THE SIGNY ISLAND TERRESTRIAL REFERENCE SITES: XI. POPULATION STUDIES ON THE ACARI

By D. G. Goddard

Abstract. The population dynamics of the Acari of two contrasting moss communities, the first a dry *Polytrichum–Chorisodontium* moss turf and the second a wet association of *Drepanocladus–Calliergidium–Calliergon* moss carpet, were investigated at Signy Island by 27 monthly samples between January 1972 and March 1974. Cores were taken to a depth of 6 cm. with occasional deeper samples and the fauna was extracted by a high-gradient heat extractor. A total of ten species of Acari was recorded: Cryptostigmata (two), Mesostigmata (one), Prostigmata (six) and Astigmata (one). The Acari populations underwent seasonal fluctuations with high summer and low winter numbers, which for the common species in the dry moss turf ranged as follows:
Nanorchestes antarcticus 300–11,436 ind. m.$^{-2}$, *Eupodes minutus* 937–9,210 ind. m.$^{-2}$, *Ereynetes macquariensis* 251–7,146 ind. m.$^{-2}$ and *Gamasellus racovitzai* 21–1,293 ind. m.$^{-2}$. Only occasional specimens of mites were recorded from the wet moss site. The Prostigmata numbers declined by *c.* 43 per cent over the study period but the Mesostigmata remained stable. Most species were confined to the top 12 cm. in the dry moss profile. The life cycles of the common species, their distribution and population dynamics are discussed in relation to the micro-climate of the habitats.

In November 1971, two terrestrial study sites were established at Signy Island, South Orkney Islands, for long-term monitoring of the dynamics of the faunal and floral components, together with selected environmental parameters. The overall aim is a total evaluation of the functioning of the ecosystem in terms of energy and nutrients. The sites are representative of two contrasting moss communities and they have been designated the Signy Island reference sites (SIRS) 1 and 2. Both sites have been described by Tilbrook (1973*a*). A number of studies of the faunal and floral components of both sites have been conducted; Smith (1973*a*, *b*) discussed the Protozoa, Spaull (1973) the Nematoda, Broady (1977, 1979) the terrestrial algae, and Jennings (1979) the Tardigrada. Information on the respiratory physiology of a common collembolan of these sites has been given by Block and Tilbrook (1975), on a species of Tardigrada by Jennings (1975), and on several species of Acari by Block (1976, 1979) and by Goddard (1977*a*, *b*). This paper presents data on the species composition, population dynamics and depth distribution of the Acari of SIRS 1 and 2, and is the first comprehensive long-term study on Acari in the Antarctic.

Tilbrook (1973*b*) conducted a survey of the terrestrial invertebrate fauna of Signy Island and recorded four species of Collembola and 16 species of Acari. Although there are a number of accounts of the population dynamics of terrestrial Acari in temperate areas (e.g. Macfadyen, 1952; Sheals, 1957; Davis, 1963), studies of tundra mite populations are limited (Hammer, 1944; Stockli, 1957; Block, 1966*a*; and various papers in Rosswall and Heal (1975)). In the Antarctic, terrestrial Acari populations have been studied by Janetschek (1967), Tilbrook (1967*a*, *b*) and Rounsevell (1977).

The present study was undertaken during the period January 1972–March 1974 and the aims were three-fold: first, to determine the species composition and population structure of the terrestrial Acari of SIRS 1 and 2, and its variation throughout the year; secondly, to obtain information on the life histories of the component species; and thirdly, to evaluate the importance of the Acari in the energy flow of typical Antarctic moss communities.

METHODS

Sample sites

SIRS 1 and 2 are situated on Gourlay Peninsula in the south-east of Signy Island. SIRS 1, on a north-west-facing slope at approximately 53 m. a.s.l., is a relatively dry *Polytrichum alpestre–Chorisodontium aciphyllum* moss-turf bank. It has patchy lichen cover and is broken by areas of dead moss, melt-water runnels and lichen-encrusted stones together with rock outcrops. SIRS 2, at 25 m. a.s.l., is situated in a shallow drainage basin below McLeod

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Glacier, *c.* 360 m. south-west of SIRS 1, and is a permanently wet *Calliergon sarmentosum–Calliergidium austro-stramineum–Drepanocladus uncinatus* moss carpet broken by areas of senescent moss and growths of the liverwort *Cephaloziella varians*. Areas of standing water, varying in extent, were present throughout the three summers of the study period on SIRS 2. During the spring melt, drainage streams flowed across the area, flushing out large numbers of arthropods from the moss. A description of the physical characteristics of these sites has given by Tilbrook (1973*a*).

Sampling method

The sampling areas on SIRS 1 and 2 consisted of 150 squares each of 1 m.^{2} area arranged in strips of varying length. This enabled sampling to be undertaken without disturbance and trampling. Each metre square was subdivided into squares each of 10 cm.^{2} area, which were located by placing a grid over the metre square during sampling. Having selected the 10 cm. squares by random numbers, a single sample core was taken from each. The core was 0·002 m.^{2} ($=\frac{1}{500}$ m.^{2}) in area.

During summer a conventional hand-operated corer with polythene rings was used. When the substrate froze, however, a corer with tungsten carbide cutting teeth was attached to a hand-operated brace for lightly frozen moss in autumn, and an electric drill powered by a portable petrol generator was utilized in winter when the moss was frozen hard. In these cases, polythene rings could not be used, so the frozen sample cores were fitted into the rings after their removal from the corer. The frozen cores were much less susceptible to mechanical damage.

During winter both sites were covered with up to 1 m. of snow and ice, and to gain access to the moss surface a hole was dug to the ice layer which was fragmented with an axe. A 1–2 cm. thick layer of ice was always left in the hole base to prevent maceration of the moss surface by the tungsten carbide teeth of the corer. After removal of the core, the hole was re-filled with snow. Initially, cores were transported back to the laboratory in aluminium screw-top containers but, since these quickly wore out and were impractical to use at low temperatures, the numbered cores were subsequently transported in separate small polythene bags.

Faunal extraction

Prior to its insertion into a high-gradient multi-canister extractor (Macfadyen, 1961), each core was divided with a knife into two vertical 3 cm. sections and individually weighed. Cores were loaded into the extractor with the vegetation surface downwards. The samples from the first 5 months were loaded into the extractor immediately after weighing, but during the first winter (1972) problems were encountered in extracting deep-frozen cores. The core surface nearest the heat source in the extractor would thaw out and heat up quickly whilst the core base remained frozen, so seriously reducing extraction efficiency. To overcome this, weighed cores were prepared for the extractor and the exposed surfaces of the core sealed with inert parafilm sealing tape. The cores were then thawed out for 24 hr. in a constant-temperature room between 2° and 5° C before the faunal extraction commenced. To maintain comparability, this practice was employed for all subsequent samples. Individual cores were weighed wet, before extraction and dry after extraction to determine their water content.

The cores were extracted for 6 days, after which time they were completely dry. The heat source in the extractor was one 40 W electric bulb, 8 cm. above each core, and the heating was regulated with a Variac transformer using the following voltage changes at 24-hr. intervals: 60, 80, 120 and 160 V for 48 hr., after which the voltage was reduced to 120 V and the coolant flow in the extractor was switched off to dry out the base of the cores. This was necessary because the polythene rings containing the cores suffered heat damage after prolonged exposure at the 160 V heating level, and the extraction time was impractically long at 120 V. The temperature of the upper surface of the core at 160 V was approximately 70° C.

The temperature gradients (temperature difference between upper and lower surfaces) established in sample cores (from SIRS 1 and 2) during extraction were monitored throughout a typical 6-day summer extraction period. The techniques used were similar to those of Block (1966*b*) working on moorland soil samples in England. Thermistors were placed centrally at the upper, middle and lower surfaces of a 0–3 cm. core, the two remaining available thermistors being located at the middle and lower surface of a 3–6 cm. core, on the assumption that the core surface temperature would be similar. The temperature at these points was monitored on a 5-channel portable Grant temperature recorder, readings being made hourly for the 6-day extraction. Temperature gradients in cores from both SIRS 1 and 2 were measured.

Faunal analysis

In the extractor, animals were collected into a 50 per cent solution of picric acid in the canisters. Before counting, the contents of each core section were filtered through Nybolt gauze (operative mesh size 30 μm.) and each extract placed in 70 per cent ethanol and 5 per cent glycerol. The fauna was counted under ×25 and ×50 magnification in a dish with a counting grid and specimens were identified as far as possible to life stage and sex. Difficult specimens were mounted on slides in Hoyers medium for detailed examination under ×100 and ×400 phase-contrast magnification. The extracted Acari and Collembola from each core section were sorted and placed separately in ethanol in labelled tubes.

Environmental monitoring

Throughout the study various micro-climate parameters of the sites were measured. Moss temperatures were recorded hourly at the following depths: surface (0 cm.) and at 1·5, 4·5, 7·5 and 10·5 cm. below the surface, together with air temperature at 1·8 m. above the surface and incident solar radiation. The instrument was a battery-operated Grant autographic recorder model D with 20 channels, which was housed in a hut between SIRS 1 and 2.

On each sampling occasion, the snow depth was measured at six points on each site by permanent snow stakes, and in addition the extent of standing water on SIRS 1 and 2 was noted as well as the presence of temporary melt-water streams.

RESULTS

Extraction temperature gradients

The temperatures during a typical 6-day extraction of 3 cm. cores from SIRS 1 and 2 are shown in Fig. 1. A gradient between the upper and lower surface of the core was established immediately after the heating commenced and it steepened at each heat increment as the voltage was increased for the first 2 days with the SIRS 1 core, and for the first 3 days with the SIRS 2 core. This difference may be correlated with different water contents of cores from the two sites (see Fig. 8). After this the temperature gradient gradually steepened coincident with the drying out of the upper core surface near the heat source. There were no differences in the temperatures recorded at comparable levels in the 0–3 and 3–6 cm. core sections for both SIRS 1 and 2 samples. The final temperature gradient (the temperature difference between the upper and lower core surface) was approximately 40° C for the 3-cm. SIRS 1 core and 35° C for the 3-cm. SIRS 2 core. This was higher than the gradient (20–30° C) recorded by Macfadyen (1961) but less than that (80° C) for a 3-cm. core measured by Block (1966*b*), although more powerful 60 W electric bulbs were used in the latter work.

The decline in temperature at the start of the SIRS 1 extraction and at the end of the SIRS 2 extraction was probably caused by condensation of moisture at the base of the core. The peat cores used by Block (1966*b*) were dried out in 3 days compared with 6 days for the SIRS

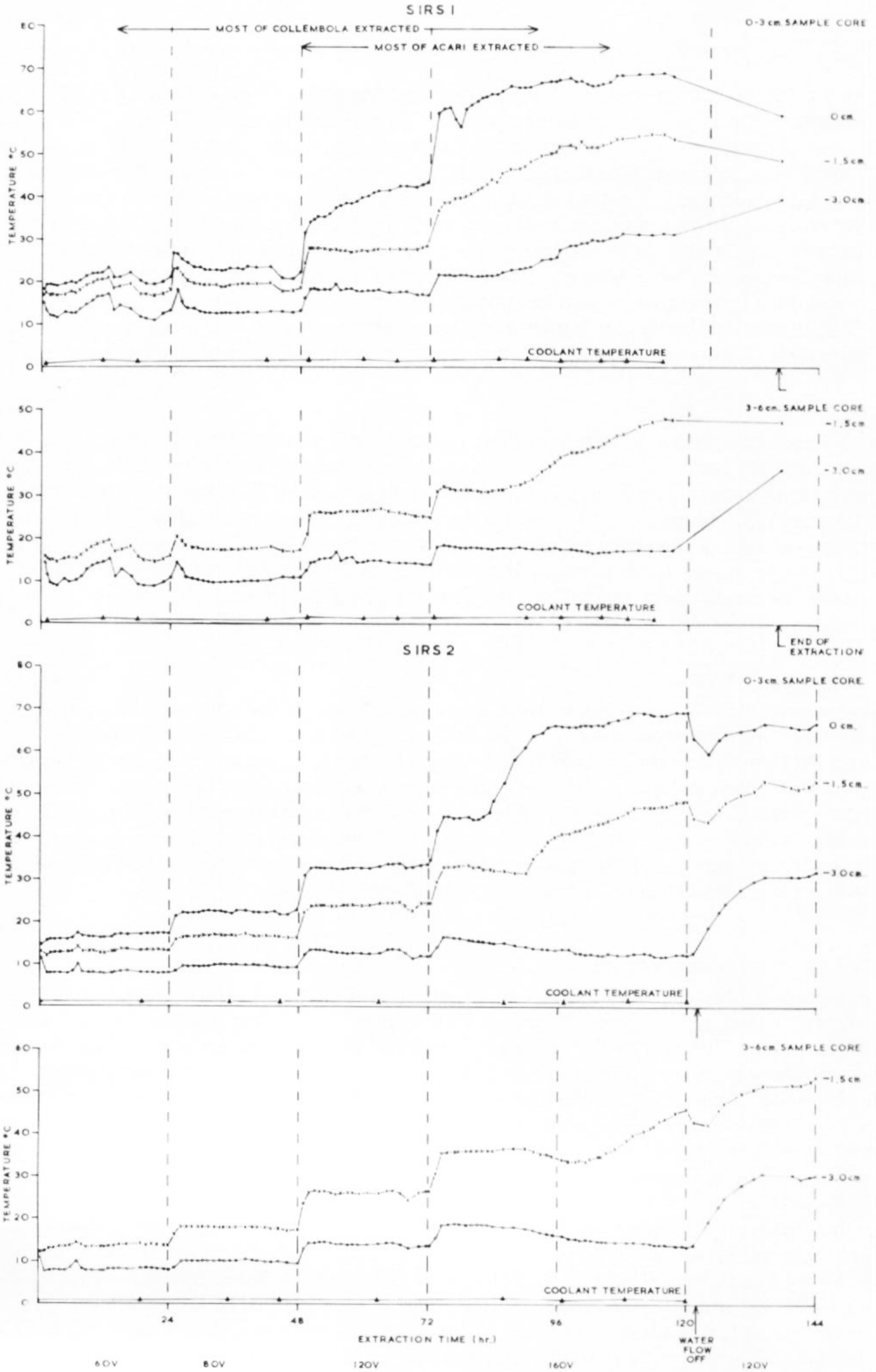

Fig. 1. Temperatures recorded in sample moss cores from 0–3 and 3–6 cm. sections of the SIRS 1 and 2 profiles during faunal extraction in the high-gradient extractor. Temperatures were recorded at the upper surface (0 cm.), 1·5 and 3·0 cm. below the surface, and in the extractor coolant.

cores, which may reflect differences in core structure, composition and stronger heating. However, the general pattern of the establishment and maintenance of temperature gradients in the cores were essentially similar in the two studies. The coolant temperature was also monitored during the extraction experiments (Fig. 1). The sea-water used as coolant remained at a constant temperature of 1–2° C. This was much lower than the coolant temperature for previous studies; 15–18° C. During winter, the sea-water supply at Signy Island became unusable for cooling and a re-cycling fresh-water cooling system was established with a temperature of *c*. 14° C. The drying time of the cores was not affected and it was assumed that extraction efficiency was similar. The temperature of the upper surface of the core was always *c*. 70° C after 6 days. The main disadvantage of the sea-water coolant was an increase in condensation on the sides of the collecting canisters and at the base of the core towards the end of the extraction.

Species composition and population dynamics

Table I lists the species of Acari recorded on SIRS 1 and 2 during the 2-year study period, with an indication of their relative abundance in different areas on the sites. Four species of mite were regularly recorded in large numbers in the SIRS 1 samples; these were the predatory mesostigmatid *Gamasellus racovitzai* (Trouessart) and the prostigmatids *Nanorchestes antarcticus* (Strandtmann), *Eupodes minutus* (Strandtmann) and *Ereynetes macquariensis* (Fain). A fourth species of Prostigmata, *Tydeus tilbrooki* (Strandtmann), was represented by a few individuals in most SIRS 1 samples. Individuals of another five species were recorded occasionally in monthly samples, although species such as *Stereotydeus villosus* (Trouessart) occurred in large aggregations under stones on the site, and *G. racovitzai* was also more numerous under stones than in moss samples. No Acari were recorded regularly from the SIRS 2 samples and during the whole study period a total of only 15 specimens of seven species was found. The only arthropod found regularly in large numbers on SIRS 2 was the collembolan *Cryptopygus antarcticus* (Willem). This species was also the most numerous arthropod in the SIRS 1 samples, the only other collembolan recorded from the samples being *Freisia* sp.

Table II shows the mean annual population densities for the total Acari and the four common species at SIRS 1. The Acari number as a whole declined by 43 per cent from 1972 to 1973; this was caused mainly by a large decrease (60 per cent) in the populations of *N. antarcticus* and *E. macquariensis*. Conversely, the *E. minutus* population declined by 19 per cent, while *G. racovitzai* maintained a stable annual population mean of around 470 ind. m.$^{-2}$.

Fig. 2 shows the mean (±1 S.E.) population density for the various Acari on SIRS 1 during the study period. The data are mean numbers m.$^{-2}$ for 0–6 cm. depth and population trends are indicated by 3-month running means. The total Acari data and those for individual species all indicate that there were higher numbers of mites in the summer months (November–April) than during the winter (May–October).

Over the 2 years there was a gradual decrease in population density of Acari. The summer peak in 1972–73 was much lower (13,000 ind. m.$^{-2}$) than in the previous summer (28,000 ind. m.$^{-2}$) and the maximum population density in the summer of 1973–74 was also lower (8,000 ind. m.$^{-2}$). The contribution of the individual species to this general pattern is indicated in Fig. 2.

The most numerous of the three species of Prostigmata was *E. minutus* (Fig. 2), which reached a maximum population density of 9,000 ind. m.$^{-2}$ in February 1972, with a decline in numbers during winter to a minimum density of *c*. 1,000 ind. m.$^{-2}$ in July 1972, rising to a peak of *c*. 7,000 ind. m.$^{-2}$ in the following summer. The trend in the second winter (1973) was for a slightly higher population density, although the minimum (1,500 ind. m.$^{-2}$) level was similar to that in 1972. The maximum density reached in the 1973–74 summer was 5,500 ind. m.$^{-2}$. The seasonal pattern of *E. minutus* was characterized by wide fluctuations in numbers associated with large S.E.'s on the means. The mean annual density of *E. minutus* over the 27-

Table I. The species of Acari collected on SIRS 1 and 2 during 1972–74 with their relative abundance in different habitats on the sites

Species	*In regular monthly moss samples*	*Under stones on moss or peat*	*On lichens*	*Under stones on scree*	*Elsewhere on site, e.g. near melt runnels*
		SIRS 1			
Cryptostigmata					
Alaskozetes antarcticus (Michael)	**	***	***	**	***
Halozetes belgicae (Michael)	**	***	***	—	***
Mesostigmata					
Gamasellus racovitzai (Trouessart)	****	****	***	***	***
Prostigmata					
Nanorchestes antarcticus (Strandtmann)	****	***	***	****	****
Eupodes minutus (Strandtmann)	****	***	***	***	***
Halotydeus signiensis (Strandtmann)	**	—	—	—	**
Ereynetes macquariensis (Fain)	****	***	***	***	***
Stereotydeus villosus (Trouessart)	**	****	***	***	***
Tydeus tilbrooki (Strandtmann)	***	***	****	**	***
Astigmata					
Neocalvolia antarctica (Hughes and Tilbrook)	*	—	—	—	—
		SIRS 2			
Cryptostigmata					
Alaskozetes antarcticus (Michael)	—	***	—	***	—
Halozetes belgicae (Michael)	*	***	—	**	—
Mesostigmata					
Gamasellus racovitzai (Trouessart)	*	****	***	***	—
Prostigmata					
Nanorchestes antarcticus (Strandtmann)	*	***	****	****	—
Eupodes minutus (Strandtmann)	**	**	****	***	—
Halotydeus signiensis (Strandtmann)	**	—	—	***	—
Ereynetes macquariensis (Fain)	**	**	****	***	—
Stereotydeus villosus (Trouessart)	—	***	***	****	—
Tydeus tilbrooki (Strandtmann)	*	—	**	****	—
Astigmata					
Neocalvolia antarctica (Hughes and Tilbrook)	—	—	—	—	—

**** Regularly present in large numbers
*** Regularly present in small numbers.
** Represented by occasional individuals.
* Single individual only.
— Not recorded.

Table II. Mean annual population densities for the four common species of Acari found in the SIRS 1 samples

Year	*Numbers of individuals m.$^{-2}$*				*Total*
	Nanorchestes antarcticus	*Ereynetes macquariensis*	*Eupodes minutus*	*Gamasellus racovitzai*	
1972	3,376	2,752	3,877	464	10,469
1973	1,278	1,086	3,144	469	5,977
1972 and 1973	2,327	1,919	3,510	467	8,223
All samples (27 months)	2,200	1,823	3,492	485	8,069

month sampling period was 3,492 ind. m.$^{-2}$ (Table II) with a 19 per cent decline in numbers between 1972 and 1973. The seasonal variation in the population of *E. macquariensis* (Fig. 2) was more regular than *E. minutus* with much smaller S.E.'s on the means. A maximum density of 7,700 ind. m.$^{-2}$ in the summer of 1972–73 declined to a minimum of 500 ind. m.$^{-2}$ during the following winter, the trend being maximum numbers in summer and winter minima with a general decrease in number over the study period. The mean density of this species over the study period was 1,823 ind. m.$^{-2}$ with approximately a 60 per cent decline in numbers between 1972 and 1973. The seasonal pattern shown by *N. antarcticus* (Fig. 2d) was essentially similar to that of *E. macquariensis* with relatively small S.E.'s on the means and a decline from 11,000 ind. m.$^{-2}$ in the summer of 1971–72 to 250 ind. m.$^{-2}$ during the following winter, with only a slight increase in the summer of 1972–73. During the winter of 1973 the decline continued to a minimum of 84 ind. m.$^{-2}$ and reached a peak of 1,500 ind. m.$^{-2}$ in the summer of 1974. The mean population density for *N. antarcticus* over the study period was 2,200 ind. m.$^{-2}$ (Table II) with a 62 per cent decline in mean annual density between years. The population of *G. racovitzai* (Fig. 2) showed a distinct seasonal pattern of high summer and low winter numbers with fairly wide variation in mean monthly density together with large S.E.'s on the means. The summer density was approximately 1,100 ind. m.$^{-2}$ and in winter it was 250 ind. m.$^{-2}$. As with *E. minutus*, the population density in the winter of 1973 was generally greater than in the winter of 1972. *G. racovitzai* was the only species which did not exhibit the general decline in population numbers during the study period. The significance of these seasonal fluctuations in numbers of the common mite species at SIRS 1 will be discussed later in relation to their distribution, life cycle and biology.

The percentage species composition of each of the 27 monthly samples over the study period is shown in Fig. 3. There was a general reduction in the proportion of *N. antarcticus* over the 2 years, broken only by a small summer increase in 1973. *E. macquariensis* followed a similar pattern, although the reduction in its percentage in the winter of 1972 was not so marked. In contrast, the proportion of *E. minutus* in the samples increased gradually during 1972 and early 1973, whilst that of *G. racovitzai* followed a seasonal pattern of summer increase and winter decrease as a proportion of the total Acari present.

Analysis of the monthly means for the four common species of Acari on SIRS 1 showed that the variance was always greater than the mean, indicating aggregation, a common feature of soil faunal populations.

Vertical distribution

The depth distribution of the four common mites at SIRS 1 during the two study years (Fig. 4) in general follows their population density changes. However, *N. antarcticus* and *G.*

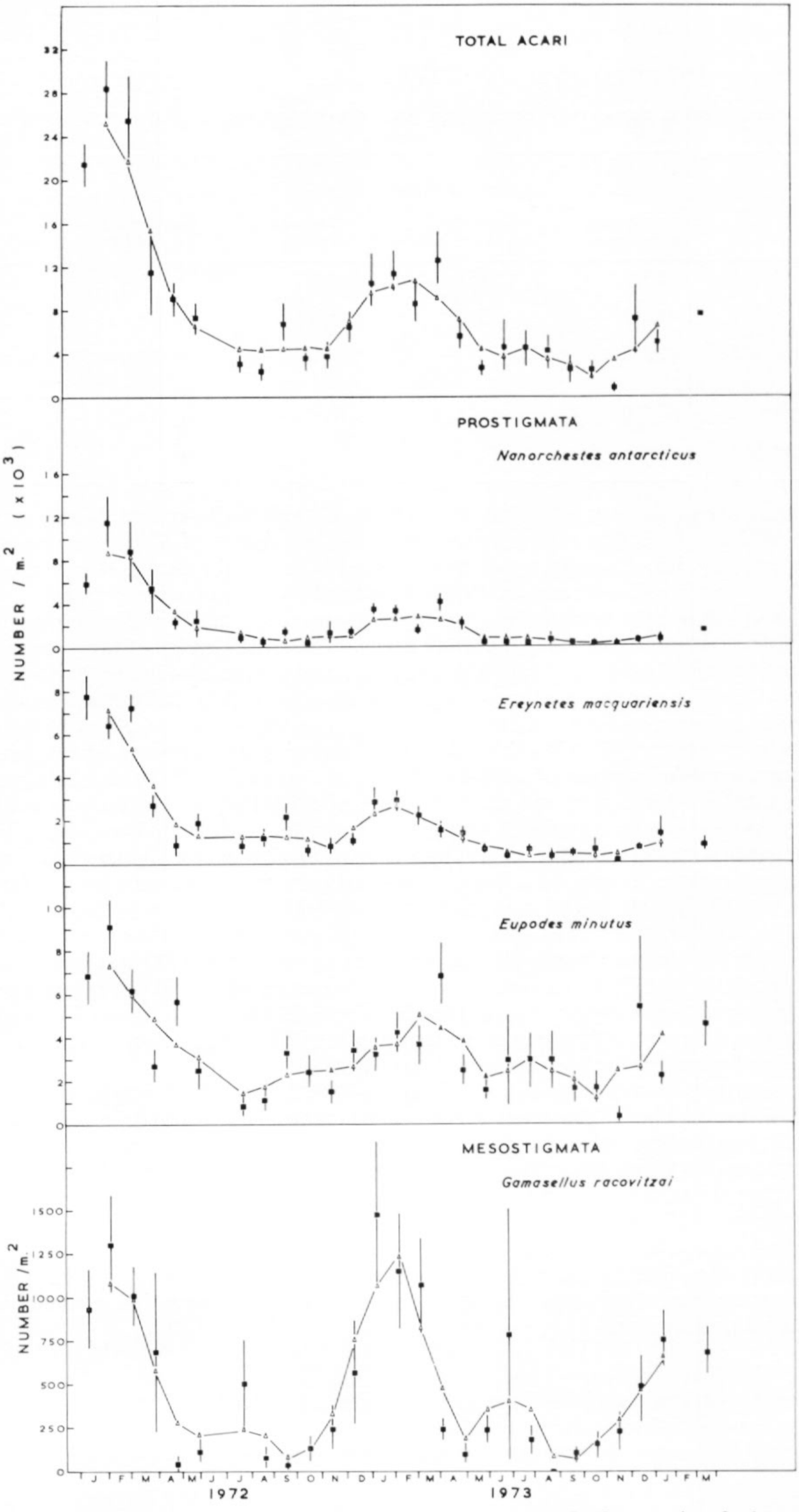

Fig. 2. Seasonal fluctuations in mean population density ($\times 10^3$ ind. m.$^{-2}$) for four species of mites and for the total Acari occurring on SIRS 1 during 1972–74. Single standard errors on the means are shown and trends are indicated by three-point running means.

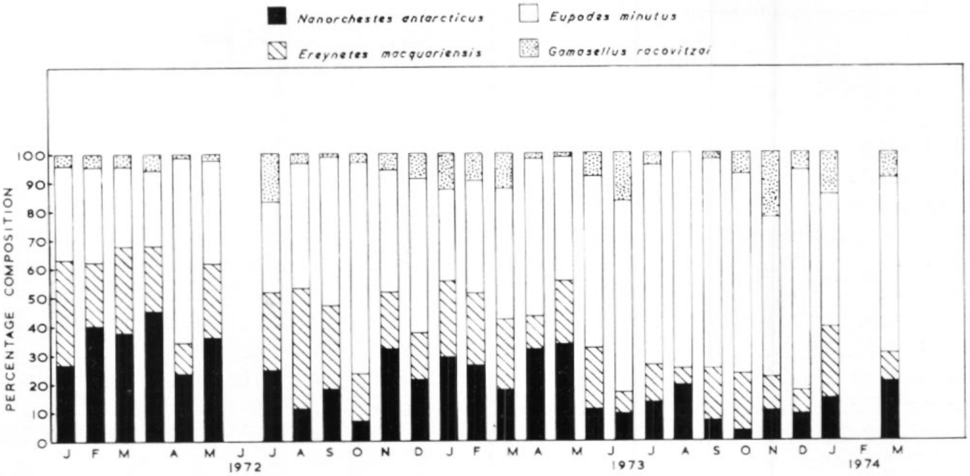

Fig. 3. Variation in percentage species composition of the Acari on SIRS 1 during 1972–74.

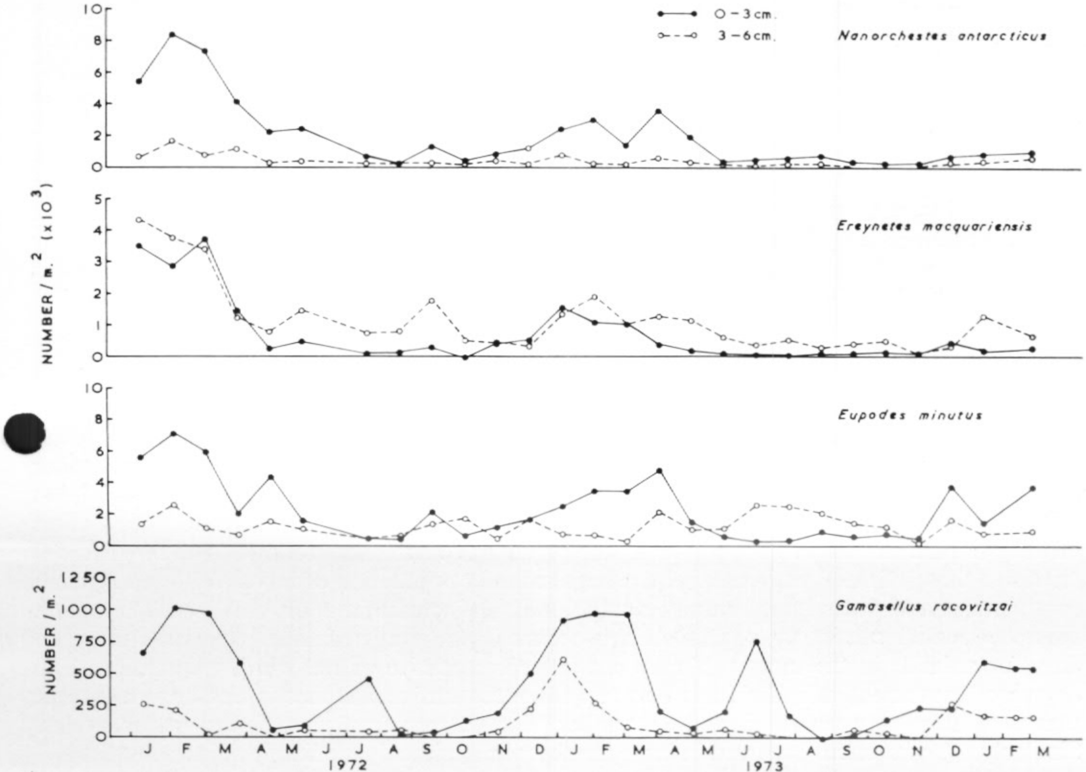

Fig. 4. Seasonal fluctuations in mean population density of four species of Acari occurring at two levels in the moss profile (0–3 and 3–6 cm.) on SIRS 1 during 1972–74.

racovitzai tended to remain in the upper (0–3 cm.) layer, whilst *E. macquariensis* predominated in the lower (3–6 cm.) layer especially during winter, although in summer its density was similar in both levels. *E. minutus* was generally found in the upper layer except in the winter of 1972, when similar numbers existed in both layers, and in the winter of 1973, when it followed *E. macquariensis* with most individuals at 3–6 cm. The depth distribution in percentage form for each species together with the total Acari (Fig. 5) shows that more mites were found in the lower layer in winter and in the upper layer in summer. This was especially evident in *E. macquariensis* and *E. minutus*.

The depth distribution of mites on SIRS 1 and 2 was examined on four occasions by core sampling to a depth in excess of 6 cm. The maximum depth on SIRS 1 sampled was 24 cm. (the length of the corer) and 18 cm. on SIRS 2. The results were expressed as the mean number of individuals m.$^{-2}$ but care must be taken in any comparison with regular monthly sample data as the number of cores was smaller: from seven to 11. Two samples were collected from unfrozen moss in summer, one sample in 1973 and one in 1974; in the intervening winter two samples of frozen moss cores were collected. The results for SIRS 1 are depicted in Fig. 6 together with the mean moisture content of cores at each depth expressed as a percentage of the mean dry weight of the cores.

N. antarcticus was virtually restricted to the upper 6 cm. of the profile and it was never recorded below 9 cm. in depth. No specimens of *N. antarcticus* were found in the last two samples: 19 September 1973 and 11 January 1974. This was probably related to the low population density of the species in the summer of 1974 (Fig. 2). *E. macquariensis* and *E. minutus* occurred at similar depths, being recorded down to 18 cm. The former species was found in larger numbers between 6 and 12 cm. than the latter species which was more numerous in the 0–6 cm. part of the profile. *G. racovitzai* was virtually absent from the frozen moss samples in winter.

The majority of the Acari at SIRS 1 were located in the top 12 cm. of the moss profile, below which only a few individuals were found (a mean of 6 per cent for the four sampling occasions). The moisture content of the cores remained fairly constant with depth and is typically high (80 per cent) in the winter samples compared with the summer samples (40 per cent).

No Acari were recorded in the four SIRS 2 depth samples; only Collembola were found. The moisture content of the cores from the 0–9 cm. section of the profile remained relatively constant in all four samples from SIRS 1. However, below 9 cm. the moisture content decreased in the late summer and early winter samples. The moisture content in all four SIRS 2 samples decreased with increasing depth in the profile.

Life-stage distribution

Fig. 7 depicts the fluctuations in numbers of the life stages of the four common Acari species at SIRS 1 during the study period. The pattern for the three prostigmatid species is similar and, as expected, shows high nymphal populations compared to larval and adult stages. Within species, the data for the three nymphal stages are combined as reliable separation of the nymphal instars was not possible. The predator *G. racovitzai* followed similar seasonal trends to those of the Prostigmata with a large summer population of larvae followed by high protonymph and deutonymph numbers and finally an increase in adult numbers. These data must be treated cautiously as this species occurs in large aggregations beneath stones, so data for animals in the moss turf may not be representative of the whole population. The degree of movement of individuals between the moss turf and stones is not known, except that in winter (between April and September) few *G. racovitzai* were found under stones. Similarly, *N. antarcticus* occurred in large numbers in habitats immediately adjacent to SIRS 1 (barren scree and glacial drift) and its population level in the moss turf did not reflect this.

In all species (Fig. 7) the larvae increased in number at the beginning of summer, whilst the

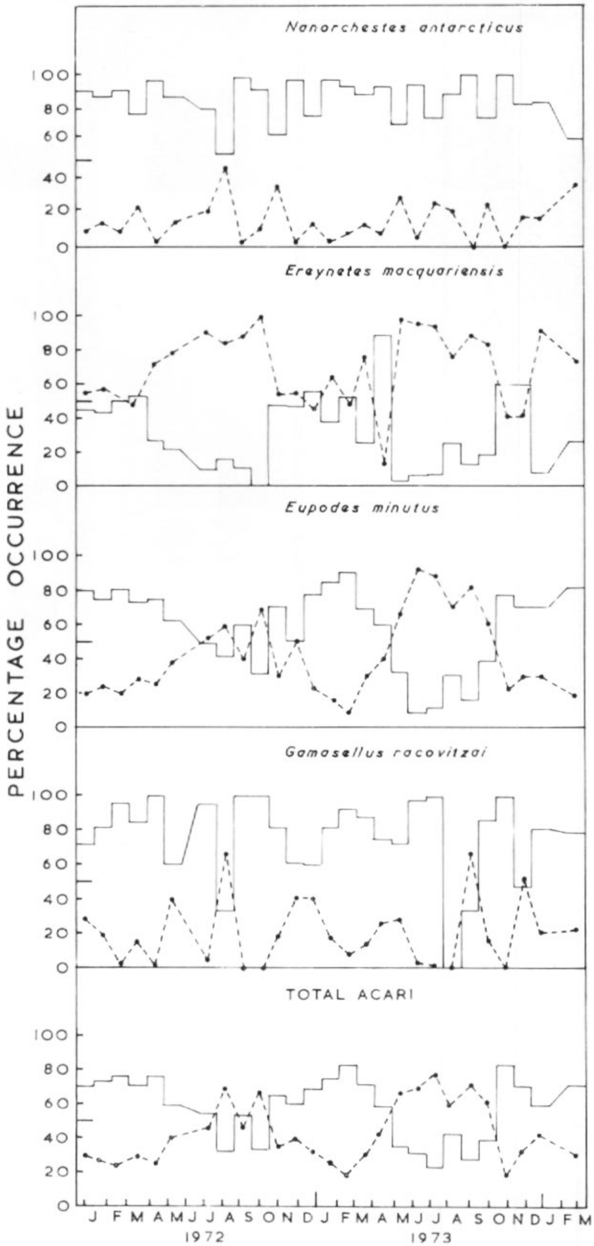

Fig. 5. Vertical distribution of four species of mites and total Acari occurring on SIRS 1 during 1972–74. The percentage of each species is shown in the 0–3 and 3–6 cm. sections of the profile.

nymphs were the main overwintering stage. Analysis of field samples of the Prostigmata showed that the protonymph and deutonumph were the main wintering instars with the exception of *T. tilbrooki*, in which the adult was the main wintering stage. It has been suggested (Goddard, 1977*a*) that for *G. racovitzai* the deutonymph is the main wintering instar, but the population data show that both protonymphs and deutonymphs were present during winter.

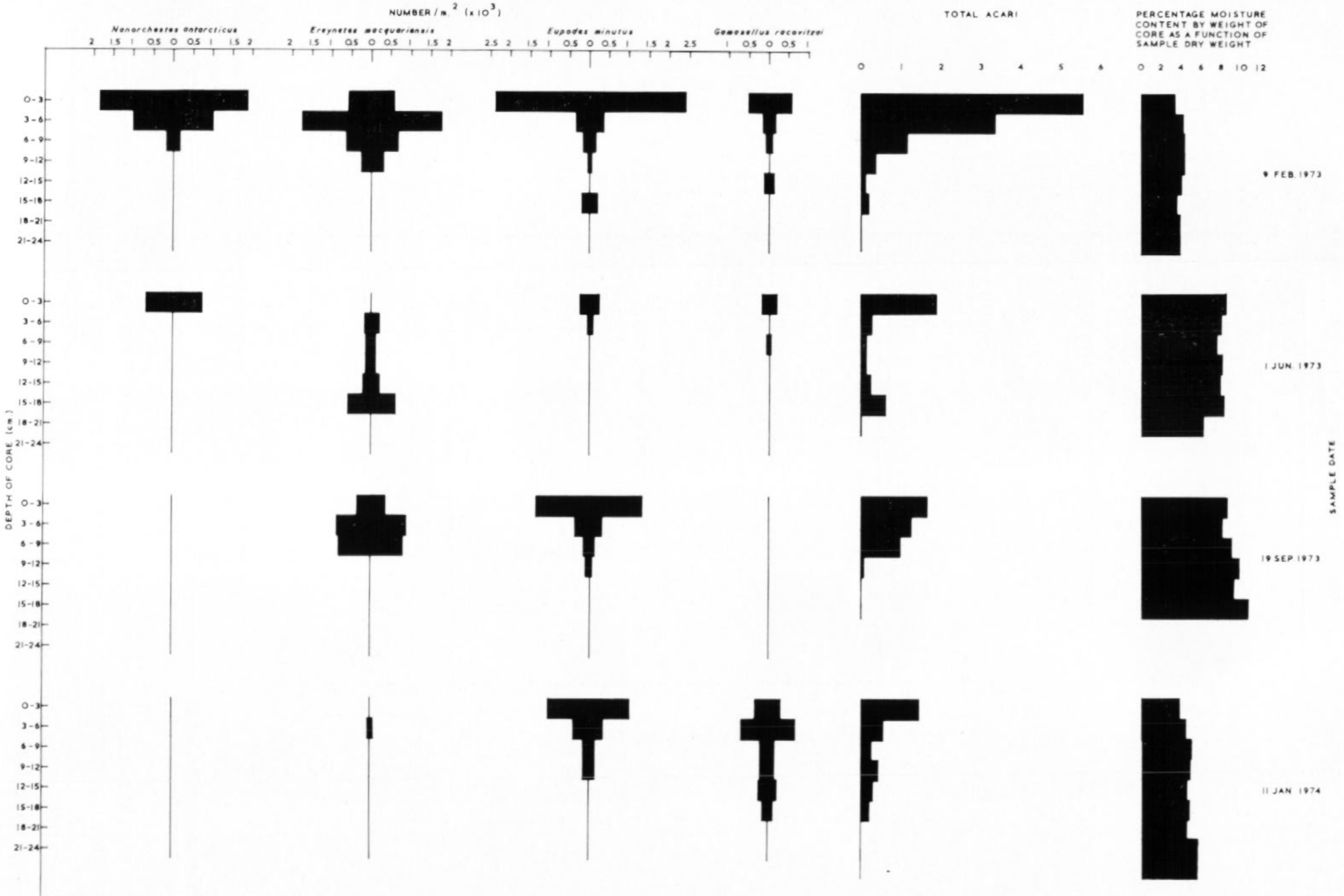

Fig. 6. Vertical distribution of four species of mite and total Acari in 24 cm. deep moss samples on SIRS 1. Samples were collected on four occasions, two in winter and two in summer[illegible]e percentage water content on the basis [illegible] mean dry weight for each 3 cm. section of the profile is also g[illegible]n.

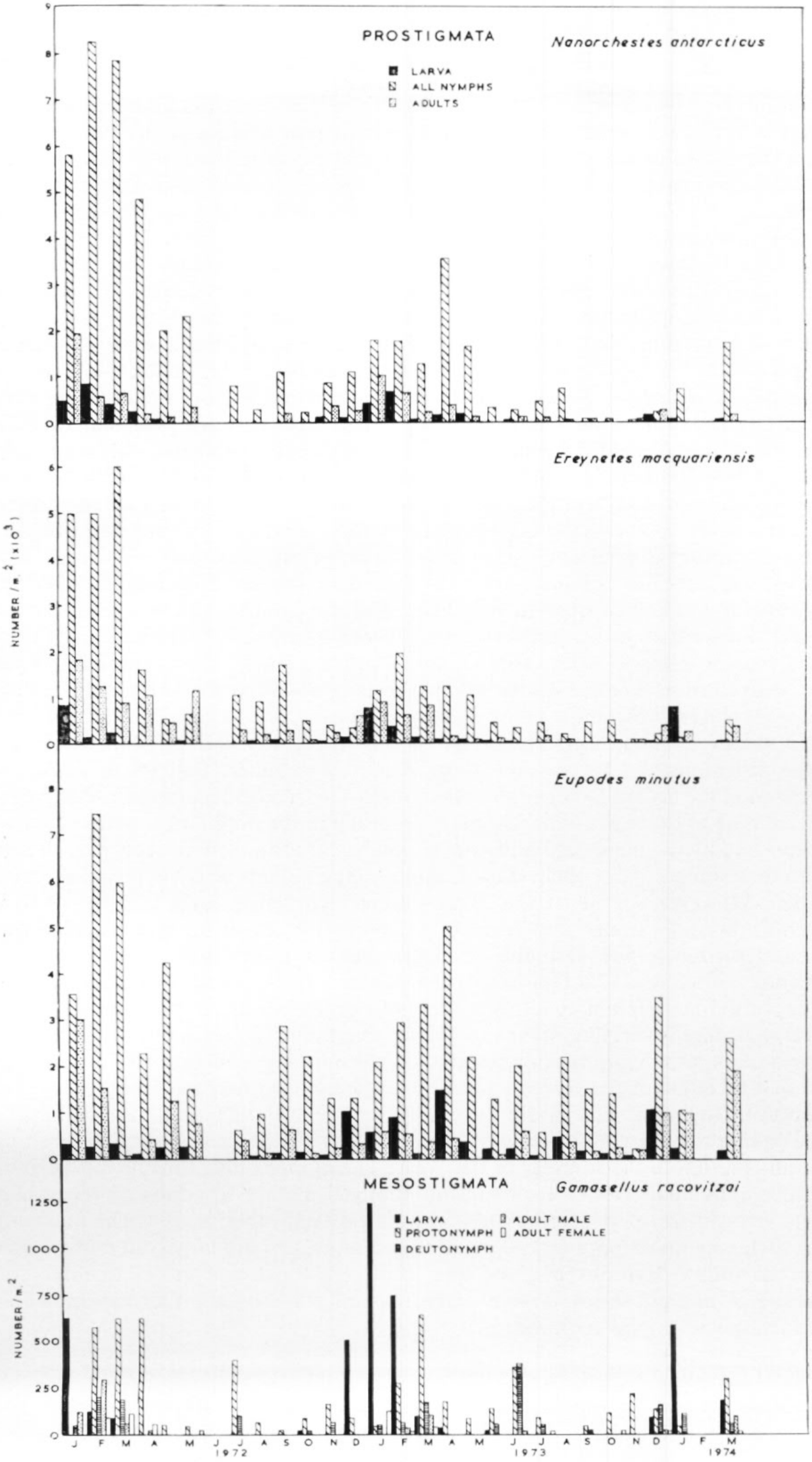

Fig. 7. Life-stage composition of four species of Acari on SIRS 1 during 1972–74.

The larvae of *E. minutus* and *E. macquariensis* found in winter sample extractions indicate either that larvae are present in the field in winter or that heating of the sample core during extraction causes ova to hatch. Similarly, nymphs may undergo moulting during the extraction process, thus making the findings unrepresentative of the actual life-stage composition of the field population on the sampling occasion. This problem becomes more acute with extension of the extraction time.

The detailed life histories of *E. minutus* and *E. macquariensis* are not known at present, but from field observations and laboratory cultures the pattern appears complex, with individuals of all life stages being present throughout the year. However, in general, large numbers of larvae are only present in summer (December–March), suggesting an early summer oviposition period. As the larval stage is the most fragile and therefore vulnerable, it is reasonable to assume that it requires a period of time at the relatively higher summer temperatures for development and to metamorphose into the more resistant nymphal stages. Laboratory observations on ova of field-collected *T. tilbrooki*, which are deposited containing pre-larvae in batches of 100–300 from October to December, showed that they required 3–4 weeks to hatch, moulting to protonymph in 1–2 weeks, and to deutonymph in a similar time. Several females contributed to the same egg batch in culture. Tritonymphs appeared in the culture approximately 12 weeks after oviposition and adults shortly afterwards. However, individuals required varying times to complete their life cycle and development time from deutonymph to tritonymph and to adult varied greatly. The cultures contained sufficient algal food (*Prasiola crispa*, etc.) and were at varied temperatures between 5° and 25° C. Laboratory development times may bear no relation to the field situation so these observations can only be related to field data with caution. Female *T. tilbrooki* were never observed carrying more than three ova at one time. It is not known how many ova a female can produce in a summer but, as the egg is retained within the body until the pre-larva is formed, it is unlikely that fecundity is high due to the development time and the short Antarctic summer. Batches of *T. tilbrooki* ova were observed in the field in October and November. This may explain the large aggregations of adults and larvae of other prostigmatid mites recorded in the population samples.

Ova deposited by the mesostigmatid mite *G. racovitzai* contained no recognizable structures, so they were assumed to be undeveloped, and a single female may oviposit several times in the summer. However, larvae of this species were recorded in large numbers only in early summer, both beneath stones and in moss samples, thus ensuring that the majority of the fragile, unsclerotized larvae were able to metamorphose to the protonymph or deutonymph before winter. Tilbrook (1973*b*) has suggested this may be the result of synchronous hatching of eggs deposited at different times. It is thought that in Antarctic Prostigmata the duration of the nymphal stage is variable, some individuals remaining longer in one instar than in others. This results in mixed nymphal populations of overlapping generations and several instars being present throughout the year. In addition, some nymphs may overwinter more than once before moulting to adults. This mixed nymphal component of the population will thus increase with time so that there are more nymphs present in any 1 year than could have been produced by the adults present in the summer of that year. The nymphs may thus be regarded as a pool of immature individuals from which varying numbers mature to adults or successive instars and adults, dependent upon micro-climatic conditions and other factors. The mortality effects acting on such a nymphal pool will be variable and at present are largely unknown for Antarctic terrestrial mites. Nymphs may be able to tolerate extreme environmental conditions which larvae or adults cannot survive. Experimental work on the thermal and other tolerances of such species is now required.

Micro-climate

Fig. 8 shows the mean monthly moisture content of the core samples collected from SIRS 1 and 2, water content being expressed as a percentage of the mean dry weight of the sample.

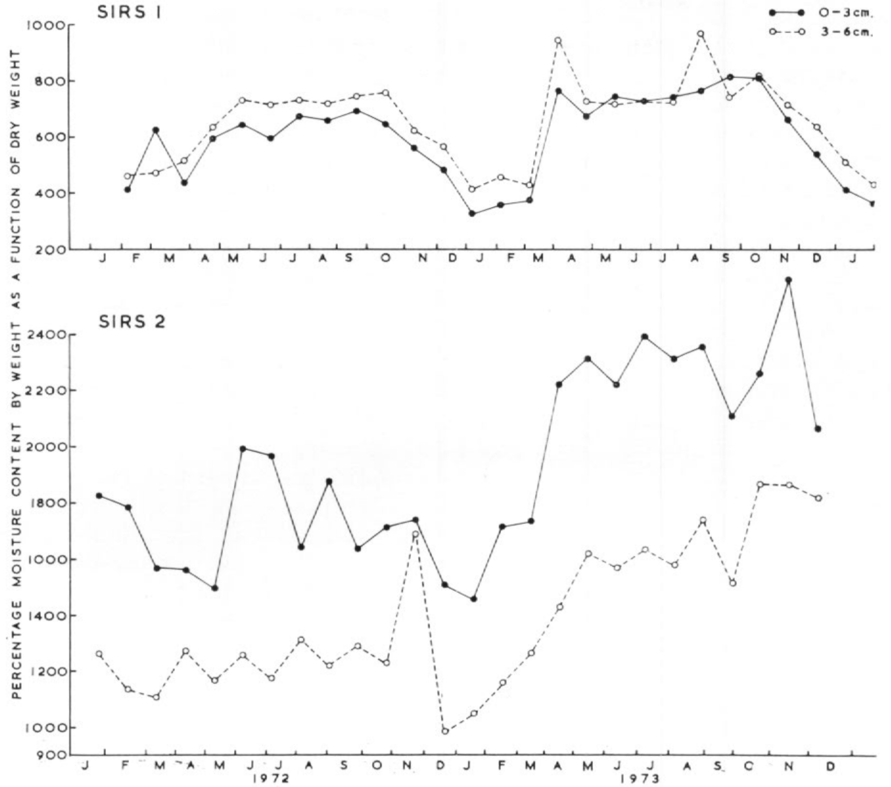

Fig. 8. Variation in mean percentage water content of the regular monthly core samples for the mite-population study on SIRS 1 and 2 during 1972–74. Data are percentage of the mean dry weight of the 0–3 and 3–6 cm. sections of the profile sample.

It is clear that in the second year (1973) both sites were much wetter than in the first year of the study and this was especially so for SIRS 2. Standing water was observed on SIRS 2 at various times during the study and more so in 1973 than in 1972. This was not necessarily caused by a greater precipitation in 1973 as the moisture content of the samples increased in March and April at the time when the sites were frozen. A larger melt or a rain-storm at the end of summer may have caused a larger than normal amount of water to be trapped and frozen in the substrate. This frozen water would be recorded in every subsequent sample while the substrate remained frozen, and this may partially explain the increased water content for 1973 (see Fig. 8). On SIRS 1, water drains freely and regularly through the upper moss layer and the sloping ground ensures good surface-water drainage. When the summer thaw began in October 1973, the moisture content of SIRS 1 cores decreased rapidly to a level similar to that of the previous two summers as the melt water drained away.

At SIRS 2, standing water remained on the surface after the thaw as the site is situated in a small drainage basin receiving melt water from surrounding areas. The moisture content of SIRS 2 cores in the 1973–74 summer was greater than in the two previous summers and remained at the winter level. The increased substrate moisture content at SIRS 1 in winter may have contributed to the general decline in the numbers of the Prostigmata. At SIRS 1, the moisture content of the two core sections was approximately equal, although the lower section tended to be slightly wetter than the upper 0–3 cm. In contrast, the 0–3 cm. section of SIRS 2 cores held more water than the lower 3–6 cm. This may be accounted for by differences in substrate density between sites (*Polytrichum–Chorisodontium* shoots are much denser and more closely packed than the wet-site mosses), or between different depths in the profile on the same site or by ice trapped in the concavities in the irregular moss surface. A 3 cm. SIRS 1 core from either level in the profile was generally heavier than a 3 cm. SIRS 2 core both in terms of dry weight and ash content. Also, the SIRS 1 cores from both levels were within similar weight ranges and thus were of similar densities, while the 3–6 cm. cores were generally heavier than the 0–3 cm. cores from SIRS 2. It is assumed that the lighter the core the greater was its moisture-holding potential under field conditions, hence the greater moisture content of the 0–3 cm. section of the SIRS 2 samples. At Signy Island in 1973, there was more precipitation as rain than in 1972, which led to an increased amount of drainage from SIRS 1 at the end of winter. The run-off water was generally confined to the surface layers of the moss, especially in early summer when the lower layers of the profile were still frozen. This undoubtedly had a flushing effect on the terrestrial invertebrates, particularly on those species inhabiting the surface layers, e.g. *N. antarcticus* and the collembolan *C. antarcticus*. This process could explain the dramatic decline in numbers of *N. antarcticus* compared to other species which were distributed over a greater depth in the profile. To test this, *c.* 10 l. [illegible] run-off water were collected over different periods during the summer of 1973–74, the water was filtered and the filtrate examined for micro-arthropods. Few Acari were recorded but in *c.* 50 l. sampled the collembolan *C. antarcticus* was found in large numbers. This does not mean that flushing had no effect on the Acari in the surface layers of the moss; melt water runs off the site for long periods in the summer and only a minute fraction of it was examined for micro-arthropods. The Collembola were generally more numerous on the site and were much more easily seen in the melt-water collections. The only Acari recorded in the melt water were *N. antarcticus* and *G. racovitzai*. This is interesting as these two species predominate in the surface layers of the moss profile, where the flushing effect would be maximal. On the scree below the SIRS 1 site, large numbers of *N. antarcticus* were found under stones alongside melt runnels and pools fed from the surface drainage. Some of these animals were probably flushed from the site. Fewer *N. antarcticus* were found beneath loose rocks above this area.

A summary of the temperature conditions at five depths in the SIRS 1 profile together with the air temperature and incident solar radiation is given in Fig. 9. The mean data are for 10-day periods together with maximum and minimum values. The general trend for temperature at all levels in the profile is for a warmer second summer (1973), although the period of time when the sites were below 0° C was similar for both years. With increasing depth in the profile, a damping of temperature response was recorded, which was reflected in both maximum and minimum values. Table III summarizes the temperature data as annual mean values for both SIRS 1 and 2 for 1972 and 1973. The temperature range was much greater in 1972 than i[illegible] 1973 so, although 1973 was generally warmer, the annual mean temperature of the site was slightly lower than in 1972. The higher 1973 temperatures were more noticeable from the air-temperature values than from the moss-profile temperatures. The decrease in the Prostigmata populations in 1973 may be partly explained by the lower winter temperatures for 1972, which could have limited the breeding in the 1972–73 summer, as the profile would take longer to reach its summer temperature. This would be especially critical for early summer breeding species. Fitzsimons (1971) recorded *N. antarcticus* active at −20° C, so low temperatures would probably not cause the population to decline unless it limited reproduction. Field and laboratory observations of *G. racovitzai* at Signy Island showed that it became inactive at 0° C and it was killed if the temperature was much lower. However, this species, which showed no population decline, probably was quiescent over winter and was therefore less susceptible to environmental changes than a species such as *N. antarcticus* which remained active during winter. It is evident that environmental changes during summer, e.g. increased moisture together with flooding and larger temperature variations, will have a greater effect

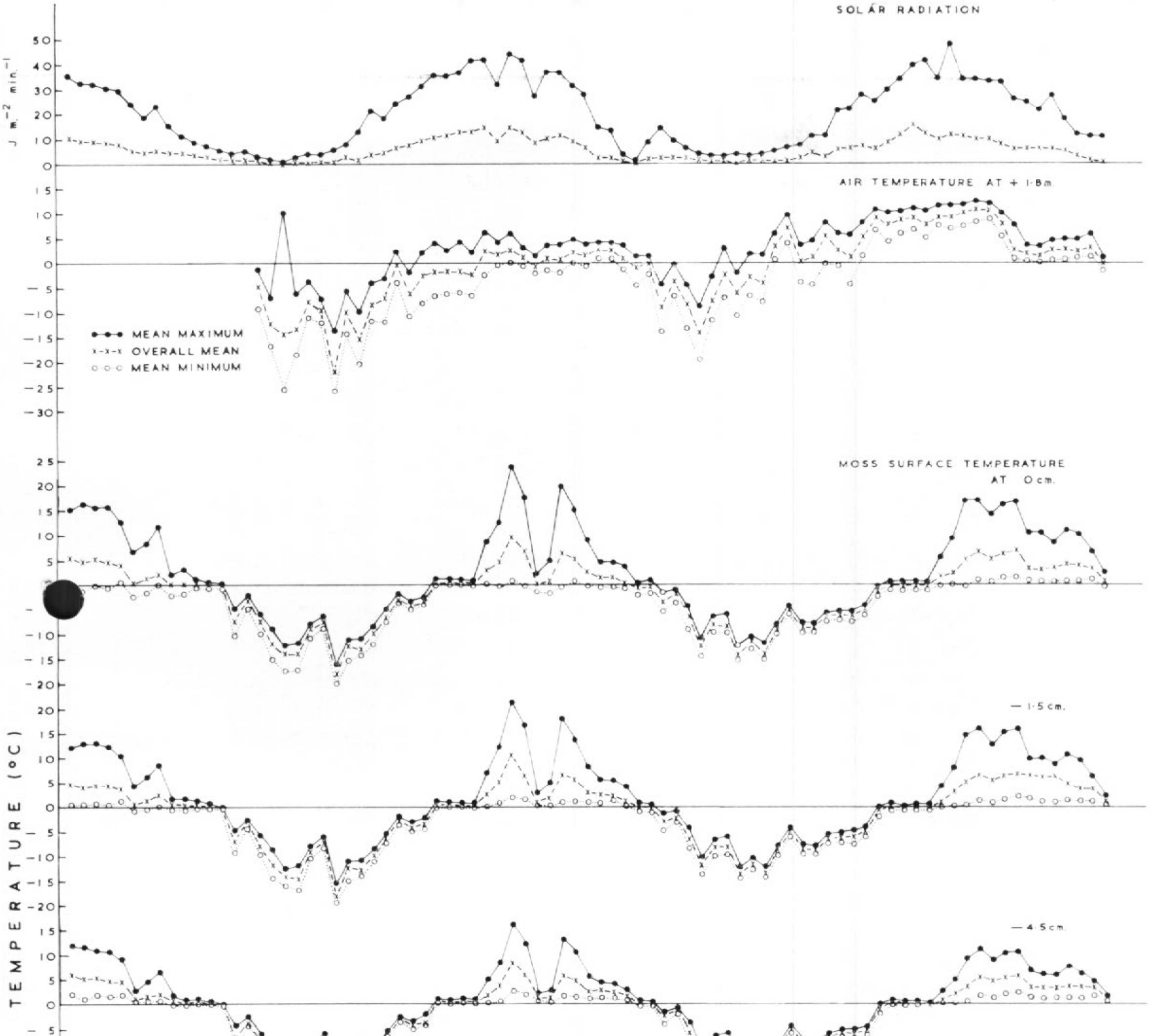

Fig. 9. Summary of the micro-climatic data recorded at SIRS 1 during 1972–74. Incoming solar radiation and air temperature at +1·8 m. are given, together with temperatures at 0 cm. (surface), 1·5, 4·5, 7·5 and 10·5 cm. below the surface in the moss profile. All temperatures are 10-day averages and data for mean maximum, mean minimum and overall mean temperature are shown.

TABLE III. MEAN ANNUAL MAXIMUM AND MINIMUM TEMPERATURES AT SELECTED DEPTHS IN THE PROFILES OF SIRS 1 AND 2 FOR 1972 AND 1973

	Temperature (°C)							
	SIRS 1				*SIRS 2*			
Depth (cm.)	1972		1973		1972		1973	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
1·8 m. above surface	*	*	5·4	−1·3	*	*	*	*
Surface	1·1	−5·0	0·3	−4·4	0·1	−3·8	−0·3	−2·6
1·5 cm. below surface	0·5	−4·6	−0·1	−3·9	−0·8	−3·7	−0·4	−2·3
4·5 cm. below surface	−0·2	−4·0	−0·8	−3·7	−1·4	−3·5	−1·0	−2·4
7·5 cm. below surface	−1·3	−3·9	−1·1	−3·5	−1·7	−3·5	−1·2	−2·4
10·5 cm. below surface	−1·7	−3·9	−2·0	−3·4	−1·7	−3·3	−1·2	−2·3

* Data not available. The air-temperature probe was situated mid-way between SIRS 1 and 2.

on population density than extreme winter conditions, although these may have a direct effect upon the subsequent summer micro-climate. Fitzsimons (1971) noted that *N. antarcticus* was more sensitive to rapid temperature changes than to the extremes of a temperature gradient. Clearly, further studies are required on the effects of cooling and warming regimes on the survival of such micro-arthropods.

In general, the majority of micro-arthropods at SIRS 1 were in the 0–6 cm. level of the profile and Table III shows that below 4·5 cm. in the profile the mean annual temperature was $<0°$ C. This may have had a limiting effect on their effective breeding season and hence the population structure, so the greatest population increases may be expected in species inhabiting the warmer upper layers of the profile. Thus the *N. antarcticus* population in summer 1972 was higher than the other species. The upper layers of the moss were less well insulated against environmental temperature changes, so species limited to these levels may exhibit the largest population fluctuations as observed with *N. antarcticus*. *E. minutus* and *E. macquariensis* which inhabit a greater depth range in the moss profile (Fig. 6), are better able to replace individuals lost from the upper layers by emigration from lower layers of the profile. Although these species had lower population densities than *N. antarcticus* in favourable years, their density fluctuations were less marked. Therefore, in unfavourable years, species inhabiting a greater depth range may become numerically dominant at this site. Similarly, *G. racovitzai*, which inhabits a wide range of habitats on the sites and is highly mobile, will tend to rapidly r[illegible] colonize areas from which it has been removed. This may partially explain the relative stability of its population in the moss turf.

DISCUSSION

The considerable literature relating to Antarctic Acari is mostly taxonomic or biogeographical. Gressitt (1967, 1971) summarized much of this information. Data on the dynamics of Antarctic mite populations are sparse and, apart from the work of Tilbrook (1973*b*) and Rounsevell (1977), it consists mainly of summer observations. Covarrubias (1966) estimated Acari numbers in an unidentified moss on the South Shetland Islands as 2×10^4 ind. m.$^{-2}$ and Janetschek (1967) gave biomass estimates for Acari in South Victoria Land, while Matsuda (1977) presented preliminary data for two species of *Tydeus* and *Nanorchestes antarcticus* at Syowa station, Enderby Land, Antarctica. Matsuda made observations in a number of habitats during summer; in unidentified algae he recorded numbers ranging from 100 to 800 ind.

m.$^{-2}$ for *N. antarcticus* and 1,100 to 2,700 ind. m.$^{-2}$ and 400 ind. m.$^{-2}$, respectively, for the two species of *Tydeus*. In soil, *N. antarcticus* ranged from 100 to 500 ind. m.$^{-2}$ and the *Tydeus* species varied from 100 ind. m.$^{-2}$ for one species to 200–700 ind. m.$^{-2}$ for the other. In an unidentified moss, the numbers of *N. antarcticus* were 1,000–1,200 ind. m.$^{-2}$ and the two *Tydeus* species were 100 ind. m.$^{-2}$ and 700–1,300 ind. m.$^{-2}$, respectively. Rounsevell's data were more comprehensive and covered a 10-month period, although he only quoted numbers for *N. antarcticus* ranging from $12{\cdot}7 \times 10^{3}$ ind. m.$^{-2}$ in August to $27{\cdot}7 \times 10^{3}$ ind. m.$^{-2}$ in November and December at one site, and $158{\cdot}6 \times 10^{3}$ ind. m.$^{-2}$ (January) to $46{\cdot}9 \times 10^{3}$ ind. m.$^{-2}$ (April) at a second site. These population densities are much higher than those recorded for this species in the present study but Rounsevell's sample sites were sandy and barren with *N. antarcticus* being the only species present. The moss-turf habitats at Signy Island are not comparable but from field observations *N. antarcticus* was the only species present and in large numbers in similar barren situations at Signy Island. The only work with which the present study is comparable is that of Tilbrook (1973*b*,) although direct comparisons must be treated with care as he used cores of a different size and with fewer replicates. Tilbrook's study was a terrestrial invertebrate survey of Signy Island together with other terrestrial maritime Antarctic habitats, whereas the present work was an intensive study of the Acari populations at two main sites.

Part of the study site used by Tilbrook (1973*b*) was a dry moss turf composed mainly of *Polytrichum alpestre–Chorisodontium aciphyllum* with lichen encrustations in places. This was essentially similar in vegetative composition to SIRS 1. The other part of Tilbrook's study site was assignable to the moss-carpet sub-formation and, although it consisted of a pure stand of the pleurocarpous species *Pohlia nutans*, it resembled SIRS 2 in many respects, particularly its waterlogged nature. As in the present study, he recorded very few Acari in this wet moss site, although generally more individuals were present. He did, however, examine several other drier *Drepanocladus–Calliergon* sites on Signy Island and these supported more species at higher population densities. The causes of the very low Acari populations at SIRS 2 are complex but it seems that the site was consistently too wet with a very high water content of the moss compared with SIRS 1 (Fig. 8). The mean annual water content as a percentage of the moss-core dry weight for the 2 study years at SIRS 2 were 1,480 per cent (1972) and 1,842 per cent (1973), and at SIRS 1 they were 609 per cent (1972) and 666 per cent (1973). The large amount of standing water on SIRS 2 would tend to restrict the air spaces in the moss available for Acari and regular flushing of the site with swift flowing streams during the spring melt was observed to flush out large numbers of Collembola and some Acari. At depths greater than 6 cm. in the profile, conditions were virtually anaerobic (Broady, 1979) and the peat remained frozen until almost mid-summer. The moss tended to be denser and more waterlogged below 6 cm., such an environment being unsuitable for the Acari species occurring at Signy Island. On SIRS 1, below a depth of 4·5 cm., the mean annual temperature of the moss never rose above 0° C and below this level the numbers of mites present decreased rapidly. At the SIRS 2 site the mean annual temperature for the whole moss profile was below 0° C (Table III). This may be an important factor influencing the occurrence and distribution of mites on this site.

Tilbrook (1973*b*) found that three species of prostigmatid mite comprised 96 per cent of the total Acari collected on his *Polytrichum–Chorisodontium* site. In the present study, the same three species (*E. minutus*, *E. macquariensis* and *N. antarcticus*) were 94 per cent of the total Acari collected in the 27-month sampling period. *E. minutus* was the commonest species in Tilbrook's study, forming 56 per cent of the total collections, and in the present study it was 43 per cent of the total Acari. The other two species of Prostigmata were present in approximately equal proportions, *N. antarcticus* being 27 per cent and *E. macquariensis* being 23 per cent. The life-stage distribution of the Prostigmata at SIRS 1 and 2 and in Tilbrook's study differed, low numbers of nymphs being recorded in winter by Tilbrook (1973*b*), whereas in the present study high numbers of nymphs and few adults were found in the winter samples. However, the life-stage data from heat-extracted samples must be treated with care as moulting and egg hatch may occur during extraction.

The life-stage distribution and population density of the mesostigmatid mite (*G. racovitzai*) recorded by Tilbrook were similar to that in the present study. Tilbrook found larvae present between November and January when approximately 85 per cent of the population were larvae. At SIRS 1, larvae were found from the end of November to mid-February, their proportion in the samples ranging from 65 to 84 per cent. Tilbrook suggested that high larval numbers were associated with synchronous egg hatching at the onset of favourable summer conditions. He found a gradual development from protonymphal maxima in January–March to deutonymphal maxima in March–April. This was not so apparent from the SIRS 1 sample cores, where after a March protonymph peak the picture was obscured because of low numbers of individuals in the samples. However, field observations support Tilbrook's findings. Most individuals collected in both this and the earlier study were from summer samples; Tilbrook recorded only nymphs in winter samples but in the present study all life stages except larvae were recorded in winter samples. Tilbrook suggested that the main overwintering stages were the egg and nymphs, although this is not confirmed by population data from the present study. Field observations suggest that the deutonymph is the main overwintering stage with small numbers of protonymphs being present. At the onset of winter, large aggregations of deutonymphs were found under stones with similar aggregations (which initially do not contain adults) being found in early spring (October). As summer advanced, the proportion of adults in these aggregations increased considerably and it is suggested that these adults originated from spring moults of the winter deutonymph population, and that they were responsible for the increased numbers of larvae in January and February rather than overwintering ova. Larvae found in November may have originated from overwintering eggs or eggs deposited by adults in October–November.

Strong (1967) suggested that *G. racovitzai* was active below 0° C. Adults of this species at Signy Island were observed to become torpid at or below 0° C and death followed if they spent prolonged periods (1–7 days) at or below this temperature. The deutonymph stage appeared to be able to tolerate low temperatures and there was a different respiratory response to temperature changes in the deutonymph compared with the other life stages (Goddard, 1977*a*). Ova of *G. racovitzai* were never found in the field and females could not be induced to lay eggs in laboratory cultures.

The general population trend in Tilbrook's study was for seasonal fluctuations of high summer and low winter density for all species and he did not record the general decline in numbers as found in the present study. However, as Tilbrook (1973*b*) pointed out, the sample size was small and the standard errors on the means were high, whereas in the present study the sample size was larger with much smaller standard errors on the means. In view of this only broad comparisons can be made.

At the onset of spring, different parts of SIRS 1 lost the winter snow accumulation at different rates, so part of the site was snow-free with thawed moss while part was still frozen with up to 1 m. of snow. In places, a greenhouse effect was observed with Acari active in air spaces on the surface of the thawed moss below a thin sheet of transparent ice situated a few millimetres above the moss surface. These conditions would produce a complex thermal regime in the moss profile, both horizontally and vertically, with some micro-habitats favourable for Acari reproduction and others not, and these may in part account for the aggregations of juvenile mites found in the sample cores. Furthermore, cores from sample quadrats which had prolonged snow cover generally contained fewer Acari than did cores from quadrats which became snow-free early in the summer or from those which experienced a greenhouse effect. The micro-climatic data provide only a general indication of temperature conditions at SIRS 1 and 2, as there was only one set of probes per site. The moss above the probes at

SIRS 1 was free of snow before most of the remainder of the site during the study period and the probe area did not experience a greenhouse effect.

A general decline in the population densities of prostigmatid mites was observed during the 27-month study period, while the population of the mesostigmatid mite remained relatively stable. The possible causes of these population declines have been advanced but more information on the biology of Acari species in such polar habitats is required, together with a detailed study of the physiological responses of individuals to seasonal changes in environmental conditions.

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