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Ecology of Enchytraeids in meadow forest soil in southern Finland

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The fauna of Enchytraeids and their ecology was studied for 13 months in two meadow forest habitats in southern Finland. There were 18 species in the moister habitat and 21 in the drier one. The species *Stercutus niveus* was found in Finland for the first time. *S. niveus* has its maximum abundance in winter, thus differing from the other species. In both habitats the genus *Fridericia* covered more than half of the total numbers and about 90 % of the biomass. The mean density was 8 044 individuals per m² in the drier habitat and 5 711 individuals in the moister one. The mean annual biomasses were 1.74 g/m² and 1.28 g/m². Some vertical migration occurred at the onset of frost. The horizontal distribution was aggregated.

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1. Introduction

The effective extraction methods developed by NIELSEN (1952—1953) and O'CONNOR (1955) made reliable ecological studies of Enchytraeids possible. Since then, extensive studies have been made on biotopes of different kinds (NIELSEN 1954, 1955a, 1955b, O'CONNOR 1957, 1958, PEACHEY 1963, NURMINEN 1967a, SPRINGETT 1970, ABRAHAMSEN 1972, DASH & GRAGG 1972, DOZSA-FARKAS 1973a, 1973c, STANDEN 1973). However, ecological research on Enchytraeids in Finland has been confined to the communities of conifer forests and bogs. The only work dealing extensively with this group of soil animals is NURMINEN's (1967a) study of the ecology of Enchytraeids in Finnish conifer forest soil. In addition there are some ecological studies on soil animals in general which include data on Enchytraeids. Effects of silvicultural practices have been examined by HUHTA *et al.* (1967, 1969), HUHTA (1976) and VILKAMAA (1976). HUHTA & KOSKENNIEMI (1975) have studied soil animals in spruce forests at two latitudes in Finland. On the other hand, studies of the richer biotopes are solely faunistic (NURMINEN 1967b, 1970).

This study was concerned with the general ecological features of the Enchytraeid community of the meadow forest in southern Finland: structure of the community, species composition, vertical and horizontal distribution, seasonal variation in numbers and biomass, and the effects of moisture and temperature upon abundance.

2. Material and methods

A. Study area

The study area is situated in Lammi commune in southern Finland (61°03″N, 25°03″E). The annual precipitation as a long-term mean is 596 mm and the mean temperature +3.8°C (HEINO 1976). The monthly precipitation and the monthly mean temperature for the survey time are presented in Fig. 1.

One sampling station (area 1) is situated in a stand of *Corylus avellana* and the other, moister area 2 in a luxuriant stand of *Filipendula ulmaria* and *Athyrium filix-femina*. The difference in soil moisture between these two areas according to tensiometer values was significant ($t = 3.28^{**}$, $n = 36$) in the surface layer (0—5 cm) and highly significant ($t = 3.85^{***}$, $n = 36$) in the deeper layer (5—10 cm).

The soil in the study areas is mull type humus, the average grain size being 0.2 mm. The litter layer in both areas is very thin. In area 1 the A_1 layer is about 30 cm thick and below this is the light brown layer of mull about 30 cm thick. In area 2 the rich mull layer is thinner, about 15 cm, and beneath this is a grey layer, where spots of $Fe(OH)_3$ show the effect

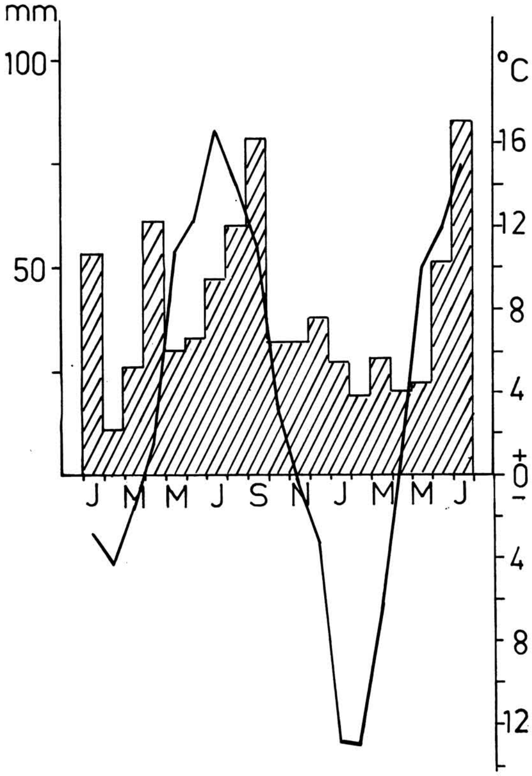

Fig. 1. Monthly precipitation and mean temperatures during the survey (January 1975—July 1976).

Table 1. Some chemical and physical properties of the soil in the humus layer in the study areas in August 1975.

	Area 1	Area 2
pH (water extraction)	5.4	5.1
Organic matter % of dry weight	10.8	14.7
Water-holding capacity % of volume	41.2	40.3
Porosity volume %	74.6	80.3
Particle volume %	25.4	19.6

of the ground water. Some chemical and physical properties of the soil are presented in Table 1.

In area 1 there are many species of trees and bushes: *Betula pubescens, Picea abies, Pinus silvestris, Corylus avellana, Prunus padus, Alnus incana, Ribes spicatum, Daphne mezereum, Sorbus aucuparia.* The most abundant species of the field layer are *Aegopodium podagraria, Oxalis acetosella, Urtica dioica, Pulmonaria officinalis, Hepatica nobilis, Maianthemum bifolia, Athyrium filix-femina* and *Lastrea dryopteris.* The ground layer is poor, consisting mainly of the moss *Brachythecium curtum.* Area 2 is characterized by luxuriant *Athyrium filix-femina* and *Filipendula ulmaria.* It supports all species growing in area 1 and also *Ranunculus cassubicus.* The species of the ground layer are *Brachythecium curtum, Rhodobryum roseum* and *Mnium* spp.

B. Sampling and extraction

Samples were taken between 6.VI.1975 and 9.VII.1976 at least monthly from ice-free soil and once from frozen soil. The exact sampling dates were 6 June, 7 July, 27 July, 10 Aug., 12 Sept., 10 Oct., 16 Nov. 1975, 30 Feb., 6 May, 29 May, 9 July. According to O'Connor (1971), monthly sampling gives sufficient information about the trend in population density, although frequency should be increased at times of rapidly changing temperature and moisture conditions.

Representative sites were 10 × 10 m in both sampling areas. Sample units were taken at random. Each sample consisted of 15 units, with the exception of 9 units from frozen soil in February. The optimal number of units was calculated for every sampling date with the equation

$$n = 25 \left(\frac{1}{\bar{x}} + \frac{1}{k}\right), \text{ where } k = \frac{\bar{x}^2}{s^2 - \bar{x}} \text{ (Elliot 1971).}$$

The mean of these optimal values was 11.11 ± 4.13 (SD) (n = 22). So 15 units was a statistically adequate number.

Samples were taken with a cylindrical steel corer (diam. 6 cm) to a depth of 8 cm. With plastic rings inside the corer it was possible to divide the sample core exactly into four equal pieces of 2 cm each. These subsamples were stored in separate plastic bags in a refrigerator for 8 days at most before treatment (cf. Abrahamsen 1972). The Enchytraeids were extracted with the wet funnel technique of O'Connor (1962).

The water content of soil on each sampling date was measured by weighing. In addition, the moisture was measured with tensiometers placed at depths of 0—5 cm and 5—10 cm (see Ahti 1971). The soil temperature was measured on the sampling dates and between 13.00 and 14.00 about every third day in summer. For precipitation and mean temperature the daily observations made at Lammi Biological Station were used.

C. Identification and estimation of biomasses

The living worms were identified and measured, and examined for maturity. Identification was according to Nielsen & Christensen (1959, 1961), Nurminen (1970) and Dozsa-Farkas (1973c). Biomasses were estimated from length measurements with Abrahamsen's (1973) equations of volume and density for different species. Because the immatures of the genus *Fridericia* could not be identified, they were treated as a unit and given the values of Abrahamsen's class D.

3. Results and discussion

A. Species composition

In area 1 there were 21 species, of which 7 were accidentals (fewer than 10 individuals

Table 2a. The proportions (%) of the different species in areas 1 and 2. Under 1 % = +.

Species	Area 1	Area 2
Fridericia	68	60
Buchholzia appendiculata (Buchholz 1862)	8	9
Stercutus niveus (Michaelsen 1884)	7	2
Enchytraeus minutus (Nielsen & Christensen 1961)	5	6
Achaeta eiseni (Vejdovsky 1877)	4	6
Cognettia sphagnetorum (Vejdovsky 1877)	3	13
Enchytronia parva (Nielsen & Christensen 1959)	3	2
Mesenchytraeus flavus (Levinsen 1884)	1	+
M. pelicensis (Issel 1905)	+	+
Henlea nasuta (Eisen 1878)	+	1
H. perpusilla (Friend 1911, augm. Cerncsvitov 1939)	+	1
Cognettia glandulosa (Michaelsen 1888)	+	–
Bryodrilus ehlersi (Ude 1892)	+	+

Table 2b. The proportions (%) of species of the genus *Fridericia*.

	Area 1	Area 2
Fridericia bisetosa (Levinsen 1884)	39	26
F. paroniana (Isse 1904)	23	31
F. bulbosa (Rosa 1887)	16	23
F. nemoralis (Nurminen 1970)	15	3
F. ratzeli (Eisen 1872)	5	12
F. bulboides (Nielsen & Christensen 1959)	2	4
F. galba (Hoffmeister 1843)	+	1
F. alata (Nielsen & Christensen 1959)	+	–
F. callosa (Eisen 1878)	+	–

during the whole period), and the corresponding values for area 2 were 18 and 4. According to NURMINEN (1967b), Finnish conifer forest soil harbours four species of Enchytraeids. In calcareous soil of the Hungarian *Quercetum petraeae cerris* forest the number of species was 21 (DOZSA-FARKAS 1973a). ABRAHAMSEN (1968) also noticed that the number of Enchytraeid species is higher in deciduous forest soil than in pine forests as a result of the better moisture conditions and more diversified food supply.

According to NURMINEN (1967b), the communities of north European meadow forests are dominated by the genus *Fridericia.* This genus accounted for 68 % of the total numbers in area 1 and 60 % in area 2 (Table 2). *F. bisetosa* was the dominant species in area 1 and the proportion of *F. paroniana* was also considerable. These two species amounted to 53 % of the total number. Another group consisted of 11 common species, which together made up 46 % of the whole community. Accidental species accounted for about 1 % of the total number. In area 2 there was no single dominant species, as NURMINEN (1967b) also noticed in meadow forest soil. The combined proportion of the four most abundant species was 53 %. These were *F. paroniana*, *F. bisetosa*, *F. bulbosa* and *Cognettia sphagnetorum*. Four other common species made up 25 % of the community and the remaining 10 species contributed 11 %. Thus in area 2 the proportions of the different species were more even than in area 1.

In area 2 the number of species near the surface (0—4 cm) was significantly greater than in the deeper layers (4—8 cm) (Table 3). In area 1 the difference between the layers was not so clear. The difference between the two areas in this respect was attributed to the difference in the thickness of the humus layers: The food conditions in the thick A_1 layer in area 1 are more homogeneous than in the thinner and more concentrated humus layer in area 2.

The Enchytraeid species form characteristic communities according to their habitat preferences (NURMINEN 1973). These preferences are stronger in rare species (NIELSEN 1955a). The communities of the areas studied included several of the species of rich biotopes found in the studies of DE GUNST (1965), NURMINEN (1967b, 1970), ABRAHAMSEN (1968), SPRINGETT (1970) and DOZSA-FARKAS (1973c). Typical species preferring mull soil occurring in both areas abundantly were *Enchytronia parva*, *Enchytraeus minutus*, *Fridericia ratzeli*, *Achaeta eiseni* and *Buchholzia appendiculata*. In addition to the species of the above-mentioned studies, *Fridericia nemoralis* was especially abundant in area 1. *F. nemoralis* has been met as yet only in stands of *Corylus avellana* in Finland (NURMINEN 1970) and central Sweden (NURMINEN personal

Table 3. The number of species in the surface layer (0–4 cm) and in the deeper layer (4–8 cm).

	Mean	SD	SE		
Area 1					
0–4 cm	9.8	2.28	0.739	t = 2.297*	df = 20
4–8 cm	7.4	2.60	0.739		
Area 2					
0–4 cm	9.8	1.81	0.534	t = 4.556***	df = 20
4–8 cm	6.4	1.73	0.534		

report). *Stercutus niveus* was found for the first time in Finland and probably also in Northern Europe. The species was identified according to Dozsa-Farkas (1973c). *Cognettia glandulosa* and *Henlea perpusilla*, which are common in the rich north-European forest soils, were only accidentals.

B. Numbers

The mean density of the Enchytraeid community was 8 044 ind/m^2 in area 1 and 5 711 ind/m^2 in area 2; the difference is statistically highly significant. In the survey year, which was very dry, the community of the normally very moist area 2 presumably suffered more from drought than the community in area 1. No definite reason can be given for the smaller numbers in area 2, because there is no information about food supply, chemical properties of the soil, predation or other soil animals.

The numbers are known to fluctuate strongly according to weather conditions, and in addition to this intra-annual fluctuation there is a great inter-annual variation (Nurminen 1967a). This study covered only one year, and a long-term survey might change the mean values. The numbers correspond well to those in an OMT-spruce stand at Lammi (Huhta & Koskenniemi 1975), but it must be considered that the study in question was made in an exceptionally dry year. The density of Enchytraeids in a moister MT-spruce stand was about twice as great (Huhta & Koskenniemi 1975). Nielsen (1955a) has actually shown that the density is permanently lower in rich mull soils than in the acid humus of conifer forests.

Seasonal variations in numbers. In both areas numbers showed a summer minimum (Fig. 2).

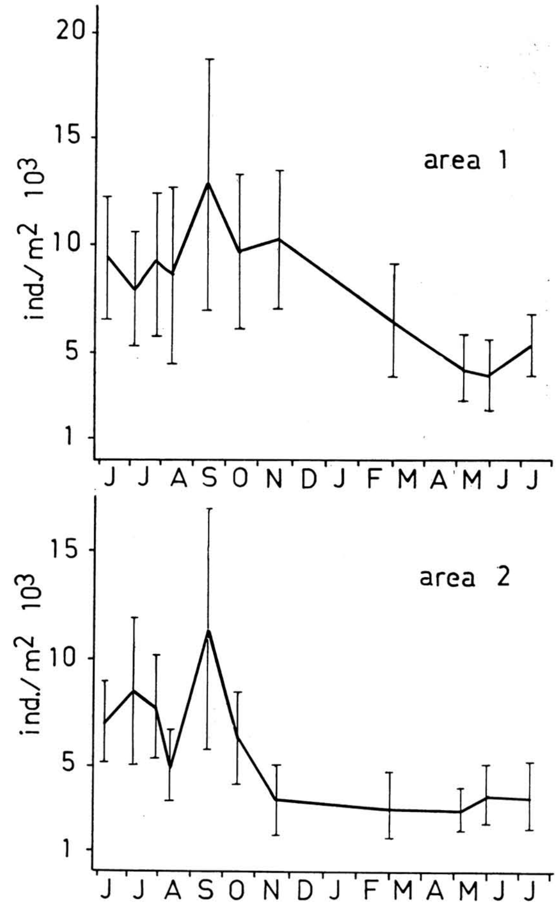

Fig. 2. Seasonal variation in total numbers of Enchytraeids (95 % confidence limit).

which is typical of Enchytraeids during a dry spell (e.g. Nielsen 1955a, Nurminen 1967a, Abrahamsen 1972). In summer 1975 the soil became very dry, and by the end of the summer the ground water level was low. At that time there was a strong minimum in area 2. In the drier area 1 the numbers remained relatively low all through the summer. In September, there was a clear maximum in both communities. Rapid changes in density are known to occur in response to changes in soil moisture (Nielsen 1955a, O'connor 1957b etc.)

The winter minimum was lower than the summer one, a fact also observed by Nurminen (1967a) in conifer forest soil. In laboratory studies Dozsa-Farkas (1973b) found that the species *F. galba* and *F. hegemon* perish in 24 h when exposed to —4 to —5°. The exception was *Stercutus niveus*, which tolerates this low temperature well. This species reaches its maximum abundance in winter (see Fig. 4), as DOZSA-FARKAS (1973a) also noticed. According to O'CONNOR (1967), low temperatures do not kill worms, but inhibit their reproduction. Similarly, NIELSEN (1955a) did not observe an abrupt decrease in numbers during a frost period (—10 to —18°C) lasting 28 days. In spring 1976 no sharp increase in numbers occurred, in contrast to the general model of the seasonal fluctuations of Enchytraeids in Finnish forest soil (NURMINEN 1967a). The absence of a spring maximum in 1976 was probably due to the strong and prolonged ground frost and low air temperatures in spring. When the temperature fell below zero in winter there was no insulating snow cover. At the end of February the frozen layer was 20—25 cm thick in area 1 and 30—35 cm thick in area 2. At the beginning of May 1976 the ground was frozen to a depth of 10—12 cm in area 1 and 6 cm in area 2. During the 4 weeks before sampling (6. V. 1976) the mean temperature of the air was only +2.3°C, whereas at the same time in the previous year it was +10.5°C.

Correlation of numbers with moisture and temperature. The effect of moisture and temperature upon the abundance of Enchytraeids was analysed in three different ways:

1. The numbers were compared with the soil water content measured on the sampling dates, and expressed as percentages of the water-holding capacity. There was no correlation between these two variables. According to ABRAHAMSEN (1971), Enchytraeids do not survive if the soil water content is less than 10 % of the water-holding capacity (WHC). The percentage in this study did not fall below 39 %. NURMINEN (1967a) considered the gravimetric method unreliable because it gives only the situation at the moment of sampling.

2. The effects of precipitation and temperature, both separately and combined, on total numbers were tested with three-dimensional regression analysis (SNEDECOR & COCHRAN 1967). Total precipitation was measured for 2 weeks before sampling, and the temperatures of the soil on the sampling dates were used as temperature values. Precipitation and temperature together explained 73.1 % of the changes in numbers in area 1 and 69 % in area 2, respectively. NIELSEN (1955b) has also observed that soil moisture is the most important factor regulating abundance. Temperature alone explained the changes better in the moister area 2 (9.4 %) than in the drier one (2.0 %). The explanation was somewhat better if account was taken of the temperature values of the cold part of the year. The dependence in the moister area was statistically almost significant ($r = 0.65$* n =11). In constantly moist habitats, according to O'CONNOR (1957), the changes in abundance correspond to seasonal variations in temperature. Thus temperature affects fecundity. In the drier area 1 no dependence was noticed. High temperatures are not a limiting factor in Finland, because the lethal temperature for Enchytraeids would be 25—30 °C (NIELSEN 1955a).

3. The dependence of numbers on moisture and temperature was also measured with a modification of the humidity index of Martonne[1] (see HUHTA *et al.* 1967). The index was calculated from macroclimatic data for periods of 2 and 4 weeks before sampling. Only the values for the warm part of the year (May-October) were used. The numbers correlated better with the index values for the shorter period (2 weeks: $r_1 = 0.86^{**}$ $r_2 = 0.77^{*}$, 4 weeks: $r_1 = 0.79^{*}$ $r_2 = 0.68^{\circ}$) as KOSKENNIEMI (1973) has also shown. Thus Enchytraeids react rapidly to changes in moisture (cf. HUHTA *et al.* 1967).

Reproduction. According to REYNOLDSON (1943), the optimum temperature for reproduction of the sewage species *Lumbricillus lineatus* and *Enchytraeus albidus* is about +18 °C. In the study area the soil did not reach this temperature until late July and early August. Then drought prevented excessive reproduction. The rains in August and September allowed a rapid increase in autumn. At that time the temperature of the soil (+10 °C) was still high enough for reproduction. According to REYNOLDSON (1943), the minimum temperature for reproduction in *L. lineatus* and *E. albidus* is +5—7 °C. With the species *Cognettia*

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[1]) Index of Martonne $\frac{S}{T+10}$

S = precipitation during the 2/4 weeks before the sampling date

T = mean temperature of the same period

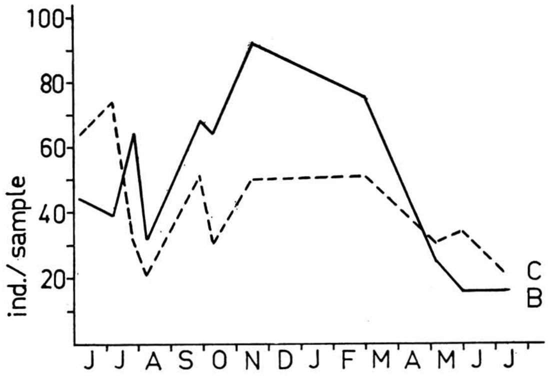

Fig. 3. Seasonal variation in numbers of *Buchholzia appendiculata* (B) and *Cognettia sphagnetorum* (C) Numbers are expressed as individuals/sample and the February samples are corrected to correspond to 15 sample units.

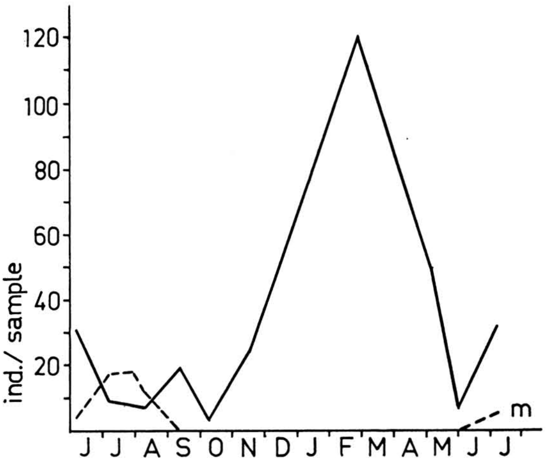

Fig. 4. Seasonal variation in numbers of mature (— — —) and immature (——) *Stercutus niveus*. The February samples corrected as in Fig. 3.

sphagnetorum ABRAHAMSEN (1971) has also shown that asexual reproduction is very weak at +6 °C.

The proportion of mature individuals was at all times small. But this proportion and its variation (12—45 %) did not exactly correspond to periods of reproduction, which varied from species to species.

CHRISTENSEN (1959, 1961) showed that the species *Buchholzia appendiculata* and *Cognettia sphagnetorum* reproduce asexually by fragmentation; in *C. sphagnetorum* this is the only mode of reproduction, because the cocoons perish after a few days. In the present study no mature individuals of these species were observed, but regenerating tail and head segments were found. The combined proportion of these species in the communities was 11 % in area 1 and 22 % in area 2. At the end of the summer the numbers of both species were minimal. Recovery took place in autumn. A huge increase occurred in *Buchholzia appendiculata* as late as November (Fig. 3). The numbers in summer 1976 were notably lower than in the previous year.

Mature individuals of *Stercutus niveus* with eggs were observed from July to September. DOZSA-FARKAS (1973c) found sexually mature individuals from the end of July till October and ovigerous ones by the end of August. In early July 1976 several "premature" worms were observed, with their chloragogen cells detached from the clitellar region (cf. DOZSA-FARKAS 1973c). The samples collected in November and February contained several individuals whose chloragogen cells were shorter and rounder than usual. These were either juveniles or worms which had already oviposited and which exhibit a phenomenon known as ananeosis (DOZSA-FARKAS 1973c). *Stercutus niveus* had its maximum abundance during the winter (Fig. 4). DOZSA-FARKAS (1973c) has noticed that this species has a prolonged inactive state from April or May until July or August. This probably explains the very low numbers in summer. As the material examined was very sparse no reliable conclusions can be drawn.

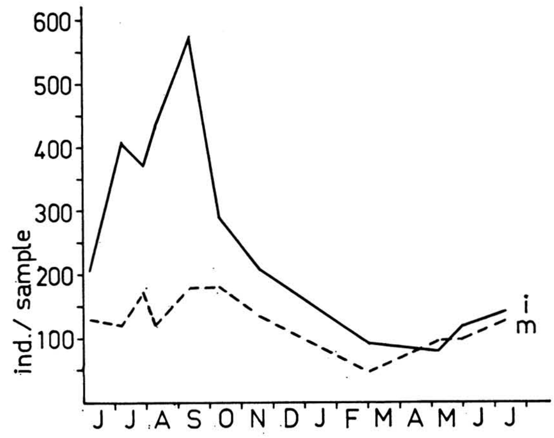

Fig. 5. Seasonal variation in numbers of mature (— — —) and immature (——) *Fridericia* species. The February samples corrected as in Fig. 3.

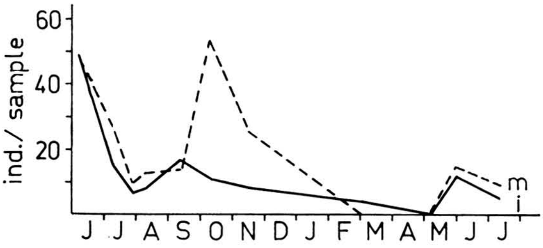

Fig. 6. Seasonal variation in numbers of mature (— — —) and immature (——) *Enchytraeus minutus*. The February samples corrected as in Fig. 3.

In the genus *Fridericia* the numbers of immature worms increased greatly during August-September. Before this, mature worms were numerous, so oviposition probably occurred in late July. Eggs hatched throughout the summer. The potential for reproduction was greatest in area 2 in October and in area 1 in September-October, and the eggs may have been laid then. Eggs could not hatch during the winter. In spring 1976 the soil was frozen for an exceptionally long period and, when it eventually became warm enough, the increase in numbers was slight (Fig. 5). So it appears likely that, because the minimum temperature for reproduction was reached much later than usual, a high proportion of the eggs had been destroyed.

Enchytraeus minutus differed from the other species in that mature worms were almost continuously more numerous than immature ones (Fig. 6). In October and November there were exceptionally large numbers of mature individuals, but before this peak of abundance no abundance of immature worms was found. Peachey (1962) has shown that the Nielsen extractor is more efficient for newly emerged individuals and small species than the standard method used in this study. Possibly some of the immature *E. minutus* were not removed from the soil samples or were overlooked when counts were made.

Vertical distribution and its seasonal variation. According to Nielsen (1955a), 70—90 % of the Enchytraeid population lives in the upper 5 cm of the soil. The vertical distribution of Enchytraeids in the study areas was calculated

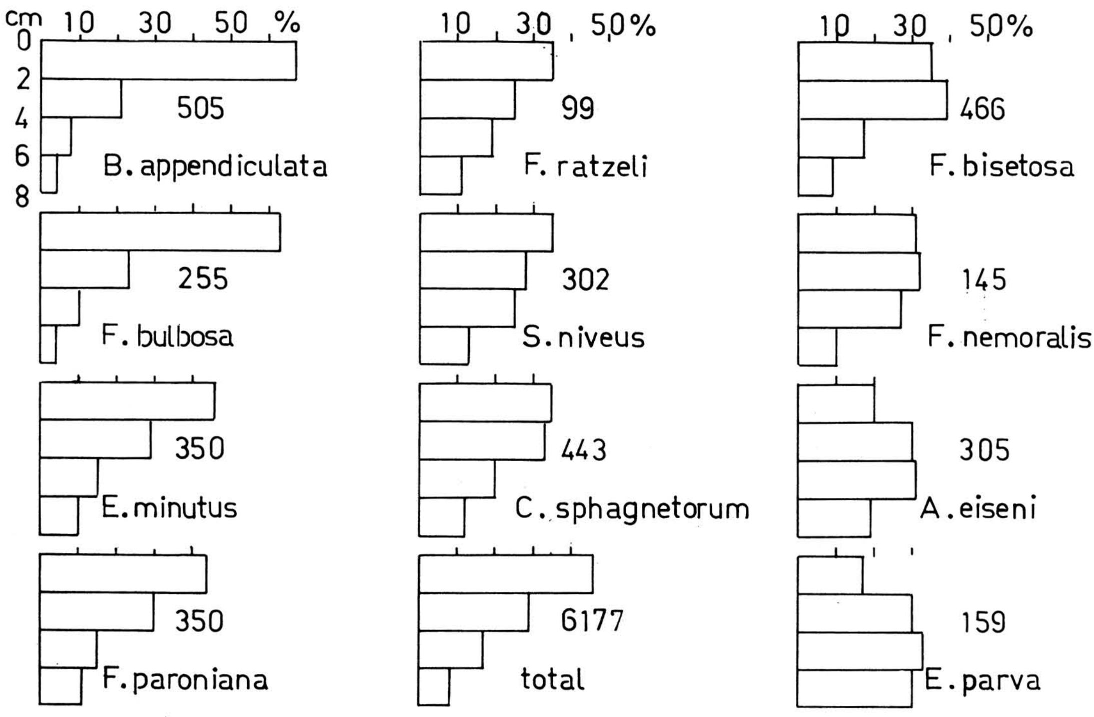

Fig. 7. Vertical distribution of Enchytraeids in meadow forest soil. The numbers of individuals found are given beside the diagrams.

for the material as a whole (Fig. 7). The numbers of worms at a depth of 8—10 cm were estimated by extrapolation. The result showed that the occurrence is restricted to the upper 10 cm, the proportion in the 8—10 cm layer being neglible.

SPRINGETT (1970) and ABRAHAMSEN (1972) have found that different species tend to inhabit different layers of soil. According to ABRAHAMSEN (1972), *Buchholzia appendiculata* has a more epedaphic distribution (preference for surface layers in soil) than the other species. Typical euedaphic (preference for deeper layers) species are *Enchytronia parva* and the genus *Achaeta*. The present results lend support to these observations (Fig. 7). Samples taken from 8—10 cm depth at the beginning of May contained only a few individuals of *Achaeta* and no other species at all. The distribution of *F. bisetosa* differed from ABRAHAMSEN's (1972) results; the worms did not concentrate in the surface layer (0—2 cm). It must be noticed, however, that the results for the distribution of *Fridericia* species referred only to mature worms.

Seasonal variation in vertical distribution may be caused either by migration or by differential mortality and reproduction rates in different layers. According to O'CONNOR (1963), drying of the soil does not cause migration; the variation in distribution is due to mortality. NIELSEN (1955a) and ABRAHAMSEN (1972) noticed that worms near the surface have a tendency to move deeper in dry periods. SPRINGETT *et al.* (1970) showed that the worms move several centimetres in a few hours, according to moisture. During these rapid movements the size of the population remains constant, so that the changes in distribution cannot be explained by differences in mortality or reproduction. The seasonal variation in the vertical distribution of the present study areas is shown in Fig. 8.

At the beginning of July, when moisture was limited, the proportion of worms in the surface layer (0—2 cm) was notably lower than in June (Fig. 8). The change occurred in both areas. In the moister area 2, however, the actual numbers in July were significantly greater than in June in all but the surface layer, where they remained about the same. The tensiometer values indicated that moisture conditions were more favourable in the deeper layers (5—10 cm, pF about 2.4) than at the surface (0—5 cm, pF about 2.6). The change

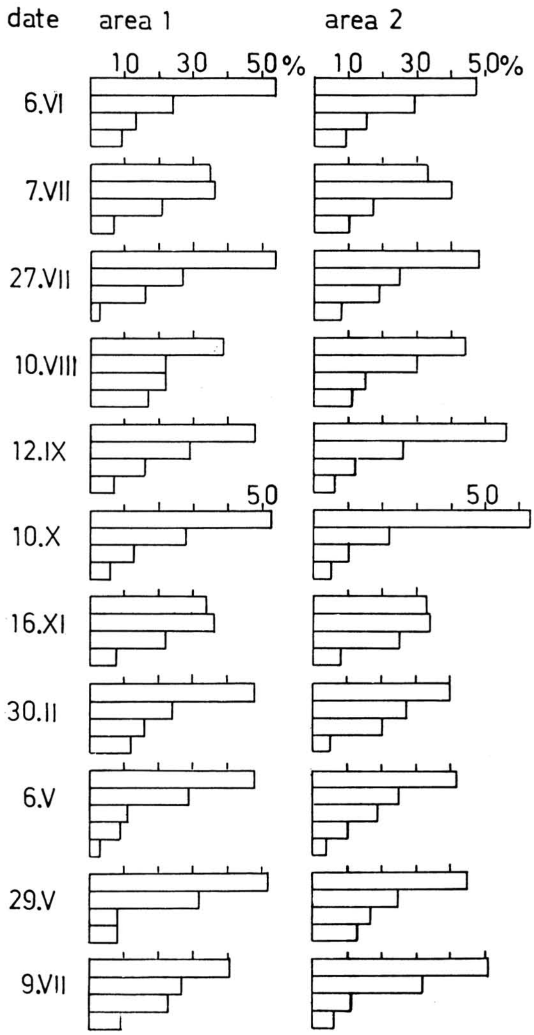

Fig. 8. Seasonal variation in the vertical distribution of Enchytraeids in meadow forest soil.

in the vertical distribution could thus be explained by reproduction but also by migration. In the drier area 1 the tensiometers showed pF values of over 2.9 (maximum measurable) both at the surface and deeper. The density at the surface had decreased notably, but at 2—6 cm depth the numbers had increased a little, so that some vertical migration may have taken place.

NURMINEN (1967a) noticed changes in the vertical distribution when the temperature of the surface layer fell below zero or rose above it. In his opinion (NURMINEN 1967a), some vertical migration may occur at the onset of frosts when the deeper layers are still warm. SPRINGETT *et al.* (1970) also suppose that the deeper penetration of *Cernosvitoviella briganta* and *Cognettia sphagnetorum* in January and February is caused by vertical migration to escape frost in moorland soils. In area 1 the numbers in the surface layer (0—2 cm) decreased significantly from October to November, whereas the numbers in the deeper layers increased. The total number was almost the same. As there was hardly any reproduction in November because of the low temperatures, the change may have been caused by vertical migration. In area 2 the Enchytraeids were notably less abundant in the surface layer in November than in October, but the numbers in the other layers remained almost the same. The result does not show whether the change in distribution was caused by mortality alone or combined with migration.

The high proportion in the surface layer in February is probably due to the abundance of the species *Stercutus niveus* and its concentration at the surface. DOZSA-FARKAS (1973a) observed the same phenomenon in the cold part of the year with this species.

Horizontal distribution. The horizontal distribution was aggregated. The frequency distribution of the observations about the sample means corresponded perfectly with the results of O'CONNOR (1967). The aggregated distribution was expressed in terms of the disturbance index of Lexis (DEBAUCHE 1962). The index values ranged from 1.84 to 4.98 (mean 3.03) in area 1 and 1.77 to 5.01 (mean 2.60) in area 2. They were smaller than those obtained by NURMINEN (1967a) for the Enchytraeids of conifer forest soil (mean 7.43), but showed an aggregated distribution with high significance (see HUHTA *et al.* 1967).

C. Biomasses

The annual mean biomass of the Enchytraeid community expressed as fresh weight was 1.74 g/m² in area 1 and 1.28 g/m² in area 2. The biomass of area 1 was nearly twice that of a population with almost the same density in an OMT spruce forest studied by HUHTA & KOSKENNIEMI (1975). The difference can be explained by the species composition: The

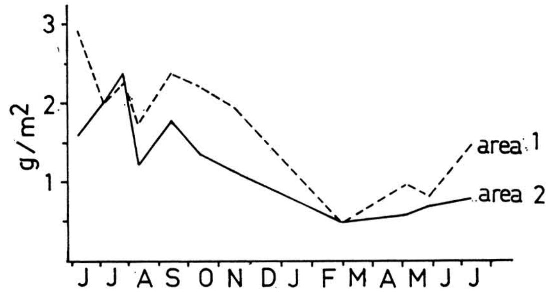

Fig. 9. Seasonal variation in biomass in the Enchytraeid communities of areas 1 (— — —) and 2 (——).

community in coniferous forests consists almost exclusively of the small species *Cognettia sphagnetorum* (NURMINEN 1967a), whereas in this study it included many large species, for instance *F. bisetosa*, *F. nemoralis* and *F. ratzeli*. NIELSEN (1955a) has shown that in rich biotopes the biomasses are greater than would be expected from the numbers alone. The seasonal variation in biomass did not correspond well to the variation in numbers. This was caused by the varied occurrence of the large species. At the beginning of June, for instance, the biomass was maximal in area 1 owing to the abundant occurrence of *Mesenchytraeus flavus*. Similarly in area 2 the sample taken on 27 June 1975 yielded large numbers of *F. ratzeli*. In February, on the other hand, the biomass in area 1 was very low in relation to numbers, owing to the high proportions of immature worms and of the small-sized *S. niveus* (Fig. 9). The vertical distribution of the biomass was the same as that of the numbers: 73 % of the biomass in area 1 and 74 % in area 2 was in the uppermost 4 cm.

The biomass figures emphasize the importance of the genus *Fridericia*. In both areas the genus covered about 90 % of the total biomasses, whereas the proportions of the smallest species e.g. *Enchytraeus minutus* and *S. niveus*, were very low, about 1 %.

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References

ABRAHAMSEN, G. 1968: Records of Enchytraeidae (Oligochaeta) in Norway. — Medd. Norske Skogforsøksvesen 89 (25):211—230.

—»— 1971: The influence of temperature and soil moisture on the population density of Cognettia sphagnetorum (Oligochaeta: Enchytraeidae) in cultures with homogenized raw humus. — Pedobiologia 11:417—424.

—»— 1972: Ecological study of Enchytraeidae (Oligochaeta) in Norwegian coniferous forest soils. — Pedobiologia 12:26—82.

—»— 1973: Studies on body-volume, body-surface area, density and live-weight of Enchytraeidae (Oligochaeta). — Pedobiologia 13:6—15.

AHTI, E. 1971: Use of a tensiometer in measuring soil water tension. — Folia Forestalia 112.

CHRISTENSEN, B. 1959: Asexual reproduction in the Enchytraeidae (Oligochaeta). — Nature 184: 1159—1160.

—»— 1961: Studies on cyto-taxonomy and reproduction in the Enchytraeidae. — Hereditas 47:387—450.

DASH, M. C. & GRAGG, J. B. 1972: Ecology of Enchytraeidae (Oligochaeta) in Canadian Rocky Mountain soils. — Pedobiologia 12:323—335.

DEBAUCHE, H. R. 1962: The structural analysis of animal communities of the soil. — In: MURPHY, P. W. (ed.), Progress in Soil Zoology: 10—25. London.

DÓZSA-FARGAS, K. 1973a: Saisondynamische Untersuchungen des Enchytraeiden-Besatzes im Boden eines ungarischen Quercetum petraeae cerris. — Pedobiologia 13:361—367.

—»— 1973b: Communicationes Breves. Some preliminary data on the frost tolerance of Enchytraeidae. — Opusc. Zool. Budapest 9:1—2.

—»— 1973c: Ananeosis, a new phenomenon in the life-history of the Enchytraeids (Oligochaeta). — Opusc. Zool. Budapest 12:1—2.

ELLIOT, J. M. 1971: Some methods for the statistical analysis of benthic invertebrates. — Freshwater Biol. Ass., Scient Publ. 25:128—131.

DE GUNST, J. H. 1965: Enchytraeidae of the Netherlands (Annelida: Oligochaeta). — Beaufortia 13: 5—12.

HEINO, R. 1976: Climatological tables in Finland, 1961—1975. — Supplement to the Meteorological Yearbook of Finland 75, 1a. The Finnish Meteorological Institute. Helsinki.

HUHTA, V. 1976: Effect of clear-cutting on numbers, biomass and community respiration of soil invertebrates. — Ann. Zool. Fennici 13:63—80.

HUHTA, V., KARPPINEN, E., NURMINEN, M., VALPAS, A. 1967: Effect of silvicultural practices upon arthropod, annelid and nematode populations in coniferous forest soil. — Ann. Zool. Fennici 4:87—143.

HUHTA, V., NURMINEN, M., VALPAS, A. 1969: Further notes on the effect of silvicultural practices upon the fauna of coniferous forest soil. — Ann. Zool. Fennici 6:327—334.

HUHTA, V. & KOSKENNIEMI, A. 1975: Numbers, biomass and community respiration of soil invertebrates in spruce forest at two latitudes in Finland. — Ann. Zool. Fennici 12:164—182.

KOSKENNIEMI, A. 1973: OMT-kuusikon maaperäeläimistön kvantitatiivinen analyysi. — Manuscript, Dept. Zool. Univ. Helsinki.

NIELSEN, C. O. 1952-1953: Studies on Enchytraeidae 1. A technique for extracting Enchytraeidae from soil samples. — Oikos 4:187—196.

—»— 1954: Studies on Enchytraeidae 3. The microdistribution of Enchytraeidae. — Oikos 5: 167—178.

—»— 1955a: Studies on Enchytraeidae 2. Field studies. – Natura Jutlandica 4—5:1—58.

—»— 1955b: Studies on Enchytraeidae 5. Factors causing seasonal fluctuations in numbers. — Oikos 6:153—159.

NIELSEN, C. O. & CHRISTENSEN, B. 1959: The Enchytraeidae. Critical revision and taxonomy of European species. — Natura Jutlandica 8—9:1—160.

—»— 1961: The Enchytraeidae. Critical revision and taxonomy of European species. Suppl. 1. — Natura Jutlandica 10:1—23.

NURMINEN, M. 1967a: Ecology of Enchytraeids (Oligochaeta) in Finnish coniferous forest soil. — Ann. Zool. Fennici 4:147—157.

—»— 1967b: Faunistic notes on North-European Enchytraeids (Oligochaeta). — Ann. Zool. Fennici 4:567—587.

—»— 1970: Four new Enchytraeids (Oligochaeta) from southern Finland. — Ann. Zool. Fennici 7:378—381.

—»— 1973: Distribution of northern Enchytraeids (Oligochaeta). — Ann. Zool. Fennici 10: 483—486.

O'CONNOR, F. B. 1955: Extraction of Enchytraeid worms from a coniferous forest soil. — Nature (Lond.) 175:815—816.

—»— 1957: An ecological study of the Enchytraeid worm population of a coniferous forest soil. — Oikos 8:161—199.

—»— 1962: The extraction of Enchytraeidae from soil. — In: MURPHY, P. W. (ed.), Progress in Soil Zoology: 279—285.

—»— 1967: The Enchytraeidae. — In: BURGES, A. & RAW, F. (eds.), Soil Biology: 213—257. London.

—»— 1971: The Enchytraeids. — In: PHILLIPSON, J. (ed.), Methods of Study in Quantitative Soil Ecology: Population, Production and Energy Flow. IBP Handbook 18:83—106.

PEACHEY, J. E. 1962: A comparison of two techniques for extracting Enchytraeidae from moorland soils. — In: MURPHY, P. W. (ed.), Progress in Soil Zoology: 286—293.

—»— 1963: Studies on the Enchytraeidae (Oligochaeta) of moorland soils. — Pedobiologia 2:81—95.

REYNOLDSON, T. B. 1939: On the life-history and ecology of Lumbricillus lineatus Mull. (Oligochaeta). – Ann. Appl. Biol. 26:782—799.

—»— 1943: A comparative account of the life cycle of Lumbricillus lineatus Mull. and Enchytraeus albidus Henle in relation to temperature. — Ann. Appl. Biol. 30:60—66.

SNEDECOR, G. W. & COCHRAN, W. G. 1967: Statistical Methods. — 381 pp. — Ames, Iowa, USA.

SPRINGETT, J. A. 1970: The distribution and life histories of some moorland Enchytraeidae (Oligochaeta). — J. Animal Ecol. 39:725—737.

SPRINGETT, J. A., BRITTAIN, J. E., SPRINGETT, B. P. 1970: The vertical movement of Enchytraeidae (Oligochaeta) in moorland soils. — Oikos 21: 16—21. Copenhagen.

STANDEN, V. 1973: The production and respiration of an Enchytraeid population in blanket bog. — J. Animal Ecol. 42:219—245.

VILKAMAA, P. 1976: Ojituksen vaikutus rämeen maaperäeläinten yksilömääriin ja biomassoihin. — Manuscript, Dept. Zool. Univ. Helsinki.

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