DISTRIBUTION OF NEMATODE FEEDING GROUPS AT SIGNY ISLAND, SOUTH ORKNEY ISLANDS, WITH AN ESTIMATE OF THEIR BIOMASS AND OXYGEN CONSUMPTION

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ABSTRACT. The Signy Island nematode fauna can be divided into four feeding groups: omnivores, predators, microbial and fungal feeders; plant feeders were absent. Microbial feeders were the most abundant group in almost all the habitats examined. Omnivores were more numerous in cushion-forming mosses and in soil associated with the two Antarctic vascular plants than in other sites. Both fungal feeders and predators generally formed less than 4 per cent of the total numbers. The majority of the nematodes of each of the feeding groups occurred in the surface 3 cm. of the soil and vegetation, and there was no apparent seasonal variation in the relative abundance of the groups. Estimates of nematode biomass in the soil and vegetation at Signy Island range from $0 \cdot 16$ to $8 \cdot 25$ g./m.^{2}, and oxygen consumption from 54 to 2,014 μl./m.^{2}/hr. at 5° C. By comparing nematode respiration with that of the soil total, it has been estimated that the nematodes are only responsible for $0 \cdot 08$ to $0 \cdot 21$ per cent of the total oxygen respired. Observations on the omnivore, *Mesodorylaimus* sp., and the predator, *Clarkus gerlachei*, showed that these two species fed on a variety of organisms, including dead Collembola.

THE quantitative contribution that a group of soil-dwelling animals makes toward the economy of the soil may be assessed from estimates of their oxygen consumption, relative to that of the soil total, whilst some indication of their qualitative contribution can be obtained from knowledge of their feeding biology.

Judging by the relatively small contribution they make towards the total soil respiration, nematodes play only a minor role in the energy turnover of temperate moorland soil (Banage, 1963). The numbers of nematodes in the soil at Signy Island are of a similar magnitude to those occurring in temperate moor soils (Tilbrook, 1967; Spaull, 1973a). On this island, which lies within the maritime Antarctic (Holdgate, 1964), the soil fauna is limited to Collembola, mites, nematodes, rotifers, tardigrades and Protozoa, there being no oligochaetes or larger arthropods which are found in temperate soils. It seems likely that, in the absence of these ecologically important elements of the soil fauna, nematodes may play a proportionally greater part in the economy of the soil than they do in temperate regions (Cragg, 1961).

According to the type of food they take, soil nematodes can be divided into five ecological groups (based on the schemes given by Nielsen (1949), Banage (1963), Yeates (1967) and Wasilewska (1971)):

i. *Plant feeders*—known or suspected plant parasites, plant browsers or plant pathogens; includes many of the Tylenchida and some of the Dorylaimida.
ii. *Fungal feeders*—nematodes known or thought to feed predominantly on filamentous fungi; includes various Tylenchida. Wasilewska (1971) has drawn attention to the fact that the line of demarcation between the plant-feeding group and the fungal-feeding group is not sharply defined.
iii. *Microbial feeders*—nematodes known or thought to feed predominantly on bacteria, although their diet may also include algae, yeasts, filamentous fungi and possibly detritus.
iv. *Omnivores*—nematodes with a heterogenous diet which may include bacteria, fungi, algae, higher plants, Protozoa, rotifers and possibly detritus; includes most of the Dorylaimoidea.
v. *Predators*—nematodes known or thought to feed predominantly on members of the soil fauna such as other nematodes, enchytraeids, rotifers, tardigrades and Protozoa, but they may also eat fungi, algae and bacteria, and possibly detritus.

The distribution and relative abundance of the nematode feeding groups at Signy Island are presented in this paper, together with observations on the diet of nematodes and an estimation of their biomass and rate of respiration.

FEEDING GROUP DISTRIBUTION

Horizontal distribution

Spaull (1973b) recorded the distribution and abundance of the nematode genera in a variety of habitats at Signy Island. Based on data given by Neilsen (1949), Banage (1963) and Goodey (1963), and on personal observations, these genera have been assigned to the appropriate feeding group, according to the classification outlined above (Table I).

TABLE I. GENERIC COMPOSITION OF THE FEEDING GROUPS ON SIGNY ISLAND

Microbial feeders	Fungal feeders	Omnivores	Predators
Plectus	*Aphelenchoides*	*Eudorylaimus*	*Clarkus*
Teratocephalus	*Ditylenchus*	*Mesodorylaimus*	
Monhystera	*Tylenchus*	*Enchodelus*	
Prismatolaimus	*Antarctenchus*		
Amphidelus			
Cervidellus			
Rhabdolaimus			
Panagrolaimus			
Caenorhabditis			
Monhysterid genus "A"			

Apart from *Aphelenchoides* sp. A, which was successfully maintained on a fungal culture, the food source of the other four tylenchid species, *Ditylenchus* sp., *Tylenchus* sp., *Aphelenchoides* sp. B and *Antarctenchus hooperi* Spaull, 1972, is not definitely known but they are probably fungal feeders. A few species of moss and the roots, stems and leaves of *Deschampsia antarctica* Desv. and *Colobanthus quitensis* (Kunth) Bartl. (the only two Antarctic vascular plants) were stained with cotton blue (Hooper, 1970) but there was no evidence of parasitic nematodes. It is true that this does not exclude the possibility that these nematodes may browse on moss and vascular plant tissue but, in the absence of any contradictory data, these four tylenchids have been included with *Aphelenchoides* sp. A in the fungal-feeding group.

The few unidentified nematodes that were found in the samples were all very small juveniles; they did not belong to either the predacious or omnivorous feeding groups because, at Signy Island, the nematodes of these two groups are all relatively large and easily recognized. The stylet-bearing unidentified juveniles have therefore been grouped with the fungal feeders and the remainder with the microbial feeders.

Using the above information, the horizontal distribution and relative abundance of the feeding groups in 19 sample sites have been calculated (Table II); the moss and vascular plant sites have been divided into four vegetation sub-formations according to the classification of Gimingham and Smith (1970).

The outstanding feature of the distribution is the overall dominance of the microbial feeders in practically all of the sample sites. Complete dominance of this group occurred in the soils associated with the chinstrap penguin rookery and elephant seal wallow. The fungal feeders formed a greater proportion of the nematode fauna in the turf-forming mosses than in the other habitats, while the omnivores in these mosses were relatively unimportant. The omnivores were much more numerous in the soil associated with the vascular plants and in the cushion-forming mosses than elsewhere. Except for two instances, predators were numerically unimportant in the sample sites.

Vertical distribution

The vertical distribution of the feeding groups in a moss-carpet community composed of *Calliergon sarmentosum* and *Calliergidium austro-stramineum* (sample site 1; Spaull, 1973b) and a moss-turf community composed of *Chorisodontium aciphyllum* and *Polytrichum alpestre* (from unpublished data) is shown in Table III. In both sites the majority of the nematodes of each of the feeding groups occurred in the surface 3 cm. and the microbial feeders were the dominant group at all depths. Predators were absent from the moss turf and in the moss carpet they formed only a minor part of the fauna at all depths.

TABLE II. DISTRIBUTION AND PERCENTAGE ABUNDANCE OF NEMATODE FEEDING GROUPS

Vegetation sub-formation	Sample site and sample site number*	Feeding group			
		Microbial	Fungal	Omnivore	Predator
Moss turf	*Chorisodontium aciphyllum* (Hook. f. and Wils.) Broth. (4)	89·9	9·2	0·9	—
	C. aciphyllum and *Polytrichum alpestre* Hoppe (5)	63·6	28·7	7·6	0·1
	P. alpestre (6)	64·0	34·3	1·7	—
Moss carpet	*Calliergon sarmentosum* (Wahlenb.) Kindb. and *Calliergidium austro-stramineum* (C. Muell.) Bartr. (1)	75·7	7·4	15·4	1·5
	Drepanocladus uncinatus (Hedw.) Warnst. (2)	87·5	2·5	8·0	2·0
	Calliergon sp. (7)	86·3	1·6	11·7	0·3
Moss cushion	*Andreaea gainii* Card. (3)	69·0	2·2	28·8	—
	Grimmia antarctici Card. (11)	78·1	1·3	20·6	—
	Tortula excelsa Card. (12)	59·2	2·3	38·3	0·2
	Bryum algens Card. (13)	79·9	—	20·0	0·1
Vascular plants	*Deschampsia antarctica* Desv. (8)	81·9	3·9	14·2	—
	D. antarctica (9)	52·4	1·6	45·9	0·1
	Colobanthus quitensis (Kunth) Bartl. (10)	55·9	3·4	40·5	0·2
	Elephant seal (*Mirounga leonina* (Linn.)) wallow (16)	100·0	—	—	—
	Chinstrap penguin (*Pygoscelis antarcticus* (Forster)) rookery (17)	100·0	—	—	—
	Prasiola crispa Meneghini near cape pigeon (*Daption capensis* Linn.) nest (14)	97·3	0·2	1·9	0·6
	P. crispa near elephant seal wallow (15)	99·3	0·05	0·05	0·6
	P. crispa from melt stream (18)	35·8	—	37·9	26·3
	P. crispa from melt stream (19)	0·2	—	11·5	88·3

* These numbers correspond to those given by Spaull (1973*b*).

Seasonal variation

The seasonal variation of the relative abundance of the four feeding groups in the *Calliergon–Calliergidium* site is shown in Table IV, based on data given by Spaull (1973*a*). Over the 2 year period the microbial feeders remained the dominant group throughout the year, but the difference between the relative abundance of the omnivores and fungal feeders is not as large as indicated by the result of the February 1969 sample, which is used in Table II. Predators never exceeded 3 per cent of the population. There does not appear to be any clear seasonal change in the relative abundance of the feeding groups. The rate of increase of the omnivores and predators from the time of the spring melt to the middle of the summer was similar in both years; however, the rate of increase of the fungal and microbial feeders was greater in the first summer than the second.

ESTIMATION OF BIOMASS AND RATE OF RESPIRATION

The weights of the Signy Island genera were estimated using the formula devised by Andrassy (1956). This formula is simply the square of the greatest body width, multiplied by the distance from the lips to the anus with a conoid extension equal in volume to that of the tail, divided by $1 \cdot 6$ million. The measurements are in μm. and the result in μg. Measurements of the smaller, thinner nematodes were taken from mounted specimens; flattening of the body

TABLE III. VERTICAL DISTRIBUTION OF FEEDING GROUPS IN TWO MOSS COMMUNITIES

	Calliergon–Calliergidium community (February 1969)				
Feeding group	*Percentage abundance*				*Total numbers* 0–12 cm.
	0–3 cm.	3–6 cm.	6–9 cm.	9–12 cm.	(mean of 4, 4·2 cm. diam. cores)
Microbial feeders	83·7	14·0	1·8	0·5	4,863
Fungal feeders	94·2	4·7	0·9	0·2	686
Omnivores	69·1	27·0	3·6	0·3	1,281
Predators	97·6	1·2	1·2	0	66
TOTAL	82·1	15·3	2·1	0·5	6,896

	Chorisodontium–Polytrichum community (January 1970)				
Feeding group	*Percentage abundance*				*Total numbers* 0–12 cm.
	0–3 cm.	3–6 cm.	6–9 cm.	9–12 cm.	(mean of 8, 4·2 cm. diam. cores)
Microbial feeders	69·0	13·4	9·6	8·0	799
Fungal feeders	91·6	5·5	2·3	0·6	347
Omnivores	67·7	20·7	9·8	1·8	28
Predators	0	0	0	0	0
TOTAL	75·6	11·3	7·4	5·7	1,174

was prevented by supporting the cover glass with over-size glass wool. The large nematodes were measured without a cover glass.

Biomass estimates were derived from the product of the number of individuals and average measurements of adult specimens. The presence of juveniles was allowed for by dividing the mass by 2·23, the average factor by which adult female populations were heavier than mixed populations in experiments (Wasilewska, 1971). Where several different-sized species had been counted together, the counts were proportioned according to the estimated relative abundance of the species in the group (Table V).

Klekowski and others (1972) measured the respiration rates of 22 species of soil nematode and, incorporating data from other studies on a further 46 species, they calculated a general regression equation for nematode respiration. This equation, $R = 1·40\ W^{0·72}$ (where R is the amount of oxygen consumed per individual, measured in $\mu l./hr.$ at 20° C, and W is the wet weight of the individual measured in $\mu g.$), has been used to estimate the oxygen consumption of the Signy Island nematodes (Table V).

Using the data on the qualitative and quantitative distribution of the nematode genera at Signy Island (Spaull, 1973*b*) and the data compiled in Tables II and V, the estimated biomass and oxygen consumption of the feeding groups and total numbers of nematodes in 14 sample sites have been calculated (Table VI). Allowance has been made for the unidentified nematodes.

Nematode biomass

At most sites the biomass of the different feeding groups reflects the overall numerical dominance of the microbial feeders, but the omnivores form a greater proportion of the total biomass than their numbers indicate (cf. Tables II and VI). In fact, in the moss-cushion and vascular plant sites, where the omnivores were relatively abundant, omnivore biomass often forms the largest proportion of the total. This is not unexpected since the omnivores are relatively heavy nematodes. Due either to their small size and/or low numbers, the fungal feeders and predators generally formed only a small proportion of the total biomass.

In the vegetated sites the greatest nematode biomass occurred in the vascular plant soils and the smallest in the turf-forming mosses. This is due to a combination of greater numbers and a larger proportion of omnivores in the former. The estimated biomass in the penguin

TABLE IV. VARIATION OF NUMBERS AND RELATIVE ABUNDANCE OF FEEDING GROUPS IN THE *Calliergon–Calliergidium* SITE DURING THE SUMMER MONTHS AND FIRST AND LAST MONTH OF WINTER

(In the 1968 winter the moss was frozen from the first week of April to the first week of October and in the 1969 winter from the third week of March to the third week of November. Rate of increase calculated from numbers present at the time of the spring melt to those present at the beginning of February. Figures for February, March and April 1968 are the mean of 4, 4·2 cm. diam. cores 0–6 cm. deep, while those from October 1968 to March 1970 are the mean of eight such cores.)

| | | | 1968 | | | | | 1969 | | | | | | 1970 | | |
		Feb.	Mar.	Apr.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Nov.	Dec.	Jan.	Feb.	Mar.
Fungal feeders	Number	140	165	150	73	138	201	440	402	377	274	138	279	166	381	309
	Rate of increase						×5·5							×2·8		
	Per cent of total	9·3	6·5	6·8	5·7	6·2	6·8	9·2	7·4	9·9	9·9	8·1	8·4	6·4	8·7	6·7
Microbial feeders	Number	1,219	2,081	1,862	1,023	1,936	2,354	3,803	4,097	3,035	2,358	1,428	2,753	1,997	3,312	3,721
	Rate of increase						×4·0							×2·3		
	Per cent of total	81·3	82·2	84·9	79·3	87·4	80·1	79·8	75·7	79·4	85·4	83·5	82·6	77·2	75·8	80·7
Omnivores	Number	123	245	159	160	114	351	474	834	326	82	112	266	378	576	487
	Rate of increase						×5·2							×5·1		
	Per cent of total	8·2	9·7	7·3	12·4	5·1	11·9	9·9	15·4	8·5	3·0	6·5	8·0	14·6	13·2	10·6
Predators	Number	18	40	21	34	28	32	50	78	84	46	33	36	46	99	93
	Rate of increase						×2·3							×3·0		
	Per cent of total	1·2	1·6	1·0	2·6	1·3	1·1	1·0	1·5	2·2	1·7	1·9	1·1	1·8	2·3	2·0
TOTAL NUMBER		1,500	2,531	2,192	1,290	2,216	2,938	4,767	5,411	3,822	2,760	1,711	3,334	2,587	4,368	4,610

	Measurements from:		Mean and range of weights of adults (μg.)	Rough estimate of percentage abundance of species in populations with sample site number	Corrected average weight per individual (see text) (μg.)	Estimated oxygen consumption per individual (μl. $\times 10^{-3}$ hr. at 20° C)
Tylenchus sp.	6♀	6♂	0·08 (0·02–0·13)	50 per cent Tylenchus (1, 3 and 12)	0·14	0·33
				80 per cent Tylenchus (5, 7, 8, 9 and 11)	0·07	0·22
*Antarctenchus hooperi Spaull, 1972	10♀	10♂	0·52 (0·35–0·81)	100 per cent Tylenchus (2, 4, 6, 10 and 13)	0·03	0·12
*Aphelenchoides sp. A	12♀		0·17 (0·05–0·56)			
*Aphelenchoides sp. B	4♀	1♂	0·19 (0·17–0·23)	Equal proportions all sites	0·08	0·23
Ditylenchus sp.	7♀	5♂	0·43 (0·23–0·79)		0·19	0·43
Plectus parietinus Bastian, 1865	6♀		3·43 (3·01–3·85)	30 per cent		
Plectus antarcticus de Man, 1904	16♀	2♂	0·82 (0·46–1·33)	50 per cent		
Plectus armatus Butschli, 1873	7♀		0·22 (0·13–0·31)	5 per cent		
*Plectus sp. A	6♀		0·11 (0·07–0·15)	5 per cent — All sites	0·69	1·07
Plectus sp. B	5♀		1·15 (0·77–1·55)	5 per cent		
Plectus sp. C	6♀		0·28 (0·15–0·34)	5 per cent		
Teratocephalus near lirellus Anderson, 1969						
*Teratocephalus sp. A	17♀	2♂	0·19 (0·10–0·35)	Equal proportions all sites	0·09	0·24
Teratocephalus sp. B						
Monhystera sp. A	10♀		0·33 (0·27–0·49)			
*Monhystera sp. B	7♀		0·07 (0·05–0·10)	Equal proportions all sites	0·07	0·20
Prismatolaimus sp.	6♀		0·04 (0·04–0·06)			
Unidentified monhysterid sp.	5♀	2♂	0·81 (0·69–0·90)		0·37	0·68
Amphidelus sp.	7♀	5♂	0·81 (0·46–1·26)		0·37	0·68
Cervidellus sp.	11♀		0·25 (0·19–0·35)		0·11	0·29
Rhabdolaimus sp.	10♀		0·14 (0·12–0·18)		0·06	0·19
Panagrolaimus sp.	5♀	5♂	0·66 (0·35–0·97)		0·30	0·58
Caenorhabditis sp.	10♀	10♂	4·55 (2·69–10·53)		2·04	2·34
Eudorylaimus sp. A	5♀	5♂	2·64 (1·66–4·98)	60 per cent spp. A and B (3, 11 and 12)	3·11	3·17
*Eudorylaimus sp. B				90 per cent spp. A and B (5, 7, 8, 9 and 13)	1·67	2·02
Eudorylaimus sp. C	5♀	1♂	13·36 (9·44–17·33)	100 per cent spp. A and B (1, 2, 4, 6 and 10)	1·19	1·58
Mesodorylaimus sp.	6♀		2·56 (2·26–2·83)		1·15	1·55
Enchodelus sp.	8♀		2·49 (1·84–3·05)		1·12	1·52
Clarkus gerlachei (de Man, 1904)	5♀	5♂	21·64 (13·86–28·23)		9·70	7·19

* These brackets group those species, or genera, which were counted together.

		Moss carpet			Moss turf			Moss cushion				Vascular plants			
	Sample site (Sample site number)	(1)	(2)	(7)	(4)	(5)	(6)	(3)	(11)	(12)	(13)	(8)	(9)	(10)	(17)
	Feeding group	Calliergon and Calliergidium	Drepanocladus	Calliergon	Chorisodontium	Chorisodontium and Polytrichum	Polytrichum	Andreaea	Grimmia	Tortula	Bryum	Deschampsia	Deschampsia	Colobanthus	Penguin rookery
Numbers of nematodes (millions/m.²)		3·904	2·222	2·145	0·802	0·483	2·658	2·247	2·234	1·764	1·221	4·786	7·470	5·835	4·040
Percentage of total biomass	Fungal feeders	1·8	0·3	0·3	2·1	7·2	16·5	0·3	0·2	0·3	—	0·6	0·2	0·2	
	Microbial feeders	41·6	61·3	57·0	93·8	52·6	73·6	9·7	13·3	24·9	57·3	67·6	30·3	28·5	100·0
	Omnivores	32·0	12·4	37·1	4·1	35·7	9·9	90·0	86·5	72·4	41·7	31·8	69·4	69·0	—
	Predators	24·6	26·0	5·6	—	4·5	—	—	—	2·4	1·0	—	0·1	2·3	—
Total biomass (mg./m.²)		2,227·2	1,693·0	1,117·0	207·1	157·0	529·8	2,231·7	1,649·7	1,767·5	720·3	2,756·1	5,707·4	3,924·7	8,249·7
Biomass/million nematodes (mg.)		570·5	761·9	520·8	258·2	325·1	199·3	993·2	738·4	1,002·0	589·9	575·9	764·0	672·6	2,042·0
Percentage of total oxygen consumed	Fungal feeders	3·2	0·9	0·5	3·4	12·4	22·3	0·7	0·5	0·7	—	1·0	0·3	0·5	
	Microbial feeders	53·0	72·7	67·2	93·6	59·3	71·0	20·2	27·5	34·2	63·2	72·3	34·8	33·8	100·0
	Omnivores	30·8	12·2	29·5	3·0	26·3	6·7	79·1	72·0	63·7	36·3	26·7	64·8	64·6	—
	Predators	13·0	14·2	2·8	—	2·0	—	—	—	1·4	0·5	—	0·1	1·1	—
Total oxygen consumed (μl./hr./m.² at 20° C)		3,094·2	2,295·4	1,639·9	379·6	255·0	1,046·1	2,436·7	1,901·6	2,155·5	1,079·3	4,208·6	8,206·2	5,649·7	9,456·9
Total oxygen consumed (μl./hr./m.² at 5° C)		659·1	488·9	349·3	80·9	54·3	222·8	519·0	405·0	459·1	229·9	896·4	1,747·9	1,203·4	2,014·3

rookery soil is larger than in any of the other sites examined; apart from a few isolated individuals of *Panagrolaimus* sp., *Caenorhabditis* sp. was the only species found in this habitat, where it occurred in large numbers, and was the third heaviest nematode at Signy Island.

Nematode oxygen consumption

The estimated oxygen consumption of the nematode fauna in the different habitats at Signy Island ranged from 255 to 9,457 μl./m.^{2}/hr. at 20° C (Table VI). A general pattern can be seen in Table VI, which groups the carpet- and turf-forming mosses with greater oxygen consumption by microbial feeders than omnivores, and cushion-forming mosses and vascular plants with greater consumption by omnivores than microbial feeders. Since the oxygen-consumption estimates are based on the weight of the nematodes, a similar grouping of habitats is demonstrated when biomass is considered. There is one cushion-forming moss, sample site 13, and one vascular plant, sample site 8, that differ from this pattern (Table VI); the difference in site 13 may be partly explained by the relatively low number of dorylaims, particularly the large *Eudorylaimus* sp. C (Table V; Spaull, 1973*b*) and in site 8 by the relatively small number of *Mesodorylaimus* (Spaull, 1973*b*). The fungal feeders and predators rarely consumed more than 4 per cent of the total nematode consumption.

The oxygen-consumption estimates given in Table VI are based on data for nematode respiration at 20° C. However, oxygen consumption by nematodes generally decreases with temperature (Nielsen, 1949; Bhatt and Rohde, 1970; Marks, 1971) and, since the average monthly temperature in the moss and soil at Signy Island never reaches 20° C, a correction must be made to give more realistic estimates. The average annual monthly temperature at a depth of 2·5 cm. in moss at Signy Island may range from $-1\cdot0°$ C (in 1963 in an unnamed moss (Chambers, 1966)), to $-3\cdot0°$ C (in 1969 in a moss carpet community (Spaull, 1973*a*)). These averages include at least 6 months of the year when the ground was frozen, during which nematode respiration would be minimal. Activity of the soil fauna and flora at Signy Island is probably almost entirely restricted to the summer months, when soil temperatures are above freezing point. Consequently, consideration of nematode respiration will be limited to that which occurs during the summer.

The average temperature at a depth of 2·5 cm. in moss from the time of the spring melt until the onset of the winter freeze was approximately $+1\cdot4°$ C in the 1968–69 summer and $+3\cdot3°$ C in the 1969–70 summer (Spaull, 1973*a*). It seems reasonable to assume a certain amount of cold adaptation by the Signy Island nematodes. This may be allowed for by assuming a higher average summer soil temperature; $+5°$ C has been chosen for this purpose. This was also the temperature used by J. H. Baker (personal communication) during the measurement of the oxygen consumption of complete cores of *Chorisodontium aciphyllum* peat and *Deschampsia antarctica* soil at Signy Island.

The estimated oxygen consumption of the nematodes has been corrected for temperature using Krogh's (1914) temperature–metabolism curve; multiplying the 20° C oxygen-consumption figures given in Table VI by 0·213 gives the estimated consumption at $+5°$ C. Thus at this temperature the respiration rate of the Signy Island nematodes ranged from 54·3 μl./m.^{2}/hr. in the *Chorisodontium–Polytrichum* community, to 2,014·3 μl./m.^{2}/hr. in the penguin rookery soil (Table VI).

The oxygen-uptake estimates given by Baker (1970*a*, fig. 3) for *C. aciphyllum* peat, derived from the 3–9 cm. layer, are expressed in μl./g. dry weight/hr. (personal communication from J. H. Baker); therefore the average amount of oxygen consumed during the period from after the spring melt in December 1966 until the onset of the winter freeze in 1967 was 19·1 μl./g. dry weight/hr. (Baker, 1970*a*). Assuming the density of the peat in the 3–9 cm. layer is the same as that in the 6–7 cm. layer, namely 0·086g. dry weight/cm.^{3} (Baker, 1970*b*), then during the summer the average respiration rate of the *Chorisodontium* peat, 3–9 cm. deep, is 101×10^3 μl. O_2/m.^{2}/hr. The estimated oxygen consumption of the nematodes in the 0–6 cm. layer of a different *Chorisodontium* peat at 5° C is 80·9 μl./m.^{2}/hr. Using these figures, nematodes would seem to contribute less than 0·08 per cent of the total respiration in peat. It is unlikely that the different moss and depth would greatly alter the scale of respiration.

Baker (personal communication) found that during the 1966 winter the oxygen uptake in

Deschampsia antarctica soil from Lynch Island (lat. 60°40′S., long. 45°38′W.), South Orkney Islands, was 55·9 μl./g. dry weight/hr. at 5° C. The density of the soil below *D. antarctica* is approximately 0·247 g. dry weight/cm.³ (unpublished data of V. W. Spaull), which means that the oxygen consumption in this soil is approximately $828 \times 10^3 \mu$l./m.²/hr. At 5° C the nematodes in *D. antarctica* from Factory Cove (sample site 9) consumed 1,747·9 μl. O_2/m.²/hr., which, discounting differences in time and space, indicates that the nematodes are responsible for 0·21 per cent of the total oxygen respired.

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SOME OBSERVATIONS ON THE FEEDING AND GUT
CONTENTS OF NEMATODES FROM SIGNY ISLAND

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The food of Mesodorylaimus sp.

Whilst making counts of the different genera from the various sample sites, it was noted that the intestine of a number of individuals of *Mesodorylaimus* sp. contained dark blue-coloured granules. In some cases the granules filled almost the whole gut. Blue granules were also occasionally seen in the intestine of *Clarkus gerlachei* (de Man, 1904) Jairajpuri, 1970, *Eudorylaimus* spp. and to a much lesser extent in *Plectus parietinus* Bastian, 1865 and monhysterid genus "A". These granules resemble those present in the deeply pigmented collembolan, *Cryptopygus antarcticus* Willem, 1902, which occurs in large numbers on Signy Island. The following observation indicates that the granules in the nematode intestines originate from this collembolan.

About 30 *C. antarcticus* were added to a mixed culture of fungi, algae and bacteria on 5 per cent *Deschampsia*–soil agar in a petri dish. The Collembola were then squashed, such that the haemocoel was ruptured. Ten female *Mesodorylaimus* sp., without any coloured granules in their intestines, were added to the agar plate and observed under a dissecting microscope. Some of the *Mesodorylaimus* were seen feeding on very small coccoid algal (?) cells that were abundant in the culture. When the nematodes were observed feeding in the vicinity of a squashed collembolan, blue granules from the ruptured haemocoel were clearly seen to be ingested as the oesophagus pulsated. When the culture was examined 24 hr. later, the nematodes, with their intestines partly or almost completely filled with the granules, resembled those that had been found in the sample sites.

In another similar culture it was noted that the oesophagus of a female *Mesodorylaimus* pulsated without there being any visible food source (e.g. fungal spores, algae, Protozoa, etc.); possibly the nematode was feeding on bacteria. When the nematode was surrounded by a ring of blue granules, these were seen to be ingested as it traversed the ring. On another occasion a female *Mesodorylaimus* was seen in culture feeding on a fungal spore and a juvenile was observed feeding on a bdelloid rotifer; complete removal of the body contents of the rotifer took more than 30 min. A female *Mesodorylaimus* was observed apparently feeding on the body contents of a dead *C. gerlachei*.

Gut-content analysis of Clarkus gerlachei

C. gerlachei is a relatively large nematode (3·05–4·00 mm.) with a barrel-shaped buccal cavity armed with a single dorsal tooth. It belongs to a family of nematodes, the Mononchidae, the members of which are commonly predacious, although many also feed on soil micro-organisms (Thorne, 1927; Banage, 1963). Examination of the intestine of a number of preserved *C. gerlachei*, obtained from a mat of the thallose alga, *Prasiola crispa*, at Signy Island, indicated that this species is a facultative predator.

A total of 128 adult specimens were examined and 45 of these had no visible solid gut content; of the remaining 83 specimens, algae were present in the intestine of 23 per cent, fungal hyphae or spores in 9 per cent, blue granules from Collembola in 34 per cent, arthropod cuticular hairs in 29 per cent, rotifer trophi in 12 per cent, tardigrade claws in 7 per cent and unidentified solid objects in 81 per cent. Also in the intestine of a female specimen from Signy Island and three females from Elephant Island (lat. 61°10′S., long. 55°14′W.) there was an odontostyle from a dorylaim. Recognizable remains of three individuals of the genus *Plectus* were found in the intestine of a male *C. gerlachei* collected from Elephant Island. A juvenile

C. gerlachei was observed ingesting the semi-liquid surface material of an agar culture that had been seeded with an unknown variety of micro-organisms.

DISCUSSION

Besides the availability of suitable food, soil factors that are thought to affect the distribution and relative abundance of nematode feeding groups include pH and water content (Banage, 1963), organic content (Yeates, 1967), associated vegetation (Mankau and Mankau, 1963; Yuen, 1966; Egunjobi, 1971) and possibly soil texture (Norton and others, 1971). A number of these factors will have a direct effect on the feeding groups via their effect on the distribution and abundance of the food supply; however, they will also have an indirect effect by influencing the non-feeding activities of the nematodes within the groups. For example, Mountain and Boyce (1958) found that, although peach seedlings grew equally well in coarse- and fine-textured soil (and thus the potential food supply for plant-feeding nematodes was similar in both soil types), the population increase of the migratory root feeder, *Pratylenchus penetrans* (Cobb, 1917) Sher and Allen, 1953, was much greater in the coarse-textured soil; the difference was probably due to the smaller pore size and less suitable moisture characteristics of the fine soil which limited nematode movement (Townshend and Webber, 1971).

Furthermore, the distribution and relative abundance of the feeding groups may partly reflect inherent differences between taxonomic groups; Norton and others (1971) and Oteifa and others (1964) noted that the plant-feeding nematodes of the Tylenchoidea differed from those of the Dorylaimoidea in their response to various soil factors. Possibly such behavioural differences exist between the plant- and fungal-feeding Tylenchoidea and the omnivorous nematodes of the Dorylaimoidea.

Banage (1963) found that, in English moorland soils, plant feeders (which included fungal-feeding tylenchids) were the dominant group, while in a series of Danish soils Nielsen (1949) recorded a dominance of microbial feeders. Banage (1963) suggested that this difference was due to the more acid nature of the moorland soils which favoured the activity of fungi more than that of bacteria. But the range in pH of the moorland soils studied by Banage is similar to that of the Signy Island soils, and yet at Signy Island the microbial feeders are the dominant group. However, it is of interest to note that in the more acid turf-forming mosses at Signy Island the fungal feeders attained their greatest relative abundance.

Since microbial feeders may feed on yeasts as well as other components of the soil micro-flora, their predominance in moss turf may be related to the much greater biomass of yeasts than bacteria that has been recorded in this type of vegetation at Signy Island (Baker, 1970*b*). This is supported by the fact that the vertical distribution of the microbial feeders in a moss turf is similar to that of the yeasts, whereas bacteria show a contrasting gradient (Baker, 1970*b*). However, temperature may be the primary factor affecting the vertical distribution of the nematodes at Signy Island (Spaull, 1973*b*).

The nematode biomass estimates for the Signy Island habitats are within the range found for a variety of other habitats by several authors (Wasilewska, 1971, table I; Ferris and Ferris, 1972; Yeates, 1972, tables I and II). The range in weight per million nematodes is also similar (Table VI).

The Signy Island nematodes consume an estimated $0 \cdot 08 - 0 \cdot 21$ per cent of the total oxygen respired in the soil. Banage (1963) reported that nematodes consume $0 \cdot 7$ per cent of the total oxygen used in *Juncus* moor soil. At first sight, this difference is rather surprising since enchytraeids and the larger soil arthropods, which consumed 96 per cent of the oxygen respired by the soil fauna in *Juncus* soil (Cragg, 1961), are absent from Signy Island.

However, the total soil respiration figure of approximately 80 cm.^{3} O_2/m.^{2}/hr. at 20° C given by Banage (1963)* apparently refers only to the oxygen consumed in a 1 cm. layer, within the

* In fact, Banage (1963) cited Cragg (1961) as the authority for the "total soil respiration" value in *Juncus* soil. However, Cragg's total value of "107 mg. O_2" (= $74 \cdot 9$ cm.^{3} O_2) refers only to the sum of the oxygen consumption of the larger members of the soil fauna at 13° C (Cragg, 1961, table IX corrected). Bearing in mind that bacteria and fungi may be responsible for 80–90 per cent of the total soil metabolism (Macfadyen, 1963), the figure given by Cragg seems rather high compared with data for the total *Juncus* soil respiration (Latter and Cragg, 1967; Latter and others, 1967).

surface 3 cm., per square metre of *Juncus* soil (Latter and others, 1967). But Banage's (1963) nematode respiration estimate of $0\cdot4937$ cm.^{3}/m.^{2}/hr. at $16°$ C is based on population density to a depth of 6 cm. (Banage, 1966). Using the data from Latter and others (1967, table I) and Latter and Cragg (1967, fig. 4), the combined oxygen consumption of each of the horizons in the 0–6 cm. layer of *Juncus* soil is estimated to be 340 cm.^{3}/m.^{2}/hr. at $20°$ C. Thus an improved estimate for the contribution that soil nematodes make towards the total respiration in *Juncus* soil is approximately $0\cdot2$ per cent.

The biomass estimates given by Banage (1963) were derived from measurements (according to the method of Andrassy (1956)) for adult nematodes (Banage, 1960). If the biomass correction factor, which was used in the present study to include the weight of juvenile nematodes, is applied to the data given by Banage (1963, table IV), nematode oxygen consumption in *Juncus* soil is further reduced to approximately $0\cdot07$ per cent of the total. Thus, despite the absence of oligochaetes and larger soil arthropods in Signy Island soils, there is not a conspicuous increase in the contribution that nematodes make towards the total soil respiration.

As far as is known, Bunt (1954) was the only other person to compare nematode respiration with total soil respiration. He estimated, by extrapolating from data given for Danish soils by Nielsen (1949), that the soil nematodes at Macquarie Island were responsible for $0\cdot5$–$1\cdot2$ per cent of the total soil respiration. However, it is not known how much reliance can be attached to these estimates since oxygen consumption by adult nematodes is proportional to body weight (Klekowski and others, 1972), and body weight may vary between species by a factor of 500 (Table V); the errors associated with extrapolating respiration data directly from one nematode fauna to another will therefore be large.

Nematodes at Signy Island occur in a wide variety of habitats and are present in large numbers. Since they feed on most of the other elements of the soil biota, their influence on the functioning of the soil ecosystem will be widespread. But, judging by their limited contribution to the total soil respiration, the magnitude of this influence is small. However, soil nematodes at Signy Island are the food source of predacious fungi (Duddington and others, 1973) and, when dead, of saprophytic bacteria and fungi; also, as suggested by Macfadyen (1961), nematodes may, together with other members of the soil fauna, have a catalytic effect on microbial activity by enriching the substrate with excreta, by grazing on senescent bacterial colonies and by the transport of microbes to favourable sites; the resulting increased metabolism could be several times that of the animals themselves.

The general regression equation for nematode respiration formulated by Klekowski and others (1972) is based on data for adult nematodes. However, juvenile nematodes have a greater respiratory metabolism than adults (Nielsen, 1949; Wieser and Kanwisher, 1960), so the Signy Island oxygen-consumption figures given in Table VI, which are derived from the general equation, are probably underestimates. Also the oxygen consumption will have been further underestimated if low-temperature adaptation by the nematode fauna is greater than that considered here. These possibilities can be resolved by a practical study of the respiration rates of the nematodes at Signy Island.

The fact that *Mesodorylaimus* sp. feeds on the blue granules from ruptured Collembola and the isolated observation of an individual apparently feeding on a dead *C. gerlachei* suggests that this species is partly necrophagous. It is possible, however, that the nematodes were feeding on the saprophagous micro-organisms associated with the dead animals. Many more *Mesodorylaimus* than microbial-feeding nematodes were seen with blue granules in their intestines, which indicates that the granules, or the associated micro-organisms, are ingested selectively.

The analysis of the intestinal contents of *C. gerlachei* showed that this species fed on a variety of organisms. Of the material that could be identified, blue granules from Collembola had the highest frequency of occurrence. The ability of Collembola to make rapid movements suggests that it is most unlikely that *C. gerlachei* can prey on live individuals; necrophagy seems more probable. If this is the case, and in view of the fact that a notable proportion of this species fed on algae, perhaps *C. gerlachei* should have been grouped with the omnivores. However, as shown by Young and others (1964), visual analysis of gut contents of predators may be misleading; if the predator frequently feeds solely on the colourless body fluids and soft tissues of one type of animal and occasionally on the whole or part of another which has

identifiable undigestible structures, only the latter would be recognized in the gut. Young and others (1964) overcame this problem by using a serological technique to detect the food of predators.

Both *Mesodorylaimus* sp. and *C. gerlachei* may feed on bacteria together with the organic and inorganic compounds surrounding the bacteria. It is possible that such compounds may be utilized by all omnivores and predators that are "ingesters" rather than "piercers" (Yeates, 1971). Yeates suggested that these compounds may be the real food source of nematodes that ingest bacteria. However, microbial-feeding nematodes rely, to some extent at least, on compounds that are synthesized by bacteria; for example, an unidentified nutritional requirement of *Caenorhabditis briggsae* is present in the bacterium *Klebsiella aerogenes*, upon which the nematode can be cultured, but it is absent from the culture fluid surrounding the bacteria (Nicholas and others, 1959). A similar nutritional dependence on bacterial cell content was found with *C. briggsae* and a gram negative yellow-pigmented bacterium (Zuckerman and others, 1969).

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