SEASONAL VARIATION IN NUMBERS OF SOIL NEMATODES AT SIGNY ISLAND, SOUTH ORKNEY ISLANDS

By V. W. SPAULL

ABSTRACT. The generic composition of the nematode fauna of three moss habitats on Signy Island is given. Total numbers are comparable with those from temperate moor soils ($0 \cdot 25–1 \cdot 97 \times 10^6$/m.^{2}). Monthly sampling showed that the size of the nematode population varied during the year. Maximum numbers occurred in the summer but during the winter, when the moss was frozen, there was a decline in numbers reaching a minimum just before the spring melt. This decline in numbers was greater in the 0–3 cm. layer than the 3–6 cm. layer, due, it is thought, to autumn freeze-thaw cycles that are more frequent in the surface layer. There was evidence of a partial upward migration of some of the genera during the spring and a partial downward migration in the autumn.

IT is perhaps indicative of the early stage of development of Antarctic nematology that most reports on soil nematodes describe new species whilst others add new records to the Antarctic fauna. Timm (1971) reviewed these papers and added three species to the list of Antarctic nematodes, two of which were new to science. More recently, Spaull (1972) described a species collected at Signy Island (lat. 60°43′S., long. 45°38′W.) that belonged to a new genus and sub-family.

The only quantitative data have been given for Signy Island by Tilbrook (1967*a*, *b*, 1970), who reported that nematodes occurred in large numbers, showing a preference for the wetter bryophytes and soil associated with vascular plants. There was no evidence of a seasonal change in numbers but the vertical distribution altered during the year.

The climate and vegetation of Signy Island is typical of the maritime Antarctic; the mean temperature of the warmest month is a little above freezing point and that of the coldest month rarely falls below −10° C. Precipitation is frequent and in summer it may fall as rain. The vegetation is dominated by lichens and mosses, although liverworts do occur and two flowering plants are locally abundant in sheltered lowland areas.

This paper reports a more detailed investigation of the ecology of the soil nematodes on Signy Island, especially in relation to their seasonal variation in numbers under the rather severe climatic conditions.

MATERIALS AND METHODS

Sample sites

Samples were taken from sites representing three of the main plant communities in the maritime Antarctic (Gimingham and Smith, 1970). The primary sample site was a moss-carpet sub-formation composed of a mixed stand of *Calliergon sarmentosum* (Wahlenb.) Kindb. and *Calliergidium austro-stramineum* (C. Muell.) Bartr., the former constituting about 80 per cent of the vegetation. The site was on a very slight north-facing slope, approximately 18 m. above sea-level on the eastern side of the island near the British Antarctic Survey station at Factory Cove. The vegetation extended to a maximum depth of 20 cm. with quartz-mica-schist as the bedrock. The pH was $4 \cdot 65$ at a depth of $2 \cdot 5$ cm. and $4 \cdot 36$ at $5 \cdot 0$ cm. (mean of eight readings taken in February 1970).

The moss was nearly always wet and often waterlogged. There was a marked seasonal change in the water content, with a maximum in winter and a minimum in summer (Fig. 1). It is possible that the high winter values for the water content of the 0–3 cm. layer are partly due to ice frozen to the surface of the moss, although an effort was made to remove all such extraneous ice.

During the period of study the temperature in the moss at a depth of $2 \cdot 0$–$2 \cdot 5$ cm. was recorded using a thermistor attached to a Wheatstone bridge; resistance readings were taken daily. When the thermistor was calibrated, it was found that its characteristics had altered slightly. The temperature data presented here are therefore approximate but they are sufficient to indicate the general trends in the moss (Fig. 1). The mean monthly air temperatures in the 1969 winter were lower than those in 1968, resulting in lower moss temperatures. In the winter

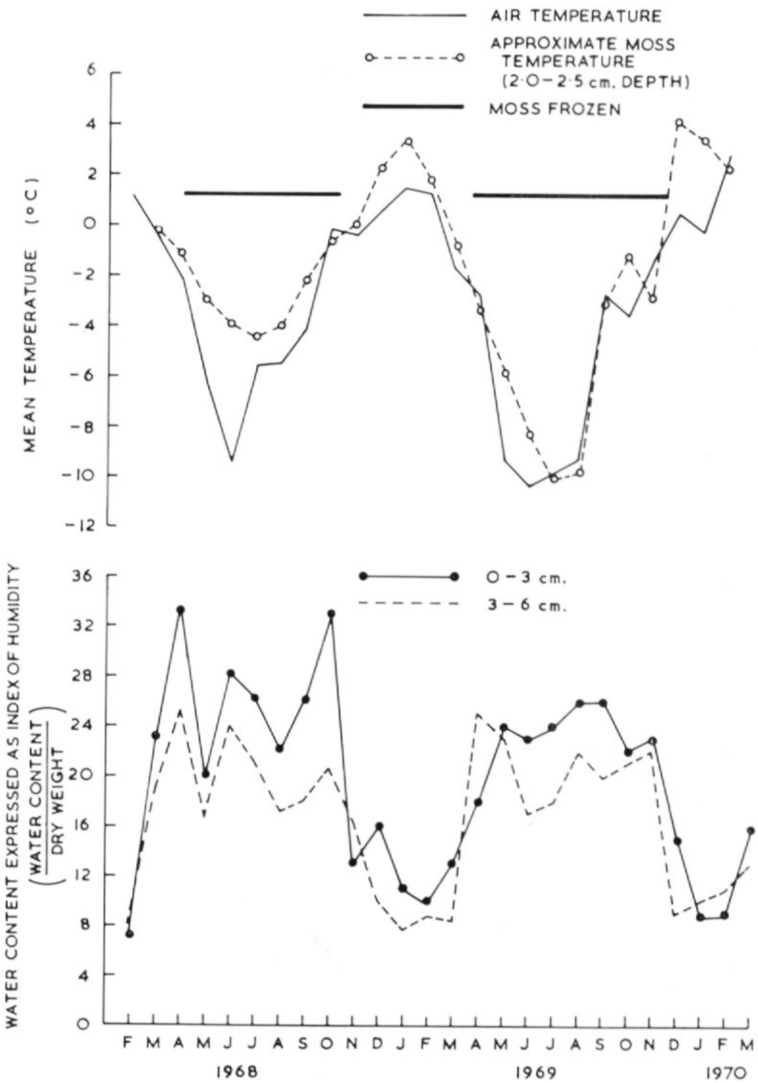

Fig. 1. Temperature, water content and duration of the winter freeze in the *Calliergon–Calliergidium* site.

of 1968 the minimum temperature at 2·0 cm. was −16·5° C and in 1969 it was −19·0° C (readings taken from a minimum thermometer left in the moss over winter). The site was snow-covered in both winters to an average depth of approximately 9 cm. During the course of the winter the deeper layers of snow were converted to ice.

The two secondary sample sites were a moss-turf sub-formation composed of *Chorisodontium aciphyllum* (Hook. f. et Wils.) Broth. and *Polytrichum alpestre* Hoppe, and a moss-cushion sub-formation composed almost entirely of *Andreaea gainii* Card. At a depth of 2·5 cm. the pH was 4·08 in the *Chorisodontium–Polytrichum* site and 4·96 in the *Andreaea* site. The water content of these two sites was lower than in the *Calliergon–Calliergidium* site but it showed similar seasonal variation. The depth of snow cover on the *Andreaea* and *Calliergon–Calliergidium* sites was similar but it was considerably greater on the *Chorisodontium–Polytrichum* site.

Sampling, extraction and counting

Four, 4·2 cm. diameter cores were taken at random from the three sites at monthly intervals from February 1968 until February 1969. The cores were taken to a depth of 6 cm., except in the *Andreaea* site where they were only taken to 3 cm. because the moss rarely exceeded this depth. Sampling was continued at the *Calliergon–Calliergidium* site until March 1970. In September 1968 and subsequent months the number of cores taken from the *Calliergon–Calliergidium* site was increased to eight per month in an effort to overcome the wide variation in numbers of nematodes per core within months. During the summer the cores were obtained using a simple steel cylindrical corer but in winter, when the moss was frozen, a modified corer had to be used. This consisted of a hardened steel, toothed cylinder attached to a modified carpenter's brace (see Baker, 1970).

The 6 cm. cores were divided in half horizontally, to provide data on the vertical distribution, and the nematodes were extracted using a modified Baermann funnel similar to that used by Whitehead and Hemming (1965). The cores were teased apart on a "Kleenex" paper tissue (the two halves being treated separately), supported on thick nylon gauze in a plastic tray. Water at approximately 15° C was added so that it just covered the vegetation.

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

After thoroughly mixing the nematode suspension, by bubbling air through it, a proportion, generally not less than one-eighth, was pipetted into a counting tray. The numbers of each genera were then counted but the numbers of each species were not recorded. The species composition of these and other sites on Signy Island will be presented later.

RESULTS

Nematode fauna of the Calliergon–Calliergidium site

The fauna of this site was composed of 12 genera: *Ditylenchus*, *Tylenchus*, *Antarctenchus*, *Aphelenchoides*, *Eudorylaimus*, *Amphidelus*, *Plectus*, *Teratocephalus*, *Monhystera*, *Prismatolaimus*, *Clarkus* and an unidentified monhysterid here referred to as monhysterid genus "A". (Whilst making the monthly counts, *Tylenchus* was not separated from *Antarctenchus*, nor *Monhystera* from *Prismatolaimus*.)

There were an estimated 1·97 ± 0·08 million nematodes per square metre, 6 cm. deep, in the *Calliergon–Calliergidium* site (mean and standard error of 180 sample units). *Plectus* comprised 35·2 per cent of the total population, *Teratocephalus* 33·8 per cent, *Eudorylaimus* 8·8 per cent and *Monhystera/Prismatolaimus* 7·8 per cent. The remaining genera individually constituted less than 5 per cent.

Seasonal variation in numbers

Fig. 2 shows the seasonal variation in total numbers from February 1968 to March 1970. Allowing for the erratic fluctuations, which are thought to be due to sampling errors rather than any change in actual numbers, there was a decline in numbers during the winter, reaching a minimum just before the spring melt. This was followed by an increase in the summer, maximum numbers occurring in February or March. The population level was much higher in the 1968–69 summer than in the previous one. The fall in numbers during the winter was of a similar magnitude in both years, although there were differences between individual genera, within and between years (Table I).

As for the seasonal variation of the component genera, *Plectus* showed a similar pattern to the total fauna (Fig. 3); *Eudorylaimus* and *Monhystera/Prismatolaimus* differed from this in that minimum numbers were reached just before, or soon after, the onset of winter (Fig. 3). Although less marked, the seasonal variation of *Tylenchus/Antarctenchus*, *Amphidelus* and monhysterid genus "A" was similar to that of *Eudorylaimus;* the remaining genera, apart from increasing in numbers after the 1968 winter, showed no clear seasonal trends.

The increase in total numbers from the end of the winter to the beginning of February was

TABLE I. NUMBERS OF NEMATODES PRESENT IN THE SAMPLE SITES AT THE BEGINNING AND END OF WINTER AND AT THE HEIGHT OF SUMMER (MEAN OF FOUR OR EIGHT CORES, 1/721·5 m.², 6 cm. DEEP, TO THE NEAREST WHOLE NUMBER)

Genus	*Calliergon–Calliergidium*						*Chorisodontium–Polytrichum*			*Andreaea* (*3 cm. deep*)		
	April 1968	Oct. 1968	Feb. 1969	April 1969	Nov. 1969	Feb. 1970	April 1968	Oct. 1968	Feb. 1969	April 1968	Oct. 1968	Feb. 1969
Ditylenchus	45	26	97	90	85	224	0	1	8	0	1	0
Tylenchus/Antarctenchus	103	45	256	116	47	148	2	2	106	35	13	68
Aphelenchoides	2	2	49	68	6	9	42	17	78	0	1	0
Plectus	1,369	629	1,433	1,142	487	1,049	79	35	130	112	38	80
Teratocephalus	305	340	1,361	1,082	817	1,731	138	81	293	1,056	723	1,582
Monhystera/Prismatolaimus	110	10	973	8	4	338	0	1	3	48	11	232
Monhysterid genus "A"	47	34	260	116	117	167	0	1	0	112	47	180
Amphidelus	31	10	70	10	3	27	0	1	0	35	38	76
Eudorylaimus	159	160	834	82	112	576	7	4	38	318	140	896
Enchodelus	—	—	—	—	—	—	2	17	13	0	1	0
Clarkus	21	34	78	46	33	99	0	0	1	0	0	0
TOTAL NEMATODES	2,192	1,290	5,411	2,760	1,711	4,368	270	160	670	1,716	1,013	3,114

— Absent for sample site.
0 Not found in sample but recorded on another sampling occasion.

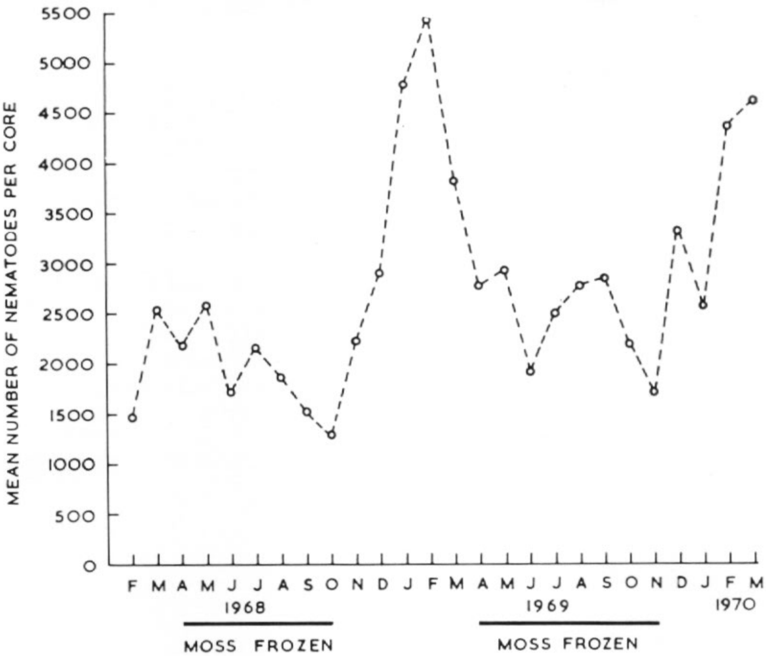

Fig. 2. Seasonal variation in numbers of nematodes from the *Calliergon–Calliergidium* site, 0–6 cm.

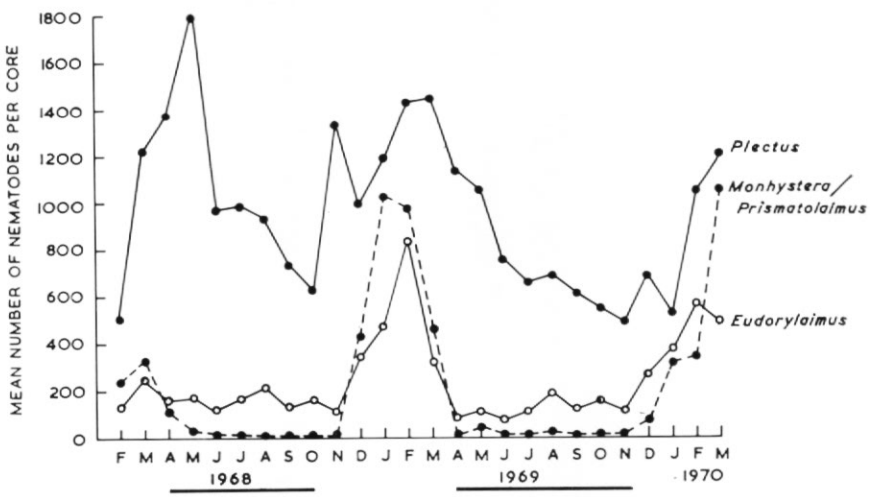

Fig. 3. Seasonal variation in numbers of *Plectus*, *Eudorylaimus* and *Monhystera/Prismatolaimus* from the *Calliergon–Calliergidium* site, 0–6 cm.

greater in the 1968–69 summer than in the following one, and there was considerable variation in the degree to which the individual genera increased during both of these periods (Table I).

Seasonal variation in the vertical distribution

During the year there was a change in the distribution of the nematodes in the 0–3 and 3–6 cm. layers of the *Calliergon–Calliergidium* community. This is most clearly shown by comparing the percentage distribution of the nematodes at the two depths (Fig. 4). In the summer about 80 per cent of the nematodes occurred in the surface 3 cm. of the moss. During the autumn and early winter the proportion in this layer decreased and by the end of the winter the majority were found in the lower layer. The distribution reverted to the summer condition after the spring melt.

Tilbrook (1967*b*) found a similar seasonal variation in the vertical distribution of nematodes on Signy Island and he suggested (Tilbrook, 1970) that this was due to a differential mortality. However, data obtained from the present study indicate that this is not the complete explanation.

Immediately after the spring melt in October 1968 the sharp increase in the proportion of nematodes in the 0–3 cm. layer was due to a large increase in numbers in this layer associated with a decrease in the 3–6 cm. layer (Fig. 5). This is taken as evidence of a partial upward

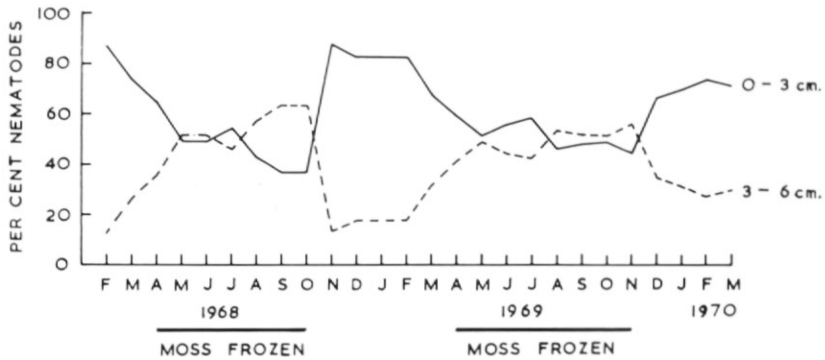

Fig. 4. Seasonal variation in nematode distribution in the 0–3 and 3–6 cm. layers of the *Calliergon–Calliergidium* site (expressed as a percentage of the total).

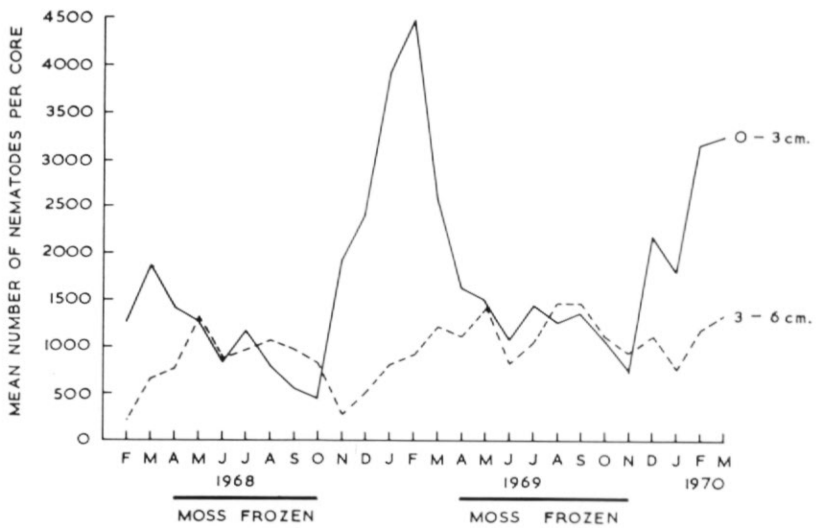

Fig. 5. Seasonal variation in nematode distribution in the 0–3 and 3–6 cm. layers of the *Calliergon–Calliergidium* site.

migration. After this, the percentage numbers in the two layers did not alter appreciably owing to a proportional increase in numbers at both depths. During the autumn, before the onset of the winter freeze, the decrease in the proportion of nematodes in the 0–3 cm. layer was due to a continued increase in numbers in the 3–6 cm. layer associated with a decrease in the surface layer. This is taken as evidence of a partial downward migration.

Of the individual genera, *Clarkus*, *Plectus* and monhysterid genus "A" clearly showed signs of a partial spring and autumn migration (Fig. 6). Apart from *Ditylenchus* and *Aphelenchoides*, there was some evidence of a partial vertical migration of the remaining genera on at least one occasion.

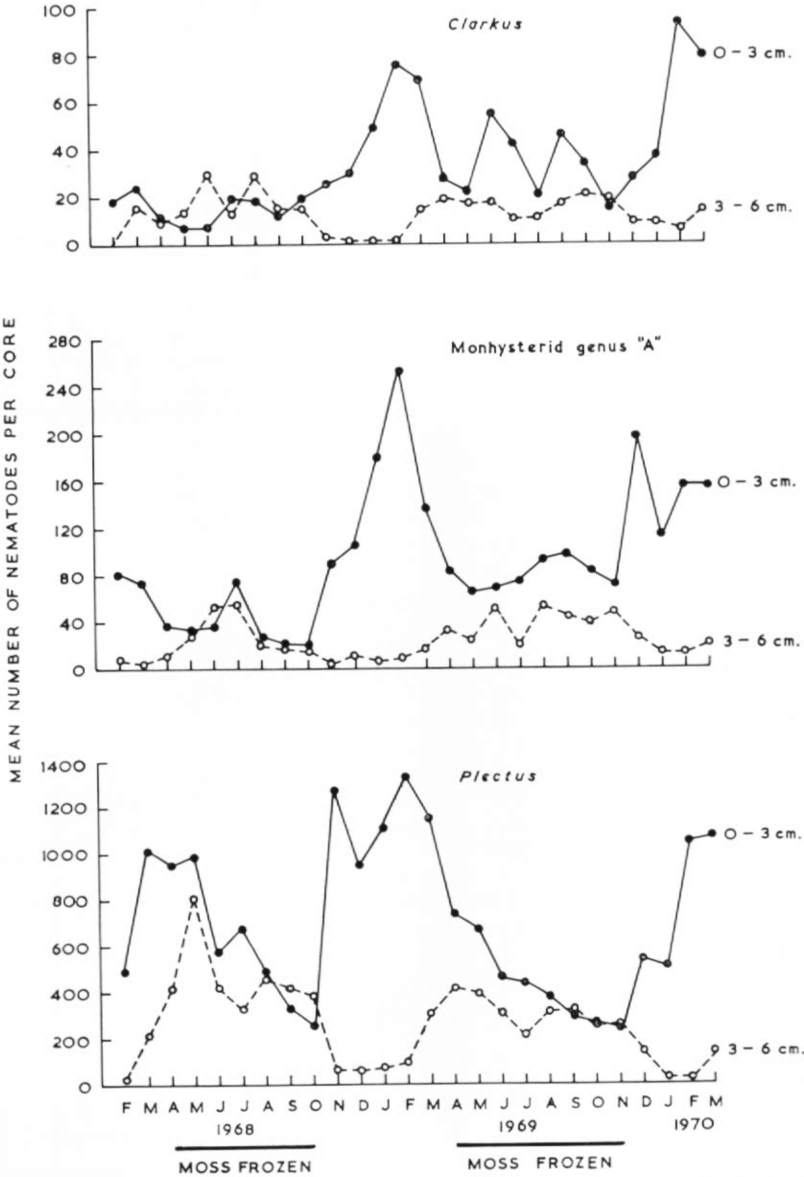

Fig. 6. Seasonal variation of *Plectus*, *Clarkus* and monhysterid genus "A" at two depths in the *Calliergon–Calliergidium* site.

The numbers of *Clarkus*, *Plectus* and monhysterid genus "A" did not increase in the 3–6 cm. layer for the first 4 months of the summer, whereas there was an increase in numbers of the other genera in this layer. Possibly these three genera continue to migrate upwards during the summer.

The continued change in the vertical distribution of nematodes that occurred during the winter cannot be explained by migration or reproduction since the moss was frozen during this period. In fact, the change was due to a relatively greater decline in numbers in the 0–3 cm. layer compared with the 3–6 cm. layer. During the 1968 winter there was a 67 per cent reduction in numbers in the 0–3 cm. layer with no apparent decline in the 3–6 cm. layer. In the following winter there was a 54 per cent reduction in numbers in the 0–3 cm. layer and only a 14 per cent reduction in the 3–6 cm. layer. In both winters nearly all of the genera showed a greater decline in numbers in the surface layer.

Nematode fauna and seasonal variation in the Chorisodontium–Polytrichum and Andreaea sites

The fauna of these two sites was similar to that of the *Calliergon–Calliergidium* site, although the percentage abundance of the genera was different. In the *Chorisodontium–Polytrichum* site, *Teratocephalus* comprised 50·0 per cent of the total population and *Plectus* 27·8 per cent. In the *Andreaea* site, *Teratocephalus* comprised 58·7 per cent of the total, *Eudorylaimus* 21·3 per cent and *Plectus* only 3·8 per cent.

There was an estimated 0·25 ± 0·03 million nematodes per square metre, 6 cm. deep in the *Chorisodontium–Polytrichum* site and 1·21 ± 0·11 million per square metre, 3 cm. deep in the *Andreaea* site (each the mean and standard error of 52 sample units).

The seasonal variation of the total numbers and of the commonly occurring genera in both sites was similar to that in the *Calliergon–Calliergidium* site. In fact, both the population decrease during the winter and the population increase during the summer were very much the same in all three sites (Table I).

In the *Chorisodontium–Polytrichum* site, where samples were taken to a depth of 6 cm., there was a differential decline in numbers in the 0–3 and 3–6 cm. layers but it was less marked than in the *Calliergon–Calliergidium* site. There was no apparent spring or autumn vertical migration in the *Chorisodontium–Polytrichum* site.

Discussion

The seasonal change in numbers of nematodes found on Signy Island is similar to that recorded by Burkhalter (1928) and Yeates (1968). It differs from the seasonal variation recorded by Banage (1966) and Winslow (1964) in that they found minimum numbers in mid or late summer with a rise to maximum in the autumn.

Temperature was probably the over-riding factor that caused the seasonal change in numbers on Signy Island, since it restricted nematode activity to a few months in the summer. This limited period of activity may have caused the similar patterns of seasonal variation shown by the nematode genera in the *Calliergon–Calliergidium* site. However, some difference did occur as shown by the rapid autumn decline of *Eudorylaimus* and *Monhystera/Prismatolaimus* compared with the more gradual decline of *Plectus*. During the autumn the top few centimetres of the moss may freeze then thaw several times before attaining a continuous frozen state (Chambers, 1966). Freeze-thaw cycles are damaging to nematodes and may be more injurious to some genera than others (Hwang, 1970); the autumn decline of *Eudorylaimus* and *Monhystera/Primatolaimus* may partly be a result of these cycles. As the cycles occur more frequently in the surface layer (Chambers, 1966), they may perhaps be the cause of the differential decline in numbers in the winter; nematodes subjected to freeze-thaw cycles, if not killed at once, would presumably be less able to survive the winter conditions and would therefore show a greater decline in the surface layer.

Some juvenile nematodes are better able to survive sub-zero temperatures than adults (Rhoades and Linford, 1961; Burns, 1964; Hwang and Sayre, 1969). On Signy Island, life stages of all the genera, except *Monhystera*, appeared to be present throughout the winter, and actual counts made of the males, females and juveniles of *Eudorylaimus* showed that there was no apparent difference in their ability to overwinter. Although juveniles of *Monhystera* were very occasionally counted as *Prismatolaimus*, and the counts have therefore been combined, it was noted that throughout the winter no adults of *Monhystera* occurred in any of the mosses subjected to the normal extraction period and it is possible that no juveniles occurred either. However, when cores of *Calliergon–Calliergidium* were thawed at 12° C for 24 hr. prior to extraction, juvenile *Monhystera* were found to be present and in cores kept for several days at 12° C adults were also found. It may be that this genus overwinters in a quiescent juvenile stage; the much larger increase in numbers of *Monhystera/Primatolaimus* after the spring melt, compared with the other genera, lends support to this idea.

Sayre (1964) discussed several ways by which soil nematodes may be protected from freezing temperatures, and he divided them into three groups according to their response to falling temperatures. Since the Signy Island nematodes survive the winter freeze, they must belong either to the "freezing-susceptible" or to the "freezing-resistant" group; the former survive by supercooling while the latter are not injured by the formation of small internal ice crystals. It seems probable that the Signy Island nematodes are freezing resistant, since winter soil temperatures fall below the level to which nematodes usually supercool; eggs of nematodes may, however, supercool to much lower temperatures (Sayre, 1964).

The partial vertical migrations that occurred with some of the genera in the *Calliergon–Calliergidium* site are similar to those found for *Ditylenchus dipsaci* in organic soil in North America (Lewis and Mai, 1960). The upward spring migration may have been in response to slightly higher daytime temperatures that occur in the surface layer (Longton and Holdgate, 1967) and the downward migration may possibly have resulted from a reversal of this gradient which may occur in the autumn (Tilbrook, 1967*b*).

The rate at which the total nematode populations increased after the spring melt was broadly similar in the three sample sites, but there were differences between genera. These differences probably reflect the way in which the varying reproductive potential of the genera is limited by temperature, moisture and availability of food. Observations indicate that low temperatures may not be quite as inhibiting as might be thought; over a period of 22 weeks, at a temperature that ranged between $-0\cdot25°$ and $-2\cdot0°$ C, a few juvenile *Plectus* (probably *P. antarcticus* de Man, 1904) in culture developed into females and some of these females produced eggs. Thus development may take place below 0° C, albeit slowly.

The total population estimates are of a similar magnitude to those previously recorded from Signy Island (Tilbrook, 1967*a*) and to those recorded from English moorland soils (Banage, 1966).

The considerably lower numbers in the 1967–68 summer, compared with the following one, may have been due to the fact that there was a mid-winter melt in 1967 and that the spring melt at the beginning of the 1967–68 summer began in early November, that is about 4 weeks later than in the following year (Baker, 1970). The thawing and re-freezing of the moss in the 1967 winter probably killed off some of the nematodes, resulting in a smaller initial summer population, and the later melt delayed the resumption of activity of this population.

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