

## ORIGINAL PAPER

S.J. Coulson · I.D. Hodkinson · N.R. Webb · W. Block  
J.S. Bale · A.T. Strathdee · M.R. Worland · C. Wooley

## Effects of experimental temperature elevation on high-arctic soil microarthropod populations

Received: 13 May 1994/Accepted: 18 May 1995

**Abstract** An experiment was conducted to measure the effects of summer warming on the total population densities of soil-dwelling microarthropods in the high Arctic and to compare these results with those from natural between-year and between-site variations. Small polythene tents were used to elevate summer temperatures over 3 years on polar semi-desert and tundra heath in West Spitsbergen, Svalbard, Norway. Soil cores were taken at regular intervals from tented and untented (control) plots and heat extracted for mites (Acarina: Oribatida) and springtails (Collembola). Species present were similar at both sites, but at the start of the experiment total springtail populations were greater at the polar semi-desert whilst oribatid mite densities were equal at both sites. No significant effect of temperature elevation on oribatid mite populations emerged, even after 3 years. By contrast, springtail numbers were significantly lower on tented versus control plots at the polar semi-desert at the end of year 3, but not so at the tundra heath. Collembola numbers declined at both sites during the warm dry midsummers of 1992/1993 and this was most marked at the better drained polar semi-desert site. Over the equivalent period total oribatid mite populations, while

relatively more stable, increased significantly at the polar semi-desert as a result of an increase in the number of juveniles. Results are interpreted in the context of the ecophysiological adaptations of oribatid mites and springtails to soil temperature and moisture. The resulting survival characteristics are considered in relation to the temperature and moisture characteristics of the two sites. The experiment demonstrated that year to year variation in climate, interacting with physical differences between sites, produced an equal or greater effect on microarthropod numbers at any one site than the 8–10% increase in “heat availability” (day degrees above zero) resulting from the summer tent treatment. The limitations of the use of tents to elevate soil temperatures are discussed. Comparisons are made with microarthropod population data from other polar and alpine sites.

### Introduction

The effects of global warming are predicted to be most marked at high northern latitudes where the most recent Global Circulation Models suggest that by the middle of the next century, mean summer temperatures will have risen by 1.5–4.5°C (Mitchell et al. 1990; Kareiva et al. 1993). This has profound implications for the organisms living at such latitudes (Callaghan et al. 1992; Chapin et al 1992; Danks 1992). We have already demonstrated that, on Spitsbergen, the above-ground aphid herbivore *Acyrtosiphon svalbardicum* Heikkinheimo, feeding on *Dryas octopetala* L., responds rapidly and positively to elevated summer temperatures within one season by increasing its rates of development and reproduction (Strathdee et al. 1993a, b). This paper describes the results of a parallel 3-year experiment, using small polythene tents, to examine the response of the numerically dominant oribatid mites and Collembola in the soil to enhanced summer temperatures. Most of these soil microarthropods, unlike the aphid

S.J. Coulson · I.D. Hodkinson (✉) · C. Wooley  
School of Biological and Earth Sciences,  
Liverpool John Moores University,  
Byrom St. Liverpool L3 3AF, UK FAX-0151298-1014

N.R. Webb  
Furzebrook Research Station, NERC,  
Institute of Terrestrial Ecology, Wareham,  
Dorset BH20 5AS, UK

W. Block · M.R. Worland  
British Antarctic Survey,  
Natural Environment Research Council,  
High Cross, Madingley Road, Cambridge CB3 0ET, UK

J.S. Bale · A.T. Strathdee  
School of Biological Sciences, University of Birmingham,  
Edgbaston, Birmingham, B15 2TT, UK

that completes more than one generation per year, probably have life-cycles extending over 2 or more years (e.g. Hammer 1944; Addison 1981). They may, therefore, be expected to have a slower initial response to warming. Furthermore, soil temperatures during the experiment were generally lower than those in the surface vegetation mat and were more strongly buffered against change (Coulson et al. 1993).

Detailed long-term studies on Arctic microarthropod populations are few (Addison 1977; Danks 1981), although comparative data sets are available for some Antarctic species (Goddard 1979; Block 1982). Previous studies on the mites and Collembola of Spitsbergen have listed the faunas associated with various plant communities (Thor 1930; Stach 1962; Karppinen 1967; Valpas 1967; Sendstad 1976) or provided single estimates of total population densities (Bengtson et al. 1974; Hinz 1976; Seniczak and Plichta 1978; Wüthrich 1989). Manipulative experiments are confined to investigations on the effects of the removal of lichen cover on Collembola populations (Sendstad 1981) or the specialised feeding biology of selected species (Hodkinson et al. 1994a). The aim of the present experiment was to measure the effects of summer warming on total populations of soil-dwelling mites and springtails in the Arctic and to compare observed changes with those resulting from natural between-site and between-season variation.

## Materials and methods

### Study site and methods

Small, polythene, geodesic dome tents with a 1.5 m × 1.5 m basal area were used to elevate soil temperatures on plots at two sites, a polar semi-desert (Outer Fjord) and a tundra heath (Inner Fjord) adjacent to the settlement of Ny Ålesund, West Spitsbergen, Svalbard. Full descriptions of tents, experimental protocols and the effects on summer soil temperature are given by Coulson et al. (1993). Briefly, the polar semi-desert site supported a sparse vegetation cover (76%), predominantly *Dryas octopetala* and lichens growing on a gravelly mineral soil. By contrast, the tundra heath site had complete vegetation cover (136%), with several vascular species, particularly *Cassiope tetragona* and *Salix polaris*, growing amongst a surface mat of mixed bryophytes in which *Racomitrium lanuginosum* was dominant. Tents were first set up on 2 July 1991, immediately following snow melt, and maintained on the same plots throughout the 1991, 1992 and 1993 growing seasons. Summer heat budgets (day degrees above 0°C) in the soil at 3 cm depth were increased by 10% and 8% at the Inner and Outer Fjord Sites respectively, while corresponding figures for the vegetation mat were 39% and 30%.

A 9-cm-diameter soil core (maximum depth 8 cm, dependent on soil thickness) was taken from each of twelve randomly located tented and untented (control) plots at each site on ten occasions during 1991–1993. Sampling, for logistic reasons, was staggered by up to about 1 week between the two sites during 1991 but for between-site comparisons the samples were regarded as belonging to the same sampling ‘period’. For the 1992 and 1993 seasons both sites were sampled on the same day. During 1991, soil arthropods were slowly extracted in sets of Tullgren apparatus from the cores over 1 week. These were replaced by equivalent-size Macfadyen high

**Table 1** The dominant species of Oribatida and Collembola recorded at the Inner and Outer Fjord Sites

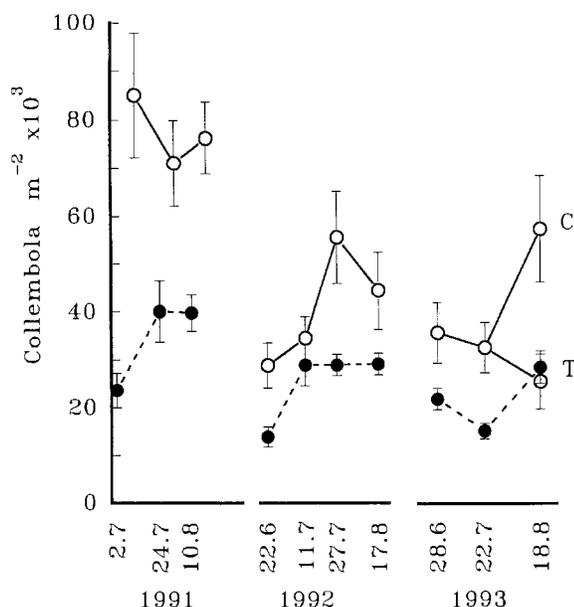
ACARI:ORIBATIDA	
<i>Mycobates sarekensis</i> (Trägårdh) = <i>Calyptozetes sarekensis</i>	
<i>Camisia anomia</i> Colloff	
<i>Ceratoppia hoeli</i> Thor	
<i>Diapterobates notatus</i> (Thorell)	
<i>Hermannia reticulata</i> Thorell	
<i>Oppiella nova</i> (Oudemans)	
COLLEMBOLA	
<i>Anurida polaris</i> (Hammer)	
<i>Onychiurus arcticus</i> (Tullberg)	
<i>O. groenlandicus</i> (Tullberg)	
<i>Folsomia quadrioculata</i> (Tullberg)	
<i>F. bisetosa</i> Gisin	
<i>F. stella</i> Grow & Christiansen	
<i>Hypogastrura tullbergi</i> (Schäffer)	
<i>Isotoma anglicana</i> Lubbock	
<i>I. nansenii</i> Fjellberg	
<i>Lepidocyrtus lignorum</i> (Fabricius)	
<i>Sminthurinus concolor</i> (Meinert)	

gradient extractors in 1992. This did not materially affect extraction efficiencies as the Tullgren extractors were operated in a cooled environment (5°C), providing a similar temperature gradient through the cores to that in the Macfadyen extractors. Total counts of Oribatida and Collembola were made to allow comparison, using one-way ANOVA, between tented and control treatments and between the polar semi-desert and tundra heath sites. Except where stated, Collembola and Oribatida ‘populations’ are totals for all the dominant species listed in Table 1 and include both adult and immature forms. The soft-bodied immature stages of *Opiella* rapidly desiccated during extraction and were poorly represented in the samples.

## Results

The dominant Oribatida (6 species) and Collembola (11 species) were similar at both sites (Table 1). There was no significant difference, on any sampling occasion, in the mean number of Collembola in tented versus untented plots at either the polar semi-desert ( $F < 3.7$ ,  $P > 0.07$ ) or the tundra heath ( $F < 3.2$ ,  $P > 0.09$ ) site during 1991 or 1992 (Fig. 1). A similar pattern was recorded at the tundra heath in 1993 ( $F < 1.5$ ,  $P > 0.11$ ) but at the polar semi-desert, while the first two sample dates showed no significant difference ( $F < 3.7$ ,  $P > 0.06$ ), by sampling date 3 the numbers of springtails inside the tents were significantly lower than in the controls ( $F = 6.4$ ,  $P = 0.02$ ). As the variances of treatment and control plot means were similar for all date-site pairings, except for the final sample in 1993 at the polar semi-desert, the two underlying sets of data, except the last, were combined before further analysis, thereby doubling the replication of samples.

For any given sampling date, except the final one, Collembola numbers were consistently and significantly higher at the polar semi-desert ( $30\text{--}83 \times 10^3 \text{ m}^{-2}$ ) than at the tundra heath ( $14\text{--}40 \times 10^3 \text{ m}^{-2}$ ) ( $F > 4.4$ ,  $P < 0.05$ ). These differences were greater in 1991 than in 1992 or 1993.

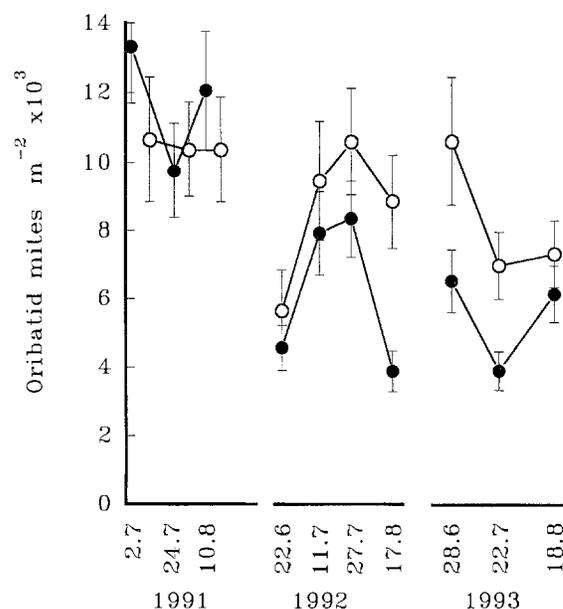


**Fig. 1** Changes in mean Collembola population densities at the polar semi-desert (○) and tundra heath sites (●) during 1991/1993. Error bars represent the standard error of the mean. For the 18 August 1993 sample, means for tented (T) and untented control (C) plots at the polar semi-desert are significantly different and are therefore plotted separately

At the tundra heath site there was a significant difference between the mean numbers of Collembola present on successive sampling dates within 1991, 1992 and 1993 ( $F > 3.9$ ,  $P < 0.025$ ), with a rise from an early summer low to a mid-season peak followed by a late season decline in the first 2 years but not in 1993 (Fig. 1). A similar seasonal pattern was evident at the polar semi-desert during 1992 ( $F = 2.6$ ,  $P = 0.05$ ), but in 1991 and for the initial two samples of 1993 differences between dates were not significant ( $F < 0.8$ ,  $P > 0.48$ ).

Collembola numbers declined significantly ( $F = 28.2$ ,  $P < 0.001$ ;  $F = 35.7$ ,  $P < 0.001$ ) between the last 1991 sample and the first sample of 1992 at the polar semi-desert and tundra heath, respectively. This heavy winter/early spring mortality was similar at both sites, 62% and 65% respectively. By contrast, apparent mortality (17–20%) over the winter 1992–1993, while of the same order at both sites, was not significant ( $F < 1.4$ ,  $P > 0.39$ ).

Total oribatid populations (Fig. 2) showed parallel trends between sites but there were no significant differences over the 3 years between treatment and control plots at the polar semi-desert ( $F < 1.7$ ,  $P > 0.20$ ) or the tundra heath ( $F < 1.3$ ,  $P > 0.27$ ), and data were again combined. For 1991, no significant differences in total oribatid densities were found between the sites in any sample period ( $F < 1.8$ ,  $P > 0.19$ ), but in 1992 a trend towards comparatively higher numbers at the polar semi-desert became apparent. On the first three sampling dates the difference was non-significant ( $F < 1.7$ ,



**Fig. 2** Changes in mean total oribatid mite (adult plus immature stages) population densities at the polar semi-desert (○) and tundra heath (●) sites during 1991/1993. Error bars represent the standard error of the mean

$P > 0.19$ ) but by the last sample of the season significance was established ( $F = 11.0$ ,  $P = 0.002$ ). This difference was perpetuated in the first two sample dates of 1993 ( $F > 4.0$ ,  $P < 0.05$ ) but became non-significant by the final date in August ( $F = 0.91$ ,  $P = 0.34$ ). Typical oribatid populations lay within the range  $5\text{--}11 \times 10^3 \text{ m}^{-2}$  and  $4\text{--}14 \times 10^3 \text{ m}^{-2}$  at the polar semi-desert and the tundra heath, respectively.

At the polar semi-desert, total oribatid densities did not vary significantly between dates within 1991 ( $F = 0.01$ ,  $P = 0.99$ ), 1992 ( $F = 2.1$ ,  $P = 0.11$ ) or 1993 ( $F = 2.27$ ,  $P = 0.11$ ). A similar stable population was observed at the tundra heath in 1991 ( $F = 1.3$ ,  $P = 0.27$ ), but in 1992 and 1993 there was a significant difference between dates ( $F = 5.8$ ,  $P < 0.001$ ;  $F = 3.3$ ,  $P = 0.04$ , respectively), with a notable significant decline between the last two dates in 1992 ( $F = 12.3$ ,  $P = 0.001$ ), which contributed to the between-site difference already mentioned.

To investigate seasonal patterns of recruitment, the numbers of immature oribatid mites were separated from the total and analysed independently (Fig. 3). Numbers of immatures did not differ significantly between treatments and controls ( $F < 1.9$ ,  $P > 0.18$ ) and data were again combined. Within-year differences in population density were non-significant for the tundra heath in 1991 ( $F = 1.8$ ,  $P = 0.18$ ) and 1993 ( $F = 0.6$ ,  $P = 0.51$ ) and the polar semi-desert in 1992 ( $F = 1.1$ ,  $P = 0.03$ ) and 1993 ( $F = 0.33$ ,  $P = 0.72$ ), although at both sites the trend was for an increase as the summer progressed. This seasonal rise was significant at the polar semi-desert in 1991 ( $F = 5.5$ ,  $P = 0.006$ ) and was apparent over the first three sampling occasions at the

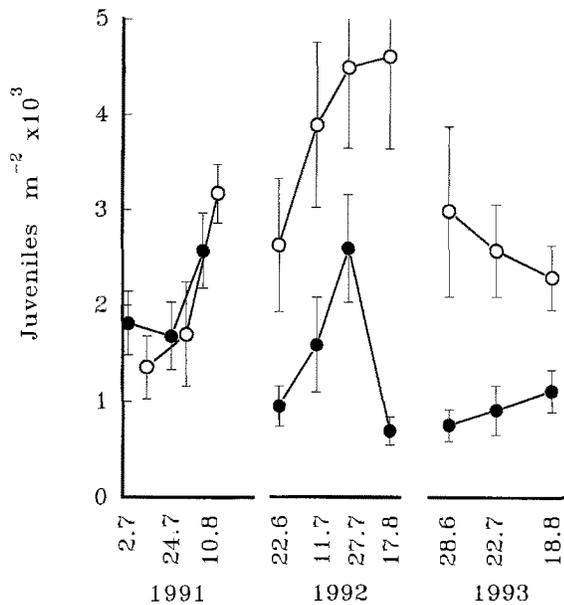


Fig. 3 Changes in mean immature oribatid mite population densities at the polar semi-desert (○) and tundra heath (●) sites during 1991/1993. Error bars represent the standard error of the mean

tundra heath in 1992 before it was followed by a steep and significant decrease. This contributed markedly to the decline in total oribatid population already noted and produced a significant difference between dates ( $F = 4.7$ ,  $P = 0.004$ ). Data for the polar semi-desert in 1992 suggest a similar steep rise in numbers but variances are high and differences were not significant.

Mortality over the winter 1991/1992 for the total oribatid population was significant at both sites, ranging from 46% ( $F = 6.7$ ,  $P = 0.012$ ) at the polar semi-desert to 62% ( $F = 16.8$ ,  $P < 0.001$ ) at the tundra heath. Equivalent figures for the immature stages alone were 17% ( $F = 0.38$ ,  $P = 0.54$ , not significant) to 63% ( $F = 13.2$ ,  $P = 0.001$ , significant). The lower winter mite mortality at the polar semi-desert thus appeared to result from a lower mortality among juveniles. By contrast, overwintering mortality of juveniles in 1992/1993 was not significant at either site ( $F < 1.5$ ,  $P > 0.22$ ). However, adult numbers at both sites showed a significant increase ( $F > 2.1$ ,  $P < 0.02$ ). By comparison with the previous winter, this was reflected in a significant increase in total oribatid population at the tundra heath ( $F = 5.8$ ,  $P = 0.02$ ) but a non-significant change at the polar semi-desert ( $F = 0.5$ ,  $P = 0.45$ ).

## Discussion

The temperature manipulation experiment produced some counter-intuitive results. The tent treatment, which increased the heat budget available to the soil animals by around 10%, had no measurable effect on the total soil oribatid mite populations at either the

polar semi-desert or tundra heath sites, even after 3 years. By contrast, springtail numbers declined significantly in warmed plots on the polar semi-desert, but only after three summers. Equivalent effects were not demonstrated on the tundra heath. Many high-Arctic oribatids and springtails probably have extended life-cycles of 2 or more years, with correspondingly slow development rates (e.g. Addison 1981). It appears that these organisms, living in the thermally buffered soil environment may be inherently slower to respond to temperature enhancement than their herbivore counterparts above ground, which experience higher temperatures and accelerated host-plant growth (Wookey et al. 1993; Strathdee et al. 1993b). This is despite the often high respiratory  $Q_{10}$  values they exhibit (Petersen and Luxton 1982; Block et al. 1994). Such an explanation is, however, incomplete as significant within- and between-season trends in population density were demonstrated, independent of the tent experiment, and between-site differences emerged within 3 years. The data suggest that inter-annual changes in climate produced measurable effects on both oribatid and springtail populations but the effects were mediated by site characteristics and the differing responses of the animal groups.

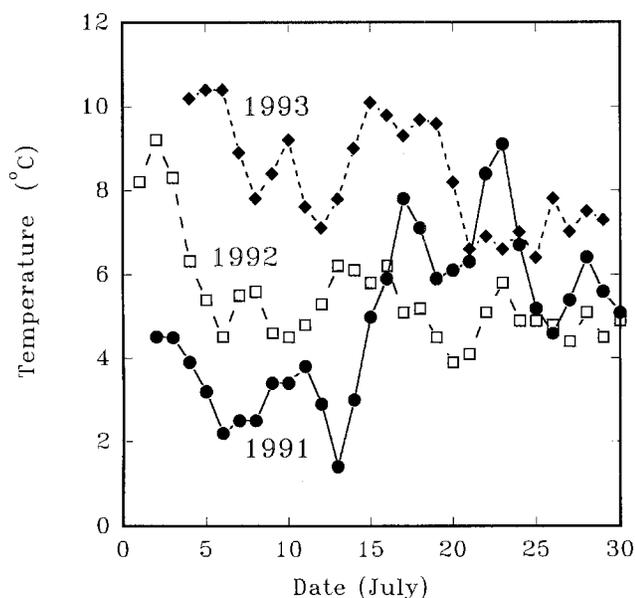
The observed changes were subtle and their interpretation requires an understanding of: (a) the adaptive physiology of the dominant oribatid and springtail species, particularly their survival response to temperature and humidity, (b) the macroclimatic differences between the 1991/1993 summer seasons, and (c) the differences in the soil environment at the two sites.

Detailed ecophysiological studies on the microarthropods have shown that, in general, the oribatid mites were significantly less susceptible to high temperatures and desiccation than were the springtails (Hodkinson et al. 1994b; Block et al. 1994; Hodkinson et al. unpublished). Bengtson et al. (1974) also pointed out that Arctic Collembola were highly susceptible to desiccation and that their population densities in sites near Ny Ålesund appeared positively correlated with soil moisture status. Hammer (1944), while recognising this phenomenon, urged caution and drew attention to dry sites in Greenland with high Collembola populations.

Table 2 compares monthly mean temperature and precipitation data for June/August during 1991/1993 with mean values for the previous 30 years. Snow melt-off at most sites is from mid- to late June with the date of clearance determined primarily by June temperatures. The main growing season is July when temperature and precipitation are particularly critical for the soil fauna. Activity tails off towards the end of August. In 1991, following a warm dry June, July was particularly cool and wet. Above average precipitation persisted into a warmer August. During 1992, a warm wet June was followed by a July of average temperature and precipitation, and August was cool and dry. By comparison, 1993 was an exceptional year with July

**Table 2** Comparison of mean monthly temperature and precipitation for June, July and August 1991–1993 with the long-term means for Ny Ålesund (1960–1990). The figure in parentheses following a temperature mean is the percentage frequency with which that value has been equalled or exceeded during the previous 30 years and gives a measure of how “typical” the value is. For precipitation the equivalent figure indicates frequency of years that have been equally dry or drier. Data are from Det Norske Meteorologiske Institutt climate station

	June	July	August
Temperature (°C)			
1991	2.6(23)	3.9(95)	5.1(5)
1992	2.6(23)	4.8(73)	3.6(73)
1993	2.3(27)	5.8(18)	5.0(5)
Mean 1961–1990	1.4	4.7	3.9
Precipitation (mm)			
1991	3(18)	37(91)	52(86)
1992	33(91)	27(68)	36(55)
1993	17(64)	8(5)	64(91)
Mean 1961–1990	19	29	40



**Fig. 4** Comparison of July temperatures in the tundra heath soil at 3-cm-depth ● 1991, □ 1992, ◆ 1993. Data points are daily means of readings taken at 15-min intervals

and August temperatures well above average and with July unusually dry. Figure 4 compares mean daily soil temperatures in 1991/1993 at 3-cm-depth on the tundra heath during July. Viewed in conjunction with Table 2, it highlights how soil temperatures magnify differences in screen temperatures and reinforces the very different midsummer temperature environment in each of the 3 years. Thus, the first growing season (1991) was typically colder and wetter than average whereas the subsequent two seasons were significantly warmer, with lower than average July precipitation, and this resulted in a general drying of the tundra soils, especially at well-drained sites, particularly during 1993. The

exposed mineral soil at the polar semi-desert was freely drained and swiftly absorbed heat, leading to rapid warming following snow melt (Coulson et al. 1993). At the tundra heath, the combination of an insulating vegetation mat and a wet, poorly drained soil overlying permafrost ensured that temperatures were slower to rise in the spring and remained slightly lower throughout the growing season. Furthermore, snow melt occurred consistently earlier at the polar semi-desert. Thus, paradoxically, the soil temperature at the more sheltered tundra heath on the Inner Fjord was lower, and the growing season was slightly shorter, than at the climatically less favourable polar semi-desert site on the Outer Fjord (Coulson et al. 1993).

Collembola numbers during 1991 were highest at the climatically more favourable polar semi-desert site. However, in the 2 succeeding years numbers declined, particularly at the polar semi-desert where the trend was accentuated on the tented plots. These plots received identical precipitation to the controls, but increased evapotranspiration, resulting from the higher temperature, probably ensured drier soil conditions. The decline in springtail numbers was associated with warmer and drier conditions, with the effect most marked at the polar semi-desert. Soil moisture at this site during “average” years, such as 1991, appears sufficient to allow the Collembola better to exploit the thermal advantages of the site. However, in warmer and drier years this advantage disappears and moisture probably becomes limiting, with sites like the tundra heath providing a cooler but moister refuge for at least some species.

By contrast with the springtails, oribatid mite numbers were less variable. However, while numbers in 1991 were similar at both sites, a between-site difference developed in 1992/1993, with significantly more animals at the polar semi-desert. This is consistent with the idea that the oribatids are better adapted to exploit the thermally advantageous conditions at the polar semi-desert, despite the drier conditions in the latter two seasons.

Seasonal trends across and between years showed recognisable patterns but some inconsistencies. Collembola usually showed a rise in numbers as the season progressed, indicating continuing recruitment. The largest change at both sites occurred over winter/early season 1991/1992 when significant mortality (62–65%) was recorded. This coincided, in part, with an exceptionally dry and warm spell before the first sample of 1992 was taken (Table 2). Apparent overwintering mortality in 1992/1993 (17–20%) was, by contrast, non-significant.

Seasonal changes in total oribatid populations are more difficult to interpret. Overwintering mortality during 1991/1992 (46–62%) paralleled that in the Collembola but was highest at the tundra heath where mortality among juveniles was similarly greater. This was followed in 1992 by a parallel rise in oribatid

**Table 3** Comparison of densities of soil Acari (Oribatida) and Collembola (numbers  $\times 10^{-3} \text{ m}^{-2}$ ) in high-Arctic, alpine and Antarctic sites

Site/vegetation type	Acari	Collembola	Authority
Spitsbergen, Svalbard			
Polar semi-desert	4–14	30–83	Present study
Tundra heath	5–11	14–40	Present study
Oligotrophic tundra	7	40	Wüthrich 1989
Lichen tundra	21–24	20–38	Bengtson et al. 1974
Wet moss tundra	22	243	Bengtson et al. 1974
Grassland	247	268	Bengtson et al. 1974
Lichen tundra	–	10–40	Sendstad 1981
Moss-lichen tundra	18–81	–	Seniczak & Plichta 1978
Devon Island, Canada			
Cushion plant-lichen	–	2–14	Addison 1977
Cushion plant-moss	–	9–20	Addison 1977
Sedge-moss	–	2–8	Addison 1977
Polar desert	–	0–30	Addison 1977
Signy Island, Antarctica			
Moss turf (dry)	1–28	20–99	Goddard 1979
Moss carpet (wet)	usually absent	0.04–65	& Block 1982
Various low arctic/alpine sites	0–220	0–220	MacLean 1981 Fjellberg 1975

numbers at both sites and includes a significant increase in the numbers of juveniles. By comparison with 1991/1992, the winter/early season period in 1992/1993 produced an apparent increase in total oribatid numbers that was significant at the tundra heath, suggesting very late, or early season, recruitment. However, the consistently low ratio of immature to adult mites suggests a slow rate of recruitment that is insufficient to explain this increase. One explanation is an early season moult of immatures through to adults, which were then extracted with a relatively higher efficiency.

Our results highlight some of the problems involved in measuring, and ultimately predicting, the effects of climate change on Arctic soil microarthropods. These animals are adapted to live in a harsh and unpredictably variable temperature and moisture environment and cope with much year to year variation. They are also generalists, spreading their risk by living in a variety of contrasting habitat types. Even a large temperature manipulation experiment may represent a minor perturbation compared with natural changes that occur continually. Given the variability inherent in population data for soil microarthropods, experiments may need to run for several years before trends become discernible, as the fauna adjusts to new background conditions.

Despite the variability, it is instructive to compare our data with Oribatida and Collembola population estimates for similar polar and alpine vegetation types, usually sampled on a single occasion, by other workers (Table 3). This variability is increasingly being recognised as a reflection of the variable micro-distribution patterns of individual species and should be recognised as a consequence of their survival strategy rather than a statistical feature (Seniczak and Plichta 1978). Total oribatid population densities at the polar semi-desert

and tundra heath were generally lower than at most other tundra sites but were comparable with densities recorded by Wüthrich (1989), in an area adjacent to our polar semi-desert site. Collembola numbers are similar to those of Wüthrich and to those recorded by Bengtson et al. (1974) and Sendstad (1981) for lichen tundra, but are much lower than densities recorded from wet moss tundra and grassland (Bengtson et al. 1974). In general, Collembola densities at Ny Alesund are higher than at similar sites on Devon Island, Canada (Addison 1977). There are clear parallels, in total population densities, with comparable habitats on Signy Island, Antarctica. Numbers of oribatids and Collembola at the drier polar semi-desert site were similar to those in dry moss turf at Signy Island, whereas numbers in the wetter tundra heath were lower and similar to those recorded from wet moss carpet in the Antarctic (Block 1982) (Table 3).

**Acknowledgements** This work was supported by the Arctic Terrestrial Ecology Special Topic Programme of the Natural Environment Research Council (Grant GR3/02/534). We thank Drs. A Fjellberg, M. Colloff and J. Stary for confirming the identities of the microarthropod species. The British Antarctic Survey provided additional support for fieldwork (W.B. and M.R.W.) and the Institute of Terrestrial Ecology, South loaned sets of Tullgren extractors. Drs. T. Solhøy and M. Luxton made helpful comments on the manuscript.

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