THE SIGNY ISLAND TERRESTRIAL REFERENCE SITES: XIII. POPULATION DYNAMICS OF THE NEMATODE FAUNA

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ABSTRACT. Two contrasting moss sites, the first a dry *Polytrichum–Chorisodontium*-dominated moss turf and the second a wet association of *Drepanocladus–Calliergidium–Calliergon* moss carpet, were sampled over 2 years to determine the spatial and temporal distribution of the nematode fauna. Twelve genera were recorded, one being a new record from the sites. Bacterial feeders were numerically the most important group on both sites, frequently forming 90% of the population and fungal feeders were locally abundant. Omnivores, represented by the genus *Eudorylaimus*, were widely distributed but the predator *Coomansus gerlachei* occurred only on the wet site. Experiments on laboratory cultures of *Plectus antarcticus* were carried out to provide information on fecundity and birth rate, and the results are discussed as a possible explanation for seasonal fluctuations in nematode populations as a response to temperature. The effects of sampling and extraction techniques on the accurate estimation of field density of nematodes are discussed.

THE two Signy Island terrestrial reference sites (SIRS) were established at Signy Island, South Orkney Islands, in 1970 and 1971 for long-term monitoring of the various biotic and abiotic components of Antarctic moss-peat communities. The results of the nematode project reported here will contribute to the development of ecosystem models for these sites.

SIRS 1 is a well-drained moss-turf community composed primarily of *Polytrichum alpestre* Hoppe and *Chorisodontium aciphyllum* (Hook. f. et Wils.) Broth. SIRS 2 is a low-lying wet moss carpet of *Drepanocladus uncinatus* (Hedw.) Warnst., *Calliergon sarmentosum* (Wahlenb.) Kindb. and *Calliergon austro-stramineum* (C. Muell.) Bartr. with areas of the hepatic *Cephaloziella varians* (Gottsche) Steph., which are frequently waterlogged in summer. For a full description of the sites see Tilbrook (1973*a*). Previous research on the two sites has investigated the Protozoa (Smith, 1973), algae (Broady, 1977, 1979), tardigrades and rotifers (Jennings, 1979) and mites (Goddard, 1979). Spaull (1973*b*) conducted an initial survey of the nematode fauna and Maslen (1981) produced a comprehensive species list and examined variations in summer populations.

The present investigation of the distribution of nematode populations of the SIRS was undertaken during the period January 1976–April 1978. In addition to providing information for the study of energy flow through the ecosystem, fluctuations in nematode density are explained as a response to temperature, and this hypothesis is supported by laboratory experiments with a species common to both sites (*Plectus antarcticus* de Man, 1904).

MATERIALS AND METHODS

SIRS population study

Between 9 March 1976 and 25 February 1977 random samples were collected from almost pure stands of *Polytrichum* and *Chorisodontium* on SIRS 1 and from *Drepanocladus* and *Calliergon* on SIRS 2. During the summer of 1976–77 the limits of SIRS 2 were expanded as much of the previously sampled area was waterlogged and now dominated by *Cephaloziella,* this change in the vegetation having occurred since the sites were established in 1970–71. Three new sampling strata, each of 10 m^2 area, were designated A, B and C, being dominated by *Drepanocladus, Calliergidium* and *Calliergon,* respectively. Each stratum was marked by stakes and contained ten quadrats each of 1 m^2. From 9 June 1977 to 23 March 1978, random samples were taken from three quadrats on SIRS 1, and from one quadrat from each of the areas A, B and C on SIRS 2 between 5 April 1977 and 23 March 1978. These quadrats were numbered 23, 136 and 149 on SIRS 1 and A10, B14 and C29 on SIRS 2. The percentage cover of plant species from these areas and quadrats is given in Table I.

Sharpened copper corers (internal diameter 3.2 cm) with a 12 cm by 1 cm slit (after Michelbacher, 1939) were used for collection of samples during summer, the cores remaining in the tubes for transportation to the laboratory. During autumn and winter the substrate was

TABLE I. PERCENTAGE COVER OF PLANT SPECIES ON SELECTED QUADRATS OF SIRS 1 AND 2

	1976–77				1977–78					
	SIRS 1		SIRS 2		SIRS 1			SIRS 2		
Quadrat / Plant species	*Polytrichum*	*Chorisodontium*	*Calliergon*	*Drepanocladus*	23	136	149	A10	B14	C29
Polytrichum	80	3	—	—	85	22	15	—	—	—
Chorisodontium	18	90	—	—	5	40	80	—	—	—
Calliergon	—	—	95	15	—	—	—	15	8	70
Drepanocladus	—	—	5	85	—	—	—	85	—	2
Calliergidium	—	—	—	—	—	—	—	—	85	30
Cephaloziella	—	—	<1	—	—	—	—	—	8	<1
Crustose lichens	<1	4	—	—	10	35	9	—	—	—

frozen, so cores were obtained using a stainless steel corer with tungsten carbide cutting teeth, driven by an electric drill powered by a petrol generator. Five 7 cm cores were collected from each quadrat on each sampling occasion during 1976–77 but this was reduced to four 3 cm replicates in the second year, due to the time available for processing the cores. To provide information on the vertical distribution of nematodes, the larger cores were separated into 1–4 and 4–7 cm depths, and the smaller cores into 1 cm sections.

Nematodes were extracted from individual core sections by the modified Baermann funnel technique (Whitehead and Hemming, 1965), the moss and peat being teased apart on a single thickness of paper tissue supported by a thick nylon mesh (5 mm aperture). The larger core sections were extracted in plastic trays (36.5 cm by 22.5 cm by 6.0 cm) and the smaller ones in 9 cm plastic Petri dishes. Water at *c.* 15°C was added and extraction continued for 36 h for the larger samples and for 24 h for the 1 cm sections. The water containing nematodes was decanted into 1 l glass measuring cylinders and allowed to settle for at least 3 h, the excess water then being removed with a fixed-volume siphon and the remainder decanted into 7.5 cm by 2.5 cm sample tubes. The Petri dish extractions did not require concentration. All extracts were stored at 2°C until counted, normally within 14 d, except for the last 4 months' samples of the 1977–78 summer. These worms were heat-killed at 64°C and preserved in formal-acetic 4 : 1 (Hooper, 1970) for transport to the United Kingdom.

Extraction efficiency was tested by extracting samples for 12, 24, 36, 48 and 72 h and was 58% and 43%, respectively, for the 2 years; however, this may have varied seasonally. Extracted worms were counted in a Doncaster counting dish under ×25 magnification and identified to genus using keys by Spaull (1969) and Maslen (1980). Sub-samples were taken only when an excessive number of worms was present, never less than one-quarter of the sample being counted. The nematodes were also assigned to one of the four feeding groups (plant parasitic/fungal feeders, bacterial feeders, omnivores and predators) proposed by Banage (1963).

Nematodes in laboratory culture

Laboratory experiments were conducted, both on Signy Island and in the United Kingdom, on the feeding and growth of *Plectus antarcticus* (de Man, 1904), a species that was easily cultured and was common to both SIRS 1 and 2. In the Antarctic the nematodes were extracted from fresh *Polytrichum* collected from beneath Factory Bluffs near to the British Antarctic Survey scientific station. Individuals were maintained in filtered moss water (expressed from fresh moss by squeezing) and fed regularly with a mixed bacterial flora grown in nutrient broth. The nema-

todes were cultured at 15°and 22°C for a period of several weeks and the eggs produced were counted at regular intervals

For work in the United Kingdom, cores of *Polytrichum* were collected in April 1978 and kept at 0°C during transportation and subsequent storage. The nematodes were later extracted at 10°C and gravid females of *Plectus* transferred to liquid inorganic Collins medium. Three strains of bacteria isolated from Antarctic peat were used initially as food organisms but one proved to be toxic, the nematodes dying within a few hours of it being introduced. The bacteria used were slender gold-pigmented gram-negative rods (0.8–2.5 μm by 0.2 μm) showing a tendency to form stellate micro-colonies. They were grown on casein peptone starch medium at an incubation temperature of 15°C and harvested at 14 d by scraping the colonies from the agar surface and suspending them in Collins medium. Individual females were transferred from stock culture to the chambers of Perspex haemagglutination trays and fed regularly at a bacterial concentration of at least 8×10^6 cells ml^{-1}, being estimated with a Helber counting chamber (Jones, 1979). The nematodes were observed under a dissecting microscope at 1 or 2 d intervals and regularly moved to fresh chambers to avoid a possible build up of toxic substances from unused food material. The number of eggs laid per female was recorded at three temperatures (0°, 5° and 10°C).

Freshly hatched juveniles were also maintained at 10°C until maturity, some of known ages being heat-killed to determine their growth rate. This was done by measuring their length and width with an opisometer in conjunction with a microscope drawing tube and calculating their live weight by the technique of Andrássy (1956).

Results

SIRS population study

1976–77

Bacterial feeding nematodes were the most abundant group in all four quadrats (Table II); only in *Polytrichum* peat were they <90% of the population, due to an increased proportion of fungal feeders. Fungal feeders were only found in significant numbers on SIRS 1 (Table II), similar numbers occurring in both of the dominant mosses. The predominance of bacterial feeders was due mainly to the high numbers of *Teratocephalus* found in almost all the cores (maximum 4.4×10^6 m^{-2} in *Chorisodontium*). *Plectus* and *Monhystera* were the other genera in this group, the former being more common on SIRS 1 and the latter, although regularly found in SIRS 2 samples and in *Polytrichum*, was virtually absent from *Chorisodontium*. Of the fungal feeders, *Ditylenchus* sp. was rarely found, and only one specimen of *Antarctenchus hooperi*

TABLE II. PERCENTAGE CONTRIBUTION OF EACH FEEDING GROUP TO THE TOTAL NEMATODE POPULATION OF SIRS 1 AND 2 DURING 1976–78

	1976–77				*1977–78*					
	SIRS 1		*SIRS 2*		*SIRS 1*			*SIRS 2*		
Feeding group / *Quadrat*	*Polytrichum*	*Chorisodontium*	*Calliergon*	*Drepanocladus*	23	136	149	A10	B14	C29
Fungal feeders	16.4	5.9	0.4	0.6	33.0	58.1	42.1	0.7	22.1	0.5
Bacterial feeders	79.0	91.8	96.3	94.7	63.3	39.4	51.8	96.6	75.4	95.4
Omnivores	4.7	3.2	3.2	4.7	3.7	2.5	6.1	2.4	1.9	4.0
Predator	—	—	0.1	0.1	—	—	—	0.4	0.7	0.1

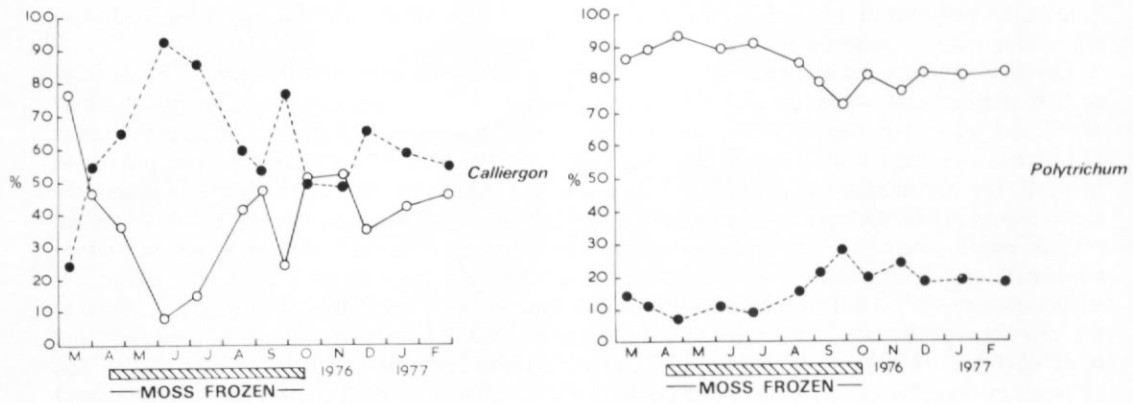


Fig. 1. Seasonal changes in vertical distribution of total nematodes during 1976–77 in *Calliergon* (SIRS 2) and *Polytrichum* (SIRS 1) peat at Signy Island.
○——○ 1–4 cm depth; ●– – –● 4–7 cm depth.

Spaull, 1972 was extracted, this coming from *Drepanocladus*. The omnivores, represented by several species of *Eudorylaimus*, were regularly present in small numbers in all quadrats but amounted to <5% of the total nematode fauna; and the predator, *Coomansus gerlachei* (de Man, 1904), was only occasionally found in *Drepanocladus*, rarely in *Calliergon* and was absent from SIRS 1.

The vertical distribution of the nematodes in the two sites (Fig. 1) was markedly different. At SIRS 1 an average 81% of the population was in the upper (1–4 cm) horizon, whereas in SIRS 2 the greater proportion (62% on average) was found in the lower (4–7 cm) horizon. This pattern on SIRS 2 was due almost entirely to *Teratocephalus*, the other bacterial feeders being more numerous in the upper horizon. *Eudorylaimus* occurred in similar numbers in both horizons of SIRS 2 and the numbers of other genera were insufficient for a pattern to be discerned. On SIRS 1 all genera were more abundant in the upper horizon. The difference in nematode distribution between the two major moss types probably reflected the physical nature of the substrate, *Chorisodontium* having a more loose, open structure than *Polytrichum*. Although the mean population density for each quadrat during 1976–77 fluctuated considerably, there was no clear seasonal pattern as has been reported previously for nematodes in other Signy Island communities (Spaull, 1973*a*; Tilbrook, 1973*b*).

This study of the two sites in 1976–77 provided a basis for a more detailed investigation in 1977–78.

1977–78

SIRS 1

In Table II it is seen that, as in the previous year, the bacterial feeders were the predominant nematode group on the *Polytrichum* and *Chorisodontium*-dominated quadrats 23 and 149 but fungal feeders were better represented, forming 33% and 42%, respectively, of the nematode population of these quadrats. On quadrat 136, with a relatively high lichen cover (Table I), the fungal feeders were the most abundant group, comprising over 58% of the nematode fauna. Quadrat 23 had the highest mean population density (maximum 3.97×10^6 m^{-2} on 18 January 1978) composed mainly of *Teratocephalus* (38%), *Aphelenchoides* (23%) and *Plectus* (19%). Similar numbers were found on quadrat 136 but here *Plectus* was less important, the main genera being *Aphelenchoides* (33%), *Teratocephalus* (31%) and *Tylenchus* (18%).

The nematode population of quadrat 149 was lower than either of 23 or 136, having a

monthly mean of 436.7×10^3 m^{-2} as compared to 1 695.8 and 1 262.1 $\times 10^3$ m^{-2}, respectively, and the dominant genera were again *Teratocephalus* (39%) and *Aphelenchoides* (34%). *Plectus*, the third most important genus here, only accounted for 8% of the population.

The omnivore group, represented by several species of *Eudorylaimus* and an occasional specimen of *Mesodorylaimus signatus* Loof, 1975, were regularly encountered in the samples but only formed 4, 2 and 6% of the nematodes in each of the three quadrats 23, 136 and 149. No specimens of the predator *Coomansus* were extracted from SIRS 1 cores.

The vertical distribution of the nematodes showed a similar pattern in each of the SIRS 1 quadrats, most of the worms being in the top centimetre which is the actively growing region of the moss (Table III). Over 90% of the fungal feeders were found in this zone, the bacterial feeders and omnivores being slightly less restricted.

The relatively small number of replicates collected and the high degree of aggregation of SIRS nematodes (Maslen, 1981) resulted in considerable variability between samples and between monthly mean population estimates. Certain trends can be determined, however, which indicate a seasonal change in nematode numbers, this being particularly evident in quadrat 23 and to a lesser extent in quadrat 149 (Fig. 2). There was no clear seasonal pattern in quadrat 136 which may reflect the more heterogeneous nature of this habitat. As the majority of worms were found in the top centimetre and as this part of the moss-peat profile on SIRS 1 also experiences the maximum extremes of temperature throughout the year (Walton, 1977), it is to be expected that this zone displays clear seasonal variations in nematode numbers, from a low winter population to a higher summer density. In quadrats 23 and 149, the summer nematode populations were 50–100% higher than their winter levels, this change being caused by increases in the numbers of the four main genera, *Teratocephalus, Aphelenchoides, Plectus* and *Tylenchus*. The less common genera, *Eudorylaimus, Monhystera* and *Ditylenchus*, showed no obvious seasonal pattern.

SIRS 2

Teratocephalus was the dominant genus on all quadrats: 65, 67 and 69% of the total nematode population of the 0–3 cm horizon of quadrats A10, B14 and C29, respectively. On

TABLE III. PERCENTAGE OF FEEDING GROUPS OF NEMATODES IN THREE DEPTHS OF SIRS 1 AND 2 IN 1977–78

Quadrat	*Depth* (cm)	*Fungal feeders*	*Bacterial feeders*	*Omnivores*	*Predator*
SIRS 1					
23	0–1	89.3	70.6	68.1	—
	1–2	8.7	21.3	22.9	—
	2–3	2.0	8.1	9.0	—
136	0–1	92.6	74.8	72.3	—
	1–2	5.8	19.5	18.3	—
	2–3	1.6	5.8	9.4	—
149	0–1	90.6	61.2	75.3	—
	1–2	7.8	28.2	17.1	—
	2–3	1.6	10.7	7.6	—
SIRS 2					
A10	0–1	29.0	16.2	21.2	50.9
	1–2	44.1	26.2	29.5	24.6
	2–3	26.9	57.7	48.8	24.6
B14	0–1	90.2	15.4	27.1	46.7
	1–2	5.4	39.2	40.4	31.7
	2–3	4.4	45.4	32.6	21.6
C29	0–1	30.9	13.1	26.0	46.1
	1–2	36.9	38.5	42.6	17.8
	2–3	32.3	48.5	31.4	38.2

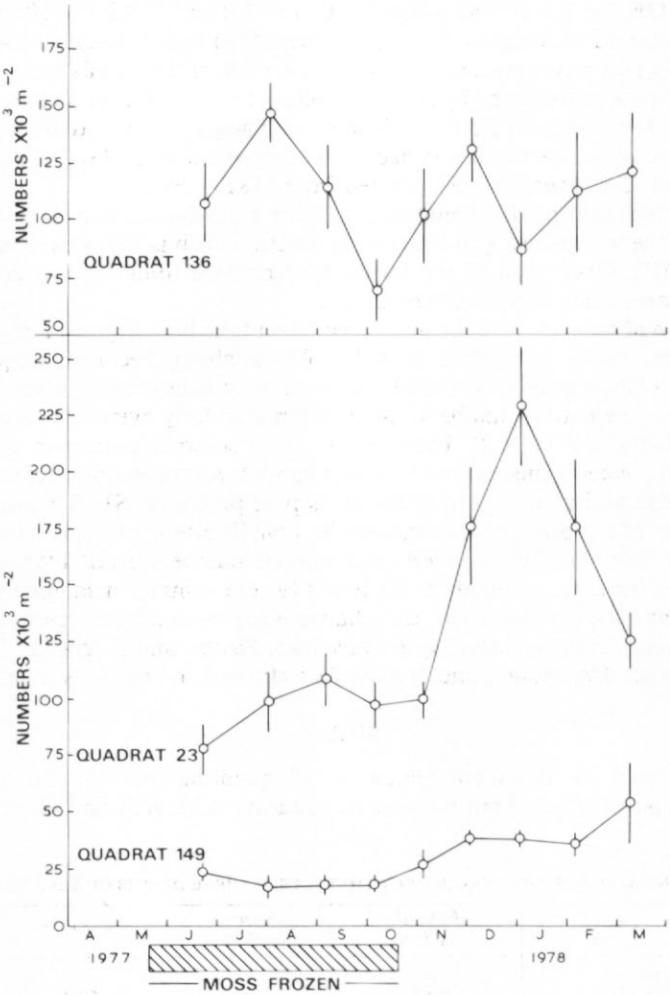


Fig. 2. Variation in mean (± 1 SE) nematode population density in 0–1 cm horizon of SIRS 1 during 1977–78. Quadrat 136 was lichen-encrusted *Chorisodontium*, quadrat 23 was mainly *Polytrichum* and quadrat 149 was mainly *Chorisodontium*.

A10 the remaining bacterial feeding nematodes *Monhystera* and *Plectus* accounted for 16% and 15%, but fungal feeders were rare, making up *c.* 1% of the population. Eudorylaimids occurred regularly in all three quadrats as did *Coomansus gerlachei,* although the latter species was never abundant. On quadrat C29 the numbers of *Plectus* were small (only *c.* 2% of the total nematodes) but *Monhystera* was relatively more important (24%). Here, too, fungal feeders were rare, contributing <1%. Fungal feeders were an important component of the fauna on quadrat B14. Although few *Aphelenchoides* were found, *Ditylenchus* and *Tylenchus* were abundant and represented 22% of the nematode population in the 0–3 cm horizon.

The vertical distribution pattern of SIRS 2 differed from that of SIRS 1 (Table III), the greatest numbers being found below 1 cm depth. This, however, reflected the distribution pattern of *Teratocephalus* which accounted for over 75% of the population in the 2–3 cm layer, the other nematodes being more evenly distributed throughout the three horizons with the exception

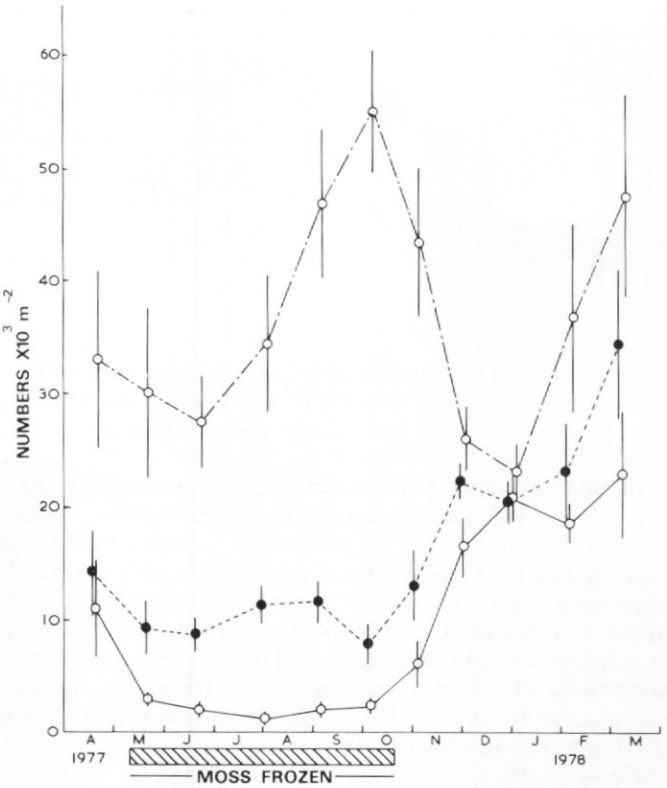


Fig. 3. Variation in mean (± 1 SE) nematode population density in three horizons of SIRS 2 quadrat A10 (dominated by *Drepanocladus*) during 1977–78.
○——○ 0–1 cm; ●- - -● 1–2 cm; ○-·-·-○ 2–3 cm.

of the fungal feeders in quadrat B14. Here, 72% of *Tylenchus* and 93% of *Ditylenchus* were found in the top centimetre of the profile.

A clear seasonal pattern in nematode density was apparent on quadrat A10 (Fig. 3), the population in the top centimetre being low from May until October 1977 and then increasing steadily throughout the Antarctic summer. This pattern was repeated in the 1–2 cm horizon but was not evident in the 2–3 cm horizon due to considerable variation in the numbers of the common genera. *Eudorylaimus*, however, showed a clear increase in numbers in the three horizons after the thaw in October 1977, but this had little effect on total nematode numbers. There was a steady increase in overall nematode density in the top centimetre of quadrat B14 during the months following thawing, but the seasonal pattern was unclear due to variation in numbers from the winter cores. Although the mean temperature is lower, the nematodes of SIRS 2 do not have to tolerate the extremes of temperature as those of SIRS 1 (Walton, 1977), and thus seasonal changes in numbers may be less marked. However, it is again the upper 1 cm horizon that experiences the greatest variation in temperature and water content, and showed the most marked seasonal changes in population density.

Nematode feeding and growth experiments

The results of the experiments with *P. antarcticus* are summarized in Table IV. The mean daily egg-production rate rose from 0.5 at 2°C to 2.3 at 10°C, above which it was constant.

TABLE IV. DEVELOPMENT OF *Plectus antarcticus* AT VARIOUS TEMPERATURES

Temperature (°C)	2	5	10	10	15	22
Source of material*	a	c	c	a	b	b
Mean number of eggs d^{-1}	0.5	0.6	1.2	2.3	2.3	2.3
Maximum number of eggs d^{-1}	2	2	—	6	6	6
Incubation period (d)	—	31.6	13.4	10.4	—	8.3
Maturation period (d)	—	63.9	36.9	33.0	—	26.0
Life cycle (d)	—	95.5	50.3	43.3	—	34.3

* a Young adults from laboratory culture.
b Extracted from fresh *Polytrichum*.
c Extracted from cores stored for 12 months at 0–4°C.

Similarly, the maximum number of eggs produced by an individual increased from 2 to 6 d^{-1} but did not increase further at temperatures above 10°C; this may be the optimum temperature for this species. The main effect of increased temperatures was to reduce larval development time, the period from egg to adult taking 95.5 d at 5°C but only 34 d at 22°C. Field temperatures on Signy Island during summer are rarely in excess of 5°C for long periods, the mean summer air temperature being 1.5°C. Having reached maximum egg production, usually within 10 d of depositing the first egg at 10°C, the age of the female had no effect on the number of eggs produced each day. After 86 d at 10°C, 38% of the worms were alive and producing eggs, some individuals having produced >200. Nematode fecundity appeared to be influenced by prior temperature acclimation, worms from eggs laid in laboratory culture at 10°C producing eggs at twice the rate at this temperature than those extracted from cores stored for 12 months at 0°C. Egg production also provided an indication of food quality (Duncan and others, 1974), falling to zero if the worms were accidently fed with dead bacterial cells. Mortality during the experiments appeared to be due to an internal fungal infection.

The growth rate of juvenile *Plectus* at 10°C in United Kingdom culture is shown in Fig. 4. Little change occurred during the first few days followed by a steady increase in size until maximum length was attained after 32 d. This corresponds well with the time of 33–37 d taken from hatching to maturity in earlier United Kingdom experiments. Live weight of newly hatched nematodes was 0.035 µg with a length at 310 µm. Mean weight at maturity was 0.55 µg, an increase of 0.016 µg d^{-1}.

DISCUSSION

The quadrats investigated in this study are typical of the SIRS which were chosen to represent two of the major vegetation types of the maritime Antarctic (Tilbrook, 1973*a*). On SIRS 1 the green apical portion of the moss is approximately 1 cm in length, below which is dense peat consolidated with a tomentum of rhizoids. The peat raises the moss surface clear of most drainage water and the position of the site, on the side of a hill, means that melt-water run-off is rapid. *Chorisodontium* peat has a much more open structure than *Polytrichum* peat and thus more habitat space is available to the nematodes; population density might therefore be greater under *Chorisodontium*, and this was clearly demonstrated by the results from 1976–77.

On SIRS 2 the moss stems are very loosely packed below the top 5 mm apical growing portion and the peat is completely permeated by drainage water. In each of the quadrats studied the peat was very similar in texture, although quadrat B14 had a greater weight of organic material per core. The water content of the SIRS 2 moss and peat was always high (1 200–1 700%, Tilbrook, 1973*a*; 906–2 361%, personal communication from D. D. Wynn-Williams; 1 032–2 299%, present study) and is unlikely to be a limiting factor. However, most areas of SIRS 2 undergo occasional flooding and worms at the moss surface may be periodically washed away.

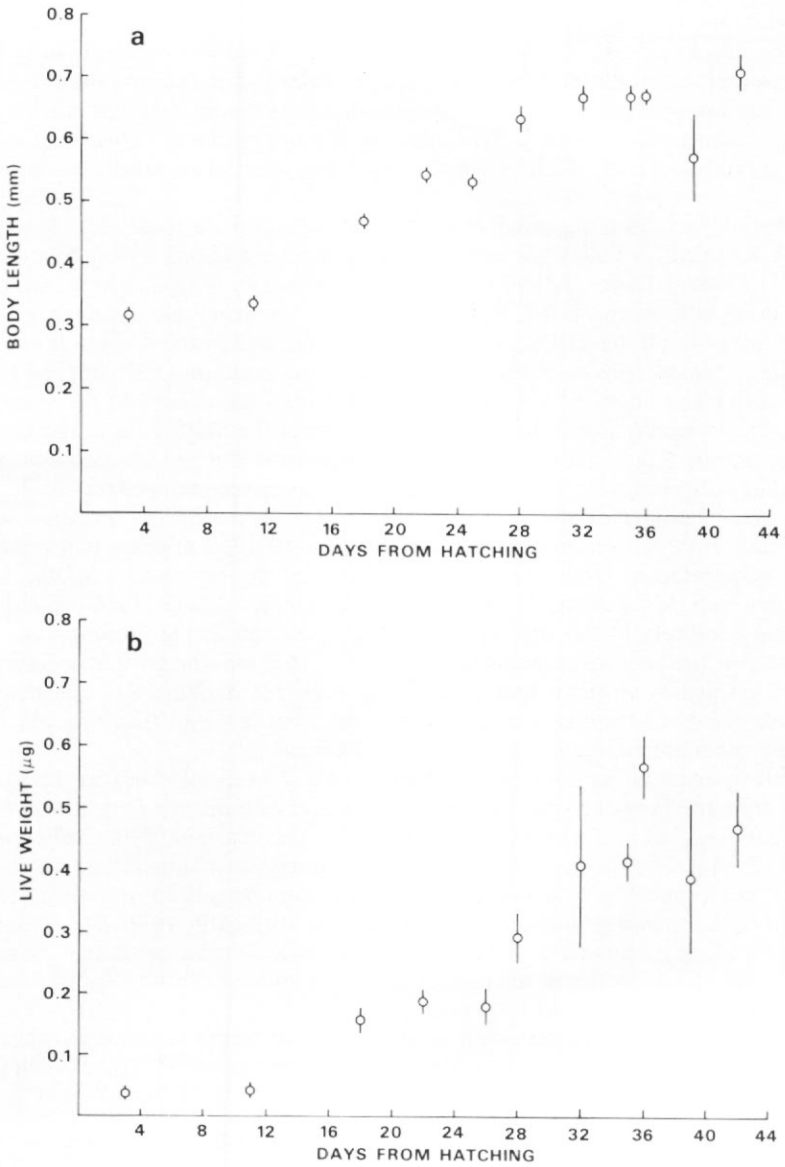


Fig. 4. Mean (± 1 SE) increase in body length (a) and live weight (b) of *Plectus antarcticus* at 10°C.

Maslen (1981) listed 15 nematode genera from the SIRS of which *Ditylenchus, Tylenchus, Aphelenchoides, Plectus, Teratocephalus, Monhystera* and *Eudorylaimus* were commonly found on both sites. Although he reported *Coomansus* in one core from SIRS 1, neither Spaull nor the present author found it on this site and it is possible that a wetter flushed area was sampled on that occasion. The three rhabditid species found on single occasions by Maslen were not encountered during the current study and it is apparent from Spaull (1969) that *Cervidellus* sp. favours soils associated with the higher plants *Deschampsia antarctica* Desv. and *Colobanthus crassifolius* (D'Urv) Hook. f. *Amphidelus* sp. is abundant in mosses such as *Andreaea* and

Grimmia which are virtually absent from the sites (personal communication from R. I. Smith), and *Rhabditis* subgenus A sp. (called *Caenorhabditis* by Spaull) is predominantly found in penguin rookeries and seal wallows. One additional genus was found during the present study: this was *Panagrolaimus* sp. which is commonly associated with soils contaminated by vertebrates, e.g. close to seabird nests. This is true also of *Mesodorylaimus signatus* Loof, 1975, and *Enchodelus signyensis* Loof, 1975, of which only a few specimens have been recorded in SIRS cores.

Teratocephalus has been reported from several high-latitude sites, e.g. Macquarie Island (Bunt, 1954), Kościeliska Valley (Brzeski, 1962), Spitzbergen (Loof, 1971), Stordalen (Lagerlöf and others, 1975) and Devon Island (Proctor, 1977), and both Spaull and Maslen found this genus to be dominant on the SIRS. The present study confirms this dominance below the top centimetre of moss in all the SIRS quadrats investigated, and in the 4–7 cm horizon of SIRS 2 *Teratocephalus* formed >90% of the total nematode population. This implies that it is well adapted to survive conditions of low oxygen and relatively high pH (4.9; personal communication from D. D. Wynn-Williams) that are characteristic of the SIRS 2 peat. The occurrence of a single species dominating a habitat is generally uncommon but not unknown at Signy Island, where *Rhabditis* subgenus A sp. is the only nematode associated with penguin rookery soil.

From the small number of species that are common on the SIRS compared with the total number recorded from the maritime Antarctic (Maslen, 1980), it appears that many have fairly rigid habitat requirements, and this is demonstrated by the distribution of the fungal feeder *Ditylenchus* sp. and *Monhystera villosa*, a bacterial feeder. Spaull (1969) found *Ditylenchus* restricted almost entirely to the top 3 cm of his samples and in the present study most of the population was in the topmost centimetre (Table V). This may mean that it feeds upon living moss cells or on yeasts or fungi that mainly occur in this horizon. *M. villosa*, a very active nematode, was evenly distributed throughout the top 3 cm of the quadrats in which it occurred and was rarely encountered in the presence of *Ditylenchus*.

It is difficult to draw direct comparisons between the 2 years of study as the sampling areas were slightly different. However, the changes in vertical distribution in *Drepanocladus* were similar in both years (Fig. 5) and were also comparable to the distribution in *Calliergon–Calliergidium* (Spaull, 1973*a*). The results from *Polytrichum* can also be compared as the two areas were within 1 m of each other. Fig. 6 shows the mean population density for the strata studied in each year, and below the growing portion of the moss (not studied in 1976–77), the numbers and distribution of feeding groups were very similar. Nematode distribution in this substrate is probably limited by the dense nature of the peat; in the top centimetre shoot density would be a more important factor governing nematode numbers.

Seasonal changes in population density, with low winter numbers followed by an increase in spring, have been shown for Antarctic nematodes by Tilbrook (1973*b*) and Spaull (1973*a*) as

TABLE V. MEAN POPULATION DENSITY ($\times 10^3$ m^{-2}) OF *Monhystera villosa* AND *Ditylenchus* sp. AT SIRS 1 AND 2 IN 1977–78

Quadrat	*Depth* (cm)	*M. villosa*	*Ditylenchus* sp.	*Quadrat*	*M. villosa*	*Ditylenchus* sp.
23	0–1	452.8	90.2	A10	270.2	8.3
	1–2	361.4	—		342.4	2.4
	2–3	235.1	1.4		421.5	0.6
136	0–1	2.6	865.4	B14	2.9	132.2
	1–2	2.1	17.9		1.3	7.2
	2–3	0.7	11.6		0.8	3.4
149	0–1	91.2	4.2	C29	33.3	0.4
	1–2	79.8	0.7		62.0	0.3
	2–3	32.1	—		51.6	0.1

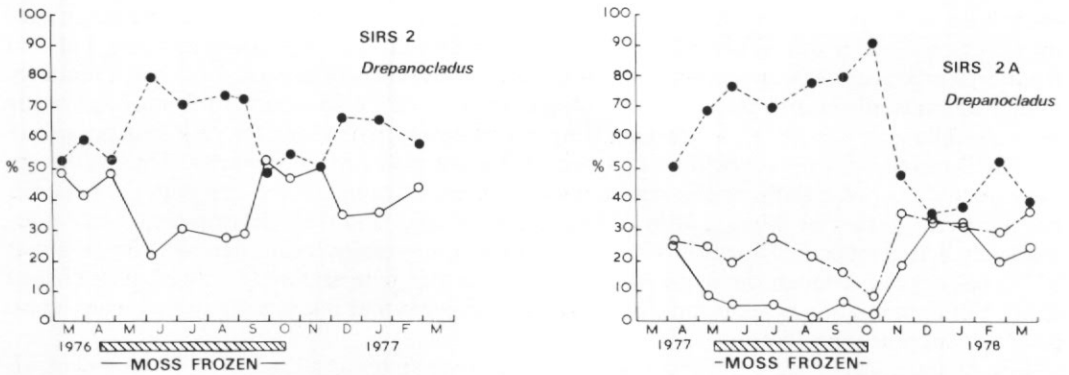
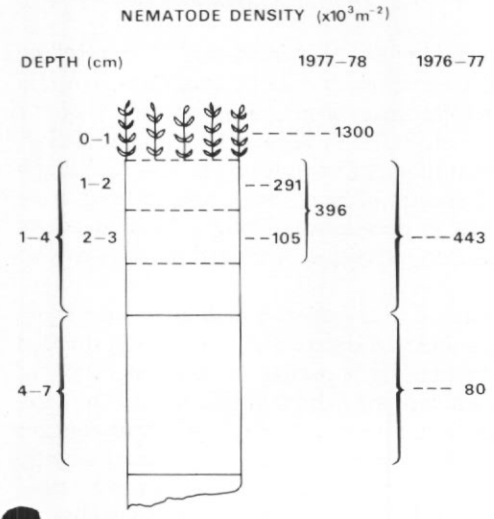


Fig. 5. Vertical distribution of nematodes (as percentages in each horizon) in *Drepanocladus* on SIRS 2 during 1976/77 and in quadrat A 10 (SIRS 2A) in 1977–78.
SIRS 2 ○——○ 1–4 cm; ●- - - -● 4–7 cm.
SIRS 2A ○——○ 0–1 cm; ○——○ 1–2 cm; ●- - -● 2–3 cm.



PERCENTAGE OF NEMATODE POPULATION

	1977-78 (1–3 cm)	1976-77 (1–4 cm)
Feeding group		
Fungal	15.0	18.0
Bacterial	79.9	77.2
Omnivore	5.1	4.8

Fig. 6. Vertical distribution of nematodes in *Polytrichum* of SIRS 1 during 1976–78.

well as the current study. Although not occurring in all the quadrats studied, these changes were most evident in the top centimetre of the moss (Figs 2 and 3), which suggests that temperature is the most important factor controlling nematode density. Freeze–thaw cycles occur more frequently and extremes of temperature are more severe at the moss surface and consequently there is a greater mortality here in autumn and winter than lower down in the peat profile. Conversely, the top centimetre experiences higher summer temperatures, so that growth, development and egg production will be greater here. At the onset of spring there is a massive increase in microbial activity (personal communication from D. D. Wynn-Williams), which would provide a rich source of food material. Experiments with *P. antarcticus* suggest that eggs laid during this period would not hatch for at least 30 d, even if the temperature remained near to 5°C, and thus would

contribute to the peak in numbers between 1 and 3 months after the thaw. Maximum egg production would occur at this period as well as recruitment into the population of young hatched from eggs produced in the previous year. However, the juvenile worms would not reach maturity until after midsummer and perhaps not until late autumn. In a cold summer this may not occur until the following year. Even at 10°C, a temperature rarely maintained for very long periods in the SIRS mosses, 6 weeks would be required for the worms to reach maturity. Thus, although the nematode population fluctuates seasonally in response to temperature, this may not occur as rapidly as suggested by Maslen (1981). Production of eggs and their development time varies markedly between species. Spaull (1969) showed that *Panagrolaimus* eggs hatched after 4–5 d at 12°C but eggs of *Coomansus* required at least 19 d at this temperature (Caldwell, unpublished data). Futhermore, observations on *Teratocephalus* indicate that this species has a longer larval development time than *Plectus*.

Results from winter cores suggest that nematodes overwinter at all stages of development, although the techniques used do not extract eggs of quiescent stages. Spaull (1973*a*) found no specimens of *Monhystera villosa* in fresh winter cores unless they were allowed to thaw at 12°C for at least 24 h, after which time juveniles were extracted and, after storing thawed cores at this temperature for several days, adults were extracted. This led him to postulate that *M. villosa* overwinters as eggs or quiescent juveniles. During the 1977 winter, however, this species was frequently extracted, the only exceptions being when it was not found on two occasions in the cores from quadrat B14. As it was normally uncommon at this site (Table V), it is likely that Spaull's results were due to its restricted distribution pattern.

Although temperature, and to a lesser extent water content, are important in controlling nematode populations, other factors may be involved. The predatory mite *Gamasellus racovitzai* (Trouessart) is found on SIRS 1 (Goddard, 1979) and the carnivorous tardigrade *Macrobiotus furciger* J. Murr. occurs on both sites (1.1×10^4 m^{-2} on SIRS 1; 8.7×10^4 m^{-2} on SIRS 2; Jennings, 1979). Their effect cannot be assessed nor can that of *Coomansus gerlachei*, although this species only occurs in low numbers. At least 12 species of nematode-trapping fungi have been reported from Antarctic mosses (Gray and others, in press), but although the precence of these was seen in some of the SIRS worms, the extraction technique precluded most worms so affected.

Tilbrook (1967) found seasonal variations in the vertical distribution of nematodes on Signy Island and he suggested (Tilbrook, 1970) that this was due to a differential mortality in the 0–3 and 3–6 cm horizons. Spaull (1973*a*) suggested that there is a partial upward migration of nematodes at the spring thaw and a corresponding downward movement during the late autumn, a view supported by Maslen (1981). However, Maslen found no statistically significant changes in population density in the lower stratum, and Spaull's 3–6 cm figures only varied slightly during the 2 years of his study. Large seasonal fluctuations in numbers were shown in Spaull's 0–3 cm horizon and were evident in the present study but this is not necessarily an indication of vertical migration. This large increase during spring (Spaull, 1973*a*) corresponded with only a small decrease in the lower strata, and is consistent with the deeper layers thawing more slowly (Walton, 1977) and not experiencing increased microbial activity. Conversely, in late autumn, numbers in the lower horizon continued to increase slightly while more severe temperatures in the upper horizon induced a rapid population decline.

Simple corers used in the past on Signy Island tended to compress severely the deeper layers of peat which could result in artificially high population estimates when compared to winter samples where no such compressing occurred. This problem was surmounted by use of slit corers which also enabled the peat horizons to be marked before the cores were expressed from the tubes. Care was needed with the use of the winter corer to avoid erosion of the moss surface as this would lead to an underestimate of population size, especially in *Polytrichum*.

The efficiency of extraction is one of the major factors influencing the estimated density and, unless it is known, direct comparisons between population studies are of uncertain value. It is

improbable that all stages of SIRS nematodes were extracted at the same rate by the modified Baermann technique, as juveniles undoubtedly move more quickly than adults, and very active free-swimming species such as *M. villosa* might be extracted more efficiently than larger/slower species such as *Eudorylaimus* or *Teratocephalus* and *Plectus* that attach themselves to the substrate. Extraction should be undertaken at a constant temperature throughout the year, and at an optimum temperature for nematode activity. This, however, may not be similar for all species. Nematodes from recently thawed winter cores may behave differently from those collected during summer and thus apparent population changes could be an artefact of the extraction technique. Finally, the nature of the peat itself may affect extraction efficiency. A densely packed peat like *Polytrichum* may retain a greater proportion of the nematode population than the more loosely structured peat of SIRS 2 and thus give an artificially low value. No perfect test of the modified Baermann technique exists because of the variables mentioned above, and values of its efficiency in the literature range from 34% (Procter, 1977) to 90% (Banage, 1963).

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REFERENCES

ANDRÁSSY, I. 1956. Die Rauminhalts-und Gewichtbestimmung der Fadenwürmer (Nematoden). *Acta zool. hung.*, **2,** Nos. 1–3, 1–15. English translation: The determination of volume and weight of nematodes. (*In* ZUCKERMAN, B. M., BRZESKI, M. W. *and* K. H. DEUBERT. 1967. *English translation of selected East European papers in nematology*. Massachusetts, University of Massachusetts, 73–84.)

BANAGE, W. B. 1963. The ecological importance of free-living soil nematodes with special reference to those of moorland soil. *J. Anim. Ecol.*, **32,** No. 1, 133–40.

BROADY, P. A. 1977. The Signy Island terrestrial reference sites: VII. The ecology of the algae of site 1, a moss turf. *British Antarctic Survey Bulletin*, No. 45, 47–62.

———. 1979. The Signy Island terrestrial reference sites: IX. The ecology of the algae of site 2, a moss carpet. *British Antarctic Survey Bulletin*, No. 47, 13–29.

BRZESKI, M. 1962. The nematodes of the peat-mosses in Kościeliska Valley (western Tatra). *Acta zool. cracov.*, 87, No. 2, 23–37.

BUNT, J. S. 1954. The soil-inhabiting nematodes of Macquarie Island. *Aust. J. Zool.*, **2,** No. 2, 264–74.

DE MAN, J. G. 1904. Nematodes libres. *Résult. Voyage S. Y. Belgica*, Zoologie, 55 pp.

DUNCAN, A., SCHIEMER, F. *and* R. Z. KLEKOWSKI. 1974. A preliminary study of feeding rates on bacterial food by adult females of a benthic nematode *Plectus palustris* de Man 1880. *Polskie Archwm Hydrobiol.*, **21,** No. 2, 249–58.

GODDARD, D. G. 1979. The Signy Island terrestrial reference sites: XI. Population studies on the Acari. *British Antarctic Survey Bulletin*, No. 48, 71–92.

GRAY, N. H., WYBORN, C. H. E. *and* R. I. L. SMITH. In press. An ecological study of nematophagous fungi from the maritime Antarctic. *Oikos*.

HOOPER, D. J. 1970. Handling, fixing, staining and mounting nematodes. (*In* SOUTHEY, J. F., *ed.* Laboratory methods for work with plant and soil nematodes. *Tech. Bull. Min. Agric. Fish & Food*, No. 2, 39–54.)

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.

JONES, J. G. 1979. A guide to methods for estimating microbial numbers and biomass in fresh water. *Scient. Publ. Freshwat. biol. Ass.*, No. 3, 112 pp.

LAGERLÖF, J., MAGNUSSON, C. *and* T. ROSSWALL. 1975. Investigation of nematodes at the Stordalen site. *International Biological Programme, Swedish Tundra Biome Project. Technical Report*, No. 18, 32 pp.

LOOF, P. A. A. 1971. Freeliving and plant parasitic nematodes from Spitzbergen, collected by Mr H. van Rossen. *Meded. LandbHoogesch. Wageningen*, **71–7,** 1–86.

MASLEN, N. R. 1980. Additions to the nematode fauna of the Antarctic region with keys to taxa. *British Antarctic Survey Bulletin*, No. 49, 207–29.

———. 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.

MICHELBACHER, A. E. 1939. Seasonal variation in the distribution of two species of *Symphyla* found in California. *J. econ. Ent.*, **32,** No. 1, 53–57.

PROCTER, D. L. C. 1977. Nematode densities and production on Truelove Lowland. (*In* BLISS, L. C., *ed. Truelove Lowland, Devon Island, Canada: a High Arctic ecosystem.* Calgary, The University of Alberta Press, 347–61.)

SMITH, H. G. 1973. The Signy Island terrestrial reference sites: II. The Protozoa. *British Antarctic Survey Bulletin*, Nos. 33 and 34, 83–87.

SPAULL, V. W. 1969. Soil nematodes of Signy Island, an interim report (B.A.S. No. N6/1969/H), 30pp. [Unpublished.]

———. 1973*a*. Seasonal variation in numbers of soil nematodes at Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin*, Nos. 33 and 34, 47–56.

———. 1973*b*. The Signy Island terrestrial reference sites: IV. The nematode fauna. *British Antarctic Survey Bulletin*, No. 37, 94–96.

TILBROOK, P. J. 1967. 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 terrestrial environment and invertebrate fauna of the maritime Antarctic. (*In* HOLDGATE, M. W., *ed. Antarctic ecology*. London and New York, Academic Press, 886–96.)

———. 1973*a*. The Signy Island terrestrial reference sites: I. An introduction. *British Antarctic Survey Bulletin*, Nos. 33 and 34, 65–76.

———. 1973*b*. *Terrestrial arthropod ecology at Signy Island, South Orkney Islands*, Ph.D. thesis, University of London, 254 pp. [Unpublished.]

WALTON, D. W. H. 1977. Radiation and soil temperatures 1972–74: Signy Island terrestrial reference site. *British Antarctic Survey Data*, No. 1, 51 pp.

WHITEHEAD, A. G. *and* J. R. HEMMING. 1965. A comparison of some quantitative methods of extracting small vermiform nematodes from soil. *Ann. appl. Biol.*, **55,** No. 1, 25–38.