THE RESPIRATION OF SOME PLANKTONIC COPEPODS

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(Text-figs. 1, 2)

The respiratory rates of zooplankton organisms are of considerable interest, if only in so far as they permit an assessment of the metabolic requirements of the zooplankton, which forms a vital link in the economy of the sea. Yet very little information is available on the respiratory rates even of copepods, which usually comprise the bulk of a zooplankton community. Data exist only for a few species of copepods, and even then only for a few stages in the life histories of the species. The first measurements of the respiration of a selected species, as distinct from mixed plankton catches, were made by Marshall, Nicholls & Orr (1935). They worked with *Calanus finmarchicus* (Gunner), adults (male and female) and Stage V. In 1939, Clarke & Bonnet published a further series of measurements of the respiration of Stage V *C. finmarchicus*, giving figures slightly higher than those of Marshall *et al.* Zeuthen (1947) included some observations on copepods in his study of size and metabolic rates, but he determined the species of only a few of the animals he used.

In this paper the study of respiration in the Copepoda has been extended to a species much larger than *Calanus*, viz. *Euchaeta norvegica* Boeck, and to two smaller species, *Centropages typicus* Kroyer and *C. hamatus* (Lilljeborg), and in the two larger species, *Calanus* and *Euchaeta*, an additional copepodite stage has been included. In this and further papers a survey will be made of the respiration of the more important species of planktonic copepods, throughout their life histories and under varying environmental conditions. In this way, in time, a picture may be built up of the food requirements of the planktonic population in the sea.

MATERIAL AND METHODS

Copepods were taken by townet in the Fairlie Channel, or off Garroch Head, both grounds within half an hour's run from the laboratory. The tow-nettings were well diluted for transport. In the laboratory, with the larger forms,

vigorous specimens of the desired species and stage were picked out as soon as possible and put in jars of sea water filtered through Whatman No. 1 filter-papers. The labour of sorting individually large numbers of *Centropages hamatus* was very great; and for them, after the larger copepods and any possible predators such as medusae had been picked out, the townettings were well diluted with filtered sea water, and the *Centropages* picked out only as required. The jars were kept in a sink of running water where the temperature rarely changed by more than 1° C. in 24 hr. No copepods were used until at least the day following capture. An attempt was made not to use the same catch for more than 2 days, but unfortunately rough weather prevented fresh hauls being taken on several occasions, and, especially at the end of the experiments, copepods had to be used that had been captured 4–5 days before.

Respiration was measured manometrically, in Dixon-Haldane constant pressure respirometers, the apparatus being arranged as outlined by Dixon (1943). Clarke & Bonnet (1939), who used this apparatus for their measurement of the respiration of *Calanus*, found that the presence or absence of KOH in the flasks had no effect on the readings observed. We were not satisfied on this point and KOH was always used in the annular cup in the neck of the flask. The respiration flasks were completely immersed in a bath of running water, as no means of maintaining a water-bath at constant temperatures below room temperature was readily available. It was possible by this means to keep the temperature well below 20° C. The maximum range of temperature observed in the bath during any experiment was 0·5° C., which was sufficiently constant to have no disturbing effect on the accuracy of the readings. The greatest disadvantage of this arrangement was the day-to-day variation in the temperature which fell more or less steadily from 19° C. at the beginning of the series of experiments to 15·5° C. towards the end.

The respirometers were attached to a Barcroft shaking-apparatus and shaken with an amplitude of 2 cm. at a frequency of 100 per min. Contrary to the observation of Clarke & Bonnet (1939), this shaking appeared to have no ill effect on the copepods, which survived well—only 10 out of a total of over 600 copepods used in the experiments died during the experiment, and the vast majority of them were alive and active the day following the experiment in which they had been used. However, in view of Clarke & Bonnet's experience, copepods were never used a second time for normal experiments. After closing the respirometer taps, readings were made every 30 min. for 3 hr. and the total change was converted to volume of dry gas at N.T.P. In the first nine measurements, where the respirometer taps were closed 5 min. after the flasks had been attached, as recommended by Dixon, it was found that the first reading of the manometer, 30 min. after the taps were closed, showed a very large change—sometimes two or three times that found for the subsequent 30 min. periods. The period of equilibration was therefore increased to 15 min., and the large initial change was eliminated. In the early experiments where the

equilibration period was only 5 min., and an abnormally large change was recorded in the first 30 min., the first half hour has been neglected and the calculations have been based on the last $2\frac{1}{2}$ hr. experiment.

The respiration flasks usually contained 5 ml. of filtered sea water, but the number of copepods varied with their size—usually 2–5 *Euchaeta*, 10 *Calanus* (adults, Stage V and Stage IV), 20–25 *Centropages typicus* and 50 *C. hamatus*.

For each experiment the copepods were picked out of the jars by eye, but when there was any doubt in identification they were checked under a low-power microscope before being counted into the respiration flasks. In the experiment with *C. hamatus*, in order to save time and damage to the animals, they were sorted by eye only, but were fixed in formalin at the end of the experiment for checking and counting. Any animals which were to be measured after an experiment were similarly fixed and measured with an eyepiece micro-meter.

RESULTS

In all, sixty-five separate determinations of respiration were made, and results are listed in Table I. In the table, the fifth column gives the amounts of oxygen in microlitres consumed by one copepod in 1 hr., for the temperature at which the experiment was made. A correction for temperature was made from the curve of respiration of *Calanus* with temperature, given by Marshall *et al*. The sixth column shows the data for respiration corrected to 17° C. Table II gives the mean values for each of these groups of observations, together with the standard deviation of the observations from their mean; the second figure in each pair is that obtained from the data corrected to 17° C. In the discussion which follows reference will be made only to the figures corrected to 17 °C.

More determinations were made on the respiration of *Calanus* Stage V than on any other form, and they include two small groups in which the conditions were changed. In the first special group (Exps. 36–39) the experiments were conducted in the dark, and in the second (Exps. 40–42) the respiration flasks were not shaken at all during the experiment. The group of experiments done in the dark give a mean respiration rate of $0.54\,\mu$l./cop./hr. as compared with $0.53\,\mu$l./cop./hr. for those in the light; there is no significant difference between these two means ($d/\sigma_d = 0.11$). This confirms the finding of Marshall *et al*. that the respiration of *Calanus* Stage V is not affected by light. The mean respiration rate when the respirometers were not shaken was $0.67\,\mu$l./cop./hr.; this is significantly higher than that for the rest of the measurements ($d/\sigma_d = 3.14$). The number of observations on *Calanus* adult males and on the stages of *Euchaeta* was severely limited by the difficulty of obtaining material; neverthe-less, it was decided that the data obtained were worth including.

It has already been explained that, owing to the difficulty of identifying rapidly the stages of *Centropages*, almost all the experiments on *C. hamatus*

TABLE I. LIST OF EXPERIMENTS AND RESPIRATORY RATES OBTAINED

Exp. no.	Number and stage	Date	Temp. (°C.)	Respiratory rate (μl./cop./hr.)	Corrected respiratory rate (17° C.) (μl./cop./hr.)
			Euchaeta norvegica		
1	2 adult females	15. ix.	15·85	4·284	4·785
2	4 adult females	10. ix.	16·35	3·077	3·277
3	4 adult females	10. ix.	16·35	2·999	3·194
4	4 Stage V	15. ix.	16·0	2·137	2·351
5	5 Stage V	15. ix.	15·85	2·326	2·598
6	2 Stage IV	15. ix.	16·0	1·069	1·175
			Calanus finmarchicus		
7	10 adult females	27. viii.	18·95	(0·429)	(0·362)
8	8 adult females	8. ix.	16·65	0·759	0·785
9	7 adult females	8. ix.	16·65	0·751	0·777
10	9 adult females	11. ix.	16·0	0·728	0·801
11	10 adult females	11. ix.	16·0	0·967	1·064
12	6 adult males	8. ix.	16·65	0·841	0·870
13	10 Stage V	24. viii.	19·0	0·550	0·426
14	,,	24. viii.	19·0	0·513	0·431
15	,,	24. viii.	19·0	0·844	0·708
16	,,	25. viii.	18·9	0·735	0·622
17	,,	25. viii.	18·9	0·478	0·404
18	,,	25. viii.	18·9	0·542	0·458
19	,,	26. viii.	18·8	0·512	0·437
20	,,	26. viii.	18·8	0·505	0·432
21	,,	26. viii.	18·8	0·551	0·471
22	,,	28. viii.	18·25	0·645	0·577
23	,,	28. viii.	18·25	0·615	0·550
24	,,	28. viii.	18·25	0·676	0·571
25	,,	30. viii.	18·2	0·615	0·552
26	,,	30. viii.	18·2	0·717	0·644
27	,,	30. viii.	17·9	0·521	0·479
28	,,	30. viii.	17·9	0·613	0·568
29	,,	30. viii.	17·9	0·490	0·451
30	,,	31. viii.	17·8	0·493	0·458
31	,,	31. viii.	17·8	0·524	0·486
32	,,	31. viii.	17·8	0·585	0·544
33	,,	1. ix.	17·5	0·643	0·614
34	,,	1. ix.	17·5	0·487	0·466
35	,,	1. ix.	17·5	0·548	0·525
36	,,	1. ix.	17·5	0·609	0·583 Dark
37	,,	1. ix.	17·5	0·457	0·437 Dark
38	,,	1. ix.	17·5	0·579	0·553 Dark
39	,,	2. ix.	16·9	0·578	0·583 Dark
40	,,	9. ix.	16·4	0·682	0·722
41	,,	9. ix.	16·4	0·617	0·654
42	,,	9. ix.	16·4	0·586	0·621 Dark
43	15 Stage IV	6. ix.	17·9	0·262	0·242
44	,,	6. ix.	18·0	0·198	0·180
45	,,	6. ix.	18·0	0·187	0·170
46	,,	11. ix.	16·0	0·270	0·297
47	,,	14. ix.	15·9	0·326	0·362
			Centropages typicus		
48	32♀	8. ix.	16·55	0·317	0·332
49	18♀	9. ix.	16·2	0·273	0·295
50	12♀, 5♂, 1..V	9. ix.	16·2	0·222	0·240
51	9♀, 4♂ 1..V	9. ix.	16·2	0·308	0·332
52	25♀	12. ix.	15·9	0·167	0·186
53	25♀	12. ix.	15·9	0·158	0·175
54	20♀	13. ix.	15·6	0·187	0·215
55	20♀	13. ix.	15·6	0·172	0·187
56	20♀	14. ix.	15·8	0·169	0·190
57	20♀	14. ix.	15·8	0·110	0·124
58	29♀	14. ix.	15·9	0·222	0·247
			Centropages hamatus		
59	26♀ 10♂, 64 V	2. ix.	16·85	0·079	0·082
60	17♀	2. ix.	16·85	0·125	0·135
61	13♀, 16♂, 31 V	2. ix.	16·85	0·066	0·068
62	15♀, 11♂, 29 V	5. ix.	17·25	0·107	0·105
63	35♀, 5♂, 17 V	5. ix.	17·25	0·112	0·110
64	22♀, 7♂, 5 V	6. ix.	18·0	0·118	0·108
65	15♀, 8♂	8. ix.	16·55	0·134	0·140

and the earlier ones on *C. typicus* were done on groups of animals which included adult males, females and Stage V. The data concerning *C. typicus* fall into two well-marked groups, but for reasons other than this mixing of adults and Stage V. Exps. 48–51 and 58 form one group in which there is a range in the rate of respiration from 0·24 to 0·33 μl./cop./hr. (mean = 0·29), and Exps. 52–57 form a second group in which the rate of respiration is much lower, ranging from 0·12 to 0·22 (mean = 0·18). This difference in respiration rate cannot be explained as a consequence of a difference in the proportionate number of adult and Stage V animals used in the different experiments, since in Exps. 48, 49 and 58 of the first group, and in all the Exps. 52–57 of the second group, the animals were exclusively adult females, yet the rate of respiration was high in the first group and low in the second. Or again, within the first

TABLE II. MEAN VALUE OF RESPIRATORY RATE

Species	Stages	Respiratory rate (μl.O_2/cop./hr.)		Standard deviation σ	
		Observed	Corrected to 17° C.	Observed	Corrected to 17° C.
Euchaeta norvegica	Adult ♀	4·284	4·785	—	—
	Adult ♂	3·038	3·235	—	—
	V	2·232	2·474	—	—
	IV	1·069	1·157	—	—
Calanus finmarchicus	Adult ♀	0·801*	0·857	0·111	0·139*
	Adult ♂	0·814	0·870	—	—
	V (13–35)	0·578	0·517	0·089	0·080
	V (36–39)	0·556	0·539	0·067	0·069
	V (13–39)	0·578	0·521	0·090	0·076
	V (40–42)	0·628	0·666	0·049	0·051
	IV	0·249	0·250	0·057	0·081
Centropages typicus	A (48–51, 58)	0·268	0·289	0·031	0·044
	B (52–57)	0·161	0·180	0·025	0·030
C. hamatus		0·106	0·107	0·025	0·026

* Omitting Exp. 7.

group itself, the rate of respiration in Exps. 50 and 51 in which animals were not all adult females was not significantly different from that in Exps. 48, 49 and 58 in which only adult females were present.

Originally it was thought that the lower rate of respiration in the second group of experiments might be due to starvation of the copepods used, with a consequent reduction in metabolism. In the first four, Exps. 48–51, the measurements of respiration were all made on animals caught during the previous day, whereas in Exps. 52–57 carried out on 12–14 September, the animals used had been caught on 10 September. Those used in Exps. 52 and 53 had been kept for 48 hr. in filtered sea water and had therefore not fed for this period; those in Exps. 54 and 55 had been picked out of the diluted townet catches that had been standing in running water for 72 hr., and although there may have been some phytoplankton in the diluted townetting for the copepods to eat, the

amount may well have been inadequate. The animals used in the four experiments, Exps. 52–55, were therefore transferred to a jar containing a thick suspension of a culture of *Chlamydomonas* and on the following day, after having been fed for 20 hr., the most active of these were picked out and used for Exps. 56 and 57. At the same time Exp. 58 was carried out with fresh animals picked out from a townetting taken the previous day (i.e. 13 September) and fed for 20 hr. The respiration rates in Exps. 56 and 57 were no different from those in Exps. 52–55; in Exp. 58 it was distinctly higher and agreed well with the rates observed in Exps. 48–51 (Table I). It is apparent therefore that starvation was not the cause of the lower respiration rate, or that, if starvation was the causative factor, one day's feeding in a rich suspension of food was insufficient for recovery.

It might be suggested that the lower rate of respiration was due to a size difference in the copepods, but it is unlikely that the animals caught on 10 September were for any reason smaller than those caught at other times. In the first place they were caught in the same locality, and, in the absence of currents passing through the area, there is no reason to expect that they came from a population different from those caught on 9 September. Secondly, the two species of *Centropages* were always separated initially by the naked eye without difficulty, since the greater size of *C. typicus* clearly distinguished it from *C. hamatus*. It is shown later that the respiratory rate is roughly proportional to the square of the length. If the observed difference in the rate of the two groups of *C. typicus* were due to size, those copepods caught on 10 September should have had a mean length of *c.* 1 mm., as compared with a mean length of 1·25 mm. for those caught on 9 September. But *C. typicus* of mean size 1 mm. would be no different in size from *C. hamatus*, and the normal separation of the two species on 10 September without microscopical examination would have been impossible.

It is clear that the two groups of *C. typicus* did not differ appreciably in mean length, and it is more likely that marked differences in respiratory rate are in some way correlated with the handling and retention of the copepods in the laboratory. It may be suggested, and support for this suggestion will be given in a later section, that the lower rate of respiration is the more correct one and that *Centropages* takes longer to regain its normal respiratory rate after the excitement of capture and handling than does *Calanus* for which 24 hr. appears to be sufficient.

These differences in the respiratory rates of *Centropages typicus* adult females necessitated a careful scrutiny of the earlier observations in order to see whether such differences could be detected in any other species. Only one result was clearly anomalous, namely Exp. 7 with *Calanus* females (27 September) where the respiratory rate was 0·36 μl./cop./hr. as compared with a mean for the other four experiments on adult females (Exps. 8–11) of 0·86 μl./cop./hr. Again the animals used in Exps. 7 had been kept for more than 24 hr. before the measure-

ments were made. On the other hand, all the experiments done with Stage V
Calanus from 28 August up to and including 1 September were done with
animals taken from an unusually good townetting taken on 27 August, and no
significant decline of the respiration rate is detectable in this group (cf. Table I,
col. 5, Exps. 22–35). It may be incorrect, however, to compare Stage V *Calanus*
with adult copepods. Stage V copepodites may be better able to maintain
a constant metabolic rate under conditions of stress, for it must be remembered
that Stage V copepodites obtained in late summer were part of an overwintering
stock (cf. Marshall *et al.* 1934) which pass into deep water and possibly live at
a lowered metabolic level (cf. Gross & Raymont, 1942).

TABLE III. LENGTH MEASUREMENTS

Species and stage (no. of observations)	Total length		Cephalothorax	
	Mean	σ	Mean	σ
Euchaeta norvegica:				
Female (2)	7·45	0·038	5·10	0·0
Male (8)	6·14	0·259	4·36	0·184
Stage V (5)	5·75	0·148	4·15	0·121
Calanus finmarchicus:				
Female (19)	3·12	0·118	2·45	0·091
Stage V (19)	2·66	0·225	2·06	0·175
Stage IV (31)	2·03	0·138	1·63	0·226
Centropages typicus:				
Female (37)	1·86	0·111	1·25	0·095
Male (8)	1·74	0·089	1·21	0·040
Stage V (2)	1·66	0·186	1·21	0·074
Stage IV (1)	1·32	—	0·95	
Centropages hamatus:				
Female (10)	1·47	0·096	1·06	0·097
Male (8)	1·29	0·089	0·94	0·076
Stage V (1)	1·16	—	0·79	—

Table III gives the mean lengths of the groups of copepods measured. Two
measurements are given for each group: (1) the length of the cephalosome and
metasome, i.e. the 'cephalothorax'; and (2) the total length including the
urosome. The advantages of measurements of the 'cephalothorax' are three-
fold: it is the bodily dimension that is easiest to measure accurately; it is the
dimension most commonly used in measuring copepods; and thirdly, if the
respiration rate is to be related to any power of a linear dimension, it will be
more closely associated with some power of the length of the cephalothorax
than with a power of the total length, since the cephalothorax makes up by far
the greater part of the bulk of the animal. Our measurements agree reasonably
well with previous measurements of copepods in the Clyde area (Marshall
1933, 1949; Nicholls, 1934).

DISCUSSION

The measurements made of the respiratory rate of *Calanus finmarchicus* agree
well with those determined previously by Marshall *et al.* (1935), and by
Clarke & Bonnet (1939). On both previous occasions measurements were

given in ml./1000 cops./hr.; these are numerically the same when expressed in μl./cop./hr. Marshall *et al.* made no observations at 17° C., but their curve for the relationship between temperature and respiratory rate gives a value of 0·44 μl./cop./hr. for *Calanus* Stage V, which does not differ significantly from the mean value of our measurements, 0·52 μl./cop./hr. ($d/\sigma_d = 1·05$). Clarke & Bonnet's experiments at 16·8° C. give a rather higher respiration rate, (0·80 μl./cop./hr.), the difference from that given by the present observation being statistically significant ($d/\sigma_d = 3·4$). However, the order of magnitude is the same, and in the present poor state of knowledge of the physiology of plankton, the agreement can be regarded as reasonably satisfactory. The respiration rates for male and female *Calanus* found by us were both higher than those given by Marshall *et al.*, that for females (0·86 as compared with 0·66 μl./cop./hr.) being significantly so, but again the agreement is reasonably good.[1]

Zeuthen (1947) quotes one measurement of the respiration of *Centropages hamatus*, giving a mean respiration rate of 0·08 μl./cop./hr. at 16° C. This agrees fairly well with the measurements here recorded which have a mean of 0·11 μl./cop./hr. This agreement too becomes even closer when account is taken of the size of the animals: Zeuthen's copepod was 0·86 mm. long (presumably total length) compared with the mean total length of 1·30 mm. for the *C. hamatus* given here.

Marshall *et al.* (1935) found marked falling off in respiration with time after capture, especially between the time of capture and 24 hr. later. Clarke & Bonnet (1939) found no such decline but their results are hardly comparable, as they did not use animals until the day after capture—the practice followed in the experiments reported here. Zeuthen (1947), citing a single measurement of the respiratory rate of *C. hamatus*, found a decline during the course of his experiment. In the present series of observations, there was no very obvious decline during the course of individual experiments. However, if the mean oxygen consumption is calculated at the end of each 30 min. period for the experiments with *Calanus* Stage V, the rate of consumption appears to fall (Fig. 1), since the points for times shorter than the mean time (1·75 hr.) lie above and two of those for longer times lie below the straight line drawn from the origin through the means (1·75 hr. and 11·38 μl. O_2 consumed). But closer examination shows that only one of the means differs from the corresponding point on the straight line by as much as its standard error, and the deviation of this one, that for the second group, is less than three times its standard error so that the differences are insignificant. It is therefore improbable that there was any real falling off in the respiration rate during our experiments.

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[1] Comparison is made more difficult by the fact that the curve drawn by Marshall *et al.* showing the relationship between temperature and respiratory rate appears to be based on a single experiment, while different respiratory rates are given for other experiments at a given temperature. Thus the respiratory rates of female *Calanus* at 15° C. is given on p. 8 as 0·57, on p. 12 as about 0·70 (for normally saturated sea water), while on p. 15 a value of 0·74 is given for a temperature of only 12° C.

It is generally true that the respiratory rate of animals is related approximately to their surface area. Hence, since the copepods used in the experiments described above are all closely comparable in shape, some relationship may
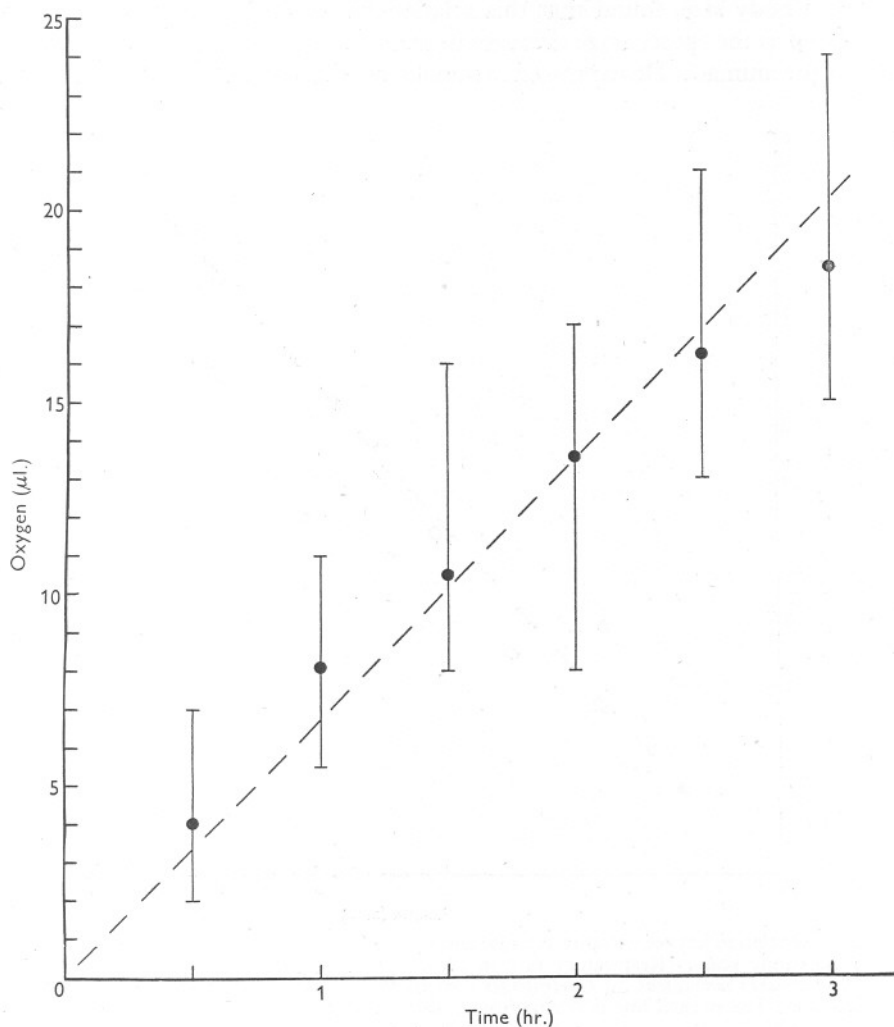

Fig. 1. Oxygen consumption by ten copepods at half-hourly intervals after start of an experiment.

be expected between their respiratory rate and the square, or some power close to the square, of their length. In Fig. 2 the respiratory rate is plotted against the length, on logarithmic co-ordinates, and it can be seen at once that the observed values lie very nearly on a straight line. The calculated regression line of the logarithm of the respiratory rate (R) on the logarithm of the length (L) is

$$\log R = 2 \cdot 193 \log L - 0 \cdot 9278,$$

from which it can be seen that in these measurements the respiratory rate was related to the length to the power of 2·19.

Zeuthen (1947, p. 81), in his analysis of the relationship between respiratory rate and body size, found that this relationship could be most satisfactorily expressed as the 'percentage decrease in metabolic rate at ten times magnification of the animal'. He expressed metabolic rate in terms of oxygen consumed
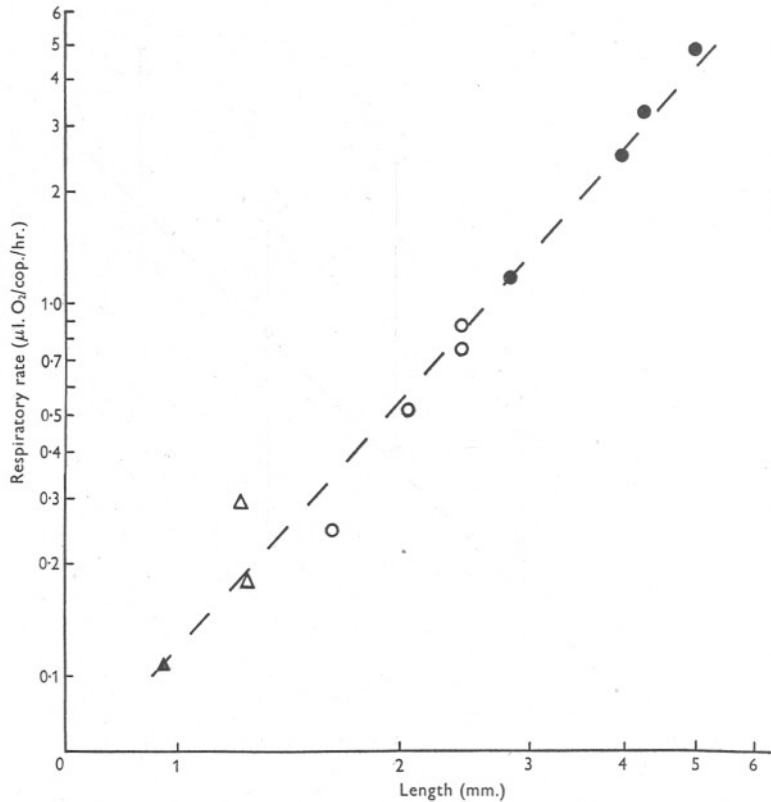

Fig. 2. The relation between respiratory rate and size of different copepods, plotted on a double logarithmic scale. (Respiratory rate in μl. O₂ per copepod per hour; length in mm.) ○, *Euchaeta norvegica*; △, *Centropages typicus*; ●, *Calanus finmarchicus*; ▲, *Centropages hamatus*. The pecked line is the regression line, given by

$$\log R = 2\cdot19 \log L - 0\cdot928.$$

per unit nitrogen content $\left(\dfrac{\mu l.\ O_2 \times 10^{-2}/hr}{\gamma N} \right)$ or per unit of weight, and showed that for a ten times magnification of the body size, the percentage decrease declined fairly steadily from *c.* 52 % for medium-sized animals (10 g.– 1000 g. wt.) to only *c.* 20 % for small copepods. The percentage decrease for animals of the size range used in this present investigation he found to be

30–40 %. In the experiments described here no measurements of weights or nitrogen contents were made, but weight is usually closely proportional to the cube of the length for animals of similar shape so that a rough comparison with Zeuthen's results can be made by expressing metabolic rate as rate of oxygen consumption divided by the cube of the length.

In the measurements made above there are three pairs of figures from which percentage decrease in the metabolic rate for a ten-times magnification of size can be calculated. *Euchaeta* females are very nearly ten times the size (as given by the cube of the length) of *Calanus* females, *Euchaeta* males are just less than ten times the size of *Calanus* Stage V and *Calanus* Stage V are nearly ten times the size of *Centropages hamatus*. The decreases in metabolic rate (expressed by respiratory rate divided by the length cubed) found for these pairs are 30, 35·75 and 49·75 % respectively, with a mean of 38·5 %. The decrease in metabolic rate for a ten times increase in size calculated from the regression of respiratory rate on length given above is 46 %. These figures agree very well with Zeuthen's figure of 30–40 % for animals of the range of size represented by the copepods used in the present experiment.

The difference between the respiratory rates of the two groups of experiments with *C. typicus* has been discussed above. The distribution of the observed points given in Fig. 2 suggests that the lower value might be the more correct one, or at least that corresponding to the figures found for the other species. The deviation of the higher value (0·29 μl. O_2/cop./hr.) from the regression line

$$\log R = 2 \cdot 193 \log L - 0 \cdot 9278$$

is 0·19, twice the standard error of estimate (0·09), whereas that for the lower value (0·18 μl. O_2/cop./hr.) is only 0·03. The agreement of the lower rather than the higher respiratory rate for *C. typicus* with those for the other species is made even clearer by calculating a regression omitting the higher value. This makes a slight but not clearly significant improvement in the correlation coefficient and gives regression equation

$$\log R = 2 \cdot 302 \log L - 0 \cdot 9901.$$

The deviation of the higher respiratory rate from this line is more than three times the standard error of estimate, i.e. this value almost certainly differs from the group of values represented by this regression line, while the deviation of the lower value is less than half the standard error of estimate.

Several suggestions could be made to account for an enhanced respiratory rate in *Centropages* as found in Exps. 48–51 and 58—for instance, that *C. typicus* is excited more easily than other species by handling or by light, but in the absence of any information about the factors which might have produced the increase of the respiratory rate, further discussion is not profitable.

The question as to which of the two respiratory rates found for *C. typicus*

represent the 'true' value leads to the wider question, namely how far the rates as determined for the other species (*Calanus*, *Euchaeta*, *Centropages hamatus*) are true for these copepods living under natural conditions in the sea. Any future discussion of nutritional requirements based on respiratory rates (cf. Pütter, 1909) must imply that the metabolic rates determined in the laboratory are true for the copepods under natural conditions. The curve given by Marshall *et al.* (1935) for respiration and temperature would permit us to calculate approximately the respiration rates for the various temperatures at which the different species are living over the seasons of the year. But there are many other factors apart from temperature that might also affect respiration. Of these some attention has been given to such internal factors as sex and developmental stage. As regards environmental conditions, there are indications that light has little effect on Stage V *Calanus* (cf. also Marshall *et al.*), though no experiments were made using bright sunlight. However, the precise effects of light as well as of such factors as feeding, season, etc., must await further study.

There remains the very pertinent question as to how far the experimental conditions in a closed respirometer may modify the metabolic rate. The experiments on *Calanus* by Marshall *et al.* seemed to show that lowered O_2 tension had little or no effect unless the concentration fell below about 3 ml. O_2/l.—a value which would never even be approached in our 3-hourly experiments. There is also the possible disturbing effect on metabolism of handling the animals. This would appear to be slight (with the possible exception of *Centropages typicus*) in view of the fact that no clear reduction in respiratory rate with time was observed in our experiments, and also since our results (for *Calanus*) agree very well with those of Marshall *et al.* who employed the Winkler technique where animals were left undisturbed for relatively much longer periods of time. From the results of a few experiments with Stage V *Calanus* (Table I, Exps. 40–42) where shaking was limited to a few minutes immediately prior to final reading of the manometers, it is apparent that shaking depressed the respiratory rate of the copepods. But no permanent injury appears to have been caused by it, since the great bulk of our experimental copepods were active and healthy after being in the respirometers, and indeed, if used for a second experiment, gave a result usually showing good agreement with the original determination. The shaking of the respirometers may have reduced respiration by interfering with the physical activity of the copepods in the respirometer flask rather than by injury of the animal.

It is obvious, of course, that we were measuring the respiratory rates of the copepods in a state of activity, but how far their activity in the respirometer corresponds to their normal activity in the sea is not easy to determine. In these measurements, as in those of Marshall *et al.* and Clarke & Bonnet, the copepods were enclosed in a very small volume of water, of the order of 1 ml. per copepod, while in the sea the water in which the copepod is swimming is

effectively infinite and its distance from its nearest neighbour is probably of the order of ten or possibly a hundred times as great as it is in the respiro-meter. In consequence the probability of contact with the walls of the respirometer or with other copepods is very much greater than it is in nature. This repeated stimulus of contact may keep the copepods in a comparatively excited condition and this may produce a rise in the respiratory rate.

SUMMARY

The respiratory rates of four species of planktonic copepods were measured. In two of the species measurements were made with two copepodite stages, and with adult male and female specimens.

The rate for *Calanus finmarchicus* Stage V at 17° C. was found to be 0·52 µl./cop./hr., a figure which agreed with previous measurements.

For all the species and stages studied the respiratory rate was found to be closely proportional to the length to the power of 2·2.

The relevance of such measurements to conditions in the sea is briefly discussed.

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