An ecological study of moorland enchytraeidae

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AN ECOLOGICAL STUDY OF

MOORLAND ENCHYTRAEIDAE

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CONTENTS

INTRODUCTION

The Enchytraeidae are a family of small Oligochaeta particularly abundant on moist 'mor' type soils. Since the latter part of the nineteenth century many workers have drawn attention to the numbers of Enchytraeidae present in the soil and their obvious importance in the break-down of organic material.

The fundamental role of Enchytraeidae in the breakdown of organic matter in sewage beds has been clearly demonstrated by Reynoldson (1939-1958). It has been assumed that soil Enchytraeidae can be classed as secondary decomposers (Nielsen 1962, Macfadyen 1963) utilising nutrients released from raw plant material by bacterial and fungal activity. Recently Kurir (1964) has suggested that Fridericia galba (Hoffmeister, 1843) can be parasitic on forest seedlings, but it is not clear whether infestation by Fridericia galba occurs before or after attack by micro-organisms.

With the development of extraction techniques for dealing with soil Enchytraeidae (Nielsen 1952, O'Connor 1955) studies on the population densities of soil Enchytraeidae became possible. Such studies were made by Nielsen (1954, 1955) O'Connor (1957, 1958, 1963) and Peachey (1959, 1963). A review of the taxonomy of the European species has recently been made by Nielsen and Christensen (1959, 1961).

Peachey's studies on the Enchytraeidae of moorland soils on the Moor House National Nature Reserve were carried out before the publication of Nielsen and Christensen's taxonomic review. Because of the taxonomic difficulties Peachey's work dealt mainly with the numbers and spatial distribution of total Enchytraeidae. His work also involved a detailed comparison of the efficiencies of the available extraction techniques for moorland soils, and a subsequent modification of O'Connor's wet funnel method. The present work on the Enchytraeidae of moorland soils at Moor House N.N.R. was carried out using the wet funnel method.

Measurements of the respiratory activity of enchytraeid worms have been made by Nielsen (1961) and O'Connor (1963) and the population metabolism estimated. Figures of this type are of particular importance when they can be compared with similar ones for other groups of soil animals and especially so when all the animals are from one soil site.

In this thesis the work on Enchytraeidae which took place between October 1961 and October 1964 is described in seven parts, dealing with the study area and climate, sampling and extraction techniques, species distribution, the horizontal distribution of Enchytraeidae, life cycles of the worms, seasonal variations in numbers of worms and the vertical distribution and migration of Enchytraeidae.

The nomenclature of the higher plants follows that of Clapham et al (1952) and the mosses that of Watson (1955).

I. THE STUDY AREA

THE STUDY AREA

Location and Physiography

This study was made on sites selected on the Moor House National Nature Reserve (Nr.80) in the northern Pennines. The Reserve lies 12 miles east of Penrith and 11 miles south of Alston (Nat. Grid Ref. NY/758329). The major part of the Reserve's 10,000 acres (4,000 hectares) slopes eastwards from the three fells, from north to south; Little Dun Fell (2,761 ft.; 842m.), Great Dun Fell (2,780 ft.; 845m.) and Knock Fell (2,604 ft.; 794m.). No part of the Reserve lies below 1,600 ft. (533m.). The area is heavily dissected by streams, those of the western, scarp slope draining to the River Eden; and those of the eastern, dip slope, feeding the River Tees and its main tributaries, Troutbeck, Moss Burn and Force Burn.

The scarp and dip slopes are formed by the Yoredale series of Carboniferous sandstones, shales and limestones. These are mostly covered by glacial drift deposits which are in turn covered by blanket peat. Mineral soils occur on the fell tops, the occasional limestone and sandstone outcrops, and on the terraces of the many small streams.

The soils on the limestone outcrops are probably of skeletal origin, while the alluvial soils of the stream terraces contain various amounts of redistributed peat. The blanket peats have plant associations of

Calluna vulgaris and Vaccinium myrtilis on the upper dry slopes and shallow peat and Calluna and Eriophorum vaginatum and E. angustifolium on the deeper peats, (Lewis 1904). The areas of blanket peat are in various stages of erosion and recolonisation. On the higher slopes, and along the stream valleys, shallower peat or mineral soils allow rush and grass dominated areas to develop, (Juncus effusus, J. squarrosus, Nardus stricta, Festuca ovina and Agrostis tenuis). Further descriptions of the reserve can be found in Conway (1955), Cragg (1961) and Johnson and Dunham (1963).

The Sample Sites

Sample sites were chosen to be characteristic of the types of soil and vegetation found on the Moor House reserve. Five sites were selected for routine sampling; two mineral soils and three peat soils.

1. Limestone grassland - lime poor mull
2. Nardus grassland - peaty alluvium
3. Juncus squarrosus moor - peat mor - disturbed shallow peat on Moor edge
4. Mixed moor - blanket peat
5. Bare peat - eroded blanket peat

The exact location of each site is marked on the map of the reserve, Fig. I. The soil profiles of these sites are described in Appendix I, after Cragg (1961) and the chemical properties in Table I adapted from Banage (1960).

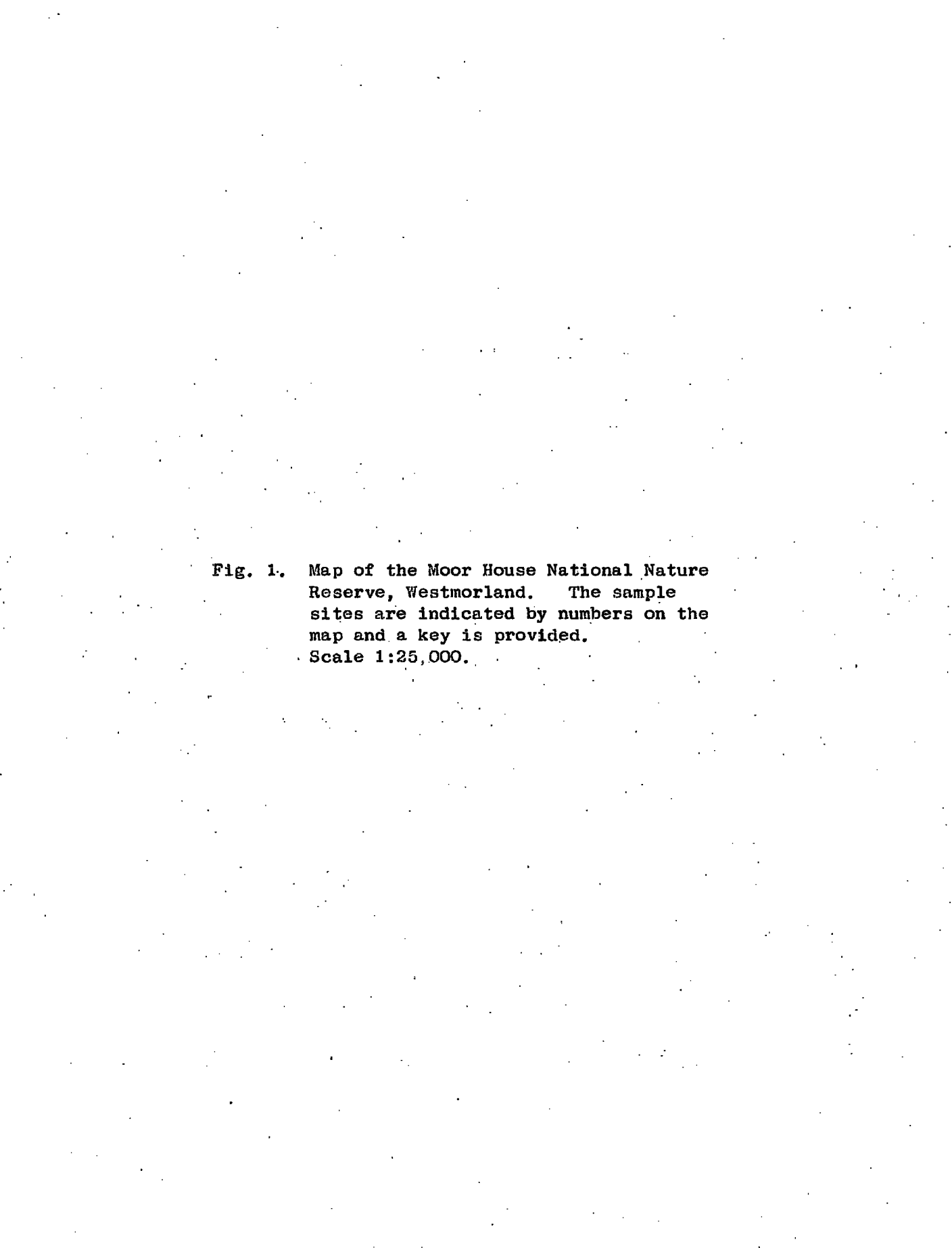


Fig. 1. Map of the Moor House National Nature Reserve, Westmorland. The sample sites are indicated by numbers on the map and a key is provided. Scale 1:25,000.

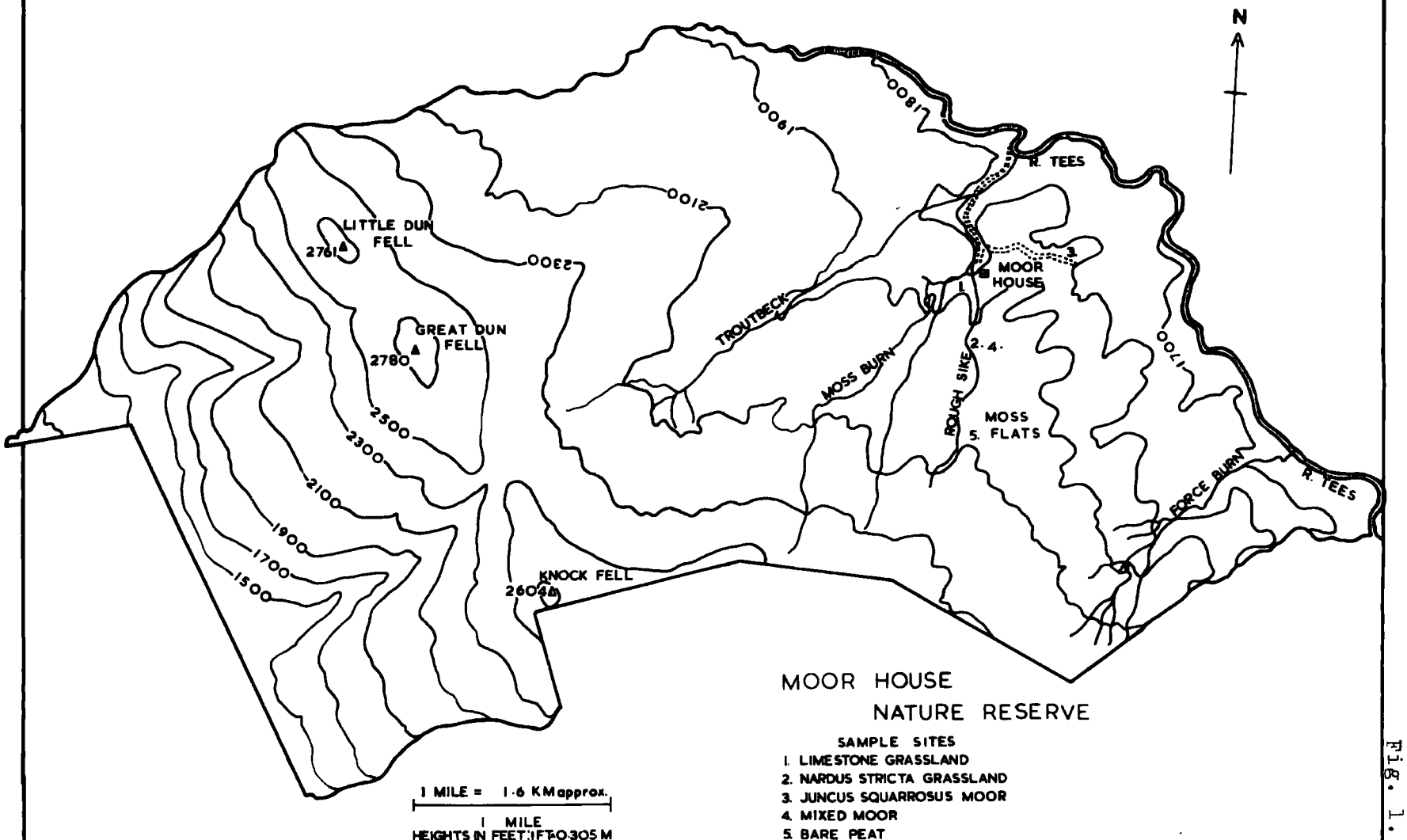

N
R. TEES
1800
1900
2100
2300
LITTLE DUN FELL
2761
GREAT DUN FELL
2780
KNOCK FELL
2604
TROUTBECK
MOSS BURN
ROUGH SIKE
MOOR HOUSE
MOSS FLATS
FORCE BURN
R. TEES
2500
2300
2100
1900
1700
1500
1 MILE = 1·6 K M approx.
1 MILE
HEIGHTS IN FEET: 1 FT = 0·305 M
MOOR HOUSE
NATURE RESERVE
SAMPLE SITES
1. LIMESTONE GRASSLAND
2. NARDUS STRICTA GRASSLAND
3. JUNCUS SQUARROSUS MOOR
4. MIXED MOOR
5. BARE PEAT

Fig. 1.

Table 1

The chemical properties of the soils on the sampling areas after Banage (1960)

Index	Limestone grassland	Nardus grassland	Juncus squarrosus	Mixed Moor	Bare Peat
pH	5.8-6.0	3.0-4.8	6.7-4.4	5.0-4.4	4.6-4.3
Percentage carbon	3.2-7.4	7.5-16.3	27.0-30.0	30.9-35.1	35.9-38.3
Percentage nitrogen	0.44-0.98	0.45-0.98	2.05-2.31	2.02-2.38	1.12-1.33
C/N	6-8	14-18	12-15	14-17	28-34
Index of Humidity	< 1.6	< 1.8	< 7.0	< 10.0	< 7.0

1. Limestone grassland sample site (1,825 ft., 556m.) Plate 1a

Located on an outcrop of Tyne Bottom Limestone, this site is near Moor House Field Station and between Moss Burn and Rough Sike, the well aerated soil has a relatively high pH (5.0-5.8) and both earthworms and moles are present. This typical Festuca-Agrostis grassland has a vegetation mat about three centimetres thick which is kept close cropped by sheep. The vegetation is:-

Dominant

Festuca ovina, Agrostis tenuis.

Abundant

Agrostis canina, Thymus drucei, Polytrichum commune, Potentilla repens.

Plate 1a. The Limestone grassland site, looking north with Moss Burn directly in front. Scale x 1/30.

Plate 1b. The *Nardus* grassland and Mixed moor sample sites. The *Nardus* site is in the foreground, with the Mixed moor site slightly above and behind. The view is taken looking north-east. Scale x 1/30.

Plate 1a

Plate 1b

Others

Selaginella selaginoides, Anthoxanthum odoratum, Galium hercynicum, Euphrasia confusa, Rumex acetosilla, Luzula campestris, Achillea millefolium, Carex caryophylla, Veronica officinalis, Cirsium arvense, Cerastium vulgatum, Cardamine pratense, Prunella vulgaris, Viola riviniana, V. lutea, Alchemilla vestita.

Mosses

Rhacomitrium lanuginosum, Mnium undulatum, M. punctatum.

2. Nardus grassland site (1,975 ft., 602m.) Plate 1b

This is an imperfectly drained peaty alluvium, upstream from Moor House on the east bank of Rough Sike. The site is occasionally flooded by the nearby stream when in spate. There is a thick vegetation mat with Nardus stricta the dominant grass. The litter layer is about 3 cm. thick and composed principally of the remains of N. stricta and Galium saxatile. Other species present are:- Deschampsia flexuosa, Juncus squarrosus, J. effusus, Agrostis canina, Potentilla erecta, Anthoxanthum odoratum, Luzula campestris, Rumex acetosa, Polytrichum commune, Viola riviniana.

3. Juncus squarrosus moor site (1,800 ft., 549m.) Plate 2a

This is an area of shallow peat on a south-east facing slope below a hill covered with blanket bog and Calluna moor. The site has poor drainage but there is considerable run off. Juncus squarrosus and Festuca ovina are dominant. Other species are: Agrostis tenuis, A. canina, Deschampsia

Fig. 2a. The Juncus squarrosus moor sample site, looking north, at Dodgen Pot. The sample area lies between the dark Calluna moor in the background and the tall Juncus effusus in the foreground. The area is a moor edge zone, on shallow peat with poor drainage. Scale x 1/40.

Plate 2b. The Bare peat sample site at Moss Flats looking south-west. The samples were taken from the flat peat surface between the Calluna covered residual hummocks. Scale x 1/40.

Plate 2a

Plate 2b

flexuosa, Galium saxatile, Nardus stricta, Potentilla erecta, Sphagnum spp., Polytrichum commune, Lophocolea bidentata.

4. Mixed moor sample site (1,980 ft., 604m.) Plate 1b

This site is situated on the east bank of Rough Sike, above the Nardus site. The site has typical blanket bog vegetation with Calluna vulgaris dominant, other species are: Eriophorum vaginatum, E. angustifolium, Vaccinium myrtilis, Empetrum nigrum, Rubus chamaemorus, Sphagnum spp., Cladonia sylvatica, C. impexa, C. uncialis.

5. Bare peat sample site (2,075 ft., 633m.) Plate 2b

This is an area of eroded peat near the head of Rough Sike. The peat has been denuded and re-distributed over the wind swept surface. It was from these flat areas of eroded peat that the samples were taken.

The Climate at Moor House

Introduction

Situated as it is in the upland of England, a severe climate at Moor House is to be expected. It is characteristically cold and wet and Pearsall (1950) has shown it to be typical of the montane zone of Great Britain. The summary of climatic data for 1953-1963 and the monthly means for 1962 and 1963 are given in Table 2. Daily meteorological readings have been taken at Moor House since 1953 and these are referred to in the present work.

Table 2

Summary of meteorological data for Moor House
1962 and 1963 and 13 year mean 1953-1965

	1962	1963	13 year mean 1953-65
Annual rainfall inches	77	74	74
No. of days on which rain fell	251	266	247
Potential evaporation inches	15.3	17.7	18.4 (1957-65)
Mean maximum temperature °C	7.5	7.2	8.4
Mean minimum temperature °C	1.1	1.0	1.9
Mean daily temperature °C	4.3	4.2	5.1
Snow cover (days)	79	96	62
Ground frost (days)	205	179	186
Average daily sunshine (hours)	2.9	3.1	3.2
Average earth temperature 1 ft. at 09.00 hr. G.M.T. °C	5.5	5.6	6.2

Temperature

The mean monthly temperatures for 1962 and 1963 are shown in Fig. 2. Snow may lie until May and there is no month in which frost may not occur. During 1962-1963 the highest monthly mean temperatures were 8.3°C. (46.9°F.) August 1962 and 11.8°C. (53.2°F.) July 1963. The coldest monthly means were -1.4°C. (29.5°F.) in March 1962 and -5.3°C. (22.5°F.) in February 1963. The winter of 1962-63 was extraordinarily severe, even for Moor House.

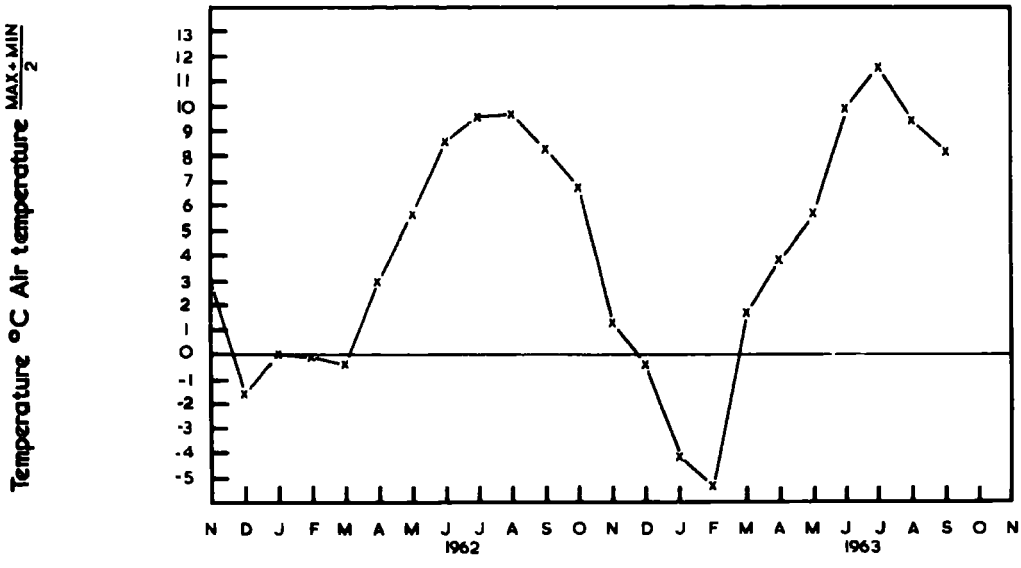
Precipitation and Evaporation

The amount of water in the soil is of prime importance to enchytraeids and the ratio of precipitation to evaporation gives an indication of this. The mean annual precipitation (10 years) is 74.8 inches and the mean potential evaporation rate is 17 inches. Thus the mean annual precipitation to evaporation ratio (P/E) is 4.41, that is, the soil is gaining more than four times as much water from the atmosphere as it is losing to it by evaporation. However, on occasions the P/E ratio drops below unity, in 1959 the P/E ratio was less than unity in three months, May P/E: 0.4, August P/E: 0.5, September P/E: 0.5. In 1962 and 1963 none of the monthly mean P/E ratios were below unity. The lowest values were June 1962 P/E = 1.1 and July 1963 P/E: 1.5, the latter figure includes 11 successive days on which the evaporation exceeded the rainfall. The monthly P/E ratios for 1962 and 1963 are shown in Table 3. In addition to the meteorological data on

precipitation and evaporation, the water content of the soil was measured at the time of sampling. An additional five cores were taken each month for index of humidity determination. The index of humidity of the soil is defined after Banage (1960) as the ratio of the weight of water to the dry weight after drying at 105°C. to constant weight. The indices of humidity for the soil sites for each month are shown in Table 4.

Fig. 2. Mean $\left(\frac{\text{Maximum + minimum}}{2}\right)$ monthly temperatures at Moor House for 1962 and 1963. Air temperatures and the temperatures of the earth at a depth of 1 foot are taken from the Moor House Meteorological Summaries for 1962 and 1963.

MEAN MONTHLY FIELD TEMPERATURES AT MOORHOUSE



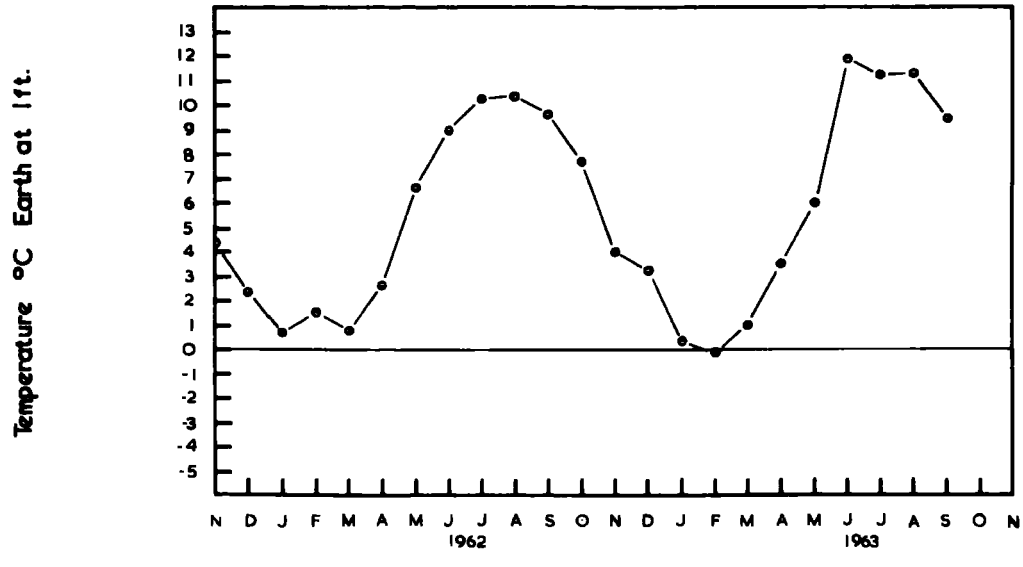


Table 3

Monthly ratio, precipitation: potential evaporation for 1962 and 1963

Figures in brackets indicate that the potential evaporation was partly estimated for that month. In January, February, March and December 1963 precipitation fell as snow and was not measured.

	1962	1963
January	(79)	-
February	(9.3)	-
March	(2.3)	-
April	(4.7)	(3.6)
May	2.7	2.0
June	(1.1)	2.4
July	(2.3)	1.4
August	6.1	3.8
September	6.9	2.9
October	4.0	4.4
November	6.7	(1.6)
December	2.5	-

Table 4

Index of humidity of soil cores
from sample sites Nov. 1961 to Nov. 1963

	Juncus squarrosus moor		*Nardus* grassland		Mixed moor		
	0-3 cm.	3-6 cm.	0-3 cm.	3-6 cm.	0-3 cm.	3-6 cm.	6-9 c.m.
November 1961	6.5	6.2	3.4	2.8	8.2	8.6	9.7
December "	6.9	5.8	-	-	9.3	9.8	8.9
February 1962	6.4	5.5	3.1	2.9	7.1	7.4	8.3
April "	6.7	5.5	2.7	1.6	7.8	8.3	8.6
May "	6.9	5.4	3.1	1.7	7.9	8.6	8.5
June "	3.6	4.0	2.9	1.8	3.6	5.9	6.2
July "	7.1	5.0	2.0	1.3	6.0	8.9	9.1
August "	6.5	5.1	2.2	1.1	9.0	9.5	9.6
September "	6.0	5.9	2.3	1.4	5.9	7.1	9.2
October "	8.4	5.0	2.7	1.2	8.8	9.8	10.2
March 1963	-	-	2.9	2.1	-	-	-
April "	7.1	5.8	2.9	2.0	9.8	8.8	8.7
May "	6.9	5.9	2.7	2.2	6.1	7.3	8.2
June "	4.4	4.8	2.5	1.6	8.6	10.0	9.3
July "	6.1	5.4	2.9	1.8	3.8	6.2	6.8
August "	5.8	5.7	2.3	1.4	5.2	7.1	7.2
September "	7.2	5.8	2.9	1.9	6.5	8.2	8.5
October "	6.5	6.0	2.8	2.0	11.3	10.2	11.5
November "	6.3	5.9	3.1	2.1	9.2	9.1	10.2

Table 4 (Cont'd) Index of humidity of soil cores from sample sites Nov. 1961 to Nov. 1963

	Limestone grassland			Bare peat	
	0-3 cm.	3-6 cm.		0-3 cm.	3-6 cm.
November 1961	1.9	1.1	November 1961	4.5	6.7
April "	1.8	1.0	December "	5.2	7.0
June "	0.6	0.5	January 1962	8.1	6.9
July "	0.4	0.4	February "	5.0	6.0
August "	1.9	0.6	June "	3.2	5.7
September "	1.8	0.9	July "	4.2	7.0
October "	2.0	1.1	August "	5.6	7.2
March 1963	1.8	1.2	September "	5.4	7.1
April "	1.9	1.0	October "	6.2	7.1
May "	1.8	1.0	April 1963	5.8	6.9
June "	1.2	0.9	May "	4.3	6.1
July "	1.5	1.0	June "	2.9	5.6
August "	0.6	0.8	July "	3.8	5.9
September "	1.5	1.0	August "	5.6	6.4
October "	2.0	1.1	September "	6.2	7.1
November "	1.9	1.2	October "	6.0	6.9

II. SAMPLING AND EXTRACTION METHODS

SAMPLING AND EXTRACTION METHODS

Collection of the soil cores in the field

The soil cores taken for estimation of the enchytraeid population were all 3.5 cm. diameter and 10 cm^2. in surface area. They were cut with a steel cylinder 25 cm. high fitted with a removable steel cutting edge and a rod handle.

The sampler was screwed into the ground to a depth of 6 cm. The soil core was slipped out of the sampler onto a polythene sheet and cut into 1.5 cm. layers. Each of these sub-cores was wrapped in a small polythene bag and the bags stacked in order in an aluminium container. Fifteen cores were taken from each sample area at monthly intervals. This number of samples was chosen as being the lowest number necessary for adequate statistical analysis which provided a manageable number of worms for counting and identification.

Extraction methods

Much work has been done on the extraction of soil animals in the past 15 years. In particular, methods for the extraction of enchytraeids have been devised by Nielsen (1952) and O'Connor (1955). Nielsen's method involves the application of heat from below the soil core, the worms being driven upwards into cooled moist gravel, from which they are easily recoverable. O'Connor used a modified Baermann funnel in which the soil

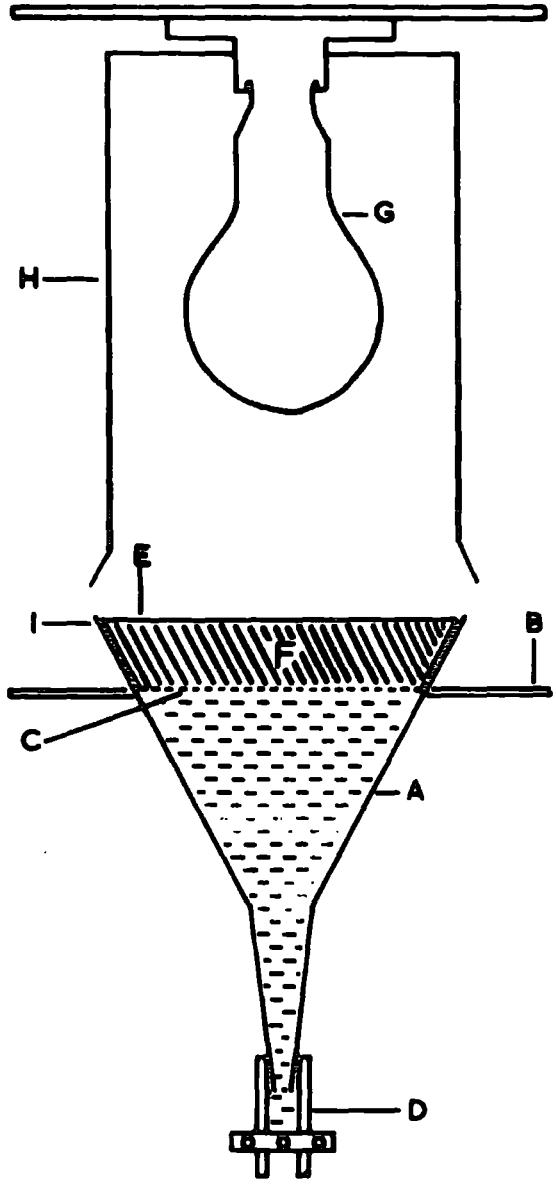
samples are submerged in a funnel filled with water and heat applied from above. The animals move away from the heat and sink through the water to the funnel base. Peachey (1959, 1963) has made a quantitative comparison of the two methods for moorland soils. He concluded that, taking into account the time factor involved and the condition of the worms after extraction, the wet funnel extractor was the most efficient for use on the sites at Moor House.

A battery of 30 extraction units, similar to those used by Peachey was used in this study. Fig. 3 is a diagrammatic representation of a single extraction unit. A is a polythene funnel 11 inches in diameter in a nine inch hole in an asbestos supporting board, B,C is a sieve with a gauze of 10 meshes/in. The funnel is filled with water, E and the sample, F placed on the gauze. The source of heat is a 60 watt bulb, G in a shade H, with a splayed lower edge I. The lower end of the funnel is closed with a screw clip D.

The lamps were wired in parallel and the current controlled by a Variac (variable induced current). The voltage through the lamps was raised twice during the extraction of two hours thirty minutes. Thirty minutes after the start of the extraction the voltage was raised from 60v. to 180v. and at 90 minutes from 180v. to 240v.

The development of a temperature gradient in the sample is shown in Fig. 4. The temperatures were measured by thermistors positioned as shown

Fig. 3. Diagrammatic representation of a single unit in the wet funnel extraction apparatus.



THE WET FUNNEL EXTRACTOR

Fig. 4. Graph of the temperatures recorded in a soil sample during extraction. The heating voltages are shown. The positions of the thermistors A-D are shown in Fig. 5.

Fig. 4.

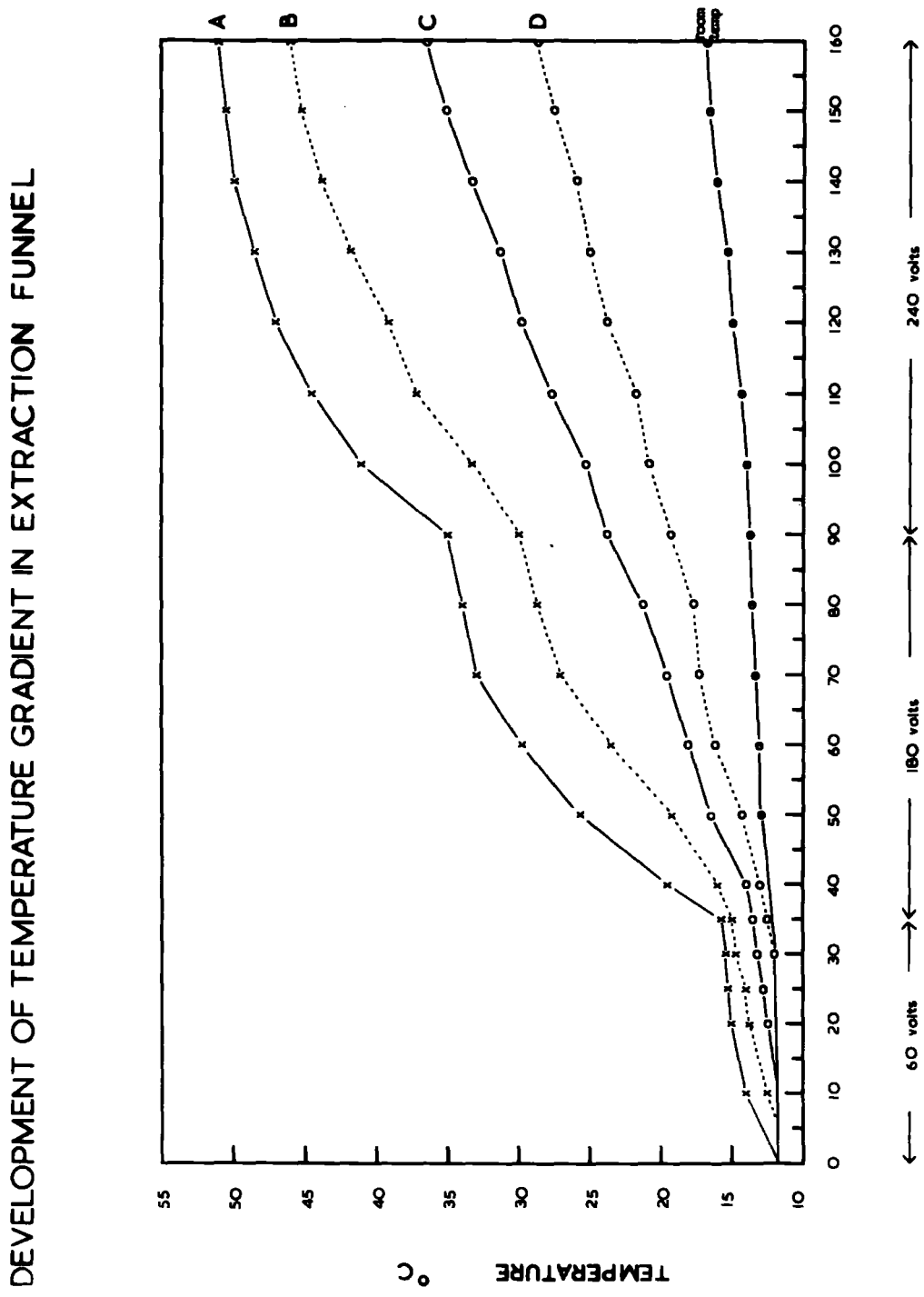
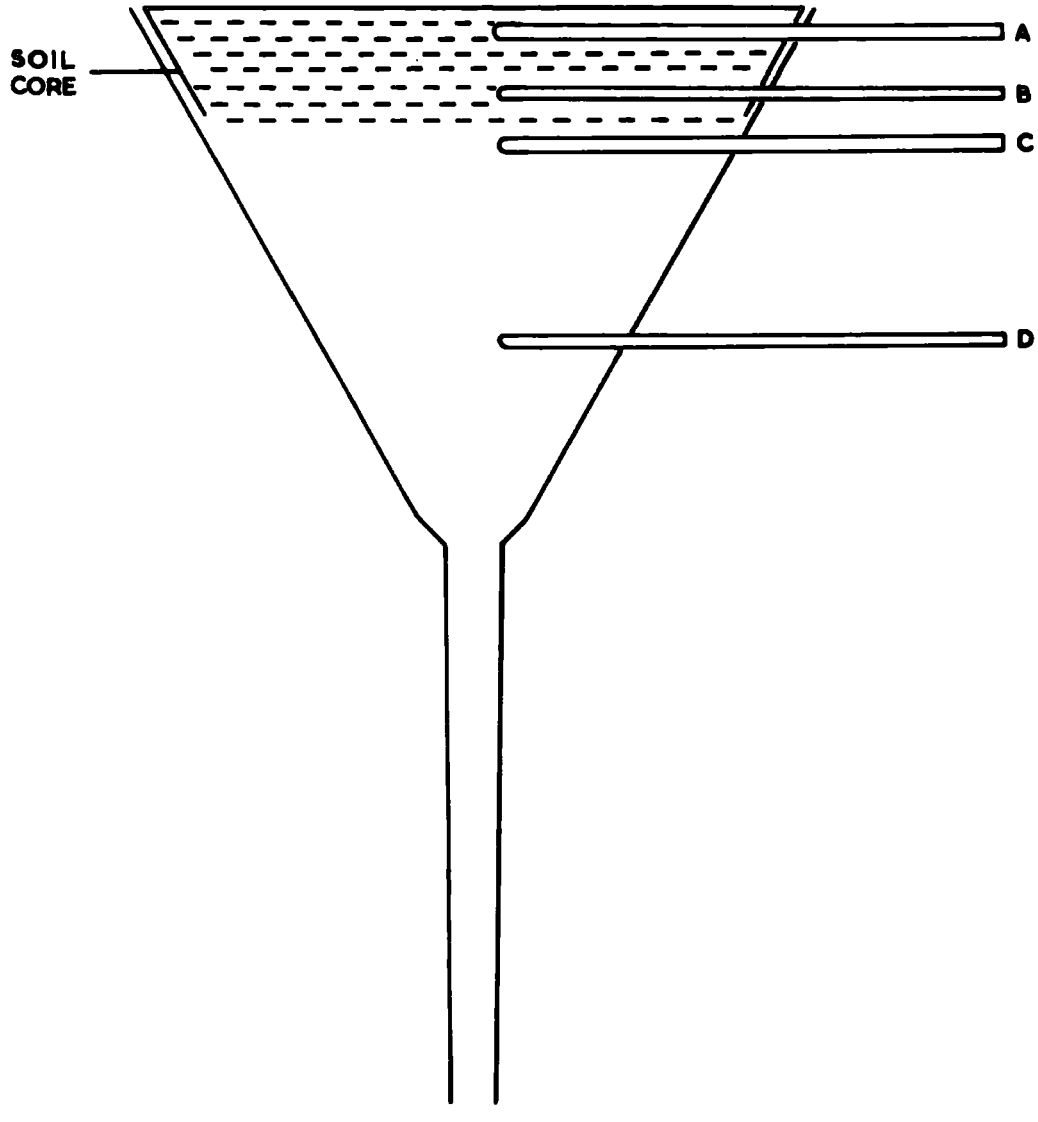

DEVELOPMENT OF TEMPERATURE GRADIENT IN EXTRACTION FUNNEL
TEMPERATURE °C
55
50
45
40
35
30
25
20
15
10
A
B
C
D
Room Temp
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
60 volts
180 volts
240 volts
TIME : MINUTES

Fig. 5. The positions of the four thermistors A, B, C, D, recording the temperatures in the wet funnel during extraction.

DIAGRAM TO SHOW THE POSITION OF THERMISTORS A B C D USED TO MEASURE THE DEVELOPMENT OF A TEMPERATURE GRADIENT IN THE EXTRACTION FUNNEL



in Fig. 5. It can be seen that between 70 and 90 minutes, and from 120 minutes to the end of the extraction (150 mins.) the temperature of the surface layer of the soil was fairly steady and sharp rises in the temperature followed the increase in voltage at 35 and at 90 minutes.

Treatment of the extracted worms

At the end of the extraction the screw clip at the base of the funnel was opened and about 90 ml. of water containing the extracted worms collected in a beaker. The worms were stored at 2°C. until they could be counted in a petri dish against a black background. They were identified alive in a film of water under a cover slip using Nielsen and Christensen's descriptions (1959 and 1961).

The emergence of worms during the extraction

To discover at what time during the extraction the worms emerge from the soil they were collected from the base of the funnel five times during the extraction. To prevent the level of water in the funnel from falling during this experiment water-filled ignition tubes were connected to the funnel stems below the screw clips. The screw clips were opened and the worms allowed to fall to the bottom of the ignition tubes. The screw clips were then closed and fresh ignition tubes full of water were fitted to the base of the funnels. Sets of cores from three of the five sample sites have been treated in this way, Mixed moor, Nardus grassland and Limestone grassland. Results have been obtained for each soil level and each of the

major species, they are shown as cumulative percentages indicating the rate at which worms were coming out of the sample during the extraction. Fig. 6, 7 and 8.

About a third of the worms come out of the soil as soon as it is placed in water, the majority emerge after the voltage has been increased for the second time. Few worms come out of the soil after the first two hours.

The worms move out of the mineral soils quickly, for example, from the Nardus and Limestone grassland layers below 3 cm. A high proportion of worms, 54 and 81 percent respectively, move out before the second voltage increase. This is in contrast to the organic layers (above 3 cm.) of these two sites where only 29 and 44 percent of the worms move out before the second increase in voltage.

If the first peak in the numbers of extracted worms is assumed to be the worms which are washed off the soil as soon as it is placed in water and the second peak to be those which are driven out by heat, then it is possible that the first peak represents worms which were moving about in the larger soil spaces and the second peak those which were in the less accessible places in the soil, e.g. inside rotting leaves and stems. If this is true it offers an explanation of why the first peak is higher in the mineral parts of the Nardus and Limestone grassland soils. The apparent contradiction in the high first peak in Mixed moor 0-1.5 cm. layer is explicable in that the surface of the Mixed moor sample is very often a

Fig. 6. The emergence of Enchytraeidae from Limestone grassland during the extraction process. The graphs show the cumulative percentage of total worms, and of total worms in each 1.5 cm. layer of the soil core. The cumulative percentage of five species is also shown. A. Cognettia sphagnetorum, B. C. cognettii, C. Marionina clavata, D. Achaeta spp., E. Fridericia spp. The heating voltages are indicated.

CUMULATIVE PERCENTAGE OF WORMS EXTRACTED IN 140 MINUTES FOR FOUR SOIL DEPTHS AND FIVE SPECIES : LIMESTONE GRASSLAND

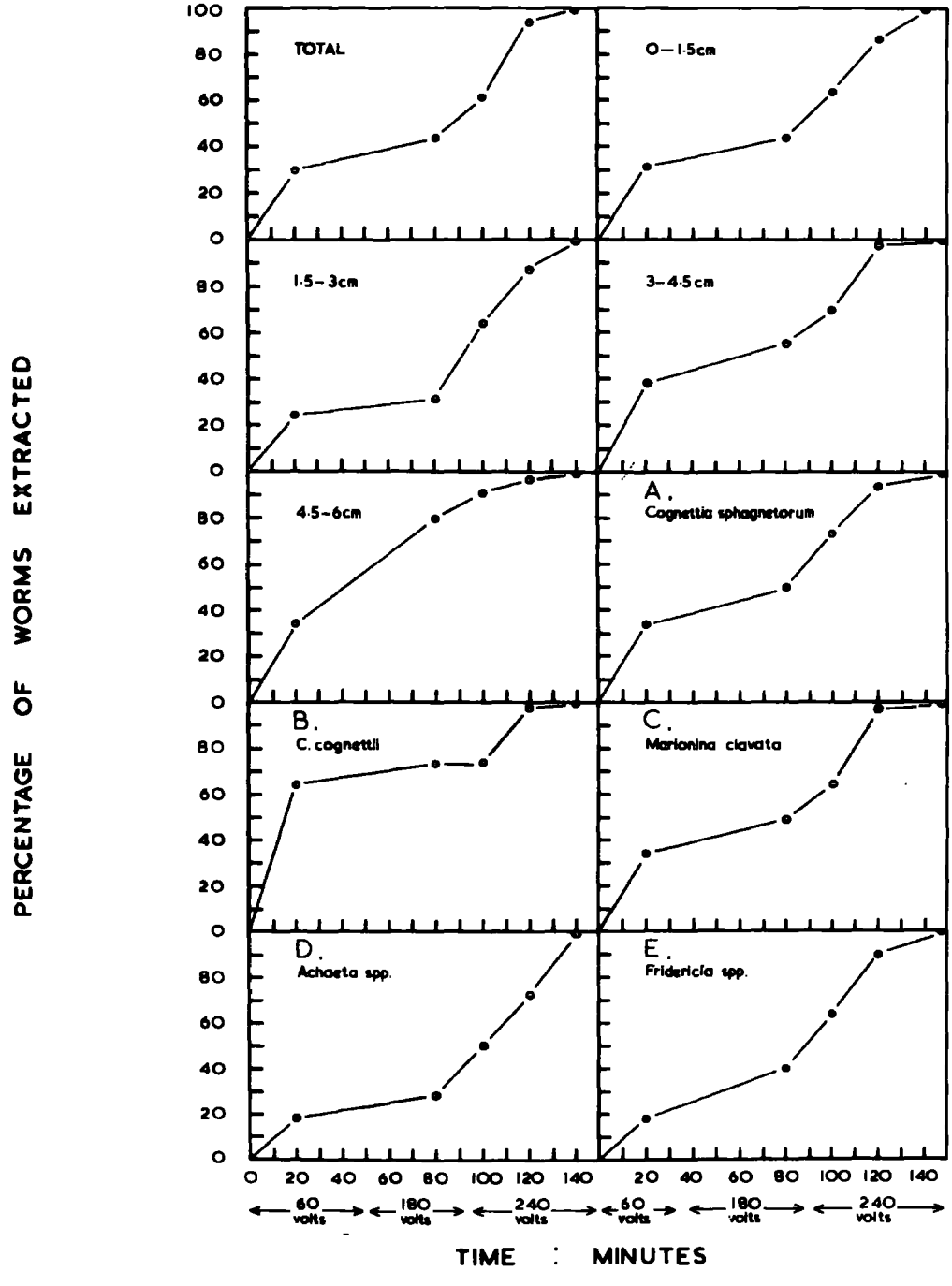


Fig. 7. The emergence of Enchytraeidae from Nardus stricta grassland during the extraction process. The graphs show the cumulative percentage of total worms, and of total worms in each 1.5 cm. layer of the soil core. The cumulative percentage of three species A. Cognettia sphagnetorum, B. Marionina clavata, C. Cognettia cognettii, is also shown.

CUMULATIVE PERCENTAGE OF WORMS EXTRACTED IN 140 MINUTES FOR FOUR SOIL DEPTHS AND THREE SPECIES : NARDUS GRASSLAND

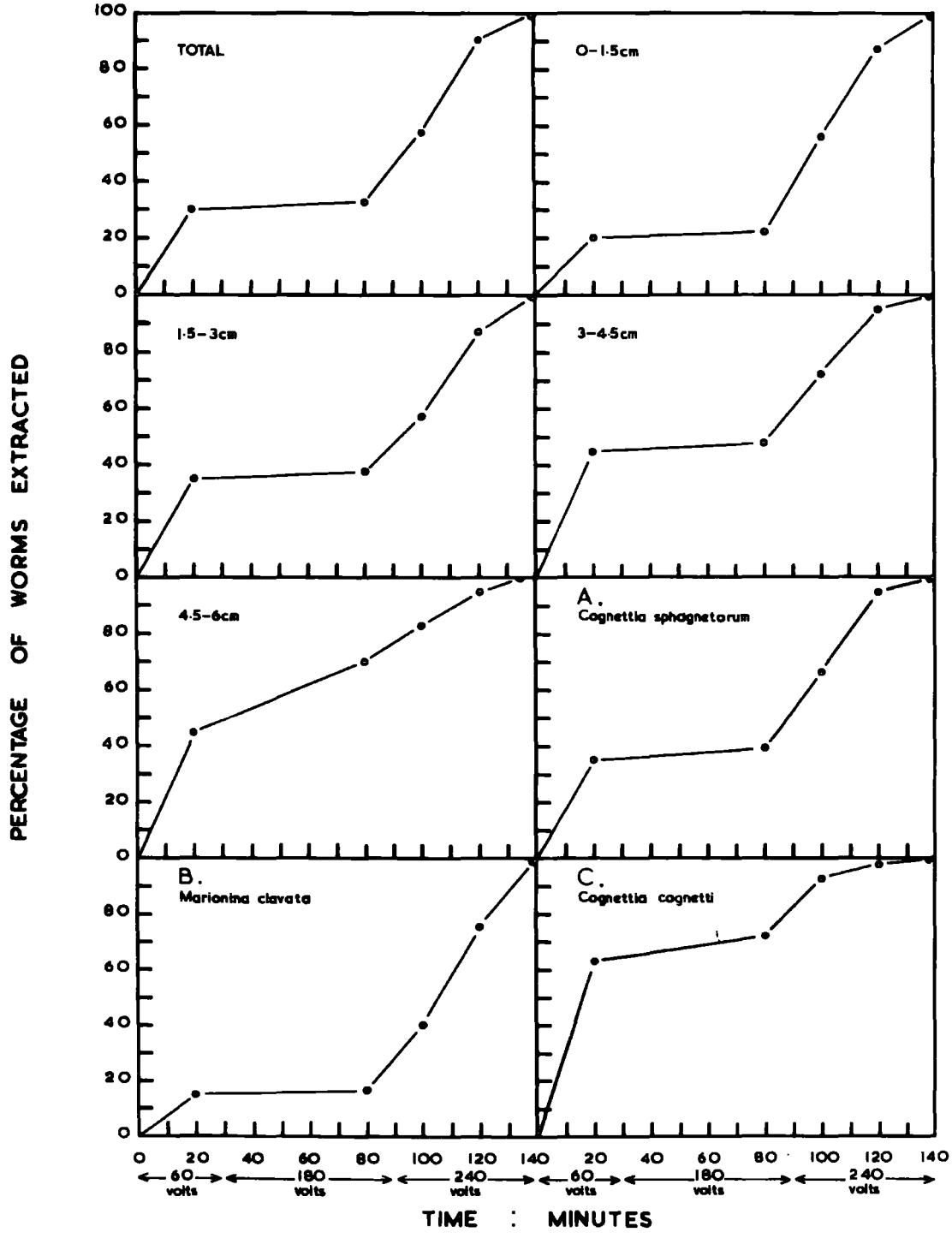
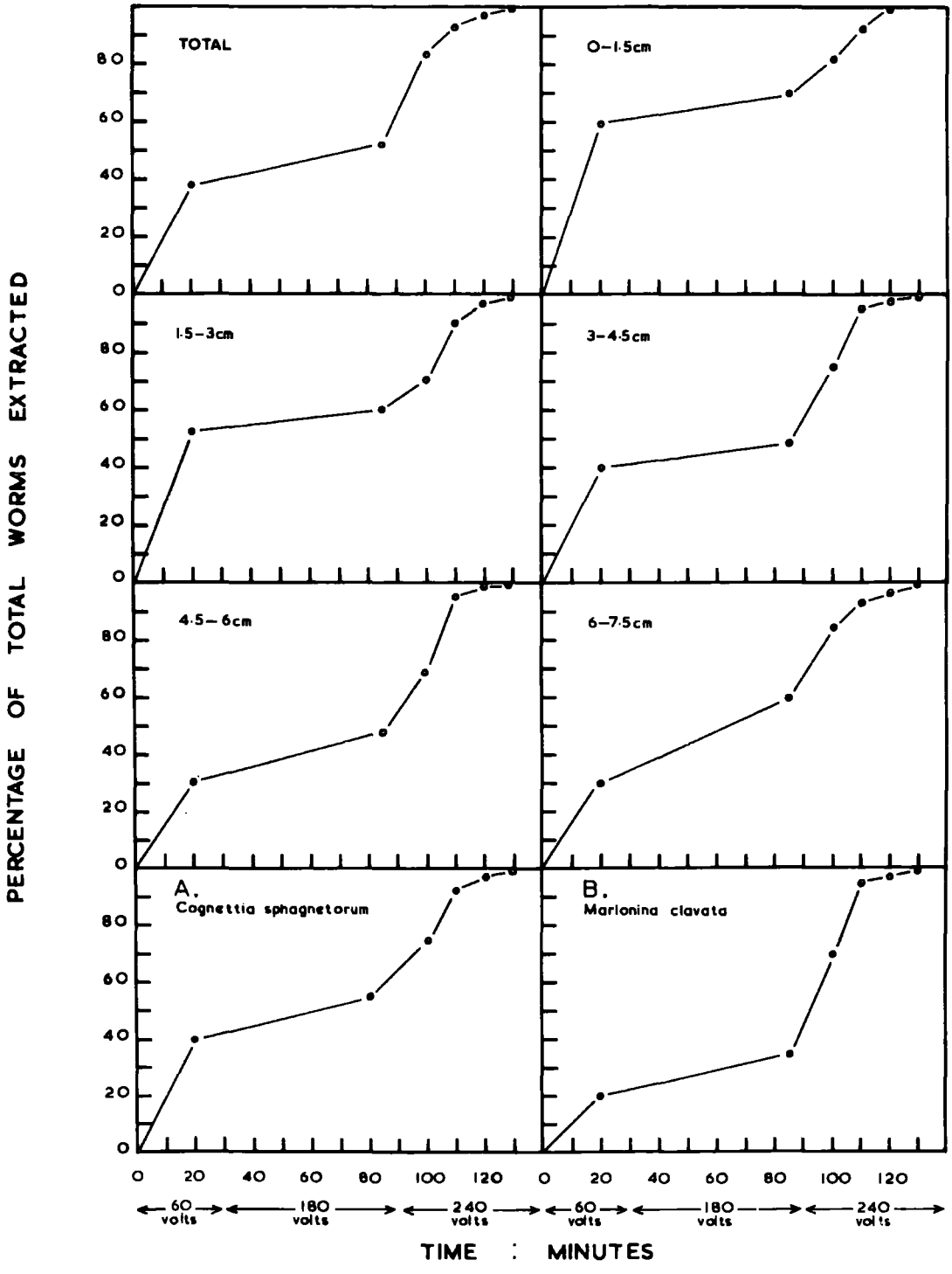


Fig. 8. The emergence of Enchytraeidae from Mixed moor during the extraction process. The graphs show the cumulative percentage of total worms, and of total worms in each 1.5 cm. layer of the soil core. The cumulative percentage of two species A. Cognettia sphagnetorum, B. Marionina clavata, is also shown. The heating voltages are indicated.

CUMULATIVE PERCENTAGE OF WORMS EXTRACTED IN 130 MINUTES FOR FIVE SOIL DEPTHS AND TWO SPECIES : MIXED MOOR



layer of fresh Sphagnum plants; in this site it would seem that the number of "hiding places" increases with depth.

On the basis of these observations some differences in the habitats of different species in the soil can be suggested. Marionina clavata Nielsen and Christenson 1961, Achaeta eiseni Vejdovsky 1877, A. affinis Nielsen and Christensen 1959, and Fridericia bisetosa (Levinsen) 1884 all tend to stay in the soil until driven out by heat, but Cognettia sphagnetorum (Vejdovsky) 1877 and C. cognettii (Issel) 1905 are mainly washed out in the first thirty minutes. A difference between M. clavata and C. sphagnetorum was seen in culture, where M. clavata burrowed into the leaf provided and C. sphagnetorum remained on the surface. The later emergence of Fridericia spp. and Achaeta spp. from the soil during the extraction is probably because these are stiff and slow moving animals.

III. TAXONOMY AND SPECIES DISTRIBUTION

TAXONOMY AND SPECIES DISTRIBUTION

In this section a check list of the Enchytraeidae of the Moor House reserve is given together with a key for the identification of worms from the five sample sites and some information on the species distribution on the reserve. During this work 20 species have been collected including four which are new to the British Isles. One species new to science has been described by the author.

A list of the species of Enchytraeidae found at Moor House.

Fridericia bisetosa (Levinsen) 1884

F. paroniana Issel 1904

F. maculata Issel 1905

F. galba (Hoffmeister) 1843

F. magna Friend 1899

F. striata (Levinsen) 1884

Mesenchytraeus armatius (Levinsen) 1884

M. flavus (Levinsen) 1884

M. glandulosus (Levinsen) 1884

M. sanguineus Nielsen and Christensen 1959

Enchytraeus buchholzi Vejdovsky 1879

Achaeta eiseni Vejdovsky 1877

A. affinis Nielsen and Christensen 1959

Cognettia cognettii (Issel) 1905

C. glandulosa (Michaelsen) 1888

C. sphagnetorum (Vejdovsky) 1877

Marionina clavata Nielsen and Christensen 1961

M. filiformis Nielsen and Christensen 1959

Henlea perpusilla Friend 1911

Cernosvitoviella briganta sp. nov

Of these 20 species three are new records for the British Isles, these being:

Achaeta affinis

Marionina clavata

M. filiformis

A species of Cernosvitoviella Nielsen and Christensen 1959, closely allied to C. atrata (Bretscher) 1903, Nielsen and Christensen 1959, was found by Nielsen and Christensen 1959 in a collection of Moor House enchytraeids sent by J. Peachey. Nielsen and Christensen did not describe the species because of lack of material. I have examined several hundred mature individuals of this species which is described below.

Cernosvitoviella briganta

Small species, 4-8 mm, segments 28-34. Colour white or intensely white. Setae 5, 6, 7, 8 9 - 5, 6, 7 8 : 5, 6, 7 - 5, 6, 7. Head pore near the tip of O. clitellum XII-XIII, glands arranged in transverse rows.

Brain concave in front deeply incised behind. Two pairs of primary septal glands, sometimes with a narrow dorsal connection, and two pairs of secondary glands. Lymphocytes spindle shaped, occasionally oval. Some lymphocytes are more elongate, as long or longer than the setae and are opaque in transmitted light. The post septal portion of the nephridium elongate, merging into the terminal efferent duct. Dorsal blood vessel originating in XIII; blood colourless or faintly red. Seminal vescicle absent. Sperm funnel small and funnel shaped, junction with the sperm duct fairly distinct, small separate glands at male pore. One or two mature eggs present at a time. The ectal duct of the spermatheca with a thick wall, no glands at the ectal orifice. The ampulla elongate extending into VII or occasionally VIII and without a distinct sperm containing lumen. (Fig. 9)

Fig. 9. A diagrammatic lateral view of Cĕrnosvitoviella briganta n.sp. showing the spermatheca extending into segment VII.

CERNOSVITOVIELLA BRIGANTA n. sp.

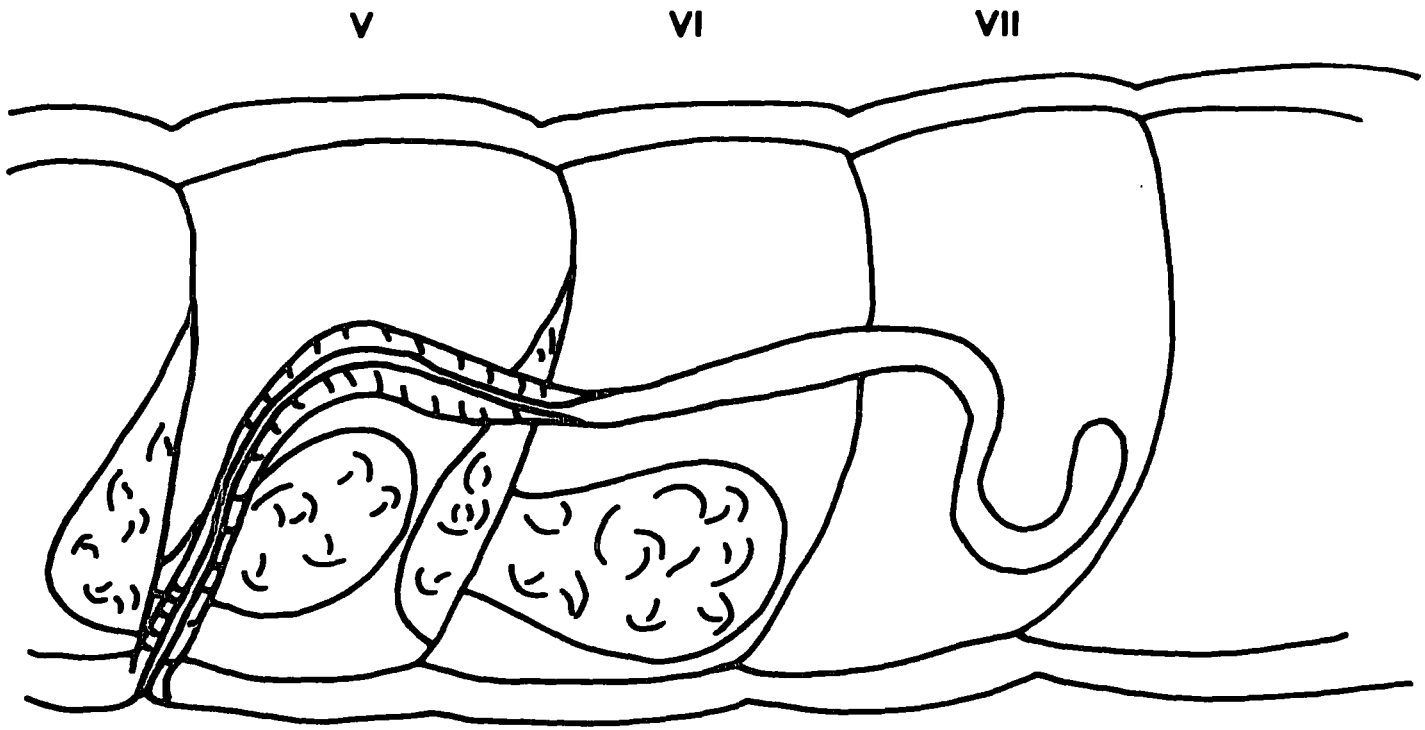


Fig. 9.

LATERAL VIEW SHOWING SPERMATHECA EXTENDING INTO SEGMENT VII

A key for the identification of Enchytraeidae from the five sampling sites used at Moor House.

1. Setae present	2.
Setae absent	Achaeta eiseni A. affinis
2. Setae straight	3.
Setae sigmoid	8.
3. Salivary glands present	4.
Salivary glands absent	5.
4. Setae in pairs with shortest in the centre, and/or loose setae in coelom, dorsal pores present	15. Fridericia
Setae not in pairs, all the same length within the bundle	Enchytraeus buchholzi
5. Two setae per bundle	6.
More than two setae per bundle	7.
6. Worm 7-12 mm. long numerous lymphocytes not dark in transmitted light	Marionina clavata
Worm 4-7 mm. long few large lymphocytes dark in transmitted light. Thin active worm.	M. filiformis
7. Dorsal vessel origin in seg. 8, heart-like expansions in 7 and 8, Lymphocytes all alike and disc shaped	Henlea perpusilla
8. Seta without nodule	9
Seta with nodule	11.
9. Primary septal glands only	Cognettia sphagnetorum
Primary and secondary septal glands	10.

10. Septal glands not fused dorsally — *C. glandulosa*

    Septal glands fused dorsally enlarged setae in segs. 3-5 — *C. cognettii*

11. Small worms less than 8 mm. long few lymphocytes dark in transmitted light. Thin active worm — *Cernosvitoviella briganta*

    Large thick worm lymphocytes small and densely packed — 12. *Mesenchytraeus*

12. Blood red, worm pink — *M. sanguineus*

    Blood colourless, worm yellow — 13.

13. More than five pairs of septal glands — *M. glandulosus*

    Not more than five pairs of septal glands — 14.

14. Enlarged setae in lateral bundles of segs. 5-7 — *M. armatus*

    No enlarged setae in segs. 5-7 — *M. flavus*

15. Fridericia species can only be separated on mature characteristics, too complicated for the present key. However, some divisions can be made using immature characters.

    2-4 setae per bundle, loose seta in the coelom — *F. bisetosa* / *F. paroniana*

    As above with greenish irridescence and red blood — *F. magna*

    4-8 setae per bundle, usually 6 few detached seta in coelom — *F. galba*

QUALITATIVE SURVEY OF SPECIES DISTRIBUTION

In addition to routine sampling for the estimation of enchytraeid densities, samples of soil were taken from several sites on the reserve. These were extracted and the mature worms in the samples identified. This was done during the summer of 1962. The sites included four soils occurring on limestone outcrops, three on alluvial deposits and three on blanket peat. A list of the species found at Moor House and the sites where they occur is given in Table 5. Differences between genera occur, Cernosvitoviella briganta was found only on peat soils or on mineral soils receiving downwash from blanket peat. Achaeta spp. were found only in soils containing mineral particles, and Fridericia spp. mainly on the limestone soils. The soils on the limestone outcrops have the highest number of species, 16, and the areas of blanket peat the lowest, one species only.

Table 5

Qualitative distribution from small samples

taken from several sites August 1962

Name of species	Limestone grassland (sample site)	Grassland and Limestone crop Knock Fell	Meadow	Alluvial Festuca grassland	Rush and Sphagnum flush from Knock Fell Limestone	Alluvial Nardus (sample site)	Moss burn gravel	Bog weir alluvial Nardus	Bare peat (sample site)	Valley bog Sphagnum	Mixed moor (sample site)	Juncus squarrosus (sample site)	Stream edge moss (Rough Sike)
1. Fridericia bisetosa	+	+	+	+									
2. F. paroniana	+	+	+										
3. F. striata	+	+	+										
4. F. galba	+	+	+										
5. F. magna	+	+	+										
6. Mesenchytraeus sanguineus					+	+		+		+	+	+	+
7. M. glandulosus	+		+									+	
8. M. flavus		+	+	+								+	
9. M. armatus	+		+										
10. Enchytraeus buchholzi	+	+	+										
11. Achaeta eiseni	+	+	+	+		+							
12. A. affinis	+	+	+	+		+							
13. Cognettia sphagnetorum	+	+	+	+	+	+	+	+	+	+	+	+	+
14. C. glandulosa	+	+	+	+	+	+					+	+	
15. C. cognettii	+	+	+	+	+	+						+	
16. Marionina clavata	+	+	+		+	+		+		+	+	+	
17. M. filiformis						+						+	
18. Henlea perpusilla	+		+										
19. Cernosvitoviella briganta						+		+		+	+	+	+
Total number of species	15	13	16	7	5	9	1	4	1	4	5	9	3

IV. HORIZONTAL DISTRIBUTION

HORIZONTAL DISTRIBUTION

Introduction

Animals are very rarely randomly distributed in the soil. Populations are patchy, with areas of relatively high density termed aggregations. Several workers have observed aggregated distributions in soil animals. Nielsen (1954), O'Connor (1957) and Peachey (1963) working on Enchytraeidae, Nielsen (1948) and Banage (1960) on Nematoda, Satchell (1955) on Lumbricidae, and Block (unpub.), Edwards (1955), Haarlov (1960), Hale (unpub.), Hughes (1962), Macfadyen (1952, 1963a), Poole (1961), all working on soil micro-arthropods. Elton (1949) has pointed out that this patchiness in distribution is to be expected and reflects the heterogeneity of the soil habitat.

There are three methods available for the study of aggregations in soil animals:

i) Complete enumeration of all animals to a known depth, followed by mapping of their positions.

ii) Use of the tie-line method to estimate the mean radius and number of animal aggregations. In this method paired samples are taken, the first randomly and the second a fixed distance away from it.

iii) The analysis of results of random sampling.

Where the random samples taken are all of the same size the presence of aggregations can be detected, but their size cannot be evaluated, and

this is the situation in the present work. Greig-Smith (1952) has emphasised the importance of the size of the sample unit in studying aggregations. Any one unit may contain more than one aggregation, only part of one, or none. Therefore for any given population there is an optimum sample size for detecting aggregations. When aggregations are detected by the analysis of random sampling data it is a real phenomenon. However, failure to detect aggregation may be the result of the sample size and does not necessarily mean that the population is randomly distributed. In the present work the horizontal distribution of Enchytraeidae has been studied by analysing the data from random sampling in two ways:

i) Using the Frequency Distribution

ii) Using the Coefficient of Dispersion

i) Detection of aggregation by using the Frequency Distribution

The frequency distribution of the sample unit values were compared with a normal distribution. The sample unit values were grouped into frequency distributions round their individual means with multiples of the standard deviation as class boundaries. Table 6 shows the results for total enchytraeids at the five sites. There is a skew in all cases with an excess of small negative deviates and of large positive deviates, and a marked asymetry in the (-1) and (+1) classes. This indicates that the enchytraeids are over-dispersed with regard to a random distribution. The same type of aggregations, using these tests and others have been found for Enchytraeidae by Nielsen (1954), O'Connor (1957), and Peachey (1959).

Table 6

Frequency distribution of the sample unit values about the mean of total Enchytraeidae

Limestone Grassland 1961-63

Standard deviation classes	Deviations from mean in standard deviations									
	-4	-3	-2	-1	0	+1	+2	+3	+4	+5
Date										
6.11.61				4	6	2	2	1		
20.4.62				3	6	4	2			
6.6.62				1	4	5	3	2		
4.7.62				3	7	2	2	1		
7.8.62				2	6	4	2	1		
19.9.62			1	1	4	2	3	3	1	
13.3.63				3	4	5	3			
5.4.63				1	8	4	1	1		
2.5.63			3	3	4	1	2	2		
2.6.63				2	4	3	5	1		
7.7.63				1	6	1	5	2		
27.7.63				2	6	2	4	1		
3.9.63			2	2	6	2	0	3		
4.10.63				2	7	3	3			
13.11.63				1	5	1	2	3	2	1
Total (observed)			6	31	83	41	39	21	3	1
									25	
Total (Expected Normal)			5	31	76	76	31	5		
X^2			0.20	0	0.14	16.11	3.06		80.00	

Total X^2 = 98.51 d.f. = 5 $P < 0.001$

Table 6 (Cont'd)

Frequency distribution of the sample unit values about the mean of total Enchytraeidae

Nardus stricta grassland 1961-63

Standard deviation classes	Deviations from mean in standard deviations								
	-4	-3	-2	-1	0	+1	+2	+3	+4
Date									
20.11.61				4	4	4	3		
13.2.62					8	6	1		
17.5.62				3	4	4	4		
12.6.62				2	5	6	2		
17.7.62				1	8	4	2		
7.8.62			1	3	4	5	2		
31.8.62				1	7	4	2	1	
3.10.62				4	3	5	3		
13.3.63				3	7	3	3		
5.4.63				2	6	4	2	1	
2.5.63				1	8	4	2		
2.6.63			1	2	3	5	1	1	
7.7.63				2	6	0	3	1	2
27.7.63					2	4	4	3	2
3.9.63			1	2	6	3	0	2	1
14.10.63				3	7	4	1	1	
12.11.63					9	3	3		
Total (observed)			3	33	97	67	36	10	5
								15	
Total (Expected Normal)			6	35	87	87	35	6	
X^2		0.67	0.19	1.15	4.60	0.29		13.50	

Total X^2 = 30.40 d.f. = 5 P < 0.01

Table 6 (Cont'd)

Frequency distribution of the sample unit values about the mean of total Enchytraeidae

Juncus squarrosus 1961-63

Standard deviation classes	Deviations from mean in standard deviations								
	-4	-3	-2	-1	0	+1	+2	+3	+4
Date									
6.11.61				4	3	5	3		
5.12.61			1	2	5	4	2	1	
13.2.62				3	4	4	3	1	
20.4.62			1	2	6	3	2	1	
7.5.62				2	6	2	2	1	
12.6.62				1	7	5	2		
17.7.62				3	6	3	3		
20.8.62				2	7	3	3		
19.9.62				2	4	6	3		
8.10.62				3	6	3	3		
5.4.63			1	1	2	6	5		
2.5.63					10	2	2	1	
6.6.63					9	3	2	1	
7.7.63				3	5	4	3		
27.7.63			2	1	4	4	4		
3.9.63				2	8	1	3	1	
14.10.63				4	4	4	3		
11.11.63				2	6	2	3	2	
Total (observed)			5	37	105	64	51	9	
Total (Expected Normal)			6	37	92	92	37	6	
X^2			0.17	0.	1.72	8.52	5.89	0.67	

Total X^2 = 16.97 d.f. = 5 P < 0.01

Table 6 (Cont'd)

Frequency distribution of the sample unit values about the mean of total Enchytraeidae

Mixed moor 1961-63

Standard deviation classes	Deviations from mean in standard deviations										
	-4	-3	-2	-1	0	+1	+2	+3	+4		
Date											
30.10.61				3	5	6	1				
5.12.61	1	1		5	6	2					
13.2.62			1	7	2	3	1	1			
14.5.62			3	6	3	4					
12.6.62			1	7	3	3	1				
17.7.62			2	7	3	3					
7.8.62			3	5	5	2					
31.8.62			2	6	2	1	2	2			
3.10.62			1	7	3	4					
5.4.63			3	4	5	1	2				
2.5.63			4	6	4		1				
2.6.63				14				1			
7.7.63			5	5	2	2	1				
27.7.63			4	5	3	2	1			+7	+8
3.9.63	2	4	3	1	2	1				1	1
14.10.63			8	3	2	1					
12.11.63			3	6	1	2	1	2			
Total (observed)	3	6	43	97	50	37	11	6		1	1
	9								19		
Total (Expected Normal)		6	35	87	87	35	6				
χ^2	1.50		1.43	1.15	15.72	0.18	28.10				

Total χ^2 = 48.13 d.f. = 5 P < 0.001

Table 6 (Cont'd)

Frequency distribution of the sample unit values about the mean of total Enchytraeidae

Bare peat 1961-63

Standard deviation classes	Deviations from mean in standard deviations								
	-4	-3	-2	-1	0	+1	+2	+3	+4
Date									
30.10.61		1	3	6	3	1	1		
11.12.61			2	3	6	3			
31 1.62				13	1				1
13.2.62		1	1	8	2	1	2		
4.6.62			2	7	3	2			
4.7.62			4	3	5	3			
7.8.62			3	3	7	2			
31.8.62			2	6	4	3			
3.10.62			2	7	3	3			
5.4.63				10	2	2	1		
2.5.63			4	6	3	2			
2.6.63			1	9	3	2			
7.7.63			3	4	5	1	2		
27.7.63			2	8	3	2			
3,9.63			3	4	5	1	1		
14.10.63			1	7	5		2		
Total (observed)		2	33	104	60	28	9	1	
								10	
Total (Expected Normal)		5	33	82	82	33		5	
X^2		1.80	0.	5.90		0.79		5.00	

Total X^2 = 13.49 d.f. = 5 P < 0.01

ii) The detection of aggregation by the Coefficient of Dispersion

The coefficient of dispersion, originally attributed to Fisher and used by Salt and Hollick (1946) in their analysis of wire worm populations is used to detect aggregations of animals. It is the ratio of the variance to the mean:

$$C.D. = \frac{(x - \bar{x})^2}{\bar{x}(n-1)}$$

$$= \frac{s^2}{\bar{x}} = \frac{\text{variance}}{\text{mean}}$$

where x is the number in each sample and n is the number of sample units. When this ratio is less than one there is under-dispersion with respect to a random population. When the ratio is unity there is a random dispersion, and when it is more than one there is aggregation or over-dispersion. Random dispersion shows a Poisson distribution and has a variance equal to the mean. The divergence from unity is regarded as being significant if it exceeds:

$$1 \mp 2\sqrt{\frac{2n}{(n-1)^2}}$$ when n = number of sample units.

For 15 sample units the value is 1 ± 0.783, i.e. lower than 0.21 and larger than 1.78.

The coefficient of dispersion has been calculated for total Enchytraeidae and for each of the major species, and their age groups, at the five sites. As only one sample size was used throughout this work, ratios of variance to mean not significantly different from unity do not

Table 7

Coefficient of dispersion for total Enchytraeidae for each site

	Juncus squarrosus moor	Nardus stricta grassland	Limestone grassland	Mixed Moor	Bare peat
November 1961	12.25	22.86	8.40	10.00	1.77
December "	6.52	-	-	1.09*	2.11
January 1962				-	3.38
February "	7.21	8.35		4.96	4.18
April "	8.00	14.91	1.54*	-	-
May "	4.36	11.47	12.52	11.12	-
June "	13.37	11.32	13.88	3.75	5.17
July "	30.00	3.13	17.10	10.56	1.68*
August "	13.27	10.79	2.15	1.25*	1.21*
September "	16.03	18.42	4.83	0.67*	3.99
October "	15.60	6.72	-	8.49	2.29
March 1963	-	9.71	4.68	-	-
April "	6.13	8.72	5.33	7.86	1.35*
May "	21.84	5.22	6.74	5.38	1.42*
June "	32.42	26.72	5.93	10.14	2.01
July "	17.54	14.56	11.95	2.38	2.50
August "	10.16	15.69	14.54	97.37	1.83
September "	17.15	10.69	23.14	13.88	2.06
October "	23.06	28.28	30.83	15.17	2.49
November "	15.17	14.62	8.12	27.00	-

The values of the coefficient of dispersion not significantly different from unity are marked *

Table 8

Coefficient of dispersion for each species and age group

Juncus squarrosus moor

	Marionina clavata				*Cernosvitoviella briganta*					*Cognettia sphagnetorum*		
	Total	Mature	Juv.	Non mature	Total	Mature	Juv.	Non mature		Total	Whole worms	Regenerating fragments
Nov. 1961	5.23	2.62		4.63	9.21	10.25		1.06	Nov.	5.12	2.35	3.42
Dec.	10.91	1.82		9.57	4.94	5.83		0.67*	Dec.	20.41	2.17	0.89*
Sept. 1962	8.89	2.11		8.92	4.31	3.47		4.44	Feb.	6.60	5.35	3.20
Apl.	12.37	5.61		8.73	3.97	3.49		2.34	Apl.	14.95	4.65	8.31
May	4.27	1.23*	0.81*	5.11	3.10	0.77*		3.51	May	5.15	10.71	4.61
June	5.54	0.78*	7.16	4.76	6.18	1.87	6.26	1.34*	June	13.92	20.47	4.62
July	4.62	2.59	9.43	3.12	15.97	1.43*	0.46	19.18	July	22.99	6.14	2.98
Aug.	3.21	1.99	2.10	2.11	3.77	3.61		1.30*	Aug.	7.05	4.97	2.07
Sept.	2.14	1.33*	2.32	3.14	20.83	13.36	10.46	2.26	Sept.	6.67	3.35	2.22
Oct.	7.59	4.16	1.56*	5.61	4.73	3.46		3.52	Oct.	4.92	23.18	1.77
Apl. 1963	1.38*	1.77		2.10	1.48*	1.33*		0.80*	Apl.	5.82	9.75	1.66*
May	6.11	0.73*	5.79	4.99	1.04*	0.70*	2.31	1.03*	May	26.23	14.10	20.56
June	3.18	-	3.94	2.87	18.12	1.31*	2.46	3.67	June	20.81	17.96	5.67
July	2.28	2.04	13.68	3.00	12.58	5.63	6.19	9.92	July	21.91	9.40	7.67
Aug.	2.98	-	1.84	4.15	6.55	5.04	1.99	9.82	Aug.	11.19	13.64	5.88
Sept.	4.40	2.63	9.41	3.96	3.62	3.51		9.82	Sept.	23.30	7.78	11.59
Oct.	4.03	2.52		4.00	6.25	5.71		3.12	Oct.	12.29	10.74	4.39
Nov.	9.12	2.62		8.92	4.94	5.06		0.54*	Nov.	17.85	8.55	5.65

The values of the coefficient of dispersion not significantly different from unity are marked *

Table 8 (Cont'd) Coefficient of dispersion for each species and age group

Nardus stricta grassland

	Cognettia sphagnetorum			Achaeta spp.			
	Total	whole worms	regenerating fragments	Total	Mature	Juv.	Non mature
Nov.	15.89	17.82	4.59	1.70*	1.34*		0.35*
Feb.	7.91	6.59	0.67*	1.38*	1.21*		1.06*
Apl.	24.32	23.21	4.49	1.21*	0.81*		0.82*
May	10.64	11.18	6.32	1.70*	0.65*		1.09*
June	7.30	8.23	4.03	2.31	2.35		0.10*
July	2.95	2.40	0.93	8.20	0.96*	13.20	1.50*
Aug.	9.04	8.71	3.56	2.35	1.73*	2.66	0.40*
Sept.	19.82	16.59	6.75	1.87	1.79		0.64*
Oct.	5.87	8.43	2.12	1.91	1.46*		0.45*
March	5.35	6.56	0.97*	-	-		
Apl.	5.38	4.39	4.29	2.02	1.83		3.30
May	3.12	6.52	1.49*	2.30	2.21		0.48*
June	7.91	8.11	1.95	2.57	1.23*	2.82	2.49
July	3.57	2.55	1.49*	10.51	1.06*	9.97	1.75
Aug.	7.17	6.99	2.89	3.10	1.42*	2.71	1.90
Sept.	10.74	12.11	2.19	1.90	1.95		0.60*
Oct.	26.44	24.22	6.88	1.84	1.96		1.80
Nov.	12.64	10.47	2.28	1.57*	1.36*		1.35*

Values of the coefficient of dispersion not significantly different from unity are marked *

Table 8 (Cont'd) Coefficient of dispersion for each species and age group

Nardus stricta grassland

	Marionina clavata				Cernosvitoviella briganta			
	Total	Mature	Juv.	Non mature	Total	Mature	Juv.	Non mature
Nov.	6.19	2.74		0.85*	6.59	5.48		0.52
Feb.	2.30	-		2.30	0.61*	0.57*		0.61*
Apl.	2.51	1.02*		2.64	-	-		-
May	9.01	0.83	4.70	3.11	-	-		-
June	3.19	1.24*		2.10	1.52*	-	2.14	0.78*
July	0.45*	0.43*		0.29*	-	-		-
Aug.	3.17	1.49*		1.79	2.15	-	2.27	0.62*
Sept.	4.41	1.96	26.35	1.44*	1.35*	1.18*		0.80*
Oct.	4.85	1.95	8.16	1.11*	1.59*	2.22		2.44
March	4.45	2.71		1.95	3.87	3.84		1.69*
Apl.	6.99	3.18		3.92	1.48*	1.40*		1.06*
May	4.19	1.34*		5.81	1.06*	1.66*		3.17
June	6.67	1.28*	5.94	0.79*	15.09	4.59	14.35	2.41
July	3.10	-	4.64	2.28	8.95	1.49*	4.19	1.59*
Aug.	3.30	1.06*	4.92	0.78*	4.49	2.09	2.88	5.56
Sept.	3.69	4.21	2.58	1.52*	7.28	2.01	12.78	3.87
Oct.	3.20	1.80*		1.99	2.48	2.18		2.48
Nov.	3.45	2.64		1.04*	2.06	2.55		2.00

Values of the coefficient of dispersion not significantly different from unity are marked *

Table 8 (Cont'd) Coefficient of dispersion for each species and age group

Limestone grassland

	Cognettia sphagnetorum			*Achaeta* spp.			
	Total	whole worms	regenerating fragments	Total	Mature	Juv.	Non mature
Nov. 1961	6.09	3.70	2.13	0.96*	0.73*	1.16*	0.88*
Feb. 1962	8.80	7.28	2.58	2.16	2.50		2.11
Apl.	0.89*	0.81*	1.47*	0.24*	0.34*		0.27*
June	3.90	1.98	2.83	1.90*	3.11		1.84
July	3.77	0.59	4.05	2.61	2.94		2.52
Aug.	1.84*	1.79	0.83*	1.88*	1.03*		1.99
Sept.	3.29	1.24*	1.75	1.06*	0.67*	2.29	1.82
Oct.	4.84	1.92	1.11*	1.98	1.33*	3.82	1.03*
Mar. 1963	6.15	1.59*	1.05*	2.62	1.01*		1.97
Apl.	2.43	2.05	0.38*	1.47*	0.76*		1.52*
May	2.93	1.86	1.63*	0.98*	0.61*		0.77*
June	4.98	2.41	2.87	0.60*	1.73*	2.55	0.83*
July	5.95	3.64	3.74	3.77	2.20	2.41	2.51
Aug.	6.34	4.17	4.35	5.74	2.86		4.38
Sept.	11.47	8.18	3.38	4.58	2.52		3.44
Oct.	16.26	9.16	7.49	4.18	1.41*		4.12
Nov.	7.18	5.32	2.16	1.16*	0.53*		1.88

The values of the coefficient of dispersion not significantly different from unity are marked *

Table 8 (Cont'd) Coefficient of dispersion for each species and age group

Limestone grassland

	Marionina clavata				*Fridericia* spp.		
	Total	Mature	Juv.	Non mature	Total	Mature	Non mature
Nov.	1.05*	1.14*		0.43*	1.56*	1.77	1.64
Feb.	2.25	2.11		1.42*	2.79	2.11	2.38
Apl.	2.38	2.47		2.27	3.38	3.42	3.41
June	1.79*	1.81		0.96*	8.11	7.18	6.89
July	2.52	2.12		1.06*	10.00	9.57	8.66
Aug.	2.02	2.50	1.72*	2.02	1.54*	0.68*	0.98*
Sept.	1.76*	1.89	5.98	0.80*	2.62	1.99	2.13
Oct.	2.17	1.82		1.05*	4.29	3.21	3.11
March	1.90	2.01		1.19*	2.12	2.42	1.87
Apl.	2.32	2.50		0.42*	1.67*	1.88	0.59*
May	1.05*	1.78		0.53*	4.88	3.92	2.11
June	1.94*	1.99	1.44*	0.50*	1.75*	1.72*	1.64*
July	2.92	2.13	3.36	0.54*	1.91	2.01	1.50*
Aug.	3.73	2.50		2.15	3.41	2.50	2.11
Sept.	7.82	6.51	3.73	6.43	2.68	1.88	2.40
Oct.	2.71	2.13		1.56*	8.97	9.12	3.12
Nov.	1.02*	1.11*		0.65*	2.15	1.83	1.94

The values of the coefficient of dispersion not significantly different from unity are marked *

Table 8 (Cont'd) Coefficient of dispersion for each species and age group

Mixed moor

	Cognettia sphagnetorum		
	Total	whole worms	regenerating fragments
Nov.	10.00	14.73	4.83
Dec.	1.09*	0.13*	1.01*
Feb.	4.96	8.89	1.10*
May	11.12	7.99	6.59
June	3.75	3.17	3.99
July	10.56	10.47	1.40
Aug.	1.25*	1.02*	0.73*
Sept.	0.67*	0.32*	0.54*
Oct.	8.49	6.46	2.87
April	7.86	7.62	2.39
May	8.38	4.94	2.00
June	10.14	10.11	7.42
July	2.38	1.95	0.62*
Aug.	97.37	29.66	8.12
Sept.	13.88	7.32	4.30
Oct.	15.17	27.74	7.77
Nov.	27.00	14.73	1.61*

Bare peat

	Cognettia sphagnetorum		
	Total	whole worms	regenerating fragments
Nov.	1.77	1.64*	2.11
Dec.	2.11	2.38	1.07*
Jan.	3.38	2.02	1.33*
Feb.	4.18	2.45	3.54
June	5.17	3.32	1.17*
July	1.68*	1.58*	2.30
Aug.	1.21*	1.61*	0.80*
Sept.	3.99	2.51	2.86
Oct.	2.29	1.99	1.49*
Apl.	1.35*	1.20*	1.32*
May	1.42*	1.97	1.15*
June	2.01	2.31	1.83
July	2.50	2.40	1.96
Aug.	1.83	2.11	1.84
Sept.	2.06	1.70*	2.00
Oct.	2.49	1.94	1.76

The values of the coefficient of dispersion not significantly different from unity are marked *

show that the population was randomly distributed, only that aggregations could not be detected by the present method.

The coefficients of dispersion for total Enchytraeidae at five sites are shown in Table 7. The occasions when the coefficient of dispersion was not significantly different from unity are marked with an asterisk. These were the two blanket peat sites, Mixed moor in December 1961, August and September 1962 and Bare peat in July and August 1962, April and May 1963 and in Limestone grassland in April 1963.

In examining the data for each species and species age group (Tables 8a-8e) more occasions are found when aggregations are not detected. For some species, aggregations were detected in most sampling months, Cognettia sphagnetorum on all five sites and Marionina clavata on the Juncus site. Achaeta species have a coefficient of dispersion below one on the majority of sampling dates on the Limestone grassland site. In general, aggregations were detected less frequently in the Limestone and Nardus grassland sites than on the Juncus site.

Discussion

The factors causing aggregations in soil animals can be divided into three classes.

1. The destruction of animals in less favourable parts of the soil, by desiccation and other adverse conditions, leaving isolated areas of survival in the soil.
2. The slow dispersal of animals from an egg batch or area of survival.

3. The active movement of animals towards a suitable food source or other environmental requirement such as a site for cocoon deposition, or area of optimum humidity or temperature.

Aggregation in Enchytraeidae has been detected through the two year sampling period at all times of the year and in all weather conditions. It can therefore be assumed that the major cause of the normal pattern of aggregation is not the patchy distribution of areas of survival. For Enchytraeidae which produce relatively few eggs per individual, it would be necessary for worms to stay in the same place in the soil for several generations to build up aggregations of the size found at Moor House with up to 70 Enchytraeidae per sample unit (10 $cm.^2$). It appears that the slow dispersal of worms from an egg batch is not the cause of aggregations of the enchytraeid worms at Moor House. The most common species of Enchytraeidae at Moor House, Cognettia sphagnetorum, reproduces asexually. It is found to be aggregated and it follows that these aggregations are caused by the movement of the animals towards an area of optimum environmental conditions.

The additional factors affecting the aggregation of sexually reproducing worms may be listed as

1. Limited numbers of suitable sites for cocoon deposition.
2. Aggregation for copulation.

3. Specialised feeding requirements for the newly hatched worms.

4. Increased susceptibility of the very young worms to adverse environmental conditions and subsequent slow dispersal from areas of survival.

Some or all of the above factors may be affecting the distribution of the sexually reproducing worms in the soil. With the available data it is not possible to distinguish the part played by any one factor.

V. LIFE CYCLE STUDIES

LIFE CYCLE STUDIES

Introduction

Previous studies on the life cycles of Enchytraeidae have been carried out by Reynoldson (1947), O'Connor (1958) and Nielsen (1955). Reynoldson's work was on Enchytraeus albidus Henle 1837 growing in sewage bacteria beds; in this habitat the numbers of cocoons can be counted. O'Connor (1958), working on a population in a coniferous forest soil, found that he could not count cocoons as they were almost impossible to see in the soil. As a measure of breeding activity he counted the number of newly hatched worms in the soil. In the present study this method has been used to study animals from field samples, and worms have also been bred in the laboratory.

Information from field samples

In order to study the life cycles of the Enchytraeidae at Moor House, extracted worms were sorted into age groups and identified by examining them alive in a drop of water under a coverslip at x100 magnification. Worms were recorded as mature if they possessed either male or female sex organs, or both. It appeared that the growth and possibly the subsequent degeneration of the sex organs was rapid, and the few individuals with partially developed sex organs were included in the "mature" class. Whole worms less than 2 mm. long were recorded as juvenile.

This is in accordance with the technique used by O'Connor (1958). Later results from cocoons hatched in culture showed that at 10°C. juvenile worms of all the major species from Moor House grew out of this size class in five to ten days. However, the soil temperatures at Moor House were less than 10°C. during some of the months when juvenile worms were present.

Table 9

Soil temperatures at 1 foot during the months when newly hatched worms were present. °C.

	1962	1963
April	2.4	3.5
May	6.5	6.9
June	10.8	11.2
July	12.5	13.3
August	12.2	12.7
September	10.0	10.0
October	7.3	7.5

The only information for relative growth rates of enchytraeids at different temperatures was obtained for the development of regenerating fragments of Cognettia sphagnetorum. The average period of development

from fragment to regenerated worm at 5°C. was 39 per cent longer than at 10°C. If the same applies to sexually reproducing worms then at 5°C. the time spent in the less than 2 mm. size class would be from seven to fourteen days instead of the five to ten days taken at 10°C. It seems unlikely that juvenile worms remain less than 2 mm. long for a whole month even at the low soil temperatures in April and May so it is probable that the same hatch would not be sampled twice. The actual hatching date of any particular juvenile worm could thus be up to fifteen days prior to sampling. The error in the estimated date of worms reaching maturity was caused by the monthly sampling period, that is, worms could have matured up to 30 days before the sampling date. A total development period recorded as 30 days from field data, could in reality be as much as 45 days but would be unlikely to be as little as 15 days. That is, both errors in estimating the development period are unlikely to operate on one worm.

In studying the changes in the numbers of worms in each age class throughout the year, it must be remembered that more than one factor may be causing the change. For example, an increase in the number of non-mature worms could be the result of the growth of juvenile worms or the loss of sex organs in mature worms. Mature worms may develop directly from juvenile worms or they may develop from non-mature worms which have previously been mature. An increase in the number of juvenile worms would only mean that cocoons had hatched during the past 15 days.

The species which reproduce sexually at Moor House and for which field data are available are: Marionina clavata, Cernosvitoviella briganta, Cognettia cognettii, Achaeta spp. (A. eiseni and A. affinis) and Fridericia spp. (F. bisetosa, F. galba). The numbers of mature, non-mature and juvenile worms for 1962 and 1963 for each species are shown in Figs. 10 to 22. The data for Cognettia cognetii are in Table 10.

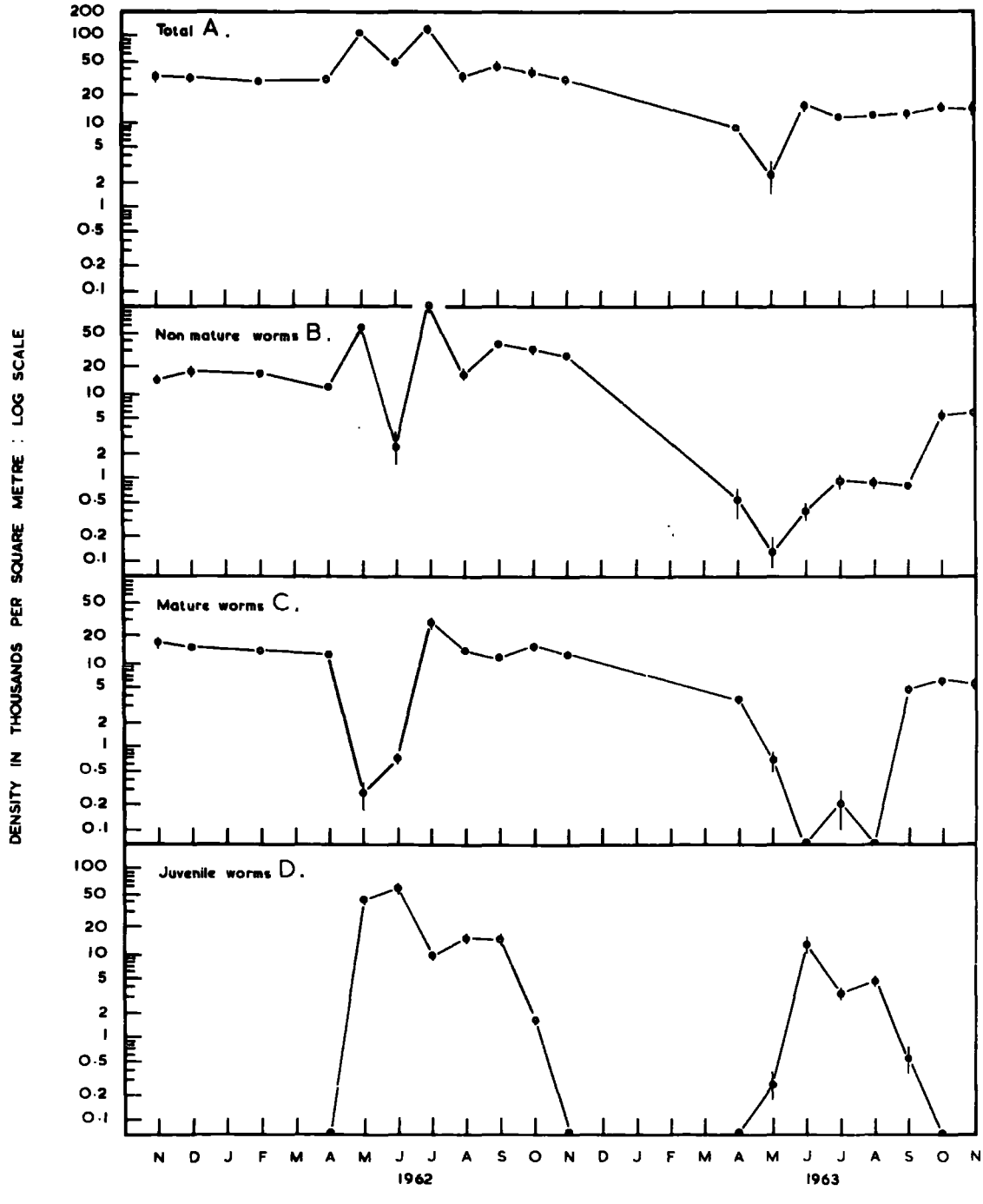
Marionina clavata

Juncus squarrosus moor site. Fig. 10.

During 1962, the total number of Marionina clavata increased in May but the number of mature animals decreased, showing that the mature worms had died or lost their sex organs and that there had been a hatch of cocoons between the April and May sampling dates. In June the number of non-mature worms fell while that of juvenile worms continued to increase. In July the numbers of non-mature and mature worms rose and juvenile worms were found in all samples until October. The mature worms found in July must have developed from the juvenile worms present in June, as in this month 95 per cent of the population was newly hatched. The development period must have been between 15 and 45 days. In May 1963 the numbers of mature and non-mature worms were low; no mature worms were recorded in June and there were also very low numbers of non-mature worms. Juvenile worms were first recorded in May and were present in all the monthly samples until September, the highest number being recorded in June.

Fig. 10. The seasonal variation in mean density of Marionina clavata, A. total worms, B. non-mature, C. mature, D. juvenile worms, in the Juncus squarrosus moor, 1962 and 1963. Density is expressed on a logarithmic scale showing thousands per square metre, a logarithmic cycle below one is included to show densities less than 1,000 per square metre. The standard errors of the means are shown.

SEASONAL VARIATIONS IN DENSITY : JUNCUS SQUARROSUS : MARIONINA CLAVATA



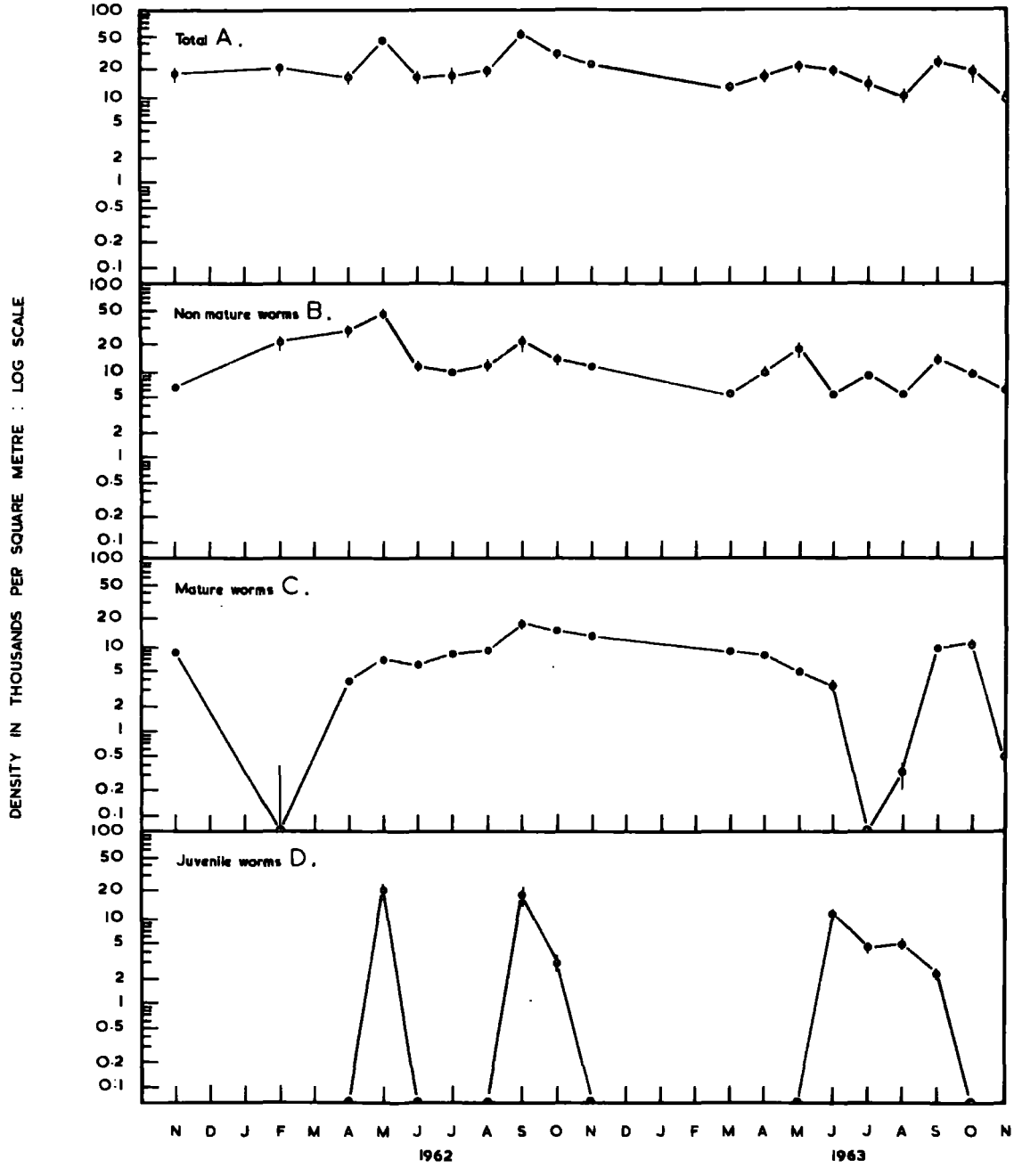
A small number of mature worms were found in July but the first large rise in numbers of mature worms occurred in September when 36 per cent of the total were mature. The mature worms present in the September samples could have developed from the juvenile worms present in the June sample. The longest possible development period would be from 15 days before the June sampling date, until the September sampling date, 105 days. If the mature worms present in July developed from the juvenile worms found in May then the longest possible development period would be 75 days. If the sampling dates are assumed to be the actual dates of development to maturity and hatching, then the two estimates of the development period are 90 days and 60 days.

Nardus grassland site. Fig. 11.

No mature worms were recorded in February 1962 but the numbers of this age class rose from April to September. Juvenile worms were found only in May, September and October. Non-mature worms were present in all months with the highest numbers in May and September. In 1963 the number of mature worms fell in June but was high in September and October. The hatch began in June and juvenile worms were found in the samples until September. Again, a high proportion of the population was in the non-mature stage throughout the year. Because of this it was not possible to estimate the development period from the field data. In 1963 there was a three month gap between the first hatching in June and the presence of

Fig. 11. The seasonal variation in mean density of Marionina clavata, A. total worms, B. non-mature, D. juvenile worms, on Nardus stricta grassland, 1962 and 1963. Density is expressed on a logarithmic scale showing thousands per square metre, a logarithmic cycle below one is included to show densities less than 1,000 per square metre. The standard errors of the means are shown.

SEASONAL VARIATIONS IN DENSITY : NARDUS GRASSLAND : MARIONINA CLAVATA



large numbers of mature worms in September, but as the numbers of non-mature worms were high from April there is no evidence to indicate that the mature worms did not develop from the reservoir of non-mature animals.

Limestone grassland site. Fig. 12.

The number of non-mature Marionina clavata was high throughout 1962 and in June both the total number of the species and of mature worms increased. It is probable that the juvenile worms were missed in the spring. It is not possible to say whether the mature worms developed from worms hatched in the spring of 1962 or from non-mature worms present during the previous winter. The number of mature worms fell in July but rose again in August when juvenile worms were also recorded. In 1963 juvenile worms were present from June. The number of non-mature worms was highest in July and the number of mature worms began to increase in August. This suggests that it took two months for newly hatched worms to become mature. However, as the number of non-mature worms was high throughout the year it was not possible to estimate the development period with certainty.

Cernosvitoviella briganta

Juncus squarrosus moor. Fig. 13.

The proportion of mature worms in the population was high in the winter months but fell during the spring and early summer. In 1963

Fig. 12. The seasonal variation in mean density of Marionina clavata, A. total worms, B. non-mature, C. mature, D. juvenile worms, on Limestone grassland, 1962 and 1963. Density is expressed on a logarithmic scale showing thousands per square metre, a logarithmic cycle below one is included to show densities below 1,000 per square metre. The standard errors of the means are shown.

Fig. 12.

SEASONAL VARIATIONS IN DENSITY: LIMESTONE GRASSLAND: MARIONINA CLAVATA

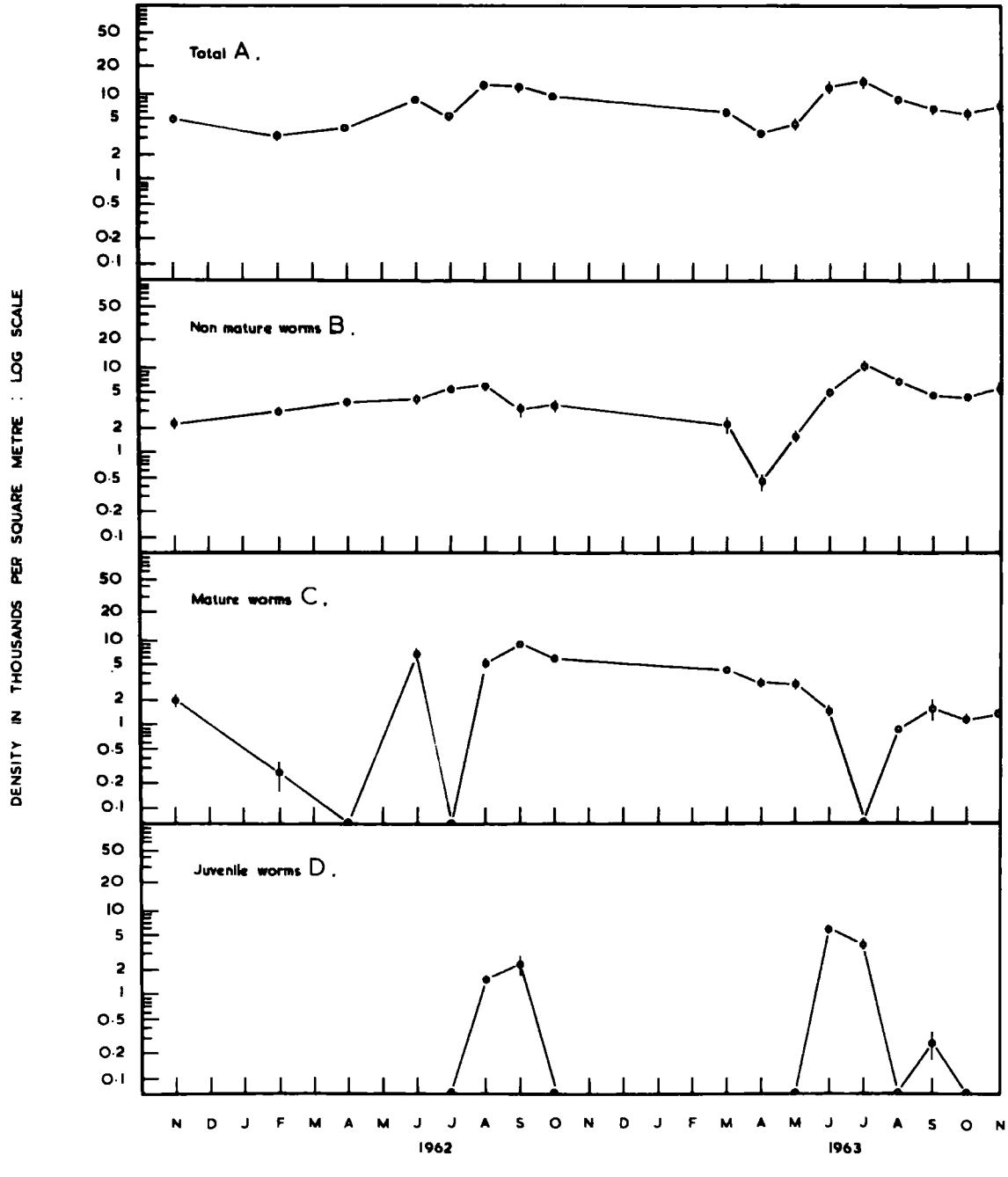
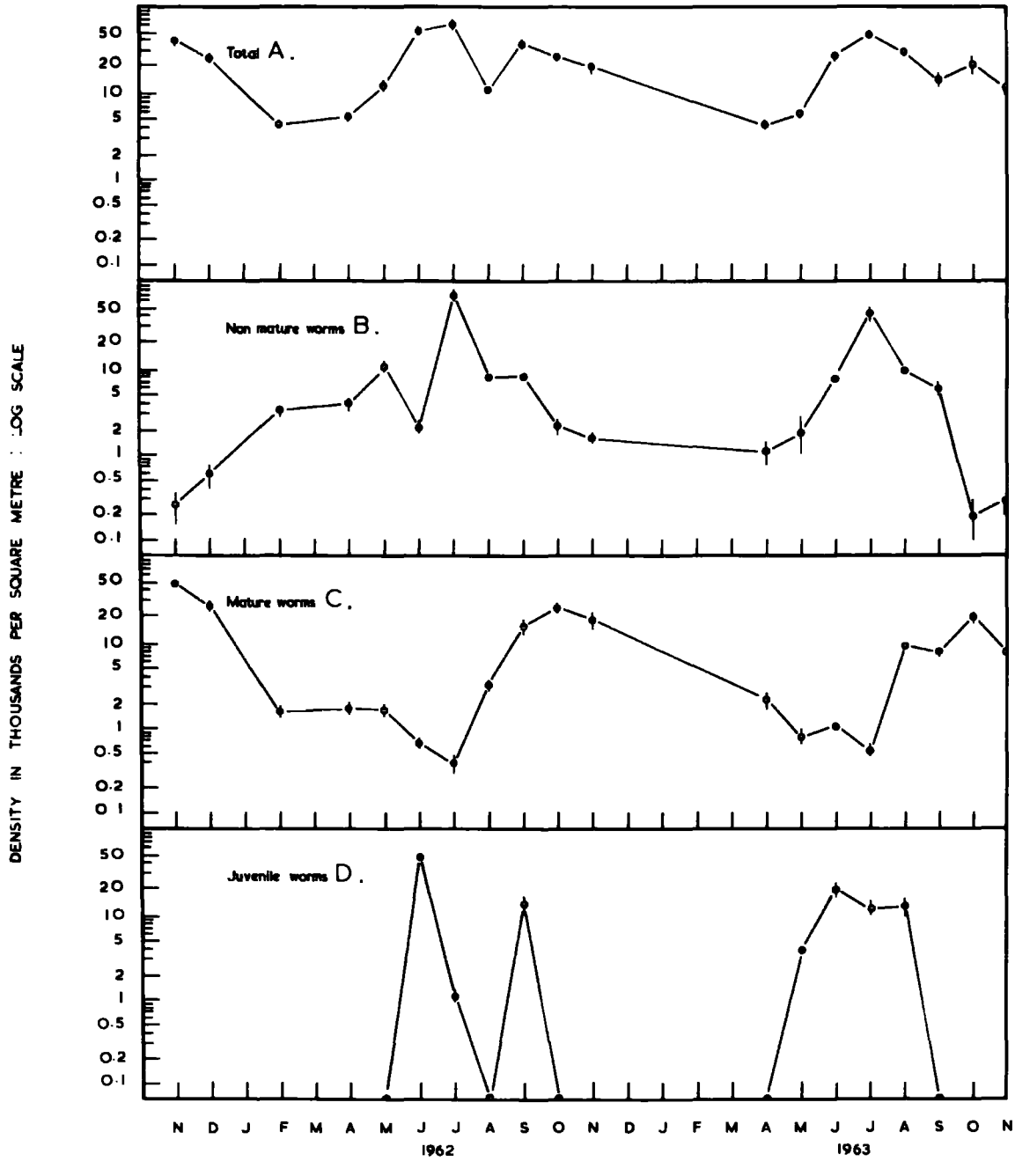


Fig. 13. The seasonal variation in mean density of Cernosvitoviella briganta, A. total worms, B. non-mature, C. mature, D. juvenile worms, on Juncus squarrosus moor, 1962 and 1963. Density is expressed on a logarithmic scale showing thousands per square metre, and a logarithmic cycle below one has been included to show densities less than 1,000 per square metre. The standard errors of the means are shown.

SEASONAL VARIATIONS IN DENSITY : JUNCUS SQUARROSUS : CERNOSVITOVIELLA BRIGANTA



the reduction in numbers of mature worms did not occur until after the first appearance of juvenile worms. The times taken for worms to develop to maturity as estimated from the first appearance of juvenile and mature worms in the samples were 60 and 90 days for 1962 and 1963 respectively.

Nardus stricta grassland. Fig. 14.

As on the Juncus squarrosus site the proportion of mature worms was high in the winter. In April and May 1962 the numbers of Cernosvitoviella briganta in the sample dropped to zero and no mature worms were found until September. In 1963 juveniles appeared in the samples before the number of mature worms decreased. The times taken for worms to develop to maturity, as estimated from field data in the two sample years, were both 90 days. It appears that on both sites the mature animals which over winter in the soil die before or just after the beginning of the spring hatch.

Cognettia cognettii

This species was found in small numbers on the Nardus and Limestone grassland sites, but was not recorded in all sampling months. The data have therefore been presented in table form and not graphically.

Fig. 14. The seasonal variation in mean density of Cernosvitoviella briganta, A. total worms, B. non-mature, C. mature, D. juvenile worms, on Nardus stricta grassland, 1962 and 1963. Density is expressed on a logarithmic scale showing thousands per square metre, and a log cycle below one has been included to show densities less than 1,000 per square metre. The standard errors of the means are shown.

SEASONAL VARIATIONS IN DENSITY : NARDUS GRASSLAND : CERNOSVITOVIELLA BRIGANTA

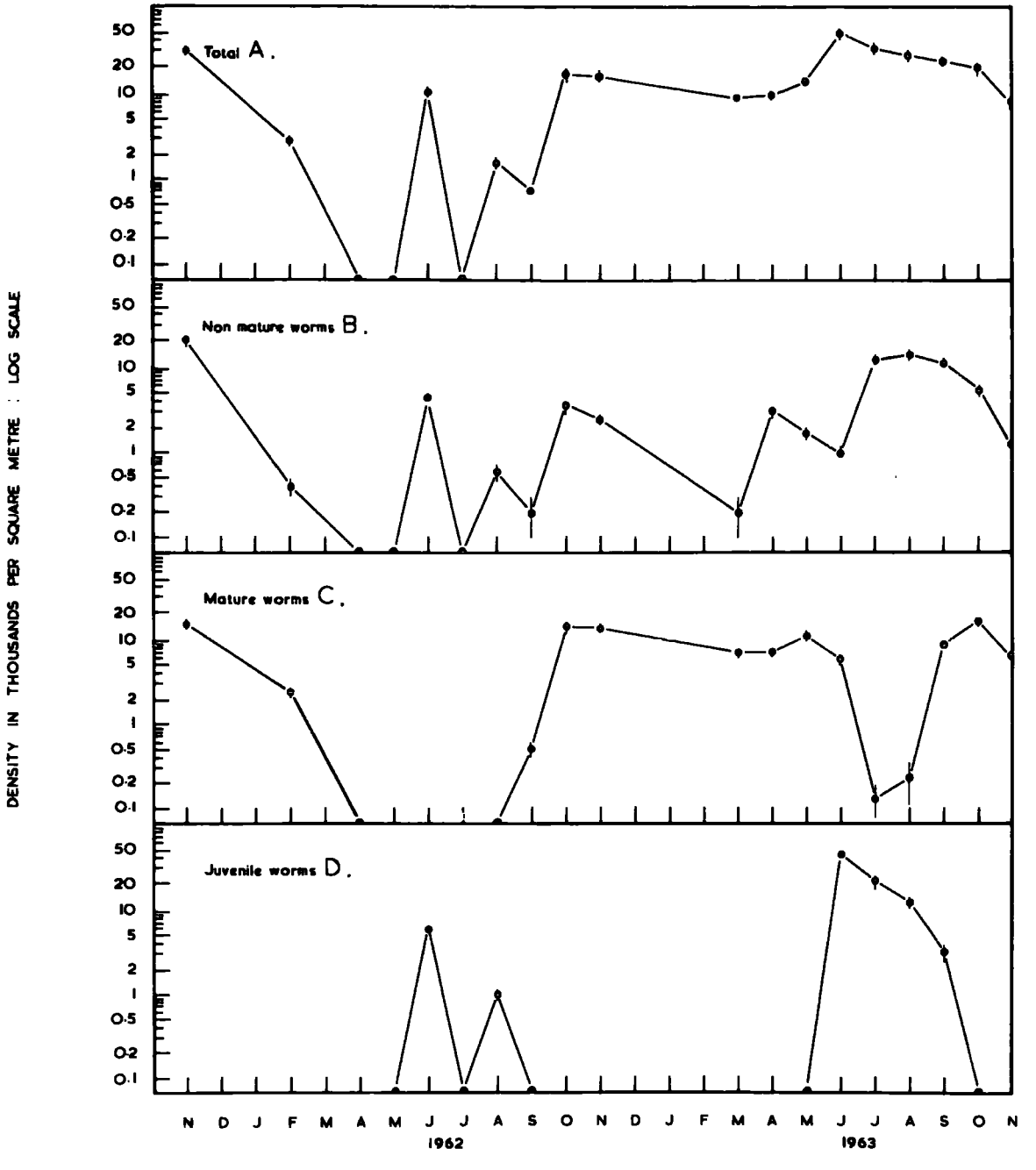


Table 10

Numbers of Cognettiia cognettii in each age group on the Nardus and Limestone grassland sites. 1962 and 1963.

Limestone grassland

	1962				1963		
	Mat.	Juv.	Non-Mat.		Mat.	Juv.	Non-Mat.
April	0	0	28	March	0	0	14
June	0	0	16	June	0	0	22
August	26	19	12	August	6	0	4
September	12	22	3	September	14	20	4
				October	0	0	3

Nardus grassland

	1962				1963		
	Mat.	Juv.	Non-Mat.		Mat.	Juv.	Non-Mat.
February	0	0	39	April	0	0	5
June	0	0	20	May	0	0	96
July	0	0	8	July	0	0	39
September	36	23	2	August	70	3	9
				September	52	64	12

In August and September 1962 and 1963 on both sites, both mature and juvenile animals were found. The mature and juvenile stages are of short duration and during most of the year this species is in the non-mature stage.

Achaeta species. Figs. 15, 16.

Two species of Achaeta (A. eiseni and A. affinis) have been recorded from Nardus (Fig. 16) and Limestone grassland (Fig. 15). They have been

Fig. 15. The seasonal variation in mean density of Achaeta spp., A. total worms, B. non-mature, C. mature, D. juvenile worms, on Limestone grassland, 1962 and 1963. Density is expressed on a logarithmic scale showing thousands per square metre, and a logarithmic cycle below one has been included to show densities less than 1,000 per square metre. The standard errors of the means are shown.

SEASONAL VARIATIONS IN DENSITY : LIMESTONE GRASSLAND : ACHAETA SPECIES

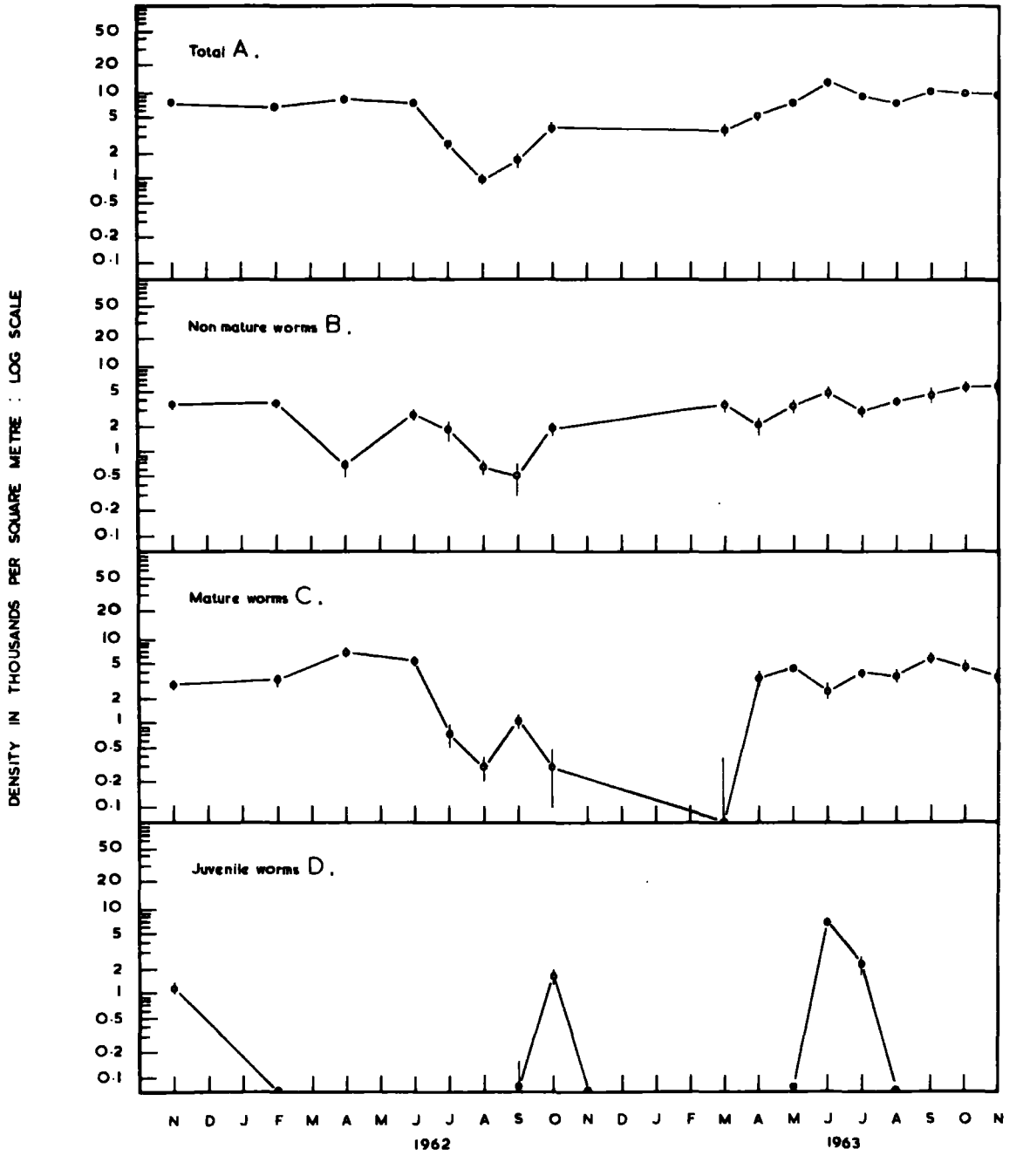
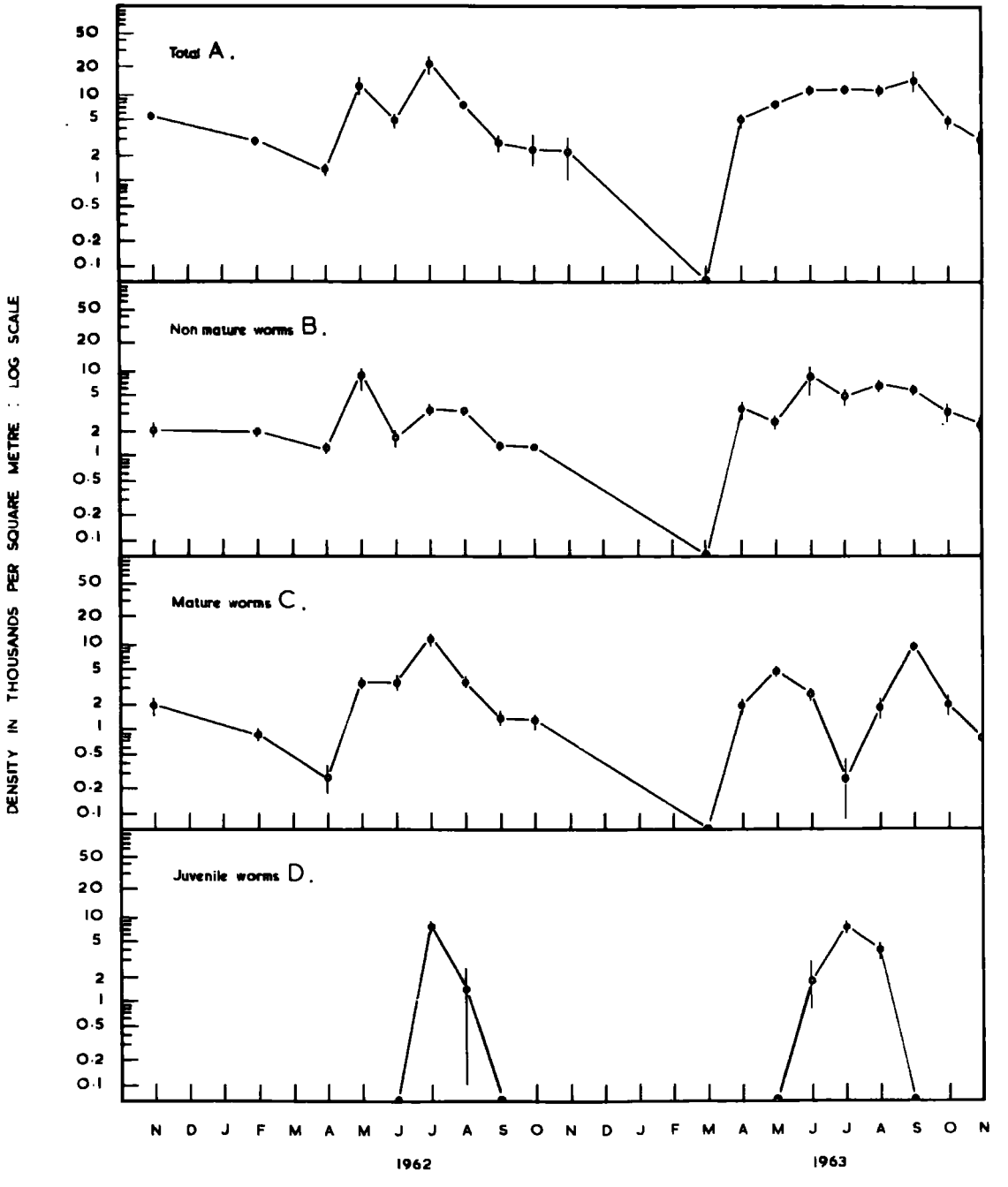


Fig. 16. The seasonal variation in mean density of Achaeta spp., A. total worms, B. non-mature, C. mature, D. juvenile worms, on Nardus stricta grassland, 1962 and 1963. Density is expressed on a logarithmic scale showing thousands per square metre, and a logarithmic cycle below one has been included to show densities less than 1,000 per square metre. The standard errors of the means are shown.

Fig. 16.

SEASONAL VARIATIONS IN DENSITY : NARDUS GRASSLAND : ACHAETA SPP.



grouped together because of the difficulty of separating even the mature animals. In both years and at both sites there was an increase in the total number of Achaeta spp. when no juvenile worms had been recorded, indicating a definite hatching period in the spring. The proportion of non-mature worms was high throughout the year and it is possible either that the time taken to develop to maturity was long, or that cocoons hatched at all times in the year with a peak in the spring.

Fridericia species. Fig. 17.

This genus occurred only on the Limestone grassland site Fridericia magna and Fridericia galba can be identified in the non-mature stages but they occurred only in very low numbers in the samples. The majority of the worms of this genus in the samples were Fridericia bisetosa, Fridericia paroniana and Fridericia maculata. The taxonomic characters used to distinguish these species are the shape of the spermathecae and the number of segments. Non-mature worms could not be identified and all the animals in the genus have been classed as one group in the population studies. No juvenile worms were found in the monthly samples even though a search was made for worms less than 5 mm. long. The proportion of non-mature worms was high throughout the sampling period and it was not possible to draw any conclusion about the life cycles of the genus.

Cognettia sphagnetorum

Cognettia sphagnetorum reproduces by fragmentation and is the most abundant species at Moor House. Numbers of whole and of regenerating

Fig. 17. The seasonal variation in mean density of Fridericia spp., A. total worms, B. non-mature, C. mature worms, on Limestone grassland, 1962 and 1963. Density is expressed on a logarithmic scale showing thousands per square metre, and a logarithmic cycle below one has been included to show densities less than 1,000 per square metre. The standard errors of the means are shown.

Fig. 17.

SEASONAL VARIATIONS IN DENSITY : LIMESTONE GRASSLAND : FRIDERICIA SPP.

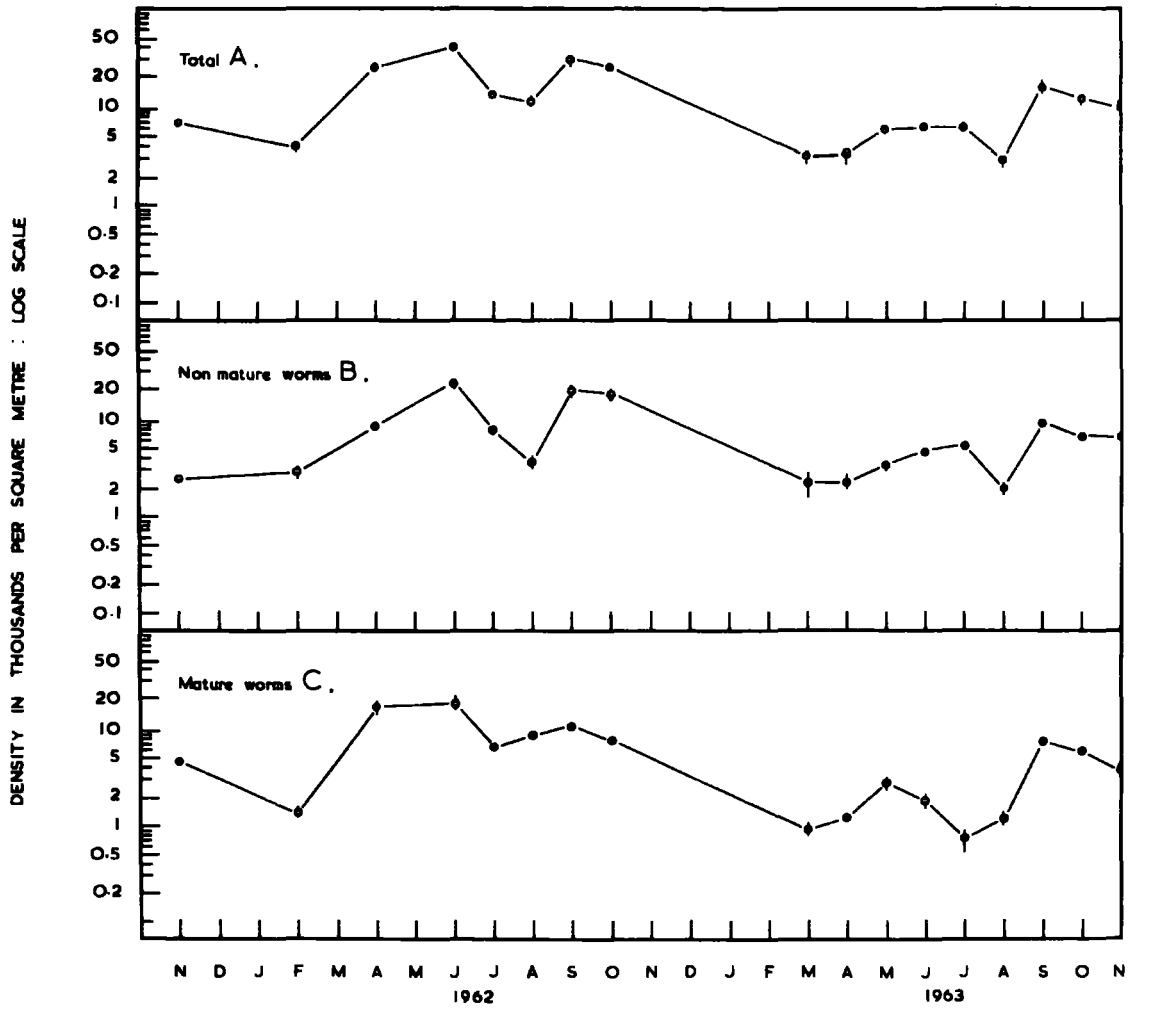


Fig. 18. The seasonal variation in mean density of Cognettia sphagnetorum, A. total worms, B. whole and C. regenerating worms, on Juncus squarrosus moor, 1962 and 1963. Density is expressed as thousands per square metre on a logarithmic scale which is larger than that in Figs. 10-17, and does not include a logarithmic cycle below one. The standard errors of the means are shown.

Fig. 18.

SEASONAL VARIATIONS IN DENSITY: JUNCUS SQUARROSUS: COGNETTIA SPHAGNETORUM

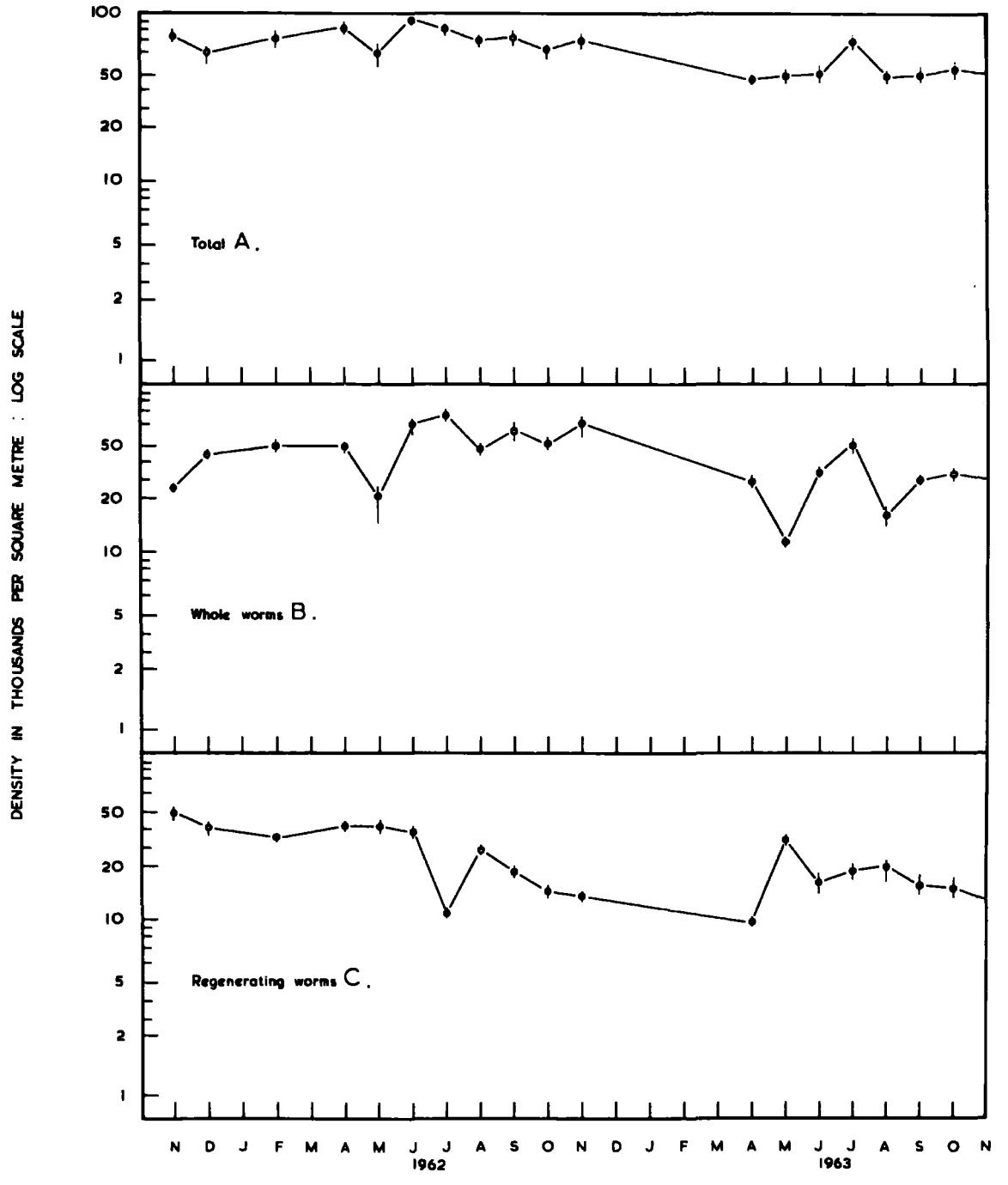


Fig. 19. The seasonal variation in mean density of Cognettia sphagnetorum, A. total worms, B. whole and C. regenerating worms, on Nardus stricta grassland, 1962 and 1963. Density is expressed as thousands per square metre on a logarithmic scale smaller than that of Fig. 18, the base line is at two for each graph.

SEASONAL VARIATIONS IN DENSITY : NARDUS GRASSLAND : COGNETTIA SPHAGNETORUM

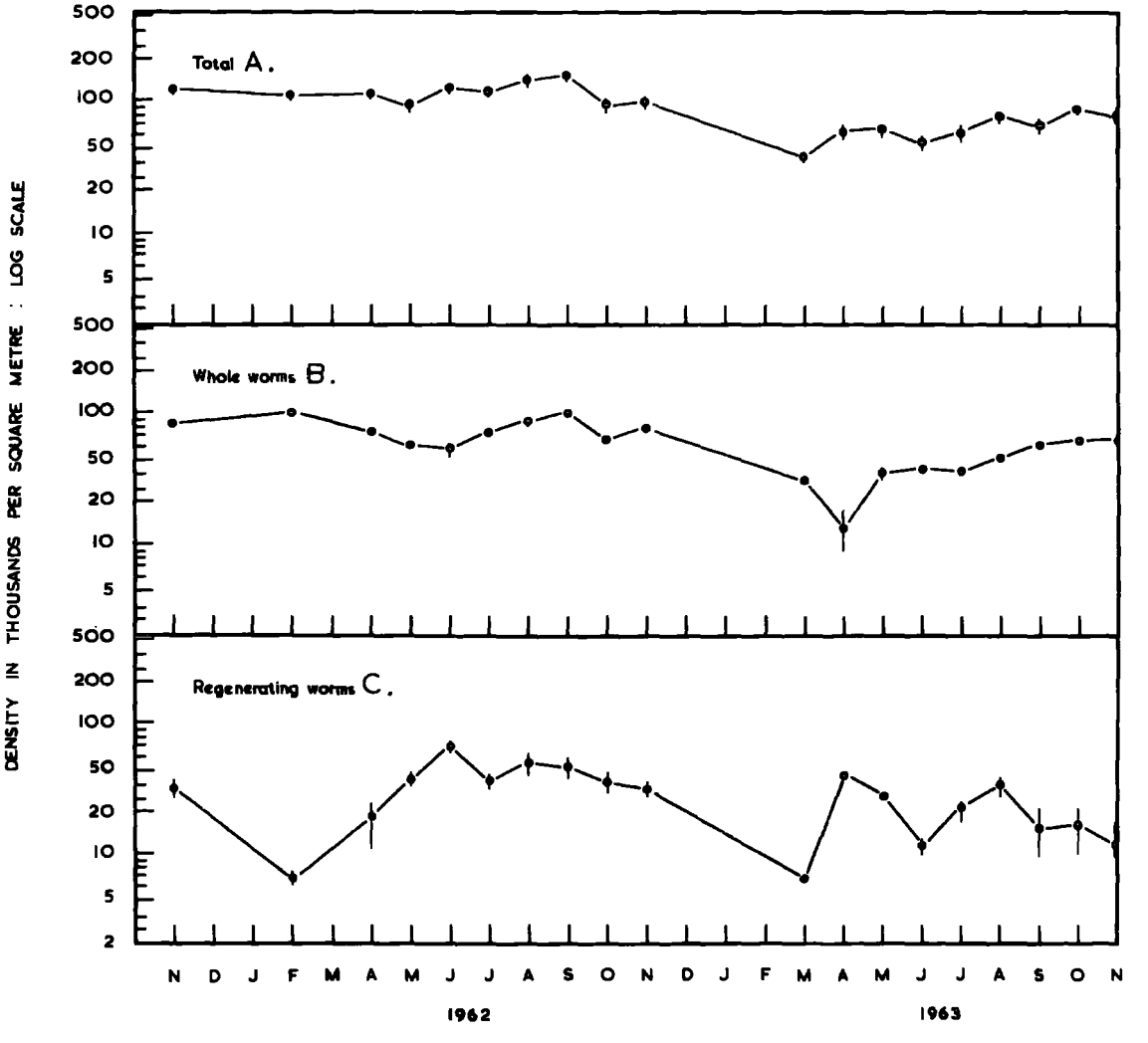


Fig. 20. The seasonal variation in mean density of Cognettia sphagnetorum, A. total worms, B. whole and C. regenerating worms, on Limestone grassland, 1962 and 1963. Density is expressed as thousands per square metre on a logarithmic scale similar to that used in Figs. 10-17.

Fig. 20.

SEASONAL VARIATIONS IN DENSITY : LIMESTONE GRASSLAND : COGNETTIA SPHAGNETORUM

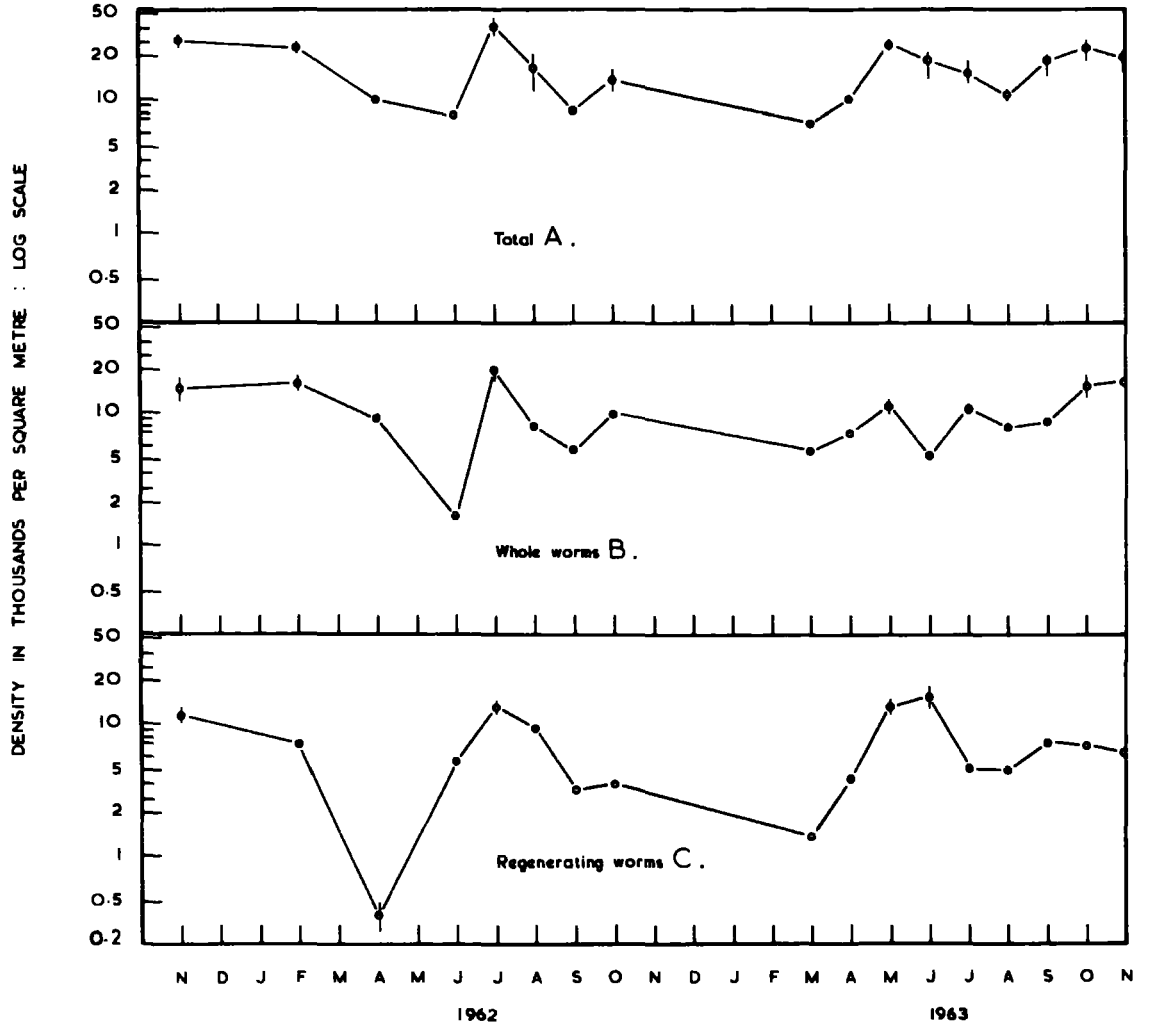


Fig. 21. The seasonal variation in mean density of Cognettia sphagnetorum, A. total worms, B. whole and C. regenerating worms, on Mixed moor, 1962 and 1963. Density is expressed as thousands per square metre on a logarithmic scale similar to that in Fig. 18. The standard errors of the means are shown.

SEASONAL VARIATIONS IN DENSITY : MIXED MOOR : COGNETTIA SPHAGNETORUM

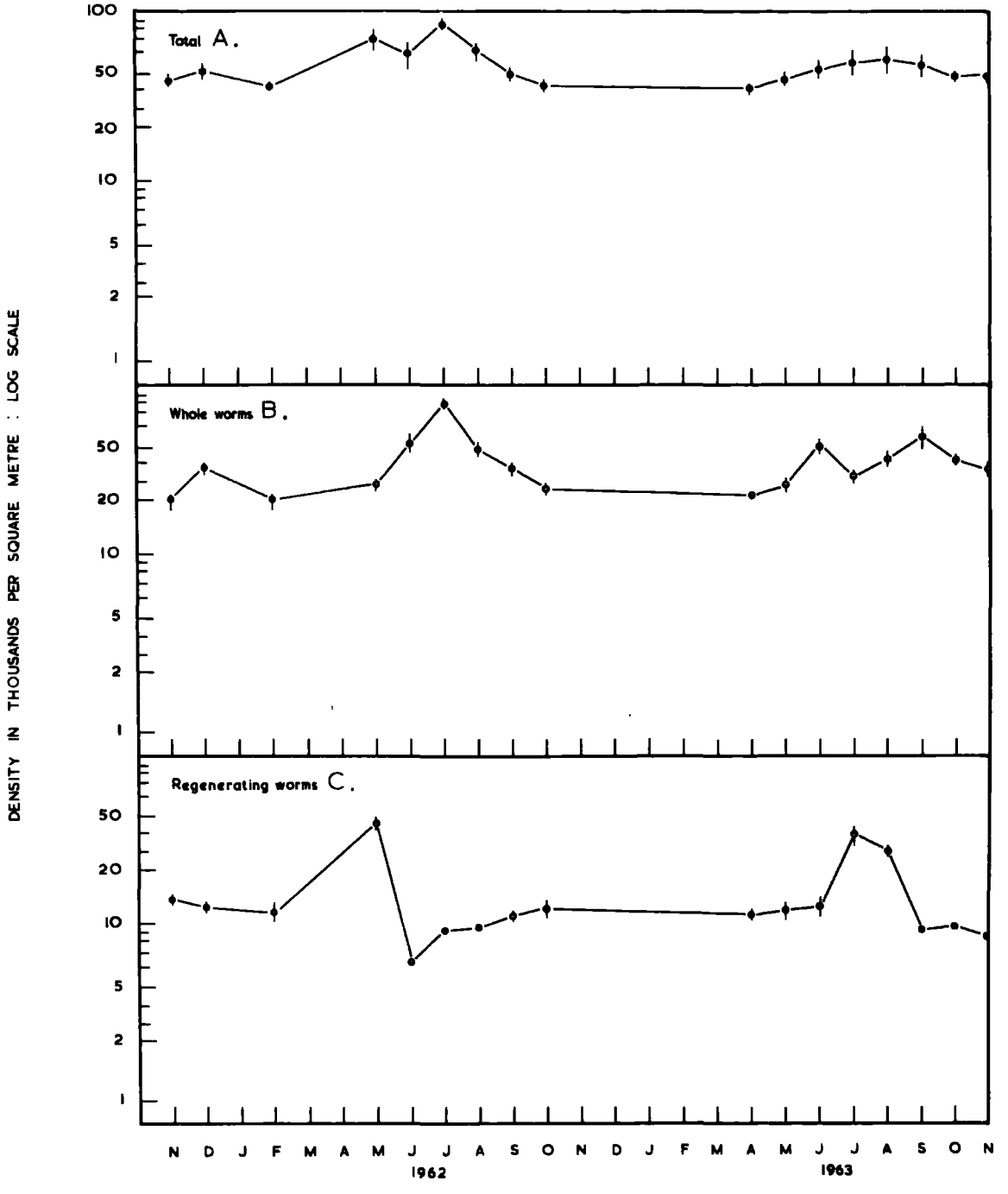
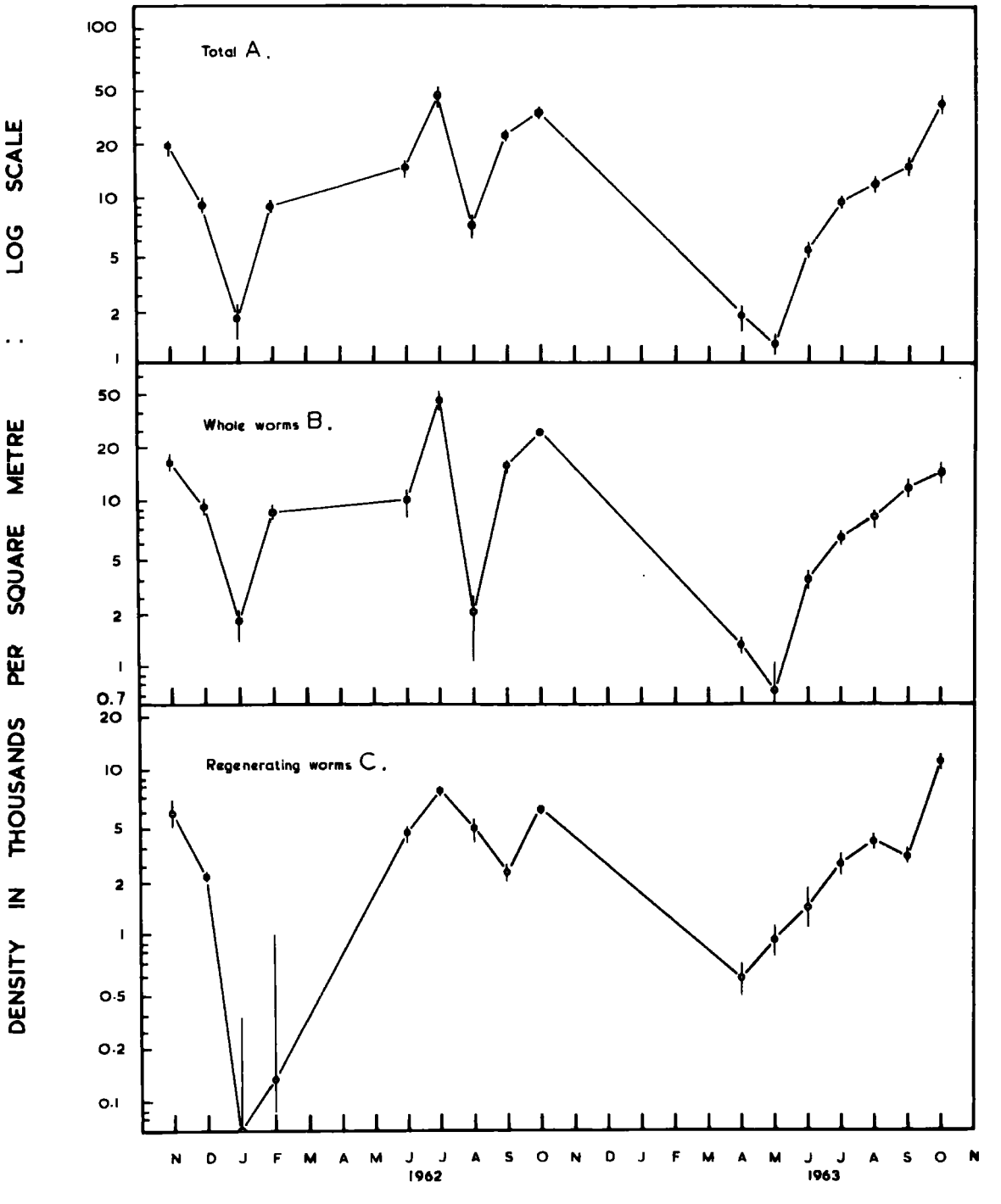


Fig. 22. The seasonal variation in mean density of Cognettia sphagnetorum, A. total worms, B. whole and C. regenerating worms on Bare peat, 1962 and 1963. Density is expressed as thousands per square metre on the larger logarithmic scale used in Figs. 18 and 21, the scale extends below 1,000 per square metre for whole and regenerating worms. The standard errors of the means are shown.

Fig. 22.

SEASONAL VARIATIONS IN DENSITY : BARE PEAT : COGNETTIA SPHAGNETORUM



fragments are plotted for the five sample sites (Figs. 18 to 22). On the Juncus, Nardus and Mixed moor sites the numbers of Cognettia sphagnetorum remained relatively constant, except for a drop in numbers during the severe winter of 1962-3. This suggests that the birth rate balances the death rate for most of the year. The numbers of regenerating fragments increased during the spring and summer, a change probably caused by higher soil temperatures. On the Bare peat and Limestone grassland sites the smaller population was less stable in numbers but still showed an increase in reproductive activity in the spring and summer, with a lower number of regenerating fragments in the winter.

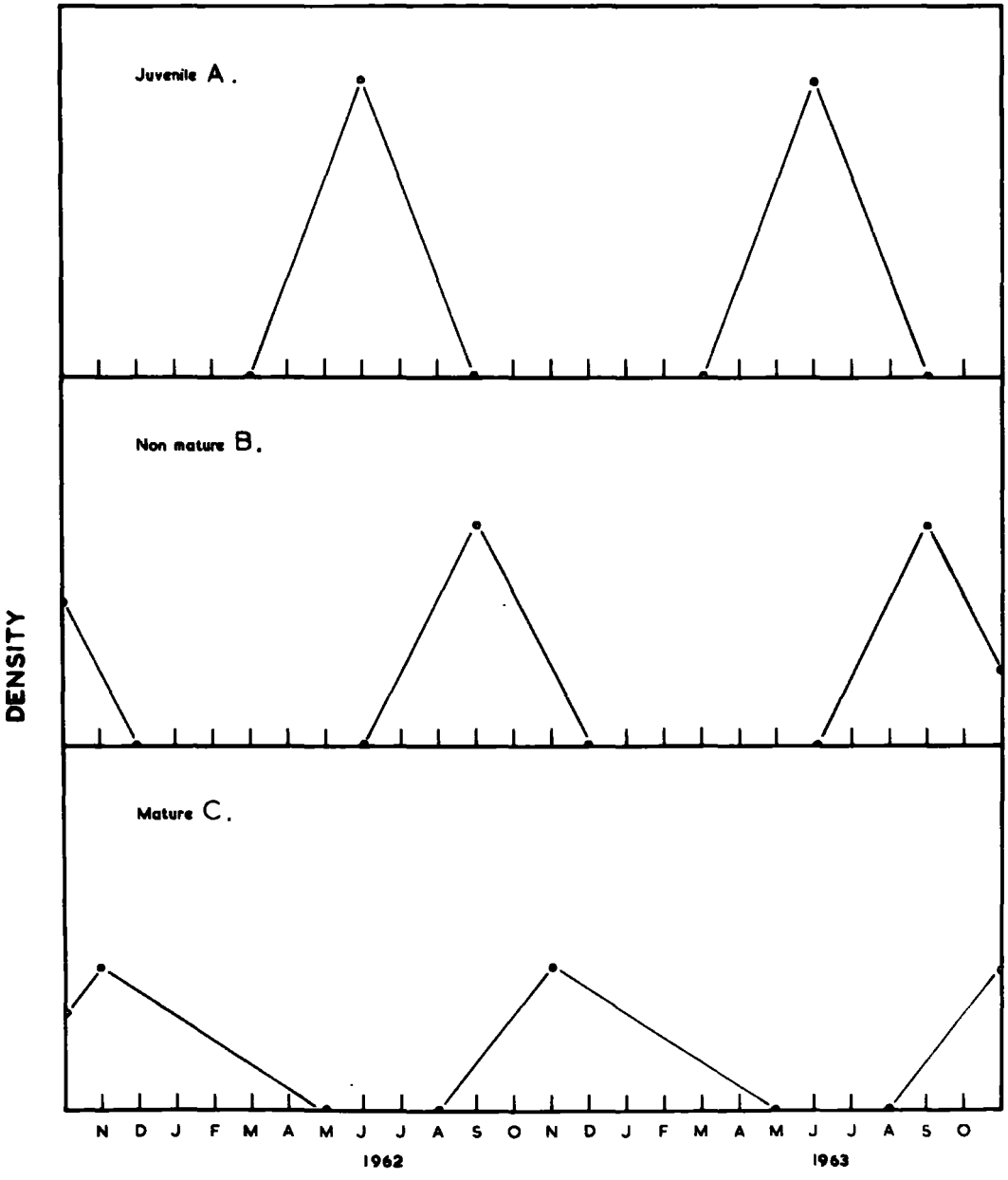
Discussion

For an enchytraeid species having a life span of one year and breeding once during that year the pattern of mature, non-mature and juvenile worms would be expected to be like that shown in Fig. 23. The non-mature class recorded in the field may include post-mature as well as pre-mature worms and the time spent as cocoons cannot be estimated from field data. The species at Moor House which has a life cycle most like that of the model is Cernosvitoviella briganta. Three successive overlapping curves for juvenile, non-mature and mature worms can be distinguished in Fig. 13 and Fig. 14. The majority of the winter population was in the mature stage and these worms died off at the beginning of, or just before, the next hatching period. Indication

Fig. 23. A diagrammatic representation of the variations in density for each age group, A. juvenile, B. non-mature, C. mature, during annual life cycles of a sexually reproducing enchytraeid over two years (1962 and 1963).

Fig. 23.

A TWO-YEAR MODEL OF THE ANNUAL LIFE-CYCLE
OF A SEXUALLY REPRODUCING ENCHYTRAEID



of three successive curves can be detected for Marionina clavata in Figs. 10-11. These however are slightly different from those of C. briganta. The proportion of non-mature worms was high during the winter, indicating that some worms matured more slowly than others or did not mature at all. The data for Achaeta spp. were insufficient to show a pattern like that of the model, even if such a pattern were present.

The field data for Cognettia cognettii, in which mature and juvenile worms occurred only during a short period, show another modification of the model. In this case breeding activity was limited to one or two months in the late summer and early autumn, and most of the year was spent in the non-mature stage. (Table 10)

Information from Laboratory cultures

Culture technique

Field data collected from monthly samples cannot provide all the information needed to form a picture of the breeding cycles of enchytraeids under moorland conditions. As initial studies indicated that most species have only one generation per year it was necessary to devise a method of culture in which the animals could be kept alive and healthy for longer than a year, and preferably in which they could be readily examined without disturbing the culture medium.

The culture methods used by other workers for gaining information on breeding and development of enchytraeids were tried. Specimen tubes

with moist cotton wool in the bottom (Reynoldson 1939), and chambers made with glass slides kept apart by frames of filter paper (Christensen 1956) were tried without success. Specimen tubes with a layer of fine glass beads in the bottom were also used as possible culture chambers. All these types of cultures were kept moist and at 10°C. Three sources of food were used: 'live' soil (free of all other enchytraeids and cocoons); mouldy bread; and yeast. In all of these cultures, worms were kept alive for up to seven weeks, but they did not feed or lay cocoons. Cognettia sphagnetorum, which reproduces by fragmentation, increased in numbers for the first four weeks, but very few worms were alive after the eighth week, and none survived the tenth.

Present culture method

A fourth type of culture method has proved successful. The culture chamber is a petri dish with a 1 per cent soil extract agar plate sprinkled with soil. To make the soil-agar one litre of soil is washed with a litre of distilled water and filtered. The filtrate is made up to one litre with distilled water. The agar is added and the mixture autoclaved at 15 lb. per square inch pressure for 30 minutes, making a sterile agar gel. The agar is then poured into the smaller halves of sterile petri dishes to a depth of about 5 mm., covered, and allowed to cool. When the agar is set, the surface is sprinkled with a thin layer of soil or leaf litter free of living enchytraeids and cocoons. (These can either be carefully removed by hand or killed by heating to 50°C. for

20 to 30 minutes). The soil on the agar must cover between 50 and 70 per cent of the surface, but not be thick enough for the worms to be hidden. Unless a large proportion of the agar is covered by soil, isolated patches of fungi, yeasts, or bacteria develop, which appear to be harmful to the worms. A full complement of soil microflora seems to be necessary for the healthy development of enchytraeids in culture. To avoid patches of infection within the agar, sterile instruments must be used to handle the worms. The agar becomes opaque where it has been scratched or pierced by dirty needles. After cooling the chambers to the required temperature (10°C. in the case of moorland worms), the enchytraeids are introduced. The dishes should be stacked with the agar in the lower dish as the worms tend to crawl downwards and out of the agar if the dishes are kept the other way up. The plates need to be moistened occasionally with sterile soil solution. If the plate begins to dry out, it can be floated off its dish, and placed on top of a new plate without disturbing the culture.

A particular advantage of the chamber is that the animals can be studied in either transmitted or reflected light.

This method of culturing enchytraeids is useful not only for breeding experiments, but also as a means of keeping worms in good condition, and this easy way of keeping the animals could be of considerable use in taxonomic studies of the group.

Ten species of Enchytraeidae have been kept in culture in the laboratory, six of which have provided some information on breeding activity. The six species which bred successfully were Marionina clavata, Cernosvitoviella briganta, Achaeta eiseni, Enchytraeus buchholzi, Cognettia cognettii and C. sphagnetorum. The four species which did not breed in culture were: Mesenchytraeus sanguineus, Achaeta affinis, Henlea perpusilla and Fridericia bisetosa.

Slight modifications to the standard culture chamber were necessary for some species before the worms would breed. The 'right' conditions were discovered by trial and error. In some cases the worms died in the 'wrong' type of chamber and in others they remained alive but did not breed. It is possible that the four species which did not breed failed to do so because the correct type of chamber was not discovered. Table 11 shows the preferred type of chamber and the types of chamber in which the worms died or failed to breed for each species.

Table 11

The type of chamber in which worms bred or failed to breed

	Bred	Failed to breed	Died
Cognettia cognettii	Flat surfaces of soft decomposing leaves from the litter layer of Juncus moor.	Soil with high mineral content or peat soil sprinkled over the agar surface.	-

Table 11 continued — The type of chamber in which worms bred or failed to breed

	Bred	Failed to breed	Died
Cernosvitoviella briganta	Very finely divided peat with free water on the agar surface.	-	Peat with large crumbs or parts of plants. No free water in the agar surface.
Marionina clavata	Decomposing leaves and stems from the litter layer of Juncus moor.	Standard chamber.	Peat crumbs sprinkled on the agar surface.
Achaeta eiseni	Thick layer of mineral soil with much organic material.	Crumbled peat.	Peat, finely divided and wet on the surface.

Enchytraeus buchholzi bred in the standard chamber at the first attempt to culture it. Cognettia sphagnetorum grew to a large size and was very healthy in the standard chamber, and in all the above mentioned modifications, but did not fragment.

Cognettia cognettii

Two cultures, kept at 10°C. were started with two large non-mature worms in each. These became mature and laid eggs within one month. In both culture chambers eggs were laid between the agar and the leaf, and the free surface of the cocoons wrapped with mucus and small particles. After 14 cocoons had been laid, the worms each developed another ripe egg

in the body but did not lay a cocoon. After three weeks, the developing cocoons were removed and placed in fresh culture chambers. Almost immediately four new cocoons were laid in the same places as the first of the 14 cocoons laid previously. After four or five eggs per worm had been laid, the adults produced no more eggs and died in eight to ten days.

Number of worms	4
Number of eggs per cocoon	1
Total number of cocoons	20
Average number of cocoons per worm	5
Average rate of laying	7.1 days/cocoon/worm
Average hatching period at 10°C.	31.8 ± 1.4 days
Average time taken to develop to maturity	321.4 ± 2.0 days

Worms were free of yolk, moved actively and started feeding immediately.

Number of segments at hatching	21 ± 3.0 segments
Length at hatching	1.7 ± 0.1 mm.
Number of segments at 5 days	22 ± 2.0 segments
Length at 5 days	2.5 ± 0.2 mm.
Number of segments at 10 days	24 ± 5.0 segments
Length at 10 days	3.0 ± 0.6 mm.
Number of segments at 30 days	27 ± 4.0 segments
Length at 30 days	4.8 ± 0.9 mm.
Number of segments when mature	40 ± 5.0 segments
Length when mature or almost mature	22 ± 4.0 mm.

The time taken to mature was 321 ± 2.0 days. Of the worms hatched in culture, only two gained full maturity and laid ripe eggs which hatched. The others began to develop sex organs but died before they became fully mature.

Marionina clavata

Two successful cultures, kept at 10°C. were each started with two non-mature worms. These were probably hatched in August 1962, but did

not mature until March 1963 when they began to lay eggs. This was a probable development period of 31 weeks (227 days). The eggs were laid singly in cocoons in burrows inside the leaves, and wrapped in mucus with a few particles of debris. Within ten days of laying the last egg the mature worms died with a few small, unripe ova in the body cavity. The cocoons hatched after an average period of 48.3 ± 4.0 days. The young worms were free of yolk, active and started feeding in the first or second day.

Number of worms	4
Number of eggs per cocoon	1
Total number cocoons	24
Average number cocoons per worm	6
Average rate of laying	13.3 days/cocoon/worm
Average hatching period	48.3 ± 4.0 days
Average time to develop to maturity	64.5 ± 3.0 days (18 worms) and 223 ± 12.0 days (6 worms)

Number of segments at hatching	14 ± 3.0 segments
Length at hatching	1.4 ± 0.1 mm.
Number of segments at 5 days	15 ± 3.0 segments
Length at 5 days	1.6 ± 0.1 mm.
Number of segments at 10 days	19 ± 4.0 segments
Length at 10 days	2.1 ± 0.2 mm.
Number of segments at 30 days	21 ± 4.0 segments
Length at 30 days	3.8 ± 0.5 mm.
Number of segments when mature	28 ± 3.0 segments
Length when mature	6 ± 1.0 mm.

Growth was slow in the first ten days, but after that 18 of the worms grew rapidly and were adult size with developing sex organs in 59 to 68 days. Six of the worms grew more slowly and did not mature for 212 to 241 days. This longer period approximates to that estimated for the original worms in the cultures. Worms with long and worms with short

developmental periods occurred in the same culture chamber. As the cultures were kept at a constant 10°C. the difference in development time could not have been caused by physical environmental factor. As all the parent worms had the longer development period it is not likely that two species were involved. From this evidence it seems possible that Marionina clavata can lay two types of eggs which differ in the time they take to develop to mature worms.

Cernosvitoviella briganta

A total of 31 cultures, each originally inoculated with ten worms, had cocoons laid in them. Twenty one cultures were kept at 10°C. and ten at 5°C. The original worms were mature when taken from the field and contained ripe eggs. Attempts to bring non-mature worms to maturity in culture were unsuccessful. Of the 65 cocoons laid at 10°C. only 10 hatched, and none of the cocoons laid at 5°C. were fertile. The mature worms died at all stages of egg laying after the start of the culture, some before laying any eggs, others after one egg had been laid, and some worms after laying several eggs.

Total number of worms	310	
Number of eggs per cocoon	1	
Total number cocoons at 10°C.	65	
Total number cocoons at 5°C.	19	
Total number of worms which laid eggs at 10°C	42	
Total number of worms which laid eggs at 5°C	19	
Number of cocoons per worm at 10°C.	1.5	
Number of cocoons per worm at 5°C.	1	
Average rate of laying at 10°C.	15.6	days/worm/cocoon
Average rate of laying at 5°C.	31.5	days/worm/cocoon
Average hatching period at 10°C.	33.7 days ± 3.0	
Average time to develop to maturity	55.6 days ± 3.0	

Growth at 10°C.	
Number of segments at hatching	12 ± 2.0 segments
Length at hatching	0.9 ± 0.1 mm.
Number of segments at 5 days	17 ± 3.0 segments
Length at 5 days	1.7 ± 0.1 mm.
Number of segments at 10 days	19 ± 3.0 segments
Length at 10 days	2.4 ± 0.1 mm.
Number of segments at 30 days	25 ± 4.0 segments
Length at 30 days	4.7 ± 0.2 mm.
Number of segments at maturity	27 ± 5.0 segments
Length at maturity	5.2 ± 0.3 mm.

The young hatched after 33.7 ± 3.0 days at 10°C., they were very active and free of yolk. Growth was rapid and mature worms appeared in 55.6 ± 4.0 days. Three newly hatched worms collected at Moor House became mature in 54.0 ± 3.0 days. The worms reared in culture failed to lay any fertile eggs.

Enchytraeus buchholzi

Four cultures were started, each with two non-mature worms. Two of the worms matured in the same culture chamber and five cocoons, each with two eggs, were laid in four weeks. The cocoons were deposited on the surface of the agar and wrapped with mucus and soil particles. The adult worms then had ripe eggs in the body but did not lay more cocoons until the first cocoons hatched. The second batch of five cocoons were laid in the same sites as the first five. The hatching period was 35 days and the young worms were active and free of yolk. In all the cocoons both worms grew to about the same size and hatched at the same time.

Total number of worms	2
Number of eggs per cocoon	2
Total number of cocoons	10
Average rate of laying	20.5 days/worm/cocoon
Hatching period	35 days
Time to develop to maturity	more than six months
Number of segments at hatching	9 ± 2.0 segments
Length at hatching	1.9 ± 0.1 mm.
Number of segments at 5 days	14 ± 3.0 segments
Length at 5 days	2.4 ± 0.2 mm.
Number of segments at 10 days	21 ± 4.0 segments
Length at 10 days	4.3 ± 0.3 mm.
Number of segments at 30 days	25 ± 5.0 segments
Length at 30 days	6.7 ± 0.5 mm.
Number of segments when mature	30 ± 4.0 segments
Length when mature	9.4 ± 1.1 mm.

None of the worms hatched in culture had matured, by August 1964, the time taken to develop to maturity in culture at 10°C. was, therefore, more than six months.

Achaeta eiseni

Five mature worms in three chambers gave information on breeding. Thirteen cocoons each with a single egg were laid on the surface of the agar and wrapped in mucus and soil. Four eggs failed to develop. The young worms hatched after an average period of 104.7 ± 9.0 days. The posterior segments still contained yolk granules and the worms moved very slowly. Because of the opacity of the yolk granules and the absence of setae it was difficult to count the number of segments. None of the worms hatched in culture matured in five months, but five newly hatched Achaeta sp. collected in the field matured in 145 ± 2.6 days but did not lay cocoons. They were identified as A. eiseni.

Number of worms	5
Number of eggs per cocoon	1
Total number of cocoons	13
Rate of laying	15 days/worm/cocoon
Hatching period 10°C.	104.7 days ± 9.0
Time to develop to maturity 10°C.	145 days ± 26.0
Number of segments at hatching	7 ± 1.0 segments
Length at hatching	1.3 ± 0.1 mm.
Number of segments at 5 days	9 ± 1.5 segments
Length at 5 days	1.7 ± 0.1 mm.
Number of segments at 10 days	12 ± 2.0 segments
Length at 10 days	2.8 ± 0.1 mm.
Number of segments at 30 days	22 ± 3.0 segments
Length at 30 days	5.6 ± 0.3 mm.
Number of segments when mature	32 ± 3.0 segments
Length when mature	10 ± 2.0 mm.

Cognettia sphagnetorum

Cognettia sphagnetorum reproduces by regenerating body fragments consisting of several segments. Spontaneous fragmentation did not occur in the culture chambers. Fragments were cut from large healthy worms, placed in new culture chambers, and the growth of new head and tail ends was measured. At 10°C. it was found that an average of 28 days was needed for the mouth to break through and the worm to start feeding. An average of 57 days was needed for a fragment to become a worm indistinguishable from a whole worm. At 5°C. the corresponding time intervals were 39 days and 76 days.

Discussion

In order to obtain a picture of life cycles of species of Enchytraeidae at Moor House the data from field and laboratory must be combined. Two estimates of the time taken to develop to maturity from

hatching are available, one from cultures and the other from field data. Information on the length of the mature and post-mature stages, and the time taken for the cocoon to develop is available only from the laboratory results. Although cultures were kept at 5°C. and 10°C. only worms kept at 10°C. provided breeding data. Table 12 shows the incubation period and both the field and laboratory estimates of the time taken to develop to maturity.

Table 12

Laboratory and field data showing the incubation period and the time taken in days, to develop from hatching to maturity, for five species of Enchytraeidae

	Incubation	Development to maturity from hatching	
		In culture 10°C.	Field estimate
Cognettia cognettii	32	321	300
Enchytraeus buchholzi	35	> 180	
Achaeta spp.	105	145	
Marionina clavata	48	65 & 223	36-89 ?
Cernosvitoviella briganta	34	56	57-90 ?

It has only been possible to make field estimates of the development period for three species, Cernosvitoviella briganta, Marionina clavata and Cognettia cognettii. The numbers of non-mature Achaeta spp. and

Fridericia spp. are too high throughout the year for any change in generations to be apparent. It is assumed that a significant rise in the total number of these species is caused by hatching even if young worms have not been recorded.

It can be seen from Table 12 that Cernosvitoviella briganta and Marionina clavata take almost three months to develop to maturity at 10°C. The lack of a second peak in the number of newly hatched worms suggests that there is only one generation per year.

As some individuals of Marionina clavata developed very slowly in culture in spite of the relatively high temperature, it seems likely that the large proportion of non-mature worms present in the winter population is caused by slow maturation rather than the loss of sex organs. This is in contrast to Cernosvitoviella briganta with 90 per cent of the population mature during the winter months and only one developmental period in culture.

The development periods measured in the laboratory indicate that it would not be possible for Cognettia cognettii, Achaeta eiseni or Enchytraeus buchholzi to have more than one generation a year. The cultures were kept at 10°C. throughout the life cycle of the worms. As 10°C. represents the maximum temperature at Moor House it is possible that at field temperatures more than one year is necessary for Achaeta eiseni and Enchytraeus buchholzi to complete their life cycles. With Cognettia cognettii however, the August and September population are composed mainly

of mature and juvenile worms so that it appears that the life cycle is an annual one.

The most abundant species of enchytraeid worm in the soils at Moor House is Cognettia sphagnetorum which reproduces asexually. The rate of reproduction, as measured by the proportion of regenerating fragments in the population, increases in the spring and summer and decreases in the winter. Culture data show that regeneration is complete in two months at 10°C. and two and a half months at 5°C. so that several cycles may be completed in a year.

The general picture of life cycles of sexually reproducing Enchytraeidae at Moor House is one in which cocoons hatch during the spring and summer and mature and non-mature worms are present during the winter. This corresponds with the situation in North Wales (O'Connor 1958) and in sewage bacteria beds (Reynoldson 1947), but because of the lower winter temperature and the shorter summer at Moor House the period during which newly hatched worms are present in the soil is shorter. Nielsen (1955) describes population densities in soils in Denmark where the summer drought conditions are an important factor in the life cycle. The Enchytraeidae populations have a spring and autumn peak and a summer minimum during the drought. A situation similar to this was seen at Moor House in 1962 in the numbers of Cernosvitoviella briganta when a minimum in the numbers of juvenile worms coincided with a period of dry weather.

VI. VARIATIONS IN THE NUMBERS OF TOTAL ENCHYTRAEIDAE

VARIATION IN NUMBERS OF TOTAL ENCHYTRAEIDAE

Introduction

The variations in the numbers of individual species at each site combine to give the variations in the number of total Enchytraeidae on each site which are shown in Fig. 24. On Bare Peat, where only one species is present, the variation is the same as that shown in Fig. 22 for total Cognettia sphagnetorum. This is also the case on the Mixed moor site, where the variation in total Cognettia sphagnetorum is the same as for Fig. 21.

On the remaining three sites the variations in numbers of each species do not necessarily coincide so that the variations of the total worms are not proportionately as great as those for the individual species on that site.

Fig. 24 shows the variation in total worms on the Nardus, Limestone grassland and Juncus sites. In 1962 there were relatively slight variations in numbers of total worms on all three sites. The summer increase in the Juncus site is more marked than on the other two sites, owing to the coincidence of the hatch of C. briganta and M. clavata. The most striking factor of the three figures is the large drop in numbers over the winter of 1962-63 and the rather more irregular pattern of increase in the summer on Nardus and Limestone sites.

Fig. 24. The seasonal variation in mean density of total Enchytraeidae on A. Juncus squarrosus moor, B. Limestone grassland and C. Mixed moor, 1962 and 1963. Density is expressed as thousands per square metre on a logarithmic scale which is different for each site. The standard errors of the mean are shown.

Fig. 24.

SEASONAL VARIATION IN DENSITY : TOTAL ENCHYTRAEIDAE

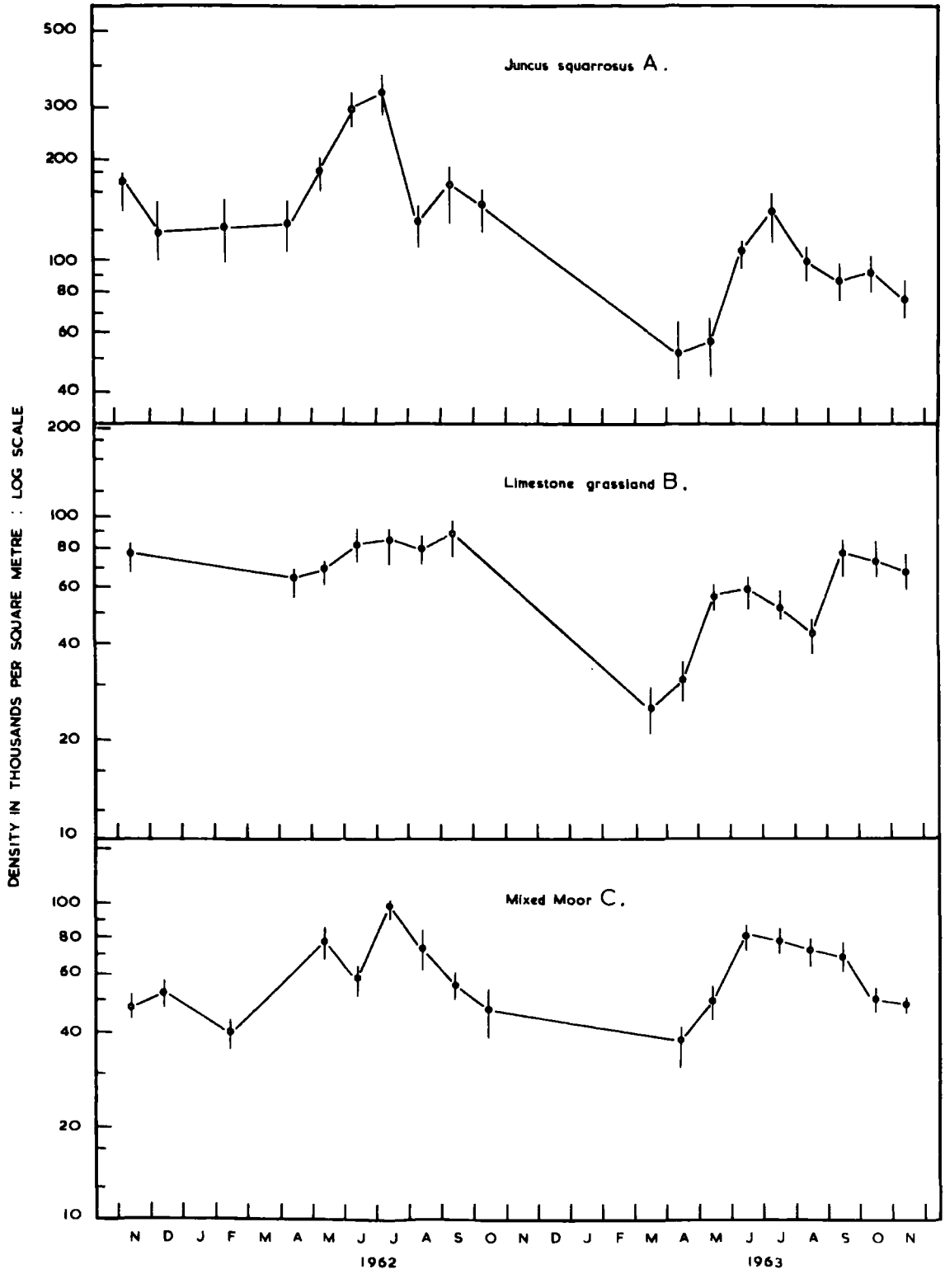
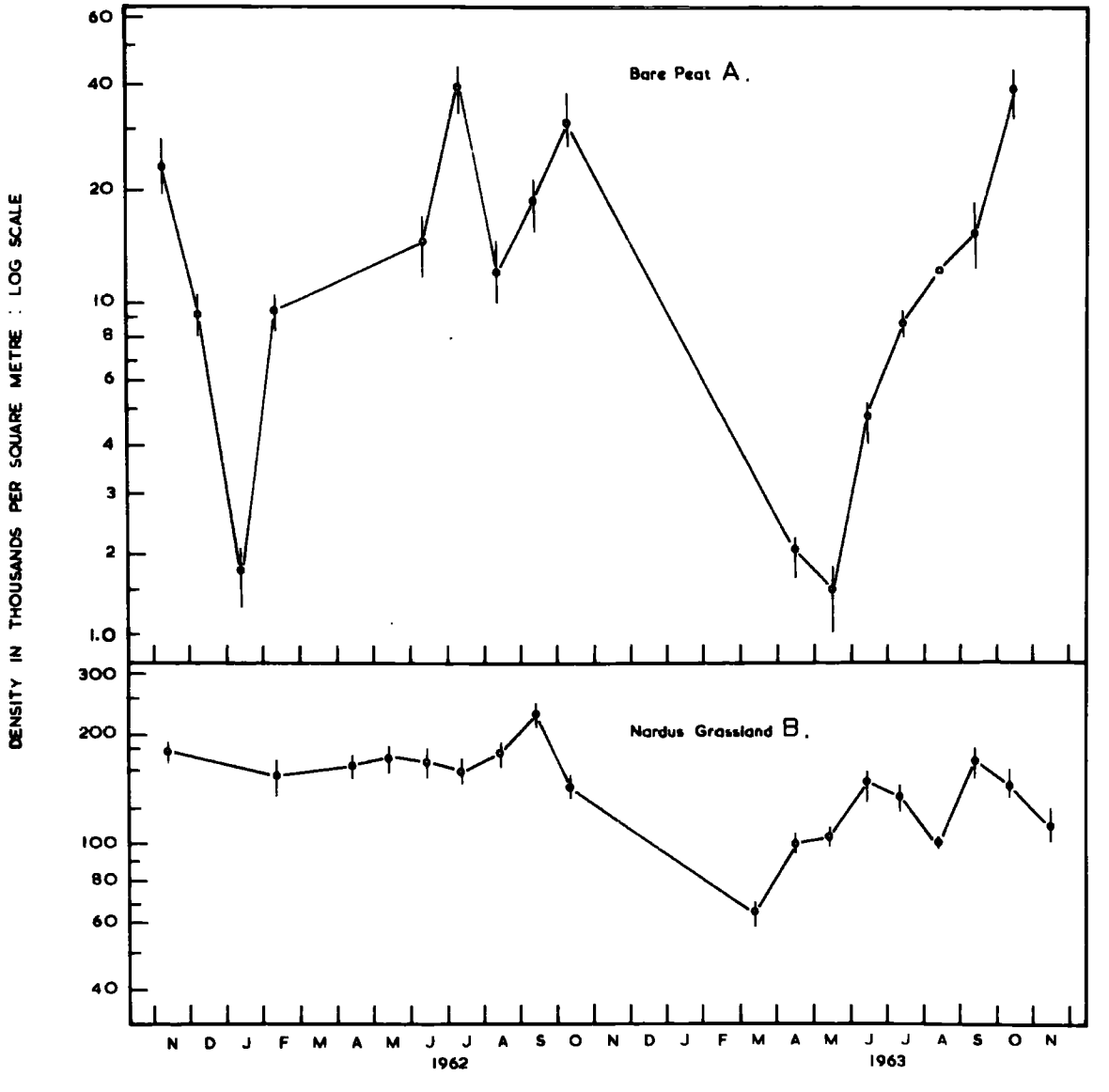


Fig. 24. The seasonal variation in mean density of total Enchytraeidae on A. Bare Peat and B. Nardus stricta grassland, 1962 and 1963. Density is expressed as thousands per square metre on a logarithmic scale which is different for each site. The standard errors of the mean are shown.

Fig. 24. contd.

SEASONAL VARIATION IN DENSITY : TOTAL ENCHYTRAEIDAE



Because of the variations amongst the breeding cycles of different species, the species composition of the sites alters throughout the year. For example the proportions of Cernosvitoviella briganta on Nardus and Juncus are very small in the winter populations and increase when the cocoons hatch in the early summer. In most cases a change in the number of one species results in a change in the total number of enchytraeids but on Limestone grassland in 1962 the proportion of Fridericia spp. and C. sphagnetorum varied inversely so that the total number of Enchytraeidae did not vary significantly.

It has been shown that Cognettia sphagnetorum forms the major part of the population during the winter months and the species which reproduce sexually are more important during the summer.

Causes of variation in total Enchytraeidae

Variations in the numbers of Enchytraeidae in the sample site are caused by breeding and mortality. Nielsen (1955) has stated that at Mols, areas of soils denuded of enchytraeids by drought have taken several years to be recolonised by worms from the surrounding soil. It appears that horizontal migration of worms can be discounted as a cause of seasonal variation in densities in the sample sites. The variations caused by breeding have already been dealt with in the section on life cycles.

The main causes of mortality are old age, predation and parasitism, and adverse physical environmental factors, such as drought, which may

cause death by desiccation. The death of old worms following reproduction has been recorded in culture. The field evidence for this has been described previously. Predation of Enchytraeidae has not been studied, although certain larvae of Tipulidae (Dipt.) and flat worms (Platyhelminthes) have been seen attacking and eating enchytraeids in culture. Nelson (pers. comm.) has found Empidae (Dipt.) at Moor House with guts full of enchytraeid seta. Enchytraeidae may compete for food but until further data on feeding of Enchytraeidae are available it is not possible to state whether the food supply limits the population density in any way.

Physical environmental factors

A series of experiments have been carried out to discover the degree of heating and desiccation which enchytraeids can withstand. The experiments were carried out with only two species from Moor House as plentiful supplies of the other species were not available. The species used were Cognettia sphagnetorum and Cernosvitoviella briganta, one medium sized and one small worm.

Heat Death

A method modified from that used by Milkman (1963) for Drosophila was used. Experiments were carried out with healthy worms which had been kept in culture chambers at 10°C. for two weeks. Fifteen worms were dropped into a test tube of tap water kept at a steady temperature

in a water bath. After 30 minutes the worms were taken out of the test tube, examined, and put back in to their culture chamber. The chamber was then placed in a cold room at 10°C. The number of dead worms were recorded and the chambers examined every two hours for the first eight hours and twice a day for two weeks. The experiment was repeated using a range of temperatures 36°C., 29°C., 24°C., 19°C., 14°C., 9°C. Further experiments using worms which had previously been kept at 2°C. or room temperature (13°-20°C.) were carried out. A control experiment in which worms were placed in test tubes of tap water at the same temperature as that of their culture chambers was carried out.

In all cases the worms immersed in water at 36°C. for 30 minutes were dead on the first examination. In all the other cases the worms were alive on the first examination and remained alive for at least two weeks after the experiment.

The maximum soil temperature at Moor House is usually in the region of 12°C., and as worms were kept in culture at 20°C. for several weeks. it can be assumed that heat death is not important in the natural ecology of Enchytraeidae on the Nature Reserve.

Desiccation

Humidity chambers were made by placing small watch glasses face down on petri dishes and sealing the edges with vaseline. Chambers with a relative humidity of 100 per cent were made by placing a large drop of distilled water on the petri dish below the watch glass. The petri

dishes were placed on wet filter paper in a large plastic container, the top of which was covered by a wet cloth. This arrangement was maintained for several hours before the worms were introduced. Single worms were blotted on filter paper and placed on the watch glass above the drop of water. The dishes were kept at 10°C., 5°C. and room temperature, approximately 18°C., and the worms examined every 15 minutes. A control series of chambers was set up with the worm in the drop of water.

The experiment was carried out with the following species, Fridericia bisetosa, Mesenchytraeus sanguineus, Cognettia sphagnetorum and Marionina clavata. In all cases the worms started to secrete mucus onto the surface of the skin as soon as they had been blotted dry. This resulted in a rapid shrivelling of the worm and death followed very quickly. The worms in the control experiments remained alive and healthy.

Table 13

Time taken for worms to die

at 100% RH at 5°C., 10°C. and 18°C.

	Time of recorded death (mins.)			
	5°C	10°C.	room temp.	number of worms used
Mesenchytraeus sanguineus	45	45	30	10
Fridericia bisetosa	60	45	30	6
Marionina clavata	45	30	15	5
Cognettia sphagnetorum	45	30	13	10

As death is so rapid at 100% RH it is obvious that the presence of free water in the soil is of prime importance to enchytraeids.

Freezing

Worms of all the major species found at Moor House have been frozen to 0°C. in water and thawed out again with no apparent ill effects. Worms have been successfully extracted from frozen soil cores.

From these laboratory experiments it can be seen that the physical factor of the greatest importance to enchytraeids is the soil moisture. Even a short period without direct contact with water can be fatal. Unfortunately it has not been possible to carry out these experiments with cocoons.

Seasonal variation of Enchytraeidae in relation to the weather

It has been seen from laboratory results that the most important physical factor influencing the mortality of Enchytraeidae is the water content of the soil.

The soil moisture content has been found at the time of sampling. Periods of drought are also indicated by the ratio of precipitation to evaporation which is recorded daily at Moor House. The days on which the evaporation is greater than precipitation are those on which the soil is drying out. However, the number of consecutive days needed to reduce the water content to a lethal level for Enchytraeidae depends on the rate of drying and the original water content. During the study period summer drought has been relatively unimportant compared with the situation recorded by Peachey (1957) when the population was drastically reduced.

It is probable that the dry spell in both summers (1962 and 1963) may have reduced the number of juvenile worms in the soil. But the major weather factor during the study period was the severe winter of 1962-63. The population level of enchytraeids in 1963 was much lower than that in 1962. As enchytraeids have been successfully frozen and thawed in the laboratory it is probably not the direct effect of cold which reduced the population. The worms were possibly trapped by ice and the ice then sublimated by winds which blew away the protective snow cover and death was most probably caused by desiccation.

The genus Cernosvitoviella was apparently better able to recover from the severe winter than Marionina. It is likely that as Cernosvitoviella has a high proportion of mature worms early in the autumn most of the cocoon deposition takes place before winter begins. Nielsen (1955) suggests that cocoons, with their protective covering are better able to withstand drought than are adult worms. It is probable that M. clavata lays more of its eggs in the spring and that the adult worms which would have laid eggs in the spring of 1963 were killed. The density of Cognettia sphagnetorum was also lower in 1963. The very low temperatures may have inhabited any reproduction which would normally have taken place. As C. sphagnetorum has no drought resistant cocoon stage in its life cycle, drought conditions would increase the mortality.

Discussion

As seen in the previous section the life cycles of the sexually reproducing Enchytraeidae at Moor House cause a spring and summer maximum

and a late winter minimum in population densities. With the asexually reproducing species, Cognettia sphagnetorum, the changes in density are not so rapid, as reproduction occurs throughout the year though at an accelerated rate in the summer.

The situation is seen to be much more like that recorded by O'Connor (1957, 1958) for Enchytraeidae in N. Wales than was recorded by Nielsen (1952) for worms in Denmark. These results endorse the view of O'Connor (1957) that in the absence of prolonged drought or other adverse environmental factors the population density of enchytraeid worms is closely correlated with temperature. However, the laboratory studies of life cycles show that a continously high temperature does not result in more than one generation per year so that the relationship for Moor House worms between temperature and densities is not as simple as it would appear. The abundance and wide distribution of the asexually reproducing species Cognettia sphagnetorum emphasizes the fact that drying of the soil is not a common occurrence at Moor House.

VII. THE VERTICAL DISTRIBUTION OF ENCHYTRAEIDAE

THE VERTICAL DISTRIBUTION OF ENCHYTRAEIDAE

Introduction

An increase in the proportion of enchytraeid populations in the subsurface layers of the soil during drought has been observed at Moor House (Peachey 1959), and in North Wales (O'Connor 1957).

It has been suggested by O'Connor (1957) that the increase in the proportion of the Enchytraeidae at low levels in the soil is caused by differential mortality and hatching. Peachey (1959) suggests that the changes in proportion are caused by vertical migration of the worms. The following work was done to investigate the vertical distribution of Enchytraeidae and their movement in response to drying. Information was obtained for each of the major species and for the total Enchytraeidae.

As previously described, soil cores six cm. deep were taken during most sampling months and cut into four layers in the field. In the summer months, May, June, July and August, cores 12 cm. deep were taken and cut into eight layers in the field.

The number of worms in each layer is expressed as a percentage of the worms in the sample, both for the total Enchytraeidae and for each of the major species.

The variations in the soil water content have already been described. Table 4 shows the indices of humidity for each sample site. Of the five sample sites, the two blanket peat sites, Mixed moor, and Bare peat, differ from the other three sites in having a lower index of humidity in

the 0-3 cm. layer than in the 3-6 cm. layer on all sampling occasions. In drought conditions the Mixed moor dries in such a way that a surface crust of dry litter 6-9 cm. thick forms and lifts away from the peat, leaving a space between the relatively moist peat and the dry litter layer. This crust acts as a protective layer and decreases the rate of drying of the peat. The remaining four sites were all in a position to receive run-off water from the blanket peat during dry weather. However, during very dry weather these sites dry out from the top without the formation of a protective crust.

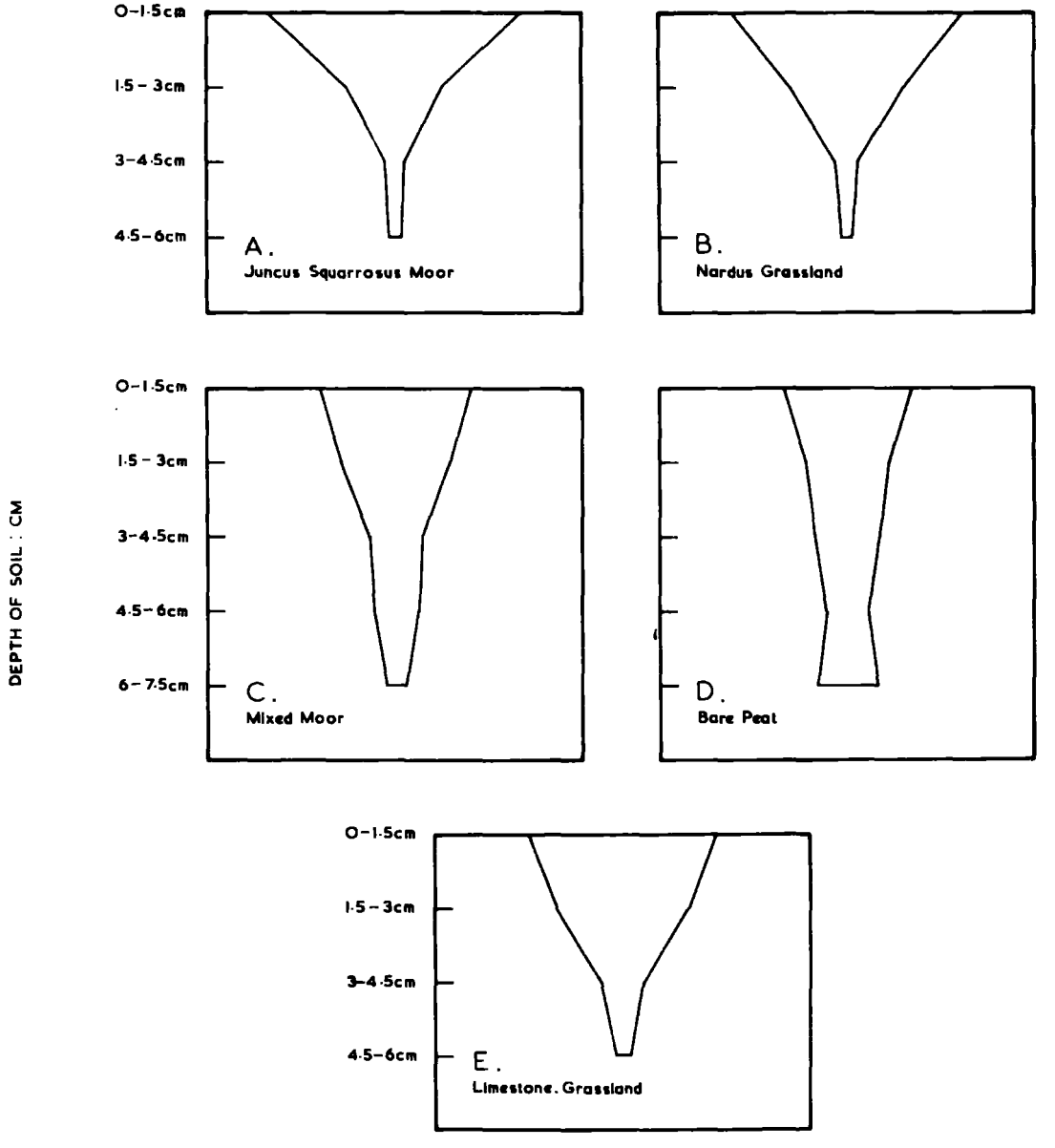
The average percentage vertical distribution of the total number of Enchytraeidae extracted

The average percentage vertical distribution of the total number of worms extracted from each sample site during the sample period is shown in Fig. 25. From Fig. 25 it can be seen that on all sites the major part of the enchytraeid population is concentrated in the top 3-5 cm. of the soil. This concentration is most marked on the Nardus and Juncus sites, the Limestone grassland, Mixed moor and Bare peat sites having, on average, a somewhat deeper distribution.

The average percentage vertical distribution over the sampling period may be affected by two factors, the migration of worms in response to environmental conditions or the occurence of appreciable numbers of worms at a low level throughout the sampling period independent of environmental conditions.

Fig. 25. The average percentage of the total worms extracted from each soil layer at each sample site, A. Juncus squarrosus moor, B. Nardus grassland, C. Mixed moor, D. Bare peat, E. Limestone grassland, during 1962 and 1963. The total horizontal axis represents 100 per cent.

PERCENTAGE OF TOTAL WORMS EXTRACTED FROM EACH SOIL LAYER DURING TWO YEAR SAMPLE PERIOD



The vertical migration of total Enchytraeidae in response to the drying of the soil

The percentage of the total number of worms extracted from each soil layer for each sampling month is shown in Table 14. It can be seen from Tables 4 and 14 that on the blanket peat sites worms were extracted from below their usual lower limit in the soil during dry weather and the population densities did not differ significantly from those found in the wet months (Fig. 24). It is because the worms were found at depths where they are normally absent that vertical migration is clearly demonstrated. Differential mortality and/or breeding would not cause worms to appear below their normal lower limit in the soil although it might alter their percentage vertical distribution within their normal habitat.

On the other three sites Juncus, Nardus and Limestone grassland, the soil surface dried out slightly and there was a slight indication of vertical migration within the top 6 cm. of soil. In these cases differential mortality cannot be entirely ruled out. It was to study vertical movement in these soils that laboratory experiments were devised.

Laboratory experiments on vertical migration

These experiments were designed to give information on the speed of movement of the worms and the amount of drying necessary to cause vertical migration.

Fig. 26. The average percentage of A. Cognettia sphagnetorum, B. Cernosvitoviella briganta and C. Marionina clavata extracted from each soil layer in the Juncus squarrosus moor sample site in 1962 and 1963. The total horizontal axis represents 100 per cent.

PERCENTAGE OF TOTAL OF EACH SPECIES EXTRACTED FROM EACH SOIL LAYER DURING TWO YEAR SAMPLE PERIOD
JUNCUS SQUARROSUS MOOR

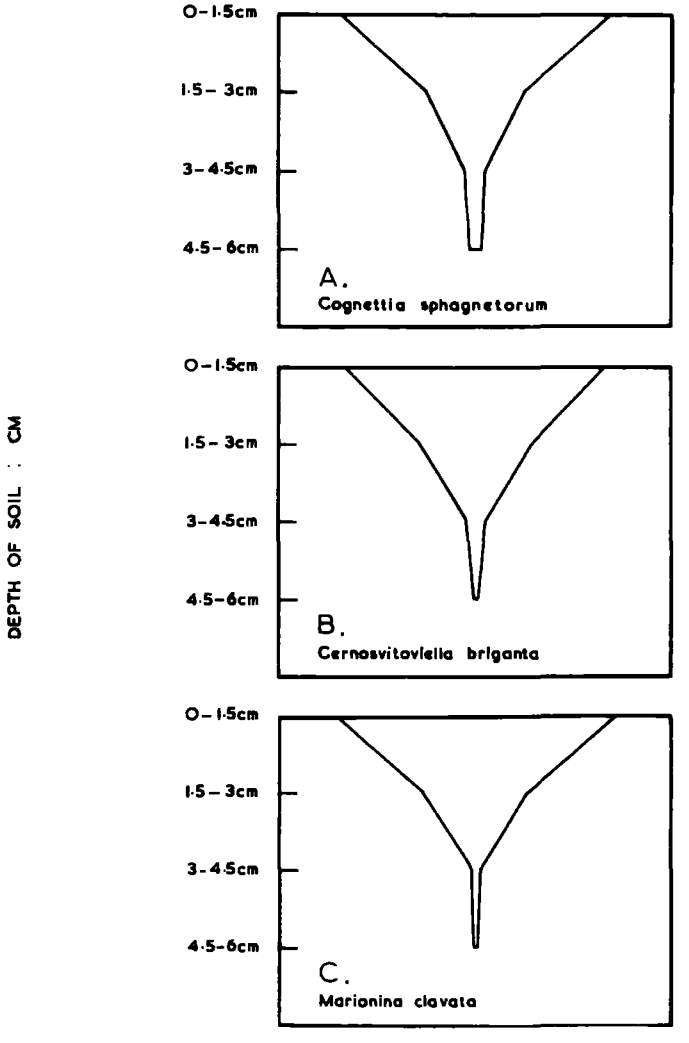


Table 14

The percentage of total Enchytraeidae in each soil layer in each sample month

Juncus squarrosus moor

	Depth in cm.			
	0-1.5	1.5-3	3-4.5	4.5-6
Nov. 1961	67	23	7	3
Feb. 1962	48	38	10	3
Apl.	50	34	9	7
May	46	46	4	4
June	36	46	9	9
July	88	10	1	1
Aug.	82	16	1	1
Sept.	79	19	1	1
Oct.	58	40	1	1
Nov.	61	35	3	1
Apl. 1963	64	31	5	1
May	80	16	2	2
June	42	28	22	7
July	74	14	11	1
Aug.	64	22	12	1
Sept.	32	13	1	4
Oct.	86	6	2	5
Nov.	76	14	8	2

Table 14 (Cont'd) The percentage of total Enchytraeidae in each soil layer in each sample month

	Depth in cm. 0-1.5	1.5-3	3-4.5	4.5-6
Limestone grassland				
Nov. 1961	43	38	14	5
Feb. 1962	24	39	24	13
Apl. 1963	33	43	14	10
June	52	28	14	6
July	46	38	10	6
Aug.	72	21	5	3
Sept.	55	24	19	1
Oct.	49	39	10	2
March 1963	50	35	12	3
Apl.	63	25	8	4
May	55	35	9	1
June	44	40	11	5
July	67	17	9	7
Aug.	47	30	12	10
Sept.	51	41	5	3
Oct.	66	23	8	2
Nov.	44	46	7	2
***Nardus stricta* grassland**				
Nov. 1961	36	52	9	2
Feb. 1962	14	55	25	5
Apl. 1962	29	57	11	2
May	53	43	4	1
June	62	28	7	3
July	49	46	3	2
Aug.	60	29	7	4
Sept.	57	35	5	2
Oct.	74	21	2	2
March 1963	91	7	1	1
Apl.	80	18	2	1
May	68	30	1	1
June	73	26	1	1
July	94	6	1	0
Aug.	61	27	10	1
Sept.	86	13	1	1
Oct.	76	15	4	5

Table 14 (Cont'd) The percentage of total Enchytraeidae in each soil layer in each sample month

Bare peat

	Depth in cm. 0-1.5	1.5-3	3-4.5	4.5-6	6-7.5	7.5-9	below 9
Oct. 1961	41	33	22	4			
11.12.61	40	36	27	7			
Jan. 1962	65	31	4	0			
Feb.	12	20	29	36	1	1	
Apl.	47	38	10	5			
May	51	39	7	3			
June	45	19	16	6	5.	4	5
July	8	7	6	9	21	24	25
Aug.	55	34	5	4	2		
Sept.	41	12	18	14	10	5	
Oct.	65	28	3	4			
Apl.	15	21	36	26	2		
May	30	30	20	19	1		
June	28	28	20	21	3		
July	11	7	27	41	9	5	
Aug.	33	37	16	10	3	1	
Sept.	73	12	7	8			
Oct.	18	39	42	1			

Mixed Moorland

Oct. 1961	40	26	19	16			
Dec. 1961	40	27	19	14			
Feb. 1962	22	43	22	13			
May	38	35	18	6	3		
June	21	20	24	22	7	5	1
July	14	13	13	27	25	6	2
Aug.	32	61	6	1	difficulty in sampling		
Sept.	51	43	3	3			
Oct.	73	20	5	2			
Apl.	62	23	12	2	1		
May	40	23	16	18	3	1	
June	34	44	10	8	3	1	
July	20	17	15	10	25	13	
Aug.	22	27	26	17	7	1	
Sept.	51	33	7	6	2		
Oct.	54	21	17	8			
Nov.	59	21	14	6			

Nine turves 300 cm.^{2} x 9 cm. deep were cut from the Nardus grassland site, placed in water-tight containers and taken to the laboratory. Two control turves, A and B, were opened just before extraction, A at the beginning and B at the end of the experiment. The surfaces of the other seven turves C, D, E, F, G, H, I were uncovered and dried for 24 hours with a current of air from an electric fan. Four turves C, D, E and F, were dried continuously throughout the experiment and after an initial period of twenty four hours were extracted at twelve hourly intervals. The three remaining turves G, H and I were dried for an initial period of twenty four hours, drying was then stopped and the turves wetted and worms extracted at twelve hourly intervals. They were given sufficient water to soak the top of the turf without flooding the container. The temperature of the turves varied between 9°C. and 11°C. throughout the experiment. The turves were cut into three equal horizontal layers just before extraction, half of each layer being used to determine the index of humidity (Table 15). The percentage of enchytraeids in each layer and the total number of worms extracted for each turf are shown in Table 16. The indices of humidity for each turf are shown in Table 15.

It can be seen from Tables 15 and 16 that in the laboratory reducing the index of humidity from 2.9 to 1.9 decreases the proportion of worms in the surface layer by 20 per cent. It appears that on Nardus,

Table 15

Index of humidity of turves during laboratory experiments on vertical migration of Enchytraeidae

Turf	depth 0-3 cm.	3-6 cm	6-9 cm.
A	2.9	2.6	1.3
B	2.9	2.5	1.5
C	2.0	2.1	1.8
D	1.9	2.2	1.4
E	2.5	2.2	1.6
F	1.7	1.3	1.9
G	2.3	2.5	1.8
H	4.2	3.6	2.4
I	4.8	3.8	2.2

Table 16

The percentage of enchytraeids in each soil layer and the total number of worms extracted from each turf

Turf code letter	0-3 cm.	3-6 cm.	6-9 cm.	Total number of worms extracted
A	41	27	32	1,110
B	51	31	18	1,165
C	23	26	51	951
D	21	42	37	1,080
E	34	36	30	936
F	24	35	43	1,007
G	36	34	30	1,014
H	54	28	18	1,072
I	65	14	23	916

the worms move out of the surface layers as the index of humidity drops below 2, as in turves C, D and F, and move back into the surface layers as the index of humidity rises above 2, as in turves E, G, H, I, and the controls A and B. In comparing these results with the field data it can be seen that the index of humidity of the sample cores was as low as 2 only on one occasion, July 1962, and was below 2.5 only in July, August, September 1962 and August 1963. In July 1962 and August 1963 there were slight indications of downward movement of the worms. The rapidity of the vertical migration of the worms in the laboratory indicates that the worms are highly mobile and capable of retreating from the soil surface at the beginning of a drought and also that they respond to short periods of drying.

Discussion

Vertical migration of Enchytraeidae in response to drying has been demonstrated in the field for the blanket peat sites and in the laboratory for the Nardus grassland site. In soils where there is a definite humidity gradient enchytraeids are capable of avoiding desiccation by moving deeper in the soil. It is probable that the worms are able to move deeper into the blanket peat sites than they can on the more compact mineral soil. However, as the peat dries out to a greater depth than on the mineral soil this is probably of little significance biologically.

The Enchytraeidae at Moor House tend to be small worms highly susceptible to drying out, and the most abundant species Cognettia sphagnetorum has no drought-resistant cocoon stage. It appears that at Moor House downward vertical migration is important in preventing death from desiccation and that worms are capable of rapid movement away from the surface in dry conditions and can return as soon as the soil becomes sufficiently wet.

Differences in the vertical distribution of different species of Enchytraeidae in the soil over the whole sampling period

The percentage vertical distribution of the total number of each species for each site is shown in Figs. 26-28. It can be seen that in some species the average percentage vertical distribution over the sampling period was different from that of the total worms, and the other species on that site. This is most clearly shown by Achaeta eiseni and A. affinis on the Nardus and Limestone grassland sites and Fridericia spp. on the Limestone grassland site. On the Limestone grassland site Marionina clavata shows some difference in vertical distribution to the other species there, and to its own distribution on the Juncus and Nardus sites. In all these cases the vertical distribution is deeper than that of the total worms on the site, that is a larger percentage of these species occurred in the lower layers of the soil.

The deeper distribution of Marionina clavata, Achaeta eiseni,

Fig. 27. The average percentage of A. Cognettia sphagnetorum, B. Marionina clavata, C. Cernosvitoviella briganta and D. Achaeta spp. extracted from each soil layer in the Nardus grassland sample site in 1962 and 1963. The total horizontal axis represents 100 per cent.

PERCENTAGE OF TOTAL OF EACH SPECIES EXTRACTED FROM EACH SOIL LAYER DURING TWO YEAR SAMPLE PERIOD : NARDUS GRASSLAND

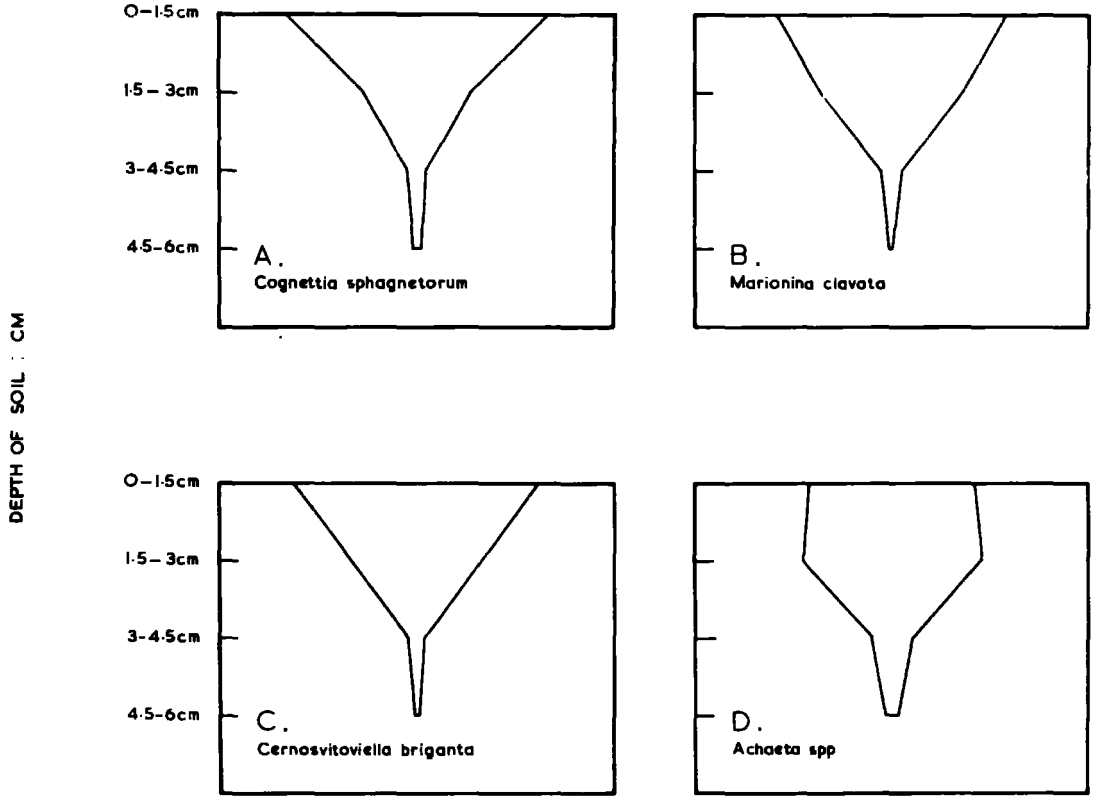
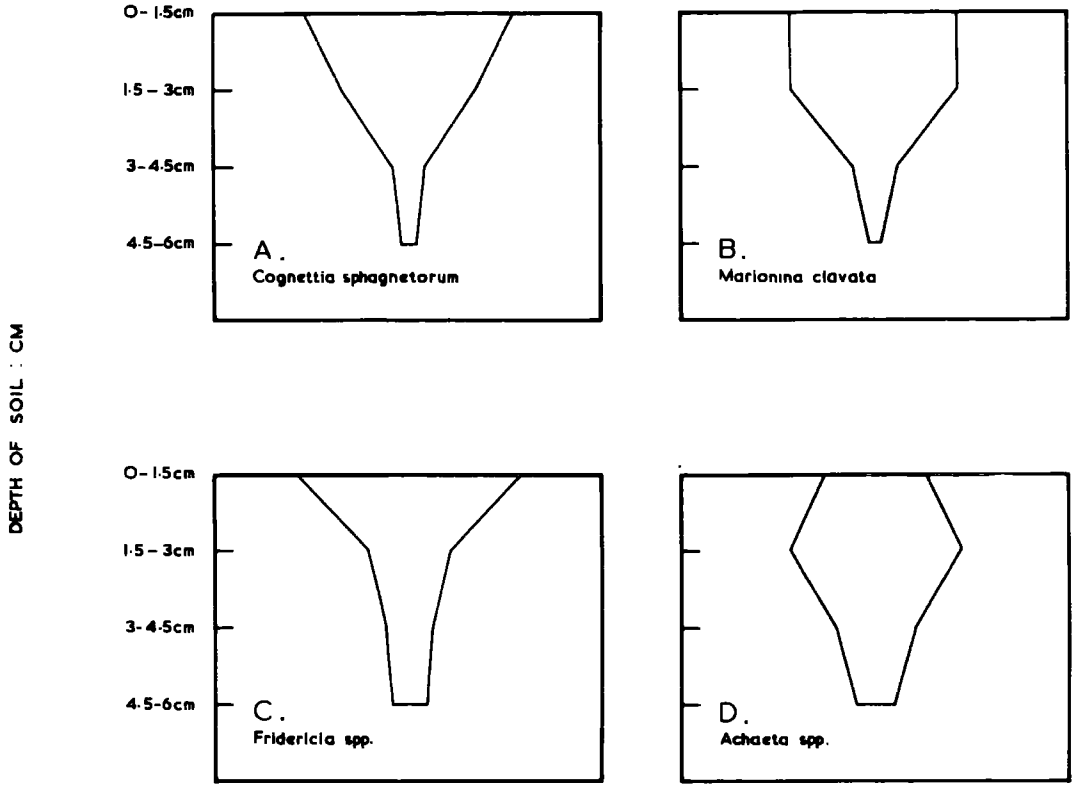


Fig. 28. The average percentage of A. Cognettia sphagnetorum, B. Marionina clavata, C. Fridericia spp. and D. Achaeta spp., extracted from each soil layer in the Limestone grassland sample site in 1962 and 1963. The total horizontal axis represents 100 per cent.

PERCENTAGE OF TOTAL OF EACH SPECIES EXTRACTED FROM EACH SOIL LAYER DURING TWO YEAR SAMPLE PERIOD : LIMESTONE GRASSLAND



A. affinis and Fridericia spp. was sufficient to make the vertical distribution of the total worms on Limestone grassland different from that on the Juncus and Nardus sites. On the Nardus site the numbers of Achaeta eiseni, A. affinis and Marionina clavata in the lower layers were not sufficient to make a difference in the vertical distribution of the total worms. On the Juncus site all the species had their greatest percentage in the surface layers.

The vertical distribution of different species

Achaeta eiseni and A. affinis

These species occurred on the mineral soils, on the Nardus stricta and Limestone grassland sites. The monthly percentage vertical distribution is shown in Table 17. On both the sites, A. eiseni and A. affinis had their largest proportion below 3 cm. in contrast to the other species on the sites. On both sites there were some months during which the greatest percentage of worms was in the surface layer of the soil, but there was no apparent pattern of vertical migration during the sampling period.

Marionina clavata

Marionina clavata was found on three sites, Nardus stricta, Juncus squarrosus moor and Limestone grassland. The average percentage vertical distribution over the sample period is shown in Figs. 26, 27, 28 and the monthly percentage vertical distribution in Table 17. The

average percentage vertical distribution over the sampling period (Fig. 24) differed for the three sites. Marionina clavata was predominantly on the surface layer in Juncus squarrosus moor, but on the Nardus site the average percentage in the 1.5-3 cm. soil layer was higher than that on the Juncus site. On the Limestone grassland site the distribution was such that the 0-1.5 cm. and 1.5-3 cm. soil layers had equal proportions of M. clavata in them.

Cognettia sphagnetorum

This species occurs in all five of the sample sites (Figs. 25-28 and Table 17). The average vertical distribution is superficial on Juncus squarrosus, Nardus stricta and Limestone grassland although a slightly higher percentage occurs in the lower layers of Limestone grassland than on the other two sites. On the Mixed moor and Bare peat sites the deeper average distribution is caused by the downward migration of worms in dry weather as can be seen from Table 14.

Cernosvitoviella briganta

C. briganta is found on the Nardus and Juncus sites (Figs. 26, 27) distribution is superficial on both sites. There is some evidence for downward migration on the Juncus site in May and June 1962 and June and August 1963.

Fridericia species

This genus is found only on the Limestone grassland site (Fig. 28).

Table 17

The percentage of each species present in each soil layer in each sample month

Juncus squarrosus moor

	Cognettia sphagnetorum				*Marionina clavata*			
	0-1.5 cm.	1.5-3 cm.	3-4.5 cm.	4.5-6 cm.	0-1.5 cm.	1.5-3 cm.	3-4.5 cm.	4.5-6 cm.
Nov.	54	35	7	4	71	15	12	2
Dec.	55	38	5	2	57	43	0	0
Feb.	44	38	11	7	69	21	0	0
Apl.	43	44	9	4	56	28	14	2
May	36	45	9	10	59	40	1	0
June	24	32	22	2	57	41	1	1
July	82	11	5	2	89	10	1	0
Aug.	93	5	1	1	79	20	1	0
Sept.	65	31	2	2	85	13	1	1
Oct.	55	40	4	1	49	39	7	5
Apl.	72	22	3	3	37	45	18	0
May	83	9	5	3	62	30	8	0
June	64	21	15	0	35	59	6	0
July	82	17	1	0	71	17	12	0
Aug.	79	18	2	1	59	18	23	0
Sept.	78	15	1	6	85	15	0	0
Oct.	85	3	2	10	77	23	0	0
Nov.	91	5	2	2	49	51	0	0

Table 17 (Cont'd) The percentage of each species present in each soil layer in each sample month

Juncus squarrosus moor

	Cernosvitoviella briganta			
	0-1.5 cm.	1.5-3 cm.	3-4.5 cm.	4-5.6 cm.
Nov.	79	18	3	0
Dec.	83	17	0	0
Feb.	84	16	0	0
Apl.	76	21	3	0
May	0	85	15	0
June	17	83	0	0
July	94	6	0	0
Aug.	83	16	1	0
Sept.	70	29	1	0
Oct.	66	34	0	0
Apl.	27	73	0	0
May	46	54	0	0
June	19	36	45	0
July	93	7	0	0
Aug.	38	26	36	0
Sept.	86	14	0	0
Oct.	93	7	0	0
Nov.	88	12	0	0

Table 17 (Cont'd) The percentage of each species present in each soil layer in each sample month

Nardus stricta grassland

	Cognettia sphagnetorum				Marionina clavata			
	0-1.5 cm.	1.5-3 cm.	3-4.5 cm.	4.5-6 cm.	0-1.5 cm.	1.5-3 cm.	3-4.5 cm.	4.5-6 cm.
Nov.	47	40	10	3	20	61	14	5
Feb.	17	49	27	7	9	80	11	0
Apl.	38	51	9	2	6	91	3	0
May	43	50	5	1	78	22	0	0
June	66	24	7	3	62	38	0	0
July	53	43	3	1	42	53	5	0
Aug.	88	6	4	2	35	60	5	0
Sept.	51	43	4	2	67	22	8	3
Oct.	83	14	1	2	75	22	2	1
March	95	4	1	0	93	5	1	1
Apl.	84	14	1	1	76	23	1	0
May	81	17	1	1	50	30	20	0
June	74	24	1	1	74	25	1	0
July	93	6	0	0	94	5	1	0
Aug.	59	30	10	1	58	39	6	2
Sept.	83	15	1	1	91	8	1	0
Oct.	91	2	1	6	39	52	8	1
Nov.	60	32	6	2	41	54	5	0

Table 17 (Cont'd) The percentage of each species present in each soil layer in each sample month

Nardus stricta grassland

	Cernosvitoviella briganta				Achaeta spp.			
	0-1.5 cm.	1.5-3 cm.	3-4.5 cm.	4.5-6 cm.	0-1.5 cm.	1.5-3 cm.	3-4.5 cm.	4.5-6 cm.
Nov.	15	85	0	0	77	23	0	0
Feb.	0	56	44	0	0	24	76	0
Apl.	-	-	-	-	0	19	69	12
May	-	-	-	-	0	96	4	0
June	20	70	7	3	62	24	10	4
July	-	-	-	-	33	64	1	2
Aug.	21	79	0	0	12	85	3	0
Sept.	0	0	0	100	33	45	10	12
Oct.	36	54	10	0	11	61	28	0
March	76	17	4	3	-	-	-	-
Apl.	62	34	4	0	60	30	9	0
May	0	98	2	0	0	98	2	0
June	70	29	1	0	72	25	1	2
July	93	5	1	1	98	2	0	0
Aug.	79	11	10	0	38	33	15	14
Sept.	93	7	0	0	82	15	3	0
Oct.	56	34	7	3	30	40	23	7
Nov.	65	18	7	0	0	49	36	15

Table 17 (Cont'd) The percentage of each species present in each soil layer in each sample month

Limestone grassland

	Cognettia sphagnetorum				*Marionina clavata*			
	0-1.5 cm.	1.5-3 cm.	3-4.5 cm.	4.5-6 cm.	0-1.5 cm.	1.5-3 cm.	3-4.5 cm.	4.5-6 cm.
Nov.	43	52	4	1	0	13	73	14
Apl.	31	38	30	11	0	0	0	0
May	42	34	18	6	NONE PRESENT			
June	34	36	26	4	4	62	15	19
July	49	29	14	8	30	54	16	0
Aug.	74	14	8	4	64	32	3	1
Sept.	39	55	2	4	75	21	3	1
Oct.	40	54	5	1	63	28	9	0
Nov.								
March					53	37	6	4
Apl.	57	34	7	2	45	36	15	4
May	59	32	8	1	42	56	12	0
June	47	36	11	6	48	46	6	0
July	72	16	6	6	58	27	11	4
Aug.	68	17	7	8	59	28	10	3
Sept.	51	44	4	1	8	80	9	3
Oct.	88	10	1	1	13	87	0	0
Nov.	53	46	0	1	34	47	19	0

Table 17 (Cont'd) The Percentage of each species present in each soil layer in each sample month

Limestone grassland

	Achaeta spp.				*Fridericia* spp.			
	0-1.5 cm.	1.5-3 cm.	3-4.5 cm.	4.5-6 cm.	0-1.5 cm.	1.5-3 cm.	3-4.5 cm.	4.5-6 cm.
Nov.	19	23	27	31	21	32	42	5
Apl.	0	34	33	33	19	33	29	19
May	25	41	23	10	39	20	12	29
June	37	44	19	0	66	6	14	14
July	0	100	0	0	58	36	6	0
Aug.	0	33	14	53	62	29	6	3
Sept.	100	0	0	0	97	0	2	1
Oct.	1	52	32	15	42	40	13	5
Nov.								
March	38	42	20	0	40	35	17	8
Apl.	20	50	19	11	52	26	9	7
M y	31	55	14	0	69	20	10	1
June	33	44	15	8	50	39	11	0
July	45	37	11	7	50	24	12	14
Aug.	0	64	25	11	0	44	17	39
Sept.	47	42	6	5	70	17	7	6
Oct.	4	48	46	2	76	16	5	3
Nov.	19	41	31	9	43	50	5	2

Fridericia spp. show a preference for the deeper soil layers below 3 cm. A similar distribution was observed by Peachey (unpub.). There is some indication of downward migration in July 1963. The numbers of Fridericia on the Limestone grassland site are large enough for their deeper distribution to be apparent in a deeper vertical distribution of the total worms on the site.

Discussion

The pattern which emerges from the data presented here is one of the superficial distribution of Enchytraeidae on the sample sites. The vertical migration of the worms in response to weather conditions has been demonstrated and it has been shown that these movements may be rapid. The speedy return to the surface layers after downward migration indicates that for most species the optimum conditions for life are found only in the superficial layers of the soil. However, it has also been shown that some species, Achaeta eiseni, A. affinis and Fridericia spp. habitually occupy the deeper layers of the soil. It can be noted that both these genera, which occur in the deeper layers of the two mineral soils have a thicker cuticle and straighter setae than those species which occur mainly in the surface layers and on the peat soils. It seems that Achaeta spp. and Fridericia spp. are better able to penetrate the mineral soils.

It has been shown that both vertical migration in response to environmental conditions and differences amongst the usual vertical distributions of different species affect the vertical distribution of the total Enchytraeidae.

VIII. GENERAL DISCUSSION

GENERAL DISCUSSION

In this thesis the densities and species composition of Enchytraeidae populations on some moorland soils have been studied. Changes in these have been related to the life cycles of the major species and to changes in environmental conditions.

In endeavouring to relate this information to the wider field of soil biology it is important to think of the relationships of Enchytraeidae to other soil organisms, their relative importance in the soil economy at Moor House when compared with microarthropods, earthworms, nematodes and other soil animals. The role of Enchytraeidae in the breakdown of litter, their influence on the microflora and their importance in soil formation are aspects of enchytraeid activity for which quantitative data are lacking but towards which present work is now tending (O'Connor 1964, Nielsen, 1962).

It is possible to compare information on Moor House Enchytraeidae with that obtained by Nielsen (1954) and O'Connor (1957) for populations of Enchytraeidae in soils in Denmark and N. Wales. O'Connor (1963) reviews the work done on enchytraeid population densities, biomass and activity by Nielsen (1961) on heath soils in Denmark and by himself on coniferous forest soils in N. Wales. He compares the total annual mean densities, biomasses and respiratory activity and also the seasonal variations in these values for three Danish sites and one Welsh site.

For the Moor House Enchytraeidae the annual population metabolism can be estimated using the respiration data from Nielsen (1961) and O'Connor (1963). None of the species for which respiration data are available occur commonly at Moor House, therefore detailed comparison is not possible, O'Connor (1963) having shown that respiration rates can vary amongst species of the same size. Mean figures for oxygen consumption by Enchytraeidae at an average annual field soil temperature of 6°C. have been obtained for three mean body live weights of 150 μg, 270 μg and 350 μg. These weights are the approximate annual mean body live weights on Juncus squarrosus moor; Nardus stricta grassland, Mixed moor and Bare peat; and Limestone grassland respectively. The figures for mean densities, biomass and respiratory activity are presented in Table 18. The final column of energy released annually in K calories per square metre is calculated using a conversion factor of 4.8 K calories per litre oxygen after Engelmann (1966).

A detailed comparison of the Enchytraeidae in the three areas is meaningless because of the differences in the species involved. However, it can be seen that the wet 'mor' type soils at Moor House are rich in Enchytraeidae particularly the moor edge sites Juncus squarrosus and Nardus stricta grasslands. The blanket peat itself is a heavily leached impoverished site but Enchytraeidae still occur in numbers comparable with those of the relatively dry heathlands of the Danish sites. The

Danish and Welsh sites, after Nielsen (1961) and O'Connor (1963).

µl O_2/g/hr. @ 6°C	ml O_2/m^2/hr. @ 6°C	l O_2/m^2/year	Kcal./m^2/year
2.35	5.63	48.9	235.2
1.64	3.37	29.3	140.6
0.70	1.83	15.9	76.4
1.64	2.05	17.9	85.7
1.64	0.66	5.7	27.4
	@ field temp.		
	3.61	31.3	151
	0.84	7	34
	1.10	10	48
	3.70	32	154

predominance of Cognettia sphagnetorum which reproduces by fragmentation and regeneration and has no drought resistant stage indicates that drying of the soil at Moor House is a rare occurrence. Enchytraeidae can reach high densities at Moor House; the reasons for this are not clear at present but it appears that the wet climate is a factor favouring the growth of enchytraeid populations on 'mor' type soils even where these soils are relatively poor. Figures are available for the seasonal changes in numbers and age categories of Enchytraeidae at Moor House but no work has been carried out on the respiratory activity of regenerating fragments of Cognettia sphagnetorum. As the size of both fragments and whole worms is very variable throughout the year it is not possible to make a detailed month by month comparison of the type presented for the Danish and Welsh soils by O'Connor (1963). However, as Moor House is not a site on which summer drought conditions are a frequent feature of the climate it can be assumed that the population metabolism follows a pattern similar to that of the permanently wet Danish station 18 and the Welsh coniferous forest soil studied by O'Connor. In these sites the population densities, biomasses and respiratory activity had summer maxima and winter minima.

When the numbers, biomass and maintenance metabolism of Enchytraeidae at Moor House are compared with similar data for other

animal groups on the same sites (Table 19) it can be seen that Enchytraeidae are of major importance in the energy turnover of the soil. On the peat and redistributed peat soils Enchytraeidae are responsible for a large proportion of the known faunal respiratory activity, 57 per cent on Juncus squarrosus, 59 per cent on Mixed moor, 82 per cent on Nardus stricta and almost 100 per cent on Bare peat. Only on the Limestone grassland 'mull' soil are other animal groups, earthworms and craneflies (Tipulidae) more important than Enchytraeidae. Even so enchytraeids are still relatively abundant on Limestone grassland, the density and respiratory activity of Enchytraeidae on Limestone grassland is of the same order as on Mixed moor and the biomass is similar to that on Juncus squarrosus and Nardus stricta. The species composition differs markedly as has been shown previously, the Enchytraeidae on Limestone grassland tending to be larger animals than those on the peat soils.

The present amount of knowledge of the exact role of Enchytraeidae in the soil is meagre, they are assumed to belong to the secondary decomposer group of fungal and/or bacterial feeders. O'Connor (pers. comm.) has frequently seen strands of fungal hyphae in the guts of worms extracted from coniferous forest soils in N. Wales. Nielsen (1962) has tested soil and litter invertebrates including Enchytraeidae for carbohydrases. He failed to demonstrate the presence in enchytraeid

Table 19

Comparison of the known respiratory activity (K cal/m^2/year) density ($10^3/m^2$) and biomass (gm live weight /m^2) of the soil fauna at Moor House after Cragg 1961 and Macfadyen 1963

	Juncus squarrosus moor	*Nardus stricta* grassland	Mixed moor	Limestone grassland	Bare peat
Acarina					
$10^3/m^2$	43	78	54	37	neg.
gm/m^2	0.9	1.9	1.1	0.9	
K cal/m^2/yr	13	21	14	8	
Collembola					
$10^3/m^2$	13	-	32	56	neg.
gm/m^2	0.1	-	0.3	0.4	
K cal/m^2/yr	4	-	10	15	
Lumbricidae					
nos/m^2	4	-	-	389	-
gm/m^2	1.2	-	-	137	-
K cal/m^2/yr	5	-	-	333	-
Nematoda					
$10^6/m^2$	3.9	3.3	1.4	2.3	0.02
gm/m^2	1.0	-	-		
K cal/m^2/yr	2.1	10	5	10	
Tipulidae					
$10^3/m^2$	1389	-	371	49	-
gm/m^2	22	-	8	36	-
K cal/m^2/yr	131	-	30	149	-
Enchytraeidae					
$10^3/m^2$	170	120	62	59	20
gm/m^2	24	20.5	12.5	26	4
K cal/m^2/yr	235	140	86	76	27
Total K cal/m^2/yr	409	171	145	591	27
% contribution of *Enchytraeidae*	57	82	59	13	ca 100

worms of enzymes capable of digesting plant structural polysaccharides. He concluded that primary decomposition is mainly carried out by the microflora and possibly molluscs, some Diptera larvae and protozoa. The majority of those soil and litter invertebrates which are not predators are secondary decomposers, feeding either on specific bacteria or fungi(some protozoa and free living nematodes (Nielsen 1949) and some mites (Karg 1963)) or ingesting large quantities of organic matter and digesting only part of it. Enchytraeidae, earthworms and some microarthropods fall into this latter category and therefore are of great importance in soil formation and the comminution of organic debris, rendering it more susceptible to attack by microbes. The relative importance of these groups of secondary decomposers is not known. It is probable that earthworms have a greater effect because of their large size and ability to mix and aerate the soil. Micro-arthropods are capable of biting and chewing plants and fungi and are probably of greater importance in comminution than Enchytraeidae which have relatively weak sucking mouth parts. The food must be in a relatively finely divided form before Enchytraeidae can ingest it. Hale (unpub.) points out that Acarina and Collembola together are slightly more numerous on Mixed moor than Enchytraeidae and that the production of faeces is probably similar. In the absence of measurements of the faeces production rate it is not possible to say definitely which is the most

important group. The respiratory rate of Enchytraeidae on Mixed moor is three times that of microarthropods and a higher rate of energy turnover would seem to indicate a greater consumption of food and subsequently a greater production of faeces. However, as Enchytraeidae extracted from Mixed moor seldom have any visible gut contents it is possible that on the peat soils food is taken largely in the form of dissolved nutrients and faeces production may therefore be low.

It is generally assumed that Enchytraeidae take over the role of earthworms in acid 'mor' type soils, and this is so, in that they are the predominant group of secondary decomposers. However, their small size and weak mouth parts probably prevents them being as efficient as earthworms in soil formation even when they occur in large numbers. Enchytraeidae are probably of greatest significance in the soil when considered as a potential food source for predators. I have observed Tipulidae and Rhabdocoela feeding on Enchytraeidae in culture and some Empidae (Diptera) larvae, numerous on Mixed moor, apparently feed exclusively on enchytraeids. (Nelson pers. comm.). Enchytraeidae must also release substantial amounts of nutrients on death and decomposition. The sexually reproducing species have only one generation per year and Cognettia sphagnetorum, the predominant worm probably has three or more generations per year, reproduction occurring at all seasons. On Mixed moor this represents a possible annual addition to the soil of approximately 30 grams per square metre of dead Enchytraeidae.

Quantitative estimates of the importance of different animal groups in moorland soils are at present limited to evaluation of the densities, biomasses and maintenance metabolisms of the populations. Nielsen (1962) states that "the chief importance of soil and litter invertebrates must be sought in their effect upon the chemical activity of the microflora". The extent to which comminution and predation on the soil microflora by each animal group effects the rate of primary decomposition is not known. To discover this the exact food requirements, the movements and the activity of the animals within the soil must be measured.

SUMMARY

SUMMARY

1. A study of the Enchytraeidae on five sites selected on the Moor House National Nature Reserve in the northern Pennines is described. The reserve is largely covered by blanket peat and has a sub arctic climate.

2. To determine population densities a wet funnel technique was used to extract worms from soil cores.

3. Differences in the behaviour of species during extraction were observed. The stiff, slow, moving species Achaeta affinis, A. eiseni and Fridericia spp. are extracted later than Cognettia sphagnetorum, C. cognettii. Marionina clavata was mostly extracted after the Cognettia species but before Achaeta spp. and Fridericia spp.

4. A list of twenty species found at Moor House is given. Of these, Achaeta affinis, Marionina clavata, and M. filiformis are new records for the British Isles. A fourth species Cernosvitoviella briganta is new to science and a description is included.

5. The distribution of enchytraeid species on thirteen sites on the reserve is described. The soils occurring on limestone outcrops have the largest number of species, 15 species being recorded from the Limestone grassland sample site. The alluvial and moor edge soils contain from five to nine species and the blanket peat sites four or less species.

6. Cognettia sphagnetorum was found at all the sites selected. Fridericia spp. were typical of the limestone soils and Cernosvitoviella briganta of the peat soils.

7. A key for the identification of Enchytraeidae from the five sample sites at Moor House is included.

8. Aggregations of Enchytraeidae have been detected by the analysis of the data from random sampling. The frequency distribution is seen to differ from the normal and the coefficient of dispersion is significantly greater than unity in the majority of cases.

9. Aggregations have been detected for the total Enchytraeidae and for each species and species age group on all the sample sites. The biological importance of aggregations in soil animals is discussed.

10. The life cycles of Enchytraeidae at Moor House have been studied using both field and laboratory methods. The sexually reproducing species appear to have annual life cycles with cocoons hatching during the warmer months of the year.

11. There are some differences in the form of annual life cycle. Cernosvitoviella briganta overwinters in the mature stage whereas mature specimens of Cognettia cognettii are found in the field only in the late summer and early autumn.

12. Cognettia sphagnetorum reproduces asexually by regeneration of body fragments, reproduction in this species occurs at all seasons though at an accelerated rate in the summer.

13. A new method for breeding Enchytraeidae in the laboratory is described. The worms are kept in a thin layer of soil on top of a 1% soil agar plate in a petri dish.

14. The variations in population densities of Enchytraeidae during 1962 and 1963 are described. Enchytraeidae at Moor House show a maximum population density in summer with a late winter and early spring minimum.

15. The highest densities have been recorded on Juncus squarrosus moor with 300,000 per square metre. The Bare peat site had the lowest number of species and the lowest densities.

16. The vertical distribution of Enchytraeidae in the soil throughout the sampling period is described. It is shown from field data that Enchytraeidae move downwards in the soil during periods of drought. Laboratory experiments verifying this conclusion for Nardus grassland are described.

17. Differences in the vertical distribution of different species are recorded, Achaeta spp., Fridericia spp. and Marionina clavata tending to occur in lower soil layers than Cognettia sphagnetorum and Cernosvitoviella briganta.

18. The importance of Enchytraeidae with respect to numbers, biomass, and population maintenance metabolism in the Moor House soils is compared with that of Enchytraeidae on other sites and with other soil invertebrates on the Moor House sites. On the peaty soils Enchytraeidae are responsible for a major proportion of the known faunal respiratory activity, 57 per cent on Juncus squarrosus 59 per cent on Mixed moor, 82 per cent on Nardus stricta grassland and almost 100 per cent on Bare peat. From this it seems that Enchytraeidae are the most important group of secondary decomposers on the peat soils at Moor House.

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APPENDIX I

Soil profiles of the sample sites from Cragg 1961

Limestone grassland

A_oL 0-3 cm. Vegetation mat, litter not distinct.

A_oF +H. 3-6 cm. Dark humic layer forming distinct band.

A_1 6-7 cm. Dark band, undulating boundary distinctly separated from the adjacent zones.

A_2 7-10 cm. Fine sandy silt layer, more leached than above. Some red iron mottling.

B_1 10-11 cm. Humus band distinct boundary.

B_2 11-65 cm. Brown sub-soil. Prominent earth-worm burrows. Small stones of shale and limestone origins.

Base Rock Tyne Bottom Limestone

Juncus squarrosus moor

A_oL 0-3 cm. Distinct litter of leaves, leaf-bases and root-stocks.

A_oF 3-4 cm. Not clearly separated from A_oL and A_oH.

A_oH 4-19 cm. Black, oxidised and crumbly, formed in situ, well humified, merges into next layer.

19-42 cm. unoxidised, less crumbly than previous zone. Betula layer at base.

A_2G 42-67 cm. Gleyed, greybuff waterlogged and plastic soil of drift origin. Some iron mottling.

Base Rock Tyne Bottom Limestone.

Nardus grassland

A_oL 0-5 cm. Mainly loosely packed living and dead portions of Nardus.

A_oF (+H) 5-6 cm. Humus being formed. Distinct layer.

A_1 6-40 cm. Dark brown, moist, sandy loam; sometimes crumbly with mixed humus of alluvial peat origin. Abundant fine, fibrous roots, particularly in upper layers.

B_2 40-53 cm. Deeper layers with prominent fine to medium iron mottling. Merges into layer of stones and boulders of sandstone origin.

Base Rock Sandstone above Single Post Limestone.

Mixed moor

A_oL 0-4 cm. Distinct litter, zone of various remains of species.

A_oF 4-5 cm. Separated from above but merging into A_oH.

A_oH 5-15 cm. Dark, humified, slightly crumbly peat with fibrous plant roots.

15-60 cm. Yellow-brown, unoxidised with Eriophorum and Calluna remains. Lower layers more compacted becoming plastic.

A_2G 60 cm. Gleyed soil overlying boulder clay.

Bed Rock Tyne Bottom Limestone

Bare peat

A_oH 0-2 cm. Black well oxidised crumbly humified peat. Largely redistributed.

2-18 cm. Peat more plastic and humified.

Below 18 cm. Brown unoxidised and stratified. Formed in situ. Contains twig remains.

Base Rock Beds of limestone, shale and limestone between Tyne Bottom and Scar Limestones.

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