

THE SIGNY ISLAND TERRESTRIAL REFERENCE SITES: XII. POPULATION ECOLOGY OF NEMATODES WITH ADDITIONS TO THE FAUNA

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ABSTRACT. A total of 27 species (15 genera) of nematode was recorded in the 1973–74 Antarctic summer from the Signy Island terrestrial reference sites (SIRS); of these, 26 species (15 genera) occurred on SIRS 1 and 22 species (12 genera) on SIRS 2; 21 species (12 genera) were common to both sites. The dominant species on SIRS 1 was *Teratocephalus tilbrooki* (mean density $373.5 \times 10^3 \text{ m}^{-2}$), that on SIRS 2 was *Teratocephalus rugosus* ($129.3 \times 10^3 \text{ m}^{-2}$) which comprised, respectively, 48.8 and 30.3% of mean total nematodes on each site. The mean population density of all nematodes was $766.9 \times 10^3 \text{ m}^{-2}$ on SIRS 1 and $447.0 \times 10^3 \text{ m}^{-2}$ on SIRS 2. The SIRS 1 mean individual live weight biomass was $0.196 \mu\text{g}$ and that on SIRS 2 was $0.675 \mu\text{g}$. Mean biomass of all nematodes was calculated to be 150.5 and 301.8 mg m^{-2} , respectively. For nematode samples from all strata, coefficients of dispersion were high, indicating considerable aggregation. Changes in vertical distribution were different on the two sites; on SIRS 1 these were negligible with approximately 80.0 (76.3–89.0) % occurring in the upper stratum throughout the summer; on SIRS 2 the proportion in the upper layer was lowest early in the study period and highest towards the end, containing on average 65.6 (41.9–83.0)%. The corresponding proportions in the 0–3 and 3–6 cm strata in terms of biomass were 78.3, 21.7 (SIRS 1) and 66.3, 33.7 (SIRS 2)%. The mean oxygen consumption of the populations at 5°C was calculated as 57.6 and $76.1 \mu\text{l h}^{-1} \text{ m}^{-2}$, respectively. The nematodes were estimated to be responsible for 0.09 (SIRS 1) and 0.21 (SIRS 2) % of total moss respiration.

THE Signy Island terrestrial reference sites (SIRS) were established to facilitate studies of the functional relationships between their biotic and abiotic components leading eventually to total ecosystem analyses. SIRS 1 is an example of a *Polytrichum alpestre*–*Chorisodontium aciphyllum* moss turf and SIRS 2 is a *Calliergidium austro-stramineum*–*Calliergon sarmentosum*–*Drepanocladus uncinatus* moss carpet; a detailed description of the sites and an introduction to this project has been given by Tilbrook (1973).

Although a number of publications concerning, or including, the nematodes of Signy Island, South Orkney Islands, have appeared in recent years (Tilbrook, 1967*a, b*, 1970; Spaul, 1972, 1973*a, b, c, d*; Loof, 1975; Maslen, 1979*a, b*), the only qualitative information dealing with the nematodes of the SIRS was given by Spaul (1973*e*). The results of this preliminary survey were from single sampling occasions at each site during separate austral summers.

This paper describes the results of a more detailed investigation of the summer ecology of the soil nematodes on the SIRS in the 1973–74 season.

MATERIALS AND METHODS

Temperature and rainfall

Moss and surface temperatures on the SIRS have been recorded hourly since 1972 (Walton, 1977). Mean mid-horizon (1.5 and 4.5 cm depth) temperatures encompassing the period of study (early December 1973–mid-April 1974) are shown in Fig. 1 for each site. The maximum temperature on SIRS 1 during the study was 26.7°C , whilst on SIRS 2 the maximum was 19.7°C (both in early January). The minimum temperatures were -1.0°C (early April) and -0.5°C (late December 1973), respectively.

Rainfall was not recorded at the SIRS but at the British Antarctic Survey station about 2 km away from the sites. 5 day rainfall equivalent totals are also given in Fig. 1 for the period under study and these can be regarded as representative of the two sites.

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After 21–24 h, the water containing the nematodes that had passed through the paper tissue was poured from the tray into a litre beaker and allowed to stand for at least 3 h. In this time the nematodes sank to the bottom of the beaker and excess water was siphoned off.

After thoroughly mixing the nematode suspension by bubbling air through it, a proportion, between one-half and one-seventh was pipetted into a counting tray. The numbers of each taxon were then identified, where possible to species level, and counted. Where it was not possible to carry out counts immediately, usually on alternate sampling dates, extracts were preserved with hot formal-acetic 4:1 (as summarized by Hooper (1970)) and stored in sample tubes. These samples were counted as described above at a later date.

Biomass determination

The weights of SIRS nematodes were estimated using the method of Andrassy (1956). This employs the formula $W^2L/16 \times 10^5$ and gives a live weight in μg when the maximum body width (W) and body length (L) are in μm . In conoid tailed specimens, L is the length from lips to tail tip. However, in other specimens, L is the length from lips to anus, plus the length of a theoretical conoid extension equal in volume to the non-conoid tail of the nematode.

Measurements were made on slide-mounted specimens and flattening of the body was prevented by supporting the cover slip with strands of glass wool or small glass beads.

Mean individual biomasses were calculated which, when corrected for an extraction efficiency of 63.3% and multiplied by the number of individuals of each taxon on each sampling date, provided estimates of biomass for both individual taxa and the total nematode population successively through the 1973–74 summer.

Calculation of oxygen consumption

The oxygen consumption at 20°C was first calculated by the method used by Klekowski and others (1972), Spaul (1973*d*) and others, using the general regression equation for individual nematode respiration in which $R=1.40 W^{0.72}$ (where R =amount of oxygen consumed per individual in $\mu\text{l h}^{-1}$ at 20°C and W =wet weight of the individual in μg). Estimated oxygen-consumption figures at 20°C were then corrected for the required temperature of 5°C by using Krogh's (1914) temperature-metabolism curve, which simply involved multiplying the 20°C values by 0.213.

RESULTS

Nematode fauna of the SIRS

A list of nematode species found on SIRS 1 and 2 is given in Table I. The fauna is composed of 27 species in 15 genera, although several species were scarce. For example, *Rhabditis* subgenus A sp., *Cervidellus* sp. and *Amphidelus* sp. were found (SIRS 1) on one sampling occasion only.

In total, 26 species in 15 genera were recorded from SIRS 1 and 22 species in 12 genera from SIRS 2. Of these, 21 species in 12 genera were common to both sites.

Feeding groups

Spaul (1973*d*) discussed the taxonomic composition, the distribution and relative abundance of nematode feeding groups in various Signy Island mosses. The relative abundance during the summer of each feeding group on the SIRS was given by Spaul (1973*e*).

The nematode species recorded from the SIRS in the present study are shown in Table I in relation to the appropriate feeding group for each genus as proposed by Spaul (1973*d*). It should be noted that comprehensive feeding studies have yet to be carried out with the Signy Island and other Antarctic nematode taxa. Spaul (1973*d*) undertook some feeding observations on *Mesodorylaimus* sp. and *Coomansus gerlachei*.

TABLE I. THE NEMATODES OF THE SIGNY ISLAND TERRESTRIAL REFERENCE SITES

Taxon	SIRS 1	SIRS 2	Feeding group
<i>Ditylenchus</i> sp.	+	+	Fungal feeders
<i>Tylenchus</i> sp.	+	+	
<i>Antarctenchus hooperi</i> Spaull, 1972	+	+	
<i>Aphelenchoides haguei</i> Maslen, 1979	+	+	
<i>Aphelenchoides helicosoma</i> Maslen, 1979	+	—	
<i>Aphelenchoides vaughani</i> Maslen, 1979	+	+	
<i>Plectus antarcticus</i> de Man, 1904	+	+	Microbial feeders
<i>Plectus parietinus</i> Bastian, 1865	+	+	
<i>Plectus</i> species D	+	—	
<i>Teratocephalus tilbrooki</i> Maslen, 1979	+	+	
<i>Teratocephalus rugosus</i> Maslen, 1979	+	+	
<i>Monhystera villosa</i> Bütschli, 1873	+	+	
<i>Monhystera</i> species A	+	+	
<i>Monhystera</i> species B	+	+	
<i>Prismatolaimus</i> sp.	+	+	
<i>Cervidellus</i> sp.	+	—	
<i>Rhabditis</i> subgenus A sp.	+	—	
<i>Amphidelus</i> sp.	+	—	
<i>Eudorylaimus pseudocarleri</i> Loof, 1975	+	+	Omnivores
<i>Eudorylaimus coniceps</i> Loof, 1975	+*	+	
<i>Eudorylaimus paradoxus</i> Loof, 1975	+	+	
<i>Eudorylaimus verrucosus</i> Loof, 1975	+	+	
<i>Eudorylaimus spaulli</i> Loof, 1975	—	+	
<i>Eudorylaimus</i> species G	+	+	
<i>Mesodorylaimus signatus</i> Loof, 1975	+	+	
<i>Enchodelus signyensis</i> Loof, 1975	+	+	
<i>Coomansus gerlachei</i> (de Man, 1904)	+	+	Predator
Number of species	26	22	
Number of genera	15	12	

+ Present. — Absent.

* Recorded by Spaull (1973e), but not found in the present study.

In Table II the relative abundance and number of taxa comprising each feeding group are compared with those found on the SIRS by Spaul (1973e). It can be seen that the number of taxa recorded on each site in the present study is at least double that previously recorded. However, the general order of abundance of feeding groups is similar. That is, on SIRS 1 the microbial feeders were most abundant followed by the fungal feeders and omnivores, then by the predator (not recorded by Spaul (1973e)). On SIRS 2, the microbial feeders were again dominant but the omnivores were slightly more numerous than the fungal feeders, and the predator was still low, although more numerous than on SIRS 1.

TABLE II. COMPARISON OF SPECIES NUMBERS AND PERCENTAGE ABUNDANCE OF NEMATODE FEEDING GROUPS IN THE 1973-74 SUMMER WITH A PREVIOUS STUDY OF SIRS NEMATODES

			<i>Fungal feeders</i>	<i>Microbial feeders</i>	<i>Omnivores</i>	<i>Predators</i>
SIRS 1	February 1970 (Spaul, 1973e)	Number of species	5	5	2	—
		Relative abundance (%)	38.8	58.2	3.0	—
	Summer 1973-74	Number of species	6	12	7	1
		Relative abundance (%)	23.5	72.2	4.3	0.1
SIRS 2	February 1973 (Spaul, 1973e)	Number of species	2	6	2	1
		Relative abundance (%)	9.5	77.2	12.4	0.9
	Summer 1973-74	Number of species	5	8	8	1
		Relative abundance (%)	9.0	80.2	10.3	0.5

Variation in numbers and horizontal distribution

The intra-seasonal variation in numbers of each taxon on SIRS 1 and 2 is shown in Tables III and IV along with the percentage composition of species within genera and total nematode numbers. A summary of mean density and relative abundance over the summer is shown in Table V. It can be seen that, in the 0-6 cm layer, highest numbers ($10.720 \times 10^5 \text{ m}^{-2}$) on SIRS 1 were recorded on 19 February 1974; on SIRS 2, highest numbers ($7.198 \times 10^5 \text{ m}^{-2}$) were recorded on 5 March 1974. The SIRS 2 maximum numbers therefore represent 67.2% of the SIRS 1 maximum. However, comparing mean numbers over the season (Tables III and IV) those on SIRS 2 represent only 58.3% of those on SIRS 1.

The commonest genus in terms of numbers on both sites (Table V) was *Teratocephalus*, with *T. tilbrooki* and *T. rugosus* as the dominant species on SIRS 1 and 2, respectively. *T. tilbrooki* accounted for 48.8% (equivalent to $3.73 \times 10^5 \text{ m}^{-2}$) of mean total nematodes on SIRS 1; *T. rugosus* accounted for 30.3% (equivalent to $1.29 \times 10^5 \text{ m}^{-2}$) of mean total nematodes on SIRS 2. On SIRS 1, the six most abundant taxa were *Teratocephalus* spp., *Plectus* spp., *Tylenchus* sp., *Aphelenchoides* spp., *Monhystera villosa* and *Eudorylaimus* spp. On SIRS 2 the corresponding abundant taxa were: *Teratocephalus* spp., *Monhystera villosa*, *Plectus* spp., *Eudorylaimus* spp., *Ditylenchus* sp. and *Aphelenchoides* spp. (Table V). The commonest species on SIRS 1 (i.e. those

TABLE V. MEAN NUMBERS AND RELATIVE ABUNDANCE OF EACH NEMATODE TAXON ON THE SIRS OVER THE 1973-74 SUMMER

Horizon	SIRS 1			SIRS 2		
	Mean number m^{-2} during season ($\times 10^3$)	Relative abundance of each taxon (%)		Mean number m^{-2} during season ($\times 10^3$)	Relative abundance of each taxon (%)	
	a	b	(a + b)	a	b	(a + b)
<i>Ditylenchus</i> sp.	10.3	0.6	1.4	29.7	4.4	8.1
<i>Tylenchus</i> sp.	83.1	8.4	12.0	3.9	0.3	1.0
<i>Antarctenchus hooperi</i>	0.5	0.5	0.1	0	< 0.1	< 0.1
<i>Aphelenchoides</i> spp.	71.5	5.4	10.0	7.0	2.4	2.2
<i>Plectus</i> spp.	84.3	26.8	14.5	39.2	9.7	11.6
<i>Teratocephalus</i> spp.	311.3	92.0	52.7	103.5	82.2	44.0
<i>Monhystera villosa</i>	23.2	11.6	4.6	76.0	13.2	21.1
<i>Monhystera</i> sp. A and B	0.9	1.0	0.3	1.9	1.6	0.8
<i>Prismatolaimus</i> sp.	0.6	0.3	0.1	1.1	0.7	0.4
<i>Rhabditis</i> subgen. A sp.	0.1	0	< 0.1	—	—	—
<i>Cervidellus</i> sp.	0.1	0	< 0.1	—	—	—
<i>Eudorylaimus</i> spp.	26.3	6.4	4.3	26.1	16.2	10.0
<i>Mesodorylaimus signatus</i>	< 0.1	0.2	< 0.1	1.3	< 0.1	0.3
<i>Enchodelus signyensis</i>	0	0.1	< 0.1	< 0.1	< 0.1	< 0.1
<i>Amphidelus</i> sp.	< 0.1	0	< 0.1	—	—	—
<i>Coomansus gerlachei</i>	0.1	0	< 0.1	1.3	0.4	0.4

For composition of species within genera refer to Tables III and IV.
a 0-3 cm horizon; b 3-6 cm horizon.

whose numbers exceeded 5% of total nematodes) were *Teratocephalus tilbrooki*, *Plectus antarcticus*, *Tylenchus* sp. and *Aphelenchoides haguei* (Table III); on SIRS 2, the corresponding species were: *Teratocephalus rugosus*, *Monhystera villosa*, *Plectus antarcticus*, *Ditylenchus* sp. and *Eudorylaimus verrucosus* (Table IV).

There were several species which were collected on a number of sampling occasions, yet were numerically unimportant (i.e. less than 0.5% of mean nematode numbers over the summer). On SIRS 1, these were *Antarctenchus hooperi*, *Monhystera* spp. A and B, *Prismatolaimus* sp., *Mesodorylaimus signatus*, *Enchodelus signyensis* and *Coomansus gerlachei*; the corresponding species on SIRS 2 were: *A. hooperi*, *Prismatolaimus* sp., *M. signatus* and *E. signyensis*.

The horizontal distribution of SIRS nematodes was found to be non-random and, with one exception (SIRS 1, 0-3 cm), non-normal. Coefficients of dispersion were calculated for each stratum on each sampling date and the extent to which the distributions satisfied a Poisson (random) model was tested by χ^2 (see Southwood, 1966), where $\chi^2 = \{S^2(N-1)\}/\bar{x}$ with one degree of freedom. If the distribution is Poisson, the coefficient of dispersion (S^2/\bar{x}) value approximates to unity, while a value significantly greater implies aggregation. On all occasions

TABLE III. SIRS I: NUMBERS OF NEMATODES ($\times 10^3$) IN EACH STAGE PER m^2 ON EACH SAMPLING DATE IN THE 0-3 AND 3-6 cm HORIZONS DURING THE 1973-74 SUMMER

Day Date	Horizon*	0 21.12.73		13 3.1.74		26 16.1.74		40 30.1.74		48 7.2.74		60 19.2.74		67 26.2.74		74 5.3.74		82 13.3.74		92 23.3.74		102 2.4.74		110 10.4.74		Mean number in summer		
		a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	
<i>Ditylenchus</i> sp.	J	—	—	2.50	—	0	0	1.16	0	6.60	0	5.78	0.50	5.78	0	8.58	0.33	23.10	1.32	23.76	0.33	1.98	1.65	4.95	0	7.65	0.41	
	F	—	—	0	—	1.16	0	0	0	2.15	0	1.82	0	2.31	0	0	0.33	3.47	0	1.98	0.33	0	0	0	0.83	1.17	0.15	
	M	—	—	0.83	—	0	0	0	0	1.16	0	0	0	3.47	0	1.98	0.33	6.93	0	1.98	0	1.98	0	0.83	0	1.74	0.03	
<i>Tylenchus</i> sp.	J	—	—	45.38	—	41.09	3.47	43.89	5.78	23.10	2.97	25.08	4.95	8.09	0	51.81	6.27	30.00	1.16	42.90	8.25	59.40	4.29	29.70	4.13	36.41	4.11	
	F	—	—	51.98	—	33.00	1.16	17.33	4.62	11.06	0	12.21	2.48	15.02	1.16	16.17	0.66	18.48	1.16	16.50	4.29	18.48	1.65	18.98	0.83	20.83	1.80	
	M	—	—	23.10	—	9.10	1.16	30.00	8.09	18.65	0	14.69	2.97	13.86	0	28.05	0.99	16.17	2.31	23.76	5.61	31.02	2.64	13.20	0.83	20.14	2.46	
<i>Antarctenchus hooperi</i>	J	—	—	0	—	0	0	0	0	0	0	0	0	0	1.16	0	0	0	0	0	0.66	0	0	0	0	0	0.06	0.12
	F	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	3.47	0	0	0	0	0	0	0	0.00	0.35
	M	—	—	0	—	0	0	1.16	0	0	0	0	0	0	0	0	0	0	0	0	0.66	0	0.66	0	0	0	0.17	0.00
<i>Aphelenchoides helicospoma</i> (15.5%) <i>Aphelenchoides haguei</i> (76.4%) <i>Aphelenchoides vaughani</i> (8.1%)	J	—	—	18.98	—	22.94	0	31.19	5.78	11.06	0	27.89	0.99	27.72	10.40	21.78	8.25	63.53	8.42	62.04	2.31	74.58	1.32	51.98	0.83	37.60	3.83	
	F	—	—	29.70	—	28.88	0	24.26	2.31	8.75	0.66	14.69	0	25.41	0	15.18	2.64	40.43	2.31	26.40	0.66	36.30	0.33	30.53	0	25.50	0.89	
	M	—	—	6.60	—	6.77	0	8.09	3.47	4.46	0	9.08	0	9.24	1.16	6.60	1.32	16.17	0	7.26	0	23.10	0	17.33	0.83	10.42	0.68	
<i>Plectus antarcticus</i> (98.0%) <i>Plectus parietinus</i> (1.2%) <i>Plectus</i> species D (0.8%)	J	—	—	32.18	—	47.19	9.24	47.36	9.24	52.80	14.69	193.71	24.92	55.44	5.78	93.72	26.07	48.51	46.53	58.74	18.15	73.26	26.40	54.45	22.28	68.85	20.33	
	F	—	—	34.65	—	27.56	15.02	23.10	3.47	3.30	1.49	45.05	17.00	18.48	3.47	11.88	2.97	19.64	6.27	5.28	2.97	7.92	6.27	9.90	5.78	18.79	6.47	
	M	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00	
<i>Teratocephalus rugosus</i> (7.4%) <i>Teratocephalus tilbrookii</i> (92.6%)	J	—	—	121.28	—	108.90	45.05	136.29	56.60	103.46	44.06	217.00	71.61	72.77	12.71	168.63	93.39	114.35	14.36	207.24	71.61	193.38	67.32	120.45	47.03	142.15	52.37	
	F	—	—	141.08	—	148.83	61.22	69.30	20.79	54.95	13.20	102.63	20.63	42.74	1.16	102.30	14.19	50.82	4.95	96.36	16.50	106.26	18.48	81.68	14.85	90.63	18.60	
	M	—	—	70.13	—	79.04	21.95	71.61	17.33	57.26	13.86	135.47	37.62	54.29	5.78	70.29	27.39	82.00	13.04	91.08	28.05	92.40	26.40	65.18	18.98	78.97	21.04	
<i>Monhystera villosa</i>	J	—	—	15.68	—	30.03	10.40	3.47	8.09	3.30	0	16.67	9.57	3.47	0	34.32	15.51	23.10	10.40	13.86	7.26	31.68	12.54	24.75	7.43	18.21	8.12	
	F	—	—	4.95	—	2.31	0	4.62	1.16	1.16	0.66	4.62	2.97	1.16	0	6.93	1.98	5.78	2.31	1.98	2.97	3.96	5.28	4.13	3.30	3.78	2.06	
	M	—	—	2.48	—	2.31	3.47	1.16	0	3.30	0	4.29	0.50	0	0	6.60	3.30	8.09	0	1.98	1.98	0	3.30	3.30	1.65	3.05	1.42	
<i>Monhystera</i> species A (50.0%) <i>Monhystera</i> species B (50.0%)	J	—	—	0	—	0	0	2.31	0	0	0	0.66	0	0	0	1.65	0	0	0	1.32	0.33	0.66	4.62	0.83	2.48	0.68	0.74	
	F	—	—	0	—	0	0	0	0	0	0.66	0	0	0	0	0.66	0	1.16	0	0	0.33	0.66	0.99	0.83	0	0.30	0.20	
	M	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00	
<i>Prismatolaimus</i> sp.	J	—	—	0	—	0	0	3.47	1.16	0	0	0	0.99	0	0	1.32	0	0	0	0	0.33	0	0	0	0	0	0.43	0.25
	F	—	—	0	—	0	0	1.16	0	0	0	0.33	0	0	0	0.66	0	0	0	0	0	0.66	0	0	0	0.26	0.00	
	M	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00	
<i>Rhabditis</i> subgenus A sp.	J	—	—	0	—	1.16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.10	0.00
	F	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00	
	M	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00	
<i>Cervidellus</i> sp.	J	—	—	0	—	0	0	0	0	1.16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.10	0.00
	F	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00	
	M	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00	
<i>Eudorylaimus pseudocarleri</i> (1.3%) <i>Eudorylaimus paradoxus</i> (2.0%) <i>Eudorylaimus verrucosus</i> (17.0%) <i>Eudorylaimus</i> species G (79.7%)	J	—	—	19.80	—	27.72	5.78	16.17	8.09	14.36	4.46	25.41	7.43	6.93	2.31	33.33	5.94	18.48	2.31	21.78	3.96	22.44	5.28	13.20	5.78	19.97	5.13	
	F	—	—	9.90	—	3.47	1.16	1.16	1.16	0	0	1.98	3.47	3.47	0	2.97	0.66	6.93	2.31	1.32	0.66	2.64	0	2.48	0.83	3.30	1.02	
	M	—	—	4.13	—	1.16	0	0	0	0	2.15	0.66	3.14	0.49	3.47	0	1.98	0.33	2.31	0	4.62	0	1.98	0.66	2.48	0	2.49	0.21
<i>Mesodorylaimus signatus</i>	J	—	—	0	—	0	0	0	0	0	0	0	0.50	0	1.16	0.99	0.33	0	0	0	0	0	0	0	0	0.09	0.20	
	F	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00	
	M	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00	
<i>Enchodelus signyensis</i>	J	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.33	0	0.33	0	0	0.00	0.07	
	F	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.66	0	0	0	0	0.00	0.07	
	M	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00	
<i>Amphidelus</i> sp.	J	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00	
	F	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0.66	0	0	0	0	0	0	0	0	0	0.06	0.00	
	M	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00	
<i>Coomansus gerlachei</i>	J	—	—	0	—	0	0	1.16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.10	0.00
	F	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00	
	M	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00	
Total nematode numbers per sampling date per m^2 ($\times 10^4$)		59.40	15.18	63.53	17.16	62.25	17.90	53.94	15.71	38.40	9.75	86.21																

TABLE IV. SIRS 2: NUMBERS OF NEMATODES ($\times 10^3$) IN EACH STAGE PER m^2 ON EACH SAMPLING DATE IN THE 0-3 AND 3-6 cm HORIZONS DURING THE 1973-74 SUMMER

Day Date	Horizon*	0 21.12.73		13 3.1.74		26 16.1.74		40 30.1.74		48 7.2.74		60 19.2.74		67 26.2.74		74 5.3.74		82 13.3.74		92 23.3.74		102 2.4.74		110 10.4.74		Mean number in summer			
		a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b		
<i>Ditylenchus</i> sp.	J	—	—	5.94	—	8.09	5.78	23.10	3.47	30.36	8.75	85.14	5.94	9.24	3.47	11.88	1.32	15.02	1.16	25.74	5.94	3.30	0	2.64	0	20.04	3.58		
	F	—	—	1.32	—	0	0	4.62	0	1.32	0.33	11.22	0	4.62	0	8.58	0.33	1.16	0	16.50	1.49	1.32	1.49	0.66	0.83	4.67	0.45		
	M	—	—	1.98	—	0	0	1.16	0	1.98	0	22.44	0.33	2.31	0	9.90	0.33	2.31	0	27.06	0.33	3.30	1.49	0.66	1.65	6.65	0.41		
<i>Tylenchus</i> sp.	J	—	—	0.66	—	0	0	0	0	0	0	0	0	1.16	0	5.94	0	2.31	0	9.24	0	7.26	0.50	3.96	0.83	2.77	0.13		
	F	—	—	0	—	0	0	0	0	0	0	0	0	1.16	0	0	0	0	0	0.66	0	2.64	0	1.98	0	0.59	0.00		
	M	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	1.16	0	2.64	0.33	3.30	0	1.32	0.83	0.77	0.12		
<i>Antarctenchus hooperi</i>	J	—	—	0	—	0	0	0	0	0	0.33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00
	F	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00
	M	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00
<i>Aphelenchoides haguei</i> (92.5%) <i>Aphelenchoides vaughani</i> (7.5%)	J	—	—	0	—	0	0	0	0	0	0	0	0	13.86	0	1.32	9.90	15.02	5.78	9.24	0	11.22	0	3.30	0	4.90	1.57		
	F	—	—	0	—	0	0	0	0	0	0	0	0	3.47	0	0.66	2.64	10.40	2.31	2.64	0.33	4.62	0	1.32	0.83	2.10	0.61		
	M	—	—	0	—	0	0	0	0	0	0	0	0.33	0	0	1.65	1.16	0	0.66	0	3.96	0	1.32	0	0.65	0.20			
<i>Plectus antarcticus</i> (86.5%) <i>Plectus parietinus</i> (13.5%)	J	—	—	11.22	—	2.31	6.93	23.10	8.09	13.20	2.97	9.90	6.27	42.74	8.09	102.96	24.42	8.09	3.47	23.10	9.57	35.64	6.11	24.42	7.43	26.97	8.33		
	F	—	—	15.18	—	12.71	2.31	13.86	0	3.30	0.50	2.64	0.33	15.02	0	39.60	5.61	3.47	1.16	4.62	2.15	11.22	0.99	9.24	0.83	11.89	1.39		
	M	—	—	0.66	—	1.16	0	0	0	0.66	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.23	0.00	
<i>Teratocephalus rugosus</i> (68.9%) <i>Teratocephalus tilbrooki</i> (31.1%)	J	—	—	22.40	—	4.62	150.15	24.26	46.20	33.00	65.18	26.40	24.92	64.68	51.98	63.36	56.10	27.72	45.05	96.36	35.97	88.44	31.19	48.18	15.68	45.40	52.24		
	F	—	—	13.20	—	11.55	32.30	35.81	18.48	22.44	20.13	17.16	11.72	34.65	11.55	56.10	15.51	24.26	16.17	34.98	8.75	56.76	3.80	31.68	17.33	30.78	15.58		
	M	—	—	7.92	—	6.93	17.33	20.79	10.40	23.10	20.13	23.10	16.17	42.74	19.64	39.60	20.46	10.40	13.86	40.26	7.76	50.82	7.59	38.28	10.73	27.63	14.40		
<i>Monhystera villosa</i>	J	—	—	66.00	—	78.54	8.09	24.26	16.17	12.54	7.76	50.16	11.06	78.54	12.71	38.94	8.91	23.10	3.47	8.58	0.66	44.22	8.91	34.32	12.38	41.75	9.01		
	F	—	—	51.48	—	28.88	6.93	5.78	1.16	0.66	0.50	7.26	2.15	27.72	2.31	9.24	2.64	5.78	0	5.94	1.16	7.26	6.60	11.88	1.65	14.71	2.51		
	M	—	—	22.40	—	21.95	1.16	17.33	1.16	4.62	0.33	9.24	4.46	15.02	0	13.86	2.97	4.62	0	3.96	0.66	5.94	0.99	3.30	4.95	11.11	1.67		
<i>Monhystera</i> species A (50.0%) <i>Monhystera</i> species B (50.0%)	J	—	—	1.98	—	0	0	1.16	2.31	0	0	0	0	0	1.16	1.32	1.32	0	1.16	0.66	2.64	0.66	0	0	0	0.83	0.53	0.94	
	F	—	—	0.66	—	0	0	0	2.31	0	0	0	0	1.16	3.47	3.96	0.66	0	0	1.98	0.33	0	0	0	0	0	0.77	0.68	
	M	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00	
<i>Prismatolaimus</i> sp.	J	—	—	1.32	—	1.16	0	1.16	1.16	0	0	0	0.66	1.16	2.31	2.64	0.33	0	0	1.98	0	0	0.50	0	0	0.86	0.50		
	F	—	—	0	—	0	0	0	1.16	0	0	0	0	0	0	0.66	0.33	0	0	0.66	0	0	0	0	0	0.12	0.15		
	M	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00	
<i>Eudorylaimus pseudocarteri</i> (1.5%) <i>Eudorylaimus coniceps</i> (0.4%) <i>Eudorylaimus paradoxus</i> (21.6%) <i>Eudorylaimus verrucosus</i> (56.9%) <i>Eudorylaimus spaulii</i> (19.3%) <i>Eudorylaimus</i> species G (0.4%)	J	—	—	8.58	—	2.31	27.72	9.24	5.78	36.30	16.83	17.82	7.76	18.48	15.02	46.86	51.15	12.71	9.24	13.86	3.30	9.90	2.31	4.62	2.48	16.42	14.16		
	F	—	—	3.96	—	8.09	2.31	4.62	0	5.94	1.65	2.64	2.64	4.62	1.16	19.14	3.30	2.31	0	1.32	0.33	0.66	0	1.32	0	4.96	1.14		
	M	—	—	4.62	—	4.47	4.62	11.55	0	2.64	1.16	2.64	0.66	1.16	0	23.76	2.64	0	0	1.98	0	0.66	0	1.32	0	4.89	0.91		
<i>Mesodorylaimus signatus</i>	J	—	—	1.32	—	0	0	0	0	2.64	0.33	1.98	0	0	0	1.32	0	0	0	0	0	0	0	0	0	0	0.66	0.03	
	F	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0.66	0	0	0	0	0	0	0	0	0	0	0.06	0.00	
	M	—	—	0.66	—	0	0	0	0	0	0	0.66	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.12	0.00	
<i>Enchodelus signyensis</i>	J	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00
	F	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0.66	0	0	0	0	0.33	0	0	0	0	0	0.06	0.03	
	M	—	—	0	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00	
<i>Coomansus gerlachei</i>	J	—	—	0.66	—	0	0	3.47	0	0.66	0	0.66	0.36	0	0	1.98	1.65	0	0	0.66	0.66	0	0	0	0	0	0.73	0.26	
	F	—	—	0	—	0	0	0	0	0	0	0	0	3.47	0	0	0	0	0	0	0	0	0	0	0	0	0.31	0.00	
	M	—	—	0	—	0	0	0	0	0	0	0	0	1.16	1.16	0.66	0	0	0	0	0	0	0	0	0	0	0.17	0.11	
Total nematode numbers per sampling date per m^2 ($\times 10^4$)		36.53	27.72	24.42	28.38	19.17	26.57	22.52	11.78	19.54	14.65	29.11	9.57	38.81	13.40	50.56	21.42	17.09	10.28	33.53	8.28	35.31	7.21	22.57	7.92	29.10	15.60		
\log_{10} total numbers per m^2		5.56	5.44	5.38	5.45	5.28	5.42	5.35	5.07	5.29	5.17	5.46	4.98	5.59	5.13	5.70	5.33	5.23	5.01	5.53	4.92	5.55	4.86	5.35	4.90				

* a 0-3 cm horizon; b 3-6 cm horizon. — Composition of taxa not determined. J Juvenile; F Female; M Male.

the coefficients of dispersion were high, indicating considerable aggregation. Comparisons of the frequency of sample unit values were made with the theoretical normal distribution. Only in the case of samples from the upper layer on SIRS 1 were the frequencies not significantly different from normal.

In this study the qualitative and quantitative distribution of SIRS nematodes has been examined more precisely than in previous studies of Antarctic nematodes, by separating the taxa into males, females and juveniles at the counting stage. Tables III and IV show the numbers of males, females and juveniles of each taxon per stratum on the various sampling dates throughout the summer season. The mean numbers of nematodes m^{-2} (0–6 cm depth) for each site during the summer are shown in Fig. 2a and b.

Statistical comparisons (*t*-tests) for seasonal variations in abundance in each of the strata revealed very few significant ($P < 0.05$) changes between consecutive sampling occasions. On SIRS 1, in the 0–3 cm layer, there was one significant decrease between 19 and 27 February 1974, and one significant increase between 26 February and 5 March 1974. In the upper layer on SIRS 2 there was one significant decrease between 5 and 13 March 1974, and one significant increase between 13 and 23 March 1974. No significant changes were demonstrated in the lower stratum of either site. On SIRS 1 (0–6 cm) there were statistically significant lower nematode

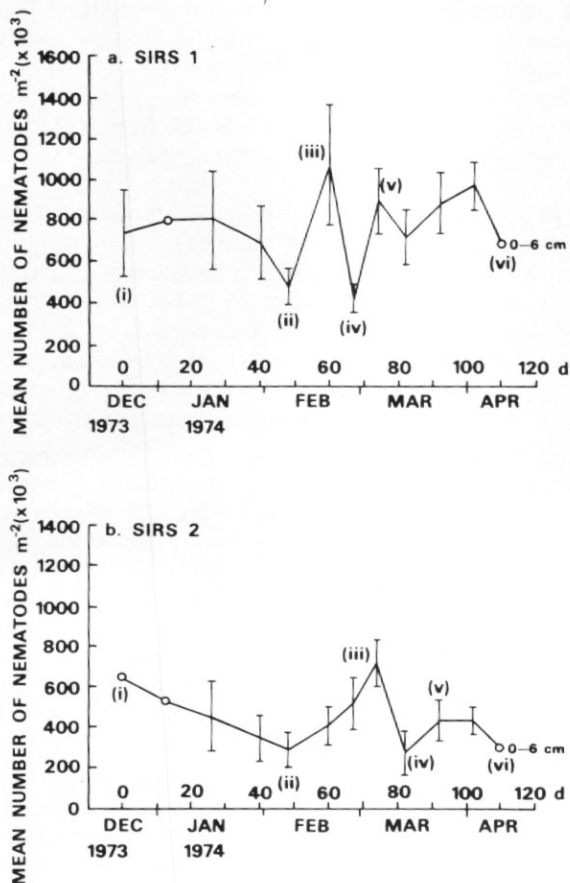


Fig. 2. a. Summer variation in mean (± 1 SE) numbers of nematodes per m^2 on SIRS 1.

b. Summer variation in mean (± 1 SE) numbers of nematodes per m^2 on SIRS 2.

densities on 27 February 1974, while the highest density occurred on 19 February 1974. On SIRS 2, lowest significant densities occurred on 13 March 1974 and highest densities on 5 March 1974.

It is possible to account for changes in nematode abundance on the SIRS over the 1973–74 austral summer and, although this is inevitably somewhat conjectural, it is intended primarily as a basis for future ecological investigation. Population changes on both sites appear to have been broadly similar, as shown in Fig. 2a and b, with corresponding phases numbered (i)–(vi). The difference in pattern between sites is attributed to the higher water content of SIRS 2, which consequently required longer to respond to an increase in ambient temperature than SIRS 1, and was therefore always at a lower temperature throughout the summer season (Fig. 1). This is thought to account for the lag in population response between the sites around February–March (Fig. 2a and b). Allowing for a delay in response to favourable weather conditions but a more rapid change with adverse conditions, population changes can be related to seasonal moss temperature and moisture changes as follows:

Phase (i)–(ii): Population levels were initially high in response to favourable (increasing) summer temperatures. However, water loss by evaporation and wind effects, reduced rainfall in mid-January 1974 (Fig. 1) and consequent reduction in aerobic conditions on the sites produced a fall in nematode numbers. There was a marked female mortality and a corresponding increase in the proportion of juveniles (Figs 4 and 5; Tables III and IV) especially in *Plectus* spp.

Phase (ii)–(iii): Continuing suitable temperatures with a peak in rainfall in early February 1974 produced optimum conditions for recruitment from eggs deposited by the high proportion of females in phase (i)–(ii). Note the 14 d lag between the peaks (iii) on SIRS 1 and 2 (Fig. 2).

Phase (iii)–(iv): Rapid population decline was probably due to a high mortality in a now large population of juveniles (Figs 4 and 5; Tables III and IV).

Phase (iv)–(v): Adequate rainfall and continuing favourable mean temperatures permitted continuation of rapid recruitment (from eggs deposited early in the summer) with some recovery to higher population levels, which was greater on SIRS 1.

Phase (v)–(vi): In this period there was probably an equilibrium between recruitment and mortality until just before the end of summer, when declining temperatures and reduced rainfall (Fig. 1) caused a reduction in population numbers on both sites.

In addition to inducing a greater lag in population response to temperature, the presence of a larger quantity of water in the substrate of SIRS 2 was probably responsible for inhibition of at least part of the population by flooding during and after the spring melt (phase (i)–(ii)). Some taxa were entirely absent or present in very low numbers in this period (e.g. *Aphelenchoides* spp., *Tylenchus* sp.). The taxa inhibited in this way were also those which showed a preference for the drier site (SIRS 1). Nielsen (1967) and Kühnelt (1976) have discussed nematodes in relation to their characteristic occurrence and preference for “wet” or “dry” habitats. The progressive reduction in numbers of other taxa in phase (i)–(ii) (e.g. *Monhystera villosa*, *Monhystera* spp. A and B) may be due to gradual development of anaerobic conditions (Spaull, 1973e).

Variation in vertical distribution

If the distribution of nematodes at the two depths is compared for each site, expressed as a percentage of total nematodes in both layers, the changes in vertical distribution can be clearly seen (Fig. 3a and b). On SIRS 1 about 80 (76.3–89.0)% of the nematodes were found in the surface 3 cm of the moss throughout the summer. On SIRS 2 the nematode distribution in both horizons was approximately 50% at the beginning of the summer. Thereafter, the percentage in the upper layer progressively increased over the season to a maximum of 83.0%, although this layer contained 75.0% of the nematodes by February (Fig. 3b).

Both Tilbrook (1967a) and Spaul (1973a) found seasonal variations in the vertical distribution of nematodes on other Signy Island sites. Monthly samples taken by Spaul (1973a) from a *Calliergon-Calliergidium* site showed a similar summer pattern to that found on SIRS 2. Data from a *Chorisodontium-Polytrichum* site investigated by Spaul (1973f) between February 1968 and February 1969 reveal a similar pattern to that found on SIRS 1 (Fig. 3c). The proportion of nematodes found in the upper layer on Spaul's *Chorisodontium-Polytrichum* site was between 81 and 96% during the summer, and 70-96% over the whole year (Fig. 3c), a slightly wider range than, but not at all dissimilar to, summer changes on SIRS 1.

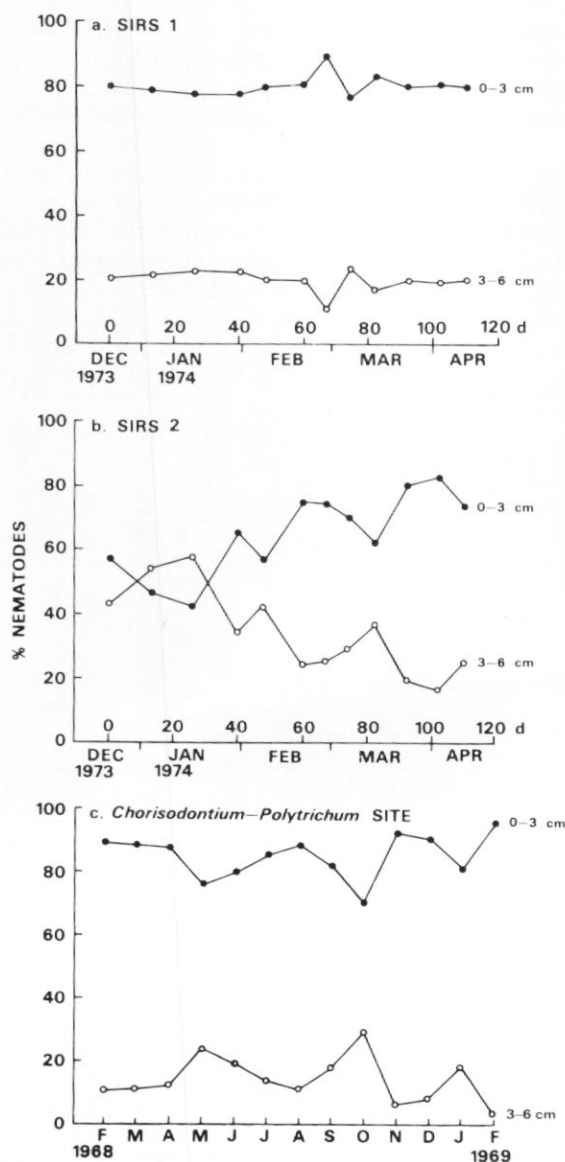


Fig. 3. Seasonal variation in vertical distribution of nematodes as proportions in the 0-3 and 3-6 cm strata. a. SIRS 1; b. SIRS 2; c. A *Chorisodontium-Polytrichum* site (data from Spaul (1973f)).

This suggests that the winter variation on SIRS 1 is unlikely to differ greatly from the summer pattern shown in Fig. 3a. The summer variation on SIRS 2 likewise compared well with that of Spaul (1973a), indicating that annual variation on SIRS 2 would be similar to his *Calliergon-Calliergidium* site.

Tilbrook (1970) suggested that seasonal variations in nematode numbers were caused by differential mortality. However, Spaul (1973a) claimed that this was not the complete explanation. He presented evidence to show that a partial upward migration occurred from the 3–6 cm to the 0–3 cm layer in the spring, followed by a partial downward migration in the autumn. It should be noted that these observations relate to a moss-carpet (*Calliergon-Calliergidium*) and not to a moss-turf community. In the present study, a spring increase in the 0–3 cm layer associated with a decrease in the 3–6 cm layer was observed in the SIRS 2 (moss-carpet) site (Table IV; Fig 3b). There was also an indication of a reversal in this process in April. No such changes were evident on the moss-turf (SIRS 1) site (Table III; Fig. 3a).

Among individual taxa on SIRS 2, there was no single sharp increase or decrease in the 0–3 cm layer relative to the 3–6 cm layer during summer which could be interpreted as upward or downward migration. Instead, there were two or more numerical increases and decreases in the 0–3 cm layer with varying changes in the 3–6 cm layer, depending upon the taxon and the time of season (Table IV). All the most abundant taxa showed evidence of large numbers in the 0–3 cm horizon corresponding with the peak just after February (Fig. 2b). Of the individual taxa, *Teratocephalus* showed a partial upward migration, exhibiting a large increase in the 0–3 cm

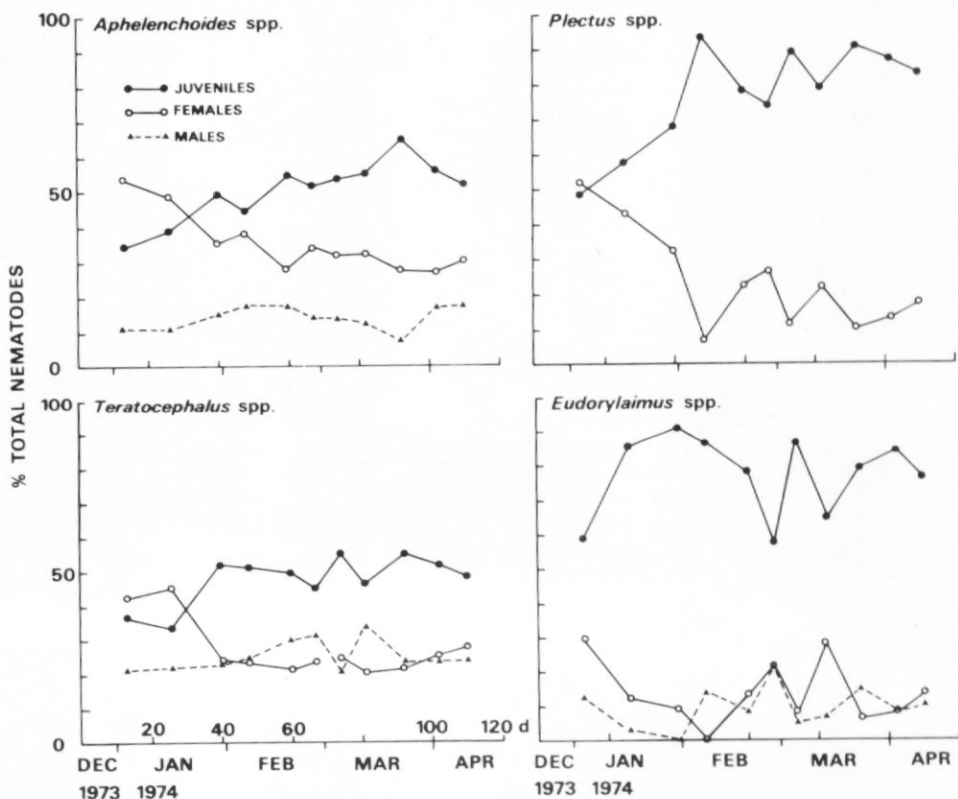


Fig. 4. Summer variation in proportions of juveniles, males and females in populations of *Aphelenchoides* spp., *Plectus* spp., *Teratocephalus* spp. and *Eudorylaimus* spp. on SIRS 1.

layer and a decrease in the 3–6 cm layer. However, this was preceded by a phase where a sharp increase in numbers in the upper horizon was accompanied by a smaller increase in the lower layer. Both events were also observed with *Monhystera villosa*, *Eudorylaimus* spp. and *Plectus* spp. In the case of *Ditylenchus* sp. there was a major increase in the upper layer with little or no change in the lower layer, which is consistent with a differential natality/mortality than a vertical migration.

Relative abundance of males, females and juveniles

The percentages of males, females and juveniles of each taxon per sampling date were calculated from tables III and IV. The changes in composition of four of the most abundant taxa on each site are shown in Figs 4 and 5. In some taxa, the percentage of juveniles was low at the beginning of the summer season, the number of females often exceeding the number of juveniles at this time (Tables III and IV). During the rest of the summer, the proportions of juveniles were generally considerably higher than either the males or females. An exception was *Ditylenchus* sp. on SIRS 2, where there was a decrease in the proportion of juveniles, and an increase in males and females, such that there were almost equal numbers of juveniles and females, and slightly fewer males towards the end of the summer.

In most taxa on both sites, the proportion of males and females was approximately equal throughout the summer, except for December. However, in the case of SIRS 1 *Aphelenchoides* spp., there were fewer males than females throughout the study (Fig. 4), while with SIRS 1

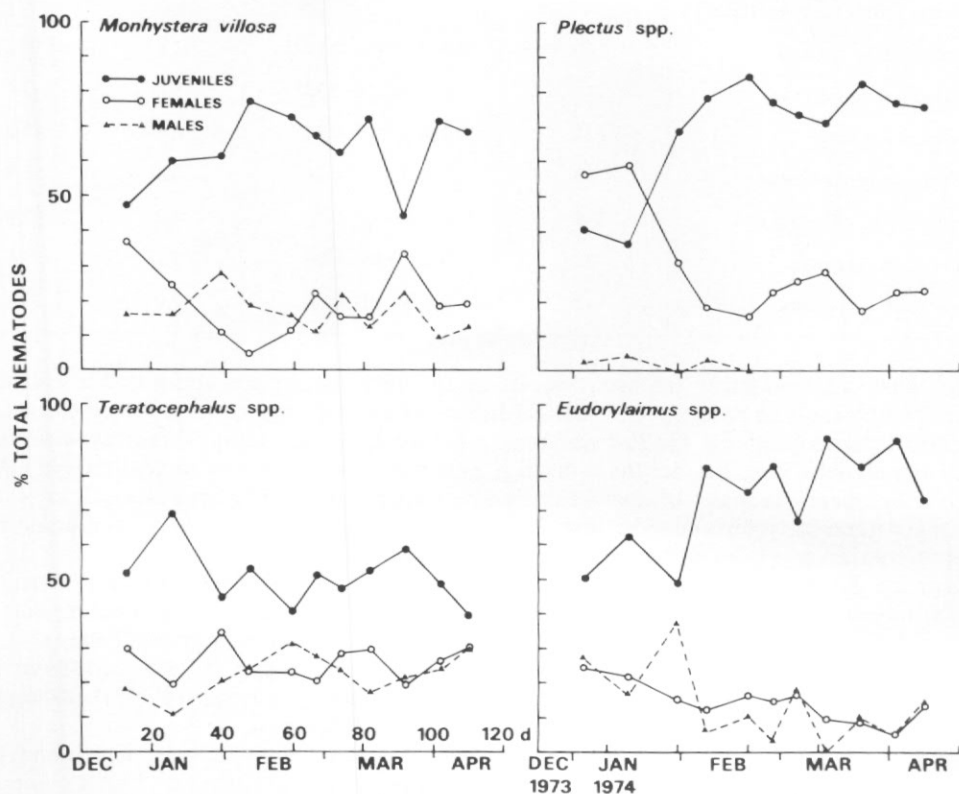


Fig. 5. Summer variation in proportions of juveniles, males and females in populations of *Monhystera villosa*, *Plectus* spp., *Teratocephalus* spp. and *Eudorylaimus* spp. on SIRS 2.

Tylenchus sp. the proportion of males was greater than females for most of the summer. On SIRS 2, males of *Plectus* spp. were found only within the first half of the summer in very low numbers (Fig. 5), while no males occurred in SIRS 1 *Plectus* spp.

Biomass

The live-weight biomass of adults and some juveniles of *Aphelenchoides haguei*, *A. vaughani*, *A. helicosoma*, *Teratocephalus tilbrooki*, *T. rugosus*, *Plectus antarcticus*, *Plectus* sp. D, *Rhabditis* subgenus A sp., *Eudorylaimus pseudocarleri*, *E. coniceps*, *E. paradoxus*, *E. verrucosus*, *E. spaulli* and *Eudorylaimus* sp. G were determined from specimens mounted on microscope slides. Mean juvenile live weights of some species are presented in Table VI, whilst mean adult biomasses are given in Table VII for all the taxa found on the SIRS (biomass data for taxa not mentioned above are taken or modified from table V in Spaul (1973d).

TABLE VI. MEAN LIVE-WEIGHT BIOMASS OF THE JUVENILES OF NUMERICALLY DOMINANT NEMATODES FROM THE SIRS

Species	Number of individuals	Mean biomass (range) (μg)	Ratio of mean adult biomass to mean juvenile biomass	Biomass ratio of largest to smallest juvenile specimen
<i>Aphelenchoides haguei</i> (91.4%)	50	0.058 (0.014–0.167)	1.7	11.9
<i>Aphelenchoides vaughani</i> (8.6%)				
<i>Teratocephalus tilbrooki</i>	160	0.054 (0.010–0.112)	1.9	11.2
<i>Teratocephalus rugosus</i>	77	0.077 (0.018–0.133)	1.8	7.4
<i>Plectus antarcticus</i>	223	0.094 (0.019–0.247)	8.5	13.0
<i>Eudorylaimus paradoxus</i>	53	2.96 (0.21–14.26)	6.4	67.9
<i>Eudorylaimus verrucosus</i>	141	2.20 (0.19–9.30)	4.2	49.0
<i>Eudorylaimus spaulli</i>	33	0.80 (0.18–3.89)	5.1	21.6
<i>Eudorylaimus</i> species G	141	1.44 (0.13–4.60)	2.0	35.4

The mean adult biomass for each species or for each genus, according to the calculated species composition on the respective SIRS (Tables III and IV), has been corrected to allow for juveniles. This was done by dividing the adult mass by 2.23, the average factor by which adult female populations were heavier than mixed populations in experiments by Wasilewska (1971). Ideally, the mean biomass of the adults and juveniles of each species should have been determined separately but only the juveniles of some of the common genera containing more than two species have been measured and their biomass calculated (Table VI).

Using the data on the distribution of the nematode taxa on SIRS 1 and 2 (Tables III and IV), and the biomass data (Table VIII), the nematode biomass per site on each sampling date was calculated (Fig. 6). The four most important SIRS 1 taxa in terms of biomass (Table VII) were *Eudorylaimus* spp. (43.1%), *Plectus* spp. (27.3%), *Teratocephalus* spp. (13.4%) and *Monhystera villosa* (8.4%). On SIRS 2 the corresponding taxa were *Eudorylaimus* spp. (67.6%), *Monhystera villosa* (10.9%), *Plectus* spp. (8.3%) and *Coomansus gerlachei* (6.4%).

The total nematode biomass on the SIRS for each sampling date is shown in Fig. 6 and Table VIII. On SIRS 1, the largest biomass in the 0–6 cm layer was 238.0 mg m⁻² on 19 February 1974; on SIRS 2, it was 893.1 mg m⁻² on 5 March 1974. The mean biomass over the season in the 0–6 cm layer was 150.5 and 301.8 mg m⁻² on SIRS 1 and 2, respectively. The SIRS 2 mean

TABLE VII. ESTIMATED MEAN ADULT BIOMASS OF NEMATODE TAXA ON THE SIRS DURING THE 1973-74 SUMMER

Horizon	SIRS 1			SIRS 2		
	Mean biomass per m ² during season (mg)	Percentage of total biomass over season	(a + b)	Mean biomass per m ² during season (mg)	Percentage of total biomass over season	(a + b)
	a	b	(a + b)	a	b	(a + b)
<i>Ditylenchus</i> sp.	2.0	0.1	1.4	5.6	0.8	2.1
<i>Tylenchus</i> sp.	3.3	0.3	2.4	0.2	< 0.1	0.1
<i>Antarctenchus hooperi</i>	0.1	0.1	0.1	0	< 0.1	< 0.1
<i>Aphelenchoides</i> spp.	3.6	0.3	2.6	0.3	0.1	0.1
<i>Plectus</i> spp.	31.2	9.9	27.3	20.2	4.9	8.3
<i>Teratocephalus</i> spp.	15.6	4.6	13.4	6.3	5.0	3.7
<i>Monhystera villosa</i>	8.4	4.2	8.4	28.5	4.6	10.9
<i>Monhystera</i> sp. A and B	0.2	0.1	0.2	0.2	0.2	0.1
<i>Prismatolaimus</i> sp.	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1	< 0.1
<i>Rhabditis</i> subgen. A sp.	0.4	0	0.3	—	—	—
<i>Cervidellus</i> sp.	< 0.1	0	< 0.1	—	—	—
<i>Eudorylaimus</i> spp.	52.3	12.7	43.1	125.8	79.0	67.6
<i>Mesodorylaimus signatus</i>	0.1	0.1	0.1	1.5	< 0.1	0.5
<i>Enchodelus signyensis</i>	0	0.2	0.1	0.1	0.1	0.1
<i>Amphidelus</i> sp.	< 0.1	0	< 0.1	—	—	—
<i>Coomansus gerlachei</i>	1.0	0	0.7	12.6	6.8	6.4

For composition of species within genera refer to Tables III and IV.
a 0-3 cm horizon; b 3-6 cm horizon.

biomass was therefore almost twice that on SIRS 1, despite the fact that mean nematode numbers over the period were 71.6% higher on SIRS 1 than SIRS 2 (Tables III and IV). This difference is also apparent in the mean individual live-weight biomass in the 0-6 cm horizon, which was 0.196 μg on SIRS 1, whereas that of SIRS 2 nematodes was 0.675 μg .

Using the energy value of 2.152 cal mg^{-1} [= 9.004 J mg^{-1}] for fresh nematode material given by Yeates (1972), the energy equivalent of the mean SIRS 1 biomass of 150.5 mg m^{-2} was calculated as 323.88 cal m^{-2} [1 355.10 J m^{-2}]; that for the mean SIRS 2 biomass of 301.8 mg m^{-2} was similarly calculated as 649.47 cal m^{-2} [2 717.4 J m^{-2}].

Nematode oxygen consumption

Using the data for the distribution of nematode taxa on SIRS 1 and 2 (Tables III and IV) and the oxygen-consumption data for individual taxa compiled in Table IX, the oxygen consumption for total nematodes on each site has been calculated for each sampling date (Table VIII). The summer mean values are also shown in this table. Spaul (1973d) used 5°C as an average summer soil temperature for comparing oxygen consumption in Signy Island nematodes. The

TABLE VIII. ESTIMATED RESPIRATION RATE AND BIOMASS OF SIRS NEMATODES DURING THE 1973-74 SUMMER

		Day Date	0 21.12.73	13 3.1.74	26 16.1.74	40 30.1.74	48 7.2.74	60 19.2.74	67 26.2.74	74 5.3.74	82 13.3.74	92 23.3.74	102 2.4.74	110 10.4.74	Summer mean	
SIRS 1	Total biomass (mg m ⁻²)	Horizon														
		0-3 cm	109.4	125.2	129.7	97.0	72.7	187.3	72.0	159.5	121.1	118.7	128.6	93.4	117.9	
		3-6 cm	(30.2)	(34.5)	34.3	32.4	20.2	50.7	11.4	40.0	36.7	29.4	38.5	32.8	32.6	
		0-6 cm	(139.6)	(159.7)	164.0	129.4	92.9	238.0	83.4	199.5	157.8	148.1	167.1	126.2	150.5	
	Total oxygen consumed (μ l h ⁻¹ m ⁻²)	at 20°C	0-3 cm	191.2	218.9	226.2	171.8	131.5	341.0	132.5	274.2	217.0	221.3	243.5	177.0	212.0
			3-6 cm	(52.9)	(60.5)	63.0	55.7	35.2	87.1	19.2	74.7	64.8	56.7	71.9	57.6	58.6
		0-6 cm	(244.1)	(279.4)	289.2	227.5	166.7	428.1	151.7	348.9	281.8	278.0	315.4	234.6	270.6	
		at 5°C	0-6 cm	(52.0)	(59.5)	61.6	48.5	35.5	91.2	32.3	74.3	60.0	59.2	67.2	50.0	57.6
SIRS 2	Total biomass (mg m ⁻²)	0-3 cm	230.9	161.1	124.9	203.2	252.6	178.2	248.0	573.9	98.8	135.1	113.8	78.9	200.0	
		3-6 cm	(116.4)	(89.8)	191.0	44.4	107.5	101.1	105.4	319.2	53.1	37.0	24.2	32.8	101.8	
		0-6 cm	(347.3)	(250.9)	315.9	247.6	360.1	279.3	353.4	893.1	151.9	172.1	138.0	111.7	301.8	
	Total oxygen consumed (μ l h ⁻¹ m ⁻²)	at 20°C	0-3 cm	301.1	213.1	169.0	227.3	259.9	227.5	307.1	623.4	121.2	182.2	173.1	140.4	245.7
			3-6 cm	(136.6)	(96.7)	209.9	61.4	118.1	103.2	114.7	316.7	62.5	47.6	37.0	42.5	111.5
			0-6 cm	(437.7)	(309.8)	378.9	288.7	378.0	330.7	421.8	940.1	183.7	229.8	210.1	182.9	357.2
	at 5°C	0-6 cm	(93.2)	(66.0)	80.7	61.5	80.5	70.4	89.8	200.2	39.1	48.9	44.8	39.0	76.1	

Figures in parentheses are interpolated from mean summer data (see text).

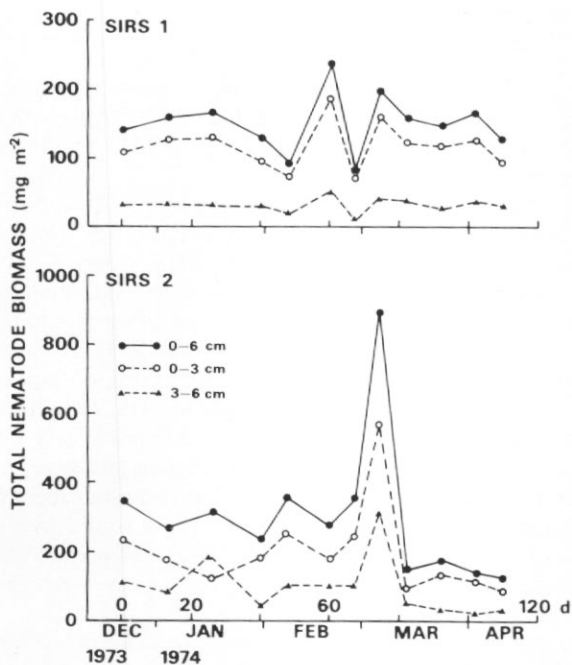


Fig. 6. Total nematode live-weight biomass per m² in the 0-3, 3-6 and 0-6 cm strata on SIRS 1 and 2 during the 1973-74 summer.

total oxygen consumption of SIRS nematodes (0-6 cm stratum) at this temperature on each sampling date was calculated using Krogh's curve and this is given in Table VIII.

The oxygen consumption by nematodes in the 0-6 cm horizon at 5°C was 57.6 (32.3-91.2) $\mu\text{l h}^{-1} \text{m}^{-2}$ on SIRS 1 and 76.1 (39.0-200.2) $\mu\text{l h}^{-1} \text{m}^{-2}$ on SIRS 2 during the 1973-74 summer. The mean SIRS 2 consumption was therefore 32.2% higher than SIRS 1, while the maximum oxygen consumption on SIRS 2 was nearly 120% greater than on SIRS 1.

Mean oxygen-uptake values at 5°C have been determined by Gilson respirometry for cores of representative mosses taken from the SIRS in the 1975-76 summer (personal communication from D. D. Wynn-Williams). The oxygen uptake was calculated from mean spring and autumn values determined for mixed or individual moss types in the 1-6 cm layer (i.e. excluding the upper 0-1 cm green-shoot layer). These mean levels have been increased to take account of the respiration contribution by the top 1 cm to that of the total profile (0-6 cm). The mean respiration at 5°C of the SIRS 1 mosses (*Chorisodontium* and *Polytrichum*) for 0-6 cm was estimated to be 63.87 $\text{ml h}^{-1} \text{m}^{-2}$. For the SIRS 2 mosses and the liverwort (*Calliergon-Calliergidium-Drepanocladus-Cephaloziella*) for 0-6 cm it was calculated to be 36.71 $\text{ml h}^{-1} \text{m}^{-2}$.

Using the mean oxygen consumption values at 5°C for the nematode populations (Table VIII), the proportion of total respiration which is contributed by nematodes in the 0-6 cm horizon on each site was calculated as 0.09% (SIRS 1) and 0.21% (SIRS 2) during the 1973-74 austral summer. These figures may be too high, as the sample-core oxygen-uptake values were probably underestimated owing to nutrients becoming rate-limiting within the Gilson chambers during consecutive experiments (personal communication from D. D. Wynn-Williams). During the summer at least, higher nematode numbers occur consistently in the 0-3 cm layer on both sites and these are probably concentrated within the 0-1 cm horizon.

DISCUSSION

Systematic sampling in the 1973–74 austral summer revealed the occurrence of 14 further nematode species and six further genera on SIRS 1, and 11 further species (four further genera) on SIRS 2 compared with a previous study (Spaull, 1973e). In the present study, 77.8% of species and 80% of genera were common to both sites.

The generic composition of the nematode feeding groups, their distribution and percentage abundance on Signy Island has been discussed by Spaull (1973d). The relative abundance, based on single sampling occasions, of feeding groups on SIRS 1 and 2 have been given by Spaull (1973e). In the present study, the microbial feeders were the dominant group which is similar to the results of Spaull (1973d, e) (see Table II). Dominance of microbial feeders was also reported by Nielsen (1949) in Danish soils and by Wasilewska (1971) in afforested dunes in Poland. However, in a study of English moorland sites by Banage (1963), plant feeders (including fungal feeders) were the dominant group. On SIRS 1 fungal feeders were the second most important group, whereas the omnivores occupied this position on SIRS 2 (Table II).

The numbers of nematodes m^{-2} recorded from SIRS 1 in this study compare well with those for the same site given by Spaull (1973e). However, the mean numbers recorded over the 1973–74 season on SIRS 2 are over 21 times greater than those found by Spaull. It is possible that nematode densities were generally low in the earlier study. However, the SIRS 2 samples were not collected or processed by Spaull (1973e) and the low numbers may be a result of a difference in extraction and decanting procedures.

Numerically, the commonest genus on both sites was *Teratocephalus*. This was also the dominant genus found on the SIRS by Spaull (1973e), although in a variety of other Signy Island mosses *Plectus* spp. were frequently the dominant taxon (Spaull, 1973b).

Tilbrook (1967a, b) and Spaull (1973b) found that nematodes were most numerous in wet moss communities, although Spaull did not show a correlation between water content of the moss and total nematodes. However, the opposite clearly applies on the SIRS, as shown by the results of this study and by Spaull (1973e).

The horizontal distribution of SIRS nematodes was aggregated and, with one exception, non-normal. This was shown by the results for both strata on SIRS 2 and the lower stratum on SIRS 1. However, if the approximation to a normal distribution in this stratum of SIRS 1 is real (i.e. not due to inadequate numbers of samples), it appears that positive skew distributions may be related to aggregations only up to certain limits of nematode population density. It was found by Proctor and Marks (1974) that skewness appears to decrease as population density increases (and also as the number of cores per sample increases). It should be noted that the mean population density of nematodes in the top stratum on SIRS 1 was about twice that in the corresponding layer on SIRS 2 and about four times that of both the lower strata from the SIRS (Tables III and IV). This higher density may have normalized the distribution in the SIRS 1 upper stratum.

Seasonal variation in a Signy Island nematode population (*Calliergon–Calliergidium* site) revealed a picture of high population densities in summer and low densities in winter (Spaull, 1973a), while a variety of other workers reported contrasting results. Banage (1966) found lowest densities in summer and highest in autumn on a moorland *Juncus* site. Yeates (1972) recorded high densities in the spring and low populations in winter in a Danish beech forest. In contrast, Berge and others (1973), in an ancient grassland habitat, and Phillipson and others (1977), in an English beech wood, found low densities in spring and high numbers in early winter. In the Antarctic, it appears that higher nematode densities occur on these sites in summer than in winter.

What are the factors responsible for these differences in the seasonal population density pattern? Banage (1966), Berge and others (1973), Spaull (1973a), Arpin (1975a, b) and Phillipson and others (1977) could not advance a simple explanation to account for seasonal

pattern in their respective studies. On the other hand, Yeates (1972) accounted for the population changes in his beech forest nematodes in terms of temperature and soil moisture. In the present study, no direct relationship could be detected (Figs 1, 2a and b). However, if an allowance was made for a delay in the effects of temperature and rainfall on the nematode fauna, an indirect relationship might be demonstrated. On the SIRS, as for other nematode fauna, such circumstantial evidence is only a first step in evaluating, and eventually predicting, population changes. Further work is required to produce quantitative information on the factors causing seasonal variation in nematode numbers on the SIRS, particularly during the period of high production in the austral summer.

The changes in vertical distribution during the summer were clearly different on SIRS 1 and 2. This is consistent with results of work on similar Signy Island sites by Spaul (1973f) and Spaul (1973a), respectively. On moss-cushion sites (e.g. SIRS 1), the proportion of nematodes in the upper 3 cm of moss has not been observed to decrease below 70% during the year (Fig. 3a and c). On moss-carpet sites (e.g. SIRS 2), there appears to be a seasonal cycle with the peak summer proportion in the 0–3 cm layer reaching 80% or higher, while the proportion in this layer frequently falls to less than 50% during the autumn, winter and late spring (Fig. 3b; Spaul, 1973a). What are the reasons for these differences in nematode behaviour in the two moss types? Spaul (1973b, d) discussed a number of interacting factors which could affect nematode distribution but he was of the opinion that the primary factor influencing the vertical distribution of Signy Island nematodes is temperature. If this is the case, temperature must act on one or more important secondary factors which are different in moss-carpet and moss-cushion sites; if this were not so, vertical changes on these sites would be similar. Figs 1 and 2b show that there was no direct correlation between the temperature in the 0–3 cm and the 3–6 cm layers and nematode vertical distribution on SIRS 2. The temperature differentials between the upper and lower layers (Fig. 1) for the two sites remain fairly constant for much of the snow-free period. While the proportion of nematodes in the two layers also remained relatively constant on SIRS 1 during this study, other work (Spaul, 1973f) (see Fig. 3c) has shown that this is a characteristic of moss-turf sites throughout the year and therefore not related to vertical temperature profiles. However, there are other factors, such as the physical nature of the moss (e.g. density and texture) and the environment within it (oxygen tension, free water, organic content and pH), which could affect both the seasonal distribution of food for the nematode fauna and the necessity (or ability) to migrate, resulting in the between-site differences in vertical distribution. Seasonal changes in vertical distribution of nematodes on moss-carpet sites have been explained in terms of differential mortality (Tilbrook, 1970) and vertical migration (Spaul, 1973a). Of these interacting factors, migration seems more important on circumstantial evidence, although on at least one occasion during this study increases in one stratum relative to another could be accounted for in terms of differential natality/mortality.

The relative proportion of juveniles, females and males was generally similar on both sites (55.8, 25.6 and 18.6%, respectively, on SIRS 1; 57.6, 21.4 and 20.9% on SIRS 2) over the study period. The eggs produced by the high number of females on both sites at the beginning of the summer are probably responsible for the "mid-summer" peaks.

The mean population biomass on SIRS 2 exceeded that of SIRS 1 by over 100%, despite the fact that mean numbers were 71.6% higher on SIRS 1. Comparison of Tables III and IV shows that this was caused by the higher proportion of relatively large nematodes (e.g. *Coomansu gerlachei*, *Mesodorylaimus signatus*, *Monhystera villosa*, *Ditylenchus* sp.) occurring on SIRS 2. In addition, the much larger individual biomass of *Eudorylaimus* spp. on SIRS 2 (Table IX) undoubtedly contributed substantially to the overall greater biomass; it can be seen that this genus contributed just over 40% of mean total biomass on SIRS 1, but nearly 70% of that on SIRS 2 (Table VII). However, the reason for the greater mean population biomass relative to numbers on SIRS 2 is more clearly appreciated by comparing the mean individual live-weight biomass for each site. The value for SIRS 2 was over 3.4 times that for SIRS 1. The mean

individual live-biomass values for the SIRS were within the range found by various authors for other habitats (Nielson, 1961; Yeates, 1972, recalculated by Phillipson and others 1977; Spaul, 1973*d*, Table VI, 1973*e*; Phillipson and others, 1977). The nematode biomasses for the SIRS in this study (Table VIII) are broadly comparable with the results of previous studies on the SIRS (Spaul, 1973*e*) and within the range for other Signy Island moss sites (Spaul, 1973*d*). They are at the lower end of the range reported for a variety of other habitats (Wasilewska, 1971; Ferris and Ferris, 1972; Yeates, 1972; Phillipson and others, 1977).

Spaul (1973*d*) has pointed out that the general regression equation for nematode respiration formulated by Klekowski and others (1972) was based on data for adults, which have a lower respiratory metabolism than juveniles, and it would therefore underestimate oxygen consumption. Metabolic adaptation to low temperatures, often assumed for soil nematodes, could also produce underestimates. However, it seems unlikely that such relatively small errors would significantly alter the nematode contribution to total moss respiration.

The SIRS nematodes consumed an estimated 0.09–0.21% of the total oxygen respired in the moss/peat. This is similar to the 0.08–0.21% for some other Signy Island nematodes estimated by Spaul (1973*d*), although it should be noted that Spaul's larger estimate was for nematodes in soil under the angiosperm *Deschampsia antarctica*, not a moss. It is also similar to the estimates (0.07–0.2%) given by Banage (1963), corrected by Spaul (1973*d*) for moorland nematodes, and those estimated for beech woodland by Phillipson and others (1977). The highest estimates were those of Bunt (1954) for Macquarie Island soil nematodes (0.5–1.2%), which were obtained by extrapolation from Nielsen's (1949) data for Danish soils. Spaul (1973*d*) has pointed out the potential for considerable error in extrapolating such data directly from one nematode fauna to another. Nevertheless, it is clear from the published work that nematodes do not make a large contribution to total soil metabolism.

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TABLE IX. LIVE WEIGHTS AND RESPIRATION RATES AT 20°C OF NEMATODES ON SIRS 1 AND 2

	Measurements from ♀ ♂		Mean and range of weights of adults (µg)	SIRS 1			SIRS 2		
				Composition of species within genera (%)	Corrected average weight per individual (see text) (µg)	Estimated oxygen consumption per individual (µl × 10 ⁻³ h ⁻¹ at 20°C)	Composition of species within genera (%)	Corrected average weight per individual (see text) (µg)	Estimated oxygen consumption per individual (µl × 10 ⁻³ h ⁻¹ at 20°C)
<i>Ditylenchus</i> sp.	7	5	0.43 (0.23–0.79)		0.19	0.42		0.19	0.42
<i>Tylenchus</i> sp.	6	6	0.08 (0.02–0.13)		0.04	0.14		0.04	0.14
<i>Antarctenchus hooperi</i>	10	10	0.52 (0.35–0.81)		0.23	0.49		0.23	0.49
<i>Aphelenchoides vaughani</i>	15		0.05 (0.04–0.07)	8.1	0.05	0.16	7.5	0.04	0.14
<i>Aphelenchoides haguei</i>	27	22	0.10 (0.08–0.22)	76.4			92.5		
<i>Aphelenchoides helicospoma</i>	14	13	0.16 (0.09–0.36)	15.5			None		
<i>Plectus parietinus</i>	6		3.43 (3.01–3.85)	1.2	0.37	0.68	13.5	0.52	0.87
<i>Plectus antarcticus</i>	20	4	0.80 (0.46–1.33)	98.0			86.5		
<i>Plectus</i> species D	2		1.17 (0.93–1.41)	0.8			None		
<i>Teratocephalus tilbrookii</i>	31	30	0.11 (0.05–0.16)	92.6	0.05	0.16	31.1	0.06	0.19
<i>Teratocephalus rugosus</i>	10	18	0.13 (0.08–0.22)	7.4			68.9		
<i>Monhystera villosa</i>	5	2	0.81 (0.69–0.90)		0.36	0.67		0.36	0.67
<i>Monhystera</i> species A	10		0.33 (0.27–0.49)	50.0	0.09	0.25	50.0	0.09	0.25
<i>Monhystera</i> species B	7		0.07 (0.05–0.10)	50.0			50.0		
<i>Prismatolaimus</i> sp.	6		0.04 (0.04–0.06)		0.02	0.08		0.02	0.08
<i>Rhabditis</i> subgenus A sp.	5	4	3.73 (2.21–5.30)		1.67	2.03	None	—	—
<i>Cervidellus</i> sp.	11		0.25 (0.19–0.35)		0.11	0.29	None	—	—
<i>Amphidelus</i> sp.	7	5	0.81 (0.46–1.26)		0.36	0.67	None	—	—
<i>Eudorylaimus pseudocarleri</i>	4	3	4.99 (4.13–5.70)	1.3	1.99	2.30	1.5	4.82	4.34
<i>Eudorylaimus coniceps</i>	3	3	6.70 (5.58–7.81)	None			0.4		
<i>Eudorylaimus paradoxus</i>	6	5	19.04 (15.00–28.18)	2.0			21.6		
<i>Eudorylaimus verrucosus</i>	6	5	10.08 (5.61–13.12)	17.0			56.9		
<i>Eudorylaimus spaulli</i>	6	5	4.10 (2.75–5.44)	None			19.3		
<i>Eudorylaimus</i> species G	5	5	2.85 (1.82–4.08)	79.7			0.4		
<i>Mesodorylaimus signatus</i>	6		2.56 (2.26–2.83)		1.15	1.55		1.15	1.55
<i>Enchodelus signyensis</i>	8		2.49 (1.84–3.05)		1.12	1.51		1.12	1.51
<i>Coomansus gerlachei</i>	5	5	21.64 (13.86–28.23)		9.70	7.19		9.70	7.19

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