

THE SIGNY ISLAND TERRESTRIAL REFERENCE SITES: XIV. POPULATION STUDIES ON THE COLLEMBOLA

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ABSTRACT. Field data for Collembola extracted from a series of 25 monthly samples of a moss turf and a moss carpet at Signy Island have been analysed to provide information on species composition, population density and biomass, size-class structure and field distribution. Three species were found: *Friesea grisea* (Schäffer), *Parisotoma octooculata* (Willem) and *Cryptopygus antarcticus* Willem, with the latter species being numerically dominant throughout the study at both sites. Population densities for all Collembola averaged 49 928 (moss turf) and 9 913 (moss carpet) individuals m^{-2} , of which *C. antarcticus* comprised 99% and almost 100%, respectively. Mean biomass equivalents were 688 and 154 mg live weight m^{-2} (250 and 56 mg dry weight m^{-2}). Size-class analyses for *C. antarcticus* showed an almost stable distribution in the moss turf, whereas summer growth was evident in the moss-carpet population. A similar degree of aggregation was observed for *C. antarcticus* at the two sites. Between 78% and 88% of the Collembola were located in the zone from the moss surface down to 6 cm depth in the turf, whilst 96–99% occurred in the same zone of the moss carpet. These findings are discussed in relation to the micro-climate and structure of the two habitats, and compared with data available for other Antarctic sites, the Arctic and temperate studies.

PREVIOUS research on the Collembola of the Antarctic region has been concerned with taxonomy and systematics (e.g. Wise, 1967, 1971), distributional ecology (e.g. Janetschek, 1967a; Tilbrook, 1967a, b), field biology (e.g. Strong, 1967; Janetschek, 1970; Tilbrook, 1970) and physiology (e.g. Marsh, 1970; Block and Tilbrook, 1975, 1978; Block 1979). Detailed investigations of the population dynamics of single species are few: on *Isotoma klovstadi* Carpenter at Hallett Station, North Victoria Land (Pryor, 1962), on *Gomphiocephalus hodgsoni* Carpenter at Cape Crozier (Ross Island) and Mount England, South Victoria Land (Janetschek, 1967b), on *G. hodgsoni* at Cape Bird, Ross Island (Peterson, 1971), and on *Cryptopygus antarcticus* Willem at Signy Island, South Orkney Islands (Tilbrook, 1977). The present paper provides information on the dynamics of the populations of two species of Collembola in two bryophyte communities at Signy Island, maritime Antarctic. One of these, *C. antarcticus*, is both the largest and the most abundant arthropod in these communities. This paper is a further contribution to the Signy Island terrestrial reference sites (SIRS) ecosystem programme, which is aimed at an analysis of the structure and function of such systems in the maritime Antarctic. The study sites have been described (Tilbrook, 1973a), and data are available on seasonal changes in the population numbers of protozoans (Smith, 1973), tardigrades and rotifers (Jennings, 1979), nematodes (Caldwell, 1981a, b; Maslen, 1981) and the mites or Acari (Goddard, 1979). Davis (1981) has made an initial synthesis of the results and the information available, which suggests that the Collembola play a relatively minor role in the turnover of material and energy in such communities. This is in contrast to their relatively high population density and biomass.

The aims of the present work were:

- i. To determine the species composition and population structure of the Collembola at the two sites.
- ii. To study seasonal variations in their numbers.
- iii. To examine the distribution of the animals in the peat profile.
- iv. To obtain information on their life cycles.

METHODS

Study sites and sampling

SIRS 1 and 2, situated on Gourlay Peninsula in the south-east of Signy Island, are a *Polytrichum-Chorisodontium* moss turf (site 1) and a *Calliergon-Calliergidium-Drepanocladus* moss carpet (site 2). The sites, each containing 100 m^2 of sample strata, have been studied for

over 10 years (Tilbrook, 1973a), and Goddard (1979) has reported on the methods for micro-arthropod sampling.

Twenty-four vegetation and peat cores, collected at random within the 1 m wide sample strata of each site, comprised a sample. Samples were collected from both sites at approximately 4-week intervals between 20 December 1971 and 7 December 1973 (25 occasions in all). Each core was 6 cm in depth from the moss surface and 0.002 m² in surface area. It was cut horizontally into two 3-cm-deep sections, and the arthropod fauna extracted separately from each section. In addition, on at least two occasions in 1973, the peat of each site was sampled to the underlying bedrock, the cores being similarly subdivided into 3-cm-deep sections. The maximum depths of peat found from these samples were 24 cm (SIRS 1) and 18 cm (SIRS 2).

Sampling was undertaken using a hand corer in summer and using a corer with tungsten carbide cutting teeth driven by an electric drill powered from a portable generator, when the moss was frozen in winter. Up to 1 m of snow and ice was present on both sites at times during winter (Block, 1980a), and this was removed before sampling.

Faunal extraction and analysis

Micro-arthropods (Acari and Collembola) were recovered from individual 3-cm core sections in a high-gradient canister extractor (Macfadyen, 1961). The sections, contained in core rings from the field, had their cut surfaces sealed with parafilm and were thawed at 2°–5°C for 24 h before extraction. The extraction regime, using increasing temperature and desiccation gradients over 6 d, has been described by Goddard (1979). The fauna was extracted into a 50% solution of picric acid in the canisters, the extracts were filtered through 30- μ m-mesh Nybolt gauze and transferred to 70% ethanol and 5% glycerol solution for analysis. Arthropods were identified and sorted under $\times 25$ to $\times 50$ magnification using a grid. The Collembola, separated into species, were individually measured in terms of body length for assignment to size class (Tilbrook and Block, 1972; Block and Tilbrook, 1975) and to derive their live and dry weights.

In the United Kingdom, data for derivation of the relationship of individual live weight to dry weight were obtained using a LM 500 micro-balance at 5°C from specimens transported live from Signy Island.

Environmental monitoring

The following parameters were monitored during the field study: hourly moss and peat temperatures recorded at the moss surface (0 cm), at -1.5, -4.5, -7.5 and -10.5 cm below the surface, and at 1.8 m in the air above the surface, together with incident solar radiation. These data were recorded by a battery-driven Grant Model D recorder, which was housed in a field hut near SIRS 1 and 2. Details of the instrument and the thermistor probes have been given in Walton (1977). Throughout the winter, frequent measurements of snow depth were made at positions on each site using permanent snow poles.

RESULTS

Species composition

Only three species of Collembola were found during the 2-year study: *Cryptopygus antarcticus* Willem, *Friesea grisea* (Schäffer) and *Parisotoma octooculata* (Willem). They are referred to by their generic names throughout this paper. These species represent c. 75% of the total collembolan fauna of Signy Island (Tilbrook, 1973b). *Parisotoma* was recorded only in the moss turf (SIRS 1) and only during summer. *Cryptopygus* was present in all the samples collected from both sites in each month of the year, whereas *Friesea* was more common in the moss turf than the moss carpet and was found only in six samples from the moss carpet during the summer of 1972.

Population density

The mean numbers of *Cryptopygus* estimated from monthly samples of the moss turf (SIRS 1) ranged from a minimum of 19 585 (September 1973) to a maximum of 98 520 (February 1972) individuals m^{-2} (Fig. 1a), whereas in the moss carpet the population density was more variable, ranging from a minimum of 40 (July 1973) to a maximum of 64 690 (December 1971) individuals m^{-2} (Fig. 1b). In the moss turf, smaller populations of *Cryptopygus* were found during winter in August 1972 and September 1973 with relatively higher numbers throughout the summer (December–March) of both years. In the moss carpet, lower population densities occurred in June and September 1972, and in July 1973. Similarly, higher numbers of *Cryptopygus* were recorded in the summers of both years. Thus, a pattern suggestive of seasonal changes in overall population numbers can be discerned (Fig. 1a and b), which is probably related to the life cycle of this species under maritime Antarctic conditions.

Cryptopygus was more abundant in the relatively drier moss turf than in the carpet community, its mean annual population being five times (1972) and 11 times (1973) larger in the former site (Table I). On an annual basis also, there were major differences in population density between years on both sites (Table I). Populations of *Cryptopygus* were just over half the size (SIRS 1) and just over one-quarter of the size (SIRS 2) in 1973 of those recorded in the previous year. Throughout the 2-year study, there was a decline in population numbers of *Cryptopygus* with time, which can be expressed as:

$$y = 78.37 - 2.21x \quad (r^2 = 0.69; P < 0.001) \text{ for SIRS 1,}$$

$$\text{and } y = 33.63 - 10.18x \quad (r^2 = 0.38; P < 0.001) \text{ for SIRS 2,}$$

where $n = 25$ in both cases, y is the population density (number $\times 10^3 m^{-2}$) and x is the time (months). Recent observations suggest that the population densities are much lower (personal communication from R. G. Booth).

Friesea occurred in both communities but in much lower population densities than *Cryptopygus* (Fig. 2). The maximum population noted was 2 335 (December 1971) and the minimum 20 (September 1973) individuals m^{-2} in the moss turf, whilst, in the moss carpet, numbers ranged from 20 to 585 individuals m^{-2} during January–May 1972. Annual mean population densities for *Friesea* (Table I) show that it was almost five times more abundant at SIRS 1 than at SIRS 2 in 1972, but it was not recorded at all on SIRS 2 in 1973. Again, as with *Cryptopygus*, a reduction (by 50%) in mean annual population density occurred between the two study years in the moss turf. The overall decline in population with time at SIRS 1 calculated for the study period may be expressed as:

$$y = 0.992 - 0.037x.$$

As a population decline occurred in both *Cryptopygus* and *Friesea*, it may be that a common factor affected the populations of both species.

The numbers of *Parisotoma* in the moss turf were very small. A total of 18 specimens was found, mostly during the summer months; it was not recorded in the samples from the moss carpet. Clearly, bryophyte-dominated communities do not afford suitable habitats for this species, and it is found in more open situations such as fellfields on Signy Island (W. Block, unpublished).

In terms of the entire Collembola community of the two sites, total numbers varied from 3 093 to 60 957 individuals m^{-2} during the study period (Table I) with mean values around 49 928 (moss turf) and 9 913 (moss carpet) individuals m^{-2} . In all cases, fewer Collembola were found in the moss carpet than in the turf.

Population biomass

Using published live-weight data for the five size classes of *Cryptopygus* (Block and Tilbrook, 1975), estimates of the population biomass for this species were calculated. Monthly population

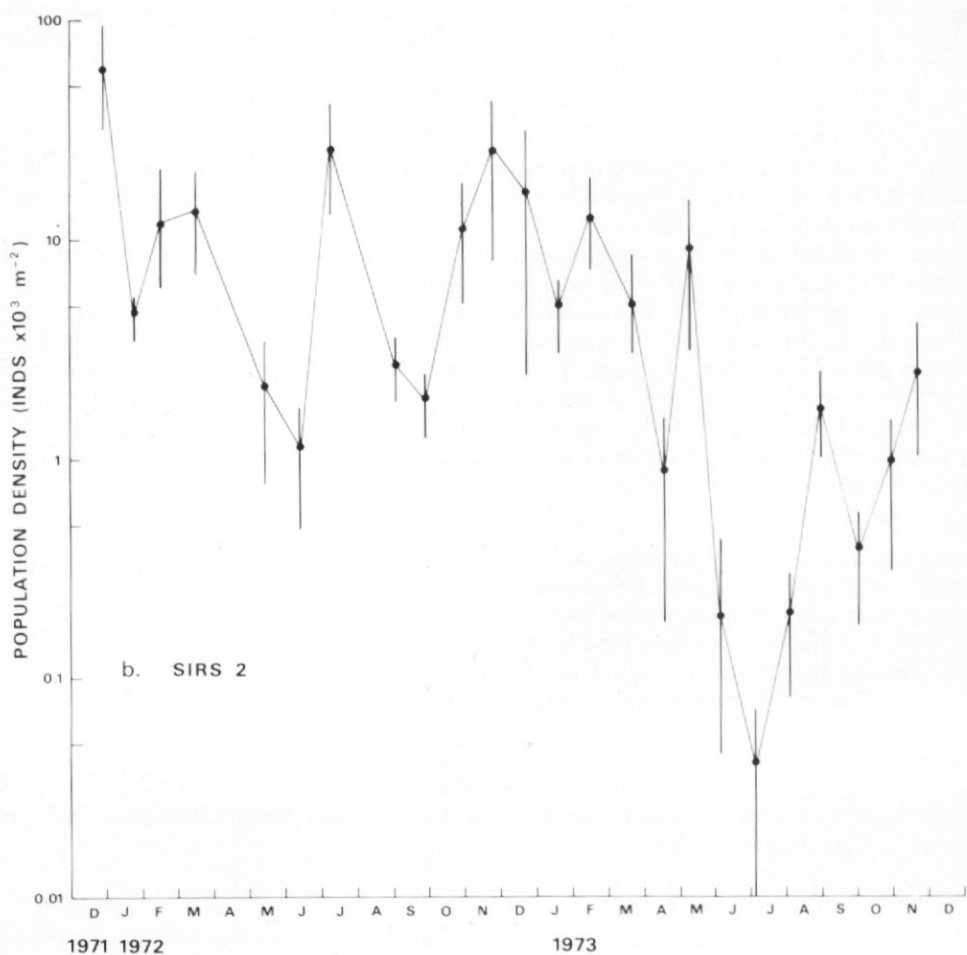
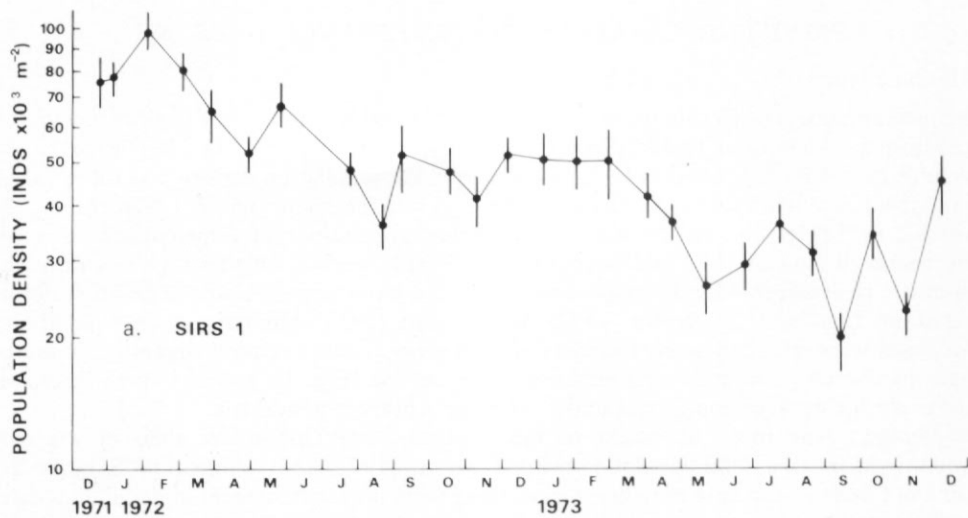


Fig. 1. Seasonal changes in population density of *Cryptopygus antarcticus* in a moss turf (SIRS 1) (Fig. 1a) and a moss carpet (SIRS 2) (Fig. 1b) during 1972-73 at Signy Island. Values are mean \pm SE and $n = 24$ for each sample.

TABLE I. MEAN ANNUAL POPULATION DENSITIES OF COLLEMBOLA IN MOSS-TURF (SIRS 1) AND MOSS-CARPET (SIRS 2) COMMUNITIES AT SIGNY ISLAND DURING 1972-73. VALUES ARE NUMBER OF INDIVIDUALS m^{-2}

Year	n	<i>Cryptopygus antarcticus</i>		<i>Friesea grisea</i>		Total <i>Collembola</i>	
		SIRS 1	SIRS 2	SIRS 1	SIRS 2	SIRS 1	SIRS 2
1972	12	60 398	12 161	567	122 (n=6)*	60 965	12 283
1973	12	36 190	3 093	297	—	36 487	3 093
Study period	25	49 420	9 908	508	5	49 928	9 913

n Number of monthly samples.

— Only a few individuals recorded.

* January-June 1972.

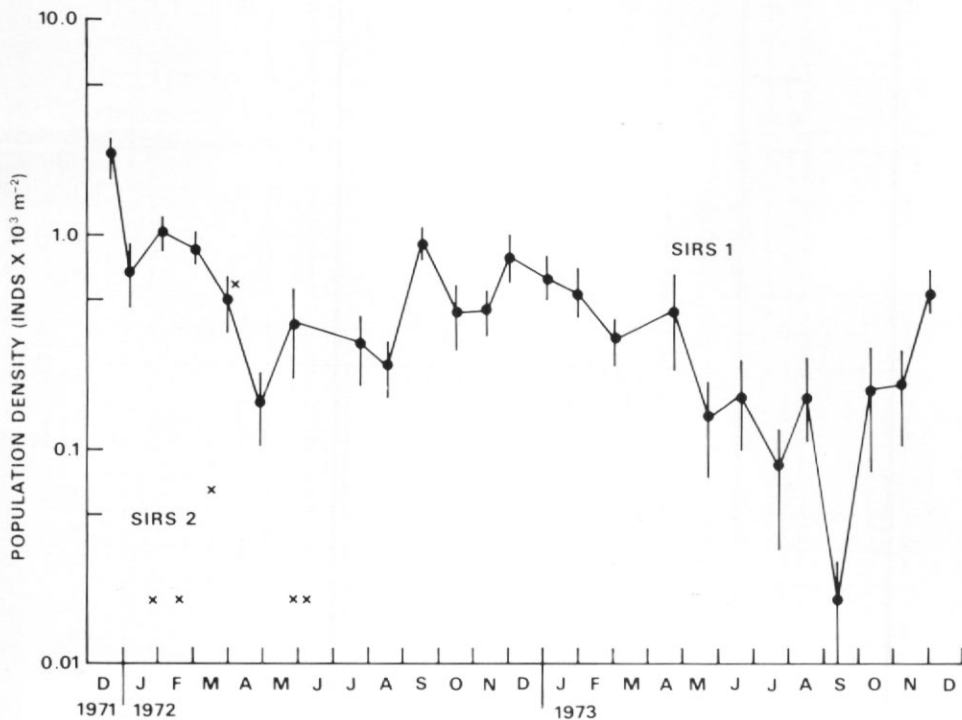


Fig. 2. Seasonal changes in population density of *Friesea grisea* in a moss turf (SIRS 1) and a moss carpet (SIRS 2) during 1972-73 at Signy Island. Values are mean \pm SE and $n = 24$ for each sample.

biomass varied from 363 to 1 125 (SIRS 1) and from 0.6 to 863 (SIRS 2) mg live weight m^{-2} , with >30% of the total being contributed by size classes 2 and 4 (SIRS 1) and by size class 3 (SIRS 2). The lowest biomass was calculated for the winter months for both sites, and the highest value was obtained during summer. On the basis of mean annual estimates of biomass (Table II), the total population estimate for *Cryptopygus* declined between the two study years at both sites, by 22% in the moss turf and by 79% in the moss carpet. Mean biomasses over the 25-month study were 688 and 154 mg live weight m^{-2} for SIRS 1 and 2, respectively. In terms of the contribution made by the size classes to total *Cryptopygus* biomass, size class 2 dominated in the moss turf by comprising *c.* 42%. In the moss carpet, size class 4 contributed >30% of the total biomass over the study period. The smallest fractions of total biomass in this species were formed from size classes 1 and 5, the smallest and largest individuals in the populations.

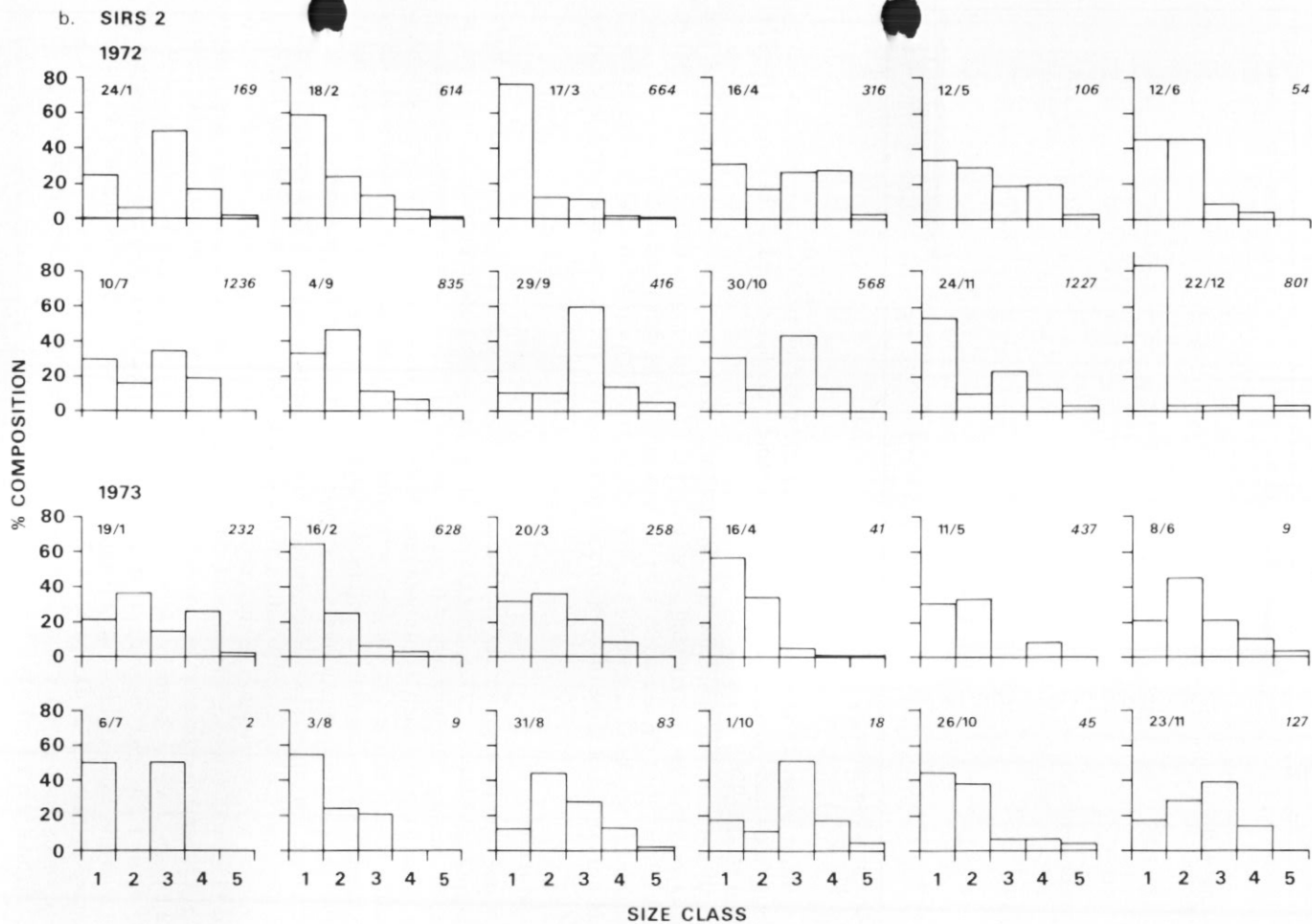


Fig. 3. Percentage composition by size class of monthly samples of the populations of *Cryptopygus antarcticus* in a moss turf (SIRS 1) (Fig. 3a) and a moss carpet (SIRS 2) (Fig. 3b) at Signy Island during 1972-73. The total number of *C. antarcticus* in each monthly sample is also shown, and $n=24$ cores per sample.

TABLE II. BIOMASS ESTIMATES (mg LIVE WEIGHT m^{-2}) FOR POPULATIONS OF *Cryptopygus antarcticus* IN MOSS-TURF (SIRS 1) AND MOSS-CARPET (SIRS 2) COMMUNITIES AT SIGNY ISLAND DURING 1972-73. THE CONTRIBUTIONS OF EACH OF THE FIVE SIZE CLASSES ARE ALSO SHOWN TOGETHER WITH MEAN INDIVIDUAL LIVE WEIGHTS

Site	Year (n)	Mean biomass per size class					Mean total biomass	
		1	2	3	4	5	Live weight	Dry weight
	Mean live weight individual ⁻¹	3.0	10.2	25.7	52.5	92.8		
SIRS 1	1972 (12)	45.0	365.0	195.5	141.0	27.4	773.9	281.5
	%	5.8	47.2	25.3	18.2	3.5		
	1973 (12)	17.8	205.3	164.8	167.8	48.4	604.1	219.7
	%	2.9	34.0	27.3	27.8	8.0		
	Study period (25)	32.9	287.9	178.3	151.6	36.9	687.6	250.1
%	4.8	41.8	25.9	22.0	5.4			
SIRS 2	1972 (12)	16.8	21.0	73.5	75.5	18.1	204.9	74.5
	%	8.2	10.2	35.9	36.8	8.8		
	1973 (12)	3.9	10.5	10.2	16.1	3.9	44.6	16.2
	%	8.7	23.5	22.8	36.0	8.7		
	Study period (25)	13.0	22.2	60.6	47.9	10.7	154.4	56.1
%	8.5	14.4	39.3	31.2	6.9			

n Number of monthly samples.

Using a mean water content for individual *Cryptopygus* of 63.6% ($n = 61$), dry-weight equivalents of the mean annual biomass estimates were calculated to be in the range 219-281 (SIRS 1) and 16-74 (SIRS 2) mg dry weight m^{-2} .

Live-weight data are not available for *Friesea* but, on the basis of general body size and length, average individuals correspond to size class 2 of *Cryptopygus*. Hence, a live weight of 10.2 μg individual⁻¹ has been used for the computation of its mean population biomass. This species contributes between 1.2 and 5.8 mg live weight m^{-2} . Thus mean annual biomasses for all Collembola are estimated to be 607-780 (moss turf) and 45-206 (moss carpet) mg live weight m^{-2} .

Size-class structure

It was hoped that, by assignment of individual *Cryptopygus* to five size classes based on body length (Tilbrook and Block, 1972), changes would be seen which could provide information on growth and life history. The numbers of *Cryptopygus* in each size class were used to calculate the proportion of each class in each monthly sample, and the results are given in Fig. 3 for both sites.

The striking feature of the *Cryptopygus* population of the moss turf over the two study years was its apparently stable size-class structure. Size class 2 (body length 750-1 060 μm) formed c. 57% of the samples throughout the study. Size classes 1 and 3 composed 20 and 15% respectively, with the larger individuals being <10% of the population. There were no obvious seasonal changes in the size-class structure of the *Cryptopygus* population in the moss turf (Fig. 3a). In contrast, the composition of the population in the moss carpet changed between study years, and there was evidence of seasonal shifts in the size-class structure. Size class 1 (body length 440-750 μm) comprised, on average, c. 39% of the samples during the 2-year period, whilst size classes 2 and 3 formed c. 23% each of the population. Larger individuals were 11% (size class 4) and 2% (size class 5) in terms of mean values. The size-class composition of *Cryptopygus* in the moss carpet (Fig. 3b) suggests that growth occurred principally in summer (e.g. February to May 1972; December 1972 to January 1973; February to June 1973), and possibly at times during winter (e.g. September to October 1972; August to October, 1973). However, caution is required when interpreting such changes based on low mean numbers per core, i.e. ≤ 2 which represents a total of ≤ 48 individuals per monthly sample, and the possibility of differential mortality should not be overlooked.

Fig. 4a and b shows the seasonal fluctuations in mean numbers per core for each size class of *Cryptopygus* at both sites. As reflected from the overall population-density levels, the moss-carpet community experienced much greater fluctuations than that of the moss turf over the 2 years. Juveniles, especially size class 1, increased in numbers during November–December 1972 at SIRS 2, which was followed by an upsurge in size class 2 individuals, but only in April 1973. No such pattern was discerned for SIRS 1.

Horizontal distribution

The range of variances about the mean populations of *Cryptopygus* was much greater for the moss carpet than for the turf. The degree of aggregation of this species at the two sites was compared by plotting monthly mean (\bar{x}) numbers core⁻¹ against variance (s^2) on a double log scale. The fitted regressions:

$\log s^2 = 11.61 + 0.42 \log \bar{x}$ ($n = 25, r^2 = 0.78$) for SIRS 1,
and $\log s^2 = 1.97 + 0.47 \log \bar{x}$ ($n = 19, r^2 = 0.95$) for SIRS 2,

indicated no significant difference in slope. Taylor's power law ($S^2 = a\bar{x}^b$) (Taylor, 1961), when applied to these data, yielded indices of aggregation of 2.82 and 3.12 for SIRS 1 and 2, respectively. It is concluded that the degree of aggregation of *Cryptopygus* is similar in both substrates. A reciprocal square-root transformation of the population data was indicated ($p = -0.41$ and -0.56 for SIRS 1 and 2, respectively), and this allowed independence of the variance from the mean.

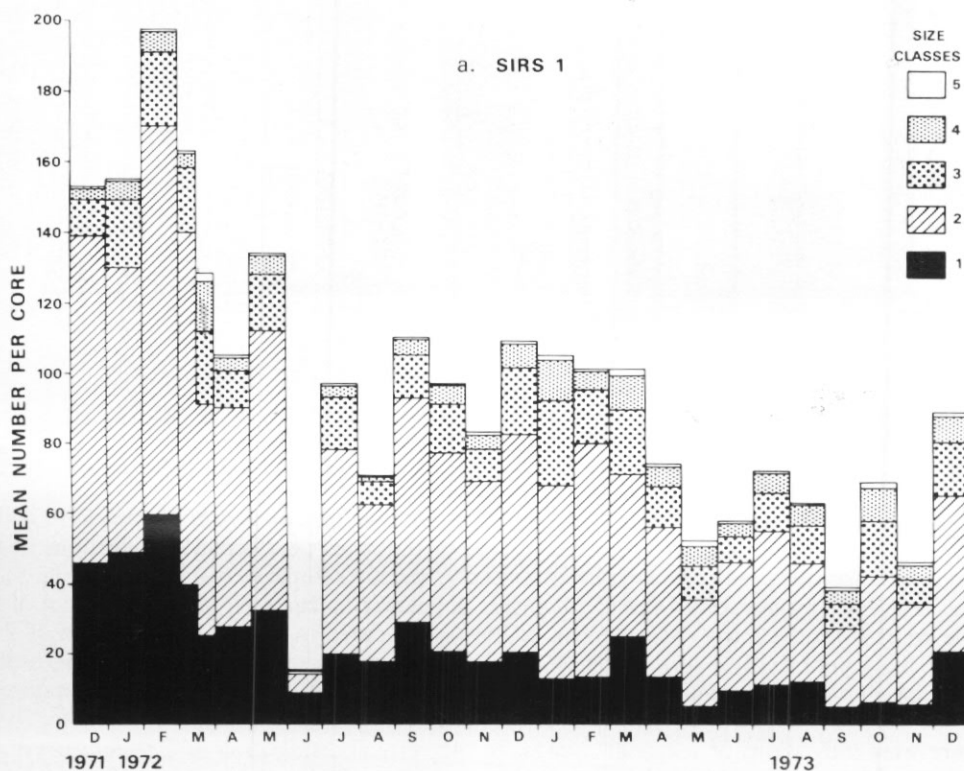


Fig. 4a.

Fig. 4. Population structure of *Cryptopygus antarcticus* on the basis of the mean numbers of each size class per core for a moss turf (SIRS 1) (Fig. 4a) and a moss carpet (SIRS 2) (Fig. 4b) at Signy Island during 1972–73.

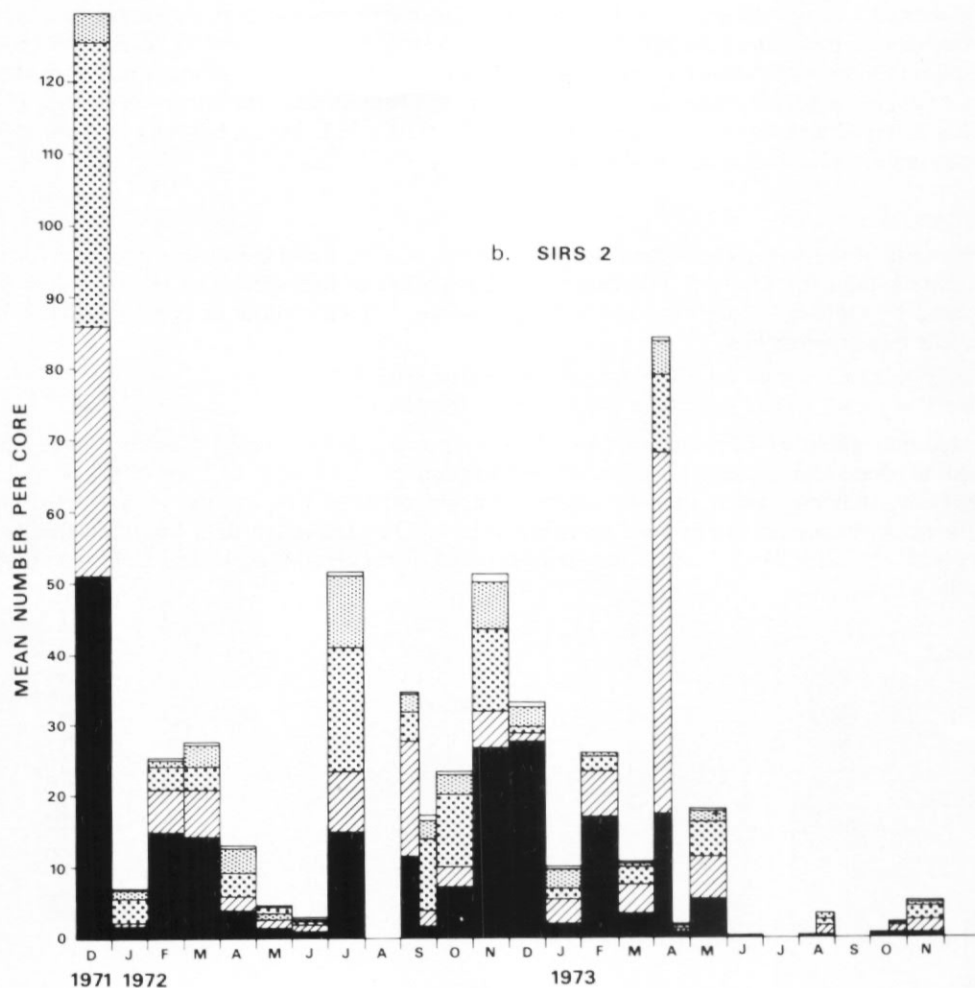


Fig. 4b.

Vertical distribution

From the monthly samples, it was possible to examine the distribution of *Cryptopygus* within the two layers, 0–3 and 3–6 cm from the surface of the moss peat profile. Proportions of the total numbers for this species in each layer for each monthly sample were calculated (Fig. 5). In general, a greater proportion of the *Cryptopygus* population occurred in the upper 3 cm of the sample cores from the moss carpet (mean of 86%), compared to the moss turf (mean of 71% over the study period). This was probably a reflection of the waterlogged nature of the peat at SIRS 2 for much of the thawed period of the year, compared to the free-draining nature of SIRS 1.

There were indications of seasonal changes in the vertical distribution of *Cryptopygus* in the moss turf (Fig. 5), with a general increase in the proportion of fauna in the upper (0–3 cm) layer during summer (maximum 94%), and a decrease in the proportion therein during winter

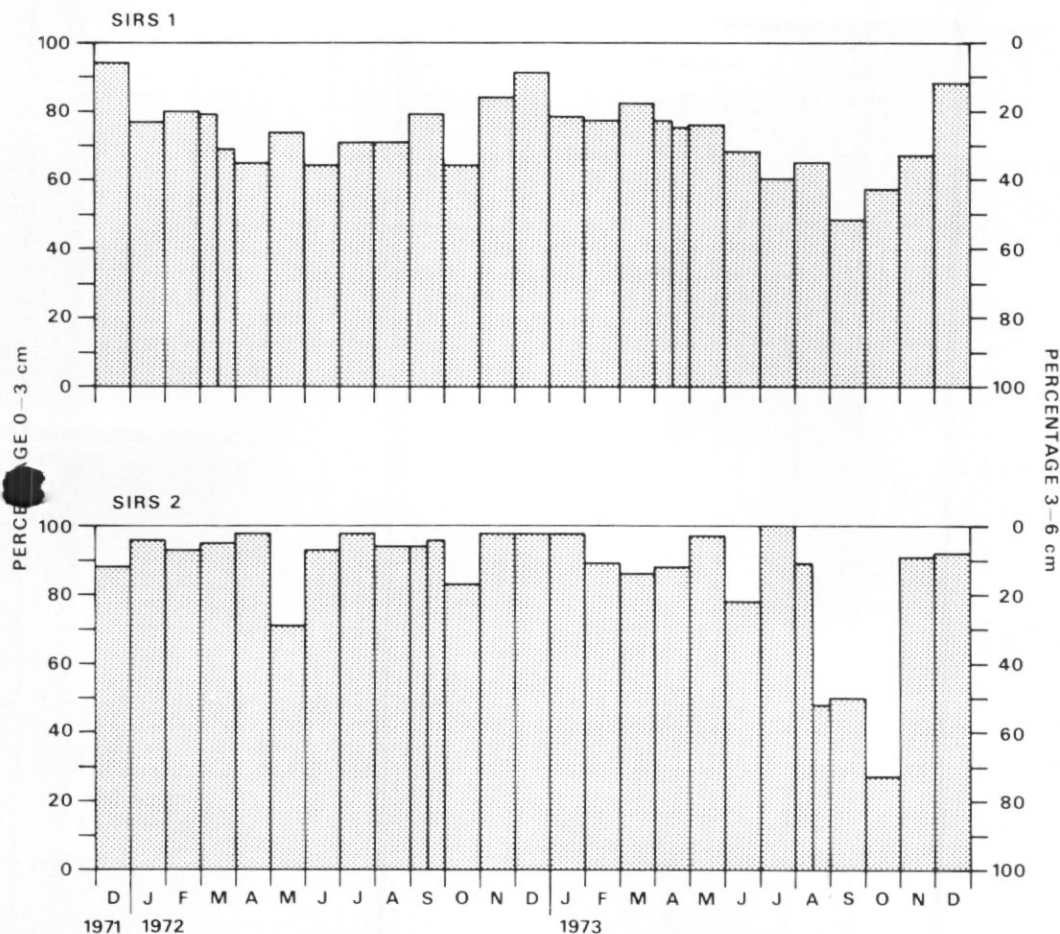


Fig. 5. Proportion of *Cryptopygus antarcticus* occurring in two vertical zones (0-3, 3-6 cm) of a moss-turf (SIRS 1) and a moss-carpet (SIRS 2) community at Signy Island during 1972-73.

(minimum 48%). There were changes in the percentages of the collembolan in the moss-carpet cores, but these were less well defined and not obviously related to season. During the late winter and early autumn of 1973 only 27-50% of the Collembola occurred in the upper 3 cm, compared to >70% for the rest of the study. This may have been caused by the accumulation of excess melt water above a frozen horizon in the peat profile at this time but, due to the low numbers involved, firm conclusions cannot be advanced. As indicated for the population-density estimates, extraction efficiency will also affect the vertical distribution of the fauna.

On five occasions, deeper cores to the underlying bedrock were collected from SIRS 1 and 2 in order to examine the distribution of Collembola in the peat profile. Three such samples to greater than 24 cm in depth were taken from the moss turf and two samples to 18 cm depth were cored from the moss carpet in 1973. The numbers of Collembola observed per 3-cm vertical section of these cores are shown in Fig. 6 together with their water contents.

Parisotoma was not found in these deeper samples at either site. In the moss turf both *Cryptopygus* and *Friesea* were found, although the latter occurred only in small numbers. *Cryptopygus* was found down to a depth of 21 cm (9 February 1973) and *Friesea* to one of 18

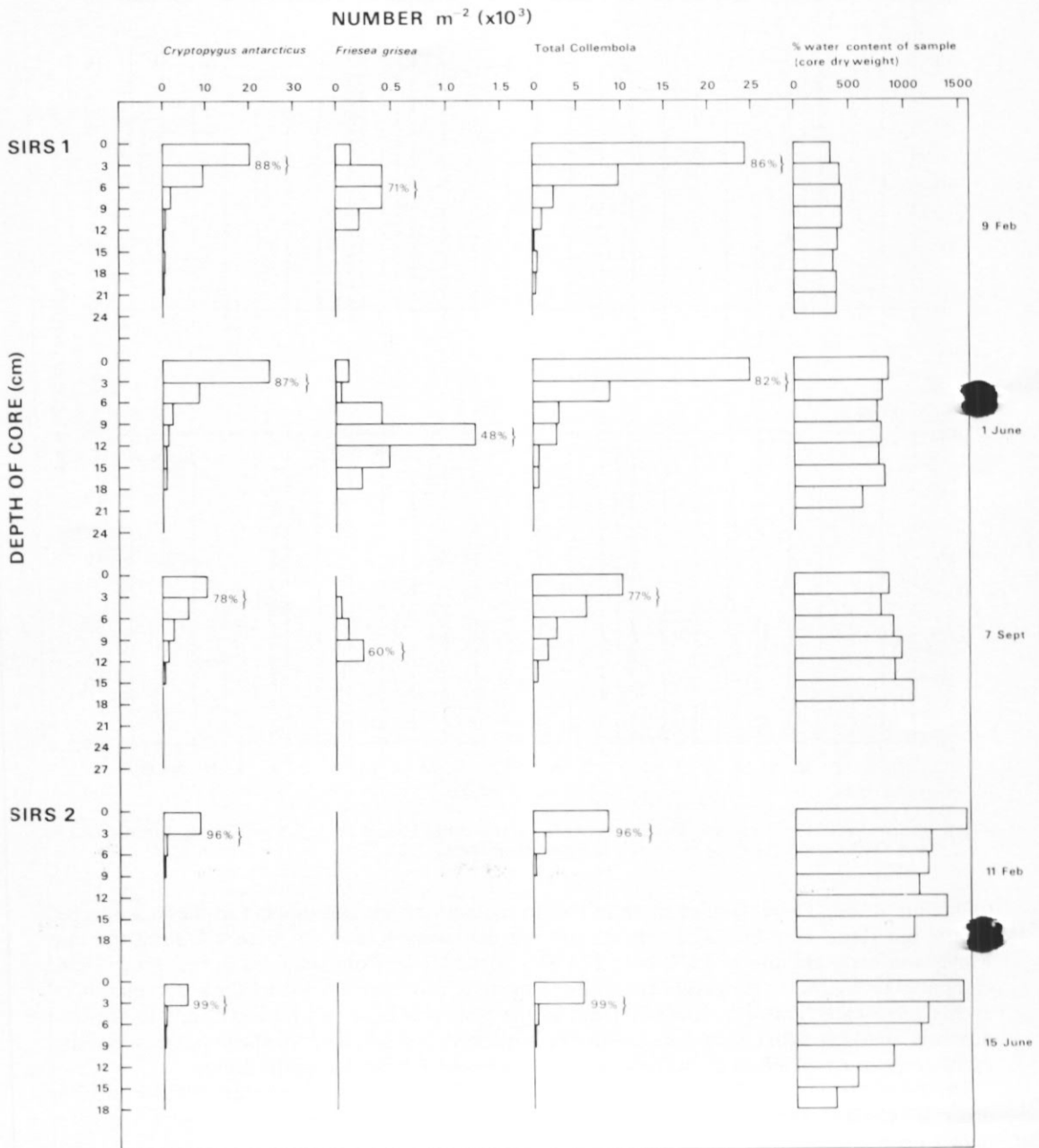


Fig. 6. Vertical distribution of two species of springtails and total Collembola in deep samples from a moss-turf (SIRS 1) and a moss-carpet (SIRS 2) community at Signy Island during 1973. The percentage water content on a dry-weight basis of each 3-cm section of the profile is also shown together with the proportion of Collembola in selected sections of the profile.

cm (1 June 1973). The majority of the *Cryptopygus* population occurred in the 0–6 cm zone (range from 78% to 88% of the total population), whilst *Friesea* was abundant in the 3–9 cm zone (71% on 9 February 1973) and at 9–12 cm on the other two sampling occasions (range from 48% to 60% of the total population). There was, therefore, a distinct contrast in the vertical distribution of *Cryptopygus* and *Friesea* in the moss turf. As *Cryptopygus* was numerically dominant at SIRS 1, the distribution pattern for total Collembola (Fig. 6) was almost identical to that for this species. The water content in the moss-peat profile varied only slightly within the samples but there was a general increase in moisture of the 1973 samples from SIRS 1.

Friesea was absent from the moss carpet and *Cryptopygus* was almost entirely restricted to the top 6 cm of the profile (range of 96% to 99% of the total population) (Fig. 6). The water contents of the SIRS 2 samples were higher than those of the moss-turf samples which were collected at similar seasons, and the data suggest a decline in moisture content from the moss surface to a depth of 18 cm at certain times of the year.

Micro-climate

Data of soil and air temperatures together with incoming solar radiation levels for the two sites 1972–73 and analyses therefrom have been presented by a variety of workers (e.g. Walton, 1977, 1982; Goddard, 1979; Jennings, 1979; Block, 1980a, b). Therefore, only information pertinent to the Collembola study will be summarized here. Generally, the moss-carpet temperatures are less extreme than those of the moss turf, probably due to the larger volume of water contained in the former and other factors such as aspect, snow depth, etc. Data from the five temperature sensors in the two profiles indicate seasonal maxima and minima around +25°C and –20°C at the moss surface (SIRS 1) over the 2 years, and slightly less for SIRS 2 (Block, 1980b). The thermal variations, especially at the ground surface, were much greater during summer (e.g. 0° to +30°C) than in winter (–13° to –16°C) for 5 d periods. In both sites, the deeper layers of the profile were buffered from the extremes of temperature characteristic of the upper layers (Goddard, 1979; Walton, 1982). For soil invertebrates, the duration of exposure to a particular temperature is especially important in relation to their activity and survival at sub-zero temperatures. Also, the thermal zone –5° to +5°C is critical to their locomotion, feeding, etc. under field conditions (Block, 1981). Calculations based on hourly data from the moss surface, show that the temperature was within this zone for 57% and 64% of 1972 and 1973, respectively, for SIRS 1 (Walton 1982). The corresponding proportions of time for SIRS 2 were 67% and 61%, respectively. The surface layers of the two sites were generally warmer in 1973 than in 1972, with a 7–9% increase in the time that the temperatures remained in the 0° to +5°C band.

The depth of snow in winter differed both between sites and years (Block, 1980a). There was approximately twice the depth of snow on both sites in 1973, and on average, the moss carpet had a larger accumulation of snow than the moss turf (range of maximal depths of 27–38 cm for SIRS 1, and 48–72 cm for SIRS 2). The increased potential insulation combined with a longer period of snow-lie may have been responsible in part for the observed temperature differences.

Incoming solar radiation was maximal in the period from late September to March, when cloud conditions allowed, with values approaching $0.66 \text{ J m}^{-2} \text{ s}^{-1}$ (Walton, 1977; Goddard, 1979). However, soil temperatures may be relatively unaffected during times of high radiation due to surface snow but, when the moss substrate is exposed after melt, it warms rapidly (Jennings, 1979).

DISCUSSION

The species diversity of Collembola in the two communities examined at Signy Island is low in comparison with some other polar sites and most temperate soil communities. Four species are found at Signy Island, of which three occurred in samples from the SIRS, with *Cryptopygus*

being dominant. Similar numbers of Collembola species were found by Pryor (1962), Wise and Shoup (1967) near Hallett Station (three species), and by Janetschek (1967a) in South Victoria Land (six species). However, in some localities only a single species of Collembola was recorded (Janetschek, 1967b; Peterson, 1971). In the Arctic, six species have been found on Bathurst Island (Danks and Byers, 1972), eight species from Ellef Ringnes Island (McAlpine, 1965), whilst 30 species occurred at Devon Island (Addison, 1977). A range of between 23 and 62 species of Collembola has been listed from tundra sites by Ryan (1981). In a temperate beech wood in Denmark, a total of 60 species has been recorded by Petersen (1980). Clearly, terrestrial habitats in polar regions are colonized by relatively few species of Collembola, which generally achieve high population numbers.

Collembola population numbers estimated for the SIRS exhibit large fluctuations, both between sites and the two study years (Figs 1 and 2). A similar decline in numbers of Acari was observed over the same time period for the SIRS (Goddard, 1979), which suggests a common influence on both groups. It is not known, however, whether these changes are part of a general trend or an unusual catastrophe. The extraction efficiency probably varies seasonally due to physical changes in the sample cores and the physiological state of the fauna, but it is unlikely to influence population levels in such a drastic regular manner.

Little data on the population densities of Antarctic Collembola are available. For *Gomphiocephalus hodgsoni*, Wise and Spain (1967) estimated maximum numbers of 304 individuals m^{-2} (Lake Penny) and 540 individuals m^{-2} (Flatiron), both in South Victoria Land. In a more detailed study, Peterson (1971) recorded a summer population range from c. 1 000 to 3 400 individuals m^{-2} of the same species at Cape Bird, Ross Island, during 1967–68. None of these populations in chalikosystem habitats (Janetschek, 1970) achieve levels of c. 10–50 000 individuals m^{-2} (Table II), as was found in the two bryosystem habitats in the maritime Antarctic. Comparable Collembola densities have been observed in Arctic sites, where the plant cover is more diverse and often more complete. A sedge–moss community in the Taimyr, USSR, supported 4 000 Collembola m^{-2} (Matveyeva, 1972), whilst habitats on Devon Island ranging from sedge–moss to a polar plateau desert had populations of 7 800 to 29 900 individuals m^{-2} (Addison, 1977). Lichen tundra in Spitsbergen contained 20 800–38 300 individuals m^{-2} (Bengston and others, 1974), and several tundra habitats at Point Barrow, Alaska, had populations of 61 100–171 900 Collembola m^{-2} (MacLean, 1980). The latter estimates are higher than those of 19 000–67 000 Collembola m^{-2} obtained for a temperate woodland (Petersen, 1980), and those of Hale (1966) for a range of British moorland sites (20 930–52 920 Collembola m^{-2}).

The only biomass information available for Antarctic Collembola are those of Tilbrook (1977) and the present study for *Cryptopygus* at Signy Island. These suggest an annual mean of c. 688 mg live weight (250 mg dry weight) m^{-2} for the moss turf, and c. 154 mg live weight (56 mg dry weight) m^{-2} for the moss carpet. By comparison, similar biomasses have been calculated for total Collembola of a temperate beech wood (76–160 mg dry weight m^{-2}) (Petersen, 1980).

Life cycles of Antarctic Collembola, including age structure and growth, have been studied (e.g. Janetschek, 1967b; Peterson, 1971) but few conclusions have emerged. The data for *Cryptopygus* show an almost constant size structure in the moss turf and evidence of growth and maturation at certain periods in the moss carpet. The differences in size-class structure of the two populations at Signy Island are difficult to explain. The approximate constant proportion of young individuals (c. one-fifth of each monthly sample) in the SIRS 1 mosses suggest that egg-hatch is possible in any season when conditions are suitable. The proportion of such small Collembola in the SIRS 2 mosses is much more variable, but nevertheless this size class predominates through the year, which supports the idea that eggs may hatch whenever environmental conditions allow. Using data for laboratory growth rates of this species, Burn (1981) proposed that at a body length of between 1 040 and 1 134 μm (approximating to the lower portion of size class 3), individuals either increase or decrease in size at subsequent moults,

which may be influenced by nutritional and/or excretory factors. If such a situation prevails in the field, the failure of the population at SIRS 1 to show significant seasonal shifts in size distribution may be explicable. It could be hypothesized that *Cryptopygus* is not limited in this way in the moss carpet (Fig. 4). Addison (1977) analysed weight data for *Hypogastrura tullbergi* Schäffer and obtained evidence of growth from field samples at Devon Island, but she concluded that individuals could remain in the population for at least 3 years after reaching sexual maturity with a total life span of *c.* 5 years. For *Cryptopygus* under maritime Antarctic conditions, a life cycle extending over 3–7 years has been postulated (Burn, 1981).

The Collembola only penetrated slightly to depths >6 cm in the SIRS profiles, and did so less than the Acari over the same period (Goddard, 1979). Whilst between 78% and 88% of the Collembola were found in the upper 6 cm of the SIRS 1 profile, some of the mites extended deeper but 94% of all the Acari were located in the 0–12 cm zone. Differences in the arthropod penetration of the moss peat in the carpet and turf may be accounted for by the seasonally anaerobic conditions which may prevail below 3–9 cm in the carpet (Wynn-Williams, 1980; Davis, 1981). Many species of Collembola are unable to survive in periodically flooded habitats (Kuhnelt, 1976), a phenomenon which occurs annually at the moss-carpet site on Signy Island.

Little can be concluded about the horizontal distribution of the Collembola in moss substrates, and a similar degree of aggregation was found in *Cryptopygus* for both sites. Evidence is accumulating on the association between species density and vegetation cover and, from the core data, the distribution of *Cryptopygus* in the moss turf and carpet is very clumped. Significantly higher numbers of *Cryptopygus* occur in core samples of moss turf containing *Polytrichum* alone, and *Chorisodontium* and surface lichens together, than in dead mosses and bare peat (personal communications from M. B. Usher and R. G. Booth). Analyses of gut contents of *Cryptopygus* suggest that this species feeds extensively in the field on unicellular green algae (personal communication from A. J. Burn), which grow epiphytically on the live shoots of these two mosses. Until more is known about the factors which influence arthropod micro-distribution in organic substrates, and the main features of their life cycle, it is difficult to draw any further conclusions. A current research project is examining the micro-arthropod distribution in moss turf in more detail. The information on the Signy Island Collembola contrasts with that of the Collembola of a beach-ridge site at Devon Island studied by Addison (1977), which were not associated with particular plant species, and which contributed to the unspecialized nature of this group in the Arctic.

It is evident that micro-climatic conditions which prevail within the habitats of both these bryophyte-dominated communities are important influences on the population density, size distribution and life cycles of the Collembola. Of the limited collembolan fauna of the maritime Antarctic (eight species; Wallwork, 1973), *C. antarcticus* is the only species to have colonized such habitats to any extent. Present research is aimed at a clarification of the biology, and especially the feeding relations, of this species, and the role of environmental factors such as temperature and moisture in its seasonally changing cold hardiness. These adaptations must be examined in detail before conclusions can be drawn concerning the processes of arthropod colonization and survival in Antarctic terrestrial ecosystems.

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REFERENCES

- ADDISON, J. A. 1977. Population dynamics and biology of Collembola on Truelove Lowland. (*In* BLISS, L. C., ed. *Truelove Lowland, Devon Island, Canada: a High Arctic ecosystem*. Calgary, The University of Alberta Press, 363–82.)
- BENGSTON, S. A., FJELLBERG, A. and T. SOLHØY. 1974. Abundance of tundra arthropods in Spitzbergen. *Entomologica Scandinavica*, **5**, 137–42.
- BLOCK, W. 1979. Oxygen consumption of the Antarctic springtail *Parisotoma octooculata* (Willem) (Isotomidae). *Revue d'Écologie et Biologie du Sol*, **16**, 227–33.
- . 1980a. Aspects of the ecology of Antarctic soil fauna. (*In* DINDAL, D. L., ed. *Soil biology as related to land use practices*. Washington, D.C., Environmental Protection Agency, 741–57.)
- . 1980b. Survival strategies in polar terrestrial arthropods. *Biological Journal of the Linnean Society*, **14**, 29–38.
- . 1981. Terrestrial arthropods and low temperature. *Cryobiology*, **18**, 436–44.
- and P. J. TILBROOK. 1975. Respiration studies on the Antarctic collembolan *Cryptopygus antarcticus*. *Oikos*, **26**, 15–25.
- and ———. 1978. Oxygen uptake by *Cryptopygus antarcticus* (Collembola) at South Georgia. *Oikos*, **30**, 61–67.
- BURN, A. J. 1981. Feeding and growth in the Antarctic collembolan *Cryptopygus antarcticus*. *Oikos*, **36**, 59–64.
- CALDWELL, J. R. 1981a. Biomass and respiration of nematode populations in two moss communities at Signy Island, maritime Antarctic. *Oikos*, **37**, 160–66.
- . 1981b. The Signy Island terrestrial reference sites. XIII. Population dynamics of the nematode fauna. 33–46.
- DANKS, H. V. and J. R. BYERS. 1972. Insects and arachnids of Bathurst Island, Canadian Arctic Archipelago. *Canadian Entomologist*, **104**, 81–88.
- DAVIS, R. C. 1981. Structure and function of two Antarctic terrestrial moss communities. *Ecological Monographs*, **51**, 125–43.
- GODDARD, D. G. 1979. The Signy Island terrestrial reference sites: XI. Population studies on the Acari. *British Antarctic Survey Bulletin*, No. 48, 71–92.
- HALE, W. G. 1966. A population study of moorland Collembola. *Pedobiologia*, **6**, 65–99.
- JANETSCHKEK, H. 1967a. Arthropod ecology of South Victoria Land. (*In* GRESSITT, J. L., ed. *Entomology of Antarctica*. Washington, D.C., American Geophysical Union, 205–93.) [Antarctic Research Series, Vol. 10.]
- . 1967b. Growth and maturity of the springtail, *Gomphiocephalus hodgsoni* Carpenter, from South Victoria Land and Ross Island. (*In* GRESSITT, J. L., ed. *Entomology of Antarctica*. Washington, D.C., American Geophysical Union, 295–305.) [Antarctic Research Series, Vol. 10.]
- . 1970. Environments and ecology of terrestrial arthropods in the High Antarctic. (*In* HOLDGATE, M. W., ed. *Antarctic ecology*. London and New York, Academic Press, 871–85.)
- JENNINGS, P. G. 1979. The Signy Island terrestrial reference sites: X. Population dynamics of Tardigrada and Rotifera. *British Antarctic Survey Bulletin*, No. 47, 89–105.
- KUHNELT, W. 1976. *Soil biology*. London, Faber and Faber.
- MCALPINE, J. F. 1965. Insects and related terrestrial invertebrates of Ellef Ringnes Island. *Arctic*, **18**, 73–103.
- MACFADYEN, A. 1961. Improved funnel-type extractors for soil arthropods. *Journal of Animal Ecology*, **30**, 171–84.
- MACLEAN, S. F. 1980. The detritus-based trophic system. (*In* BROWN, J., MILLER, P. C., TIESZEN, L. L., and F. L. BUNNEL, ed. *An Arctic ecosystem: the coastal tundra at Barrow, Alaska*. Pennsylvania, Dowden, Hutchinson and Ross, 411–57.)
- MARSH, J. B. 1970. Radioisotopic determination of the ingestion rates of three species of Antarctic arthropods: *Cryptopygus antarcticus* Willem (Collembola: Isotomidae), *Belgica antarctica* Jacobs (Diptera: Chironomidae) and *Alaskozetes antarcticus* (Michael) (Cryptostigmata: Podacaridae). M.Sc. thesis, University of California at Davis, 72 pp. [Unpublished.]
- MASLEN, N. R. 1981. The Signy Island terrestrial reference sites: XII. Population ecology of nematodes with additions to the fauna. *British Antarctic Survey Bulletin*, No. 53, 57–75.
- MATVEYEVA, N. W. 1972. The Tareya word model. (*In* WIELGOLASKI, F. E. and T. ROSSWALL, ed. *Proceedings of the IV International Meeting on the Biological Productivity of Tundra*. Stockholm, Tundra Biome Steering Committee, 156–62.)
- PETERSEN, H. 1980. Population dynamics and metabolic characterization of Collembola species in a beech forest ecosystem. (*In* DINDAL, D. L., ed. *Soil biology as related to land use practices*. Washington, D.C., Environmental Protection Agency, 806–33.)
- PETERSON, A. J. 1971. Population studies on the Antarctic collembolan *Gomphiocephalus hodgsoni* Carpenter. *Pacific Insects Monograph*, **25**, 75–98.
- PRYOR, M. E. 1962. Some environmental features of Hallett Station, Antarctica, with special reference to soil arthropods. *Pacific Insects*, **4**, 681–728.
- RYAN, J. 1981. Invertebrate faunas at I.B.P. tundra sites. (*In* BLISS, L. C., HEAL, O. W. and J. J. MOORE, ed. *Tundra ecosystems: a comparative analysis*. Cambridge, Cambridge University Press, 517–39.)
- SMITH, H. G. 1973. The Signy Island terrestrial reference sites: III. Population ecology of *Corythion dubium* (Rhizopoda: Testacida) in site 1. *British Antarctic Survey Bulletin*, Nos. 33 and 34, 123–35.
- STRONG, J. 1967. Ecology of terrestrial arthropods at Palmer Station, Antarctic Peninsula. (*In* GRESSITT, J. L., ed. *Entomology of Antarctica*. Washington, D.C., American Geophysical Union, 357–71.) [Antarctic Research Series, Vol. 10.]
- TAYLOR, L. R. 1961. Aggregation, variance and the mean. *Nature, London*, **189**, 732–35.

- TILBROOK, P. J. 1967a. The terrestrial invertebrate fauna of the maritime Antarctic. (In SMITH, J. E., organizer. A discussion on the terrestrial Antarctic ecosystem. *Philosophical Transactions of the Royal Society*, Ser. B, **252**, 261-78.)
- . 1967b. Arthropod ecology in the maritime Antarctic. (In GRESSITT, J. L., ed. *Entomology of Antarctica*. Washington, D.C., American Geophysical Union, 331-56.) [Antarctic Research Series, Vol. 10.]
- . 1970. The biology of *Cryptopygus antarcticus*. (In HOLDGATE, M. W., ed. *Antarctic ecology*. London and New York, Academic Press, 908-18.)
- . 1973a. The Signy Island terrestrial reference sites: I. An Introduction. *British Antarctic Survey Bulletin*, Nos. 33 and 34, 65-76.
- . 1973b. *Terrestrial arthropod ecology at Signy Island, South Orkney Islands*. Ph.D. thesis, University of London, 254 pp. [Unpublished.]
- . 1977. Energy flow through a population of the collembolan *Cryptopygus antarcticus*. (In LLANO, G. A., ed. *Adaptations within Antarctic ecosystems*. Houston, Texas, Gulf Publishing Company, 935-46.)
- . and W. BLOCK. 1972. Oxygen uptake in an Antarctic collembole *Cryptopygus antarcticus*. *Oikos*, **23**, 313-17.
- WALLWORK, J. A. 1973. Zoogeography of some terrestrial micro-Arthropoda in Antarctica. *Biological Reviews*, **48**, 233-59.
- WALTON, D. W. H. 1977. Radiation and soil temperatures 1972-74: Signy Island terrestrial reference site. *British Antarctic Survey Data*, No. 1, 51 pp.
- . 1982. The Signy Island terrestrial reference sites: XV. Micro-climate monitoring, 1972-74. *British Antarctic Survey Bulletin*, No. 55, 111-26.
- WISE, K. A. J. 1967. Collembola (springtails). (In GRESSITT, J. L., ed. *Entomology of Antarctica*. Washington, D.C., American Geophysical Union, 123-48.) [Antarctic Research Series, Vol. 10.]
- . 1971. The Collembola of Antarctica. *Pacific Insects Monograph*, **25**, 57-74.
- . and J. SHOUP. 1967. Distribution of Collembola at Cape Hallett. (In GRESSITT, J. L., ed. *Entomology of Antarctica*. Washington, D.C., American Geophysical Union, 325-30.) [Antarctic Research Series, Vol. 10.]
- . and A. V. SPAIN. 1967. Entomological investigations in Antarctica, 1963-64 season. *Pacific Insects*, **9**, 271-93.
- WYNN-WILLIAMS, D. D. 1980. Seasonal fluctuations in microbial activity in Antarctic moss peat. *Biological Journal of the Linnean Society*, **14**, 11-28.