THE SIGNY ISLAND TERRESTRIAL REFERENCE SITES: X. POPULATION DYNAMICS OF TARDIGRADA AND ROTIFERA

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ABSTRACT. Two contrasting moss sites (SIRS 1 and 2) at Signy Island were intensively sampled over 2 years to determine the temporal and spatial distribution of the Tardigrada and Rotifera. Population densities are reported for five species of Tardigrada which were regularly found on both sites. Total tardigrade population maxima of 309×10^3 and 713×10^3 animals m.$^{-2}$ were recorded for SIRS 1 and 2, respectively, and a general population increase of most components on both sites was observed throughout the period July 1971–March 1973. Population-density estimates and a size-class analysis of *Macrobiotus furciger* J. Murr. were used to estimate the total population metabolism of this species at both sites, yielding an annual rate of 26·63 ml. O_2 m.$^{-2}$ at SIRS 1 and 148·80 ml. O_2 m.$^{-2}$ at SIRS 2. The oxygen-uptake rate of *M. furciger* was used to derive the population metabolism of other tardigrade species present at the sites. No specific identifications were made for the Rotifera but population data are presented for four broad taxonomic groupings (Monogononta, Bdelloidea other than *Adineta*, *Adineta* and unidentified forms). Except for the tardigrade genus *Echiniscus*, no seasonal fluctuations were apparent for any of the faunal components studied.

BETWEEN June 1971 and April 1973 a sampling programme was undertaken to determine the temporal distribution of the tardigrades and rotifiers at the two Signy Island terrestrial reference sites (SIRS 1 and 2). This investigation forms part of a long-term appraisal of the functional relationships of the various faunal and floral components of these two moss communities.

Previously, Tilbrook (1973) has described both these sites, while Smith (1973*a*, *b*) has dealt with the protozoan fauna, Spaull (1973*b*) with the nematodes and other papers examined the oxygen uptake of a tardigrade species (Jennings, 1975), a collembolan (Block and Tilbrook, 1975) and the mites (Goddard, 1977*a*, *b*).

This paper is the fourth in a series (Jennings, 1975, 1976*a*, *b*) dealing with the Antarctic Tardigrada.

METHODS

Sites

The first site (SIRS 1) is a superficially dry moss turf assignable to the *Polytrichum alpestre–Chorisodontium aciphyllum* association as defined by Smith (1972), and the second (SIRS 2) is a wet moss carpet which falls within the *Calliergidium austro-stramineum–Calliergon sarmentosum–Drepanocladus uncinatus* association. These sites were originally selected as being typical of two widespread moss types and for their convenience for study.

Sampling procedure for SIRS 1. Between June 1971 and January 1972 the entire area of SIRS 1 (Fig. 1) was used for random sampling. However, after January 1972 samples were randomized within 150 m. squares so arranged that none had to be entered to collect the sample. Samples of 20 moss cores were taken from this site at 60 day intervals.

Sampling procedure for SIRS 2. Preliminary sampling of SIRS 2 showed that both tardigrade and rotifier populations were highly aggregated on this site, and a stratified sampling procedure was therefore adopted. An area of 720 m.^{2}, 12 m. wide by 60 m. long (Fig. 2), was chosen which, at the time of selection, was considerably less waterlogged that the remainder of the site and contained a representative selection of the bryophyte species encountered elsewhere on SIRS 2. This area was divided for sampling into ten consecutive strips, each 12 m. by 6 m., and samples of 20 moss cores (two random cores from each strip) were taken at 30 day intervals.

Sampling equipment

Sampling was accomplished by taking cores approximately 3·5 cm. diameter (0·001 m.^{2}) by 6 cm. deep. The summer corers, similar to the type used by Capstick (1959), were aluminium

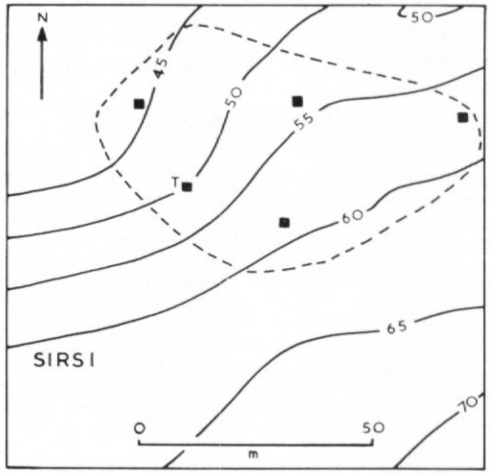

Fig. 1. Map of the Signy Island terrestrial reference site SIRS 1 (modified from Tilbrook, 1973). Contours are at 5 m. intervals.
■ Location of snow-depth markers.
T Location of thermistor probes.
— — — Boundary of site.

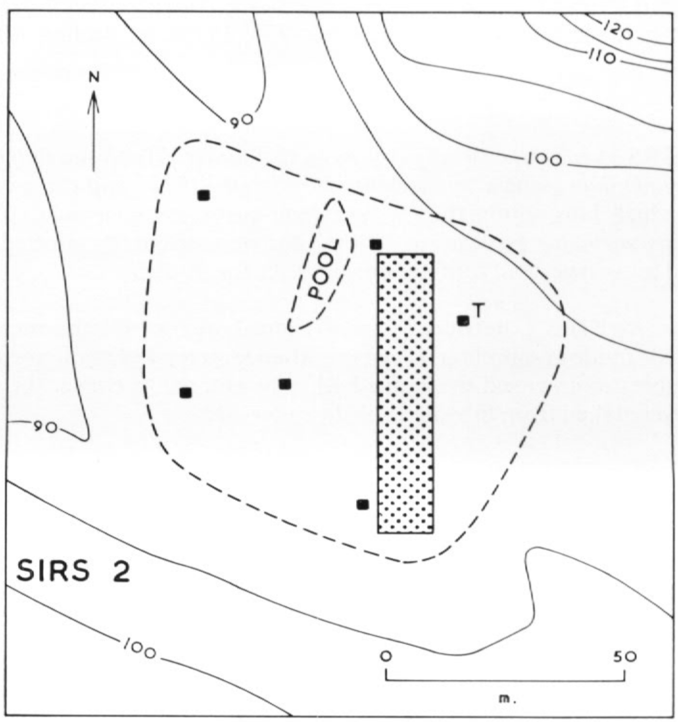

Fig. 2. Map of the Signy Island terrestrial reference site SIRS 2 (modified from Tilbrook, 1973). Contours are at 5 m. intervals. The shaded part was the sampling area used throughout study. Symbols as for Fig. 1.

tubes with one end sharpened. Since significant water loss occurred when a 6 cm. core from SIRS 2 was divided in half after removal from the corer, the upper and lower 3 cm. sections of cores from both sites were collected separately, each in a separate tube. Each core was then transported in the sampling tube by inserting a bung at one end and replacing a watertight cap at the other.

Winter sampling was carried out using a steel tube bearing a number of hardened teeth. During the 1971 winter, this corer was operated by a normal hand brace with a modified chuck, but during the 1972 winter a heavy-duty electric drill powered by a portable generator was used. The samples were collected as undivided 6 cm. cores, which were cut into upper and lower 3 cm. sections in the laboratory while the cores were still frozen.

Measurement of environmental parameters

Wet weight, dry weight (Tables I and II) and floral composition were recorded for each sample unit. Loss on ignition and pH were measured on six sample units of each sample (Tables I and II). The procedures have been described by Jennings (1976*a*). Air temperature

TABLE I. PHYSICAL CHARACTERISTICS OF SAMPLES FROM SIRS 1. MEAN VALUES FROM 20 CORES ON EACH SAMPLING OCCASION ARE GIVEN

Date	*Wet weight* (g.)	*Dry weight* (g.)	*Water* (per cent of dry weight)	*Index of humidity* (I.H. = $\frac{\text{weight water}}{\text{dry weight}}$)	*Loss on ignition* (per cent)	*pH*
5 August 1971	49·2	5·5	43·7	8·2	95·9	4·6
5 October 1971	43·4	4·9	38·5	7·9	95·2	5·1
4 December 1971	31·6	5·6	26·0	4·6	96·4	—
2 February 1972	26·5	5·3	21·2	4·0	97·6	—
4 April 1972	33·9	6·0	27·9	4·6	96·9	—
4 June 1972	47·2	5·6	41·5	7·5	95·9	—
1 August 1972	47·4	5·5	41·9	7·8	96·3	—
2 October 1972	53·5	5·9	47·6	8·3	95·8	—
30 November 1972	40·6	5·7	34·9	6·2	96·9	—
28 January 1973	30·7	6·0	24·8	4·1	96·6	—
26 March 1973	35·2	6·0	29·1	4·8	—	—
MEAN	39·9	5·6	34·3	6·2	96·3	4·8

was recorded continuously on weekly thermograph charts throughout the study period near the British Antarctic Survey's biological station *c.* 3 km. from the study sites. From January 1972 the temperature of the moss surface and at depths of 1·5, 4·5, 7·5 and 10·5 cm. was recorded hourly at both sites and incident solar radiation at a position intermediate between both sites was made on a Grant type D 20 channel recorder. Snow depth on both sites was also monitored throughout the study.

Extraction, counting and identification

Each 3 cm. section of each core was extracted for 48 hr. using the tray method (modified Baermann funnel) of Whitehead and Hemming (1965). The extraction and counting procedure

Table II. Physical characteristics of samples from SIRS 2. Mean values from 20 cores on each sampling occasion are given

Date	*Wet weight* (g.)	*Dry weight* (g.)	*Water* (per cent of dry weight)	*Index of humidity* $\left(\text{I.H.} = \frac{\text{weight water}}{\text{dry weight}}\right)$	*Loss on ignition* (per cent)	*pH*
12 July 1971	53·5	3·6	49·9	15·2	90·2	5·2
10 August 1971	46·4	2·9	43·5	17·0	92·2	5·1
9 September 1971	51·7	3·5	48·2	14·7	93·1	4·8
10 October 1971	47·6	3·4	44·1	14·1	92·8	4·6
7 November 1971	49·6	3·7	45·8	14·4	91·1	5·4
8 December 1971	50·8	3·4	47·3	15·8	92·7	6·7
7 January 1972	47·2	4·1	43·1	12·6	92·5	4·2
5 February 1972	50·4	4·2	46·2	12·7	90·5	4·1
4 March 1972	52·6	4·4	48·1	13·3	92·3	—
4 April 1972	48·8	4·2	44·6	11·7	93·8	4·2
4 May 1972	51·4	3·8	47·7	14·0	92·7	4·4
2 June 1972	57·2	4·9	52·3	11·9	94·0	4·4
4 July 1972	58·7	4·5	54·2	12·9	92·5	4·5
1 August 1972	52·4	4·5	48·0	12·1	92·9	4·3
4 September 1972	51·6	4·9	46·8	10·3	90·1	4·3
2 October 1972	50·1	4·0	46·2	12·6	91·4	4·7
31 October 1972	51·0	4·4	46·6	11·7	92·2	4·5
30 November 1972	66·8	4·4	62·4	15·6	92·7	4·3
30 December 1972	50·7	4·8	45·9	10·3	93·4	4·5
28 January 1973	62·0	7·7	54·3	11·5	93·4	4·5
28 February 1973	56·9	4·3	52·6	13·5	92·5	5·0
26 March 1973	48·2	3·4	44·8	14·3	—	—
Mean	52·5	4·2	48·3	13·3	92·3	4·7

of Jennings (1976*a*) was followed. The samples from SIRS 2 were counted at Signy Island while those from SIRS 1 were preserved in 10 per cent formalin and counted in the United Kingdom. Identifications were made during the counting using the keys in Ramazzotti (1962, 1972).

Results and Discussion

Despite a considerable volume of literature relating to the Tardigrada, comparatively little is known about the ecology of individual species. Some figures are available for tardigrade population densities in the soil and litter (Franz, 1941; Nef, 1957; Ramazzotti, 1959; Hallas and Yeates, 1972) but only the studies of Higgins (1959), Franceschi and others (1963), Morgan (1974), Hallas (1975) and Jennings (1976*a*, *b*) have provided data for their population density in mosses. Only the latter three authors have provided area-related population-density estimates for mosses, so direct comparisons are limited.

Species

Of a total of 14 tardigrade species and species groups found on Signy Island (Jennings, 1976*a*), four were recovered regularly from SIRS 1 and 2. These were *Echiniscus* (*E.*) *capillatus* Ramazzotti + *E.* (*E.*) *meridionalis* J. Murr., *Hypsibius* (*H.*) *dujardini* (Doy.), *H.* (*Diphascon*) *alpinus* J. Murr. + *H.* (*D.*) *pinguis* Marcus and *Macrobiotus furciger* J. Murr. Three other species, *H.* (*D.*) *scoticus* J. Murr., *H.* (*Isohypsibius*) *renaudi* Ramazzotti and *H.* (*I.*) *asper* (J. Murr.), were recovered from the SIRS during the sampling period. For each of these latter species, however, the number of individuals did not exceed ten, so they are not considered further in this paper.

It is generally recognized that tundra habitats lack the diversity of invertebrate species found in temperate regions. However, the Tardigrada do not follow this pattern. In this study, two tardigrade species and two species groups are reported from both SIRS, while Morgan (1974) found four species in mosses at Swansea, South Wales. Although Hallas and Yeates (1972) listed ten species from Danish forest soil and litter, this number is comparable with the most species-rich sites (the foliose alga *Prasiola crispa*) on Signy Island (Jennings, 1976*a*). Sudzuki (1964) also found that the tardigrade fauna of Antarctic mosses was similar to that of Japanese mosses.

Population studies

Previous authors have linked tardigrade population-density changes to a variety of environmental factors. These include moisture (Franceschi and others, 1963; Morgan, 1974), temperature (Franceschi and others, 1963) and availability of food organisms (Hallas and Yeates, 1972). The present work differs considerably from all previous studies in that winter conditions in the mosses at Signy Island are to some extent buffered from extreme temperature fluctuations by snow-cover (Wright, 1975). Summer conditions in the maritime Antarctic are similar to winter conditions in more temperate regions with wide diurnal fluctuations in habitat temperature and radiation input (Fig. 3), and the mosses seldom dry out completely, at least at SIRS 1 and 2. On Signy Island, the period in which tardigrades and rotifers can be active is relatively short, only 4–5 months per annum, and this is followed by a prolonged winter when moss temperatures are consistently below freezing point (Fig. 4). Even during the brief summer period, frosts and snowfalls are frequent and temporary snow-cover may reduce the temperature of the habitat for several days by reducing radiation input (Figs. 3 and 4). However, moss temperatures are generally much higher than air temperatures throughout the summer months and fluctuate around freezing point for a considerable time at the beginning and end of summer even though the sites are snow-covered.

In terms of the population density (maxima being 309×10^3 and 713×10^3 tardigrades m.$^{-2}$ for SIRS 1 and 2, respectively, these sites are intermediate between that described by Morgan (1974) with $2{,}287 \times 10^3$ animals m.$^{-2}$ in Welsh mosses and that of Hallas and Yeates (1972) with 12×10^3 animals m.$^{-2}$ in Danish forest soils and litter; however, Jennings (1976*a*) found up to 14×10^6 animals m.$^{-2}$ in one *Prasiola crispa* site at Signy Island. Morgan (1974) commented on the similarity between his increase in density from the minimum recorded to the maximum over 1 year and that of Hallas and Yeates (1972), both of whose increases were between 10 and 20 fold. He associated this with the great reproductive potential of this group under suitable conditions. In the present study, the maximum increase for all tardigrades in 1 year was only 3 to 4 fold, although, for *Echiniscus* sp. on SIRS 2, this increase was in excess of 100 fold. This was because only *Echiniscus* showed a clear annual cycle of population density at this site (Fig. 5). High numbers of this species overwintered in the wet moss carpet in 1972,

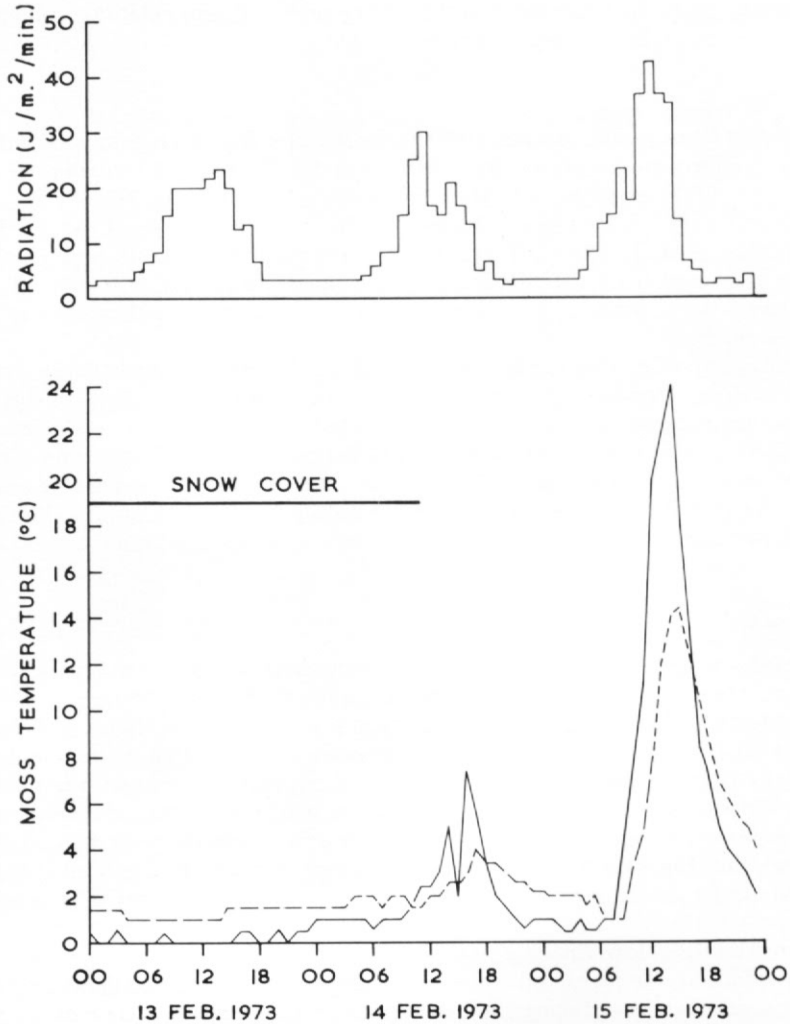

Fig. 3. Hourly temperature record (°C) and incident solar radiation (J m.$^{-2}$ min.$^{-1}$) measured at SIRS 1 on three consecutive days in February 1973. During day 1 the moss was snow-covered; this snow dispersed during day 2, and day 3 illustrates the rapid response of moss temperature to radiation input. Moss surface temperature (dashed line), temperature at $-1 \cdot 5$ cm. depth in the moss (solid line).

presumably leading to the very high numbers recovered during the following early summer. A similar but less distinct pattern is suggested for this species at SIRS 1. The relatively high density of *Echiniscus* sp. at SIRS 2 during the 1972 winter appeared to be paralleled by *M. furciger* and *H.* (*D.*) *alpinus* + *H.* (*D.*) *pinguis*. A general decline in numbers until October 1971 was recorded for both of these components, followed by a fairly sharp increase at the thaw. This higher level was maintained throughout the following winter but no further increase took place at the subsequent thaw and the population density of *H.* (*D.*) *alpinus* + *H.* (*D.*) *pinguis* declined substantially. Both *M. furciger* and *H.* (*D.*) *alpinus* + *H.* (*D.*) *pinguis* on SIRS 1 followed a similar trend of slight increase in numbers at the melt and decrease over the winter, but with an overall increase during the study period.

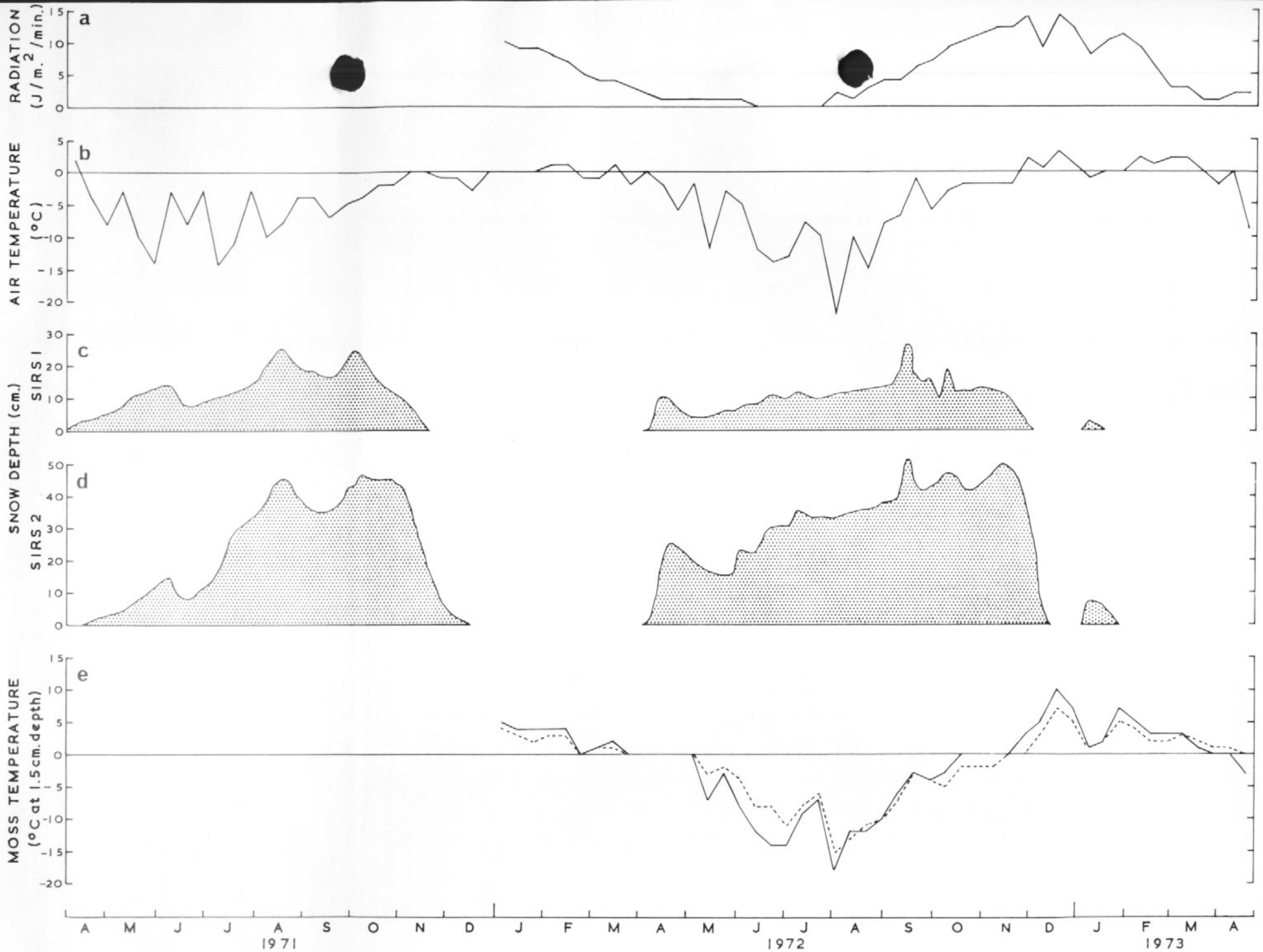

Fig. 4. Meteorological data for SIRS 1 and 2.

a. Mean radiation receipt (J m.$^{-2}$ min.$^{-1}$) over 10 day periods.

b. 10 day mean air temperature (°C).

c. and d. Snow depth (cm.).

e. 10 day mean moss temperature (°C) at $-1\cdot5$ cm. on SIRS 1 (continuous line) and SIRS 2 (pecked line).

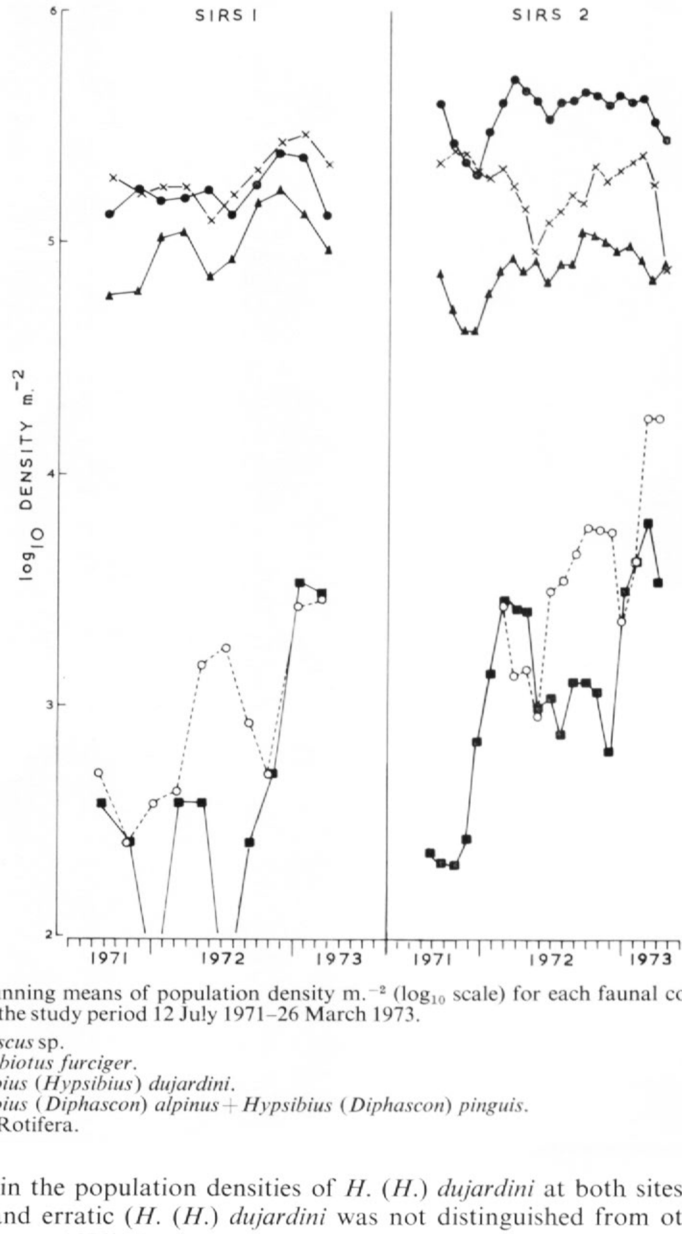

Fig. 5. 3 month running means of population density m.$^{-2}$ ($\log_{10}$ scale) for each faunal component of SIRS 1 and 2 over the study period 12 July 1971–26 March 1973.

■ *Echiniscus* sp.
▲ *Macrobiotus furciger*.
○ *Hypsibius* (*Hypsibius*) *dujardini*.
● *Hypsibius* (*Diphascon*) *alpinus* + *Hypsibius* (*Diphascon*) *pinguis*.
× Total Rotifera.

Fluctuations in the population densities of *H.* (*H.*) *dujardini* at both sites tended to be far more extreme and erratic (*H.* (*H.*) *dujardini* was not distinguished from other *Hypsibius* on SIRS 2 until January 1972). On SIRS 2 these fluctuations may be partially accounted for by the presence of a semi-permanent fresh-water pool, spanning two strata, which was rich in this species (Fig. 6) but which was not sampled in every month. Again no cyclical trend is apparent at either site (Fig. 5) but a general increase in density over the period is suggested.

It was hoped to establish in greater detail the spatial distribution and habitat preferences of each of the faunal components studied. An attempt to map the actual distribution of the tardigrades on SIRS 2 by marking each core hole was abandoned because of continual removal of the markers by brown skuas. Habitat preferences of each faunal component were then examined

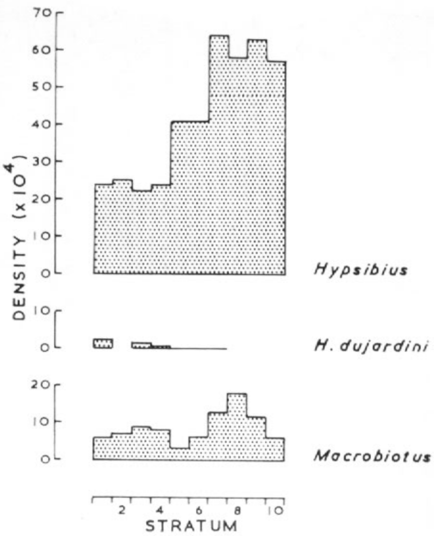

Fig. 6. Mean population density m.$^{-2}$ for three groups of tardigrades in each stratum of SIRS 2 over the study period 12 July 1971–26 March 1973. (The high density predicted in stratum 1 for *Hypsibius* (*Hypsibius*) *dujardini* resulted from a single core containing 750 individuals. This species was not recovered from the stratum at any other time.)

by combining the results from individual cores into groups, according to factors such as moisture content or vegetation composition (Tables I and II). No clear picture emerged, however, as any differences were not consistent. Clearly, variations in micro-habitat do have effects on tardigrade populations as Fig. 6 indicates, but no correlation was found between numbers of animals and any of the other measured factors.

Rotifera were also counted in this study. For SIRS 2 samples, three broad taxonomic groupings were recognized (Jennings, 1976*a*); Monogononta, Bdelloidea other than *Adineta*, *Adineta* spp. and a fourth component comprising inactive Rotifera which were impossible to identify. Since samples from SIRS 1 were preserved, it was possible only to record Rotifera as total numbers for this site. The rotifer population density of both SIRS 1 and 2 was maintained at a level similar to that recorded for the Tardigrada and here too there were no marked seasonal trends. Only the monogonont Rotifera of SIRS 2 showed any consistent pattern, reaching maximum density during the summer months of each year (Fig. 7).

Vertical distribution

It was assumed that most of the tardigrade and rotifer fauna was restricted to the upper 6 cm. of the moss. In order to test this assumption, ten 12 cm. deep cores were taken from each site on 16 March 1974 and transported at −20 °C for extraction in the United Kingdom. The results (Fig. 8) cannot be accepted as completely reliable since the distribution of the fauna in the top 6 cm. of the SIRS 1 samples differed markedly from the distribution observed over the previous 2 year period. More confidence can be placed in the results from SIRS 2, and here the population measured in the upper 6 cm. of the moss accounted for over 80 per cent of the total in the 12 cm. cores. A further point which should be considered is that the layers of organic material overlying bedrock at SIRS 1 and 2 are not uniform in depth. At SIRS 1 they have a depth of between 12 and 32 cm. (Tilbrook, 1973). Fig. 9 shows the frequency distribution of depths of organic material at the centre of 231 1 m. squares which were representative of the whole of SIRS 2. Only 21 per cent of these were less than 6 cm. deep (any core less than 6 cm.

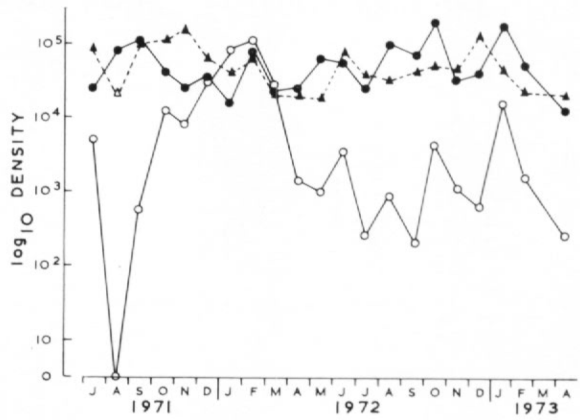

Fig. 7. 3 month running means of population density m.$^{-2}$ (log_{10} scale) for each of the rotifer groups at SIRS 2 over the study period.
▲ *Adineta.*
● Bdelloidea other than *Adineta.*
■ Monogononta.

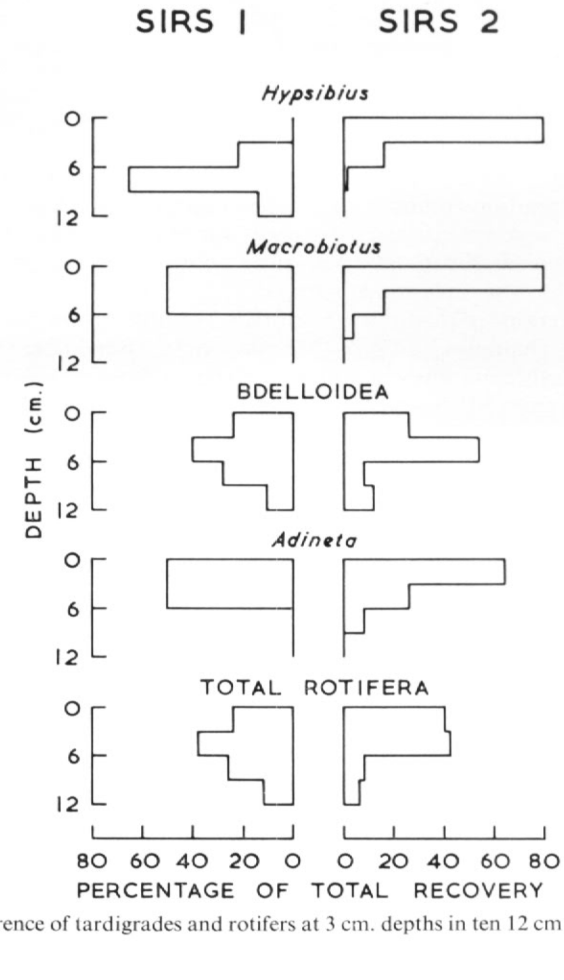

Fig. 8. Percentage occurrence of tardigrades and rotifers at 3 cm. depths in ten 12 cm. cores from each of SIRS 1 and 2.

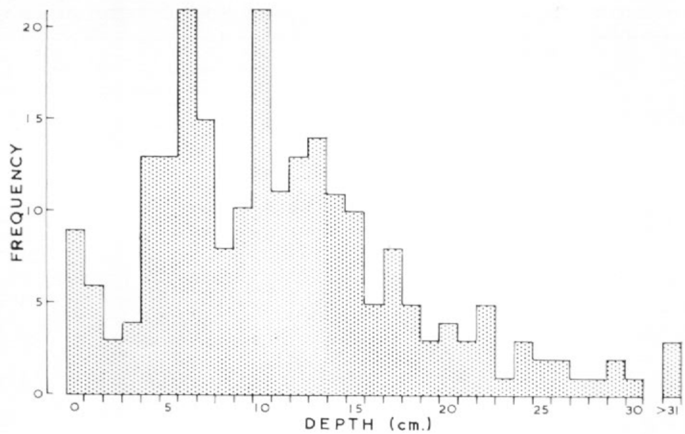

Fig. 9. Frequency distribution of the peat depth at the centre of 231 1 m. areas on SIRS 2.

deep was replaced and another taken during the sampling), and 63 per cent were less than 12 cm. deep. Thus, estimates of the total population density of tardigrades and rotifers at SIRS 2 based on 0–6 cm. cores are justified.

Whereas Spaull (1973*a*) found that at various times significant vertical migration of the nematode fauna occurred, no similar movement was apparent for either the tardigrades or rotifers on SIRS 1 and 2. In general, 70 per cent of the individual tardigrade components in both sites were found in the top 3 cm. of the moss, this percentage being slightly less for the rotifers. Although the depth of the moss and peat at SIRS 2 is over 30 cm. in places (Fig. 9), a silver plate inserted in the moss indicated that only the top 7–8 cm. layer was aerobic, and this finding was further supported by two silver wires at other locations on the site. This, combined with the lower temperatures and the decline of the micro-flora with depth (Broady, 1977, 1979), may explain the very rapid decrease of faunal populations with depth. In a pure stand of *Chorisodontium aciphyllum* (similar to SIRS 1) no anaerobic layer was detected, at least in the upper 30 cm. of moss turf (personal communication from J. H. Baker); this may be a significant reason why the decline of the fauna with depth was not as rapid at SIRS 1 as at SIRS 2.

Size-class analysis of Macrobiotus furciger

As indicated by Jennings (1975), a size/frequency histogram of the SIRS 2 *M. furciger* population did not show the pattern found by either Higgins (1959) or Franceschi and Lattes (1969) for other species of *Macrobiotus*. Consequently, estimates of the size distribution for selected months at SIRS 2 were made by sub-sampling from preserved material and grouping individuals into five equal size classes based on body-length estimates (Table III). As direct measurements of body length were unreliable, details of the buccal apparatus were used to derive body length (Jennings, 1975).

The similar percentage frequency of each size class of *M. furciger* throughout the year, particularly the consistently high proportion of individuals in size classes 3 and 4, makes size-class interpretation very difficult. A similar pattern has been noted for an Antarctic collembolan (Tilbrook, 1977) and also a temperate tardigrade (Morgan, 1974). Both authors have pointed out that this may be caused by some shortcomings in technique, leading to a loss of the smaller animals. It has been suggested by Hallas (1972) that newly hatched eutardigrades are invariably no longer than three times the egg diameter, and that egg size is controlled by environmental factors. The mean egg diameter of *M. furciger* found on Signy Island (Jennings,

TABLE III. SIZE-CLASS DISTRIBUTION OF *Macrobiotus furciger* AT SIRS 2 BASED ON BODY-LENGTH ESTIMATES

Date	Number measured	Per cent in size range (μm.)				
		1 <250	2 251–350	3 351–450	4 451–550	5 >551
7 January 1972	56	3·6	17·9	30·4	35·7	12·4
5 February 1972	85	10·6	20·0	28·2	30·6	10·6
4 May 1972	61	4·9	31·1	36·1	21·3	6·6
2 July 1972	38	7·9	21·0	28·9	34·2	7·9
4 September 1972	100	4·0	15·0	38·0	37·0	6·0
2 October 1972	42	4·8	7·1	40·5	42·9	4·8
30 December 1972	85	10·6	27·1	37·6	17·6	7·1
28 January 1973	105	14·3	29·5	34·3	16·2	5·7
28 February 1973	100	7·0	17·0	23·0	35·0	18·0
MEAN	672	7·5	20·6	33·0	30·0	8·8

1976*a*) was 96 μm., and by applying Hallas' egg size : hatchling ratio, a newly hatched animal would be 288 μm. The low proportion of specimens found in size class 1 is not, therefore, as unexpected as it may at first appear. An alternative explanation has been advanced by Tilbrook (1977) for *Cryptopyrgus antarcticus* Willem. If development after hatching was rapid compared with subsequent growth, a build-up of the medium-sized groups would result, and thereafter the more usual survivorship curve would be seen. Without a more detailed study of the life history of *M. furciger*, neither of these two suggestions can be accepted without reservation.

The similar proportion of animals within each size group throughout the year suggests a continuous recruitment period, with eggs hatching as conditions allow. It seems likely that generations span more than 1 year and that growth is sporadic because of environmental conditions.

Tardigrade population metabolism

In an earlier paper (Jennings, 1975) the respiration rate of *M. furciger* was determined at 5° and 10°C. If the Q_{10} (3·46) over this temperature range is representative of the metabolic response of this species over other habitat temperature ranges, a series of curves may be constructed relating temperature to the rate of oxygen uptake for individuals of *M. furciger* of a given size. Using these curves together with the size-class structure and population densities, the total metabolism of *M. furciger* on SIRS 2 has been calculated (Fig. 10). Pigoń and Weglarska (1953) stated that the respiration rate of cysts of *Macrobiotus dispar* J. Murr. was four times slower than the respiration of the active animals at 20°C, and that dried specimens of *Macrobiotus hufelandii* Schultz respired 600 times slower than active specimens. The physiological state of Signy Island tardigrades during the winter months is unknown, and on the basis of these findings it was assumed that tardigrade respiration below 0° C was negligible. The estimates range from 38·01 ml. O_2 m.$^{-2}$ in April 1973 to a negligible amount during the winter months. The mean monthly rate over the period January–December 1972 was 12·40 ml. O_2 m.$^{-2}$, which represents an annual uptake of 148·80 ml. O_2 m.$^{-2}$.

In the absence of published information on tardigrade energetics, apart from the physiological studies of Pigoń and Weglarska (1953, 1955*a*, *b*, 1957), the present data were used to

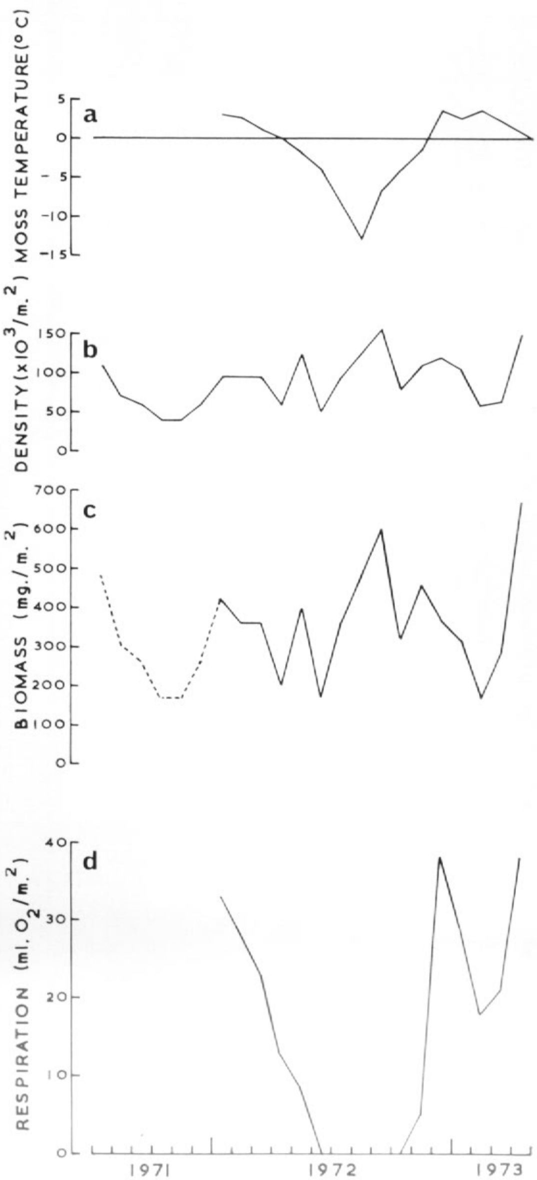

Fig. 10. Population density, biomass and respiration of *Macrobiotus furciger* on SIRS 2.
a. Mean 30 day moss temperature (°C) at $-1\cdot5$ cm. depth.
b. Fluctuations in mean population density ($\times$ 10^3 m.$^{-2}$).
c. Mean biomass (mg. m.$^{-2}$), assuming a mean tardigrade weight of $4\cdot3$ μg. (pecked line) and from size-class analysis (continuous line).
d. Total population respiration (ml. O_2 m.$^{-2}$).

extrapolate population metabolism for *M. furciger* at SIRS 1, and the total metabolism for all species of Tardigrada at both sites. It was assumed that the age-class structure of *M. furciger* at SIRS 1 was identical to that found on SIRS 2. Thus, the estimated range of population metabolism at SIRS 1 (Fig. 11) was $5\cdot02$ ml. O_2 m.$^{-2}$ in February 1973 to a negligible level in

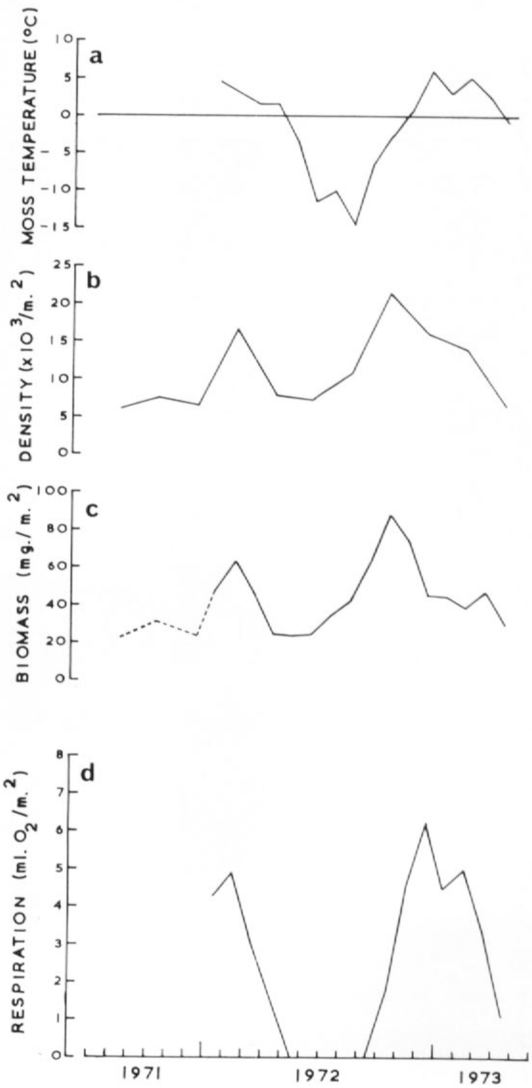

Fig. 11. Population density, biomass and respiration of *Macrobiotus furciger* on SIRS 1.
a. Mean 30 day moss temperature (°C) at $-1 \cdot 5$ cm. depth.
b. Fluctuations in mean population density ($\times$ 10^3 m.$^{-2}$).
c. Mean biomass (mg. m.$^{-2}$) assuming a mean tardigrade weight of $4 \cdot 3$ μg. (pecked line) and from size-class analysis (continuous line).
d. Total population respiration (ml. O_2 m.$^{-2}$).

the period May–September, with a monthly mean of $2 \cdot 22$ ml. O_2 m.$^{-2}$ ($26 \cdot 64$ ml. O_2 m.$^{-2}$ per annum); this was five times less than that determined for SIRS 2. Since the mean monthly density of *M. furciger* on SIRS 1 (13×10^3 animals m.$^{-2}$) was eight times less than that on SIRS 2 (102×10^3 animals m.$^{-2}$), the inference is that SIRS 1 was the more favourable habitat in terms of tardigrade activity. However, this conclusion must be treated with caution. It has been observed (Jennings, 1976*a*) that *M. furciger* activity decreased at temperatures above 15° C and the daytime temperature in the upper 3 cm. of SIRS 1 moss was often higher than

TABLE IV. TOTAL POPULATION RESPIRATION (ml. O_2 m.$^{-2}$) OVER 30 day INTERVALS AT SIRS 1 AND 2 FOR EACH TARDIGRADE SPECIES AND SPECIES GROUP. RESPIRATION WAS ASSUMED TO BE NEGLIGIBLE AT MOSS TEMPERATURES BELOW 0° C (MAY 1972 TO SEPTEMBER 1972 ON SIRS 1, JUNE 1972 TO OCTOBER 1972 ON SIRS 2)

	SIRS 1					SIRS 2				
	Echiniscus sp.	*Hypsibius (H.) dujardini*	*Hypsibius (D.) alpinus* + *Hypsibius (D.) pinguis*	*Macrobiotus furciger*	Total *Tardigrada*	*Echiniscus* sp.	*Hypsibius (H.) dujardini*	*Hypsibius (D.) alpinus* + *Hypsibius (D.) pinguis*	*Macrobiotus furciger*	Total *Tardigrada*
January 1972	0	0·10	33·94	4·34	38·38	0·21	1·08	91·55	33·12	125·95
February 1972	0	0·11	28·83	4·93	33·87	0·32	0·26	102·52	28·30	131·39
March 1972	0·05	0·11	24·24	3·00	27·40	0·61	0·31	82·05	23·45	106·42
April 1972	0·08	0·12	21·81	1·65	23·66	0·08	0·12	34·98	12·61	47·78
May 1972						0·07	0·08	21·35	8·49	29·99
October 1972	0·02	0·03	12·90	1·86	74·81					
November 1972	0·06	0·08	34·53	4·62	39·29	0·02	0·12	8·66	4·91	13·71
December 1972	0·12	0·17	62·55	6·23	69·07	0·04	0·84	116·11	37·92	154·91
January 1973	0·57	0·67	49·45	4·49	55·19	1·34	0·33	69·75	29·18	100·60
February 1973	1·70	1·48	64·35	5·02	72·13	0·71	2·06	88·68	17·89	110·34
March 1973	0·45	0·60	23·14	3·39	27·58	0·86	9·47	48·64	20·71	79·68
April 1973	0	0·08	0·20	1·08	1·35	0·04	0·22	24·51	38·01	62·78

this in both summers of the study, whereas SIRS 2 moss temperatures only rarely reached this level.

Activity, food source and basal metabolic rate are likely to vary from species to species, and this in turn would affect the rate of oxygen uptake of individuals. However, to estimate total tardigrade metabolism at the two sites, the mean weights of *Echiniscus* sp. (0·727 μg.), *H.* (*H.*) *dujardini* (1·400 μg.) and *H.* (*D.*) *alpinus* + *H.* (*D.*) *pinguis* (1·076 μg.), taken from Jennings (1976*a*), have been used to estimate their rate of oxygen uptake from the curves obtained for *M. furciger*. The resulting annual rates (Table IV) for all species are 246·48 and 610·15 ml. O_2 m.$^{-2}$ on SIRS 1 and 2, respectively, giving a mean monthly rate of 20·54 (SIRS 1) and 50·84 ml. O_2 m.$^{-2}$ (SIRS 2). The difference between these two estimates is therefore only a factor of 2·5.

Several studies similar to those undertaken at the SIRS have now been completed in tundra areas under the auspices of the International Biological Programme (*in* Rosswall and Heal, 1975). It is perhaps significant that, except for the report on Signy Island by Collins and others (1975), the Tardigrada were mentioned only once (Bliss, 1975) and no mention whatsoever was made of any rotiferan fauna, although both groups probably occurred on many of the sites investigated. This, perhaps, is a reflection of the assumed relative insignificance of these two groups in tundra ecosystems, where other mesofauna and larger hervibores are present. However, the Tardigrada are a significant faunal component in the Signy Island sites and they may warrant further investigation in other tundra areas.

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