THE SIGNY ISLAND TERRESTRIAL REFERENCE SITES: V. OXYGEN UPTAKE OF *Macrobiotus furciger* J. Murray (TARDIGRADA)

By Peter G. Jennings

Abstract. Oxygen uptake by *Macrobiotus furciger* has been measured at +5° and +10° C using a Cartesian diver micro-respirometer. From measurements of the buccal tube and lines of placoids, body length and live weight have been derived for each of the experimental animals. Mean oxygen uptake on a weight specific and an individual animal basis has then been calculated for each of five size groups. The respiration rate–body weight regression ($R = aw^b$; in μl. $O_2 \times 10^{-3}$/individual/hr. and μg. live weight) was calculated for each of the experimental temperatures. The value of "a" was 0·31 at +5° C and 0·57 at +10° C, and the exponent "b" was 0·51 at both temperatures. A Q_{10} of 3·46 has been calculated. The rate of oxygen uptake ($1{\cdot}82 \times 10^{-3}$ μl./individual/hr.) for a 600 μm. *M. furciger* at +10° C is compared to that of *Macrobiotus dispar* of a similar size at +20° C ($1{\cdot}0 \times 10^{-3}$ μl./individual/hr.).

It is generally accepted that the Tardigrada warrant a separate phylum and eight families within three orders have been recognized. According to Ramazzotti (1972), the family Macrobiotidae contained 53 per cent of all known tardigrade species. The Tardigrada are cosmopolitan in distribution and *M. furciger* has been reported from localities in Central Europe, Rumania, South America, New Zealand and the Antarctic.

As a complementary aspect of an ecological study of the Tardigrada of the Signy Island reference sites (SIRS), the oxygen uptake of *M. furciger* was measured. This will enable an estimate to be made for the population respiration of this species. *M. furciger* is robust and easily handled, and occurred in 59 per cent of all terrestrial habitats examined on Signy Island, from the very dry to the very wet, being represented on both of the reference sites. It was also found in lakes and pools.

Methods

Respirometry

The animals used for the measurement of oxygen uptake were extracted from the moss of SIRS 2 (Tilbrook, 1973) as part of a study of the temporal and spatial distribution of the Tardigrada. The extraction technique was the modified Baermann funnel method described by Whitehead and Hemming (1965) and subsequently used for Tardigrada by Hallas and Yeates (1972). In the present study the animals were extracted at room temperature which, depending on time of year, ranged from +3° to +15° C. They were then stored at +7° C until required for the experiments.

Measurements of oxygen uptake were made using a Cartesian diver micro-respirometer (Holter, 1943; Linderstrøm-Lang, 1943) in a constant-temperature room at Signy Island. Stoppered divers were used having a gas volume of 0·75–6·68 μl. and the animals were introduced into the divers by the sedimentation method described by Klekowski (1971). The divers were equilibrated in the respirometer at the experimental temperature for at least 1 hr. before readings at 30 min. intervals were undertaken.

Initially oxygen uptake of individual animals was measured, but for the size of divers in use the change in gas volume during each experiment was very small. Therefore, on all subsequent occasions measurements were made on several animals, usually five, in each diver. Unfortunately, this required considerable pre-sorting of the material under a binocular microscope in order to reduce size variation within the group. The day before they were required for respirometry the specimens were sorted into five arbitrary body-length groups. These were as follows:

1. <250 μm.
2. 251–350 μm.
3. 351–450 μm.
4. 451–550 μm.
5. >551 μm.

The respiration experiments were continued for at least 4 hr. Even with five animals in the diver, the total change in gas volume was less than 2 per cent. After each experiment the animals were removed and mounted on slides in polyvinyl-lactophenol. Unfortunately, some specimens, particularly in the smaller size groups, were lost during this procedure. The two experimental temperatures used in this study, +5° and +10° C, were chosen as being representative of summer conditions in Signy Island moss, but lack of time limited the number of measurements made at +10° C.

Length and weight derivation

During the mounting process some animals expanded in size, thus giving an overestimate of body length, and the cuticle ruptured in a few of these causing a decrease in overall length. Furthermore, all specimens shrank progressively with time. For these reasons, direct measurement of body length was unreliable, and it was necessary to find another parameter to which this could be related but which was unaffected by the mounting technique. A linear correlation exists between the muscular pharynx length and body length in *M. islandicus* Richters (Higgins, 1959) and *M. hufelandii* Schultze (Francheschi and Lattes, 1969), but the muscular pharynx is a soft structure, which is in some cases distorted during mounting. The buccal tube and placoids (Fig. 1) are both hard parts, unaffected by the mountant, and are shed and replaced before each moult. These structures were used in this study and Fig. 1 indicates the exact points from which the two measurements (A and B) were taken.

The relationships between body length of *M. furciger* and A and B were derived using preserved material from a single sample unit, all mounted at the same time and measured on the same occasion (Fig. 2). From the two resulting regression equations, two estimates of body length were derived for each experimental animal. The mean of these two lengths was then used in all subsequent calculations. As both the measured structures are lost before the moult, no body-length estimates were available for animals in the simplex stage (that period of approximately 5 days, prior to moulting when the old buccal parts have been expelled and the new ones not yet formed).

For estimating the weight of the specimens, it was assumed that their shape approximates to a cylinder. This method has been used for other Tardigrada by Hallas and Yeates (1972), who assumed (from Edwards, 1967) that their specific gravity was 1·04. To overcome the problem of both length and width being required in the calculation for volume, Hallas and Yeates used a length to width ratio of 4 : 1 for *Macrobiotus*, which is the ratio quoted by Marcus (1929) for this genus. The validity of this ratio for application in the present study was tested, again using a single sample and measured in a standard way (Fig. 3). Width measurements were taken just posterior to the first, second and third pairs of legs and the mean of these three widths was then used. Over the experimental range of 200–600 μm., a length to width ratio of 4·1 : 1 to 4·5 : 1 was indicated. In all subsequent calculations, therefore, a ratio of 4·3 : 1 was taken. The weight (W) of each animal was then given by:

$W = V \times$ s.g., where V is volume and s.g. is specific gravity,

where $V = L\pi\left(\frac{w}{2}\right)^2$, where L is length and w is width.

Since $w = \frac{1}{4 \cdot 3}.L$, $\left(\frac{w}{2}\right)^2 = \left(\frac{L}{2 \times 4 \cdot 3}\right)^2 = \left(\frac{L}{8 \cdot 6}\right)^2$.

Then $W = L\pi\left(\frac{L}{8 \cdot 6}\right)^2 \times 1 \cdot 04 \times 10^{-6}\ \mu$g.,

or $W_{4 \cdot 3:1} = L^3 \times 0 \cdot 044 \times 10^{-6}\ \mu$g.

Oxygen Uptake by *M. furciger*

A total of 55 oxygen-uptake rates was obtained, 44 at +5° C and 11 at +10° C. The relationship between log live weight and log oxygen uptake per individual is shown in Fig. 4. This

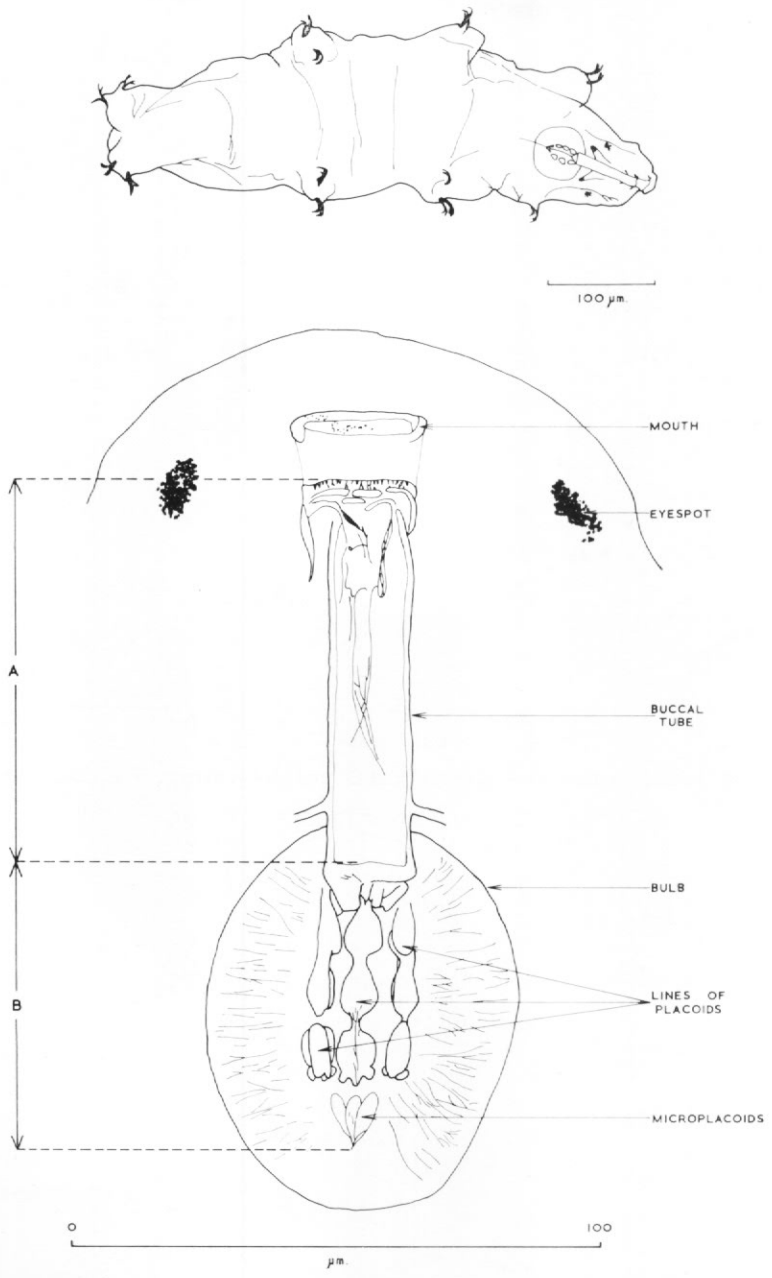

Fig. 1. *Macrobiotus furciger*. General body plan and detail of bulb and buccal tube. The two measurements from which total body lengths were derived are labelled A and B.

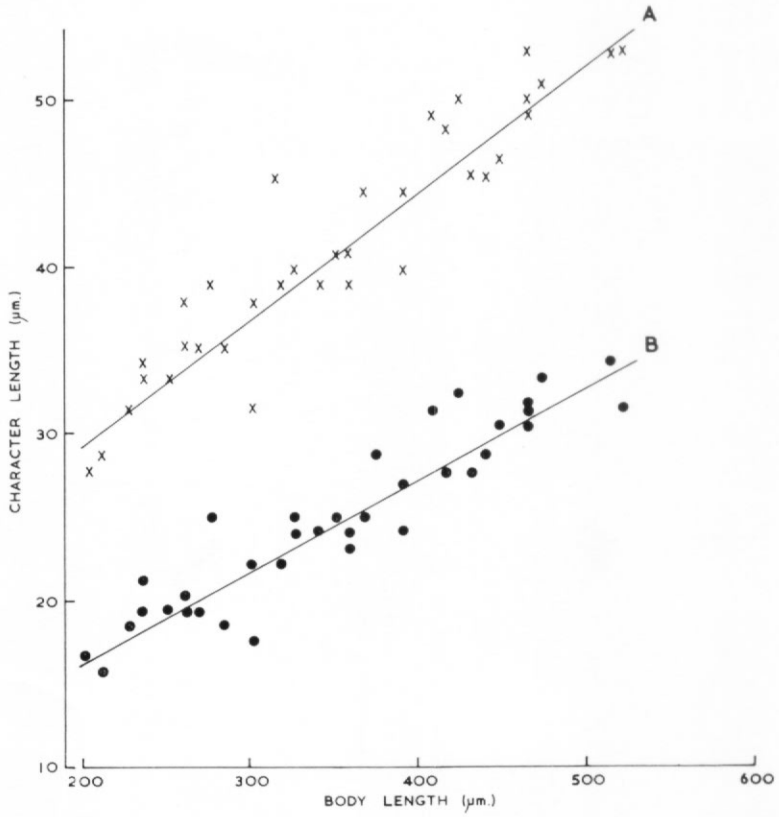

Fig. 2. Relationship between character lengths A and B and body length. The equations for the linear regressions are:

A: $y = 0{\cdot}08x + 13{\cdot}96$, $r = +0{\cdot}95$,
B: $y = 0{\cdot}05x + 5{\cdot}39$, $r = +0{\cdot}93$.

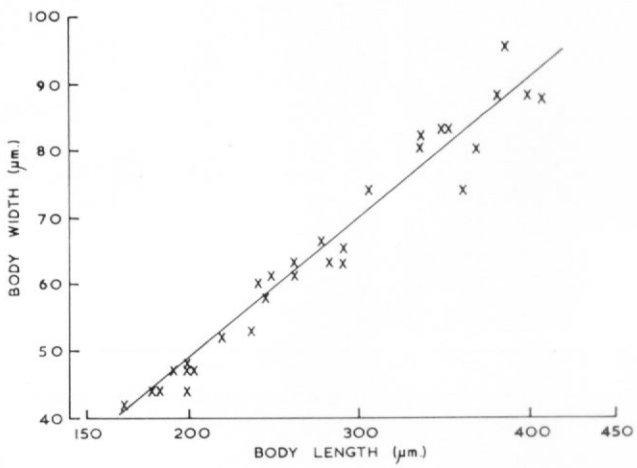

Fig. 3. Relationship between body width and body length. The equation for the linear regression is:
$y = 0{\cdot}21x + 7{\cdot}82$, $r = +0{\cdot}93$.

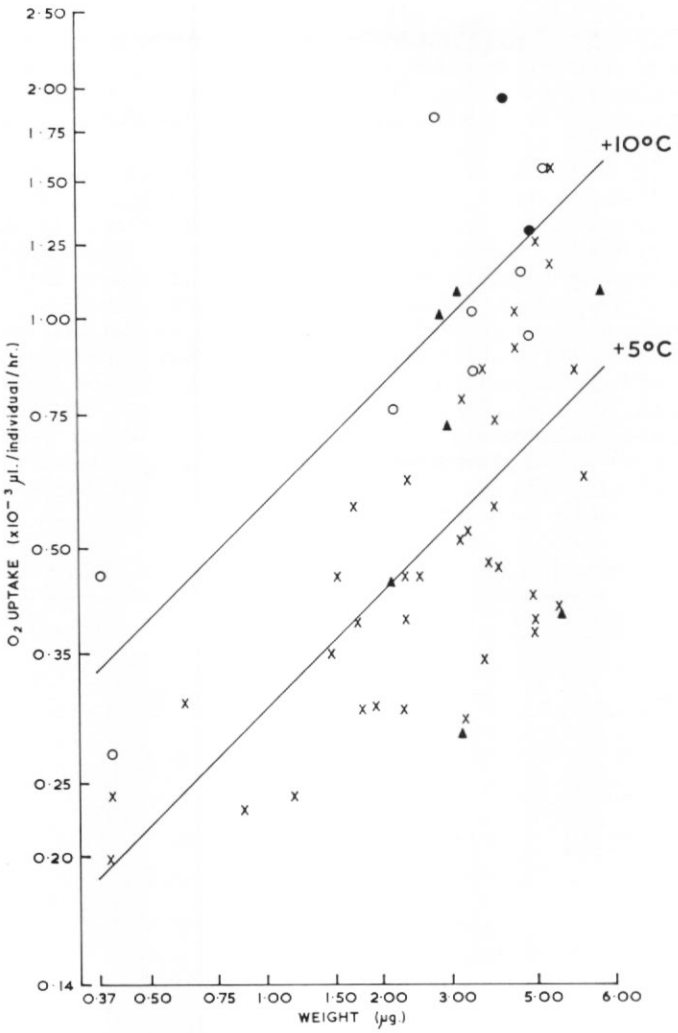

Fig. 4. Relationship between oxygen uptake per individual and live weight of *Macrobiotus furciger* at +5° and +10° C plotted on a double log scale.

▲ Rates for individuals at +5° C.
● Rates for individuals at +10° C.
× Rates for group means at +5° C.
○ Rates for group means at +10° C.

The equations for the linear regressions are:

$+5°$ C: $\log y = 0{\cdot}51 \log x - 0{\cdot}31$, $r = +0{\cdot}67$,
$+10°$ C: $\log y = 0{\cdot}51 \log x - 0{\cdot}57$, $r = +0{\cdot}89$.

includes both individual and group means and both of these have been used to calculate the two regression lines:

$R = 0{\cdot}31W^{0{\cdot}51}$ ($n = 44$, $r = 0{\cdot}67$) at $+5°$ C
and $R = 0{\cdot}57W^{0{\cdot}51}$ ($n = 11$, $r = 0{\cdot}89$) at $+10°$ C,
where R is oxygen uptake and W is live weight.

The variability in these results may partially reflect the assumptions inherent in the estimation of both length and weight. Another source of error could arise from the use of groups containing

animals of differing sizes, where the length of one or more animals is not included in the mean for the group owing to loss during recovery from the diver, or the absence of values for animals in the simplex stage. The parallel nature of the two regression lines in Fig. 4 ($t = 0{\cdot}06$ with 51 degrees of freedom) indicates that the relationship between metabolic rates at the two temperatures is constant over the whole weight range. The calculated Q_{10} for the temperature range $+5°$ to $+10°$ C is 3·46.

To determine the oxygen uptake of a given population, it is essential to know the age structure of the population. Various authors have reported estimates of the number of moults through which each species may pass, and these have been reviewed by Ramazzotti (1972). The number of moults for *Macrobiotus* is reported as being from six to 12. Using body length–frequency analysis (Higgins, 1959; Francheschi and Lattes, 1969), no pattern was distinguished in the present study, possibly because of the small sample size. Even with a large sample, the problems involved in interpreting the data are numerous, and the method has been criticized by Baumann (1961) and Hallas (1972). However, it is desirable to express the data in a form which can be applied easily to field populations. Five equal but arbitrary size groups have therefore been selected covering the body-length range of the experimental animals (although it is known that some Signy Island specimens exceed 650 μm.). Using the mid-point of each size group, a body weight has been calculated and oxygen-uptake rates per individual have been taken from Fig. 4 (Table I). Weight specific oxygen-uptake rates are also given and show the expected decrease with increasing body weight.

TABLE I. LIVE WEIGHT AND OXYGEN UPTAKE FOR THE MID-POINT OF EACH SIZE GROUP

Size group	*Body lengths* (μm.)	*Live weight* (μg.)	*Oxygen uptake*			
			μl. O_2/g./hr.		μl. $O_2 \times 10^{-3}$/individual/hr.	
			+5° C	+10° C	+5° C	+10° C
1	151–250	0·35	519·1	965·1	0·18	0·34
2	251–350	1·19	285·0	529·8	0·34	0·63
3	351–450	2·83	186·4	346·5	0·53	0·98
4	451–550	5·52	134·4	249·8	0·74	1·38
5	551–650	9·54	102·8	191·1	0·98	1·82

DISCUSSION

Of the respiratory studies completed on small metazoan poikilotherms, few relate to the terrestrial fauna. Of those which do, the majority have been undertaken at temperatures well above those used in the present investigation. Thus a comparison of this study with other works is difficult. No other oxygen-uptake–body-weight data are available for Tardigrada, but figures are presented in Table II for representatives of other mesofaunal groups which are found at the SIRS. The values of the exponent "*b*" (in the equation $R = aW^b$) for Rotifera ($b = 0{\cdot}39$) and Tardigrada ($b = 0{\cdot}51$) are lower than those usually found for small poikilotherms—0·6 to 1·0 (Hemmingsen, 1950; Zeuthen, 1953). Doohan (1973) suggested that the low value for the Rotifera examined results from the progressively higher proportion of total body weight contributed by the metabolically inactive yolk and lorica as body size increases. The low value for Tardigrada may also, in part, be attributed to an increase in yolk in the larger size groups, but it is unlikely that any proportional increase in skeletal structures takes place.

The only other measurements on the respiration rates of Tardigrada are those of Pigoń and Weglarska (1953, 1955*a*, *b*, 1957). As part of a study comparing respiration rates of tardigrades in different physiological states, they examined active animals of *M. hufelandii* and *M. dispar* J. Murray using a Cartesian diver micro-respirometer. Groups of ten individuals were used and all measurements were made at $+20°$ C. The rate for *M. hufelandii* was

TABLE II. VALUES FOR THE EXPONENT "*b*" IN THE EQUATION $R = aW^b$ FOR FIVE GROUPS OF SMALL POIKILOTHERMS

Group	*b*	*Author*	*Notes*
Rotifera	0·39	Doohan (1973)	6 reservoir species
Nematoda	0·67	Klekowski and others (1972)	22 soil species
Tardigrada	0·51	This paper	
Acari	0·70	Berthet (1964)	16 litter species
Collembola	0·75	Block and Tilbrook (1975)	1 Antarctic species

$9{\cdot}8 \times 10^{-4}$ µl. O_2/individual/hr., but as no body-size measurements are given a comparison with the present study is not possible. The specimens of *M. dispar*, however, were between 500 and 700 µm. in length and gave a mean rate of oxygen uptake of $1{\cdot}0 \times 10^{-3}$ µl./individual/hr. This rate is much less than that calculated for the largest size group of *M. furciger* at +10° C (Table I). The regression line at +10° C (Fig. 4) is based on only 11 points but nevertheless the comparison suggests some physiological adaptation of *M. furciger* to the extreme environment of the maritime Antarctic.

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