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Seasonal changes in communities of soil invertebrates in tundra ecosystems of Hornsund, Spitsbergen

ABSTRACT: Communities of soil invertebrates were studied in 4 types of tundra ecosystems on Spitsbergen (Hornsund area) during the vegetative season of 1989. Taxonomic composition, density and biomass of soil fauna were evaluated in the sites along a gradient of increase in the biogenic impact of bird colonies, i.e. in polygonal tundra, mossy/lichenous tundra, *Calliergon stramineum* moss association, and mossy associations near a colony of Little Auks (*Alle alle*). Average total biomass of soil invertebrates increased in this site sequence from 1.1 to 25.0 g wet weight $\times$ m^{-2} (mainly due to collembolans and nematodes). Seasonal dynamics of all groups of soil meso- and macrofauna (Nematoda, Enchytraeidae, Aranei, Acarina, Collembola, Coleoptera, Diptera larvae) is presented and discussed.

Key words: Arctic, Spitsbergen, tundra, soil invertebrates, ornithogenic impact.

Introduction

Zoological investigations of the soils of Spitsbergen tundra ecosystems were performed in May–August 1989 in the vicinity of Polish Polar Station (Hornsund). This study was a part of a long-term research programme of the Institute of Ecology, Polish Academy of Sciences (IE PAN), on bioenergetics of tundra ecosystems in Hornsund area. The samplings of soil fauna were carried out within four stationary experimental plots that have been under complex survey for several years by research group of the Department of Bioenergetics IE PAN (see Klekowski and Opaliński 1986, 1992). Study plots were situated on the slope (No 4) and terraces (No 1–3) of southern exposition, belonging to

Ariekamen/Fugleberget mountain system ("Fugleberget catchment"). The plots were differently located in relation to flows of surface running waters from melted snow and rains, as well as to the intensity of influence from bird colonies of Little Auk (*Alle alle*) (organic and mineral matter flow), and from Barnacle geese (*Branta leucopsis*) (trampling and grazing of vegetation). The set of plots represented the variety of soil and vegetation in the coastal tundra of Hornsund area. Here we present some basic data on soil-dwelling invertebrates (taxonomic composition, patterns of seasonal changes in their density and biomass), that may be used for subsequent calculations on bioenergetics of studied ecosystem.

Characteristics of the study area

The map and brief description of the plots under study can be found in Klekowski and Opaliński (1992).

Plot No 1: Polygonal tundra. Polygons of mineral soil (of irregular shape, 0.5–2.0 m in diameter) partly covered by compact film of algae (0.5–2.0 cm thick, mainly *Nostoc* sp.) occupied the main area of the site. Polygons (below referred to "open ground") were surrounded by cracks with rocky debris and bands or spots of vegetation. Plant associations were formed by *Salix polaris, S. reticulata, Saxifraga oppositifolia, S. caespitosa,* rarer by *S. cernua* and *S. foliosa.* Single plants of *Cardamine bellidifolia, Poa alpigena, Deschampsia alpina, Luzula confusa, Juncus biglumis* were also present. Moss cover consisted of *Drepanocladus uncinatus, Oncophorus wahlenbergii* va. *compactus, Rhacomitrium canescens, Polytrichum alpinum;* lichens were represented by *Cladina rangiferina, Cladonia* spp., *Cetraria* sp., *Stereocaulon* sp. In the first half of the season, the flowering of *Saxifraga* species was the most prolonged; polar willow flowered briefly. By the end of July, the higher plants had withered. The lichen *Ochrolechia gonatoides* became distinct and later dominant, even suppressing mosses in August. Dense moss beds of *Oncophorus compactus* and *Polytrichum* sp. were noticeable along cracks.

The mineral soil of polygons was gelic gleysol (after FAO classification). In spring it was covered only with an algal film. Later on, spots of *O. gonatoides* and single specimens of higher plants appeared here and there.

Plot No 2: Wet mossy swamp was situated in the Fuglebekken valley, along the main bed of melt snow. The total depth of the moss and turf layers was 20–30 cm, underlaid by a blue-green soil of histic gleysol type. The moss cover consisted mainly of *Calliergon stramineum;* other species were also present occupying more (*Aulacomium palustre*) or less (*Drepanocladus uncinatus, Pohlia* sp., *Ptilidium ciliare, Tritomaria quinquedentata*) moist areas. Higher plants were absent except for single specimens of *Saxifraga caespitosa.* In the end of summer, small spots of lichens (*Cladonia stricta, C. gracilis, Cetraria delisei, Peltigera* sp.) appeared.

The mossy swamp remained under snow and water longer than the other plots, and at the end of June (1st sampling date) moss layer was still water saturated. Its moisture content slightly decreased only in the middle of summer (Tab. 1). The plot was a pasture for Barnacle geese, *Branta leucopsis*, which consumed large quantities of moss and produced much of guano.

Plot No 3: Mossy/lichenous coastal tundra with compact plant cover on the soil of histic regosol type. The vegetation was composed mainly by *Salix polaris*, and rarely by *Saxifraga oppositifolia, S. caespitosa, Deschampsia alpina, Luzula confusa*. The background was formed by the lichens of *Sphaerophorus globosus, Cetraria* sp., *Cladonia* sp. and *Cladina rangiferina; Ochrolechia gonatoides* appeared and dominated in August. *Drepanocladus uncinatus* was the most common moss species. *Oncophorus compactus* and *Ptilidium ciliare* were observed in low quantities along moist rocky crevices, and small spots of *Calliergon sarmentosum* were situated close to a stream flowing from the bird colony. The plot became free from snow considerably later than plot 1, and dried easily in summer. Polar willow flowered in the end of June, its leaves fell off by the beginning of August.

Plot No 4: Associations of compact green mosses near the bird colony. Soil of histic gleysol type (with higher content of organic matter compared with plot 2) was covered with layers of mosses and turf, 8–12 cm thick. Patches of higher meadow vegetation included *Cochlearia arctica, C. groenlandica, Oxyria digyna, Cerastium alpinum, Chrysoplenium tetrandrius, Saxifraga caespitosa, S. hirculus, Polygonum viviparum, Draba alpina, Poa alpigena, Luzula confusa*. Mossy cover was formed by *Aplodon wormskioldi, Tetraplodon mnioides, Ceratodon purpurescens, Pohlia* sp., *Aulacomium turgidum, Calliergon Stramineum, Brachythecium* sp., *Mnium* sp., in the meadon associations *Drepanochadus uncinatus* and *Polytrichum alpinum* were also present. There were almost no lichens; only rarely *Cladonia* spp. was recorded. The site was situated on two narrow terraces of Ariekamen Mt., dominating over the Fuglebekken valley. Its detailed floristic description was carried out by Dubiel and Olech (1992). Plot 4 was under the greatest impact from the colony of Auks (as compared with the other plots) and the first to be free from snow in spring.

Material and methods

Samples were collected (J.B. Byzova and A.V. Uvarov) during the whole vegetative season of 1989, from snow melting in May-June till the beginning of stable frosts and snowfalls in early September. Snow disappeared on the plots in the following order: No 4 – No 1 – No 3 – No 2. Regular samplings (at intervals of 3 weeks) were performed at the plots 1, 2 and 3 (5, 4 and 5 samplings, respectively). There were 3 samplings dates at the plot 4, in early spring (May), in the middle of summer (July), and late in autumn (end of August).

Sampling methods for different groups of soil animals followed standard procedures (Gilarov and Striganova 1987). Macrofauna was collected by hand

Table 1.

Soil temperature (°C) and moisture content (% of the wet weight) in the plots under study. Symbols: P1 – P4 — plot numbers; PA — under plant associations; OG — polygons of open ground; M — moss layer, T — turf layer

Plots		Sampling dates							
		15.05	26.05	8.06	18 – 25.06	5.07	9 – 16.07	29.07 – 7.08	21 – 28.08
		Temperature							
P1	PA				4.8±0.2		7.9±0.2	7.4±0.8	7.6±0.2
P1	OG				9.0 – 9.5			8.9±0.1	8.7±0.9
P2					4.2±0.5		5.8±0.4	9.3±0.4	1.0 – 1.5
P3					4.9±0.7	5.5±0.3		8.4±0.9	7.7±0.9
P4	M	4.7±0.5				13.1±0.6			1.8±0.2
P4	T	1.4±0.8				6.3±1.0			1.0 – 2.0
		Moisture content							
P1	PA		44.6±2.5		42.7±1.6		48.9±2.1	36.6±2.2	32.6±2.1
P1	OG		19.2±0.7		25.1±1.6		22.5±1.2	22.6±1.3	18.5±0.5
P2					81.1±3.7		78.1±2.2	79.8±1.1	81.0±0.8
P3				71.5±0.6	71.0±1.4	73.9±1.8		61.1±1.4	51.8±3.1
P4	M	88.3±0.6				83.3±1.2			78.9±2.4
P4	T	85.0±0.8				82.2±1.5			73.2±4.0

sorting of square soil samples of 15 × 15 cm to the depth of the active (inhabited by animals) soil layer. Small-sized samples were preferred to larger ones in order to cover mozaics of the tundra vegetation. 15 samples were taken simultaneously on each sampling date. In plot 1, two subplots were studied separately: open ground of polygons and different plant associations surrounding them. The depth of the active layer rarely exceeded 5 cm in plots 1 to 3, and 10 cm in plot 4 where samples were subdivided into layers of "moss" and "turf".

For extraction of microarthropods and enchytraeids, samples (5 × 5 cm × depth of the acitve soil layer) were taken close to macrofauna samples, also 15 per plot on each sampling date. Microarthropods were extracted from soil by means of Tullgren funnels during 3 days and collected in a mixture of 70° alcohol and glycerol. Permanent mounts of microarthropods were made using Faure-Berlese medium. The wet funnel method was used to extract enchytraeids; the extraction lasted 1 hr with heating of samples. Animals were counted alive immediately after extraction. Samples for the extraction of nematodes (0.5 – 1.5 g fwt) were taken from every enchytraeid sample, the wet funnel method was used; extraction lasted 24 hrs without heating. Nematodes were recorded in duplicate samples; one was used for direct counts of the worms, the other was preserved in 4% formalin solution for subsequent systematic treatment of the worms.

Total number of samples was 240, 375, 375 and 750 for estimates of macrofauna, enchytraeids, microarthropods and nematodes, respectively.

On each sampling date during the season, temperature of the active soil layer was recorded. Fresh weight and water content of the samples were also determined (Tab. 1).

Live body weight of larger invertebrates was obtained by weighing individuals (macrofauna) or groups (enchytraeids, microarthropods). For small species and immature stages of microarthropods body weight was calculated using morphometric data. To calculate the body weight of oribatid mites (all the stages), body length/weight relationships for corresponding types of body shape were used (after Lebrun 1971) (Tab. 2). Body dimensions were measured in each case for not less than 20 specimens, errors of means being from 1 to 5.3%. Oribatid nymphal instars in Table 2 are indicated provisionally, being delimited to size groups. Errors due to different relative weight of integument in subsequent developmental stages (Luxton 1975) were disregarded, since certain overestimates of the juveniles' weights were believed to be somewhat compensated by underestimates of their numbers due to incomplete extraction from the substrate. Live body weight of the species of Mesostigmata and Acaroidea + Trombidiformes was calculated on the basis of our measurements (Tab. 2). Live weight of Collembola species was calculated on the basis of body length data (Tab. 3), measured according to Tamura's (1974) method. Average body

Table 2.

Live body weight (μg) of mite species collected in the study area. Calculations mainly on the basis of author's morphometric meeasurements: (*) — direct weighing; (**) — data from Luxton (1975). Symbols: I — imago, $N_1 - N_3$ — nymphal stages (data in square brackets when stages were not identified), L — larvae, n — number of measurements

Species	Stages				
Oribatei	I	N_3	N_2	N_1	L
Trichoribates spp.	464.0*	393.9	99.5	47.9	25.3
Camisia spp.	53.9*	48.3	17.0	9.7	5.6
Ceratoppia spp.	57.9*	60.9	34.1	11.7	5.5
Liochthonius spp.	1.0**		[0.5]		0.2
Oppia spp.	2.0**				
Tectocepheus velatus Michael, 1880	4.4**		[3.5]		0.5
Oribatula tibialis Nicolet, 1885	11.0**				
Zygoribatula spp.	12.0**				
Chamobates borealis (Tragardh, 1902)	6.5**				
Mesostigmata	♀	♂	N_2	N_1	L
Arctoseius multidentatus Evans, 1955	39.2	16.7	13.5	7.6	4.9
A. taimyricus Petrova et Makarova, 1991	53.5	24.6			
A. pristinus Karg, 1962	10.8	8.2			
A. weberi Evans, 1955	20.2		20.4	5.6	
Cerconopsis sp.	30.5	15.3	14.7		
Melichares sp.	14.4	9.0			
Antennoseius oudemansi Thor, 1930	56.4		68.9		
Zercon forsslundi Sellnick, 1958	19.8	10.2	9.0	4.2	2.2
Zercon sp. 1, 2	20.4	9.6	13.5		
Z. zelawaensis Sellnick, 1944	17.0				
Trombidiformes					L
Endeostigmata (n=3)	[1.4]				
Pygmephoridae (n=52)	[1.0]				
Rhagidiidae (n=34)	[26.3]				
Bdellidae (n=2)	[40.0]				
Cunaxidae (n=1)	[5.7]				
Stigmaeidae (n=20)	[4.7]				
Bryobia sp. (n=19)	[14.5]				(n=4) 1.3
Tetranychidae (n=148)	[1.5]				

weights (S.E. < 5%) are here used, seasonal fluctuations in the size structure of Collembola populations being disregarded. Average live body weight of nematode individuals was assumed to be 0.5 μg, regarding the data summarized by Petersen and Luxton (1982).

Table 3.

Average live weight (W, μg) of Collembola species within the study area.

Collembola species	n	W±SD	References
Hypogastrura viatica (Tullberg, 1871)	714	35.1±1.2	(1), (2)
H. tullbergi (Schäffer, 1900)	651	25.1±0.7	(1), (2)
Ceratophysella denticulata (Bagnall, 1941)	141	69.8±3.3	(1), (2)
Xenylla humicola (Fabricius, 1780)	372	29.4±1.3	(1), (2)
Onychiurus groenlandicus (Tullberg, 1876)	401	50.8±1.3	(3)
Anurida polaris (Hammer, 1954)	423	25.3±0.7	(3)
Micranurida pygmaea Börner, 1901	24	2.5±0.9	(3)
Folsomia quadrioculata (Tullberg, 1871)	828	13.3±0.3	(4)
Folsomia spp.	75	6.2±0.4	(4)
F. taimyrica Martynova et. al., 1973	1	27.5	(4)
Pseudanurophorus inoculatus Bödvarsson, 1957	5	1.9±0.4	(4)
Agrenia bidenticulata (Tullberg, 1876)	20	78.9±12.8	(5)
Isotoma tshernovi Martynova, 1974	88	13.6±1.5	(5)
Isotoma sp.	1	3.8	(5)
I. anglicana Lubbock, 1962	58	424.2±113.0	(5), (10)
Entomobrya sp. juv.	1	84.3	(6), (7)
Sminthurides malmgreni (Tullberg, 1876)	30	4.5±0.8	(8), (9)
Arrhopalites principalis Stach, 1945	1	17.8	(8), (9)

Note: Calculations were performed on the basis of morphometric measurements and equations after Tanaka (1970), for *Hypogastrura manubrialis* (1) and Entomobryidae (6); Edwards (1967), for Hypogastruridae (2), Entomobryidae (7) and Sminthuridae (9); Petersen (1975) for *Onychiurus armatus* (3), *Folsomia quadrioculata* (4), *Isotoma notabilis* (5) and *Sminthurinus aureus/flammeolus* (8); (10) — direct weighings included.

Results

Temperature of topsoil in the studied plots did not generally exceed 10°C, open ground (plot 1) and turf layer (plot 4) being the most warmed up and cool elements, respectively.

The water content in the topsoil correlated with the sequence of snow spring melting on the plots. On the 1st sampling date the topsoil moisture content decreased in the following plot order: No 2—No 3—No 1 (under vegetation) — No 1 (open ground). This sequence persisted during the season (Tab. 1). Differences in moisture content were significant and correlated with the degree of the development of plant cover and soil organic layer in the plots. In plot with thick mossy sod and comparatively deep turf horizon, moisture content remained high during the whole study period. In plot 1 (open ground) this parameter was also rather stable, but at the minimal level. Under vegetation (plots 1 and 3) moisture content decreased in the end of summer by ca. 1/3 from the respective maximal values.

Population density and biomass of the main groups of soil invertebrates during the vegetative season of 1989 are presented below for the studied sites.

Plot No 1. Under plant associations the macrofauna consisted of spiders and Diptera larvae (mainly Chironomidae). Spiders were represented by small

Linyphiidae: *Erigone arctica palearctica* Braendegaard, 1934, *Collinsia spitsbergensis* (Thorell, 1872) and *Hilaria glacialis* (Thorell, 1872) (one female found). Juveniles made up 93, 87, 69, 67 and 68% of the spider density, on 1st to 5th sampling dates, respectively.

Total density and biomass of macrofauna were low (Tabs. 4, and 5), spiders making up 60–100%, and the seasonal fluctuations were insignificant. Density and biomass of Enchytraeidae were more or less similar under vegetation and in the open ground of polygons, though hydrothermic regime was different: the "ground" was more dry but warmed up better. Density was maximal in midsummer corresponding with the highest soil moisture content and temperature, and retained this level until the end of the season. In the middle of summer mass reproduction of enchytraeids by fragmentation was observed, later mature specimens appeared.

Density of Nematoda under vegetation remained almost constant during the season, somewhat decreasing only in late July. It was always considerably lower in the open ground, and on 11.07. and 23.08. significant 3–4-fold differences were observed (Tab. 4).

Table 4.

Seasonal changes in the density of soil invertebrates under plant associations and on the polygons of open ground in the polygonal tundra site (Plot 1). Density expressed as: ind./g dry substrate — for Nematoda; ind./25 cm² — for Enchytraeidae and microarthropods; ind./225 cm² — for macrofauna

Group	26.05.	18.06.	11.07.	29.07.	23.08.
			Plant associations		
Nematoda	34.8±11.9	33.1±4.2	36.3±5.8	25.1±3.8	36.0±13.0
Enchytraeidae	7.3±2.2	3.3±0.8	12.3±2.3	6.6±0.9	9.2±2.2
Microarthropods					
Total	193.5±19.0	121.5±19.6	149.5±18.8	133.7±19.4	139.8±25.5
Oribatei	93.4±8.2	47.3±8.9	69.5±12.1	69.2±15.6	63.6±13.4
Gamasina	2.1±0.5	0.9±0.4	0.7±0.3	1.2±0.2	1.1±0.3
Other Acarina	10.9±0.9	16.7±6.8	13.6±2.4	18.8±4.2	19.8±2.9
Collembola	88.0±16.2	56.6±10.6	65.7±12.9	45.0±9.1	55.3±10.9
Macrofauna					
Total	1.9±0.6	2.5±0.4	1.5±0.4	1.3±0.3	2.2±0.6
Aranei	1.9±0.6	2.0±0.3	0.9	1.2±0.3	1.3±0.4
Diptera larvae	0	0.5	0.6	0.1	0.9
			Open ground		
Nematoda	13.1±2.0	15.2±4.2	11.3±2.1	18.0±2.7	9.1±1.0
Enchytraeidae	3.0±0.9	8.4±2.4	13.8±3.3	10.9±2.2	11.1±1.9
Microarthropods					
Total	52.5±0.9	28.1±4.7	41.0±4.2	48.6±5.1	39.4±7.3
Oribatei	27.2±3.3	11.1±2.2	24.3±4.1	26.9±4.4	25.1±5.8
Gamasina	0.3±0.2	0.1±0.1	0.1±0.1	0.3±0.1	0
Other Acarina	0.5±0.3	1.4±0.3	2.0±0.5	2.7±0.9	1.3±0.5
Collembola	24.7±4.4	15.5±3.0	14.6±2.1	18.7±3.3	13.0±2.6

Table 5.

Seasonal changes in the biomass of soil invertebrates under plant associations and on the polygons of open ground of the polygonal tundra site (Plot 1). Density expressed as: ind./g dry substrate — for Nematoda; ind./25 cm² — for Enchytraeidae and microarthropods; ind./225 cm² — for macrofauna

Group	26.05.	18.06.	11.07.	29.07.	23.08.
			Plant associations		
Nematoda	0.0174	0.0166	0.0182	0.0126	0.0180
Enchytraeidae	1.5±0.5	1.0±0.6	2.4±0.5	1.6±0.3	1.8±0.4
Microarthropods					
Total	2.4556	1.5185	1.8573	1.2501	1.5874
Oribatei	0.4603	0.6045	0.5144	0.4267	0.5362
Gamasina	0.0146	0.0062	0.0042	0.0057	0.0051
Other Acarina	0.0207	0.0302	0.0845	0.0903	0.0830
Collembola	1.9600	0.8776	1.2542	0.7274	0.9631
Macrofauna					
Total	1.1±0.6	1.2±0.4	1.4±0.5	1.7±0.5	1.9±0.6
Aranei	1.1±0.6	1.0±0.2	0.7	1.4±0.4	1.2±0.5
Diptera larvae	0	0.2	0.7	0.3	0.7
			Open ground		
Nematoda	0.0066	0.0076	0.0056	0.0090	0.0046
Enchytraeidae	0.3±0.1	1.8±0.4	2.6±0.5	2.1±0.5	1.5±0.2
Microarthropods					
Total	0.9498	0.5217	0.8253	0.7877	0.7833
Oribatei	0.4658	0.1936	0.4732	0.3869	0.4893
Gamasina	0.0047	0.0052	0.0013	0.0038	0
Other Acarina	0.0019	0.0110	0.0108	0.0079	0.0066
Collembola	0.4774	0.3119	0.3400	0.3891	0.2874

Total density of microarthropods under plant associations was the highest in May (Tab. 4). In June it decreased significantly and then slightly fluctuated. This initial drop was related to the decrease in the density of Oribatei and Collembola. In July the density of oribatid mites increased and then remained constant. Fluctuations of the Collembola density were not significant. Total density of other Acarina was rather low and almost constant. Acaroidea were not registered. Mesostigmata (Aceosejidae and Zerconidae) constituted 18% of the total density in May, and from 5 to 6% later on.

Microarthropod density in the open ground subplot was 4 times lower than under plant associations, diminishing proportionally for Oribatei and Collembola. The abundance of Oribatei was always somewhat higher than that of Collembola, excluding June, when springtails were more abundant than mites (Fig. 1). Gamasina and other mites usually constituted less than 5% and 5–10%, respectively. Density dynamics of microarthropods was similar to that observed under plant associations, except for the more sharp decrease in June.

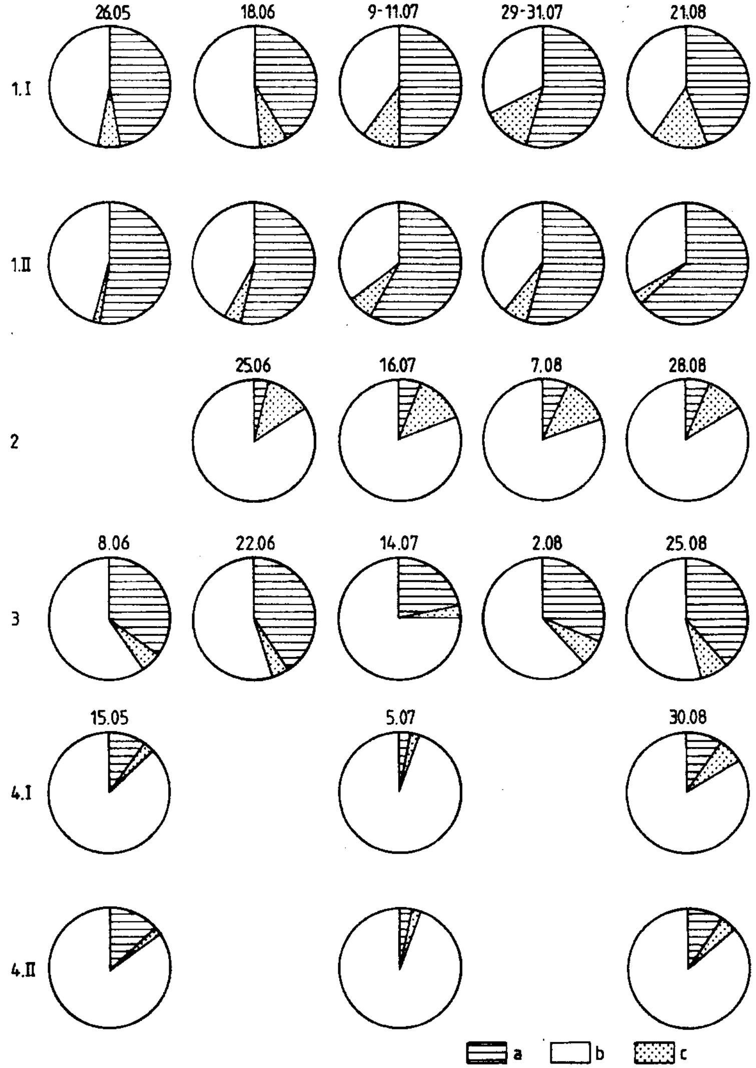

Fig. 1. Seasonal changes in the abundance (%) of microarthropod groups at different tundra sites of Hornsund. Symbols of the groups: a — Oribatei, b — Collembola, c — Acarina excluding Oribatei. Symbols of the sites: 1 — polygonal tundra (plot No 1), I — under vegetation, II — polygons of open ground; 2 — wet mossy swamp, assosciation with *Calliergon stramineum* (plot No 2); 3 — mossy/lichenous coastal tundra (plot No 3); 4 — moss associations near the bird colony (plot No 4), I — moss layer, II — turf layer

Biomass of Oribatei was almost constant in the both subplots, whereas biomass of Collembola was stable in the open ground and greatly fluctuated under vegetation (Tab. 5).

The bulk of the Oribatei population in both subplots at all the sampling dates was made by *Liochthonius* sp. ($58 \pm 4\%$ of the abundance under vegetation and 40±5% in the open ground; frequency of occurrence in the samples was 99 and 95%, respectively). *L. lapponicus* (Tragardh, 1910) prevailed, *L. muscorum* Forsslund, 1964, and *L. alpestris* (Forsslund, 1958) were also recorded. *Trichoribates novus* (Sellnick, 1928), *Camisia foveolata* Hammer, 1955, and *C. lapponica* Tragardh, 1910 (in the open ground) were the second group by abundance and frequency of occurrence (Fig. 2). The abundance of *Trichoribates* spp. group (sum of *Diapterobates notatus* Thorell, 1871, *T. novus* Sellnick, 1928, *T. trimaculatus* C.L. Koch, 1836) decreased during the season from 21–26% to 8–9%. The abundance of *Camisia* in the open ground was mostly constant (28% in the average) decreasing to 18% in the end of August. Dominance of the species of *Trichoribates, Tectocepheus, Ceratoppia* was recorded from time to time. Among Mestostigmata, *Zercon forsslundi* was almost always predominant, rarer *Arctoseius multidentatus*. Trombidiformes (Fig. 1a) were mainly represented by Tetranychidae, sometimes by Bryobiidae (*Bryobia* sp.). Under plant associations Tetranychidae were substituted by Stigmaeidae (*Ledermulleria* sp.) during the season.

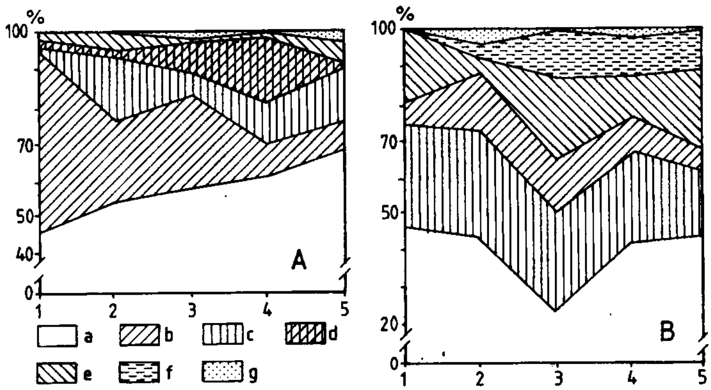

Fig. 2. Seasonal changes in the abundance (%) of Oribatei species in polygonal tundra (Plot No 1): A — under vegetation, B — polygons of open ground; 1–5 — sampling dates; a — *Liochthonius* spp., b — *Trichoribates* spp., c — *Camisia lapponica*, d — *Oppia* sp., e — *Ceratoppia hoeli*, f — *Tectocepheus velatus*, g — other Oribatei

The main part of Collembola density under vegetation was made up by *Folsomia quadrioculata* (69% by average abundance and 97% by frequency of occurrence). Among other species, *Xenylla humicola* became dominant in May (32% and 100%, respectively) but later its abundance decreased to a more or less constant level of 10 to 16%. The abundance of *Hypogastrura tullbergi* increased from 5–6 up to 17% in the end of the season. In the open ground the abundance of these three species and *Sminthurinus malmgreni* was almost equal in May (21–29%) making up together 98% of the Collembola numbers. A relative increase in the abundance of epigeic forms in spring (*S. malmgreni, H. humicola, H. tullbergi*) might be attributed to a better warming up of the open ground in contrast to the soil under vegetation. Later the first place passed to *F. quadrioculata* (39–63%) and *H. tullbergi* (20–56%). The abundance of *X. humicola* and *S. malmgreni* decreased abruptly, the latter species having disappeared before August. A similar population dynamics of *S. malmgreni* was observed under vegetation but at the lower level of abundance (Fig. 3).

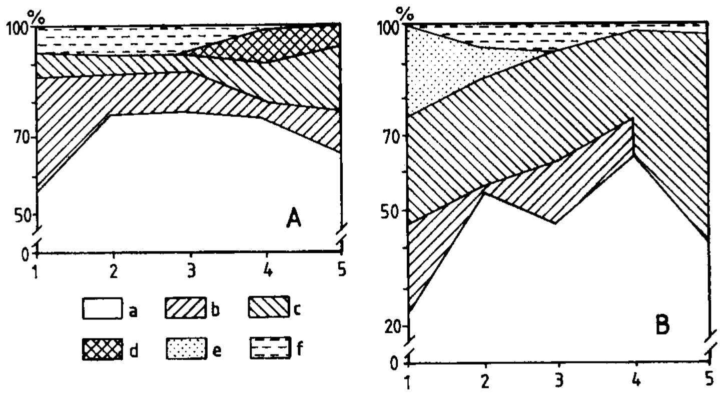

Fig. 3. Seasonal changes in the abundance (%) of Collembola species in polygonal tundra: A — under vegetation, B — polygons of open ground; 1–5 — sampling dates; a — *Folsomia quadrioculata*, b — *Xenylla humicola*, c — *Hypogastrura tullbergi*, d — *Isotoma tshernovi*, e — *Sminthurides malmgreni*, f — other Collembola

Size structure of oribatid populations under vegetation and in the open ground was generally similar. In *Liochthonius* spp. adults predominated over juveniles in the 1st half of the season. On the contrary, in the end of July (plant associations) and in August (open ground) the part of the preimaginal forms increased by 3 to 4 times. In *Trichoribates, Camisia* and *Ceratoppia* species these stages constituted a considerable part of the population at all the dates. According to the dynamics of the abundance of the larvae, the peak of hatching intensity of *Trichoribates* spp. occurried in the 1st half (both subplots) and in the end (open ground subplot) of the season. In Mesostigmata, adults constituted 44–76% of the population numbers at all the sampling dates.

Plot No 2. Mossy swamp remained under snow and water until midsummer, therefore sampling of macrofauna was possible only from the middle of July. This group was represented by larvae and pupae of several Diptera (Nematocera) species. Their density was mostly low (Tab. 6), and species composition changed in the course of the season. In the middle of July swarming of adult Chironomidae took place, their pupae and larvae predominated in the soil. A few adults of small parasitic Hymenoptera were also found in the moss layer.

Density of Enchytraeidae was high although plot 2 was characterized by the most wet and cold edaphic conditions among the sites (Tab. 6). It significantly increased during the season by 4 times. In the beginning of the season mass

Table 6.

Seasonal changes in the density and biomass of soil invertebrates in the association of *Calliergon stramineum* (Plot 2). Units of density and biomass as in Tables 4 and 5

Group	25.06.	16.07.	7.08.	28.08.
	Density			
Nematoda	173.1±26.8	260.3±34.9	176.9±14.2	255.3±28.6
Enchytraeidae	11.6±3.0	17.9±2.7	37.2±5.7	48.9±9.8
Microarthropods				
Total	886.4±162.5	824.5±118.4	1149.9±157.8	1264.4±165.4
Oribatei	29.9±0.9	53.3±16.6	54.8±12.4	47.1±10.5
Gamasina	4.6±2.1	1.7±1.3	0.3±0.3	0.7±0.3
Other Acarina	62.9±19.9	93.5±29.4	171.6±51.8	134.4±29.3
Collembola	769.0±113.6	676.0±138.1	923.2±138.1	1082.2±161.2
Macrofauna				
Diptera larvae	0	3.9±1.2	0.9±0.9	0.9±0.3
	Biomass			
Nematoda	0.0866	0.1302	0.0884	0.1276
Enchytraeidae	0.85±0.35	2.13±0.59	3.47±0.71	5.97±1.92
Microarthropods				
Total	14.2954	13.2257	17.1860	20.9777
Oribatei	0.0778	0.4985	0.2879	0.4249
Gamasina	0.0218	0.0102	0.0113	0.0066
Other Acarina	0.2803	0.4425	0.8285	0.7578
Collembola	13.9155	12.2745	16.0683	19.7884
Macrofauna				
Diptera larvae	0	2.9±1.1	1.0±0.4	1.2±0.9

reproduction of enchytraeids by means of fragmentation was observed; late in August clitellated adults appeared.

Nematodes showed two significant density peaks: in July and in the end of August (Tab. 6).

Total density of Acarina and Collembola in the mossy swamp was high in June–July, exceeding their density under plant associations of the plot 1 by 6–7 times. It increased until August (Tab. 6). Seasonal dynamics of microarthropods was determined by Collembola making up on average 84% of their total density. Oribatid density, after some initial growth, remained stable and low. Trombidiform mites (mainly *Ledermulleria* sp.) were connected with the moss cover and were comparatively abundant (from 83 to 98%) (Tab. 6, Fig. 1a). Mesostigmata (*Zercon forsslundi* and *Arctoseius multidentatus*) were found sporadically.

Biomass of the oribatid mites was low as compared with a very high biomass of Collembola (Tab. 6).

Oribatei were mainly represented by *Liochthonius* spp. (57–91%) and *Trichoribates* spp. (8–42%), with the maximum at the 1st and minimum at the 2nd sampling date. *Camisia* spp. were recorded more or less regularly, never reaching high abundance. In the population of *Liochthonius* the abundance of preimaginal stages increased up to August from 10 to 45%. Larvae and different nymph instars permanently made up 2/3 of *Trichoribates* spp. population. It seems that hatching of *Liochthonius* and *Trichoribates* larvae mainly occurred in the end and in the middle of summer for these species groups, respectively. In Mesostigmata adult mites predominated making up 52, 72 and 77% at the first, second and fourth sampling dates, respectively.

Folsomia quadrioculata predominated among Collembola species and it has determined the density dynamics of the group . Its abundance was constant (80−83%) with 100% of frequency in samples. *Hypogastrura viatica* made up 7−12% of the whole Collembola abundance. Sometimes *Onychiurus groenlandicus* and *Hypogastrura tullbergi* were also noticeable.

Plot No 3. Macrofauna consisted of spiders (Erigoninae being absolute dominants) and Diptera larvae (Tab. 7). Density of spiders was rather constant during the season and similar to that obtained under plant associations of the

Table 7.

Seasonal changes in the density and biomass of soil invertebrates in the mossy/lichenous tundra (Plot 3). Units of density and biomass as in Tables 4 and 5

Group	8.06.	22.06.	17.07.	2.08.	25.08.
			Density		
Nematoda	55.9±9.8	100.7±22.7	99.5±15.0	71.4±9.8	85.8±13.4
Enchytraeidae	20.3±5.5	28.0±2.5	58.1±11.6	40.9±5.5	16.5±3.8
Microarthropods					
Total	187.7±24.5	249.3±23.4	344.6±36.2	353.4±76.1	275.2±36.3
Oribatei	73.2±8.7	107.3±11.0	79.5±16.1	112.5±16.1	108.2±16.3
Gamasina	0.9±0.3	1.0±0.4	2.7±0.6	1.7±0.9	1.7±0.3
Other Acarina	5.5±1.3	3.1±0.8	2.4±0.9	17.9±1.3	20.2±2.8
Collembola	108.1±18.8	137.9±16.9	260.0±36.3	221.6±32.9	145.3±20.8
Macrofauna					
Total	1.5±0.3	1.8±0.3	1.3±0.5	1.7±0.5	2.1±0.9
Aranei	1.3±0.2	1.7±0.3	1.3±0.6	1.5±0.5	2.1±0.9
Diptera larvae	0.2	0.1	0	0.2	0
			Biomass		
Nematoda	0.0280	0.0504	0.0498	0.0357	0.0429
Enchytraeidae	2.1±0.6	3.3±0.4	10.7±2.4	6.1±0.9	2.2±0.6
Microarthropods					
Total	3.1983	4.8471	6.1295	6.1339	4.3398
Oribatei	0.5882	1.0497	0.8521	1.0506	0.9424
Gamasina	0.0086	0.0074	0.0329	0.0129	0.0115
Other Acarina	0.0457	0.0142	0.0445	0.1452	0.0828
Collembola	2.5558	3.7758	5.2000	4.9252	3.3031
Macrofauna					
Total	1.1±0.3	1.2±0.2	1.2±0.4	1.1±0.4	1.3±0.6
Aranei	0.8±0.2	1.2±0.4	1.2±0.4	0.9±0.4	1.3±0.6
Diptera larvae	0.3	0.01	0	0.2	0

polygonal tundra site. Juveniles comprised 79, 84, 50, 80 and 78% of the population at the first from fifth sampling dates, respectively. Among adults *Collinsia spitsbergensis* prevailed, single specimens of *Erigone arctica* were also recorded. Occurrence of Diptera larvae (mainly Chironomidae) was not regular.

Density of enchytraeids increased in the first half of the season with the peak in July, and decreased later (Tab. 7); its level exceeded the one in plots No 1 and 2.

Density of nematodes reached the maximum level in the end of June and later somewhat decreased (Tab. 7).

Total density of microarthropods increased during the season and had one peak in the end of July—beginning of August (Tab. 7). That was connected mainly with Collembola making up from 52 to 75% of microarthropod total abundance. The abundance of Oribatei fluctuated from 24 to 42% of the total for microarthropods. When comparing the densities of Oribatei and Collembola, constant predominance of the latter group was recorded during the season (Fig. 1). Density of Mesostigmata (mainly *Arctoseius multidentatus*) was low. Mites of other Acarina groups were rare in June—July and more abundant in August. Changes in the biomass of Oribatei and Collembola populations followed density of these groups.

Contrary to other sites, in the mossy/lichenous tundra species of the oppioid complex played an important role among Oribatidae (Fig. 4.1). Species of *Liochthonius* and *Trichoribates* were dominant (as in the polygonal tundra), *Camisia* species being less abundant (Fig. 2). The density of *Liochthonius* spp. was almost constant during the season; however, the proportion of immature stages increased from 9% in June to 55% in August when the highest abundance of larvae occurred. Immature mites made up 66—76% of *Trichoribates* spp. population (with peak of larval density in June) until the end of

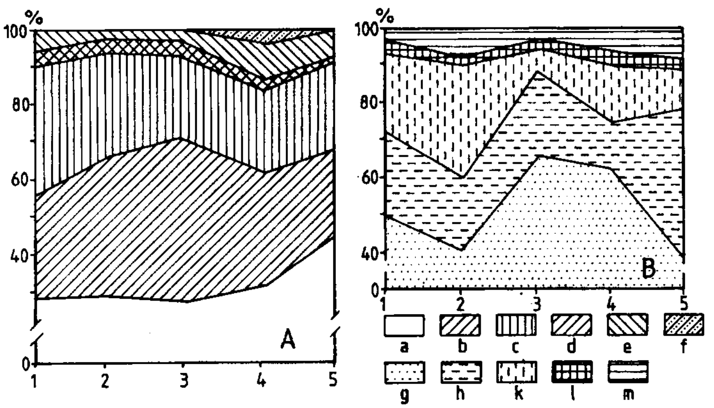

Fig. 4. Seasonal changes in the abundance (%) of Oribatei (A) and Collembola (B) in the mossy/lichenous tundra: 1—5 — sampling dates; a — *Liochthonius* spp., b — *Trichoribates* spp., c — *Oppia* spp., d — *Ceratoppia hoeli*, e — *Camisia lapponica*, f — *Tectocepheus velatus*, g — *Folsomia quadrioculata*, h — *Hypogastrura tullbergi*, k — *Xenylla humicola*, l — *Onychiurus groenlandicus*, m — other Collembola

August when adult mites were predominant (53%). The population of *Camisia* spp. consisted almost completely (June) or by 2/3 of immature individuals. In contrast, populations of oppiid mites were characterized by low percentage of preimaginal forms. The population of Mesostigmata at all the sampling dates consisted by 67–89% of adult specimens.

Among springtails, *Folsomia quadrioculata* was permanently abundant (on the average 53% of Collembola density with the maximum of 67% in July). The other dominants were *Xenylla humicola* (17%) and *Hypogastrura tullbergi* (24%), with peaks in June (39%) and in the middle and end of the season (32%), respectively (Fig. 4.2).

Plot No 4. The compact cover of mosses adjacent to the colony of Auks was inhabited by soil fauna much more abundantly comparing with all the studied plots.

Macrofauna was concentrated in the living moss and upper layer of mossy litter to the average depth of 5 cm. It was represented by spiders and larvae of Diptera; in associations of ornithogenous flora larvae and beetles of Staphylinidae (*Atheta graminicola* Gravenhorst, 1802) were also recorded (Tabs. 8 and 9). Density of Diptera larvae sharply increased from spring to autumn; Chironomidae predominated (7–55 ind./sample).

Table 8.

Seasonal changes in the density of soil invertebrates in the mossy site near the bird colony (Plot 4). Density units as in Table 4. ND — not determined

Group	15.05.	5.07.	30.08.
		Moss layer	
Nematoda	3813.8±561.8	1296.6±635.6	3190.9±1089.5
Enchytraeidae	0.4±0.2	19.4±12.3	32.4±31.7
Microarthropods			
Total	764.4±67.0	1558.0±250.0	1496.9±150.1
Oribatei	85.8±23.7	42.8±9.0	114.6±33.9
Gamasina	6.8±1.8	10.5±1.4	9.0±1.3
Other Acarina	6.8±1.6	50.6±15.9	81.0±31.6
Collembola	666.5±66.9	1482.7±258.9	1292.3±149.0
Macrofauna			
Total	6.9±2.6	ND	97.5±26.5
Aranei	0.4	ND	1.4
Diptera larvae	6.5±2.6	ND	94.5±26.8
Staphylinidae im.	0	ND	1.6
		Turf layer	
Nematoda	391.2±120.5	165.3±61.7	193.9±98.9
Enchytraeidae	0	0.9±0.1	13.4±12.9
Microarthropods			
Total	73.9±11.4	153.0±35.5	634.7±48.7
Oribatei	10.1±4.2	4.3±2.0	59.2±14.5
Other Acarina	1.2±0.3	4.0±1.0	19.4±0.9
Collembola	62.6±11.7	144.7±36.5	556.1±68.5

Aranei were not numerous, especially in summer when they were represented by juveniles of Erigonidae. In August immature specimens comprised 60% of the spider density; females of *Erigone arctica palearctica, Hilaria glacialis, Collinsia spitsbergensis* were also recorded.

Density and biomass of Enchytraeidae grew during the season (Tabs. 8 and 9). In the moss layer the increase was particularly sharp in the first half of the season. Spatial distribution of enchytraeids in the moss was quite irregular, in spring they were registered only in 2 samples, and on the 2nd and 3rd sampling dates — in 5 out of 15 samples. The maximal observed density was 412 ind. × 25 cm^{-2}, i.e. 164800 ind. × m^{-2} (August). In the turf layer a more or less abundant population was formed only in the end of the season.

Density (and biomass) of nematodes were extremely high reaching 8000–14000 ind. × g^{-1} of dry substrate (or 25–33 mln ind. × m^{-2}). They decreased in July, although remaining at a very high level (Tabs. 8 and 9). Nematodes were concentrated in the moss layer where spring and autumn peaks were recorded; in the turf their density was lower by 3–16 times and decreased during the season.

The density and biomass of microarthropods in the moss layer increased two-fold by the middle of summer and were high in the end of the season (Tabs.

Table 9.

Seasonal dynamics of the biomass of soil invertebrates in the mossy site near the bird colony (Plot 4). Biomass units as in Table 5. ND — not determined

Group	15.05.	5.07.	30.08.
		Moss layer	
Nematoda	1.9069	0.6483	1.5954
Enchytraeidae	0.5±0.5	2.9±1.7	4.8±4.3
Microarthropods			
Total	20.3060	44.9032	39.2902
Oribatei	0.1523	0.1409	0.1437
Gamasina	0.0766	0.0695	0.0875
Other Acarina	0.0155	0.0635	0.1598
Collembola	20.0616	44.6293	38.8992
Microfauna			
Total	7.5±3.2	ND	97.8±34.2
Aranei	0.3	ND	2.9
Diptera larvae	7.2±3.2	ND	95.1±35.1
Staphylinidae im.	0	ND	1.3
		Turf layer	
Nematoda	0.1956	0.0826	0.0970
Enchytraeidae	0	0.1±0.1	1.3±1.2
Microarthropods			
Total	1.9067	4.3765	17.8360
Oribatei	0.0193	0.0107	0.0606
Other Acarina	0.0031	0.0103	0.0368
Collembola	1.8843	4.3555	17.7386

8 and 9). The basis of density at all the sampling dates was formed by Collembola (Fig. 1). Among Acarina oribatid mites were predominant, their population diminished during the season. Mesostigmata (with *Arctoseius multidentatus* as constant dominant) had low population density. Other Acarina (mainly Prostigmata) increased in numbers from spring to autumn. Collembola density was maximal in the middle of summer. In the turf layer microarthropod density was much lower than in the moss; it increased 8-fold towards the end of the season due to growth in Collembola density. Dynamics of Acarina groups was similar to that observed in the moss.

The main part of the Oribatei populations consisted of the oppioid mites (56−86% in the moss, 88−97% in the turf). *Liochthonius lapponicus* was second dominant, its density increasing from the 1st to the 3rd sampling date. The constant occurrence in samples of *Ameronothrus nidicola* was apparently connected with the proximity of the bird colony. The part of the immature stages among Oribatei increased to the end of the season. Among Mesostigmata abundance of adult mites was constantly 80−83%.

Among springtails *Folsomia quadrioculata* was an absolute dominant forming more than 50% (up to 93%) of the total Collembola density at all the sampling dates.

Table 10.

Comparative data on the average numbers and biomass of soil invertebrates within the plots under study. Symbols: PA — under plant association; OG — on the open ground; (M+T) — in the moss and turf layers, totally, A — density (ind./m^2), B — biomass (mg/m^2)

	Plot 1		Plot 2	Plot 3	Plot 4
	PA	OG			M+T
A					
Aranei	65	0	0	70	30
Diptera l.	19	0	84	+	2242
Staphylinidae im.	0	0	0	0	36
Enchytraeidae	3096	3376	11560	13104	8867
Nematoda	326600	172428	848367	281425	8585096
Oribatei	27400	9168	18510	38456	42240
Other Acarina	6752	680	3481	4528	18267
Collembola	24848	6920	345040	69832	560654
B					
Aranei	48.0	0	0	47.9	40.0
Diptera l.	16.9	0	75.5	4.5	2271.0
Staphylinidae im.	0	0	0	0	28.9
Enchytraeidae	664.0	664.0	1242.0	1952.0	1280.5
Nematoda	162.8	86.2	424.2	140.7	4291.1
Oribatei	203.4	160.7	128.9	358.6	70.3
Other Acarina	25.2	3.1	231.0	26.6	38.5
Collembola	462.6	144.5	6204.7	1580.8	17009.1
Total biomass	1582.9	1058.5	8306.3	4111.1	25028.9

Discussion

Season averages (expressed per m^2) for soil fauna in the studied plots are compared in Table 10.

Soil fauna was the most abundant in the moss associations near the bird colony (plot 4). Its density and biomass decreased in the row of plot No 2 (association of *Calliergon stramineum*), plot No 3 (mossy/lichenous tundra) and plot No 1 (polygonal tundra).

Plot 4 was greatly influenced by the supply of nutrients from the bird colony. Distribution of all fauna groups showed a high level of patchiness. Macrofauna (mainly Diptera larvae) was relatively abundant and diverse. Total biomass of soil animals was higher by an order of magnitude as compared with the other plots. Collembola comprised the main part of the total biomass (69%). Nematodes were the 2nd dominant group (19%). Diptera larvae made up 11%, Enchytraeidae 6%.

The impact of bird colony on the 2nd site was somewhat intermediate between the one in the 4th site and sites 3 and 1. Collembola comprised the basic part of soil animal biomass (77%) and Enchytraeidae made up 15%. The contribution of nematodes was 5%, Chironomidae larvae contributed by only 1% in the total biomass that was 2 times lower than in the 4th plot.

In the mossy/lichenous tundra (plot 3) the main contribution to the total biomass was made by Enchytraeidae (48%) and Collembola (38%). In this site the biomass of enchytraeids was the highest comparing with other sites.

The biomass of soil-dwelling animals was the lowest in the plot 1. Assuming the approximate relative area of the 2 subplots within the site ("plant associations" and "open ground") as 0.3:0.7, the average biomass of soil fauna in the plot can be evaluated as $1.25\ g \times m^{-2}$. Under the vegetation it consisted mainly of Enchytraeidae (42%) and Collembola (29%), and on the open ground — of Enchytraeidae (60%). Nematoda made up 10 and 8% of the biomass in the respective subplots.

In all the sites phyto-saprophages were the dominant trophic group of soil fauna. The part of predators (Erigonidae spiders, trombidiform mites and Mesostigmata, mainly Aceosejidae and Zerconidae) in the total numbers and biomass was very low. In the plot 2 the whole population of soil animals could apparently suffer from the predation by Barnacle geese consuming a considerable part of the moss vegetation.

The density of nematodes in the sites 1, 2 and 3 is in the range of 10^5-10^6 $ind \times m^{-2}$ and can be considered as being at average level comparing with the data compiled by Petersen and Luxton (1982). The only exclusion is plot 4 where nematodes density is comparable with the highest recorded estimates (the level of $10^7\ ind \times m^{-2}$). Enchytraeid density and biomass at all the plots are rather moderate, with maximal values hardly reaching mean estimates found in literature for various tundra sites (Petersen and Luxton 1982).

The density of soil mites, even in the soil of plot 1 with a poor Acari population, is of the same order with those mentioned by other authors for Arctic tundra landscapes. Thus, studying mite populations in various plant associations of the mossy/lichenous coastal tundra of Hornsund, Seniczak and Plichta (1978) evaluated the density of Oribatei, Mesostigmata and Trombidiformes in the range of 18840 – 81400, 10 – 840 and 960 – 12000 ind. $\times m^{-2}$, respectively. Challet and Bohnsack (1968), and Bohnsack (1973) recorded the total density of Acari in the coastal polygonal tundra as 38372 ind. $\times m^{-2}$, Oribatei making up 63%. For the mites in the coastal tundra of Alaska Douce (1976) and Douce and Crossley (1977) obtained 70800 ind. $\times m^{-2}$ in the meadow associations, and only 5700 ind. $\times m^{-2}$ in the soil of polygons.

The density of springtails (thousands ind. $\times m^{-2}$) in the studied sites, regarding seasonal fluctuations, was observed in the range of 5 – 10 (plot 1, open ground), 48 – 80 (plot 1, plant associations), 75 – 140 (plot 3), 330 – 430 (plot 2) and 290 – 790 (plot 4). This range covers the variability of corresponding literature data for tundra landscape and polar deserts of the high Arctic and Antarctic (Challet and Bohnsack 1968, Ananeva 1971, Martynova, Gorodkov and Čelnokov 1973, Sendstad 1976, Černov, Striganova and Ananeva 1977, Petersen and Luxton 1982, Bulavincev and Babenko 1983, Ananeva, Babenko and Černov 1987, and others). The most usual records lie within the range of $10^4 – 10^5$ ind. $\times m^{-2}$ (and $10^0 – 10^{-2}$ g of dry mass $\times m^{-2}$), and are characteristic of typical tundra landscapes (plant associations of the polygonal and mossy/lichenous tundra in our study). Open ground of the polygons is evidently the most unfavourable environment with the lowest population density of springtails comparing with other tundra sites (Černov, Striganova and Ananeva 1977; open ground in our 1st plot). Collembola populations of maximal size (more than 10^5 ind. $\times m^{-2}$ and 5 g $\times m^{-2}$) were recorded in the polar ornithogenous soils (plot 4 in our study and the data of Collins, Baker and Tilbrook 1975, for Signy Island); this exceeds density estimates having been obtained for the group in almost all the types of natural ecosystems (Petersen and Luxton 1982). Decaying seaweeds (Byzova *et al.* 1986), manure heaps and composts (Černova 1977) could be only comparable natural or arthropogenous biotopes. It seems that organic matter supply and high microbial activity in the soil are mostly favourable for this group among other environmental factors. However, Collembola populations in these situations are characterized by low species diversity and by an overwhelming dominance of 1 – 2 species.

More detailed analysis of the fauna and population dynamics of separate groups of soil invertebrates in the studied region will be published elsewhere.

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Streszczenie

W prezentowanej pracy przedstawiono rozmieszczenie zgrupowań glebowych bezkręgowców w czterech różnych typach tundry arktycznej Spitsbergenu, w okresie lata arktycznego 1989. Badano sezonowe zmiany liczebności poszczególnych grup zoologicznych tego zespołu (Tab. 4–8, Rys. 1–4) a także ich biomasę (Tab. 2 i 3).