On the Biology of *Calanus finmarchicus.* V. Seasonal Distribution, Size, Weight and Chemical Composition in Loch Striven in 1933, and their Relation to the Phytoplankton.

By

S. M. Marshall, B.Sc., A. G. Nicholls, Ph.D.,

and

A. P. Orr, M.A., B.Sc., A.I.C.,

Marine Station, Millport.

With 9 Figures in the Text and Plates I and II.

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INTRODUCTION.

THE work on Calanus carried out in 1932 (Nicholls, 1933, Part I) in the Clyde Sea-Area showed that the course of events was very much the same at all four stations worked. It was felt, however, that more frequent observations would be useful for understanding the fluctuations in the population and for relating them to the food available as microplankton. Loch Striven was therefore chosen, primarily for the convenience of its position, and was visited weekly. Previous work (Marshall and Orr, 1927) has shown that this loch, although not so isolated as Loch Fyne, is little affected by ingoing or outgoing currents, and the population can be taken as self-contained. The position chosen, Station VIII (see Part I, Text-figure 1), was situated in mid-loch and had a maximum depth of about 70 metres.

Since it was known that the autumn–winter stock of Calanus starts moulting early in the year, the first visit was made in the middle of January. Weekly visits were then continued until the end of August, by which time the population had returned to its normal autumn–winter state (mainly Stage V). Two further visits in September and October confirmed this.

A series of five vertical hauls was taken each time with the Standard Net described in Part I. Five hauls were taken because of Gardiner's statement (1931) that of a large number of comparable hauls only about one in five is likely to deviate considerably from the average. Any haul which was by inspection a freak, being either much richer or much poorer than the others, was therefore rejected. On three occasions all five hauls were counted separately; on two of these there was a gradual diminution of numbers from first to last. Although the taking of a number of hauls in this way probably diminished considerably the errors inherent in the method, yet it does not do away with them entirely. The five hauls were taken within such a small area that they are not necessarily representative of the loch as a whole.

From March 27th onwards one haul in every five was taken in two sections (from the bottom to 10 metres and from there to the surface), in order to throw further light on the seasonal changes in vertical distribution. This divided haul was always counted, but when it disagreed noticeably from the average of the other four, in numbers or composition, it was ignored in estimating the average number per haul.

Samples of all the copepodite stages were taken from the standard hauls for measurement. On a few occasions in spring, when adults were scarce, additional vertical hauls were made with a one-metre stramin net to provide sufficient material for measurement. Methods of preservation, sampling, counting, and measurement were the same as described in Part I and Part II (Marshall, 1933).

Further hauls were made with the stramin net to provide material for weight determinations and chemical analyses, and these catches, suitably diluted, were taken home alive in large jars of sea-water. These hauls were usually taken horizontally in deep water, so that the Calanus caught were not necessarily a fair sample of the population. Measurements show that the majority of the Stage V and adult Calanus are caught, but that when they are small a few of the smallest may be lost by passing through the meshes of the net.

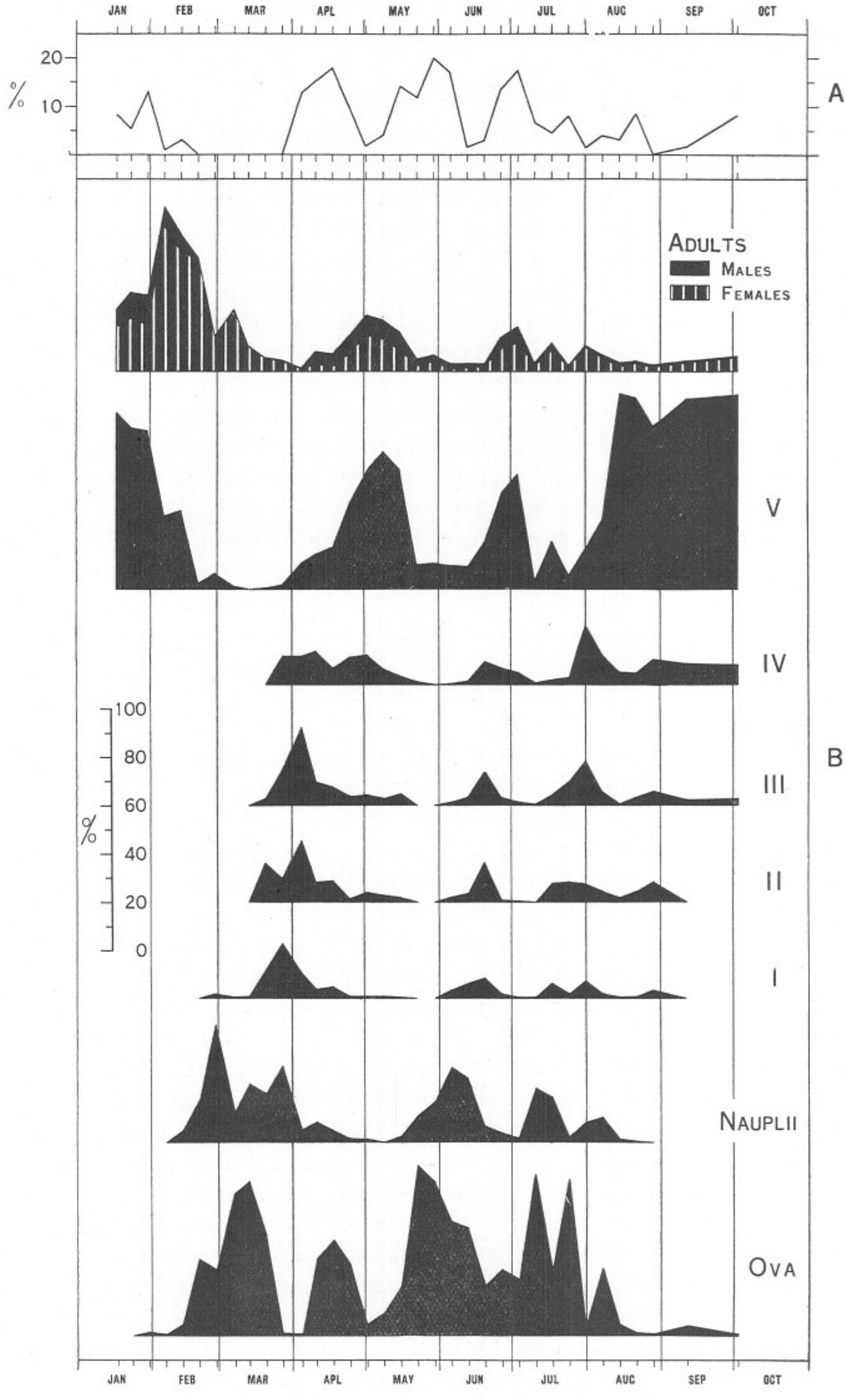
Water samples were taken with the insulating water-bottle at the surface and 30 metres, and the temperature noted. Samples from each were subsequently centrifuged and the number of organisms counted. Although counts made at only two depths do not give a detailed idea of the course of events in the microplankton, yet they are usually sufficient to show whether a diatom increase is present or not.

Seasonal Distribution.

The course of events this year was similar to that found in 1932. The autumn-winter Stage V Calanus moulted into adults through January and February and gave rise to the first brood of eggs. This is clearly seen in Plate I (percentage composition) and Tables I and II, but owing to the low numbers at that time the presence of this breeding period cannot be detected in the diagram showing numbers per haul. The first increase in numbers is seen at the end of March and beginning of April when the Calanus from the first brood of eggs were coming to maturity. One point must be mentioned about the catches from April 17th to May 1st. The number of copepodites present was much too large when we consider the number of eggs found in the previous weeks. The number of copepodites must always be *apparently* larger than the number of eggs which produced them because the copepodites stay longer in each stage than do the eggs, which remain as such only for about 24 hours, but this is not enough to account for the discrepancy. It must be noted, however, that at this time diatoms were very abundant. These would clog the meshes of the net and so reduce the amount of water filtered, particularly in the upper layers where the eggs and nauplii live (p. 814). Further, in the early part of March, from the number of females present one would have expected the number of eggs to be higher.

It will be noticed that the Calanus of the first brood of eggs were accumulating as Stage V in April and May. Only a few of these went straight through to adults and these produced a small brood of eggs during April. These eggs, however, were not followed by any considerable number of nauplii and young stages ; that is, the brood for the most part failed to develop. Only a few of the earliest eggs were found as nauplii. The failure of this brood is clearly seen in Text-figure 1. The Calanus which had accumulated as Stage V during this period moulted into adults about May 22nd and these produced the true second brood of eggs which lasted until about June 19th. This brood went through successfully to adults and these in turn produced another brood, the third, in July. Of the copepodites resulting from this brood many did not go through to the adult state but remained to form the autumn-winter stock of Stage V which was clearly established by August 14th. The few which did moult produced the small subsidiary broods of eggs in August and September, the survivors of which went to swell the stock of Stage V. One other point must be mentioned : the curious fall in numbers on July 17th. This fall is almost entirely in egg numbers since the actual numbers of nauplii and copepodites follow the usual course.

Natural mortality accounts for the fall in numbers after each breeding period and is most marked in the eggs and nauplii.



TEXT-FIG. 1.—A, The percentage of females bearing spermatophores. B, The succession of developmental stages through each breeding period.

Fertilization and Breeding.

From April onwards the female Calanus measured alive for weight determination were examined also for the condition of the ovary. They were divided into four groups (Table V): (i) early state, in which the eggs in the ovary were small and there was only one row of small eggs in the oviduct; (ii) medium state, in which the eggs in the ovary were enlarging and there were several rows of small eggs in the oviduct; (iii) mature state, in which the oviducts were full of large eggs; and (iv) spent state, in which the ovary was degenerating or had disappeared. It was not always easy to distinguish between the four types and a certain amount of overlapping must be allowed for. Rough observations from January to March, before the first breeding period, showed that on February 20th there was a large proportion of the females in the early state. On March 7th the majority were mature and on March 27th a large number was spent. This agrees well with the production of the first brood of eggs. In the same way from April 4th to May 15th there was a large proportion of early and medium state females, those which were about to produce the abortive and the true second brood, and a large proportion again on July 3rd before the third brood. After this mature females always predominated. In September the number of females decreased but the majority still remained in the mature condition. The small number of spent Calanus probably indicates that females die soon after reproduction.

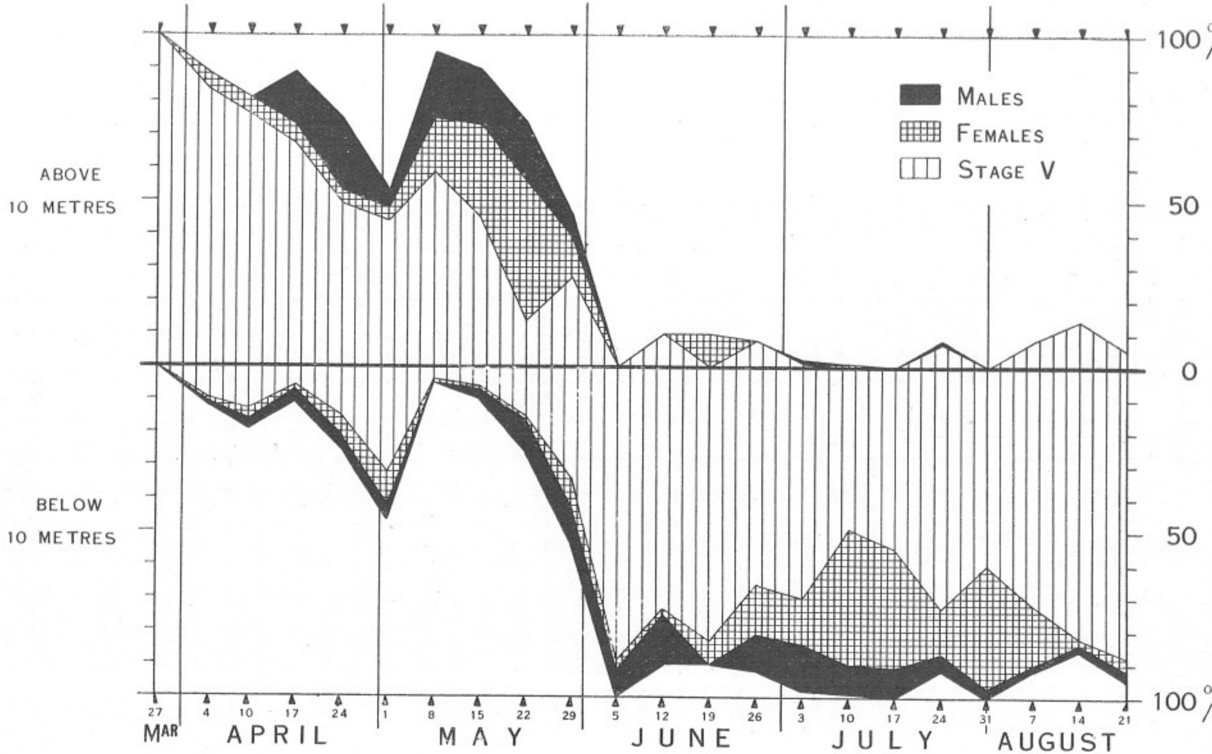
The percentage of females (in the standard hauls) bearing spermatophores rises before each brood of eggs (Table V and Text-figure 1) and is usually greatest when the proportion of males is at its maximum. Thus there is a peak in spermatophore-bearing females on January 30th before the first brood, on April 4th to 17th before the abortive beginning to the second brood, on May 15th to June 5th before and during the true second brood, and from June 26th to July 3rd before the third brood. After this the proportion was never high and the small peaks do not agree with the subsidiary broods. In this area the majority of females carry one spermatophore only, although occasionally two or three or even more are found. The males were never as numerous as the females except in April, but the disproportion is not so great as that described, for instance, in the North Sea (Gibbons, 1933). It is interesting to note that on several occasions Stage V Calanus were found with several spermatophores attached and in one case the number was as high as 13. These were usually distributed indiscriminately over the urosome and caudal furcæ but one or two were found attached to the posterior region of the thorax and fifth pair of swimming feet.

When the state of the ovary in spermatophore-bearing females is examined, it is found that spermatophores are much more frequent in the early stages than in the later. If we take early and medium state females together we find that of the 674 examined 17·4% carried spermatophores, while of the 1473 mature females less than 1% did so. One spent Calanus out of the total number of 38 had a spermatophore attached. These figures indicate clearly that the spermatophore is normally lost at a fairly early stage of development of the ovary. In recently moulted unfertilized Calanus the sacs opening on the genital segment are colourless and apparently empty, but in the great majority of the females found in the plankton they are dark in colour and appear to be full, presumably with the contents of the spermatophores. The spermatophores attached to the females are often empty. It is suggested that the sperm are stored in these sacs until spawning takes place and that some are passed out along with the eggs, but this needs confirmation by experiment. It may, however, be noted in support of this suggestion that in several other copepods the spermatozoa reach the eggs only when these are being spawned (Matscheck, 1909 ; Gray, 1929).

Immediately before the eggs are spawned they swell up and become granular in appearance. They are then squeezed out through the genital aperture as a string of sausage-shaped masses which separate and round off in a few seconds. Numerous females have been thus observed laying eggs on a slide and in several cases the numbers have been counted. The greatest number counted was 70. This agrees with the number suggested in Part I, but it is possibly exceeded at times.

Vertical Distribution.

It has been shown before (Nicholls, 1933, Part III) that during the day in this area adult and Stage V Calanus normally live in deep water, but that at certain times of the year they may be found near the surface. Text-figure 2 illustrates their vertical distribution during the period from March 27th to August 21st, during which time one haul was divided at 10 metres. Numbers (Table II) above 10 metres were multiplied by six in order to make possible a fair comparison of the density above and below this level, since there was about six times as much water below as above. Young stages were not taken into consideration since their normal distribution is above 30 metres (Part III). It will be seen that from March 27th till May 29th Calanus in Loch Striven were inhabiting the upper 10 metres continuously and almost exclusively. After that date on no occasion were they found above 10 metres to any extent. It is interesting to note that the period in which they were moving down coincided with the transition period between the first and second broods, at which time Stage V and adults from the first brood were dying out



TEXT-FIG. 2.—The vertical distribution of Calanus in the divided haul during the three main breeding periods. (Based on Table II).

and those from the second brood were appearing in the catches. This indicates clearly that it was the first brood alone which showed this unusual vertical distribution. Gardiner's (1933) results on diurnal migration in the North Sea also showed Calanus more abundant near the surface than below in May. A comparison with last year's results when the hauls were divided at 30 metres shows that this phenomenon is not of regular occurrence. On two occasions in 1932 Calanus were noticeably more abundant above 30 metres than below and these were not restricted to the first brood.

Size, Weight and Temperature.

Where possible, samples of at least one hundred of each of the six copepodite stages of Calanus taken from the standard hauls were measured. The size-frequency distribution throughout the year is shown in Plate II, and the median lengths of the cephalothorax in Table III and Text-figure 3. The small size of Stages II and III partly accounts for the high values on the size-frequency curves for these two stages. All except Stage I copepodites were measured on the same scale; Stage I were so small that they were measured under a higher magnification. This naturally makes the areas covered by their frequency distribution curves smaller than those of other stages, but the lengths of the base lines are still strictly comparable.

From January to the middle of March only Stage V and adults were present; for most of this time only females were present in numbers sufficient to measure. The sizes fluctuate considerably, but this is partly because the numbers measured were very small.

On March 20th the first of the new brood appeared as Stage I and II copepodites; by March 27th they had developed to Stages III and IV, and by April 4th to Stage V and adults. From April 4th the size of each of these stages increased and the largest Calanus were found on April 24th. The female Calanus found on this date measured 2·82 mm. as compared with 2·41 mm. on March 27th. The females during this time were a mixture of autumn–winter stock and first brood Calanus, and the dying out of the former can be seen in the frequency distribution curves (Plate II). The curves are bimodal and the lower mode corresponding to the small autumn–winter stock gradually disappears. After April 24th

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PLATES.

Plate I.—Chart showing numbers per haul and percentage composition of population of *Calanus finmarchicus* during 1933.

Plate II.—Curves showing the percentage size distribution of Calanus in Loch Striven, 1933. Left-hand side: thick line, males; thin lines, Stages V, III and I. Right-hand side: thick line, females; thin lines, Stages IV and II.

PLATE I.

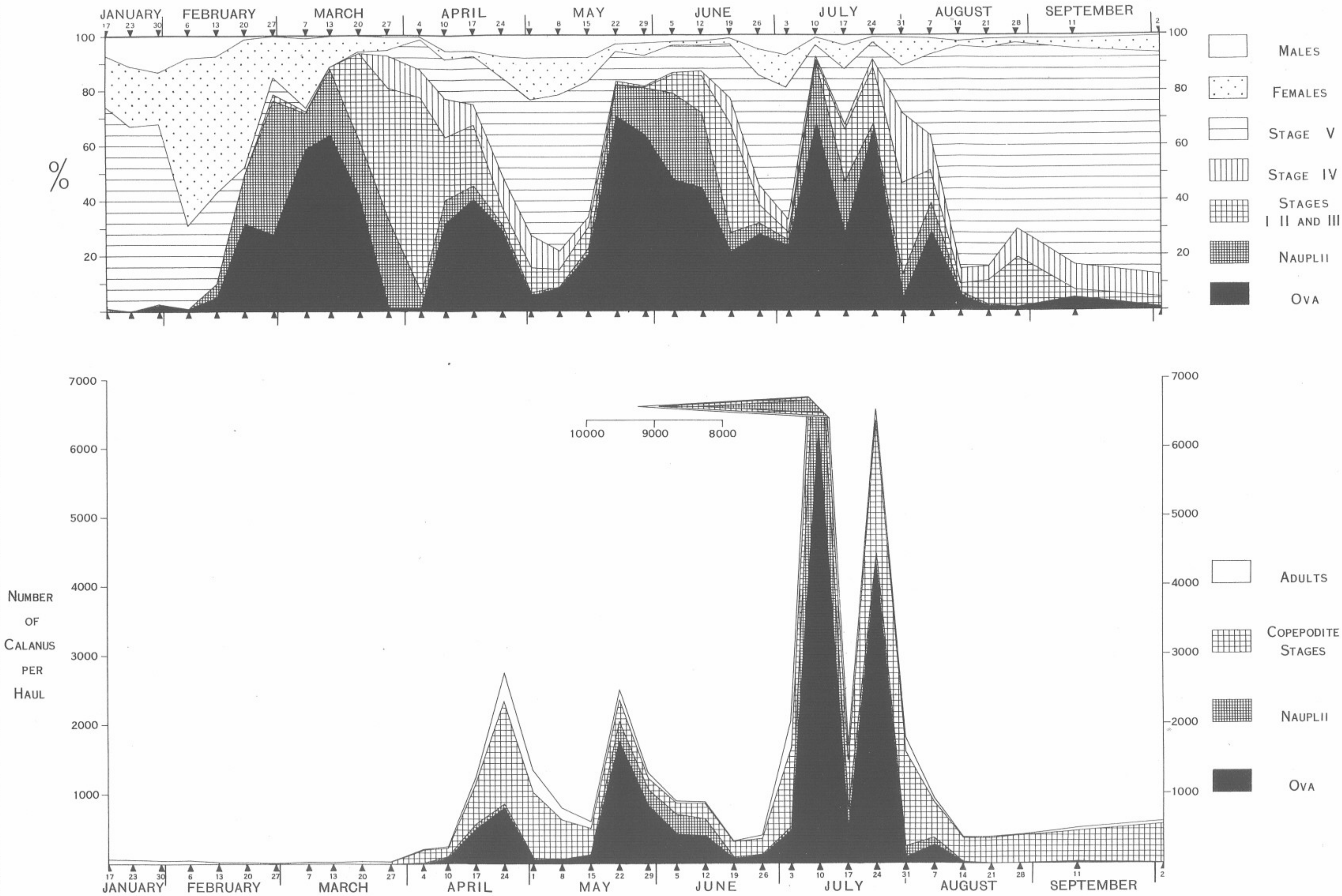
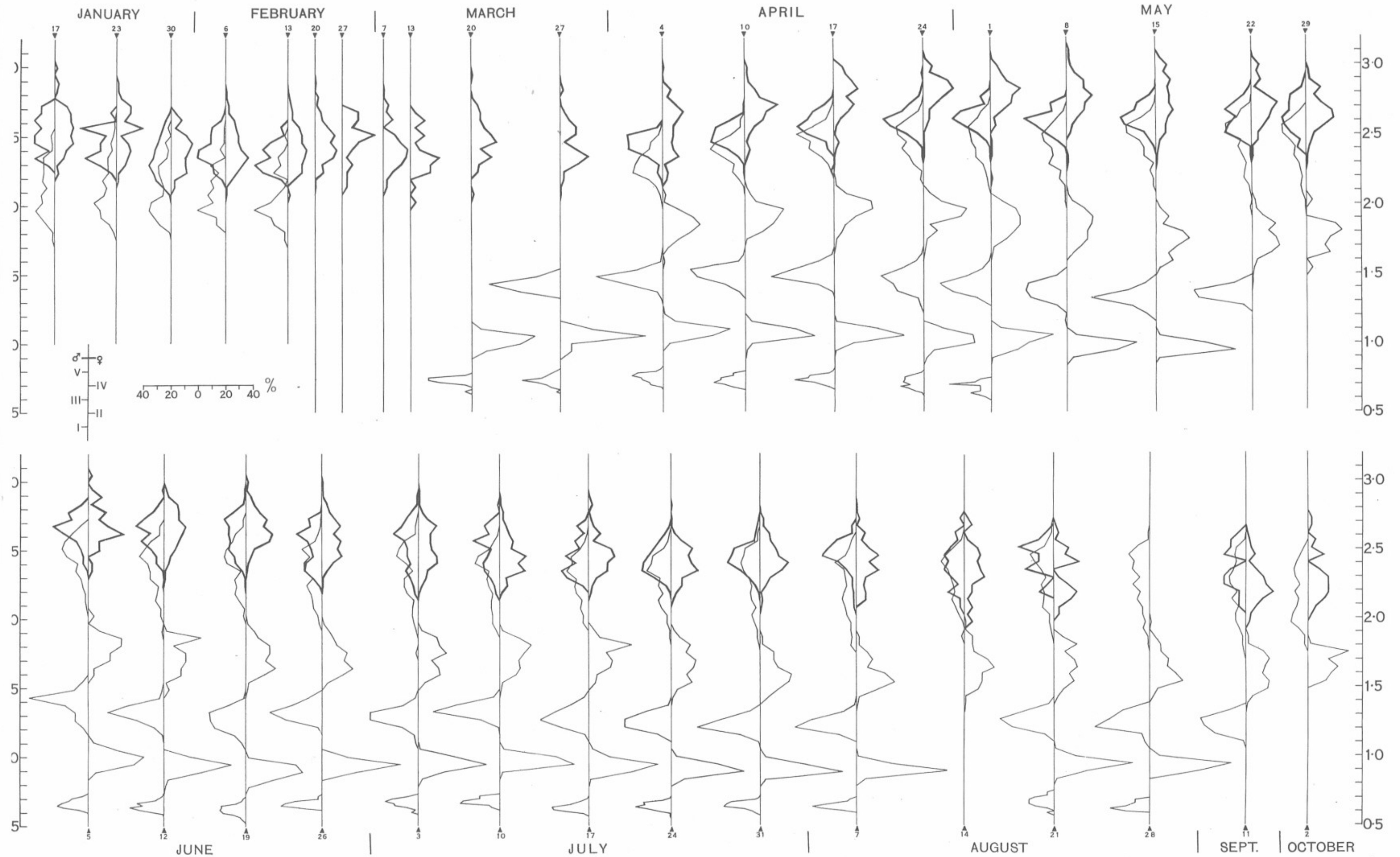

JANUARY
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
%
MALES
FEMALES
STAGE V
STAGE IV
STAGES I II AND III
NAUPLII
OVA
10000
9000
8000
NUMBER OF CALANUS PER HAUL
ADULTS
COPEPODITE STAGES
NAUPLII
OVA

PLATE II.



JANUARY
FEBRUARY
MARCH
APRIL
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3·0
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V
IV
III
II
I
40 20 0 20 40 %

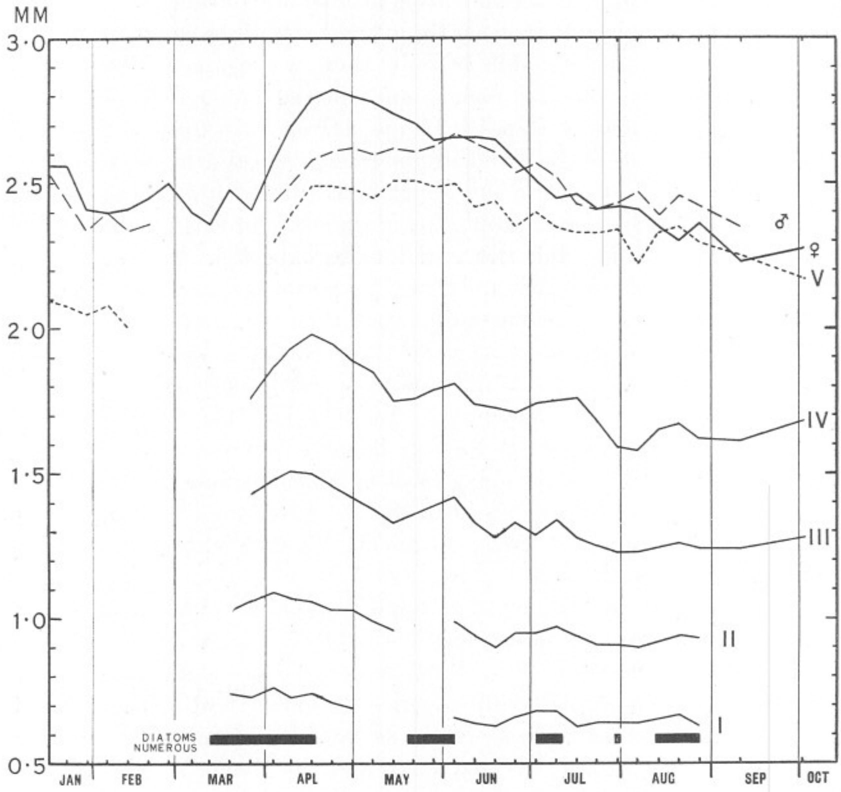
the size of all stages except Stage V and males fell until May 22nd or 29th, when the fall was checked, and in the younger stages the size actually increased a little. This corresponds to the appearance of the second brood. There were not enough of Stages I and II to measure. Males remained fairly constant in size and rose to their maximum for the year (2·67 mm.) on June 5th at the time of the second brood. The Stage V Calanus did not show the gradual fall in size either, but this is probably because in May they were accumulating instead of moulting to adults and the large ones remained to increase the average size of the stock. After the second brood, up to the middle of July, there was again a fall in size in all stages, but this was not regular and showed minor increases. The third brood appeared as Stages I, II, and III on July 10th, as Stage IV on July 17th, and as Stage V and adults, though less clearly, on July 31st. There was an indication of a subsidiary fourth brood towards the end of August. Since only a small proportion of these two broods became adults, a marked increase in adult size is not to be expected. In August and September the sizes of adults and Stage V approached each other, and in some cases the Stage V were actually larger than the females.

It seems certain, then, that while there was a gradual fall in size throughout the summer, this fall was temporarily checked at the time of the production of each new brood. In 1932 (Part II) it appeared that the Calanus from eggs spawned at the beginning of the breeding period were larger than those developing from eggs spawned at the end. This may be true in some cases this year, but it was certainly not so for the first brood in which the young stages (II–V) show that the size first increased and then decreased.

The fluctuations in dry weight of Stage V and adult Calanus are shown in Table V and Text-figure 4A. These weight determinations were made as described in Part IV (Orr, 1934) and usually on 100 individuals. The weight of Calanus naturally depends to some extent on its size, but the relation is not as close as might be expected (see below). Those which were weighed were also measured and the change in size in these samples agreed closely with the weight curves. A comparison of Text-figures 3 and 4B shows that they agreed also with the size samples from the standard hauls, especially the adults.

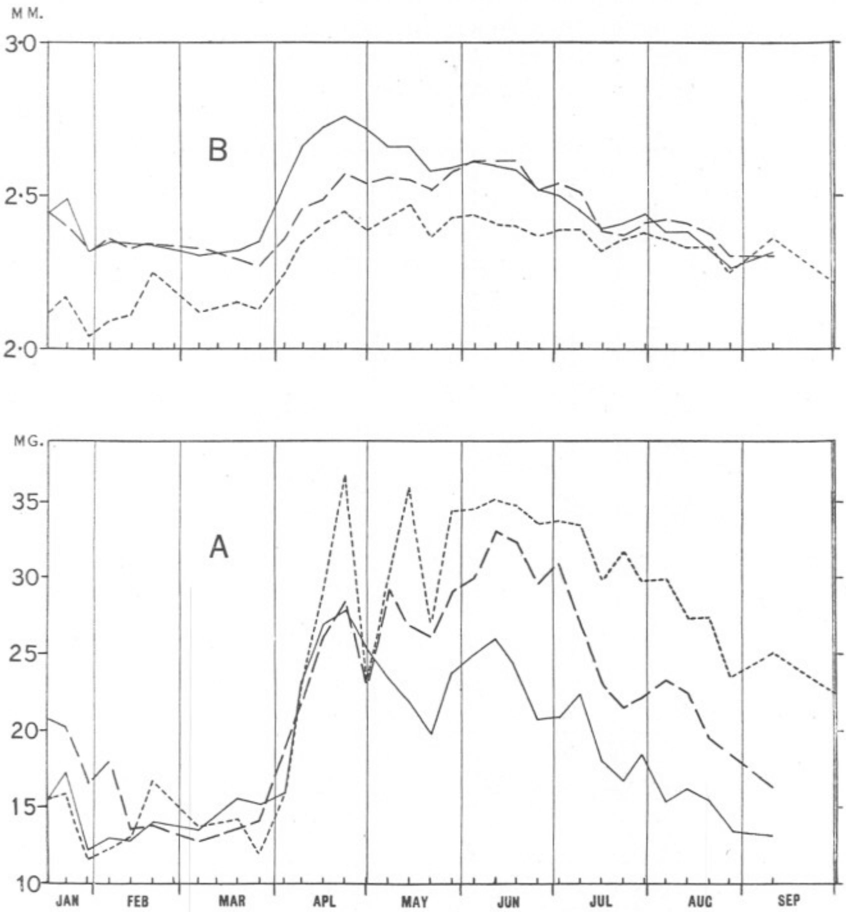
The samples were taken with a stramin and not with a fine silk net, so that one might expect them to be on the whole larger; on the other hand, these Calanus were measured alive and formalin fixation increases the size a little. Allowing for this increase after fixation the size of the adults in the two sets of measurements agrees very well. The main divergences occur in Stage V, but are, however, much larger than can be accounted for in this way, and must be caused by imperfect sampling. Stage V predominated in the catches from April onwards, and though it was often necessary to go through the whole catch to obtain sufficient adults, the required number of Stage V was obtained from one jar which represented only a small fraction of the catch.

From January to March Stage V and adults weighed very nearly the same in spite of Stage V being considerably smaller. At this time the numbers of males and Stage V available for weight determination were occasionally very small (Table V), so that the value may not be very



TEXT FIG. 3.—The median lengths of the copepodite stages of Calanus.

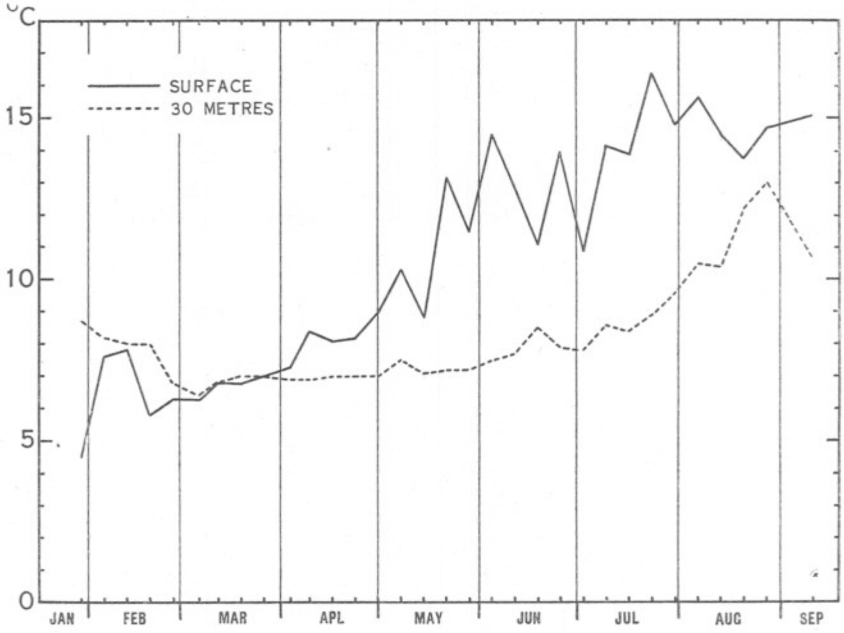
reliable. With the appearance of the first brood in the beginning of April, the weight rose rapidly, especially that of the Stage V Calanus, so that while the weight of 100 adult Calanus, male or female, rose from about 15 mg. on March 27th to 28 mg. on April 24th, 100 Stage V rose from 12 mg. to 37 mg. in the same time. After this, in accordance with size changes the weight of the females fell steadily to the end of May; it then rose to a secondary maximum in the middle of June, corresponding to the appearance of the second brood. There was a small rise in the beginning of July and another (corresponding to the beginning of the third brood) at the end of July, but otherwise the weight fell gradually until winter values were reached again in September. The weight curve for males follows the size curve for males closely, with a maximum in June. Males were distinctly heavier than females throughout the summer. After the



TEXT-FIG. 4.—Changes in median length and dry weight of 100 Calanus during the year. A, dry weight. B, median length. — — — Males; ———— Females; - - - - - Stage V.

abrupt increase in weight in April Stage V Calanus remained heavier than either male or female for the rest of the summer, apart from several curious deviations in April and May, probably to be explained by imperfect sampling. The weight remained high until mid-July and then fell gradually till September, although even then it was still above winter values.

The most striking point is, of course, that the relation of size to weight in female, male, and Stage V Calanus is *inverse*. It is obvious, therefore, that when a Stage V Calanus moults there must, at least during the summer, be a subsequent loss of organic material. It should be noted that the weights referred to above are all dry weights, and the same results do not hold if we compare wet weights. The wet weights of a number of male, female, and Stage V Calanus were determined on two occasions during the summer. About 50 Calanus were put in small drops



TEXT-FIG. 5.—The sea temperatures at the surface and 30 metres.

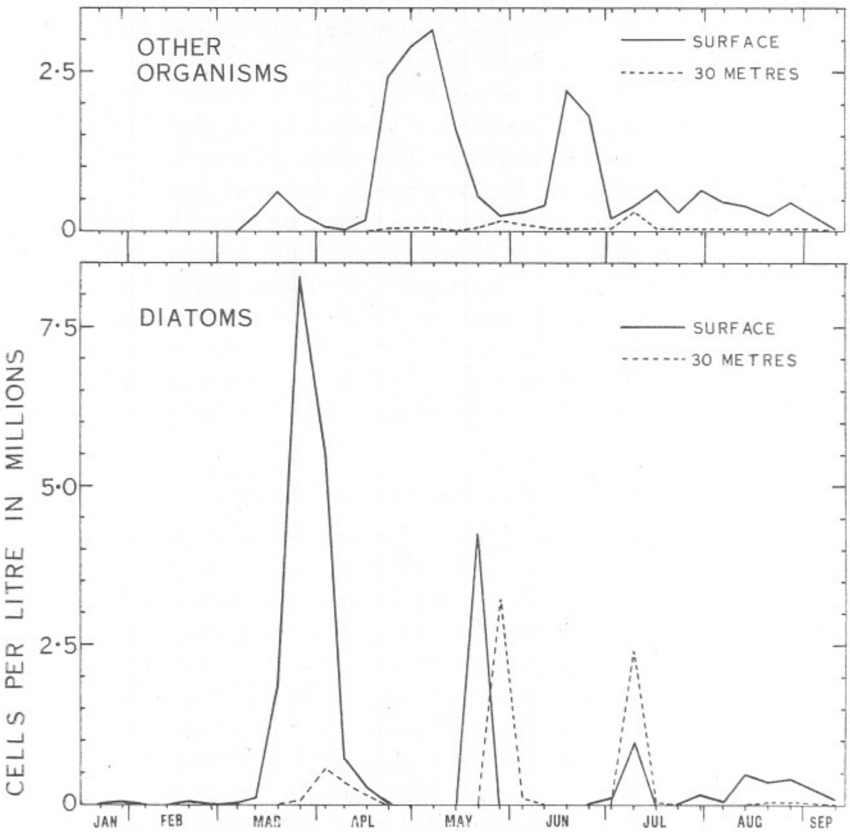
of sea-water on a slide and the sea-water removed by carefully drying with filter paper. They were weighed after a fixed time, dried at 110° C., and reweighed. The dry weight of 100 individuals, determined in the usual way, acted as a check on this and showed that the adherent sea-water had been almost completely removed by the filter paper. It was found that while Stage V Calanus contained 47 to 50% water, male Calanus had 54% and females 68 to 70%. Thus in the living state females actually weigh more than males, and males more than Stage V. Gardiner (1933) has shown that large Calanus sink more quickly than small, indicating that females have a higher specific gravity than Stage V in spite of their lower dry weight.

Throughout the year there is no constant relation between size and weight for male, female, or Stage V Calanus. In duplicate samples the agreement is good, but Calanus of the same stage and size show differences in dry weight at different times of the year which lie far beyond the experimental error of weighing or measuring. Thus of two lots of 100 Stage V Calanus with a median length of 2·35 mm. the first, on April 10th, weighed 23·0 mg., and the second, on July 24th, weighed 31·7 mg., a difference of 8·7 mg. As has been mentioned, however, the trend of the size and weight curves is similar throughout.

The temperatures taken are shown in Text-figure 5. The sea was coldest during March and April when the first brood, giving rise to the largest Calanus, was developing. Thereafter, concurrently with the warming of the sea-water, the later broods decreased in size. On this gradual fall in size are superimposed the variations caused by each brood. The Calanus found in January, February, and March were small, but these had developed from eggs laid in the previous autumn when the sea was at its warmest. Although it appears that the time taken to develop is about one month for each of the broods yet weekly visits cannot give an accurate figure for time of development which may on account of temperature be a little more for the first brood and a little less for the later ones.

Relation to the Phytoplankton.

The water samples taken weekly at the surface and 30 metres were not preserved, but 20 c.c. were centrifuged from each within 24 hours and all the organisms counted. The numbers, expressed as millions per litre, are shown in Text-figure 6 (see Table IV). Apart from minute flagellates, diatoms were the only organisms occurring in large numbers and the cycle of events was very much the same as is usual in this area, namely, a large diatom increase in spring followed by smaller increases during the summer. The main difference was in the actual numbers present which, for the spring increase at least, were much smaller than in the years from 1926 to 1931 (diatoms were not counted in 1929). The maximum number during the spring increase in these years varied from 15 to 30 million cells per litre ; in 1932, although water samples were not taken regularly, there was apparently no great increase at all, and in 1933 the maximum number was only 8·5 million cells per litre. The summer increases were also small and the year as a whole must be considered poor in diatom growth. The majority of the other organisms (Table IV and Text-figure 6) were minute flagellates which occurred in large numbers during the summer. It is possible that these flagellates are characteristic only of coastal water and would not be found in such numbers in the open sea. Many of them are colourless. Dinoflagellates did not occur in large numbers. Samples taken at only two depths can give but a general idea of the total numbers present, and there may sometimes have been more than the curves indicate. On July 3rd, for instance, the numbers counted were not particularly large at either the surface or 30 metres, but the tow-netting from 10 metres to the surface was very rich in diatoms, indicating that the maximum (which must have been greater than the



TEXT-FIG. 6.—The microplankton in Loch Striven in 1933.

figures shown at 30 metres in the following week) was a little below the surface.

Previous work (Lebour, 1922 ; Marshall, 1924) has shown that diatoms form an important part of the food of Calanus throughout the year and it might therefore be expected that the number of Calanus would bear some relation to the distribution of diatoms.

The spring increase this year, which lasted from March 13th to the middle of April, began at the time when the number of eggs was near its maximum and lasted over the period when the nauplii and young stages were developing (Plate I, Text-figure 1). These went through successfully to adults. The end of this increase overlapped the abortive beginning of the second brood which failed to produce more than a few survivors (Text-figure 1). Only the nauplii from the eggs spawned during the first few days of this production had a sufficient food supply. There was a large number of minute flagellates present during this time but they had no effect on the survival.

The second diatom increase, at the end of May, coincided with the appearance of the second brood, but did not last so long. Similarly the increase from July 3rd to 10th provided diatoms when the eggs and nauplii of the first part of the third brood were at their maximum, and these gave rise to the main bulk of the copepodite stages of this brood. Diatoms were very scarce again until July 31st, and this is reflected in the lack of nauplii from the eggs produced at the end of this brood (Plate I). Throughout August and September there was a small number of diatoms constantly present, which may have been responsible for the survival of the subsidiary fourth brood, but by this time most of the developing Calanus were not moulting into adults but remained as Stage V to form the autumn–winter stock.

Earlier work has shown that a large percentage of the diatoms produced during an increase sink to the bottom. Since the Calanus of the first brood were found almost entirely in the upper layers (Text-figure 2) the diatoms when they had sunk into deep water were of no significance to them. With the second and third broods the diatoms would be of value to the young stages when they were near the surface and in deeper water would be available for the older stages. It is curious to note that the minute flagellates, although they would appear to be suitable food, do not seem to be used.

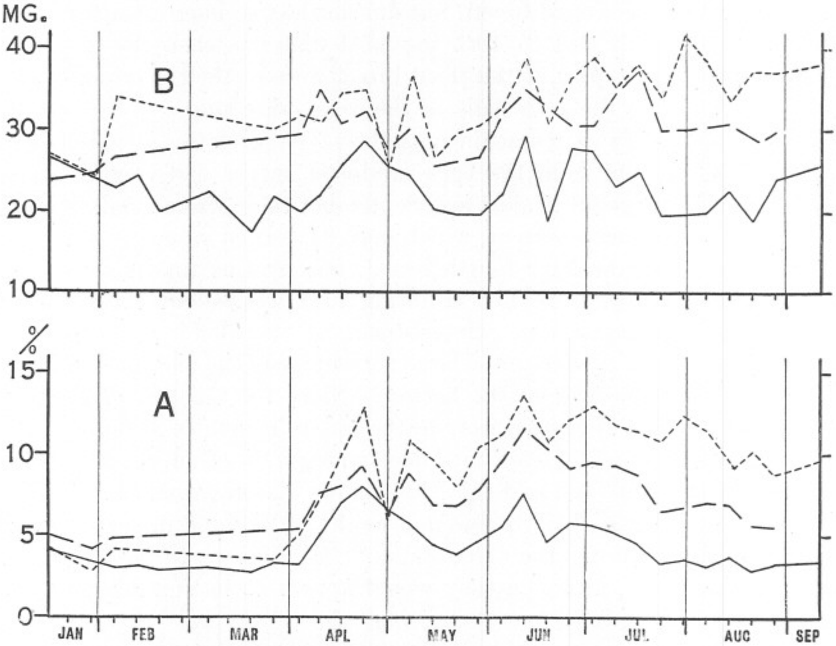
It is, of course, impossible to state what are the actual requirements of a Calanus, but the young stages, being less mobile, will require a richer supply than the later stages and adults. The critical time is therefore the period from egg to early copepodite, and the presence or absence of diatoms in the water then, means the success or failure of a brood.

The coincidence of a diatom increase with egg production (except in the case of the abortive beginning to the second brood) is interesting, but no causal relation is apparent.

In Text-figure 3 the periods when there were over 100,000 diatom cells per litre are marked in black. It can be seen that the size maxima occur shortly after these diatom-rich periods. The size maxima depend mainly on the broods, but it is possible that a rich food supply may also have a direct effect on the size.

Chemical Composition.

The fat and protein content was estimated from January to September in male, female, and Stage V Calanus. The methods used were the same as described in Part IV, but during 1933 the Calanus were not measured. The samples used for fat and protein analyses could not conveniently be weighed, so that the assumption is made that the samples of 100 Calanus used for these were strictly comparable with those used for weight and

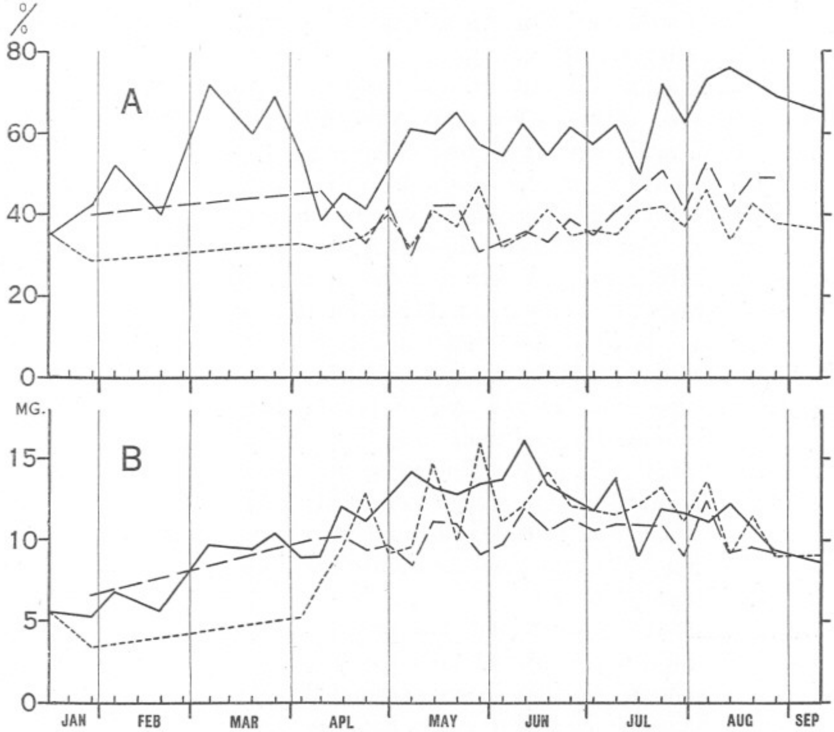


Text-Fig. 7.—Changes in fat content of Calanus during the year. A, Fat percentage. B, Weight of fat per 100 Calanus. — — — Males ; ———— Females ; - - - - - Stage V.

size determination. That this is justified is shown by the agreement between the duplicate weight samples and between the curves for weight and fat content.

The weight of fat per 100 Calanus and the percentage of fat are shown in Text-figure 7. In the early part of the year male and Stage V Calanus were scarce and it was often difficult to get sufficient for analysis. Corresponding with the low values for weight at this time of year fat content was also low. With the appearance in April of the Stage V and adult Calanus of the first brood there was a rapid increase in fat content ; thereafter the curves showing fat content of male and female Calanus agree well throughout with weight and size (Text-figure 4), while that for

Stage V shows a very good agreement except for a short period during July. Thus with male and female Calanus the three broods for the year can be recognised by the change in fat content. With Stage V, as has already been mentioned, the sampling errors are at times significant and the curve for fat content follows that for weight, which has considerable irregularities during the spring. Both the actual content and percentage of fat are lowest in females and highest in Stage V, in agreement with



TEXT-FIG. 8.—Changes in protein content of Calanus during the year. A, Protein percentage. B, Weight of protein per 100 Calanus. — — — Males ; ———— Females ; - - - - - Stage V.

weight. There is a maximum fluctuation in percentage of fat in male Calanus of 20%, in females of 13%, and in Stage V of 20%. While the curves show that the large increase in the actual fat content in April depends chiefly on the increase in weight, Text-figure 7A shows that the increases in the *percentage* of fat occur at the same time and are therefore related to broods. This is shown most clearly for the first brood of the year, less clearly for the second, and still less for the third, as was the case with sizes. These increases in the percentage of fat suggest that the abundant food provided by the spring diatom increase resulted in a storage of fat.

After the appearance of the third brood there is a general fall in the fat contents of male and female Calanus, which by September have reached approximately the same values as in early spring. The adults then die out. With Stage V, however, the value is still high in the autumn–winter stock in September, being about 6% higher than during the spring.

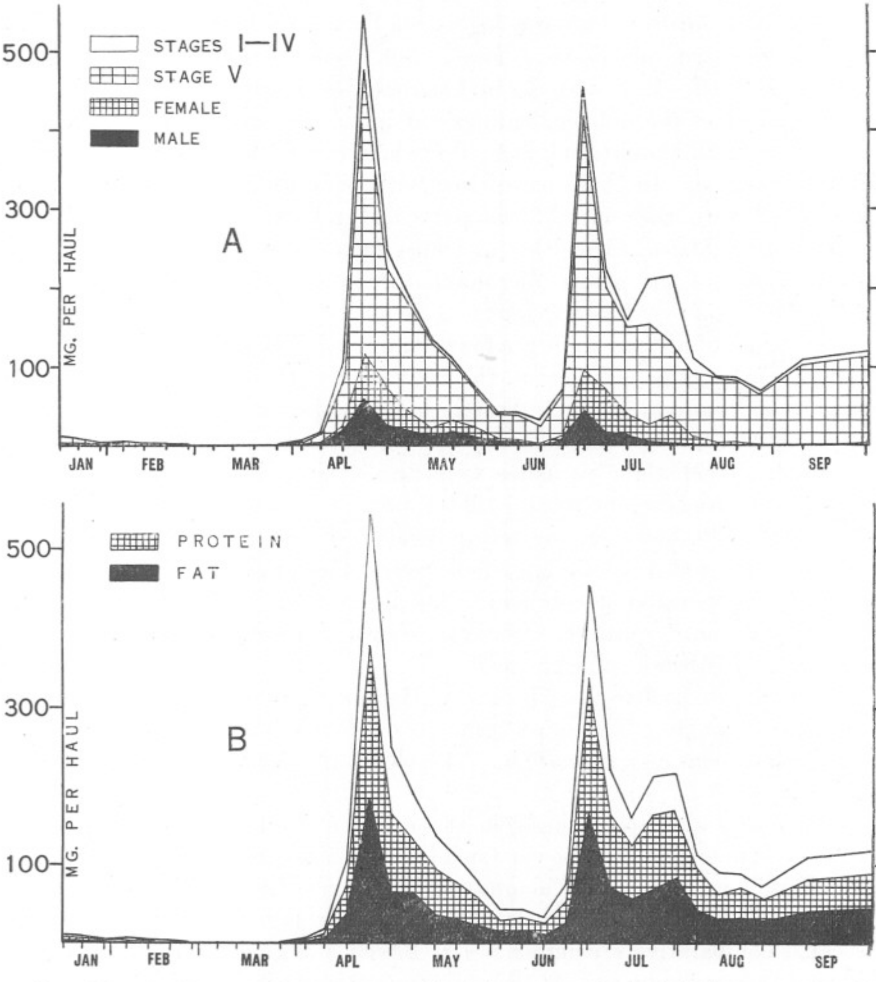
There is little or no relation shown between the fat content of female Calanus and the state of the ovaries. As is shown in Table V, there was always a high percentage of those in the mature condition, so that any changes due to the variations in this must be small and would not be shown in the curves for fat content.

The protein content of Calanus and the protein percentage are shown in Text-figure 8. There is less agreement between weight and protein than between weight and fat content. This is partly because the method of analysis was less accurate, and also because protein was estimated less frequently than fat. The agreement between protein content and weight is shown in the rise to higher values in April corresponding to the first brood, especially in Stage V. During the summer the values remained high and showed at best only a general relation to weight. After the third breeding period in July there was a fall towards winter values again. Text-figure 8B shows that, in contrast to fat, females are richest in protein and Stage V poorest. In the case of protein the difference between females on the one hand and males and Stage V Calanus on the other is more marked than with fat. The curves for protein percentage do not show any relation to the breeding periods with the possible exception of females, and their chief feature is a comparative constancy in male and Stage V Calanus. Thus the great increase of weight in spring is due more to fat than to protein.

On the basis of the weight, fat, and protein determinations, diagrams showing the total dry weight of the copepodite stages and the amount of fat and protein per haul have been constructed (Text-figure 9). The dry weights of the early copepodite stages have been calculated on the basis of Bogorov's figures (1933), while nauplius stages and eggs have been omitted, since although they were at times present in large numbers, their weight will be insignificant in comparison with copepodites and adults. During the winter the total weight (Text-figure 9A) was low because of the small numbers. The increase in the middle of April corresponded to the appearance of copepodites from the first brood. Those from the second brood, in May, caused the second weight peak on July 3rd. The third brood caused a slight increase on July 24th and 31st in which the early copepodites were of considerable importance. Thereafter the curve remained high owing chiefly to the Stage V Calanus which formed the autumn–winter stock.

The fat and protein content and the unidentified constituents of the

Calanus as a whole (Text-figure 9B) follow fairly closely the total weight curve. Of the unidentified constituents ash amounts to about 4% and chitin to about 3% (see Part IV) of the dry weight of the Calanus, while the remainder is probably largely carbohydrate (Brandt, 1898; Brandt



TEXT-FIG. 9.—Diagram showing dry weight of Calanus per haul. A, Relative weights of different copepodite stages. B, Fat and protein content.

and Raben, 1919–1922). At its maximum on April 24th the total dry weight of the copepodite stages was over 540 mg. in the whole column of water filtered (about 70 metres). This corresponds to a concentration of about 40 mg. per cubic metre, but the actual concentration will of course depend entirely on the vertical distribution of the Calanus.

Notes on Parasites.

A striking fact about Calanus is the number found parasitised. Apstein (1911) has already given a list of parasites which occur, and it may be of interest to add a few notes on those found here and their distribution.

Parasitised forms are often recognisable by their colour. Those whose body cavities contain cestode larvæ, trematodes, or dinoflagellates are all coloured red. With cestodes and trematodes the colour seems to be a development of the red pigment present in the chromatophores usually associated with the fat body, and the whole animal may be coloured a brilliant scarlet. In those parasitised with dinoflagellates the colour is associated with the mass of the parasites and varies from a pinkish yellow to bright red. The other parasites do not affect the colour at all.

An isopod of the genus Microniscus occurs occasionally throughout the year.

Two types of cestode larvæ are found, a tetraphyllid and a cyclophyllid. Both occur in large numbers in the body cavity, the cyclophyllid being smaller and more numerous. Apstein has recorded over 2000 of them in one Calanus, but the numbers here have not been more than several hundred. When these parasites were first noticed in this area, about 1924, they were rare, the tetraphyllids much rarer than the cyclophyllids. By about 1930, however, the tetraphyllids had become more numerous and in 1932 and 1933 cyclophyllids were exceedingly rare and tetraphyllids comparatively common. An interesting point about these cestode larvæ is of course the difficulty of explaining how they can occur in such large numbers in a single host.

Trematodes, probably a species of Hemiurus, occur rarely and are found only singly. The most brilliantly coloured Calanus are usually those which contain a trematode. They have also been found in Pseudocalanus.

Nematodes also occur singly in the body cavity but have no effect on the colour. They may be very small, but all sizes are found up to those which are longer than the Calanus which contains them and lie coiled up in the body cavity. These were rare until the spring of 1933, when they became comparatively common. Dr. Baylis has kindly identified this form as Contracæcum sp. At the same time this species was also common in Sagitta.

A species of gregarine is frequent in the gut and is more common in summer than in winter. It appears to have no effect on the Calanus at all.

The most common parasite of all is a species of the dinoflagellate Syndinium which occurs in masses in the body cavity. When such parasitised Calanus are kept in the laboratory they will frequently extrude the parasites as a discrete mass, but the host usually dies soon afterwards. Rarely, they extrude a mass of flagellated swarm-spores. The number of Calanus parasitised by this form is so large that it probably has a considerable effect on the mortality. The Calanus infected are usually found swimming about actively, but they are less resistant than normal specimens and die more quickly in the laboratory.

Another parasite, probably also a dinoflagellate, is *Ellobiopsis chattoni*, which is a pear-shaped body attached by a stalk usually to the antennule or one of the other cephalic appendages. It occurs most frequently in summer and was very common in the summers of 1931 and 1932. It was rare in 1933.

Except for the Syndinium, none of these parasites has much apparent effect on Calanus, which remain as active and lively as normal specimens. If they are examined more closely, however, it is usually found that the ovary remains undeveloped in females containing trematodes, cestodes, nematodes, or Syndinium. Females are found parasitised much more frequently than any other stage. Syndinium is found often in Stage V and sometimes in male Calanus, and the same may be said of nematodes and Ellobiopsis, but it is rare to find cestodes or trematodes in any but adult females.

On the whole infection is much heavier in the autumn–winter stock than in any other. These Calanus have lived much longer than those of other broods and have therefore been exposed to infection for a longer time. It is curious to notice the change which comes with the appearance of the first brood. Whereas out of a catch of a few hundred of the autumn–winter stock there may be 50 or 60 infected Calanus, out of the much larger catches of the first brood it is rare to find more than a dozen parasitised. In a catch taken on March 26th, 1931, out of 363 females, 42 were infected with Syndinium, 27 with tetraphyllids, 3 with cyclophillids, 6 with nematodes, and 1 with Ellobiopsis. Infection such as this probably accounts for a heavy mortality.

DISCUSSION.

A comparison with last year's results (Part I) shows that in general there is close agreement. The three main breeding periods, with one or more subsidiary broods, found at all Stations last year, were repeated in Loch Striven. The abortive beginning of the second brood and the accumulation of Stage V after the first brood delayed both the second and third broods by about a month, so that the autumn–winter stock was not established until August 14th (compared with July 11th in 1932). It is considered therefore that this may be regarded as a true representation of the course of breeding in the Clyde Sea-Area.

If total numbers are considered alone (Plate I) three distinct peaks appear which, except for the first, are caused mainly by large numbers of eggs. The eggs in the first are those of the abortive beginning of the second brood while the copepodites are those from the first brood, the eggs of which appeared in February and March, but were found in relatively small numbers. It has been shown that diatoms coincided with the eggs and nauplii of each brood and so aided their survival, but this will also have affected the number caught, since when diatoms are thick considerable clogging of the net is caused and its fishing capacity largely reduced. This was observed on several occasions, when the net on reaching the surface was seen to be pushing a cushion of water in front of it, and as it was hauled out brought water with it which drained away more or less slowly. This did not happen except when diatoms were very numerous. Thus while an inaccurate sample of the eggs and nauplii might have been taken because of diatoms, by the time they had developed into older copepodites diatoms had disappeared and truer samples were obtained. This applies in general to the later broods, but less to the third, since the number of diatoms at this time probably did not reach such high values as in the two preceding increases.

In the third brood alone were young stages present in sufficient numbers to produce the later copepodites and adults, and a diminution is shown from each stage to the next throughout this brood (except the first copepodites whose peak in numbers may have been missed between two successive weekly visits). In the first and second broods the reverse was the case, there being an actual increase in numbers from one stage to the next, but, as has been shown, this follows the increased efficiency of the net with decrease in diatoms. A similar state of affairs has been ascribed by Gibbons (1933) in the North Sea to immigration. It is, however, very difficult to apply this to Loch Striven. Text-figure 1 shows clearly that no large immigration of any particular stage took place at any time during the year. The broods can be followed in successive weeks from egg up to adult without any break in continuity. Apart from this it is known from previous work that hydrographic conditions in Loch Striven show no violent changes and that the micro-plankton maintains a more or less independent character, although the same general changes take place there as in the rest of the area.

The resemblances between the course of events in this and other areas have already been pointed out (Part I). Off the south coast of Ireland (Farran, 1927) the first brood appears to be so small that the copepodites resulting from it are negligible in numbers; the second brood in April and May is important and Farran states that thereafter breeding is continuous throughout the summer. His work, however, is based on collections accumulated over a number of years (1913–14 and 1920–26) and data for more than two consecutive months in any year were not obtained. They cannot, therefore, be expected to show distinct broods since these may occur at different times in different years. The recently published work of Gibbons in the North Sea (1933) does not give sufficient data for a comparison to be made. He states, however, that two broods occur, the main one in April and a secondary one in August.

On page 806 it has been shown that the phytoplankton had an effect on Calanus in 1933, mainly on the survival of the broods. In 1932 this connexion was not so obvious. There were then diatoms present during at least part of each spawning period at Stations I and II so that no brood failed completely for lack of food. At Station IV there was only one diatom increase, during May and June, which accounted for the survival of the second and third broods, but did not provide food for the first brood in March which failed. It is interesting to compare the delay in the start of breeding in Loch Fyne in 1932 and the accumulation of Stage V before the second brood in Loch Striven with the absence of diatoms in both cases.

In the open sea diatoms are less numerous than in the Clyde Sea-Area, and as a rule there is a large outburst of growth in spring and a smaller one in autumn (Gran, 1929). The sporadic increases during the summer which occur in the Clyde Sea-Area are absent. It is possible that this may have an effect on the Calanus population by delaying, or at least diminishing, one of the later broods.

In fresh water a relationship between the maxima of Cladocera and those of the phytoplankton has been shown by Krogh and Berg (1931).

It is clear that once breeding starts Calanus takes about a month to develop from egg to adult. The eggs appear after two to four weeks, spawning may last for several weeks, and the adults then die out. This sequence of events results in the production of successive broods during the summer, but owing to differences in survival these may not be apparent when only copepodites are taken into account.

The size curves show very much the same features as in 1932. They are seldom clearly unimodal except at the appearance of a new brood (Plate II, April 10th, July 31st). The Stage V and females have a particularly wide range. Although in 1933 the maxima in size correspond with diatom increases the connexion is probably indirect, for in 1932, although in several cases peaks in size corresponded with peaks in diatoms (Part II, p. 122) yet during the longest continued diatom increase there occurred a size minimum as well as a size maximum. In 1932 the connexion between broods and size was shown most clearly in females and Stage V at Station I. In 1933 it is not so clear and shows mainly in females and young copepodites.

The Stage V Calanus in Loch Striven had a considerably larger range in weight than those from Loch Fyne in 1932 (Part IV). In both cases the lowest values (10–12 mg.) were obtained in spring when numbers were low. Loch Fyne was peculiar in that there was no diatom increase until May and that the first brood was delayed and was unsuccessful. It was probably on account of this that the numbers and weight fell steadily till May and the sudden increase in weight came with the second and not with the first brood. After this the females remained much lighter than Stage V in spite of their greater size, as in 1933. The maximum weight of Stage V for the year was considerably higher in Loch Striven (37 mg. on April 24th) than in Loch Fyne (28 mg. on December 14th, 1931). The values for fat and protein percentage were comparable with those for Loch Fyne though the range was greater there. Females had low fat and high protein percentages compared with Stage V, while males occupied an intermediate position. Owing to the comparatively small numbers of analyses made in 1932, the seasonal cycle was not so well shown in Loch Fyne.

The curves for total weight per haul are very different in the two cases except for the low weights in spring. The stock of Stage V Calanus present in Loch Fyne in the winter of 1931–32 was very high when compared with the 1932–33 autumn–winter stock in Loch Striven. With the onset of breeding in spring, the total weights rose in both lochs, corresponding with the number of copepodites.

SUMMARY.

1. The seasonal changes in the population of Calanus in Loch Striven in 1933 have been investigated.

2. There were three main breeding periods. The first was in February and March, an unsuccessful beginning of the second in April, the true second brood in May to June, the third in July, and subsidiary broods in August and September.

3. Numbers were very low until April when the copepodites of the first brood caused a large increase; there was a second increase in May consisting mainly of the eggs of the second brood, and the maximum for the year came in July. The last and subsidiary broods provided the stock for the autumn and winter of 1933.

4. The reliability of the total numbers is discussed and it is concluded that a study of the percentage composition of the catch gives a reliable indication of the course of breeding.

5. A breeding period is always preceded by a large proportion of females with immature ovaries which gives way to a large proportion of mature females at the time of spawning. Spermatophores are found

chiefly on females with immature ovaries and are usually most numerous when males are abundant.

6. The Calanus of the first brood were almost entirely restricted to the upper 10 metres. This was not so for Stage V and adults of the later broods.

7. The Calanus of the first brood, which developed when the sea was at its coldest, were the largest found during the year. Thereafter there was a gradual fall, corresponding to the warming of the sea. On this fall was superimposed a series of variations caused by each brood. With the first appearance of each brood the fall in size was temporarily checked. This is shown for each copepodite stage.

8. The changes in dry weight followed the broods and changes in size, the most marked change being with the first brood in April, after which there was a general fall. Females, though largest, weighed least and Stage V, though smallest, were heaviest. This is due to differences in water content.

9. There was a spring diatom increase in March–April, followed by smaller increases in May, July and August–September. These coincided with the three main spawning periods so that the resulting nauplii had a rich food supply. The eggs spawned in April lacked diatoms and failed to develop into copepodites. The results indicate that the success or failure of a brood depends on the presence or absence of diatoms during the early stages of development.

10. The remaining constituents of the microplankton (chiefly minute flagellates) although at times numerous show no relation to breeding periods or survival.

11. The fat content of Calanus followed the changes in weight. There was also an increase in the percentage of fat with the appearance of each brood. The percentage of fat was highest in Stage V and lowest in females.

12. The protein content of Calanus followed in general the changes in weight. The percentage of protein was highest in females and lowest in Stage V.

13. The increase in percentage of fat which accompanied the increase in size and weight with the appearance of each brood suggests that a storage of fat can take place when food is plentiful.

14. The total weight of Calanus per haul is largely dependent on the number of Stage V copepodites.

15. The parasites occurring in Calanus are considered. They are most abundant in the females from the autumn–winter stock.

16. A comparison is made with previous work in this and other areas.

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TABLE I.

CALANUS IN FIVE HAULS.

Date.		Eggs.		Nauplii.		Copepodites. I.		II.		III.		IV.		V.		Adults. ♀		♂		Total.
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	
Jan.	17	–	–	2	1	–	–	–	–	–	–	1	–	223	73	57	19	22	7	305
,,	23	–	–	–	–	–	–	–	–	–	–	–	–	166	67	54	22	28	11	248
,,	30	3	2	–	–	–	–	–	–	–	–	1	1	104	65	30	19	21	13	159
Feb.	6	2	1	–	–	–	–	–	–	–	–	–	–	76	31	151	61	20	8	249
,,	13	7	5	7	5	–	–	–	–	–	–	–	–	46	33	69	50	10	7	139
,,	20	34	32	19	18	–	–	–	–	–	–	–	–	3	3	50	47	1	1	107
,,	27	13	28	23	49	1	2	–	–	–	–	–	–	3	6	7	15	–	–	47
March	7	83	59	18	13	1	1	–	–	–	–	–	–	2	1	36	26	1	1	141
,,	13	53	64	20	24	1	1	–	–	–	–	–	–	–	–	9	11	–	–	83
,,	20	79	42	39	21	23	12	31	16	6	3	–	–	1	1	11	6	–	–	190
,,	27	2	1	49	32	35	23	15	10	23	15	18	12	3	2	7	5	1	1	153
April	4	9	1	55	5	114	11	262	26	339	33	120	12	113	11	9	1	5	1	1,026
,,	10	387	32	99	8	49	4	104	9	123	10	167	14	174	14	39	3	63	5	1,205
,,	17	2,508	40	325	5	298	5	562	9	504	8	457	7	1,091	18	115	2	349	6	6,209
,,	24*	3,215	29	215	2	95	1	150	1	435	4	1,270	12	3,925	36	815	7	835	8	10,955
May	1	329	5	84	1	74	1	257	4	314	5	819	12	3,232	48	1,014	15	555	8	6,678
,,	8*	256	8	8	–	24	1	92	3	96	3	212	7	1,808	57	428	14	256	8	3,180
,,	15†	243	20	27	2	4	–	26	2	62	5	42	4	591	50	105	9	95	8	1,195
,,	22*	7,015	70	1,155	12	5	–	–	–	30	–	135	1	1,065	11	270	3	295	3	9,970
,,	29	4,168	64	1,120	17	2	–	10	–	11	–	22	–	733	11	279	4	190	3	6,535
June	5*	1,692	48	1,124	32	124	4	66	2	48	1	24	1	364	10	40	1	83	2	3,565
,,	12†	786	45	474	27	112	6	64	4	61	4	29	2	169	10	28	2	31	2	1,754
,,	19*	276	21	94	7	108	8	223	17	179	14	121	9	256	20	28	2	14	1	1,299
,,	26*	447	28	67	4	30	2	18	1	58	4	116	7	646	40	154	10	79	5	1,615
July	3*	1,910	23	180	2	40	1	30	–	140	2	400	5	3,900	48	970	12	585	7	8,155
,,	10*	25,080	68	8,310	23	180	1	85	–	165	–	410	1	1,535	4	985	3	250	1	37,000
,,	17	2,350	28	1,576	19	538	6	671	8	382	5	153	2	1,692	20	726	9	302	4	8,390
,,	24	21,516	66	776	2	709	2	2,709	8	3,225	10	983	3	2,016	6	607	2	150	1	32,691
,,	31	389	4	785	9	683	8	666	7	1,670	19	2,279	25	1,550	17	936	10	72	1	9,030
August	7	1,304	28	489	11	94	2	214	5	254	6	584	13	1,343	29	278	6	52	1	4,612
,,	14	93	5	26	1	8	–	36	2	15	1	105	6	1,540	81	35	2	42	2	1,900
,,	21	25	1	9	1	21	1	81	4	62	3	95	5	1,468	80	60	3	24	1	1,845
,,	28†	8	1	–	–	28	4	67	8	50	6	83	10	543	68	15	2	7	1	801
Sept.	11	112	4	–	–	12	1	–	–	60	2	228	9	1,996	79	96	4	24	1	2,528
Oct.	2‡	5	1	1	–	1	–	1	–	18	3	49	8	478	81	36	6	3	1	592

* Numbers in 4 hauls. † Numbers in 2 hauls. ‡ Numbers in 1 haul.

TABLE II.

Number of Calanus Above and Below 10 Metres in the Divided Haul.

Date.		Below 10 metres.									Above 10 metres.									
		Eggs.	Npl.	I.	II.	III.	IV.	V.	♀	♂	Eggs.	Npl.	I.	II.	III.	IV.	V.	♀	♂	Total.
March	27	–	1	–	1	–	–	–	–	–	1	16	13	4	3	–	1	–	–	40
April	4	–	2	1	3	8	3	13	1	2	4	18	20	61	105	31	18	1	–	291
,,	10	3	3	1	4	4	8	16	3	3	114	7	7	13	24	40	15	1	–	266
,,	17	36	8	5	3	4	8	32	5	22	480	17	45	111	128	97	63	6	15	1,085
,,	24*	224	13	1	1	1	37	164	63	46	27	2	4	26	64	88	85	8	39	893
May	1	64	19	14	21	18	84	612	197	93	–	–	–	11	71	170	140	12	17	1,543
,,	8*	79	24	–	1	1	2	33	5	3	7	1	5	19	43	65	80	21	27	416
,,	15*	19	8	–	–	1	1	11	2	6	1	–	–	6	16	4	13	8	5	101
,,	22*	81	17	–	–	–	–	25	2	18	2,915	220	1	1	–	7	4	12	5	3,308
,,	29	241	102	–	1	–	–	86	22	27	407	82	2	1	3	2	11	5	3	995
June	5*	37	97	2	1	1	1	32	1	3	4	198	18	1	–	–	–	–	–	396
,,	12	250	103	6	2	4	4	43	1	9	31	63	73	43	31	8	1	–	–	672
,,	19*	36	19	–	3	3	5	50	4	–	4	7	38	73	37	18	–	1	–	298
,,	26*	25	8	1	3	2	3	48	11	8	203	12	–	–	1	–	1	–	–	326
July	3*	22	2	3	10	18	43	529	101	103	577	15	–	–	–	–	1	–	1	1,425
,,	10*	262	309	32	43	45	80	261	221	48	277	50	1	–	–	–	–	1	–	1,630
,,	17	317	274	162	241	177	63	337	221	57	38	2	1	–	–	–	–	–	–	1,890
,,	24	935	104	88	209	254	101	301	57	19	931	2	1	–	1	2	5	–	1	3,011
,,	31	35	90	100	85	140	167	218	132	12	42	7	3	1	2	–	–	–	–	1,034
August	7	65	45	4	26	22	80	152	38	4	23	24	2	–	–	–	3	–	–	488
,,	14	13	2	–	2	1	3	103	3	2	10	2	–	–	–	–	3	–	–	144
,,	21	8	2	1	22	16	13	202	8	6	3	1	2	1	–	–	2	–	–	287

* This haul excluded from Table I.

TABLE III.

Median Lengths of Calanus in 1933.

	Males.		Females.		Stage V.		Stage IV.		Stage III.		Stage II.		Stage I.	
Date.	No. measured.	Median length.	No. measured.	Median length.	No. measured.	Median length.	No. measured.	Median length.	No. measured.	Median length.	No. measured.	Median length.	No. measured.	Median length.
17.1.33	20	2·53	58	2·56	212	2·10	—	—	—	—	—	—	—	—
23.1.33	26	2·44	55	2·56	161	2·08	—	—	—	—	—	—	—	—
30.1.33	149	2·34	98	2·41	99	2·05	—	—	—	—	—	—	—	—
6.2.33	79	2·40	593	2·40	76	2·08	—	—	—	—	—	—	—	—
13.2.33	38	2·34	184	2·41	41	2·00	—	—	—	—	—	—	—	—
20.2.33	12	2·36	217	2·45	—	—	—	—	—	—	—	—	—	—
27.2.33	—	—	25	2·50	—	—	—	—	—	—	—	—	—	—
7.3.33	—	—	71	2·40	—	—	—	—	—	—	—	—	—	—
13.3.33	—	—	27	2·36	—	—	—	—	—	—	—	—	—	—
20.3.33	—	—	86	2·48	—	—	—	—	—	—	28	1·03	22	0·74
27.3.33	—	—	68	2·41	—	—	15	1·76	23	1·43	13	1·06	29	0·73
4.4.33	72	2·44	100	2·58	105	2·30	116	1·87	113	1·48	106	1·09	87	0·76
10.4.33	175	2·50	224	2·70	146	2·40	140	1·93	111	1·51	91	1·07	44	0·73
17.4.33	101	2·58	137	2·79	197	2·49	102	1·98	123	1·50	113	1·06	106	0·74
24.4.33	152	2·61	151	2·82	174	2·49	96	1·95	81	1·46	52	1·03	87	0·71
1.5.33	78	2·62	148	2·80	195	2·48	93	1·89	125	1·42	74	1·03	26	0·69
8.5.33	85	2·60	118	2·78	165	2·45	105	1·85	68	1·38	41	0·98	—	—
15.5.33	101	2·62	144	2·74	160	2·51	74	1·75	75	1·33	33	0·96	—	—
22.5.33	168	2·61	149	2·71	189	2·51	103	1·76	31	1·36	—	—	—	—
29.5.33	141	2·63	139	2·65	141	2·49	24	1·79	—	—	—	—	—	—
5.6.33	82	2·67	39	2·66	253	2·50	25	1·81	48	1·42	63	0·99	120	0·66
12.6.33	186	2·64	169	2·66	146	2·42	45	1·74	71	1·33	68	0·94	104	0·64
19.6.33	178	2·61	186	2·65	182	2·44	101	1·73	119	1·28	113	0·90	105	0·63
26.6.33	138	2·54	139	2·58	150	2·35	107	1·71	58	1·33	21	0·95	30	0·66
3.7.33	116	2·57	184	2·51	185	2·40	118	1·74	102	1·29	70	0·95	84	0·68
10.7.33	95	2·52	196	2·45	251	2·35	162	1·75	76	1·34	58	0·97	62	0·68
17.7.33	100	2·43	207	2·46	232	2·33	77	1·76	111	1·28	133	0·94	125	0·63
24.7.33	139	2·41	107	2·41	295	2·33	97	1·68	119	1·25	106	0·91	140	0·64
31.7.33	118	2·43	131	2·42	211	2·34	163	1·59	136	1·23	84	0·91	101	0·64
7.8.33	59	2·47	97	2·41	290	2·22	106	1·58	78	1·23	72	0·90	82	0·64
14.8.33	40	2·39	33	2·35	233	2·33	83	1·65	—	—	—	—	—	—
21.8.33	19	2·46	47	2·30	194	2·35	71	1·67	54	1·26	89	0·94	22	0·67
28.8.33	—	—	14	2·36	240	2·30	78	1·62	50	1·24	61	0·93	28	0·63
11.9.33	19	2·35	104	2·23	247	2·25	202	1·61	46	1·24	—	—	—	—
2.10.33	—	—	34	2·27	235	2·17	46	1·68	17	1·28	—	—	—	—

TABLE IV.

Number of Organisms in 20 c.c. of Sea Water.

Date, 1933.	Depth in m.	All Diatoms.	Skeletonema.	Thalassiosira.	Leptocylindrus.	Rhizosolenia.	Chaetoceros.	Pennate Diatoms.	Other Diatoms.	Dinoflagellates.	Silicoflagellates.	Coccolithophores*	Unidentified flagellates.*	Ciliates.	Other organisms.	T. in °C.
23·1	0	165	125	10	—	—	24	4	2	2	3	—	61	2	1	—
23·1	30	33	9	6	—	—	—	14	4	1	—	—	1	—	1	—
30·1	0	707	673	11	—	—	—	23	—	4	3	—	210	—	—	4·50
30·1	30	25	5	5	—	—	—	26	6	6	—	—	6	—	1	8·70
6·2	0	LOST														7·63
6·2	30	22	6	11	—	—	—	11	2	7	—	—	10	—	—	8·20
13·2	0	102	66	16	—	—	—	14	6	2	—	—	8	—	—	7·80
13·2	30	36	15	5	—	—	2	13	1	7	—	—	5	—	—	8·04
20·2	0	876	809	20	—	—	8	36	3	20	—	—	260	1	—	5·80
20·2	30	36	8	8	—	—	—	20	—	2	—	—	4	1	1	7·95
27·2	0	245	142	58	—	—	3	42	—	6	—	—	26	1	1	6·32
27·2	30	334	239	35	—	—	—	58	2	5	—	—	7	1	—	6·81
7·3	0	490	365	56	—	—	7	60	2	7	—	—	51	1	1	6·32
7·3	30	355	204	80	—	—	1	70	—	1	—	—	4	—	—	6·37
13·3	0	2,048	1,794	219	—	—	23	12	—	23	—	—	5,200	9	—	6·83
13·3	30	139	89	16	—	—	—	34	—	3	—	—	39	—	—	6·82
20·3	0	37,200†	34,405	2,460	—	—	25	310	—	30	—	—	12,500	2	14	6·82
20·3	30	201	155	10	—	—	—	36	—	1	—	—	20	—	—	7·03
27·3	0	166,000†	123,800	41,450	—	—	375	375	—	29	8	90	5,300	2	9	7·02
27·3	30	822	732	67	—	—	8	15	—	—	—	—	10	1	—	7·00
4·4	0	111,000†	107,100	3,900	—	—	—	—	—	3	2	—	1,260	—	6	7·27
4·4	30	11,165	10,850	240	—	—	8	67	—	1	3	—	—	—	—	6·87
10·4	0	15,228	14,700	189	—	—	66	273	—	54	2	—	3,600	3	—	8·35
10·4	30	7,466	7,300	160	—	—	—	6	—	2	4	—	17	1	1	6·92
17·4	0	5,487	5,300	10	—	9	74	82	12	61	1	30	3,500	9	1	8·07
17·4	30	2,548	2,370	156	—	—	3	8	12	5	8	—	25	3	1	7·01
24·4	0	7	2	—	—	—	—	5	—	15	1	—	48,000	—	13	8·18
24·4	30	155	142	12	—	—	—	1	—	5	1	—	500	1	—	6·97
1·5	0	26	22	—	—	—	4	—	—	33	—	—	58,000	—	—	9·01

1·5	30	249	213	34	—	—	—	2	—	7	—	—	600	—	—	7·02
8·5	0	5	—	—	—	—	—	5	—	31	—	—	63,000	—	—	10·32
8·5	30	98	85	13	—	—	—	—	—	1	1	—	800	4	—	7·47
15·5	0	17	8	1	—	—	—	8	—	8	2	—	32,000	—	—	8·79
15·5	30	56	27	26	—	—	—	2	1	2	1	—	330	—	—	7·10
22·5	0§	85,000†	74,440	10,420	—	—	—	140	—	144	4	—	11,000	4	202	13·15
22·5	30	64	49	12	—	—	2	1	—	2	—	—	700	2	—	7·22
29·5	0	65	37	8	20	—	—	—	—	72	—	30	5,000	—	2	11·45
29·5	30	64,000†	60,660	3,215	—	—	—	125	—	8	133	—	3,000	6	—	7·20
5·6	0	19	15	1	—	—	3	—	—	91	—	—	6,000	1	9	14·51
5·6	30	2,220	1,915	292	—	—	—	13	—	4	6	—	2,000	2	1	7·53
12·6	0	2	—	2	—	—	—	—	—	50	—	—	8,000	—	2	12·90
12·6	30	96	83	9	—	—	—	3	1	9	7	—	1,000	—	2	7·71
19·6	0	26	22	2	—	—	—	2	—	31	—	100	44,000	—	1	11·10
19·6	30	59	32	26	—	—	—	1	—	6	4	100	900	—	1	8·51
26·6	0	104	2	—	96	—	3	3	—	151	1	1,400	34,600	1	2	14·04
26·6	30															7·90
3·7	0	2,167	1,761	173	29	1	16	187	—	20	1	150	4,000	—	—	10·93
3·7	30	64	45	17	—	—	—	2	—	5	1	—	600	3	1	7·78
10·7	0	19,571	45	43	19,200†	8	176	95	4	209	—	500	7,600	1	10	14·06
10·7	30	48,000†	42,780	1,370	385	—	1,240	2,225	—	1	6	300	5,700	4	—	8·63
17·7	0	107	7	11	2	1	53	33	—	73	72	600	12,400	4	1	13·90
17·7	30	555	296	153	6	—	11	89	—	6	2	30	600	—	—	8·42
24·7	0	40	4	—	17	2	8	9	—	64	—	100	6,000	3	—	16·40
24·7	30	181	77	80	—	—	6	18	—	12	1	30	700	1	—	8·90
31·7	0	3,288	3	14	35	39	3,100	95	2	385	1	500	12,500	1	1	14·80
31·7	30	122	63	34	—	—	16	9	—	15	4	—	1,000	—	—	9·57
7·8	0	536	—	1	11	3	477	43	1	58	1	500	8,500	1	—	15·71
7·8	30	49	15	15	3	—	7	9	—	16	—	—	1,000	1	—	10·51
14·8	0	9,200†	—	250	1,864	48	6,800	224	14	1,007	—	400	6,600	14	8	14·53
14·8	30	143	49	10	11	2	33	37	1	20	—	30	1,000	—	1	10·35
21·8	0	6,634	—	1	5,840	92	910	147	4	26	3	1,200	4,000	—	1	13·78
21·8	30	403	27	60	65	26	144	81	—	46	—	100	1,000	1	1	12·22
28·8	0	7,992	—	5	283	87	7,600	25	2	107	—	300	9,000	1	2	14·71
28·8	30	655	12	14	62	5	499	62	1	41	2	30	1,000	—	—	12·98
11·9	0§	1,467	13	—	296	30	1,100	25	3	59	—	—	1,000	3	5	15·12
11·9	30§	69	15	2	4	3	24	15	—	8	—	—	200	—	—	10·70

* In the surface samples from March 13th onwards and in the 30m. samples from April 24th onwards, these were counted under a higher magnification on a fraction of a ruled slide.

† Calculated from partial counts on ruled slides.

§ Sample preserved in 5% formalin.

TABLE V.

Date.	Male Calanus. Weight of 100 in mg.	Median length in mm.	Pro-tein %	Fat %	Female Calanus. Weight of 100 in mg.	Median length in mm.	Pro-tein %	Fat %	Stage V Calanus. Weight of 100 in mg.	Median length in mm.	Pro-tein %	Fat %	% carrying sperma-tophores.	Females ‖ Spermatophores and condition of ovaries. Early %	Medium %	Mature %	Spent %	Chemical composition of hauls. Calcu-lated dry weight per haul in mg.	Calcu-lated fat per haul in mg.	Calcu-lated protein per haul in mg.
17.1.33	20·8	2·44	—	20	15·2	2·42	35	27	15·6	2·14	33	27	8·6					9·7	2·6	3·5
			—	28	15·7	2·48	—	—		2·10	39	—								
23.1.33	20·3	2·40	—	—	17·3	2·49	—	—	15·9	2·17	—	—	5·5					8·5	2·2	3·1
30.1.33	16·7	2·29	40	25	12·3	2·32	43	—	11·6	2·04	29	27	13·3					3·8	1·0	1·1
	16·5	2·34	—	—						2·04	—	22								
6.2.33	17·9	2·36	—	27	13·3	2·34	52	24	12·3	2·09	—	34	1·3					6·5	1·7	2·9
					12·6	2·36		22												
13.2.33*	13·6	2·33	—	—	12·8	2·34	—	24	13·1	2·11	—	—	3·3					3·3	0·9	2·4
20.2.33†	13·8	2·34	—	—	15·6	2·32	40	19	16·7	2·25	—	—	0					1·5	0·3	0·6
							—	20												
27.2.33	—	—	—	—	—	—	—	—	—	—	—	—	0					0·3	0·0	0·1
7.3.33‡	12·8	2·33	—	—	13·8	2·29	72	22	13·8	2·12	—	—	0					1·1	0·2	0·7
					13·1	2·31	—	23												
13.3.33	—	—	—	—	—	—	—	—	—	—	—	—	0					0·2	0·0	0·1
20.3.33§	—	—	—	—	15·6	2·32	60	17	14·3	2·15	—	—	0					0·3	0·0	0·2
27.3.33	14·2	2·27	—	—	15·2	2·35	69	21	12·0	2·13	—	30	0					0·6	0·1	0·2
							—	22												
4.4.33	18·4	2·36	—	29	16·8	2·55	55	20	16·5	2·22	31	32	13·0	11	41	36	0	7·1	2·3	2·5
					15·3	2·53	—	—	15·0	2·25	35	31								
10.4.33	22·7	2·45	50	36	22·8	2·67	39	22	23·6	2·36	31	32	15·6	4	37	57	1	17·0	5·3	5·8
	20·8	2·46	42	34	23·6	2·67	39	22	22·4	2·34	33	30								
17.4.33	25·9	2·48	—	31	27·1	2·73	47	26	29·9	2·41	28	33	18·2	0	42	55	3	106·0	35·5	36·8
	26·5	2·50	—	31	26·9	2·73	43	—	28·0	2·40	38	36								
24.4.33	29·0	2·56	33	33	27·7	2·75	36	27	37·5	2·45	37	39	9·9	11	47	42	0	545·8	185·2	192·7
	27·9	2·57	—	32	28·0	2·76	45	30	36·1	2·44	33	31								
1.5.33	23·0	2·53	42	28	24·2	2·72	—	24	22·8	2·38	45	26	2·0	5	29	66	0	250·3	64·5	100·9
	23·1	2·54	—	27	26·7	2·71	—	27	23·7	2·39	35	25								
8.5.33	29·1	2·56	28	30	23·3	2·65	61	24	30·1	2·41	33	37	4·2	3	40	52	3	188·6	64·5	67·2
									28·6	2·43	—	—								
	29·4	2·55	31	—	23·7	2·66	—	25	30·9	2·44	31	36								
									30·0	2·45	—	—								

15.5.33	26·9	2·55	42	26	20·8	2·64	62	20	35·1	2·48	44	27	14·3	10	35	54	1	135·5	35·2	57·9
		2·55	42	25	23·1	2·68	58	20	36·6	2·46	38	26								
22.5.33	26·2	2·52	42	24	19·6	2·59	65	19	27·7	2·36	37	30	12·1	0	12	88	0	109·7	30·4	45·3
	25·9	2·51	—	28	19·9	2·56	—	20	26·4	2·37	—	—								
29.5.33	28·7	2·58	31	28	23·8	2·61	52	19	35·0	2·44	48	26	20·2	1	17	82	0	75·7	21·3	34·7
	29·5	2·58	—	25	23·8	2·57	61	20	33·8	2·41	45	35								
5.6.33	30·6	2·61	31	32	24·8	2·59	52	24	35·0	2·44	32	33	17·1	4	16	79	1	41·9	13·4	14·1
	29·3	2·60	34	32	25·2	2·62	58	20	34·1	2·43	—	33								
12.6.33	32·7	2·60	36	30	26·3	2·59	62	30	35·3	2·42	33	36	1·8	6	8	82	3	42·8	16·1	15·7
	33·4	2·62	—	40	25·6	2·60	—	29	35·0	2·39	36	42								
19.6.33	32·3	2·61	33	—	25·3	2·59	54	20	34·2	2·40	37	31	3·1	5	9	84	2	32·9	9·9	13·6
					23·5	2·56	56	18	35·3	2·39	45	31								
26.6.33	29·6	2·53	42	26	21·1	2·53	61	30	33·9	2·39	34	39	13·6	10	25	64	0	73·9	25·8	28·2
		2·51	35	35	20·3	2·50	—	26	33·2	2·35	36	34								
3.7.33	31·5	2·55	35	30	20·7	2·50	60	26	32·7	2·39	37	40	17·4	44	21	31	2	454·9	167·0	171·9
	30·3	2·53	34	31	20·8	2·50	54	29	34·8	2·38	34	38								
10.7.33	27·6	2·53	42	35	22·5	2·43	62	23	34·2	2·40	38	35	6·6	6	11	82	0	220·9	71·0	92·4
	26·2	2·49	40	35	22·2	2·46	—	23	32·8	2·38	31	36								
17.7.33	23·1	2·38	—	38	18·6	2·40	50	26	29·2	2·30	38	40	4·5	16	23	57	2	159·8	57·1	67·2
					17·5	2·37	—	24	30·5	2·33	43	37								
24.7.33	21·6	2·37	51	27	16·1	2·38	67	18	32·1	2·37	46	36	8·0	14	24	62	0	211·9	68·9	95·5
	21·6	2·36	—	32	17·2	2·43	76	21	31·3	2·34	38	33								
31.7.33	22·2	2·41	41	30	19·1	2·42	61	19	29·8	2·38	37	42	1·5	1	9	90	0	215·3	81·7	88·7
					17·8	2·46	65	20		2·37	—	42								
7.8.33	22·8	2·41	52	31	15·5	2·36	81	20	30·0	2·37	46	39	4·1	10	13	72	3	112·1	41·2	53·5
	23·7	2·43	54	31	15·2	2·40	64	20	29·7	2·35	45	38								
14.8.33	21·9	2·40	41	30	16·4	2·39	73	23	27·7	2·32	32	35	3·2	12	3	79	5	90·4	30·2	31·3
	22·9	2·41	43	32	15·9	2·37	78	22	26·9	2·33	36	32								
21.8.33	19·8	2·37	47	29	14·5	2·28	—	19	27·8	2·34	44	36	8·5	13	8	73	5	86·8	32·0	37·5
	19·4	2·36	50	28	16·5	2·36	—	18	26·9	2·32	41	39								
28.8.33	18·5	2·30	49	30	13·5	2·26	70	25	23·6	2·26	35	36	0	13	16	65	6	71·9	27·5	27·7
					13·5	2·26	67	23		2·23	41	38								
11.9.33	16·3	2·30	—	—	13·4	2·29	65	26	24·4	2·36	37	38	1·8	—	—	—	—	109·9	41·4	40·3
					13·0	2·32	—	—	25·7	2·35	35	39								
2.10.33	—	—	—	—	—	—	—	—	21·6	2·19	—	—	8·3	—	—	—	—	118·2	44·3	43·9
									23·0	2·23	—	—								

* Weight determined on 23 V.
† Weight determined on 42♂ and 21 V.
‡ Weight determined on 25♂ and 26 V.
§ Weight determined on 21 V.
} In all other cases more than 50 were used and usually 100.
|| Abnormal Calanus are not included in the table.