	3 } 3	176 } 195	446 } 697	153 } 170	18 } 19	1157 } 1691
·1	–	·2	11·5	41·2	10·6	1·1	100·7
7	18	6	20	226	59	28	996
·7	1·8	·6	2·0	22·7	5·9	2·8	99·9
74	186	174	163	1138	149	51	1993
3·7	9·3	8·7	8·2	57·1	7·5	2·6	100·0
–	–	14	161	617	51	7	867
3 } 3	59 } 59	141 } 155	107 } 268	36 } 653	– } 51	4 } 11	434 } 1301
·2	4·5	11·9	20·6	50·2	3·9	·8	99·9
–	–	6	351	1039	35	11	1463
6 } 6	5 } 5	15 } 21	21 } 372	33 } 1072	3 } 38	– } 11	130 } 1593
·4	·3	1·3	23·4	67·3	2·4	·7	100·0
14	18	6	650	1638	26	6	2378
·6	·8	·3	27·3	68·9	1·1	·3	100·2
–	–	5	675	2015	50	15	2760
–	–	·2	24·5	73·0	1·8	·5	100·0
–	–	–	22	755	18	–	795
–	–		2·8	94·9	2·3	–	100·0

TAB

STAT

Date.		Ova.	I.	II.	Nauplii. III.	IV.	V.	VI
3-9-31	No.	40	30	20	150	170	100	80
	%	·4	·3	·2	1·4	1·5	·9	·7
15-9-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
1-10-31	No.	100	–	–	50	10	–	–
	%	·8	–	–	·4	·1	–	–
21-10-31	No.	14	21	–	7	–	–	–
	%	·2	·3	–	·1	–	–	–
5-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
17-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
30-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
14-12-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
29-12-31	No.	–	–	–	–		–	–
	%	–	–	–	–	–	–	–
11-1-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
25-1-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
8-2-32	No.	20	–	–	–	–	–	–
	%	·7	–	–	–	–	–	–
23-2-32	No.	9	–	–	–	–	–	–
	%	·7	–	–	–	–	–	–
7-3-32	No.	156	19	4	3	2	–	–
	%	37·0	4·5	1·0	·7	·5	–	–
21-3-32	No.	226	54	66	16	1	–	–
	%	58·7	14·0	17·1	4·2	·3	–	–
5-4-32	No.	103	5	27	20	3	2	2
	%	53·4	2·6	14·0	10·4	1·6	1·0	1·0
18-4-32	No.	59	22	9	4	2	1	1
	%	38·1	14·2	5·8	2·6	1·3	·6	·6
2-5-32	No.	406	25	8	3	2	4	8
	%	74·9	4·6	1·5	·6	·4	·7	1·5
16-5-32	No.	150	50	70	80	100	60	50
	%	7·1	2·4	3·3	3·8	4·8	2·9	2·4
30-5-32	No.	455	295	65	20	25	15	15
	%	37·5	24·4	5·4	1·7	2·1	1·2	1·2
13-6-32	No.	990	115	40	25	20	15	30
	%	47·6	5·5	1·9	1·2	·9	·7	1·4
27-6-32	No.	1800	350	165	90	30	40	55
	%	58·2	11·3	5·3	2·9	1·0	1·3	1·8
11-7-32	No.	49	9	6	4	3	2	1
	%	2·2	·4	·3	·2	·1	·1	–
25-7-32	No.	3	–	–	–	–	–	–
	%	·1	–	–	–	–	–	–
8-8-32	No.	15	8	3	–	–	–	–
	%	·7	·4	·1	–	–	–	–
22-8-32	No.	3	–	–	–	–	–	–
	%	·3	–	–	–	–	–	–
5-9-32	No.	9	3	2	1	–	–	–
	%	1·0	·3	·2	·1	–	–	–
30-10-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–

TAB

STAT

Date.		Ova.	I.	II.	Nauplii. III.	IV.	V.	VI.
13-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
25-2-32	No.	2	1	–	3	–	–	1
	%	25·0	12·5	–	37·5	–	–	12·5
3-6-32	No.	921	303	120	4	–	–	2
	%	60·7	20·0	7·9	·3	–	–	·1
29-8-32	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–

STAT

16-11-31	No.	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–
22-2-32	No.	155	24	–	34	29	20	56
	%	43·6	6·8	–	9·6	8·2	5·6	15·8
30-5-32	No.	288	74	15	–	–	–	–
	%	13·4	3·4	·7	–	–	–	–
22-8-32	No.	–	1	1	2	–	2	5
	%	–	·2	·2	·3	–	·3	·9

STAT

17-11-31	No.	–	–	–	1		–	–
	%	–	–	–	10·0	–	–	–
23-2-32	No.	2	–	–	–	–	1	1
	%	20·0	–	–	–	–	10·0	10·0
30-5-32	No	5	5	–	15	15	20	25
	%	·1	·1	–	·4	·4	·6	·7
22-8-32	No	–	–	–	–	–	–	–
	%	–	–	–	–	–	–	–

LE IV.

ION IV.

		Copepodites.			Adults.		
I.	II.	III.	IV.	V.	♀	♂	Total.
120	140	170	90	9960	–	–	11070
1·1	*1·3*	*1·5*	*·8*	*90·0*	–	–	*100·1*
20	10	30	90	8310	30	–	8490
·2	*·1*	*·4*	*1·1*	*97·9*	*·4*	–	*100·1*
–	–	–	10	11970	50	10	12200
–	–	–	*·1*	*98·1*	*·4*	*·1*	*100·0*
–	7	–	7	7650	7	–	7713
–	*·1*	–	*·1*	*99·2*	*·1*	–	*100·1*
–	–	–	10	8290	10	–	8310
–	–	–	*·1*	*99·8*	*·1*	–	*100·0*
–	–	–	30	7420	–	–	7450
–	–	–	*·4*	*99·6*	–	–	*100·0*
–	–	–	15	5120	5	–	5140
–	–	–	*·3*	*99·6*	*·1*	–	*100·0*
–	–	–	30	3750	–	–	3780
–	–	–	*·8*	*99·2*	–	–	*100·0*
–	–	–	7	3087	10	10	3114
–	–	–	*·2*	*99·1*	*·3*	*·3*	*99·9*
–	–	–	2	2070	4	10	2086
–	–	–	*·1*	*99·3*	*·2*	*·5*	*100·1*
–	–	–	8	2685	37	128	2858
–	–	–	*·3*	*93·9*	*1·3*	*4·5*	*100·0*
–	–	–	10	2515	58	348	2951
–	–	–	*·3*	*85·3*	*1·9*	*11·8*	*100·0*
–	–	–	2	1056	28	113	1208
–	–	–	*·2*	*87·4*	*2·3*	*9·4*	*100·0*
1	–	–	–	142	46	48	421
·2	–	–	–	*33·8*	*10·9*	*11·4*	*100·0*
–	–	–	1	7	8	6	385
–	–	–	*·3*	*1·8*	*2·1*	*1·6*	*100·1*
10	1	–	1	8	8	3	193
5·2	*·5*	–	*·5*	*4·1*	*4·1*	*1·6*	*100·0*
–	3	2	10	22	17	3	155
–	*1·9*	*1·3*	*6·5*	*14·2*	*11·0*	*1·9*	*100·0*
6	1	5	38	21	13	2	542
1·1	*·2*	*·9*	*7·0*	*3·9*	*2·4*	*·4*	*100·1*
56	187	796	314	122	38	28	2101
2·7	*8·9*	*37·9*	*14·9*	*5·8*	*1·8*	*1·3*	*100·0*
22	53	44	39	132	16	13	1209
1·8	*4·4*	*3·6*	*3·2*	*10·9*	*1·3*	*1·1*	*99·8*
70	40	30	80	501	102	17	2075
3·4	*1·9*	*1·4*	*3·8*	*24·1*	*4·9*	*·8*	*99·5*
60	93	93	36	177	102	3	3094
1·9	*3·0*	*3·0*	*1·2*	*5·7*	*3·3*	*·1*	*100·0*
13	21	104	326	1537	127	13	2218
·6	*·9*	*4·7*	*14·7*	*69·4*	*5·7*	*·6*	*99·9*
–	3	27	682	1520	111	4	2350
–	*·1*	*1·1*	*29·0*	*64·7*	*4·7*	*·2*	*99·9*
–	1	–	610	1442	36	3	2115
–	–	–	*28·8*	*68·1*	*1·7*	*·1*	*99·9*
–	–	2	311	743	16	2	1077
–	–	*·2*	*28·9*	*69·0*	*1·5*	*·2*	*100·1*
–	4	2	290	609	19	2	941
–	*·5*	*·2*	*30·8*	*64·7*	*2·0*	*·2*	*100·0*
–	–	–	96	1110	5	1	1212
–	–	–	*7·9*	*91·6*	*·4*	*·1*	*100·0*

LE V.

ION V.

		Copepodites.			Adults		
I.	II.	III.	IV.	V.	♀	♂	Total.
–	–	2	4	22	1	-	29
–	–	*6·9*	*13·8*	*75·9*	*3·5*	-	*100·1*
–	–	–	–	–	1	–	8
–	–	–	–	–	*12·5*	–	*100·0*
2	16	59	53	15	18	1	1514
·1	*1·1*	*3·9*	*3·5*	*1·0*	*1·2*	*·1*	*99·9*
–	–	12	64	90	11	2	179
–	–	*6·7*	*35·8*	*50·3*	*6·1*	*1·1*	*100·0*

ION VI.

–	–	1	20	625	2	–	648
–	–	*·1*	*3·1*	*96·5*	*·3*	–	*100·0*
12	–	–	–	3	8	14	355
3·4	–	–	–	*·8*	*2·3*	*3·9*	*100·0*
5	81	412	607	418	247	8	2155
·2	*3·8*	*19·1*	*28·2*	*19·4*	*11·5*	*·4*	*100·1*
10	31	27	89	389	16	6	579
1·7	*5·4*	*4·7*	*15·4*	*67·2*	*2·8*	*1·0*	*100·1*

ION VII

1	–	-	-	8	–	–	10
10·0	-	-	-	*80·0*	–	–	*100·0*
–	–	–	–	5	–	1	10
–	–	–	–	*50·0*	–	*10·0*	*100·0*
165	485	1610	930	74	2	1	3352
4·9	*14·5*	*48·0*	*27·8*	*2·2*	*·1*	–	*99·8*
–	6	10	12	72		2	103
-	*5·8*	*9·7*	*11·7*	*69·9*	*1·0*	*1·9*	*100·0*