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Invertebrate activity under snow in a South-Norwegian spruce forest

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Abstract

The activity of invertebrates under snow was studied by pitfall traps during two winter seasons in a high altitude spruce forest in southern Norway. With a snow layer varying between about 30 and 150 cm during the sampling periods, the temperature in the subnivean air space stayed close to 0 °C. Traps were emptied and replaced at least once a month during the snow-covered period, from October/November to April/May. For phenological purposes, some trapping was also performed just before or after the snow period. Most invertebrate groups were identified to species level. Beneath a permanent snow cover, the most species-rich groups collected were Collembola (22 species), Acari (22 taxa), spiders (12 species) and beetles (13 species). Collembola and Acari (microarthropods) always dominated in numbers. Subnivean catches also included Opiliones, Pseudoscorpiones, Trichoceridae, Limoniidae, Brachycera, Mecoptera, Gastropoda, and Harpacticoidea (Copepoda). Beetle larvae of Cholevidae and Staphylinidae were quite common. Traps placed adjacent to natural cavities between stones etc. did not achieve higher catches than traps on flat ground with a narrow subnivean space, indicating general subnivean activity over the whole forest floor. Many Collembola and Oribatida species were actively feeding under snow, having a characteristic gut content of fungal hyphae and spores. Also the gut of Cholevidae larvae (Coleoptera) contained fungal hyphae and spores, but mixed with decaying plant material. Since fungal feeders perhaps do not need to move much, pitfall trapping may underestimate the extent of subnivean feeding. We hypothesize that certain fungi known to decompose litter beneath snow (snow molds) represent a valuable food source for winter-active Collembola, Acari and Cholevidae larvae. Some of these may be eaten by spiders. Spiders and beetle larvae are among the invertebrates known to be eaten by subnivean shrews, so we support the idea of subnivean food chains.

Key words: Winter, invertebrate activity, pitfall trap, under snow, spruce forest, Norway.

1. Introduction

When the snow layer exceeds about 20 cm (the so-called hiemal threshold), the temperature at the soil surface stabilizes at about 0 °C or a few degrees below (Coulianos & Johnels 1962, Geiger 1965, Pruitt 1970). At these temperatures, several ground-living invertebrates can be active in the air space between the ground and the snow (the subnivean habitat). Some of them migrate up into the snow layers (the intranivean habitat), or even enter the snow surface (the supranivean habitat). Among the latter fauna are certain wingless taxa which use the smooth snow surface for easy migration (Fennoscandian review by Hågvar 2010). The purpose of intranivean activity, which is mainly by Collembola, (Brummer-Korvenkontio & Brummer-Korvenkontio 1980, Leinaas 1981) may be to escape water logging or predation, but is not fully understood. The ecological meaning of subnivean activity is also unclear, although a number of more or less fragmentary studies exist.

A major part of subnivean invertebrate studies is from Manitoba, Canada (review by Aitchison, 2001). Other Canadian studies were by Olynyk & Freitag (1977) and Merriam et al. (1983). In the USA, Schmidt and Lockwood (1992) gave data from Wyoming, and Addington & Seastedt (1999) from Colorado. In Europe, Näsmark (1964) presented a pioneer study from Sweden. Smaller Nordic studies were by Waaler (1972) and Leinaas (1981) from Norway, and Viramo (1983) and Koponen (1976) from Finland. Vanin & Turchetto (2007) performed a study on subnivean activity of various invertebrates in the Italian Alps.

Several of the referred studies were either limited to one or a few groups, had a limited taxonomic resolution, or did not separate clearly between snow-covered and snow-free periods. We wished to do an in-depth study in the most common forest type of Norway, which is also characteristic for the Eurasian taiga. Which groups and species are active under snow, how regular is this activity, would studies of gut content reveal feeding activity, and can we indicate possible food chains? By placing traps partly on flat ground and partly close to natural cavities, we hoped to illustrate possible local differences in subnivean communities. The study covered the phenology during two successive winters, and most of the material was identified to species level. To our knowledge, this is the most detailed study on subnivean activity of invertebrates.

2. Material and methods

The study was performed in Votnedalen, Rollag municipality, Buskerud county, in central South Norway (60°1’0’’N, 9 °1’20’’E) in an old, rather undisturbed spruce (*Picea abies* L.) forest dominated by bilberry (*Vaccinium myrtillus* L.) vegetation at 850 m a.s.l. Here, a snow cover of 1–2 m is common, and often lasts for 5–6 months. Daily maximum and minimum temperatures during the two winter periods are shown in Fig. 1, based on an 8 km distant weather station at 220 m a.s.l., but corrected for a mean reduction of 0.6 °C per 100 m altitude. Twelve permanent pitfall traps, 8.5 cm in diameter, were run continuously for two winters (2007–2009), including some periods before and after snow cover for phenological purpose. Traps were placed 2–11 m apart, in the mean 4 m. Presence or absence of a continuous snow cover during each sampling period is indicated at the top of Tab. 2–7.

The trap design was similar to Näsmark (1964): a water-proof roof of plywood (30 x 30 cm) placed 1–3 cm over the trap had a 11 x 11 cm central hole (Fig. 2). Another square piece of 15 x 15 cm covered this hole as a lid, and a small stone kept it in place. At each sampling, the exact position of the trap was found relative to a thin pole about 30 cm distant. Due to the considerable snow depth, the insulation effect of snow was high, and the lowest snow layers were sometimes wet or icy. A saturated salt water solution with a few drops of detergent worked well as a preservative, and the animals were afterwards conserved in alcohol.

In order to study the effect of different microhabitats, two traps were placed close to natural cavities near large stones, six close to smaller cavities under roots or close to stones, and four on flat ground. The effect of microhabitats on the total catches of single traps was tested by Ordinal logistic regression, likelyhood ratio tests (JMP9, SAS Institute 2011, Cary, North Carolina, USA). Traps were usually emptied monthly. At each sampling, snow depth was measured for all traps, and the subnivean temperature was measured in one site close to the traps with a UPM weather transmitter CE 682 (Fig. 3).

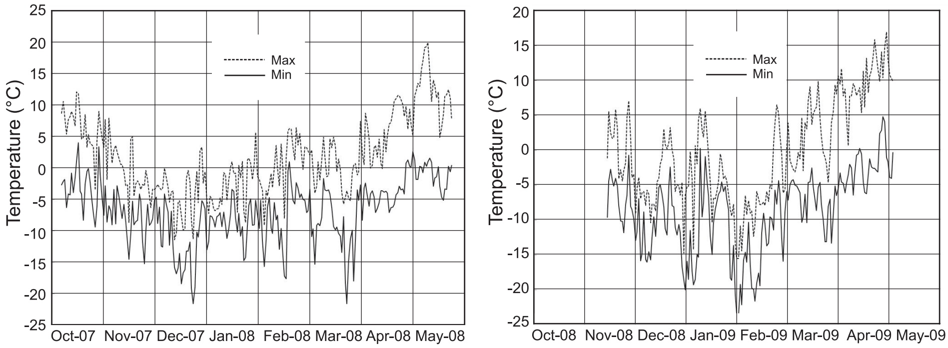

Fig. 1 Maximum and minimum air temperatures during the two winters.

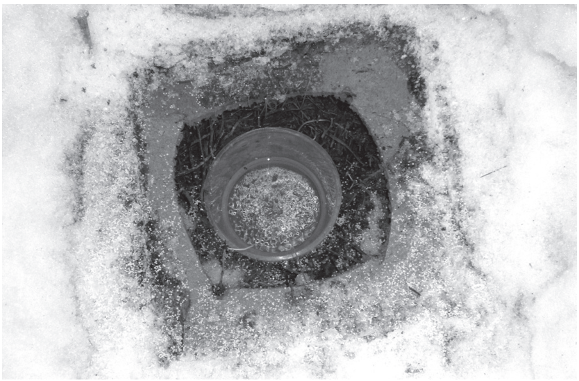

Fig. 2 Sampling procedure: A channel was dug down to the trap and the upper lid above the trap has been removed. The inner cup with the trap contents was replaced by a new one through the hole. Then the hole was covered again by the lid and the removed snow was replaced. The subnivean space around the trap was not disturbed.

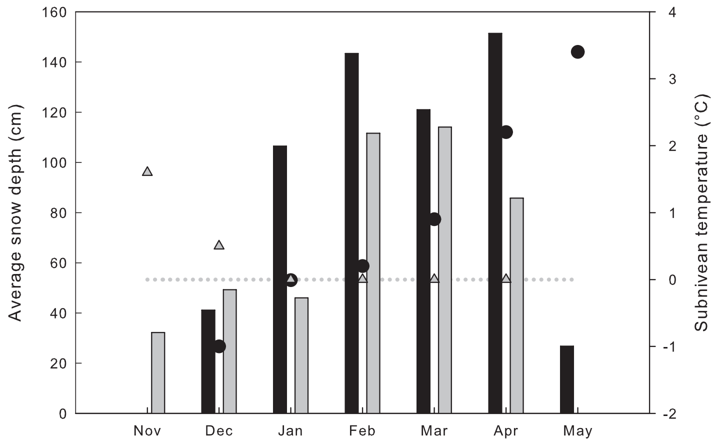

Fig. 3 Snow depth during monthly samplings in 2007/2008 (black columns) and in 2008/2009 (grey columns). Subnivean temperatures are indicated by black dots for 2007/2008 and by grey triangles for 2008/2009. The dotted horizontal line shows 0°C.

A few traps were sometimes contaminated with forest litter, probably due to subnivean activity of small mammals. These traps were excluded from the material, since we wanted to be sure that catches were due to invertebrate activity and not passive transport. For phenological comparison, all catches are presented as a calculated total (to the nearest integer) per 12 functioning traps in each sampling period.

The presence or absence of gut content was noted in Collembola (springtails), Acari (mites) and insect larvae. The gut content was further analysed at 400 x magnification, in Collembola and Acari in mounted specimens and in beetle larvae by dissecting out the content.

Sexes were distinguished among adult spiders, but most juveniles could not be identified to species or sex. Developmental stages were distinguished in Oribatida, but not in Collembola. Nomenclature of Collembola is according to Fjellberg (1998, 2007).

3. Results

3.1. Total catches

Fig. 4 shows the relative frequency (%) of different taxa at various samplings during the two winters, as well as total number of specimens. Microarthropods (Collembola and Acari) always dominated in numbers, but all main taxa were represented in all samplings. In the mean, Collembola constituted 61 % of the specimens, Acari 14 %, Araneae 10 %, insect larvae 8 %, adult Coleoptera 4 % and other invertebrates 3 %. Most individuals were collected in December and January during the second winter, when the subnivean temperature was close to zero. The May sampling in the first winter caught relatively few individuals, even though this period had the highest subnivean temperature of 2–3 °C. No significant effect of microhabitat (large, small or no natural cavities adjacent to the trap) was found, neither on total number of species ($X^2 = 0.02$, $P = 0.9$) nor on specimens per trap ($X^2 = 1.87$, $P = 0.17$) (Tab. 1).

3.2. Collembola

Tab. 2 shows the collembolan catches during periods of permanent snow cover. This group was present at all samplings, and 22 species from 8 families were collected. Throughout both winters, the most dominant species was *Lepidocyrtus lignorum*. In descending sequence, the next four dominant species were: *Desoria olivacea, Parisotoma notabilis, Hypogastrura socialis,* and *Arrhopalites pygmaeus*. Practically all species had individuals with a visible gut content, often representing the majority of the sampled individuals. Microscopic studies of mounted specimens revealed that all species with gut content had eaten a varying mixture of fungal hyphae and fungal spores. A typical gut content is shown from *Lepidocyrtus lignorum* in Fig. 5.

3.3. Acari

The mite catches during snow-covered periods (Tab. 3) were always less than Collembola. Most of the Mesostigmata and Oribatida were identified to species. Twelve taxa of Oribatida were found, and ten of Mesostigmata. In terms of individuals, Oribatida usually dominated, but Actinedida dominated in three cases. With all developmental stages being active under snow, *Platynothrus capillatus* dominated the total Oribatida material. Mesostigmata catches were rather low and unstable.

Several species of Oribatida had individuals with gut contents (Tab. 3). A varying mixture of fungal hyphae and spores was seen in *Platynothrus capillatus* (adults and the juvenile stages), *Camisia biurus* (tritonymph), *Oppiella neerlandica* (adults), *Oribatella calcarata* (proto- and

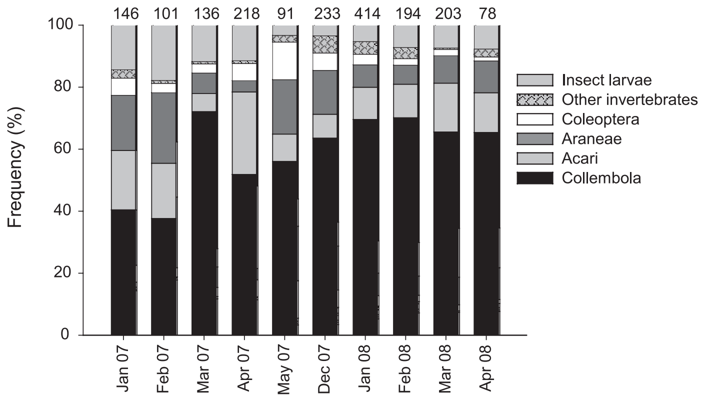

Fig. 4 Relative frequency (%) of different taxa at various samplings during the two winters, as well as total number of specimens at each sampling (on top).

Tab. 1 Total catches (species and specimens) of dominant arthropods in separate pitfall traps under snow during two winter seasons. Each trap was placed next to a large, small or no natural cavity.

Trap nr. (cavity category)	1 (large)	12 (large)	4 (small)	5 (small)	7 (small)	8 (small)	10 (small)	11(small)	2 (no)	3 (no)	6 (no)	9 (no)
Araneae, species	7	4	3	5	3	5	2	3	5	5	3	5
Araneae, specimens	22	10	4	18	7	9	14	15	7	12	10	11
Acari, Oribatida, species	3	1	5	4	1	1	4	2	3	4	4	3
Acari, Mesostigmata, species	0	0	2	2	3	1	2	5	2	2	0	0
Acari, total, species	3	1	7	6	4	2	6	7	5	6	4	3
Acari, total, specimens	17	11	24	20	31	8	31	30	17	35	15	8
Collembola, species	6	7	11	9	4	4	4	7	7	9	11	5
Lepidocyrtus lignorum, specimens	76	43	86	48	44	57	42	43	54	76	115	95
Collembola, specimens	106	66	116	73	49	62	56	73	89	128	137	103
Coleoptera, species	6	5	3	6	3	2	3	4	5	4	0	3
Coleoptera, specimens	9	7	9	6	3	6	4	8	10	13	0	3
Chionea araneoides, specimens	9	4	0	0	1	0	0	1	6	2	0	3
Boreus westwoodi, specimens	2	0	0	0	0	1	0	0	0	0	0	0
Total species	24	18	24	26	15	14	15	22	23	25	18	17
Total specimens	165	98	153	117	91	86	105	127	129	190	162	128
Ranging species	3	7	3	1	10	12	10	6	5	2	7	9
Ranging specimens	2	10	4	8	11	12	9	7	5	1	3	6

Tab. 2 Springtails (Collembola) caught in pitfall traps under snow during two winter seasons in a high altitude spruce forest, central south Norway. Numbers per 12 functioning traps. Only periods with a continuous snow cover are included. The column to the right shows the number of individuals with gut content (n) relative to the total number of individuals (tot).

Year	Winter 2007/2008						Winter 2008/2009					Gut content n/tot
Collecting period	14 Dec to 12 Jan	12 Jan to 8–10 Feb	8–10 Feb to 7–9 Mar	7–9 Mar to 4–6 Apr	4–6 Apr to 26–27 Apr	26–27 Apr to 22–23 May	14 Nov to 13 Dec	13 Dec to 17 Jan	17 Jan to 14–16 Feb	14–16 Feb to 21–22 Mar	21–22 Mar to 11–12 Apr	
Snow cover	snow	snow	snow	snow	snow	snow	snow	snow	snow	snow	snow	
ISOTOMIDAE												
Pseudanurophorus binoculatus Kseneman, 1934											1	1/1
Folsomia quadrioculata (Tullberg, 1871)								1			2	2/3
Folsomia sensibilis Kseneman, 1936											1	1/1
Parisotoma notabilis (Schäffer, 1896)			4	6	6		9	17	7	11	4	51/55
Desoria blekeni (Leinaas, 1980)		1				2	1	1				1/4
Desoria hiemalis (Schött, 1893)					1							1/1
Desoria olivacea (Tullberg, 1871)		5	21	4	2	3	3	13	18	16	4	70/74
ENTOMOBRYIDAE												
Entomobrya marginata (Tullberg, 1871)					1							0/1
Lepidocyrtus cyaneus Tullberg, 1871	2											0/1
Lepidocyrtus lignorum (Fabricius, 1793)	53	31	61	41	37	37	118	230	108	77	28	528/675
Orchesella cincta (Linnaeus, 1758)	2									1		0/2

Orchesella flavescens (Bourlet, 1839)								1				1/1
TOMOCERIDAE												
Pogonognathellus flavescens (Tullberg, 1871)		1	1	1	2	2	1	4	2	1	1	7/16
ARRHOPALITIDAE												
Arrhopalites cf. *principalis* Stach, 1945								2				1/2
Arrhopalites pygmaeus (Wankel, 1860)			4	4	1	7		6		5	6	30/31
KATIANNIDAE												
Gisinianus flammeolus (Gisin, 1957)			1	3				7	1		1	14/16
DICYRTOMIDAE												
Dicyrtoma fusca (Lubbock, 1873)	2						7	2				7/8
HYPOGASTRURIDAE												
Hypogastrura socialis (Uzel, 1891)			6	3	1		9	2		21	1	11/34
Willemia anophthalma Börner, 1901								1		1		2/2
ONYCHIURIDAE												
Micraphorura absoloni (Börner, 1901)											1	1/1
Hymenaphorura polonica Pomorski, 1990								1				1/1
Protaphorura pseudovanderdrifti (Gisin, 1957)											1	1/1
TOTAL	59	38	98	62	51	51	148	288	136	133	51	

Tab. 3 Mites (Acari) caught in pitfall traps under snow during two winter seasons in a high altitude spruce forest, central south Norway. Numbers per 12 functioning traps. Only periods with a continuous snow cover are included. Ad = adults, T = tritonymphs, D = deuteronymphs, P = protonymphs, L = larvae. The column to the right shows the number of individuals with gut content (n) relative to the total number which were suited for examination (tot).

Year		Winter 2007/2008						Winter 2008/2009					Gut content n/tot
Collecting period		14 Dec to 12 Jan	12 Jan to 8–10 Feb	8–10 Feb to 7–9 Mar	7–9 Mar to 4–6 Apr	4–6 Apr to 26–27 Apr	26–27 Apr to 22–23 May	14 Nov to 13 Dec	13 Dec to 17 Jan	17 Jan to 14–16 Feb	14–16 Feb to 21–22 Mar	21–22 Mar to 11–12 Apr	
Snow cover		snow	snow	snow	snow	snow	snow	snow	snow	snow	snow	snow	
ORIBATIDA	Stage												
Camisia biurus (C.L. Koch, 1839)	Ad	2							1				0/2
”	T			1	1								1/2
”	P										3		0/2
”	L	2											0/1
Carabodes labyrinthicus (Michael, 1879)	Ad				1				1				1/2
Carabodes marginatus (Michael, 1884)	Ad								1				0/1
Carabodes sp.	T				1								0/1
Chamobates pusillus (Berlese, 1895)	Ad				1								0/1
Eobrachychthonius borealis Forsslund, 1942	Ad								2	1			3/3
Oppiella neerlandica (Oudemans, 1900)	Ad		1		3	1					5	2	7/11
Oppiella sp.	Ad				1								1/1
Oribatella calcarata (C.L. Koch, 1835)	Ad								1				0/1
”	D								1	1	4	1	4/5

”	P									1	3	1	3/4
Platynothrus capillatus (Berlese, 1914)	Ad	2			4			3		1			4/8
”	T	2	2	2				1	2				7/9
”	D		7		1		2		4				10/11
”	P	2	2	1	2	1							7/7
”	L		1		1								2/2
Steganacarus sp.	Ad										1		1/1
Belba sp.?	Ad							1				1	0/2
”	T/juv							4	1				3/4
MESOSTIGMATA													
Mixozercon serlachii Lehtinen, submitted					1								
Zercon curiosus Trägårdh, 1910									1				
Zercon colligans Berlese, 1920									1	1			
Holoparasitus sp.								1					
Lysigamasus lapponicus (Trägårdh, 1910)				1		2			1				
Vulgarogamasus kraepelini (Berlese, 1905)		8	1					3	1		1		
Veigaia nemorensis (C.L. Koch, 1839)		2					3				1		
Trachytes aegrota (C.L. Koch, 1841)					2								
Urodiaspis tecta (Kramer, 1876)												1	
Uropodina sp., nymph		2											
ACTINEDIDA		6	4	3	33	2	3	5	25	16	14	4	
TOTAL		28	18	8	52	6	8	18	43	21	32	10	

deuteronymphs) and juveniles of '*Belba'*. The appearance of the gut contents was similar to that of Collembola (Fig. 5). Some specimens of Actinedida were also seen to have gut content, but this was not studied further.

3.4. Araneae

The spider data (Tab. 4) include some snow-free or partly bare periods for phenological purpose. Spiders were caught throughout the snow-covered period in both winters. A considerable portion consisted of juvenile Linyphiidae, especially during the second winter. Twelve species were active under snow. Eleven belonged to Linyphiidae and one to Hahniidae. Besides Linyphiidae juveniles, *Tenuiphantes alacris* (Linyphiidae) and *Cryphoeca silvicola* (Hahniidae) were the most numerous species trapped. *T. alacris* was found in all samples under snow.

Among the sixteen taxa trapped during approximately two months before the first snow in 2007, seven were also active under snow. Correspondingly, among fourteen taxa trapped during about two and a half month before snowfall in autumn 2008, eight continued to be active under snow.

3.5. Adult Coleoptera

Including about one month of bare ground in autumn 2008 and spring 2009, 27 beetle species were trapped. Of these, 13 were collected under a permanent snow cover (Tab. 5). Like spiders, beetles were trapped throughout both winters. Only two families were present in the subnivean catches: Staphylinidae with 10 species and Cholevidae with 3 species. *Olophrum assimile* (Staphylinidae) and *Choleva lederiana* (Cholevidae) dominated in numbers under snow, followed by *Oxypoda spectabilis, Arpedium quadrum, Eucnecosum brachypterum* and *Mycetoporus rufescens* (all Staphylinidae). Three species were only trapped under snow: *Choleva fagniezi, Eucnecosum brachypterum* and *Omalium caesum*.

3.6. Insect larvae

A considerable number of insect larvae were trapped under snow (Tab. 6). Most numerous were beetle larvae, which showed continuous activity under snow. The highest catches were among Cholevidae and Staphylinidae. Fourteen random Staphylinidae larvae were identified to subfamily, thirteen being Omaliinae and one Aleocharinae. Next in numbers were larvae of Nematocera. A few larvae of Brachycera and Geometridae were also collected.

A considerable fraction of the insect larvae had a visible gut content, indicating feeding under snow (right column in Tab. 6). As much as 94 % of the subnivean Cholevidae larvae had gut contents, 28 % of the Staphylinidae larvae and 71 % of the Nematocera larvae. Also in the autumn period from 6 October to 14 December 2007, which was snow-free during October and November, 29 of 30 trapped Cholevidae larvae had gut contents. The gut content of subnivean Cholevidae larvae always contained a considerable fraction of fungal hyphae and spores, mixed with heavily decayed plant fragments. Seven also contained nematode fragments and nematode eggs. Two contained various setae from invertebrates, probably insect larvae. The main food seemed to be decaying plant material, which was heavily infected with fungi. Nematodes may easily be ingested together with such food. Larvae of Staphylinidae often had an unidentifiable gut content. However, one larva of Aleocharinae and two of Omaliinae contained fungal hyphae and spores, and two of Omaliinae contained microsetae indicating predation.

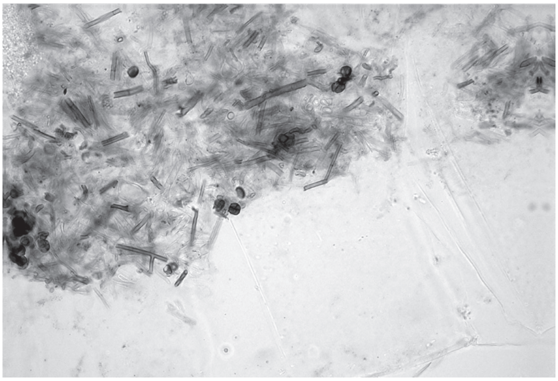

Fig. 5 Typical gut content of collembolan and oribatid species: a mixture of fungal hyphae and spores. The photo is from a specimen of *Lepidocyrtus lignorum*, the most abundant Collembola species found in the traps.

3.7. Other invertebrate groups

Tab. 7 summerizes the catches of various other groups. Opiliones were very active in the autumn, but were practically absent in subnivean catches. One species of Pseudoscorpiones was taken under snow. Among Trichoceridae, where all trapped individuals were females, two species showed subnivean activity: *Trichocera implicata* and *T. parva*.

The classic winter-active, wingless species *Chionea araneoides* (Diptera) and *Boreus westwoodi* (Mecoptera) were also collected under snow. In the second winter, *C. araneoides* was trapped in four of five snow-covered periods. A few flies (Brachycera) showed subnivean activity, but were not further identified. The gastropod specimen *Vitrina pellucida* had gut content, indicating subnivean feeding. Three specimens of Harpacticoidea, a group of Copepoda (Crustacea), which may live in moist forest floor, were also found in one trap.

4. Discussion

4.1. The subnivean space: a biologically active habitat

While strong frost in snow-free areas may halt biological activity of ground- and litter living organisms, an insulating snow cover allows a number of biological processes to go on at temperatures close to 0 ^{o}C. Decomposition beneath snow has been documented in various habitats (Bleak 1970, O'Lear & Seastedt 1994; Brooks et al. 1996). The activity of 'snow molds' may explain this. Snow molds are opportunistic parasites on dormant plants under snow and consist of diverse taxonomic groups (review by Matsumoto 2009). In a subalpine forest in Colorado, Schmidt et al. (2008) showed that their growth rate could be very high even at -2^{o}C. They proposed that fast-growing snow molds participate in plant litter decomposition under snow, receiving nutrients from the soil below them and water and oxygen from the snow above. Schmidt et al. (2009) illustrated how mats of snow molds can be formed at the soil-snow interface, and these fungi were even able to grow vertically up into the snow. The stable temperature close to zero in our study site would be favourable for snow-mold growth. In spring, we often observed dense networks of hyphae in litter and vegetation close to the ground in the study area, at the very boarder of melting snow (Fig. 6).

Tab. 4 Spiders caught in pitfall traps under snow during two winter seasons in a high altitude spruce forest, central south Norway. Numbers per 12 functioning traps. A few periods with partly snow or bare ground are included. m = males, f = females, juv = juveniles.

Year	Winter 2007/2008							Winter 2008/2009									
Collecting period	6 Oct to 14 Dec	14 Dec to 12 Jan	12 Jan to 8-10 Feb	8-10 Feb to 7-9 Mar	7-9 Mar to 4-6 Apr	4-6 Apr to 26-27 Apr	26-27 Apr to 22-23 May	24 Aug to 4 Oct	4 Oct to 17 Oct	17 Oct to 14 Nov	14 Nov to 13 Dec	13 Dec to 17 Jan	17 Jan to 14-16 Feb	14-16 Feb to 21-22 Mar	21-22 Mar to 11-12 Apr	11-12 Apr to 5 May	5 May to 5 Jun
Snow cover	snow last 10 days	snow	snow	snow	snow	snow	snow	bare	bare	partly snow	snow	snow	snow	snow	snow	partly snow	bare
LINYPHIIDAE																	
Centromerus arcanus (O.P.-Cambridge, 1873)											1f		1m			1f	7m
Centromerus sylvaticus (Blackwall, 1841)	2f								1m								
Ceratinella brevipes (Westring, 1851)	2f																
Dicymbium tibiale (Blackwall, 1836)	2f																
Diplocentria bidentata (Emerton,1882)								1f									
Diplocephalus latifrons (O.P.-Cambridge, 1863)	3m 3f							1m	1m	1m	1f						4m 2f
Gonatium rubellum (Blackwall, 1841)	2m																
Hilaira excisa (O.P.-Cambridge, 1871)														1m			
Macrargus rufus (Wider, 1834)	2m 5f		1f				2m	1f		1f						1m	1m 1f
Mecynargus paetulus (O.P.-Cambridge, 1875)																	2m

Micrargus apertus (O.P.-Cambridge, 1871)					1m									1m			4m
Oreonetides vaginatus (Thorell, 1872)	3m			1f			2m 2f	1f	1m 2f				1f	1f			24m 4f
Porrhomma cf. *montana* Jackson, 1913	3m 2f			1m				5m 1f	2m 1f	1m	1f						
Porrhomma pallidum Jackson, 1913																	2m 4f
Scotinotylus evansi (O.P.-Cambridge, 1894)	2m																
Tapinocyba pallens (O.P.-Cambridge, 1872)																	1m
Tenuiphantes alacris (Blackwall, 1853)	6m 14f	8m 5f	1m 4f	1m 2f	1f	1m	4m 4f	5f	1m 1f	2f	3f	5f	2m 2f	3m	1f		57m 29f
Tenuiphantes mengei (Kulczynski, 1887)	5m							1m	1f	1m							
Tenuiphantes tenebricola (Wider, 1834)	2m 24f	3f						1m	3f	4m 4f	3f	1f					2f
Tenuiphantes sp. juv.			1														
Thyreostenicus parasiticus (Westring, 1851)		2m														1f	
Walckenaeria nudipalpis (Westring, 1851)	3m							1m	1m	2m	1m						1f
Linyphiidae sp. juv.	42	6	5	3	4		2	10	24	21	23	23	6	12	6	2	
HAHNIIDAE																	
Cryphoeca silvicola (C. L. Koch, 1834)	8m 9f	2 juv	2m 7f 2juv	1m	1m					3f 2juv		1f			1juv		78m 2f
LYCOSIDAE																	
Lycosidae sp. juv.								1									
THERIDIIDAE																	
Robertus lividus (Blackwall, 1836)	2f																
PHILODROMIDAE																	
Philodromus sp. juv.										1							
TOTAL	146	26	23	9	7	1	16	29	39	43	33	30	12	18	8	5	225

Tab. 5 Adult beetles caught in pitfall traps under snow during two winter seasons in a high altitude spruce forest, central south Norway. Numbers per 12 functioning traps. A few periods with partly snow or bare ground are included.

Year	Winter 2007/2008						Winter 2008/2009								
Collecting period	14 Dec to 12 Jan	12 Jan to 8-10 Feb	8-10 Feb to 7-9 Mar	7-9 Mar to 4-6 Apr	4-6 Apr to 26-27 Apr	26-27 Apr to 22-23 May	4 Oct to 17 Oct	17 Oct to 14 Nov	14 Nov to 13 Dec	13 Dec to 17 Jan	17 Jan to 14-16 Feb	14-16 Feb to 21-22 Mar	21-22 Mar to 11-12 Apr	11-12 Apr to 5 May	5 May to 5 Jun
Snow cover	snow	snow	snow	snow	snow	snow	bare	partly snow	snow	snow	snow	snow	snow	partly snow	bare
CARABIDAE															
Calathus micropterus (Duftschmid, 1812)								1							1
CHOLEVIDAE															
Catops coracinus Kellner, 1846															2
Catops nigricans (Spence, 1815)	2						1	3		1					
Catops tristis (Panzer, 1793)							2								
Choleva fagniezi Jeannel, 1922									1						
Choleva lederiana Reitter, 1902				3		7	3	2		4	1	3	1	4	10
STAPHYLINIDAE															
Acidota crenata (Fabricius, 1792)								1							
Anthobium melanocephalum (Illiger, 1794)								1						1	4
Arpedium quadrum (Gravenhorst, 1806)			1	2	1	2	26	15		1				6	4

Bryoporus punctipennis Thomson, 1861															1
Eucnecosum brachypterum (Gravenhorst, 1802)	2			1						1	1				
Liogluta alpestris (Heer, 1839)								4							
Liogluta micans (Mulsant & Rey, 1852)		1			1		8	11							15
Mycetoporus rufescens (Stephens, 1832)			1	2	1		1	1	1						5
Olophrum assimile (Paykull, 1800)			1				11	21	9	7					
Olophrum fuscum (Gravenhorst, 1806)							1	1							
Olophrum piceum (Gyllenhal, 1810)															1
Omalium caesum Gravenhorst, 1806	2														
Othius myrmecophilus Kiesenwetter, 1843								1							
Oxypoda annularis (Mannerheim, 1830)							1	1						1	1
Oxypoda skalitzkyi Bernhauer, 1902			1			2									3
Oxypoda spectabilis Märkel, 1844	2	2					1	4	1		2	1			
Proteinus brachypterus (Fabricius, 1792)				1											1
Proteinus crenulatus Pandelle, 1867							2	4	1						
Zyras humeralis (Gravenhorst, 1802)															89
CRYPTOPHAGIDAE															
Cryptophagus scanicus (Linnaeus, 1758)														1	
LATRIDIIDAE															
Corticaria longicollis (Zetterstedt, 1838)															1
TOTAL	8	3	4	9	3	11	57	71	13	14	4	4	1	13	138

Tab. 6 Insect larvae caught in pitfall traps under snow during two winter seasons in a high altitude spruce forest, central south Norway. Numbers per 12 functioning traps. Right column shows the fraction of larvae with gut content.

Year	Winter 2007/2008						Winter 2008/2009					
Collecting period	14 Dec to 12 Jan	12 Jan to 8-10 Feb	8-10 Feb to 7-9 Mar	7-9 Mar to 4-6 Apr	4-6 Apr to 26-27 Apr	26-27 Apr to 22-23 May	14 Nov to 13 Dec	13 Dec to 17 Jan	17 Jan to 14-16 Feb	14-16 Feb to 21-22 Mar	21-22 Mar to 11-12 Apr	Gut content n/tot
Snow cover	snow	snow	snow	snow	snow	snow	snow	snow	snow	snow	snow	
COLEOPTERA												
Cholevidae	12	5	8	7	2		3	14	7	9		51/54
Staphylinidae, total	5	12	7	2	3	2		5	2		5	10/36
Staphylinidae, Aleocharinae								1				1/1
Staphylinidae, Omaliinae	2	4	2		1			1	1		2	8/13
Carabidae									1	4		0/3
Other Coleoptera				1			1	1				1/4
DIPTERA												
Nematocera			1	6				2	4	1	1	10/14
Brachycera						1	3					0/3
LEPIDOPTERA												
Geometridae	2	1					1					1/3
INSECTA, indet.	2				4					1		3/6

Tab. 7 Various invertebrate groups caught in pitfall traps under snow during two winter seasons in a high altitude spruce forest, central south Norway. Numbers per 12 functioning traps. A few periods with partly snow or bare ground are included.

Year	Winter 2007/2008							Winter 2008/2009									
Collecting period	6 Oct to 14 Dec	14 Dec to 12 Jan	12 Jan to 8-10 Feb	8-10 Feb to 7-9 Mar	7-9 Mar to 4-6 Apr	4-6 Apr to 26-27 Apr	26-27 Apr to 22-23 May	24 Aug to 4 Oct	4 Oct to 17 Oct	17 Oct to 14 Nov	14 Nov to 13 Dec	13 Dec to 17 Jan	17 Jan to 14-16 Feb	14-16 Feb to 21-22 Mar	21-22 Mar to 11-12 Apr	11-12 Apr to 5 May	5 May to 5 Jun
Snow cover	snow last 10 days	snow	snow	snow	snow	snow	snow	bare	bare	partly snow	snow	snow	snow	snow	snow	partly snow	bare
OPILIONES																	
Oligolophus tridens (C. L. Koch,1836)	129							92	30	47	1						9
Nemastoma lugubre (Muller,1776)	5				1			22	3	5							3
Mitopus morio (Fabricius,1799)								5	5	10							
PSEUDOSCORPIONES																	
Neobisium carcinoides (Hermann,1804)		2						1	2		1						2
TRICHOCERIDAE (Dipt.)																	
Trichocera implicata Dahl,1976												1	1				
Trichocera parva Meigen,1804	2								3	9	5	4					
Trichocera thaleri Stary 2000										1							
Trichocera sparsa Stary&Martinovsky,1996									1								

Tab. 7 (Continued previous page.) Various invertebrate groups caught in pitfall traps under snow during two winter seasons in a high altitude spruce forest, central south Norway Numbers per 12 functioning traps. A few periods with partly snow or bare ground are included.

Year	Winter 2007/2008							Winter 2008/2009									
Collecting period	6 Oct to 14 Dec	14 Dec to 12 Jan	12 Jan to 8-10 Feb	8-10 Feb to 7-9 Mar	7-9 Mar to 4-6 Apr	4-6 Apr to 26-27 Apr	26-27 Apr to 22-23 May	24 Aug to 4 Oct	4 Oct to 17 Oct	17 Oct to 14 Nov	14 Nov to 13 Dec	13 Dec to 17 Jan	17 Jan to 14-16 Feb	14-16 Feb to 21-22 Mar	21-22 Mar to 11-12 Apr	11-12 Apr to 5 May	5 May to 5 Jun
Snow cover	snow last 10 days	snow	snow	snow	snow	snow	snow	bare	bare	partly snow	snow	snow	snow	snow	snow	partly snow	bare
LIMONIIDAE (Dipt.)																	
Chionea araneoides Dalman,1816		2	1							1	5	10	5	1			
BRACHYCERA (Dipt.)						1					1	2			2		
MECOPTERA																	
Boreus westwoodi Hagen,1866				1									1				
GASTROPODA																	
Vitrina pellucida (O.F.Muller, 1774)							2										
CRUSTACEA																	
Harpacticoidea												3					

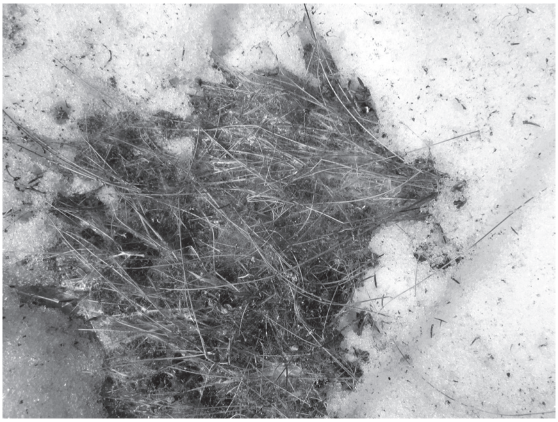

Fig. 6 At snow melt, grey mats of fungal hyphae often appear among dead vegetation close to the snow edge.

Our data not only confirm a persistent subnivean activity in a number of arthropod groups, but gut analyses document that many species of Collembola and Acari feed continuously on fungal hyphae and spores. Also beetle larvae of family Cholevidae continue to feed throughout the winter on fungal hyphae and spores, mixed with strongly decomposed plant material. We support the idea of subnivean food chains, where for instance predatory mites and spiders may eat fungi-eating springtails, and the ever-hungry shrews can eat spiders, larvae and other invertebrates (cf. Aitchison 2001). In Sweden, the stomach content of subnivean shrews studied by Ackefors (1964) contained many different invertebrate groups, most commonly beetles (larvae and adults), which also dominated in pitfall catches under snow in the same area (Näsmark 1964). This indicates that mainly active invertebrates are eaten. Our gut studies suggest that snow molds may be the base and 'driving force' of such food chains. These cold-tolerant fungi may represent a huge subnivean food resource for those being able to use it.

We were somewhat surprised that traps adjacent to natural cavities did not give higher catches than traps situated on flat ground with a rather narrow subnivean space. Arthropods seem to be active beneath snow all over the forest floor, independent of smaller or larger cavities under roots, along larger stones, etc. The main purpose of moving beneath snow, for microarthropods to mammals, may be to search for food. However, if snow molds are abundant everywhere, animals feeding on this resource do not need to move very much around. Even net-building spiders can stay within a small place. Therefore, pitfall trapping, measuring surface activity, may underestimate subnivean feeding activity and its biological importance. The subnivean habitat is also ecologically interesting by being the 'base camp' for those invertebrates which regularly use the snow layers or the snow surface as a habitat (Hågvar 2010).

4.2. Microarthropods

Also other studies have noted a dominance of microarthropods in pitfall traps beneath snow (e.g. Näsmark 1964, Aitchison 1979a,c, Leinaas 1981, Merriam et al. 1983, Viramo 1983, Schmidt & Lockwood 1992, Vanin & Turchetto 2007). Highest total catches in our study were not taken at the highest subnivean temperatures (2–3 ^{o}C), but close to zero. This may be due to snow melt leading to harmful water logging of the ground.

To our knowledge, our study is the first to document continuous fungal feeding in a number of microarthropod species beneath snow. Aitchison (1983) showed that several winter active Collembola species were able to feed down to -2 ^{o}C. In aspen litter, Whittaker (1981) showed that the collembolan *Onychiurus subtenuis* ingested hyphae and spores under snow at 0 ^{o}C. Aitchison (1979 a,c) concluded that subnivean Collembola were fully active down to at least -6 ^{o}C, and Acari down to at least -5 ^{o}C.

Leinaas (1981) showed that in a Norwegian lowland spruce forest, several Acari and all but one surface-living Collembola species moved up into the snow during winter. Pitfall trapping in that site also demonstrated a certain subnivean activity of microarthropods. The most abundant species in his traps was the same species dominating in the present study: *Lepidocyrtus lignorum*. Our material confirms that in a number of Collembola and Acari species, at least a certain part of the population remains in the subnivean space and is active there.

Desoria olivacea had the highest catches during mid-winter of both years. According to Fjellberg (pers. comm.) this species lives in moist forest patches during summer but temporarily extends its distribution during winter due to moist condition beneath snow. In this way, resources from a larger area can be reached.

4.3. Araneae

During emptying of the traps, active spiders were sometimes observed, and in a few cases a spider web had been made partly over the trap. Clearly, 0 °C is an acceptable temperature for activity in several spider species. Aitchison (1984) showed experimentally that various winter active spiders were able to feed down to -2 ^{o}C and that several Collembola species were accepted as prey.

To our knowledge, no earlier study exists at the species level regarding subnivean activity of spiders in Fennoscandian boreal forest. The following taxa trapped under snow in our study have also been collected on snow in southern Norway (Hågvar & Aakra 2006): *Cryphoeca silvicola*, *Diplocephalus latifrons, Macrargus rufus, Tenuiphantes alacris*, *Walckenaeria nudipalpis* and Linyphiidae sp. juv. However, the spider fauna active under and on snow may be very different. For instance, *Bolephthyphantes index* (Thorell 1856) is common on snow in our study site, but was not trapped under snow. This species builds webs on the snow surface to catch Collembola and other small invertebrates, and is normally quite active down to at least -5 ^{o}C (Hågvar 1973). Apparently, this species does not move horizontally under snow, but rests under snow until possibilities occur to climb to the snow surface.

Until subnivean reproduction might be demonstrated, the activity of adult spiders under snow may either be a way of overwintering, a prolonged activity of autumn breeders, or a preparation for early spring breeding. Three of the species active under snow showed a strong activity after snow melt in 2009, indicating early spring reproduction: *Oreonetides vaginatus, Tenuiphantes alacris,* and *Cryphoeca silvicola* (Tab. 4).

Also other authors have noted a considerable portion of juvenile spiders in pitfall traps during winter (see Vanin & Turchetto 2007 and references therein). Since juveniles are claimed to be the most cold-tolerant stage (Schaefer 1976), Vanin & Turchetto (2007) suggested that juvenile spiders may be well able to use certain winter food resources like Collembola, enhancing their fitness prior to spring activity.

4.4. Adult Coleoptera

According to Aitchison (1979b), certain beetles can be active down to about -3 ^{o}C. Several authors have reported subnivean catches of beetles in pitfall traps (Näsmark 1964, Aitchison

1979 b, Leinaas 1981, Merriam et al. 1983, Viramo 1983, Addington & Seastedt 1999). Especially Staphylinidae can be found active under snow throughout the winter if subnivean temperatures are not too low (Viramo 1983, Merriam et al. 1983, Addington & Seastedt 1999), as also shown in our study. The few species lists in the literature do not overlap with our material, and there is a problem that catches from snow-free periods were included (Näsmark 1964, Aitchison 1979b). To our knowledge, our study is the first to present detailed data on species level for beetles collected with certainty under snow throughout the winter.

Some species showed activity both in autumn, under snow and in spring: *Choleva lederiana, Arpedium quadrum, Liogluta micans* and *Mycetoporus rufescens*. *A. quadrum* is known to be active and even fly on sunny days in late winter (Palm 1948). The purpose of subnivean activity in adult beetles is difficult to understand. We did not check gut contents in adult beetles, but if they feed, they may be physiologically ready for early egg-laying after snow melt.

4.5. Insect larvae

Earlier pitfall studies beneath the snow also report various insect larvae, especially among beetles (Näsmark 1964, Leinaas 1981, Viramo 1983, Merriam et al. 1983). Carabidae, Cantharidae and Staphylinidae were mentioned by both Näsmark (1964) and Merriam et al. (1983). Possibly the Silphidae larvae of Näsmark (1964) could be the closely related Cholevidae. No earlier studies seem to have analysed the gut content of subnivean beetle larvae.

4.6. Other invertebrate groups

Except for Merriam et al. (1983), other studies do not report subnivean activity of Opiliones. These rather large invertebrates may not easily move in the narrow subnivean space. A few Pseudoscorpions have been trapped beneath snow in Sweden by Näsmark (1964), in Canada by Aitchison (1979d), and in Italy by Vanin & Turchetto (2007). Also some Gastropoda have been found in the subnivean space (Näsmark 1964, Aitchison 1979e, Merriam et al. 1983). Subnivean trapping of Trichoceridae has been reported in boreal forest by Viramo (pers. comm.) in Finland and Dahl (1974) in Sweden, and of the wingless *Chionea* sp. by Näsmark (1964), Schmidt and Lockwood (1992) in Wyoming, and Wiger (pers. comm.) in Norway. A number of other invertebrate groups have been recorded active beneath snow in various studies mentioned in the Introduction, but the taxonomical level varies greatly in the publications.

5. Conclusions

Our study confirmed that a rather broad spectrum of invertebrate taxa can be active in the subnivean space at temperatures close to zero. Gut analyses showed that several groups are actively feeding under snow, and we have indicated possible food chains. We further document subnivean activity of species which are typically active on the snow surface: Two species of Trichoceridae*, Chionea araneoides and Boreus westwoodi.* These regularly migrate between the subnivean and the supranivean habitat along air channels created by protruding vegetation (Hågvar 2010). Also, we have shown that not all Collembola move up into the snow layers, but that this group also shows a considerable activity in the subnivean space. Within winter ecology, subnivean ecology clearly deserves further attention.

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