Journal of the Marine Biological Association of the United Kingdom Vol 32 No 2 1953

J. Mar. biol. Ass. U.K. (1953) 32, 305–313
Printed in Great Britain

BIOMETRY OF THE COPEPOD *CALANUS FINMARCHICUS* (GUNN.) IN STAGES V AND VI

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(Text-figs. 1, 2)

There is much published information on the size of the several stages and its variation in the copepod *Calanus finmarchicus*. Marshall (1933), in the Clyde area, has found considerable variations in size even between the different generations developed throughout a single season, such variations extending to most of the copepodite stages. In general, the generations developed earliest in the season were the largest: further, the difference in size between the male and female stage VI copepodite was found to be considerable in the spring brood but almost negligible in a summer brood. Differences in size have also been reported with depth (Russell, 1928; Gardiner, 1933), and there are differences in the size of animals from distinct geographical regions. It has also been stated that the relative proportions of metasome and urosome vary. However, while some of these observations relate to the total length of the metasome and urosome taken together, most have been made on the metasome only: there appear to be no measurements of the individual segments and no consideration of the changes of size of the segments from one stage to the next. Further, the question is still open whether any sexual differentiation in size is evident in copepodite stage V.

The Materials and Experimental Methods

One of the difficulties in analysing the size variation in *Calanus* and other copepods arises from the fact that in most collections, even when obtained from a restricted area, there is often a mixture of two populations as a result of some overlap in the generations. Further, there is considerable spread, even in the sizes of individuals of a given stage from a distinct generation and this, together with the overlapping of the generations, has led to the use of overall means or modes when sizes are recorded. Certain features of the results have therefore been lost. Such an overlap of the sizes, although always likely to be present can to some extent be minimized by a choice of the time of collection.

In this work, therefore, all the results have been plotted as cumulative percentages, and in this way the presence of more than one population detected. Further, from the plots the means and standard deviations of the separate populations have been determined graphically.

The animals here referred to are *C. finmarchicus* in the sense given by Rees (1949).

The material used was collected in the Firth of Clyde at a constant depth of 100 m. with a tow-net hauled horizontally. As shown by a preliminary examination at the time of collection, late June, it consisted largely of stage VI, males and females (10·6 and 26·2% respectively), stage V (56·2%), stage IV (6·2%) and only a few of the early stages. It seems clear, from a comparison with the results of Marshall (1933) that this was the first summer generation and that the stage V population was giving rise to the population of stage VI, males and females, also present. This view is substantiated by the fact that the stage VI females showed, not only for total length but also for many of the other measurements, two populations, of which those with the larger mean size were present only to the extent of some 5%. This small population is no doubt a residuum from the larger-sized generation developed earlier in the year (Marshall, 1933). That only a single population of male stage VI was found is not surprising since, as Marshall has pointed out, the evidence indicates that these are shorter lived than the female stage VI.

The material was preserved in 5% neutral formalin as soon as possible after collection, and the measurements and any deductions derived therefrom can strictly speaking only apply to material treated in this way. The measurements were all made with the aid of a projection microscope, the image being projected on to a sheet of paper and the appropriate outlines drawn. The magnification for the metasome segments in the projected figure was $\times 103$, and for the urosome segments and the caudal rami was $\times 371$; the measurements were made from the drawings to the nearest $\frac{1}{50}$ of an inch with a precision steel ruler. One hundred animals of each of the copepodite stages to be considered, namely, stage VI male and female and stage V, were picked out at random from the sample and the following measurements made on the drawings from the projected images (Fig. 1).

From the dorsal side, the length of the head (including fused first thoracic somite) and the length of each of the five free thoracic somites (segments) were measured. The head measurement was taken from the anterior tip to the posterior border, and that of the free segments from the posterior edge of the preceding segment to the posterior border of the segment in question. On the last thoracic segment the length was taken to the centre of the posterior edge of the concave border. The drawings from which these measurements were taken were made with the animal lying flat on its ventral side, and, if necessary, any appendages which hindered keeping the animal horizontal were removed. The body shows a very slight curvature but no correction has been applied for it since tests showed that any correction was extremely small and did not affect the conclusions to be drawn from the results. Strictly speaking, however, the measurements are the lengths projected on to a horizontal plane. Also from the dorsal side the widths at the widest part of the posterior border

of all the metasome segments were measured; with the last free thoracic segment this was taken as the distance between the rounded tips. In addition, the head segment was divided into thirds and the width at each third was measured separately.

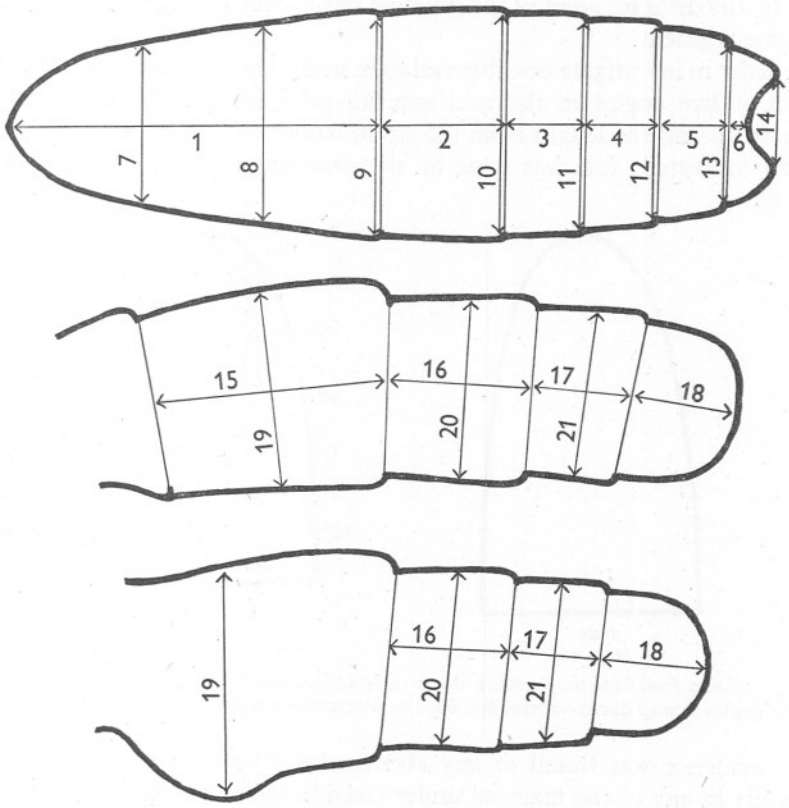

Fig. 1. To show the measurements taken on *Calanus finmarchicus* (Table I).

On preservation, the urosome often undergoes flexion, and all the measurements on this part of the animal were therefore made from drawings made with the animal lying on one side, again removing any appendages necessary in order to place the animal with its dorso-ventral axis horizontal. Even so the length of the first segment of the urosome cannot be accurately drawn in the intact animal, and it has therefore been omitted for all stages. The lengths of the other urosome segments were measured at the centres (posterior border to posterior border, again) so that there are four length measurements for stage VI male but only three for stage VI female and stage V. The depths (dorso-ventrally) at the widest part of each of these segments were also measured, and that of the widest part of the first urosome segment in the

female stage VI only (neglected in the length measurements), since here it could be clearly seen. The width of the terminal segment was not measured for any of the stages.

One further measurement was made with the animal on its ventral side, namely, the distance apart of the junction of the caudal rami with the terminal urosome segment.

In order to investigate possible variation in the shape of the head, lines were drawn at five angles to the mid anterior-posterior line from the extreme anterior tip and the length from the tip to where these lines cut the carapace border measured; this was done on the drawings from the dorsal side (see Fig. 2).

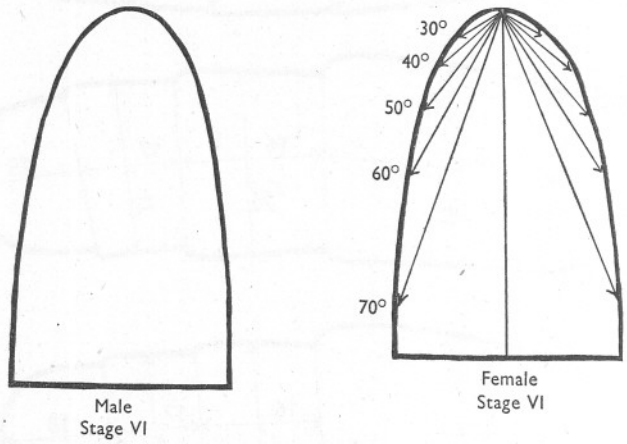

Fig. 2. *Calanus finmarchicus*, showing shape of head in stage VI male and female. Lines set off at angles to mid dorso-ventral line used to determine the shape (see text and Table II).

No evidence was found of any abnormalities such as telescoping of the segments in any of the material under consideration (Gurney, 1931).

In testing the significant differences between mean sizes, the *t*-test was used, the population means and standard errors being estimated from the graphs. For simplicity of discussion the actual units used in the measurements will always be quoted in the discussion of the sizes.

As already stated, a small larger-sized population was shown to be present in the stage VI females; only the smaller-sized and larger population (95 %) is considered in the following.

The Relations of Copepodite Stage VI Male and Female

The male and female stage VI at this time of the season do not differ in the size of the whole metasome obtained by adding together the separate segments (9·70 units males and 9·72 units females, Table I), and this is in accord with the observations of Marshall (1933) who found that the males, although

relatively smaller in the early part of the year, were in the summer brood about the same length (metasome) as the females. However, there are differences when individual segments are compared. The most striking difference is that of the head portion: this is much longer in the male (4·91 units) than in the female (4·56 units). With the exception of the first free thoracic segment in which the length of the female does not differ significantly from that of the male, the lengths of the other free segments are all slightly greater in the

TABLE I. *CALANUS FINMARCHICUS*. BODY MEASUREMENTS OF STAGES V AND VI

(In arbitrary units.)

	Stage VI		Stage V	
	Male	Female	(i)	(ii)
The metasome				
Length of metasome (by addition)	*9·700*	*9·720*	*8·990*	*8·590*
1. Length of head	4·910	4·560	4·300	3·900
2. Length of first free segment	1·550 (n.s.)	1·568	1·438	
3. Length of second free segment	1·052	1·140	1·047	
4. Length of third free segment	0·924	1·040	0·935	
5. Length of fourth free segment	0·822	0·908	0·810	
6. Length of fifth free segment	0·442	0·504	0·460	
7. Width of head one-third down	2·200 (n.s.)	2·230	2·020	
8. Width of head two-thirds down	2·720 (n.s.)	2·720	2·480	
9. Width of head posterior border	2·860 (n.s.)	2·880	2·670	
10. Width of first free segment	2·818	3·010	2·600	3·000
11. Width of second free segment	2·720	2·840	2·475	2·861
12. Width of third free segment	2·453	2·600	2·195	2·550
13. Width of fourth free segment	2·060	2·155	1·800	2·120
14. Width of fifth free segment	1·183 (n.s.)	1·170	0·920	1·300
The urosome				
15. Length of second segment	2·850	—	—	—
16. Length of antepenultimate segment	1·650 (n.s.)	1·635	2·100	
17. Length of penultimate segment	1·150 (n.s.)	1·160	1·420	
18. Length of ultimate segment	1·295	1·440	1·860	
19. Width of antepenultimate segment	2·600	2·950	—	
20. Width of penultimate segment	2·312	2·360	2·340	
21. Width of ultimate segment	2·215 (n.s.)	2·120	2·105	
22. Width apart of junction of caudal rami	1·000	0·716	0·620	

n.s., differences not significant.

female, and there is a suggestion of a relative gradient between the two sexes from anterior to posterior, the ratio changing from 0·928 in the head to 1·148 in the last free segment. It will be remembered that for the purpose of comparison within the head itself, the width was measured not only at the posterior edge but also at a distance of one-third and two-thirds its length from the anterior end. There is no significant difference between the male and female in any of these measurements, the head in both narrowing anteriorly.

In all the other segments the female is somewhat wider than the male, except in the width between the projecting terminal tips of the last free segment, where there is no significant difference.

The terminal segment of the urosome is significantly longer in the female

but there is no difference between the two preceding segments. There is no direct comparison available for the length of the second segment of the male, but it is much larger than the others. As might be expected, the width of the first segment (two fused somites) in the female, which bears the genital opening, is much larger than that of the male, although it should be remembered the comparison is between this and the second somite in the males. The widths of the penultimate and antepenultimate segments show also smaller differences, the former being slightly larger in the male (although not significant at the 0·02 level). The width apart of the caudal rami at their junction with the terminal segment (forming movable joints in the male) is much greater in the males. Indeed this, together with the difference in head length and width of the 'genital' segment of the urosome, are here the most distinguishing size differences in these male and female populations.

The Presence of Two Populations in Copepodite Stage V

The first question to be considered is whether there is any differentiation in the stage V animals in the sense that, as regards any of their size measurements, they can be divided into two distinct populations. There is a clear distinction into two populations of about 50% each in total length of the metasome (determined by adding together the separate segments), and this suggests that differentiation into potential males and females, at any rate as regards size, is evident in stage V. This separation into two distinct populations has been confirmed by the analysis of a large number of other catches taken at various times and by the analysis of published data of other workers: the lengths of the stage V metasome can almost always be separated into two populations each composing about half the total. This feature suggests sexual differentiation rather than lack of homogeneity in the material. Such a distinction, however, has not been found in copepodite stages earlier than stage V. It has been unobserved because of the considerable overlap in the sizes. A difference in the size of stage V *Calanus* has often been found in colder regions (Störmer, 1929; Bogorov, 1933), where the modes were quite distinct and has been observed by Ussing (1938) even for stage IV copepodites. In these northern regions, however, the proportions are not constantly 50/50, and the differences are probably due to lack of homogeneity, the two stage V populations having different developmental histories. Thus it has been suggested that the amount of food available at the time of production or even a 2-year development period for one population is concerned. The failure of Marshall (1933) to correlate large and small stage V with males and females in an experimental moult is due to the fact that only small numbers were used and that the differences noted above are population differences.

This differentiation in stage V does not, however, extend to all portions of the animal. It is well marked in the head length (4·30 and 3·90 units), and

this might be expected since the difference in the length of the head is the most marked feature in the metasome of stage VI males and females. There is no differentiation in the length of the other metasome segments in stage V, but the widths of all these segments except that of the head are clearly divided into two populations, of which the larger may be presumed to be the female population. There is no distinction in the lengths and breadths of the urosome segments.

Relation between the Sizes of Stage V and Stage VI Males and Females

There is no feature by which it can be known with certainty which population of stage V gives rise to the males and which to the females. There is considerable growth in the head segment from stage V to stage VI in both male and female; whereas the length of the other metasome segments (of which only one population was present in stage V) shows virtually no increase in the moult to males and only a slight increase in the moult to females. There is no difference in the widths of stage VI male and female heads and therefore it is not surprising to find only one population of these measurements in stage V and therefore the same increases must take place when passing from stage V to stage VI male or female. In the widths of the other metasome segments there are two populations in stage V, one of which is usually larger than the male stage VI and can therefore perhaps be presumed to correspond to the female population; in which case there is little change in the width on passing from stage V female to stage VI female and a moderate change in passing from stage V male to stage VI male. Only a single population was found in the stage V urosome measurements with hardly any change in width from stage V to stage VI. However, the length of all three segments measured in the urosome is much larger in stage V than the equivalent segment in stage VI male or female (as reckoned from the posterior segment). Apparently, therefore, considerable reorganization takes place in the urosome segments at moulting; but it should be remembered that the length of the first urosome segment was not measured.

The Shape of the Head in the Two Stages

The mean ratios of the lengths at 40°, 50°, 60° and 70°, set off as described previously, to that at 30°, are shown in Table II for the two stages considered, and in Fig. 2, where the 'average' head is drawn. This ratio, which increases with the angle, is always relatively smaller in the female, indicating that the head is rounder and less pointed than in the male. These lengths were plotted as for the others in stage V, and in each two populations were found present, the ratios derived from which are also shown in Table II. Clearly a round-headed

and a more pointed-headed population are present in stage V, and this further strengthens the view that there is differentiation into sexes in stage V. In the 'typical' stage V heads drawn from these figures only the narrow head is found to fit the longest head measurement; and, since the narrow head in stage VI is that of the male, the longest head in stage V may be inferred to belong to the male population.

TABLE II. *CALANUS FINMARCHICUS*. MEASUREMENTS ON THE HEAD OF STAGES V AND VI

	Stage VI		Stage V	
Ratio	Male	Female	(i)	(ii)
Length at 40°/30°	1·65	1·59	1·78	1·54
Length at 50°/30°	2·51	2·36	2·70	2·29
Length at 60°/30°	3·91	3·61	4·21	3·47
Length at 70°/30°	6·75	6·11	7·20	5·80

THE STATE OF THE ANTENNULES ON PRESERVATION

It is well known that the antennules always remain straight on preservation in formalin in stage VI males, but assume some amount of curl, often very characteristic, in the preserved stage VI females. Further, when stage V are preserved, some have curled and some straight antennules. However, it does not appear from the following observations that this can be used to differentiate the sexes in stage V. In the hundred of each stage, picked out at random, all the stage VI males had straight antennules, but so had also sixteen of the stage VI females. In the other females the antennules were curled to a varying degree. In the stage V animals 34% were straight. For all those measurements where analysis had shown that there were two populations in respect to stage V the means were separately calculated for those animals with straight and for those with curled antennules. These means were always the same; there was therefore no separation into two populations as would have been expected had the state of the antennules been correlated with sex, which in turn has been presumed to be the basis of the two population sizes.

Thanks are due to Dr S. M. Marshall for reading the manuscript and for making a number of helpful critical comments on it.

SUMMARY

One hundred each of stage VI male and female and stage V *Calanus finmarchicus* were picked at random, and, by means of a projection microscope, measurements made on a number of segments in both metasome and urosome.

The stage VI female population was mixed containing 95% of a small-sized population and 5% of a larger size-group. The males constituted a single population.

At this time of the season the stage VI male and female metasomes are the same length, but there are differences in the sizes of the individual segments, the most striking of which is that of the head.

The stage V animals in many of the measurements could be quite clearly separated into two size-groups of about 50% each and it is suggested that these are potential male and female populations. This separation at 50/50 has been noticed in numerous other collections of stage V, but it should be emphasized that the differences are population differences in regard to those measurements considered.

Evidence is presented which shows that the state of the antennules after preservation in 5% neutral formalin is unlikely in stage V animals to be a reliable guide to their sex in the next stage.

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