On the Biology of *Calanus finmarchicus*. Part IV. Seasonal Changes in the Weight and Chemical Composition in Loch Fyne.

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With 5 Figures in the Text.

The value of the zooplankton as a fish food depends not only on its distribution and numbers but also, to a large extent, on its chemical composition. Analyses of the marine plankton have already been made by Brandt (1898), Brandt and Raben (1919–22), Meyer (1914), Moberg (1926) and Wimpenny (1929). These authors worked on tow-nettings containing mixed plankton, both plant and animal. In the analyses of Brandt and of Brandt and Raben an attempt was made to assess the value of the zooplankton and of the phytoplankton apart from one another. Seasonal variations have apparently been dealt with only by Wimpenny and Moberg who had the disadvantage of dealing with mixed catches ; but the variation shown in some of the analyses given by Brandt and by Brandt and Raben suggests that seasonal variations in chemical composition take place.

The analyses given by the above authors, with the exception of those by Moberg and Wimpenny, were made on preserved material and no separation of individual species of plants and animals was possible ; in any case, the large numbers they had to deal with would have made such an attempt extremely laborious even if the method of preservation adopted had allowed of it. However, by analysing a number of catches in which certain species of plants or animals predominated, Brandt, and Brandt and Raben, were able to give an approximate figure for the chemical composition of certain groups or species.

The results in the following pages record an attempt to measure the variations in the composition of *Calanus finmarchicus* by itself. *C. finmarchicus* is an important food of certain fish and is widely distributed. In the Clyde Sea-Area it constitutes a considerable percentage of the zooplankton as a whole. The object of the work was to ascertain, in conjunction with the observations on size and distribution by Marshall (1933) and Nicholls (1933) recorded in Parts I and II of this series, what changes in weight and chemical composition took place throughout the year. Although Calanus predominated in all the catches, it was not considered that analyses of the catches as a whole would be of sufficient value and it was decided to separate the Calanus from other species. In addition, since it seemed possible that differences between male, female and the later copepodite stages of Calanus might exist, these were separated before analyses were made. Only living Calanus were used throughout. No stages younger than the fifth copepodite were dealt with largely because of the labour involved in their separation, but also because in actual weight they are relatively unimportant. The collection of material was made by Dr. A. G. Nicholls during the fortnightly visits to Loch Fyne. Very considerable help in the picking out of the Calanus was given by Miss S. M. Marshall and Dr. A. G. Nicholls. All the measurements were made by Miss S. M. Marshall. I have to thank both for making the work possible.

METHODS.

Collection of Material.

Vertical hauls with a 1-metre stramin net were made in the deep water off Strachur in Loch Fyne and the catch suitably diluted and brought to the laboratory. When sufficient numbers could not be obtained by the vertical hauls a horizontal haul was made in deep water. Vertical hauls were preferred since the material was then more likely to be similar to that used for size determination by Marshall (Part II). In the laboratory the Calanus generally lived well and could be kept for several days if the dilution was sufficiently great. If not well diluted the Calanus died off rapidly owing to oxygen depletion and decomposition of the dead ones. In addition, fat globules formed on the surface of the water and this would have vitiated fat analyses. Usually on the day following capture a series of samples of Calanus was taken from the diluted tow-nettings and separated into males, females and Stage V Calanus. Younger stages than this were rejected as it would have required a very large number for analysis and also because their occurrence was less frequent. After some practice the separation can be effected by the naked eye, but in all cases they were finally examined under the microscope. As is shown in the foregoing paper by Nicholls (Part I), the Calanus taken at Strachur consisted generally of a number of stages. At certain times males and females were scarce; sufficient for analysis could not then be obtained since it involved the examination of very many thousands of individuals. While this is to be regretted, it should be noted that at these times the very fact that they were scarce made them unimportant as a fish food. Stage V was nearly always present in sufficient numbers for analysis and except during breeding periods Calanus in this area seem to live longer in this stage than in any other (Nicholls, Part I).

Size and Weight.

Two samples of about 100 Calanus were measured under the microscope (see Marshall, Part II), each individual in a separate small drop of sea-water on a slide, and transferred alive to a small quantity of filtered sea-water. They were then collected in a sintered glass Gooch crucible, filtered free from sea-water under pressure and given several (generally three) washes with small quantities of distilled water. They were then dried to constant weight at 110° C. Washing with distilled water was necessary to get rid of the adherent sea-water but the washing should not be prolonged or the Calanus may lose some salts or may even lose some fat. Washing was usually completed in two or three minutes. The weight of the dried Calanus was measured to the nearest 0·1 mg. and was generally between 10 and 25 mg. On ignition the weight of ash was less than 1 mg. showing that the washing had been sufficiently good. On the other hand, the weight of ash was too small to be sufficiently accurate for ash determination. Drying at 110° C. was made as short as was consistent with complete removal of water since continued heating at this temperature results in a slight loss of volatile organic material.

Samples used for weight determination could not be used for any other estimations and the weight of these samples was used for determining the protein and fat percentages on separate samples. Transference (after washing with distilled water) of the undried Calanus from a Gooch crucible to a coverslip for subsequent weighing and fat or protein determination was attempted on several occasions but a loss of 1–3 mg. occurred, largely owing to splitting off of fat globules from the Calanus.

Ash.

Ash was determined on a large number of Stage V Calanus on one occasion only, the males and females being insufficient in numbers. The dry weight was obtained as above and the dry Calanus ignited to a white ash at red heat with the Bunsen burner. This procedure is likely to have resulted in a certain amount of loss by volatilisation of sodium and potassium chlorides and the ash percentage given is a minimum value for the time of year at which the estimation was made. A more elaborate procedure was not advisable with the small quantity of material available and in any case the loss is not likely to have been great.

Protein.

Protein was estimated from the total nitrogen content. Duplicate samples of 100 Calanus were combusted with sulphuric acid in the presence of potassium sulphate and a trace of copper and the ammonia formed estimated by Folin's micro-aspiration method (Plimmer, 1920). In the calculation of protein content the customary factor (N × 6·25) has been used. No allowance has been made for the presence of chitin which contains only about 6% N, whereas protein contains about 16% N. Chitin analyses could only be made on large numbers of Calanus (see below) and sufficient numbers could not be obtained regularly. Since Calanus varies in weight considerably in the course of the year, it is unsafe to make a constant correction for chitin nitrogen throughout.

Fat.

Fat was estimated by Stoddard and Drury's saponification method (1929) with some slight modifications. Duplicate samples of 100 Calanus were transferred from the microscope slide to a small basin and there ground up with the alcohol-ether mixture. The whole was then transferred to a 100 c.c. flask with the alcohol-ether mixture. The subsequent treatment was then similar to that described by Stoddard and Drury with the exception that a fat-free filter paper was used instead of the Gooch crucible suggested by them (see Stewart, Gaddie and Dunlop, 1931) and phenolphthalein was used as indicator. The factor used for conversion of titration value to fat was that for triolein. This was used by Brandt and Raben (1919–22) and is within the range given for Calanus in a recent paper by Klem (1932).

Chitin.

A large number (1000) of Stage V Calanus was treated for a short time with dilute hydrochloric acid and then for a considerable time with 15% caustic soda at 100° C. When clean, the residue was collected on a sintered glass Gooch crucible, washed successively with water, alcohol and ether, dried at 110° C. and weighed. The quantity of chitin present was small even in 1000 Calanus and the weight of the ash of the chitin on ignition lay within the experimental error of weighing.

No determinations of carbohydrate were made since a direct estimation would have involved a large number of Calanus and the indirect method of estimation employed by Brandt (1898) and others could not be adopted.

RESULTS.

Size and Weight.

The seasonal variation in the weight of male, female and fifth copepodite Calanus is shown in Figure 1 and Tables I, II and III. As has been mentioned, only Stage V Calanus could be obtained in sufficient numbers regularly and the curves for male and female Calanus are incomplete.

Adult male Calanus were obtained in sufficient numbers for analysis on only four occasions and the dry weight varied from 23·5 mg. to 18 mg. per 100 Calanus. There was a gradual fall in weight from February to May which is related directly to a decrease in size during that time. They were also largest and heaviest during their period of maximum abundance for the year.

Adult female Calanus were obtained fairly regularly from the beginning of March till the end of August. The weight of 100 Calanus varied from 19·5 mg. to about 11 mg. The variation in weight is irregular with a pronounced high peak in May and a fall thereafter. The curve for weight again shows a relation to size especially in the pronounced high peak in May. There is, however, only a slight correspondence between weight and numbers; the May peak in weight and size is associated with a very small increase in numbers of females.

Stage V Calanus show greater variations in weight than either males or females and they were available over a much longer period. In the winter of 1931 the greatest weight was 28 mg. per 100 Calanus. This was associated with their presence in very large numbers at this time. During the period from January to April the weight of 100 Calanus rapidly fell and the minimum was reached early in May when 100 Stage V Calanus weighed only about 10 mg. which is approximately a third of the winter value. After this the weight increased rapidly and reached the maximum for the autumn of 1932 in August and September at 23·5 mg. per 100 Calanus. There is a certain correspondence between numbers of Stage V Calanus and weight. The spring decrease in weight is coincident with the rapid disappearance of the large winter stock of Stage V Calanus. According to Nicholls (Part I) the first breeding period of Calanus for the year began early in March so that the nadir of the weight curve (May 2nd) came on a date when the Stage V Calanus would be expected to consist of individuals belonging to the end of this breeding period. Sufficient numbers for weight determinations were not obtained between the beginning of March and the beginning of April so that the weights during this period could not be obtained. Even on May 2nd only 60 individuals were available for weighing and some doubt exists as to the true state of affairs during this period. With the arrival of the second brood, weight rose rapidly though it was still well below winter values. The increase in weight continued thereafter, but the values ultimately reached were considerably lower than those of the previous winter. This again appears to correspond with numbers to some extent for the stock of Calanus late in 1932 was much lower than that of the winter of 1931–32. The relation of size to weight for Stage V Calanus is not so marked as with males and females but there is a general correspondence of the curves. As has already been mentioned, the catches used for analysis were not the same as those used by Marshall (Part II) for size determination and, as might be expected, the relation between weight and size in the samples actually weighed is closer than that between weight and size in the samples measured and recorded by Marshall (Part II). This is to be explained partly by the fact that the stramin net used for the capture of specimens for analyses probably exerts a certain selection on fifth copepodite Calanus; in addition the samples used for weight determination were measured alive while those used for size measurement by Marshall (Part II) were preserved in formalin which causes a slight swelling of the Calanus.

Although it has been shown that when taken separately, there is a relation between size and weight in male, female and Stage V Calanus, the curves (Fig. 1) demonstrate clearly that the weight depends chiefly on the kind of Calanus being dealt with (male, female or Stage V) and the time of year. Thus, for example, on August 22nd the average size of 100 female Calanus was 2·34 mm. and the weight 11·3 mg.; on the same date 100 Stage V Calanus had an average size of only 2·24 mm. (0·10 mm. *less* than that of the females) and yet the weight (23·5 mg.) was more than *double* that of the females. This anomalous relationship of size to weight between female and Stage V Calanus held from late May till the end of August and probably continued later in the season when females were scarce. It is probably to be accounted for by differences in water content.

During the period from March to May when Stage V Calanus were very light, both males and females were from 50–100% heavier than they; males were somewhat lighter than Stage V Calanus in May in spite of the fact that they were definitely larger. So far as can be said from the small number of observations available, male Calanus are heavier than female Calanus in spite of the fact that the latter are generally larger.

From the above remarks it is obvious that dry weight determinations on a catch containing males, females and Stage V Calanus without a preliminary separation of these, must lead to results which are of little value. It is also apparent that the food value of Calanus does not depend entirely on the numbers present but is influenced very considerably by the dry weights of the different stages at different times of the year.

It was unfortunate that the collection of samples for analysis was limited to Loch Fyne, for, as is shown by Nicholls (Part I), the catches there showed less numerous fluctuations and the variations in the sizes of the different broods were also small (Marshall, Part II).

Hitherto no direct weighings of dried Calanus have been available but some estimations of the weights of copepods without reference to species have been made by Brandt (1898). According to him one gram of dry material is contained in between 3×10^5 and 7×10^5 copepods with a probability that the range is only from 3×10^5 to 5×10^5. In the observations on Calanus from Loch Fyne, the numbers per gram dry weight were

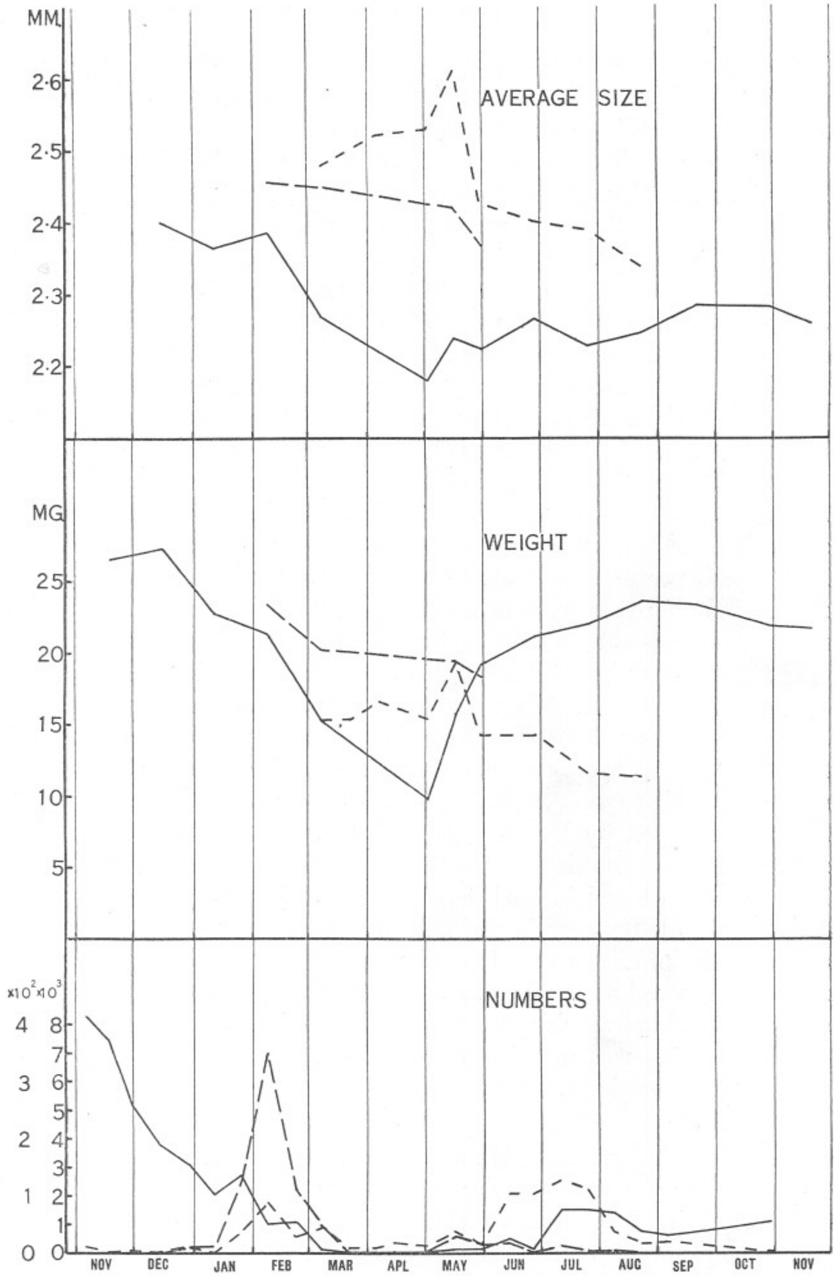

FIG. 1.—Size, weight and numbers of Calanus from Strachur, Loch Fyne.
——— StageV, — — — VI ♂, - - - - - - VI ♀.
Average size in mm. of ca. 100 individuals.
Weight in mg. per 100 individuals.
Numbers taken in one vertical haul (Part I) (V, $\times 10^3$, VI ♂ and VI ♀, $\times 10^2$.).

found to be very much smaller; one gram dry material was contained in 3500 Calanus as a minimum and in 10,000 as a maximum. It should be remembered in this connection, however, that *Calanus finmarchicus* is large compared with the average size of the copepods of the southern North Sea and that the earlier copepodite stages of Calanus have not been dealt with in the analyses from Loch Fyne.

Estimations of the wet weight of Calanus from the Barents Sea have recently been made by Bogorov (1933). The method of weighing adopted by this author (fixation in formalin and drying with filter paper) does not allow of a high degree of accuracy, but is useful in comparing the changes in weight through the copepodite stages to adult. His results showed that adult female Calanus were lighter than Stage V Calanus as has also been found in this area. In the Barents Sea, however, the females were *smaller* than the Stage V Calanus indicating that in this case the females which were lighter probably belonged to a different brood. A close comparison of the results is not possible since his observations were based on a single haul and no seasonal observations were made. His results show that to obtain a suitable quantity of material for analyses of the earlier copepodite stages of Calanus several thousand individuals would be required.

The size measurements in the present paper are those of the length of the cephalothorax while Bogorov measured the length from the head to the tips of the caudal furcæ. It has been found (by Miss S. M. Marshall) that this makes Bogorov's measurements some 20% greater than those recorded in this paper. As has already been mentioned, the method of fixation employed by Bogorov (formalin) may cause a slight swelling of the Calanus. Allowing for these corrections, the largest Stage V and female Calanus found in Loch Fyne are only about 90% of the size of those found by Bogorov in the Barents Sea. If we compare the dry weight of the largest Calanus found in Loch Fyne with the wet weight of the Calanus weighed by Bogorov, we find that about 80% consists of water. This, however, is not a reliable figure for the degree of drying used by Bogorov was empirical and the effect of the formalin on weight may also be appreciable.

Ash.

Since the ash percentage is low, a large number of Stage V Calanus (over 1500) were separated from a catch and collected on a sintered glass Gooch crucible. They were washed several times with distilled water as rapidly as possible and then dried to constant weight at 110° C. The dry mass was then gently ignited till free from carbon, cooled and weighed. The ash was white and weighed 12·9 mg. which was 3·6% of the dry weight of the Calanus. No estimations could be made on male or female Calanus as they were relatively scarce. No analyses of the inorganic constituents of the ash were made.

Figures for the percentage of ash in the plankton have already been given by Brandt (1898), Brandt and Raben (1919–22), Moberg (1926) and others. For a haul rich in copepods, Brandt gives a corrected figure of 7·12% and an average for copepods of 9·3%; Brandt and Raben in their tables give values of 4·24 and 6·42% which are fairly close to those obtained by using *Calanus finmarchicus* alone. Moberg, using material from tow-nettings taken 10 miles off La Jolla, obtained a minimum value of 4% but does not state the composition of the catch. The inshore values obtained by Moberg are very high and are no doubt caused by the silt present.

While the value found (3·6%) in Stage V Calanus probably holds for the major part of the winter, it is possible that there will be changes in ash content associated with the changes in weight.

Fat.

Analyses on adult males and females were limited owing to the difficulty in obtaining specimens in sufficient numbers. Stage V, however, were obtained more regularly. The results of the fat determinations on these are shown in Table III and Figures 2 and 3. The fat content follows the weight curve in general with two exceptions. At the beginning of March with Stage V Calanus the fat content was considerably higher than would be expected had it followed the weight curve and this is shown more clearly on the curve for fat percentage. The lowest value for fat coincided with the lowest point on the weight curve but the lowest percentage of fat was a fortnight later. It is not possible to say whether the peak in fat in March is associated with the spring increase in the phytoplankton, but the fact that the fat content was lowest during the summer when diatoms though not abundant are rarely absent does not support this conclusion. The agreement with the weight curve is to be expected though the high average value for fat content in the autumn and winter is puzzling when we consider that at that time plant food is scarce. Further work will be necessary before the relationship if any of the fat content of Calanus to abundance of phytoplankton can be found.

Analyses of female Calanus were not sufficiently numerous to show whether or not the fat content varied with the state of maturity. They do show, however, that contrary to expectation, female Calanus were less rich in fat than either male or Stage V Calanus.

The results recorded in the present paper are considerably higher than those given by Brandt and by Brandt and Raben for mixed plankton catches in the southern North Sea. They are considerably higher than those of Wimpenny who also worked on mixed catches. A possible objection to the method adopted in the present paper is that the assumption is made that the samples of 100 Calanus used for fat determination have the same weight as the samples used for weight determinations. The difference in weight in duplicate samples taken from a single tow-netting is seldom great (Tables I, II and III) and only exceeded 2 mg. on one occasion (8% error) so that this is not the explanation of the difference. The explanation more probably is that in the present work one stage of a

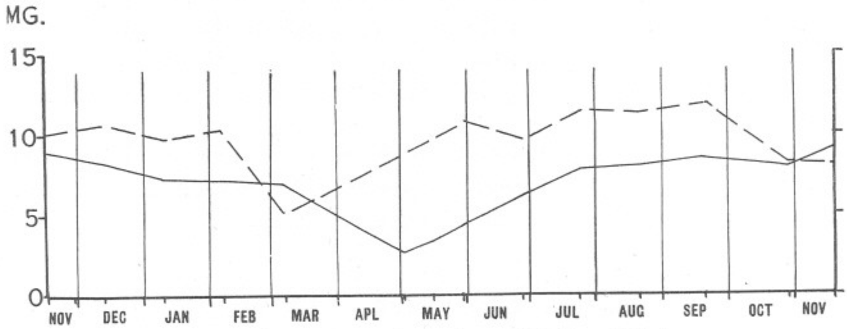

Fig. 2.—Weight of fat and protein per 100 Stage V Calanus.
Fat ———. Protein — — —.

single species is dealt with while the above-mentioned authors dealt with mixed catches.

Seasonal observations have been made by Wimpenny (1929) and he records his results as mg. fat per 1000 zooplankton individuals. The maximum fat content in the North Sea was found in August and the

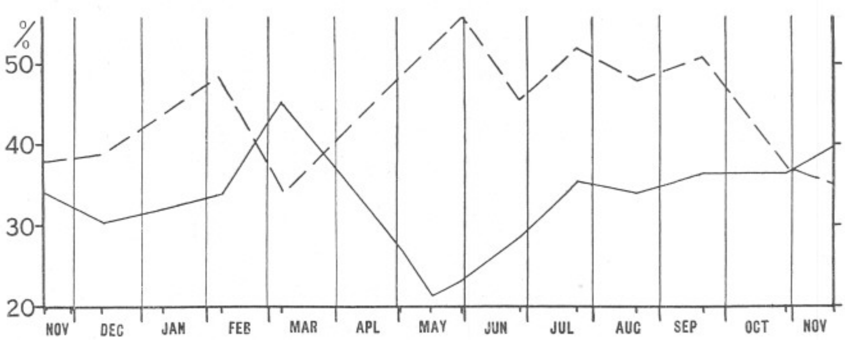

Fig. 3.—Percentage of fat and protein in Stage V Calanus.
Fat ———. Protein — — —.

minimum in October. Stage V Calanus in the Clyde Sea-Area on the other hand had its maximum fat content in March while the results in spring and autumn were uniformly high. Wimpenny's results, however, are based on the weight of fat per 1000 individuals; since he dealt with mixed catches of varying composition and since as shown in the present paper the weight of a given number of individuals may vary considerably in the course of a year, his results should be interpreted with caution.

There is no obvious relation between the percentage of fat in Stage V Calanus and the different broods throughout the year. The first brood of Stage V Calanus had low fat values and thereafter later broods were fatter till the autumn-winter brood with the usual high fat values appeared. Stage V Calanus appears, in the Clyde Sea-Area at any rate, to be the most numerous stage of this important fish food for the major part of the year (Nicholls, Part I) and in view of the results of other authors on mixed plankton catches, it must be classed as one rich in fat.

The results of fat determinations on adult male and female Calanus are not numerous enough for any seasonal changes to be deduced. In adult male Calanus the value fluctuated between 18 and 34% and in adult females between 11 and 30%. Both are less fat on the whole than Stage V Calanus. The low fat values in females were unexpected and the changes recorded showed no relationship to the breeding periods recorded by Nicholls (Part I).

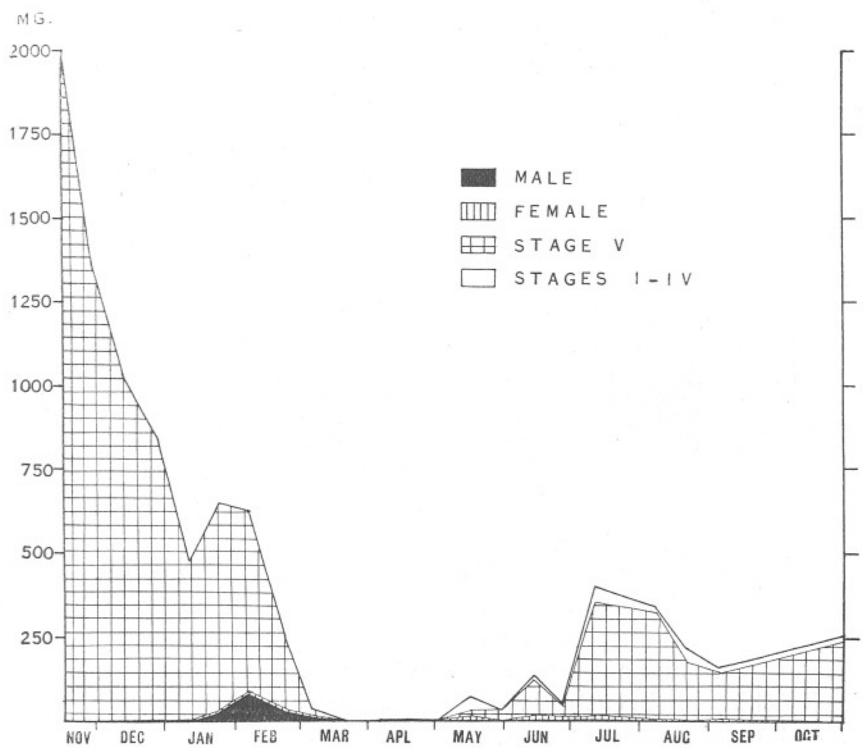

FIG. 4.—Calculated dry weight in mg. of vertical hauls throughout the year showing weight of different sexes and stages.

Protein.

Like fat estimations, nitrogen determinations could only be made on a few occasions with adult male and female Calanus. Even with Stage V Calanus more numerous estimations would have been desirable. The results are shown in Tables I, II and III, and Figures 2 and 3. No reliable estimations could be obtained between February and May when the changes in weight and fat content were most marked. Protein values

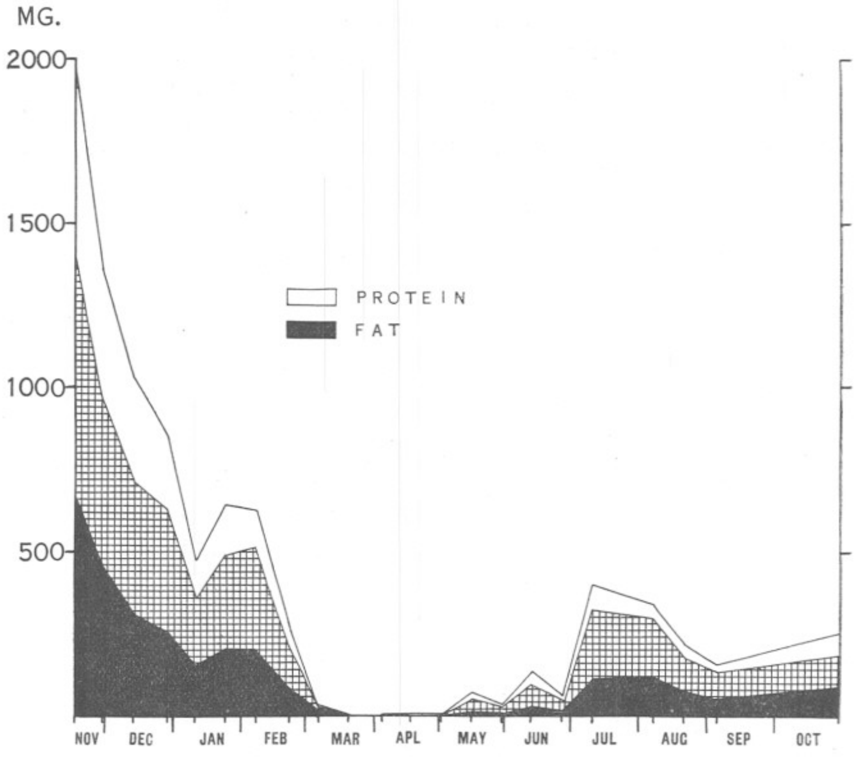

Fig. 5.—Calculated weight of protein and fat per vertical haul.

generally amounted to about 50% of the dry weight of the Stage V Calanus and fluctuated between 35 and 55%. A low value was obtained in the beginning of March on the same date as that on which the fat content was unusually high and in the autumn of 1932 values fell from 50 to 35%. This fall in protein content was not shown in the autumn and winter of 1931–32 when numbers were very much higher.

Adult female Calanus were richer in protein than Stage V Calanus and the level remained high (75%) on all four occasions on which estimations could be made. Adult male Calanus were much the same as Stage V with values varying from 40–70%.

The figures given for protein content of Calanus are considerably lower than those recorded by Brandt and by Brandt and Raben. The explanation of this discrepancy lies apparently in the fact that Calanus is richer in fat than the mixed plankton catches analysed by these authors. No seasonal observations have hitherto been recorded in protein content of plankton.

In the figures given above and in Tables I, II and III no correction is made for the nitrogen present in the chitinous parts of the Calanus.

Chitin.

An analysis of the chitin was made on only one occasion and on Stage V Calanus alone since it was necessary to use at least 1000 individuals. The Stage V Calanus used for the determination were from the winter stock and the chitin content is probably fairly constant then since they do not moult till early in the year. The amount of chitin in 1000 Stage V Calanus was 6·1 mg., equivalent to 2·98% of the dry weight of the Calanus. This is somewhat lower than the figures given by Brandt and Raben (1919–22) which are 4·37% and 5·02%.

The object of the chitin determination was to find out what fraction of the organic material could definitely be classed as indigestible. Only a comparatively small number of animals is able to digest chitin and with most animals it appears to be excreted unchanged.

The Food Value of Calanus in Loch Fyne in 1932.

In Figures 4 and 5 and Table IV is shown the calculated total dry weight of the Calanus in the tow-nettings made by Nicholls (Part I) at Strachur in Loch Fyne. Figure 4 shows the weight composition of the catch as male, female, Stage V and Stages I–IV Calanus. The weights have been calculated from the dry weight determinations on 100 individuals except for Stages I–IV when the calculations have been based on Bogorov's (1933) figures making allowance for the water content. According to his figures,

1 Stage V Calanus equals in dry weight about 1·8 Stage IV.
1 ,, V ,, ,, ,, ,, ,, 11 Stage III.
1 ,, V ,, ,, ,, ,, ,, 42 Stage II.
I ,, V ,, ,, ,, ,, ,, 60 Stage I.

The weight figures for Stages I–IV are probably not very accurate but the diagram (Fig. 4) shows that they are relatively unimportant. The nauplius stages of Calanus and the eggs must weigh very much less individually and even the very high numbers met with at times (Nicholls, Part I) will have but little effect on the total weight curve.

Stage V Calanus is responsible for the bulk of the weight except for a short period from the middle of March to the end of April when the total weight of the catch was also very low ; males and females were of importance only spasmodically. During the autumn and winter practically the whole weight of the catch was due to Stage V Calanus. In the winter of 1931 they were very much more numerous and also somewhat heavier than in the winter of 1932 which suggests that there may be considerable fluctuations from year to year.

In Figure 5 and Table IV are shown the weights of fat and protein in the catch throughout the year. The curves for these run fairly parallel to the total weight curve. The fraction unaccounted for will consist partly of ash and chitin and probably to a large extent of carbohydrate (Brandt, 1898). The net used filtered an area of 0·196 sq.m. so that the figures represent the weight of Calanus and of protein and fat below each 0·196 sq.m. of surface. The average depth at Strachur was 130 m. so that the material was distributed through 25·5 cubic metres of water.

SUMMARY.

1. The dry weight of 100 male, female and Stage V Calanus in Loch Fyne fluctuated throughout the year. 100 Stage V Calanus in May weighed only about $\frac{1}{3}$ of what they did in December. Male and female Calanus also fluctuated considerably in weight.

2. Stage V Calanus is usually largest and heaviest when it is most abundant. With male and female Calanus size and weight are related.

3. Stage V Calanus, in spite of being smaller than female Calanus, was from the beginning of June till the end of August considerably heavier (over 100%). When Stage V Calanus was at its lightest and smallest, it weighed less than female Calanus at the same time.

4. The weight of Stage V Calanus fell during the spring and did not increase again till after the end of the first breeding period.

5. The fat and protein content of Calanus depends chiefly on dry weight. The values obtained for fat content were considerably higher than those hitherto recorded for zooplankton and those of protein lower.

6. The ash content is about 3·6% and the chitin content about 3% of the dry weight.

7. Stage V Calanus accounted for by far the most important part of the total weight of the catch throughout the year.

8. The total food value of the Calanus in Loch Fyne probably varies very considerably from year to year.

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TABLE I

Weight and Composition of Male Calanus.

Date.	Dry weight of 100 in mg.	Average length in mm.	Fat %.	Protein %.
8.2.32 . .	22·5	2·45	21·9	56
	24·0	2·46	–	53
7.3.32 . .	20·2	2·45	33·7	–
	20·3	2·45	31·7	–
	20·1	2·45		
16.5.32 . .	19·4	2·42	19·6	69
			18·0	–
30.5.32 . .	18·8	2·36	22·9	59
	17·8	2·37	23·5	54

TABLE II.

Weight and Composition of Female Calanus.

Date.	Dry weight of 100 in mg.	Average length in mm.	Fat %.	Protein %.
7.3.32 . .	15·2	2·48	29·6	–
		2·48	24·3	–
21.3.32 . .	15·2	2·51	16·3	–
	15·5	2·49	16·3	–
5.4.32 . .	17·7	2·54	11·4	74
	15·5	2·51	12·6	73
2.5.32 . .	15·4	2·53	21·4	–
16.5.32 . .	19·4	2·61	12·4	–
			12·9	–
30.5.32 . .	14·6	2·41	21·1	77
	13·9	2·44	17·6	74
27.6.32 . .	14·2	2·40	13·3	79
	14·3	2·40	10·5	69
25.7.32 . .	11·7	2·39	15·6	77
	11·3	2·39	–	–

TABLE III

Weight and Composition of Stage V Calanus.

Date.	Dry weight of 100 in mg.	Average length in mm.	Fat %.	Protein %.
17.11.31 . .	25·4 27·5	– –	34·4 33·6	32 44
14.12.31. . .	26·6 28·0	2·40 2·40	28·9 31·5	42 36
11.1.32 . .	22·9 22·5	2·36 2·37	31·2 33·0	44 44
8.2.32 . .	21·0 21·5	2·39 2·38	34·4 33·4	48 49
7.3.32 . .	15·2	2·27	46·6 44·1	34 –
2.5.32 . .	9·7	2·18	26·8	–
16.5.32 . .	15·7 15·2	2·22 2·25	22·7 20·1	– –
30.5.32 . .	19·1 –	2·20 2·25	23·1 –	56 –
27.6.32 . .	21·7 20·4	2·27 2·26	26·1 31·3	46 45
25.7.32 . .	22·2 21·7	2·24 2·22	35·5 –	52 –
22.8.32 . .	23·4 23·6	2·25 2·24	34·9 32·8	46 50
21.9.32 . .	23·6 23·0	2·28 2·29	33·9 38·6	51 –
30.10.32 . .	21·6 21·9	2·26 2·30	36·8 35·8	30 44
21.11.32 . .	22·1 23·1 20·4	2·24 2·28	39·8 –	35 35

TABLE IV.

Weight and Composition of Vertical Hauls taken in Loch Fyne.

Date.	No of individuals per vertical haul.	Calculated total weight per vertical haul in mg.	Calculated weight of protein per vertical haul in mg.	Calculated weight of fat per vertical haul in mg.
17.11.31 . .	V. 7420	1962·6	747·6	668·5
	IV. 30	4·4		
		1967		
30.11.31 . .	♀ 5	0·8	0·6	0·2
	V. 5120	1354·2	515·4	461·2
	IV. 15	2·3		
		1357·3	516·0	461·4
14.12.31 . .	V. 3750	1023·8	401·5	310·3
	IV. 30	4·5		
		1028·3		
29.12.31 . .	♂ 10	2·3	1·3	0·5
	♀ 10	1·5	1·1	0·4
	V. 3087	842·8	369·2	254·8
	IV. 7	1·0		
		847·6	371·6	255·7
11.1.32 . .	♂ 10	2·3	1·3	0·5
	♀ 4	0·6	0·4	0·2
	V. 2070	469·9	205·7	150·8
	IV. 2	0·3		
		473·1	207·4	151·5
25.1.32 . .	♂ 128	29·8	16·2	6·5
	♀ 37	5·6	4·1	1·5
	V. 2685	609·4	267·1	195·9
	IV. 8	1·0		
		645·8	287·4	203·9
8.2.32 . .	♂ 348	80·9	44·1	17·7
	♀ 58	8·8	6·5	2·4
	V. 2515	534·4	261·9	181·4
	IV. 10	1·2		
		625·3	312·5	201·5
23.2.32 . .	♂ 113	26·3	14·3	5·8
	♀ 28	4·6	3·4	1·2
	V. 1056	224·4	109·8	76·1
	IV. 2	0·2		
		255·5	127·5	83·1

Date.		No. of individuals per vertical haul.	Calculated total weight per vertical haul in mg.	Calculated weight of protein per vertical haul in mg.	Calculated weight of fat per vertical haul in mg.
7.3.32 . .	♂	48	9·7	5·2	3·2
	♀	46	7·0	5·1	1·9
	V.	142	21·6	7·4	9·8
	I.	1	0·0		
			38·3	17·7	14·9
21.3.32 . .	♂	6	1·2	0·7	0·4
	♀	8	1·2	0·9	0·2
	V.	7	1·1	0·4	0·5
	IV.	1	0·1		
			3·6	2·0	1·1
5.4.32 . .	♂	3	0·6	0·3	0·2
	♀	8	1·3	0·9	0·2
	V.	8	1·2		
	IV.	1	0·1	0·4	0·6
	II.	1	0·0		
	I.	10	0·0		
			3·2	1·6	1·0
18.4.32 . .	♂	3	0·6	·3	0·2
	♀	17	2·8	2·1	0·3
	V.	22	3·3		
	IV.	10	0·8	1·4	1·9
	III.	2	0·0		
	II.	3	0·0		
			7·5	3·8	2·4
2.5.32 . .	♂	2	0·4	0·3	0·1
	♀	13	2·0	1·4	0·4
	V.	21	2·0		
	IV.	38	2·0		
	III.	5	0·0	2·3	1·1
	II.	1	0·0		
	I.	6	0·0		
			6·4	4·0	1·6
16.5.32 . .	♂	28	5·4	3·7	1·0
	♀	38	7·4	5·4	0·9
	V.	122	18·8		
	IV.	314	26·8		
	III.	796	10·9	32·3	12·3
	II.	187	0·7		
	I.	56	0·1		
			70·1	41·4	14·2
30.5.32 . .	♂	13	2·4	1·4	0·6
	♀	16	2·3	1·7	0·4
	V.	132	25·2		
	IV.	39	4·1		
	III.	44	0·7	17·1	7·0
	II.	53	0·2		
	I.	22	0·1		
			35·0	20·2	8·0

Date.	No. of individuals per vertical haul.		Calculated total weight per vertical haul in mg.	Calculated weight of protein per vertical haul in mg.	Calculated weight of fat per vertical haul in mg.
13.6.32 . .	♂	17	3·1	1·8	0·7
	♀	102	14·5	10·9	2·8
	V.	501	105·4		
	IV.	80	9·3		
	III.	30	0·6	53·1	26·7
	II.	40	0·2		
	I.	70	0·2		
			133·3	65·8	30·2
27.6.32 . .	♂	3	0·5	0·3	0·1
	♀	102	14·5	10·9	1·7
	V.	177	37·3		
	IV.	36	4·2		
	III.	93	1·7	20·2	12·6
	II.	93	0·5		
	I.	60	0·2		
			58·9	31·4	14·4
11.7.32 . .	♂	13	2·4	1·4	0·6
	♀	127	18·1	13·4	2·2
	V.	1537	337·4		
	IV.	326	39·5		
	III.	104	2·0	196·7	108·8
	II.	21	0·1		
	I.	13	0·0		
			399·5	211·5	111·6
8.8.32 . .	♂	3	0·5	0·3	0·1
	♀	36	4·1	3·1	0·6
	V.	1442	316·5		
	IV.	160	19·3	174·3	119·2
	II.	1	0·0		
			340·4	177·7	119·9
22.8.32 . .	♂	2	0·4	0·2	0·1
	♀	16	1·8	1·3	0·3
	V.	743	174·6		
	IV.	311	40·4	103·0	72·7
	III.	2	0·0		
			217·2	104·5	73·1
5.9.32 . .	♂	2	0·4	0·2	0·1
	♀	19	2·1	1·6	0·3
	V.	609	141·9		
	IV.	90	11·6	78·8	52·0
	III.	2	0·1		
	II.	4	0·0		
			156·1	80·6	52·4
30.10.32 . .	♂	1	0·2	0·1	0·0
	♀	5	0·5	0·4	0·1
	V.	1110	241·4	93·6	91·9
	IV.	96	11·5		
			253·6	94·1	92·0