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An Energy Budget for Adult *Brachionus plicatilis* Muller (Rotatoria)

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Summary. An energy budget is presented for adult *Brachionus plicatilis* Muller, a brackish water rotifer. At 20° C the hourly consumption of *Dunaliella salina* by an individual rotifer was found to be 332.79 ± 93.25 cal. The assimilation rate was 64.43 ± 9.95 cal per hour when measured, and 62.88 cal per hour when calculated from $P+R$. The difference between these two values is 2.4%. Respiration rate per individual per hour was 26.375 ± 2.4 cal and egg production cost 36.5 cal per hour. The amount of faecal matter produced in an hour was obtained by subtraction $(C-A)$. Ecological efficiencies are calculated and discussed in relation to those of animals of similar feeding habits.

Introduction

Brachionus plicatilis is a rotifer found in brackish water in estuaries and transient saline ponds. Along with other rotifers it is a useful experimental animal because of its rapid life history and high reproductive potential. Rotifers may be of considerable importance in the energy flow through pond and lake ecosystems but whilst some data are available on feeding, respiration and production of these animals (references in text), so far no complete energy budget has been published. King (1967) provided comprehensive data on *Euchlanis dilatata* omitting respiration but giving very useful observations and a valuable discussion of ecological efficiencies in rotifers. The present paper provides complete data for an energy budget and ecological efficiencies of adult *Brachionus plicatilis*.

Material and Methods

Brachionus plicatilis was obtained from stock cultures at the Biologische Station, Lunz-am-See, of the Austrian Academy of Sciences by courtesy of Prof. A. Ruttner-Kolisko. Cultures were maintained at 20° C in sea water and fed on excess *Dunaliella salina*. Experimental work was performed at 20° C on animals whose ages were known to the nearest hour.

a) Oxygen Consumption

This was determined in stoppered Cartesian divers [Linderstrom-Lang, 1943; Zeuthen, 1950; Holter and Zeuthen, 1966 (review); Klekowski, 1971]. The divers used in the present work had a gas phase of less than 0.7 µl and were constructed without the expanded head to reduce the chance of rapidly swimming

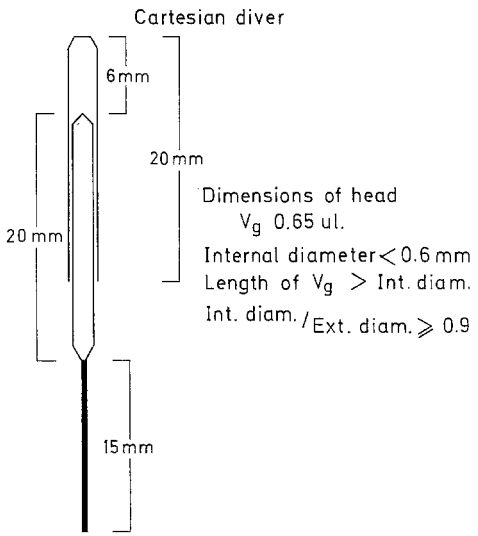

Fig. 1. Cartesian diver respirometer

animals leaving the diver head before the insertion of the gas phase. The reduced gas phase made necessary a modification of the original diver plan according to the proportions shown in Fig. 1. The sizes given approximate to those used for divers with a gas phase of 0.625 µl but the proportions need further modification as the ratio of the internal to the external diameter of the Pyrex glass capillary approaches 0.9.

Divers are usually loaded in two stages, first with the animal then the gas phase using different braking pipettes. This method was unsuitable due to the rapid movement of the rotifers. A calibrated braking pipette was therefore loaded first with the *Vg* required to float the diver then an individual rotifer was picked up with the same braking pipette. Careful breath control was necessary to prevent excess water being taken into the braking pipette so overloading the diver head. It was found that a length of water up to 10 mm containing the rotifer was satisfactory. With more water there is danger of flushing out the rotifer before the air bubble has been inserted, or placing the bubble so low in the diver that its centre of gravity is disturbed and it will not float upright.

The length of the air bubble in the braking pipette can be read with an accuracy of ± 0.25 mm. This introduces errors into the size of the *Vg* recorded for the diver, the magnitude of the error varying in proportion to the relative sizes of the *Vg* and the calibration of the braking pipette used. That used throughout this work had a calibration of 0.125 µl/mm. The diver *Vg* was 0.625 and therefore the error of the *Vg* was

$$\frac{0.25 \times 0.125}{0.625} \times 100 = \pm 5\%.$$

The manometer could be read with an accuracy of 0.5 mm of Brodie's fluid. The smallest change recorded was 21 mm giving an error of $\pm 2.3\%$. Therefore the maximum error in any individual respiration rate recorded here is $\pm 5.5\%$.

Respiration rates of adults were measured using one animal per diver; the egg rates were measured in groups of three or four. All measurements were carried out in sea water with no food and the maximum time in the respirometer was five hours. This was reduced for animals with high respiration rates so that the oxygen tension in the diver was never below 80% saturation. All ancillary operations were performed at about 20° C but even so a period of one to two hours was found to be necessary to allow complete acclimation in the diver set-up reliable respiration data could be obtained.

Ivlev's (1945) oxycalorific coefficient was used to convert hourly oxygen consumption to calories.

b) Food Consumption

Dunaliella salina, a naked green flagellate with a volume of about 140 μ^3 was used as food. Cultures of Dunaliella were labelled with ^{14}C sodium bicarbonate solution (specific activity 10 μCi per ml), 0.5 ml being added to 50 ml of Dunaliella culture. The algae were used for feeding after twenty-four hours. The fragility of the algae prevented their being filtered from the labelled medium and resuspended in sea water, but it was found that the uptake of ^{14}C from the medium was negligible provided adequate washing procedures were employed, and therefore feeding rates were measured in the labelled medium.

Feeding experiments were conducted in haemagglutination trays with cavities of 1 ml capacity. Before feeding, 5 ml of labelled Dunaliella culture were filtered onto an HA Millipore filter and washed under pressure in 45 ml of distilled water. The filter was then dried at 50° C for three hours and placed in a sealed polythene envelope for subsequent counting. Haemocytometer counts of the cell concentration were made on the same culture and so the specific activity of the algal cells was determined.

Groups of four rotifers were fed in each 1 ml cavity if the haemagglutination tray for one hour. They were then removed and washed first in sea water then in three changes of distilled water to remove salts which crystallise on the filters. The final washings were done under pressure on an HA Millipore filter and 30 ml of distilled water were washed through. About sixteen rotifers were collected on each filter which was then removed from the filter flask and dried as described above.

Radioactive counts were done on a Panax liquid scintillation counter in 10 ml of toluene-based scintillant containing 0.5 gm per litre POPOP and 4 gm per litre paraterphenyl. To maintain a counting accuracy of greater than 94%, the time taken to record one thousand counts was noted in each case, (Lund *et al.*, 1958). Prior to counting, vials were acclimated to 5° C, the temperature giving optimal counting efficiency of 85% for the counter in use.

Each experiment consisted of the following sets of counts:

a) Source—3 × 1000 counts to test machine efficiency;

b) background—clean HA Millipore filter in scintillant;

c) algal count;

d) rotifer count;

e) last washing water. In early trials this was found to differ negligibly from a) and thereafter it was omitted.

Feeding rates were calculated as follows:

$$\text{Cells ingested per animal per hour} = \frac{60}{t} \times \frac{R_R \cdot V \cdot N_A}{N_R \cdot R_A}$$

where t = length of the experiment in minutes

R_R = c.p.m. in rotifer vial

N_R = Number of rotifers in vial

V = Volume of algae counted
N_A = Number of algae per ml
R_A = c.p.m. in algae vial.

The volume of water cleared by an animal in an hour was calculated from the same formula omitting the term N_A.

The number of cells consumed per hour was converted into calories taking the calorific value of Dunaliella to be 0.436×10^{-6} cal per cell. This is one third that of Chlamydomonas (Richman, 1958) to which Dunaliella is related and of which it is about one third the volume.

c) Assimilation

Groups of four animals were fed for 2, 4, 6, 24, 26, 28, 41, 43 and 45 hours in 1 ml of radioactivity labelled algal suspension. They were then transferred to unlabelled food for an hour before washing, drying and counting as described above. The assimilation per hour was determined using the same formula as for consumption, but since radioactive food in the gut was replaced by unlabelled algae the result is the amount of food already assimilated. This was converted to calories in the same way as consumption.

d) Production

Dry weights of adults and of adults with eggs were obtained by cumulation (Doohan and Rainbow, 1971) on a Cahn Gram electrobalance, and the weight of an egg obtained by subtraction. Assuming 50% of the dry weight to be carbon, the calorific values of adults and eggs were obtained. When rotifers are mature increase in length virtually ceases (Ruttner-Kolisko, 1972) and for the purposes of the present paper only reproductive production has been considered.

Results

Table 1 shows the respiration rates of individual adult *Brachionus plicatilis* in microlitres $\times 10^{-4}$ of oxygen per hour and in calories $\times 10^{-6}$ per hour. Prior to egg production the rates are relatively uniform but ovigerous females have a rate more than double this. The higher rate appears to be independent of the number of eggs the female is carrying since 95% confidence limits of the mean of all ovigerous females cover the range of values contained in each separate category of ovigerous female although the number of determination is low. The mean respiration rate of all ovigerous females is therefore used in the budget, since in an actively growing culture mature females are seldom without an egg.

The consumption data in Table 2 show much greater variability than either respiration or assimilation, but since the variation was not closely correlated with the concentration of the feeding suspension a mean value for all the experiments was calculated.

According to Galkovskaya (1963) feeding intensity of *Brachionus calyciflorus* Pallas is dependent on cell concentration in the medium up to 0.5×10^6 cells per ml. Above this concentration feeding intensity is maximal. The lowest concentration used in the present work is within the maximal range given for this related rotifer species.

Table 1. Respiration rates of individual *Brachionus plicatilis* in μl $O_2 \times 10^{-4}$ per individual per hour

Stage	Egg	Adult	Adult + one egg	Adult + two eggs	Adult + three eggs	Post oviger-ous adult	Senile adult	Total oviger-ous adults
	5.242	20.405	43.725	54.219	59.758	53.224	13.281	
	7.652	29.15	47.223	61.215	54.802	57.318	12.826	
		31.482	59.47	71.126	63.839	47.066	12.243	
		23.3	51.26	50.049		43.338		
		20.504	47.532	58.25		65.005		
		21.669	35.416	61.215				
		23.766						
		24.698						
		27.494						
		25.069						
		23.32						
Mean ± S.E. Mean	6.447	26.623 ± 2.36	47.438 ± 8.37	59.346 ± 7.56	59.466	53.190	12.783	54.607 ± 4.97
S.D. × t			±20.49	±18.52				±19.25
Mean ± S.E. in cal × 10^{-6}	3.11	11.89 ± 1.14	22.91 ± 4.04	28.66 ± 3.65	28.72	25.69	6.17	26.375 ± 2.4

Table 2. Consumption of *Dunaliella salina* by *Brachionus plicatilis*

Rotifers per experi-ment	Food cells × 10^3 per ml	Activ-ity in C.P.M. per ml	Activ-ity in C.P.M. per rotifer	μl cleared/ ind./hr	Cells eaten/ ind./hr	Con-sump-tion — Mean assimil.	Con-sump-tion in cals × 10^{-6}
16	1440	24907	11.72	0.94	1353.6	1205.7	525.69
15	1440	24907	8.58	0.68	979.2	831.3	362.45
13	775	14925	16.96	1.14	883.5	735.6	320.72
13	775	14925	18.41	1.23	928.7	780.8	340.43
13	970	16000	12.04	0.75	727.5	579.6	252.71
12	970	16000	10.20	0.64	620.8	472.9	206.18
23	590	9600	14.44	1.5	885.0	737.1	321.38

Mean consumption = 763.28 cells/ind./hr. Mean ± S.E. (mean) = 332.79 ± 93.25 cals × 10^{-6}/ind./hr. S.D. × t = ± 246.7.

Table 3. Assimilation of *Dunaliella salina* by *Brachionus plicatilis*

Rotifers per experiment	Time in labelled food (hrs)	Food cells $\times 10^3$ per ml	Activity in C.P.M. per ml	Activity in C.P.M. per rotifer	µl per ind. per hr assimil.	Cells per ind. per hr assimil.	Cal^2 $\times 10^{-6}$ assimil. per hr
24	2	350	8230	9.12	0.56	196	85.46
22	4			12.36	0.38	133	57.99
24	6			20.49	0.42	147	64.09
16	24	590	9600	43.37	0.19	112	48.83
12	26			68.50	0.27	159	69.32
12	28			72.80	0.27	159	69.32
15	41			76.89	0.20	118	51.45
16	43			106.74	0.26	153	66.71
15	45			113.03	0.26	153	66.71

Mean assimilation = 147.9 cells/ind./hr. Mean $\pm$ S.E.(mean) = 64.43 $\pm$ 9.95 cals $\times 10^{-6}$/ind./hr. S.D. $\times t = \pm 29.85$.

The concentration of food used in the assimilation experiments (Table 3) was lower than in most of the feeding experiments but again there is no regular variation with concentration. The accuracy of the mean value (S.E. = $\pm$ 15%) coupled with the irregularity of the variation in the data, does not justify rejection of values from the lower food concentrations.

Schindler (1968) points out that in *Daphnia magna* respiration of assimilated ^{14}C begins after 16–24 hours after which true assimilation cannot be measured. The results presented here do not suggest that this has occurred during the period of the experiment since there was no fall off in activity of the rotifers. This probably requires further investigation.

Table 4 shows the dry weights obtained by cumulation and the calorific values of individual adults and eggs. These values provided the basis for production estimates. Egg development time in rotifers has been shown to be closely dependent on temperature (Edmondson, 1960). In cultures of *Brachionus plicatilis* kept at 20° C, Ruttner-Kolisko (personal communication) found that the eggs take 24–26 hours from laying to hatching. The percentage of egg development occurring in one hour will vary according to the number of eggs the female is carrying. This data is recorded in Table 5, and the hourly production converted to calories using the data from Table 4. As for the respiration data, ovigerous females were treated as one group irrespective of the number of eggs they were carrying.

Table 4. Data for production estimates for *Brachionus plicatilis*

Category	Mean dry weight (μg)	Calculated cal. value (assuming 50% d. weight = carbon)
Adult	0.158	790×10^{-6} cal.
Adult + 1 egg	0.250	1290×10^{-6} cal.
Egg	0.092	500×10^{-6} cal.

Table 5. Hourly reproductive production of *B. plicatilis*

Category	Proportion of egg produced per hour	Mean (%)	Cal. val. of egg (cals)	Hourly production of egg (cals)
Female + 1 egg	4% of an egg			
2 eggs	8% of an egg	7.3		36.5×10^{-6}
3 eggs	16% of an egg		500×10^{-6}	

Table 6. Elements of an energy budget for adult *Brachionus plicatilis* in cal $\times 10^{-6}$ per adult per hour

		Measured $\pm$ S.E.	Calculated
Consumption	(C)	332.79 ± 93.25	
Assimilation	(A)	64.43 ± 9.95	62.875 ($P+R$)
Respiration	(R)	26.375 ± 2.4	
Production (eggs)	(Pr)	36.5	34.9
Faeces	(F)		268.36 ($C-A$)
Efficiencies:	$A/C = 0.194$	Pr/C (K_1) = 0,11	Pr/A (K_2) = 0.57

Table 6 shows the elements of an energy budget for reproducing adult *Brachionus plicatilis*. The second estimate of reproductive production was calculated by Winberg's "physiological method" applied by Galkovskaya (1971) to rotifer populations in the field. This involves the determination of net production efficiency (K_2 or P/A) and the metabolic loss (T) or respiration rate, production is then equal to $\frac{TK_2}{1-K_2}$ The result obtained by this method is very close to that determined from dry weight and calorific values of the eggs.

Assimilation calculated as $P+R$ is within the limits of accuracy of the mean assimilation measured radioactively and differs from it by only 2.4%. However the assimilation measured radioactively must also include

some kind of growth factor when measurements were continued for several hours. This could be metabolic activity in the ovary or vitellarium since growth in size has definitely stopped by the time eggs are produced.

Discussion

a) Respiration

Respiration rates of rotifers have previously been determined using large numbers of animals in micro-Winkler titrations (Pourriot and Deluzarches, 1970) or using large Cartesian divers with several animals in each (Belyatskaya, 1959; Galkovskaya, 1963, 1971). Pourriot and Deluzarches demonstrated the effect of crowding on the respiratory rates of several rotifer species as Zeiss (1963) had done for *Daphnia magna*. The former authors showed that in the case of rotifers, the reduced rate in more concentrated cultures was not correlated with reduced oxygen tension in the medium. The value of the small divers used in the present work lies in their elimination of the crowding effect, and since planktonic rotifers are constantly active even in the relatively confined space of the diver head, an accurate assessment of a fairly normal active respiratory rate is feasible. Using animals of known age individual differences between animals of the same age became apparent and also differences between adults.

When the respiration rate of all the eggs carried by a female is subtracted from the total respiratory rate, the rate for an ovigerous female is still higher than that of a pre-ovigerous adult. This is probably due to increased metabolic activity in the ovary and vitellarium, which continues for about fortyeight hours after the laying of the last egg. During the postovigerous period, the body of the female seems to accumulate large quantities of yolk and the respiratory rate is as high as that of the reproducing females. As the animal stages, the yolk is dispersed but the gut remains empty and at this stage the respiratory rate decreases below that of young adults without eggs. Apart from that of the older adults, these different respiratory rates all fall within the range of values obtained by Pourriot and Deluzarches for large numbers of *Brachionus calyciflorus* of unknown age distribution under different experimental conditions (1.57–6.2 $\mu l \times 10^{-3}$/ind/h.). The values obtained by Belyatskaya (2.24×10^{-3} μl) and Galkovskaya (5.04×10^{-3}) for the same species also fall within this range. It is important therefore that mean respiratory values for a population even of animals as small as rotifers be determined on animals of known state if they cannot be measured individually. This is even more important where actively growing cultures are concerned, since the age-specific respiratory rate is even more variable (cf. Ruttner-Kolisko, 1972).

b) Feeding

The only published work on the feeding rate of *B. plicatilis* is that of Ito (1955) in which the food was *Synechococcus* sp. The mean volume filtered per individual per hour was 3.04 µl, corresponding to a cell consumption of 24.32×10^3 in a food concentration of 8×10^6 cells per ml. This is very much higher than the values obtained in the present work using *Dunaliella salina*. Galkovskaya (1961) suggests that the food consumption of *Brachionus calyciflorus* increases with cell concentration in the feeding medium, up to a maximum at about 0.5×10^6 cells per ml, when the rate levels off. King (1967) found a similar effect with *Euchlaris dilatata* feeding on *Chlamydomonas reinhardii*, but no levelling off occurrred with *Euglena* as food in the concentrations he used. This indicates, as Erman (1962) suggested, that when interspecific comparisons of food are made, feeding rate varies more with the quality of the food offerred than with its concentration. He found that in the case of *B. calyciflorus* the filtering rate ranged from 1.3 → 13.3 µl/ind./h according to the nature of the food offered. The difference between Ito's results and the ones presented here are probably a consequence of the differences between the quality of the food offered rather than of its concentration.

With a food concentration greater than 0.5×10^6 cells/ml the filtering rate of *Brachionus calyciflorus* (Galkovskaya, 1963) and of *B. rubens* (Erman, 1956) is about 1 µl/individual/h. Rates obtained for *B. plicatilis* agree with this but the results of Galkovskaya and Erman show considerable variation despite the large numbers of animals used for each determination. The maximum feeding rates obtained by Galkovskaya vary by a factor of ten. The variability of the *B. plicatilis* results is much reduced by the use of radioactive techniques and these, together with rates obtained by Pennington (1941) for *B. calyciflorus* and the present author's unpublished data for *B. rubens* and *Keratella quadrata* all fall within the same range. Until more refined methods are available for the determination of feeding rates of very small animals, it is probable that all Brachionidae will fit Galkovskaya's graph. As with respiration data, the need to use large numbers covers individual variation. Small animals vary by small amounts, but have proportionately the same variability as larger ones. Refined techniques would demonstrate individual variation whereas accurate techniques used with large samples mask individual variation by substituting a spuriously accurate mean. This is probably the case with the results of the radioactive work used here.

c) Assimilation and Assimilation Efficiency

Galkovskaya (1963, 1971) gives assimilation efficiencies A/C for *B. calyciflorus* ranging from 0.21→ 0.78 with the lower efficiencies appar-

ently occurring in higher food concentrations. The only other value for rotifers is given by Sorokin and Mordukhay-Boltovskaya (1962) for *Asplanchna* which is a predator. Their values, quoted by Galkovskaya, are 0.16→0.22. The efficiency of *B. plicatilis* (Table 6) is very low, particularly for an animal feeding on a naked alga. This is probably due to the excess of available food in the medium. Feeding is a continuous process in planktonic rotifers and little or no rejection of particles of the right size and nature occurs in the gullet. In excess food therefore, particles pass through the gut too quickly to be effectively digested. King (1967) noted that undigested algae appeared in the faeces of *Euchlanis dilatata* only at the most concentrated food level. Many cells of *Dunlaliella* seen in the faeces of *B. plicatilis* were still green and apparently intact, but they were no longer motile and therefore not available as food. The assimilation data might have been checked using the relation $A = C-F$ if labelled faeces had been collected during experiments, but the difficulties of separating faecal material from labelled algae and medium were not overcome. The similarity between the calculated assimilation $(P + R)$ and the experimental result gives confidence in the radioactive technique employed.

McNeill (1970) found that the assimilation efficiency of *Leptopterna dolabrata*, a mirid, ranged from 0.28 to 0.36. Since the mirid feeds largely on cell contents only, one would expect its efficiency to compare well with that of an animal feeding on a naked cell. Similarly Wiegert's (1964) work on *Philaenus spumarius* a plant fluid feeder, shows a very high assimilation efficiency, 0.30→0.36 for nymphs, 0.66 for adults. However neither of these animals feeds continuously and again it is the rate of movement of food through the gut in a rotifer which reduces the assimilation efficiency relative to that of other species feeding on readily assimilated food material.

d) Production and Production Efficiencies

Since the present paper deals with adult rotifers, only reproductive production has been calculated. The gross production efficiency P/C or K_1 (Ivlev, 1945) is quite low for a herbivore but is nevertheless within the range of values given by Galkovskaya (1963) for *B. calyciflorus*, 0.04→0.36, which probably also excludes body growth. The low efficiency is clearly a function of the poor assimilation efficiency since the nett production efficiency P/A, or K_2 (Ivlev, 1945) corresponds to the higher range of values given for *B. calyciflorus* 0.20→0.69, and corresponds closely to the values for the growth of *Philaenus spumarius* nymphs (Wiegert, 1945) 0.53 and to McNeill's (1970) values for *Leptopterna dolabrata* 0.50→0.58 which include both growth and reproduction. Although increase in size is not negligible in a rotifer it is nevertheless

small in comparison with its extraordinary reproductive potential. It is therefore theoretically possible that Pr/A for an adult rotifer should equal $\frac{Pg+Pr}{A}$ where Pg is growth for other animals feeding on easily assimilated material, or the Pg/A for an actively growing nymph of similar feeding habits. McNeill relates the high nett efficiency of his animal to the fact that the mirid is sedentary. This is hardly the case in a rotifer. Though *B. plicatilis* has a foot and can remain attached to a surface, this seldom occurs in a healthy growing culture and when it does ciliary currents continue at the same rate as when the animal is moving.

Adult *B. plicatilis* is highly efficient at converting assimilated food into reproductive production, but much less efficient at converting available food material into body material which could be used by the next trophic level. Under conditions where food is less readily available, the gross production efficiency may be higher. Galkovskaya (1963) found that *B. calyciflorus* achieved maximal reproductive production in the highest food concentrations (3×10^6 cells/ml). This coincided with both maximal consumption and maximal gross and nett production efficiencies. However the work recorded by her in 1971 does not show correspondence between K_1, K_2 and food concentration but shows a steady increase in K_1 as food concentration decreases while K_2 fluctuates irregularly showing no correlation with either of the other parameters. This seems to be more realistic since K_2 is a measure of the physiological state of the animal and therefore would be affected only indirectly by environmental conditions. Further work on animals cultured in different food levels is needed to ascertain the quantity of available food which gives maximal K_1 without reducing K_2. A budget determined at this food level would give the energy relations of an animal at its most efficient, and provide a standard for comparison with field situations.

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