Studies on the enchytraeidae of moorland soils

J. E. Peachey

STUDIES ON THE ENCHYTRAEIDAE OF MOORLAND SOILS

by

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E R R A T A

p.26, line 11 : delete "in IV(8), insert "on p.119".
p.60, line 9 : delete "standard mean", insert "standard deviation".
p.66, line 4 : delete "31", insert"41".
line 6 : delete "164", insert"162".
Fig. 24 : delete "53" in 7th sample row down and insert "55".
p.67, Fig. 25 : delete "177, 129 & 198" in 3rd. & 4th. rows down, respectively, and insert "172, 179 & 200" respectively.
p.116, line 17: delete "(Lotka 1925)", insert "(Nicholson 1933)". (J.Anim.Ecol., 2, 132.)

STUDIES ON THE ENCHYTRAEIDAE OF MOORLAND SOILS

(J. E. Peachey, B.Sc., Hatfield College)

Summary of thesis

The study began with a detailed comparison of sampling and extraction methods during the season 1956-1957. Over the whole of the season the wet funnel method (O'Connor 1955) was more efficient than the Nielsen (1952) method at extracting enchytraeids from soils containing large amounts of peat. There was little to choose between the two methods for mineral soils, though the Nielsen method with relatively more effort gave higher yields on these soils. In the periods of increasing density, the Nielsen method increased considerably in relative efficiency, extracting a greater number of smaller (younger) worms. The wet funnel method was more efficient in the extraction of larger species (Mesenchytraeus and Fridericia). The thickness of the soil core to be extracted and the distribution of the worms in the core were found to affect extraction efficiency.

The enchytraeids, in selected sites of the Moor House National Nature Reserve are shown to be important members of the moorland soil fauna, with maximum densities of nearly 300,000 per m^2, representing a biomass of 50 g. live weight. Their distribution in time and space was examined. The worms were found to be aggregated and distributed mainly in the litter and fermentation layers of the soil, except when driven deeper by the threat of desiccation or temperature. The effect

of the dry and hot summer of 1955 was shown to have profoundly reduced some populations, but evidence was obtained which requires the postulation of density dependent control particularly in physically favourable habitats.

C O N T E N T S

INTRODUCTION

"I have lain in the soil and criticised the worm"

T. S. Eliot.

Perhaps the best known enchytraeid is the white worm found in decaying seaweed or round the dead or decaying roots of garden plants, or breeding in porridge or mashed potato in a school culture. This is the Enchytraeus albidus named by Henle in 1837.

Following Henle other genera and species of worms were described from many varied habitats. This work was summarised and developed by two workers; Vejdovsky, who published his "Monographie der Enchytraeiden" in Prague in 1879, and Michaelsen, who published "Synopsis der Enchytraeiden" in 1889 and "Oligochaeta" in 1900. These works form the basis of Ude's key to the family, published in 1929, (Dahl 1929) which is still used.

Friend in various papers (1897-1924) described and named many new species and records for this country, which in the absence of further collecting and study, must remain somewhat doubtful, as there is difficulty in assessing the status of some of the species. Moszyński (1930) drew up a species list for differing habitats and Černosvitov (1945) has published records for the Lake District area.

The collection and identification of the worms naturally led to studies concerned more with the ecology of the family. As far back as 1900 Bretscher observed that the enchytraeids were found in far greater numbers than the lumbricids. This and later work (Jegen 1920,

Moszyński 1930) showed the family to be important members of the soil fauna and other work (Friend 1916, Reynoldson 1939-1948) demonstrated the importance of the worms in the breakdown of organic material, Reynoldson's work being particularly concerned with the enchytraeids of wrack and sewage beds.

The next stage in the development of the study of enchytraeids was facilitated by the extraction methods developed by Nielsen (1952) and O'Connor (1955) which made possible the quantitative approach of these workers and the present author. This work is in turn leading to the review of the taxonomy of the group, using chromosome numbers as a guide, (Christensen & Nielsen 1955) and the laboratory investigation of eco-physiological problems, such as respiration and reproduction. Meanwhile approaching the study from the needs of Soviet pisciculture, Ivleva (1953a & b) has produced useful information on the biology of Enchytraeus albidus.

Because wherever moist organic soils have been sampled (Bretscher 1900, Jegen 1920a, Nielsen 1955a, O'Connor 1957) enchytraeid worms have been found in large numbers, it was decided to study these worms in peaty soils. An interesting piece of early work had shown,

"that Marionina (Enchytraeoides) sphagnetorum is to be found in many moorlands" as a "characteristic member of the alpine fauna of Ireland. It is almost invariably found in the soils of moors and hills above 500 feet" (Southern 1909).

In this thesis the work is described in four parts, dealing with

the study area and climate, general information on the enchytraeids, the sampling and extraction of the worms and the compilation of the sampling data into observations on the quantitative distribution of moorland Enchytraeidae.

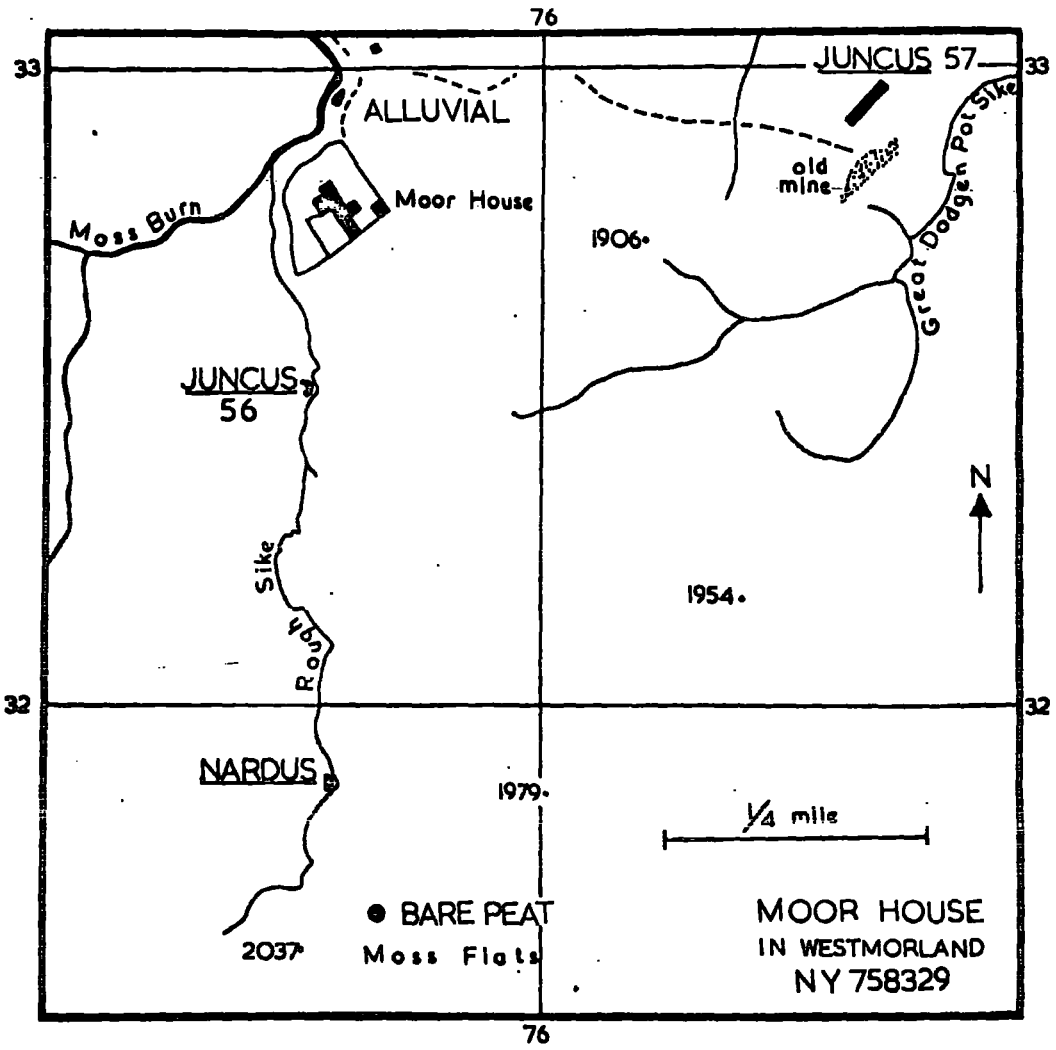


Fig. 1. The Moor House study area.

PART I

THE STUDY AREA

The Moor House National Nature Reserve, Westmorland (Grid ref: NY 73.32) is approached by road and track from Garrigill (near Alston, Cumberland). The W., S.W. and S. boundaries of the reserve are situated on Great Dun Fell (2780 ft.), Little Dun Fell (2761 ft.) and Knock Fell (2604 ft.). From the fell tops, generally covered with poor grassland, the reserve slopes E. to the R. Tees which forms its N. and E. boundaries. This area, on the N.E. dip slope of the Yordale series of Carboniferous sandstones, shales and limestones, is covered with blanket peat (Calluna, Eriophorum, Sphagnum) in various stages of erosion and recolonisation, and traversed by many streams running N.E. into the R. Tees. Along the stream sides where the peat cover is thin, or absent, or occasionally flooded; Nardus, Juncus, Deschampsia, Festuca and Agrostis are common.

(1) SAMPLE AREAS

From the study area described 5 sample sites, each 75-100 m^2, were selected. (Fig. 1 & 2). Their location, site characteristics and soil profiles are further described in Tables 1-8.

The sample sites may be considered as a transect from blanket bog to stream edge, though of course they do not all come from the same transect. (Table 1.)

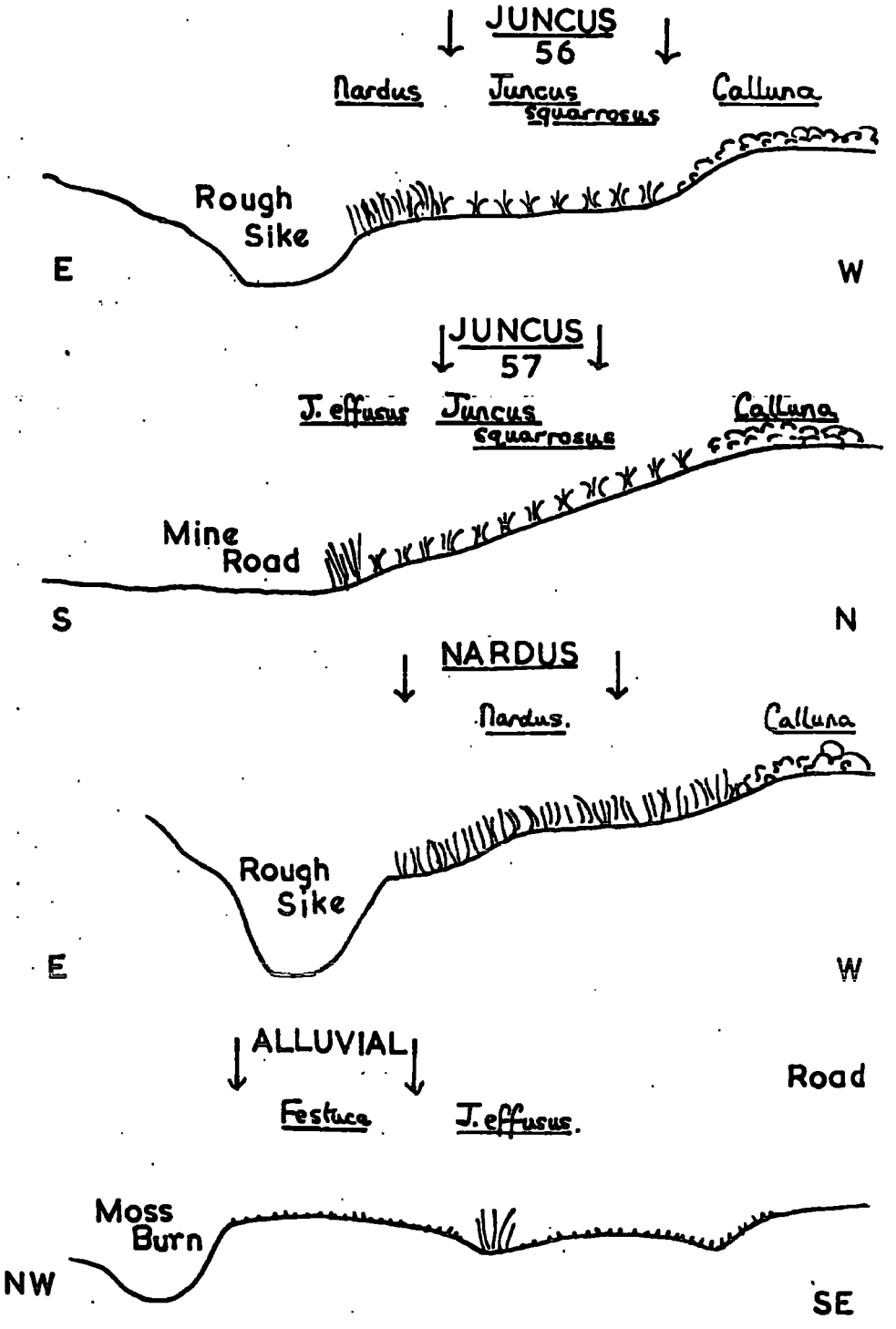


Fig. 2. Sample site characteristics.

Table 1. Sample sites considered as an idealised transect

Sample Site Type	Zonation
Bare peat	eroded blanket peat
(*Calluna* moor)	blanket peat
Juncus squarrosus	edge of peat
Nardus grassland	mineral soil on edge of stream
Alluvial grassland	

Table 2. Description of sample areas (Fig. 1 & 2, Plates 1-6)

Sample area	Juncus 56	Juncus 57	Bare Peat	Alluvial grassland	Nardus grassland
Locality	375 m upstream from Moor House on W. bank of Rough Sike	100 m N.N.W. of old Sun Mine waste heaps on N. side of road to mine	125 m S.S.E. of Nardus site in centre of Moss Flats	100 m N.N.W. of Moor House on E. bank of Moss Burn opposite Netherhearth shop	1000 m upstream from Moor House on W. bank of Rough Sike
Elevation O D	1850	1825	2075	1800	1975
Slope	Regular slight E. facing sheltered	Regular gentle (9°) E. facing sheltered	Plane - Very exposed	Plane - Sheltered	Convex-concave E. facing exposed
Drainage of site	Receiving site, some run off	Receiving site, some run off	Normal site	Normal site	Normal site, occasional flooding
Drainage of soil	Waterlogged peat on freely drained mineral soil	Waterlogged peat on very poorly drained mineral soil	Waterlogged peat on very poorly drained mineral soil	Freely drained mineral soil	Imperfectly drained mineral soil
Parent material of mineral soil	Alluvium of Yordale sandstone and shale	Glacial and solifluction deposits	Glacial and solifluction deposits	Occasionally active alluvium of Yordale sandstone limestone and shale	Sandstone above Single Post Limestone
Underlying rock (all Carboniferous)	Tyne Bottom Plate	Base of Tyne Bottom limestone or beds immediately below	Alternating beds of limestone, shales and sandstone, lying between Tyne Bottom and Scar limestones	Sandstone and shale below Tyne Bottom Limestone	Sandstone above Single Post Limestone

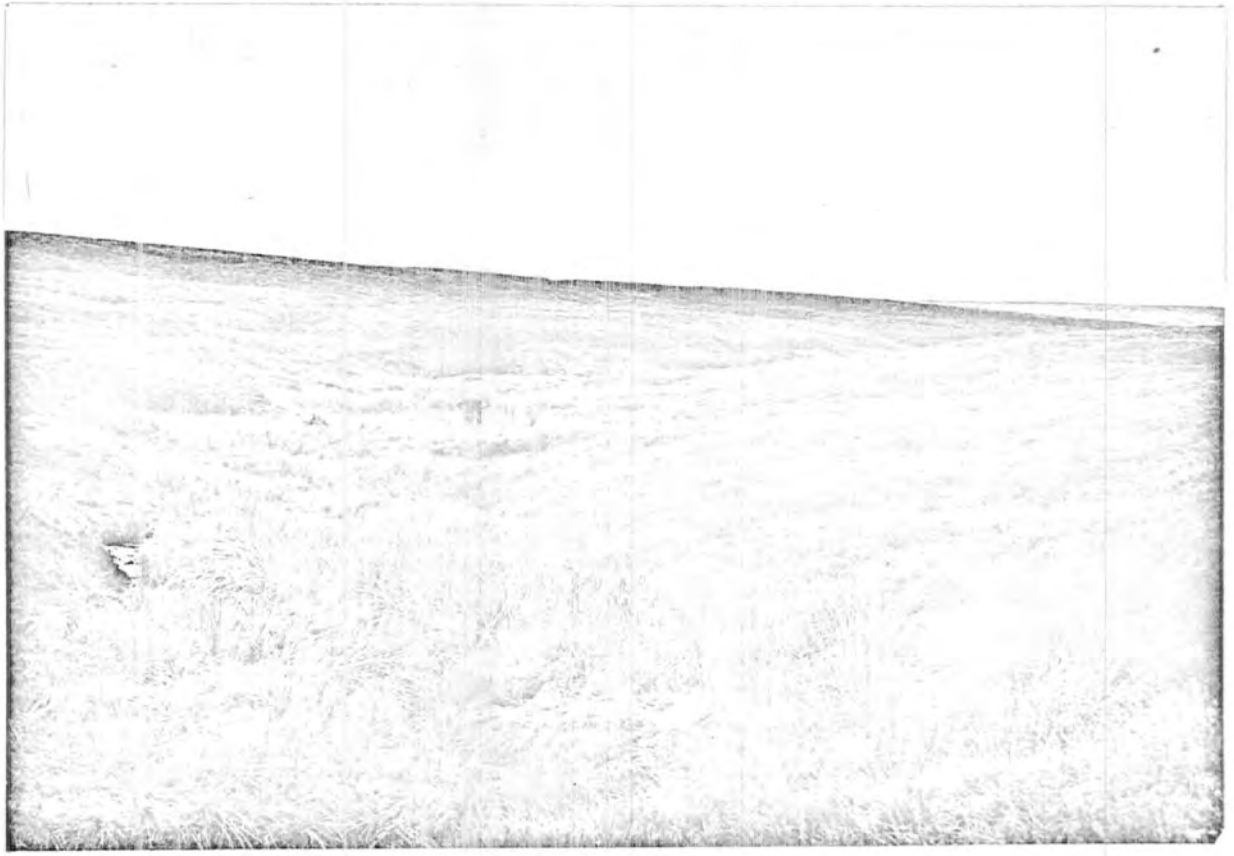


Plate 1. General view of *Juncus* 56 site looking up Rough Sike. N.B. *Calluna* moor above.

Plate 2. General view of Juncus 57 site from mine road. N.B. sample site strata and Calluna above.

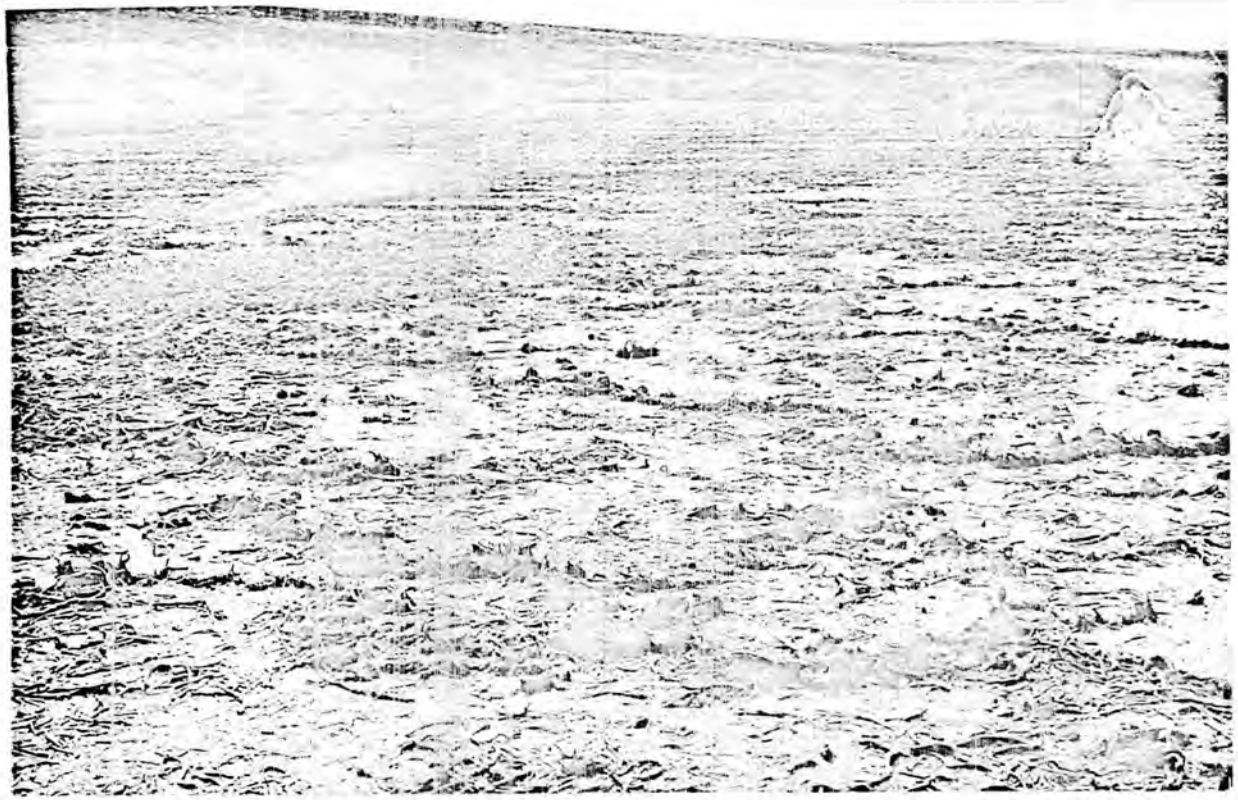


Plate 3. General view of Bare peat area on Moss Flats.

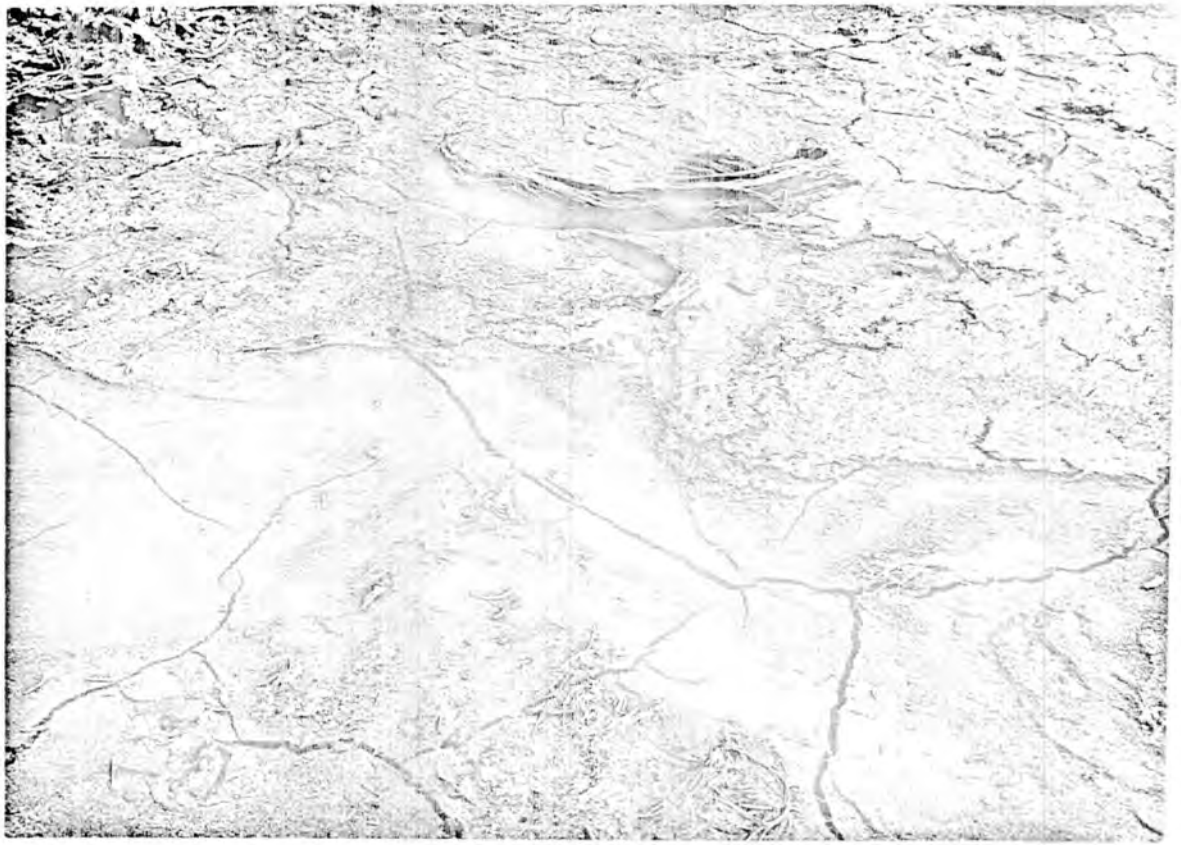


Plate 4. Part of the same area of Bare peat after a dry period to show the effect of flooding and drying out.

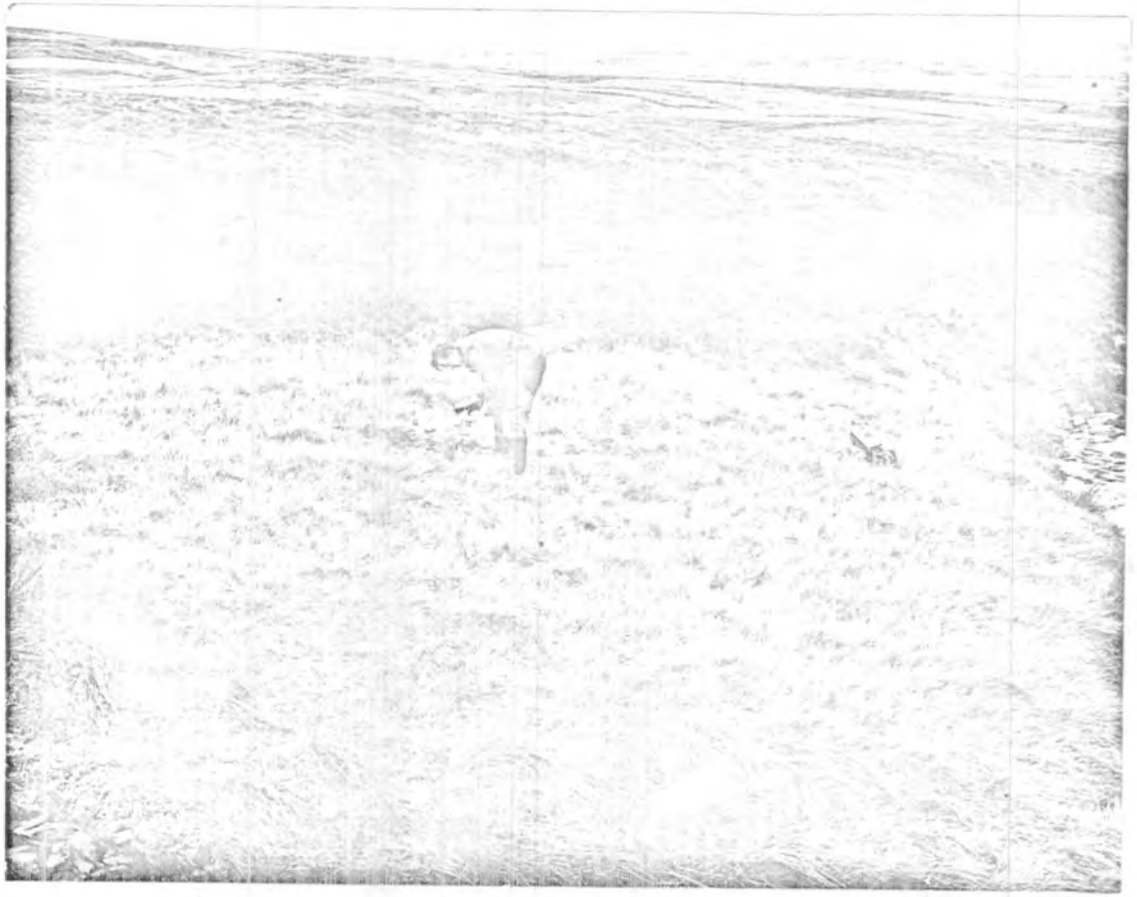


Plate 5. General view of *Nardus* grassland site. Rough Sike flows downstream on the right of the picture. N.B. *Calluna* above.

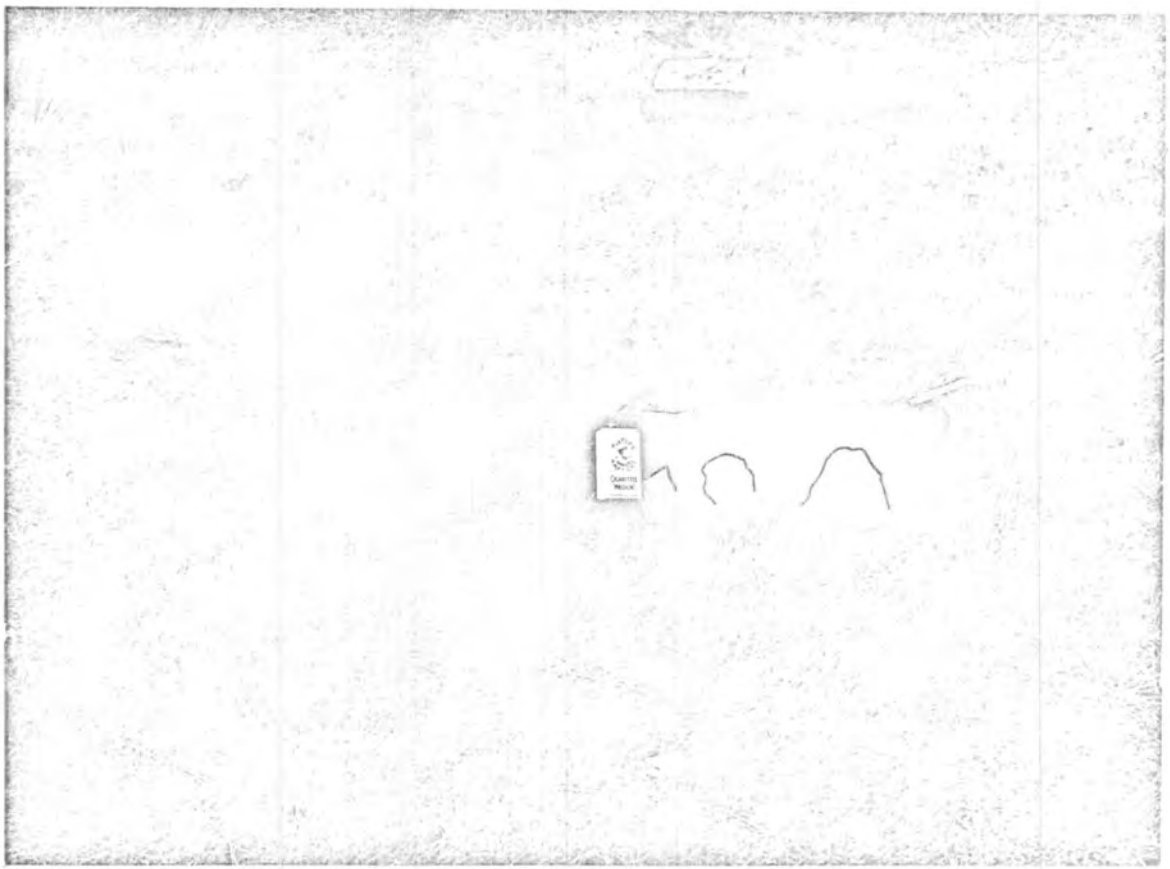


Plate 6. Alluvial grassland area and soil profile. Pencil indicates thickness of vegetation mat, and L + F layers. N.B. boulders of sandstone just below the surface.

Table 3. The vegetation of the sample areas. (Plates 6-11)

Name of site	Juncus 56	Juncus 57
Dominant	Juncus squarrosus	
Abundant	Polytrichum commune Deschampsia flexuosa	Deschampsia flexuosa Festuca ovina
Others	Nardus stricta Galium saxatile Potentilla erecta Festuca ovina Agrostis canina Juncus effusus Carex echinata Carex nigra Eriophorum angustifolium	Galium saxatile Polytrichum commune Potentilla erecta Eriophorum angustifolium
Thickness of vegetation mat.	3 cm.	3-4 cm.

Name of site	Alluvial grassland	Nardus grassland
Dominant	Festuca ovina	Nardus stricta
Abundant	Thymus serpyllum	Galium saxatile
Others	Nardus stricta Hypnum cupressiforme Agrostis tenuis Potentilla erecta Galium saxatile Polytrichium urnigerum Equisetum palustre Cirsium arvense Trifolium repens Polygala serpyllifolia Cerastium vulgatum Luzula sp.	Deschampsia flexuosa Juncus squarrosus Potentilla erecta Agrostis canina Anthoxanthum odoratum Pleurozium schreberi Juncus effusus Luzula campestris Rumex acetosa Polytrichum commune Viola riviniana
Thickness of vegetation mat.	0.5 cm.	5 cm.

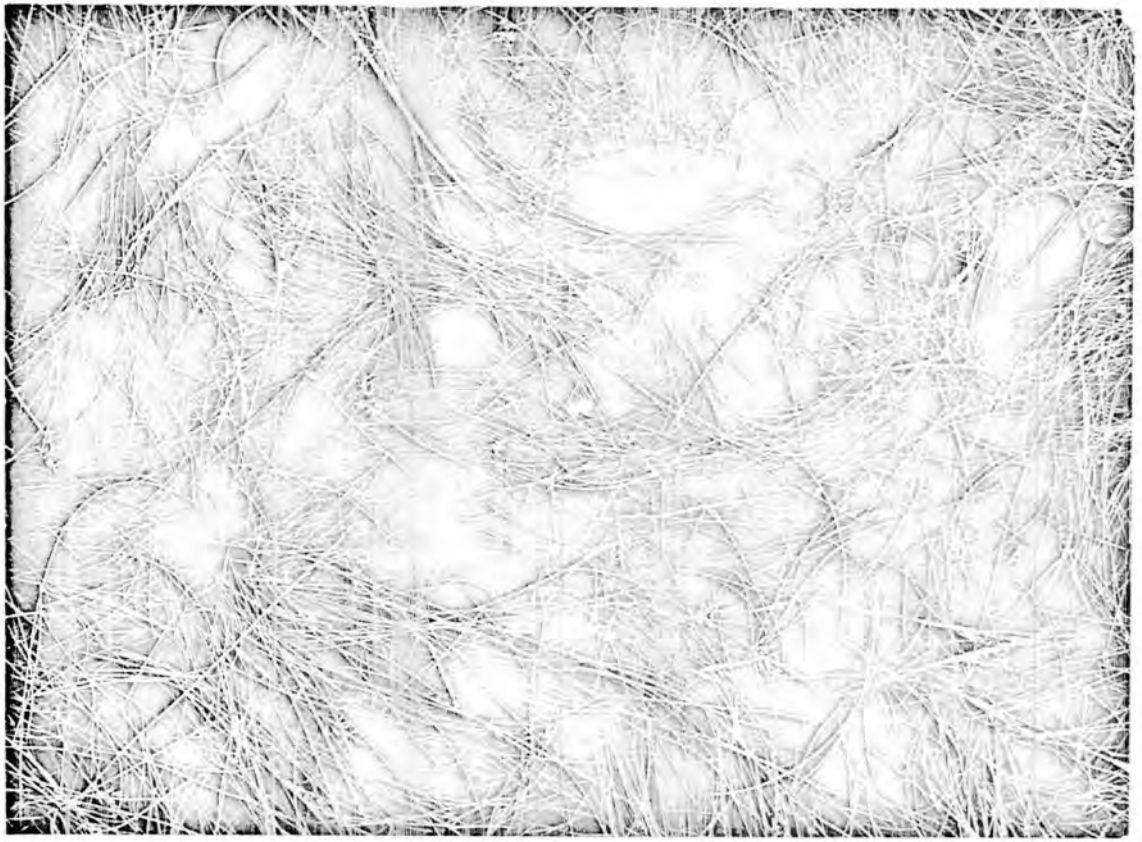


Plate 7. Close up of vegetation of Juncus 56 site (July). Notice Juncus squarrosus, Deschampsia, and Galium

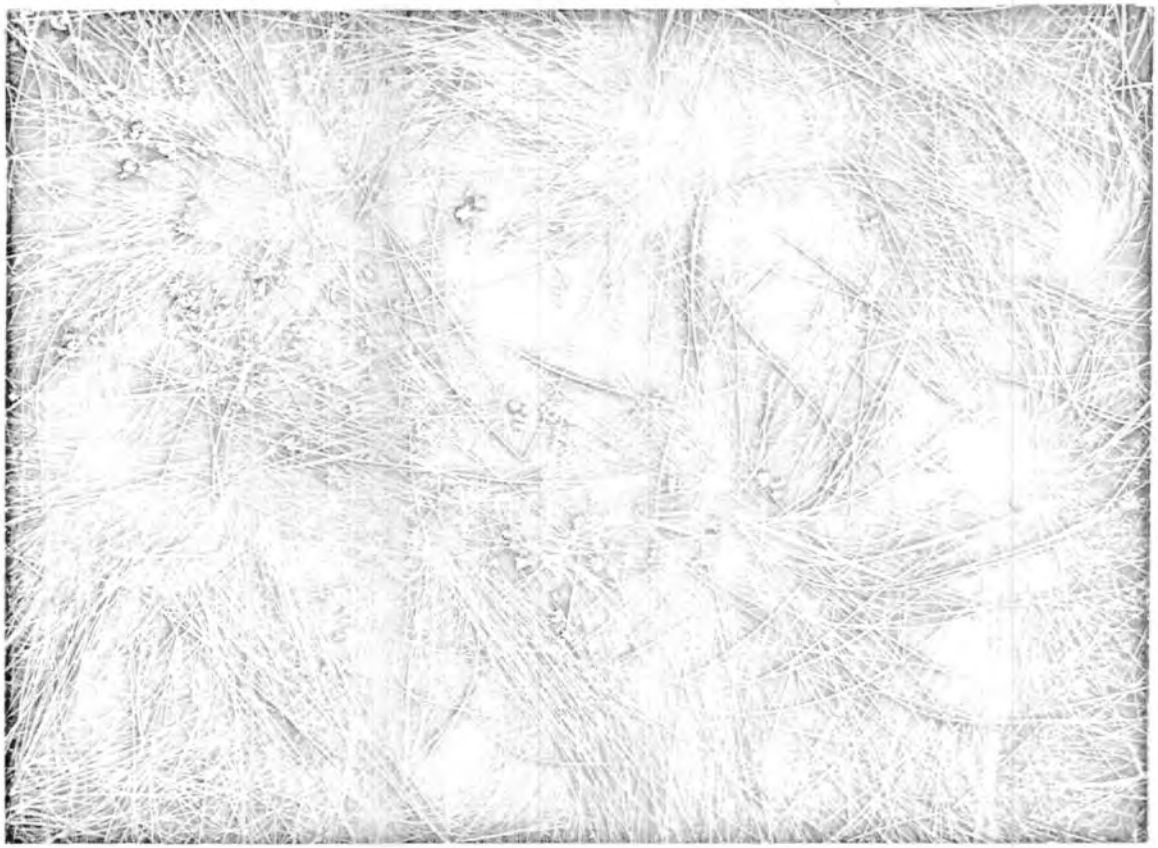


Plate 8. Close-up of vegetation of Nardus grassland site. N.B. Nardus and Galium in flower.

Table 4. Soil Profile of Juncus 56. (Plate 9)

A_o L	(0- 3 cm.)	Litter mainly composed of leaves, leaf bases and rootstock of *Juncus squarrosus* and non humified (H 2)* boundary merging
A_o F	(3- 4 cm.)	Fermentation layer as above but very slightly humified (H 3) boundary merging
A_o H	(4-10 cm.)	Black, oxidised, stratified, "grass type" peat formed *in situ*, with abundant small fibrous and fleshy roots, and slightly humified (H 4) boundary merging
A_o H	(10-80 cm.)	As above with thin bands of sandy alluvium mixed with the peat which is brown, less oxidised and more humified (H 5) boundary clear
A_1	(80 cm.)	Dark grey sandy, clayey alluvium with tabular fragments of shale and sub angular boulders.

* H is a relative measure of humification

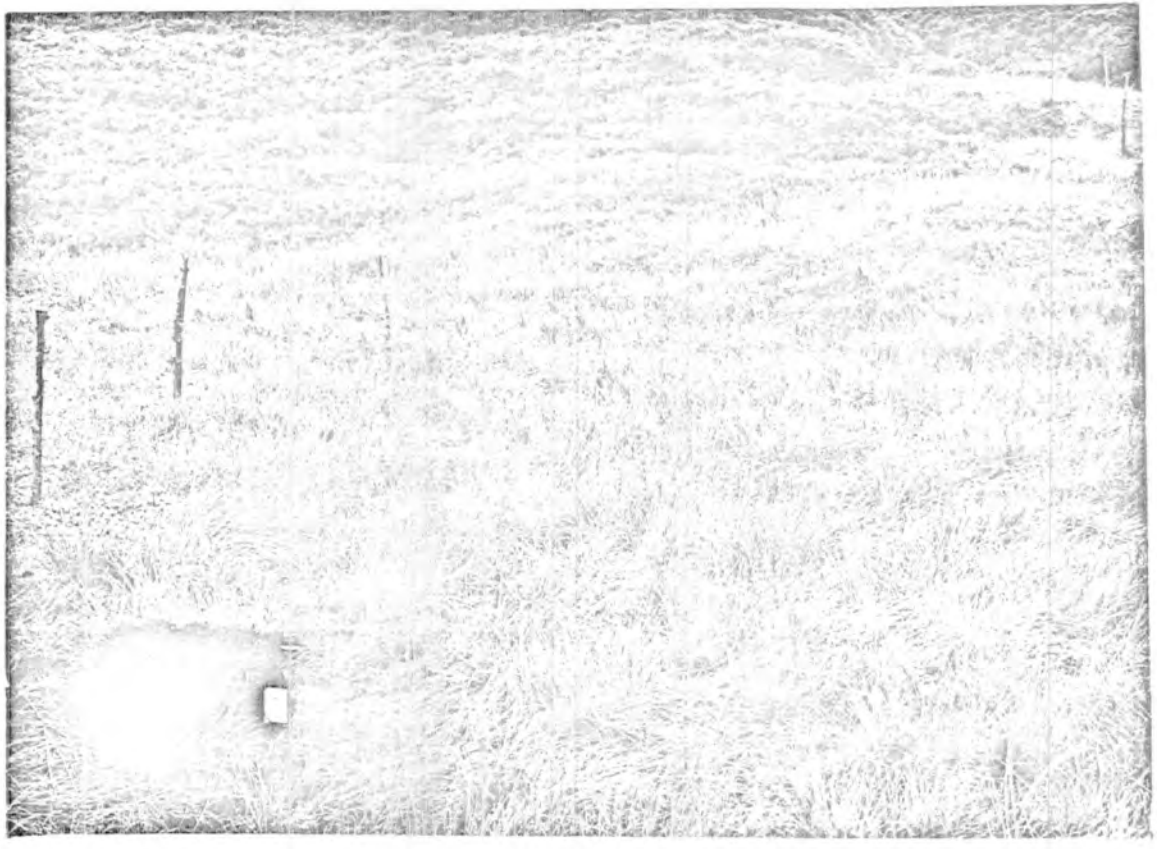


Plate 9. Close-up of Juncus 56 sample area and soil profile.
N.B. stratified peat below thick vegetation mat, litter and fermentation layers.

Table 5. Soil Profile of Juncus 57. (Plate 10)

A_o L	(0- 3 cm.)	Litter mainly composed of leaves, leaf bases and rootstock of *Juncus squarrosus* and *Deschampsia flexuosa* non humified (H 2) boundary merging
A_o F	(3- 4 cm.)	Fermentation layer as above but very slightly humified (H 3) boundary merging
A_o H	(4-19 cm.)	Black oxidised crumbly "grass type" peat formed *in situ*, with abundant fine and small fibrous and fleshy roots, and well humified (H 6) boundary merging
A_o H	(19-42 cm.)	Peat as above, but brown unoxidised less crumbly, stratified well humified (H 7) with *Betula* twig layer at base, boundary clear
A_2 G_3	(42-67 cm.)	Gleyed grey - buff waterlogged clayey and sandy plastic soil with many iron mottles and iron encrustations about the fine small roots (incidence of mottling decreases with depth) and angular stones.

N.B. A_o horizon could be compressed to 2-3 cm. thickness.

Water table at base of profile pit (60 cm. deep).

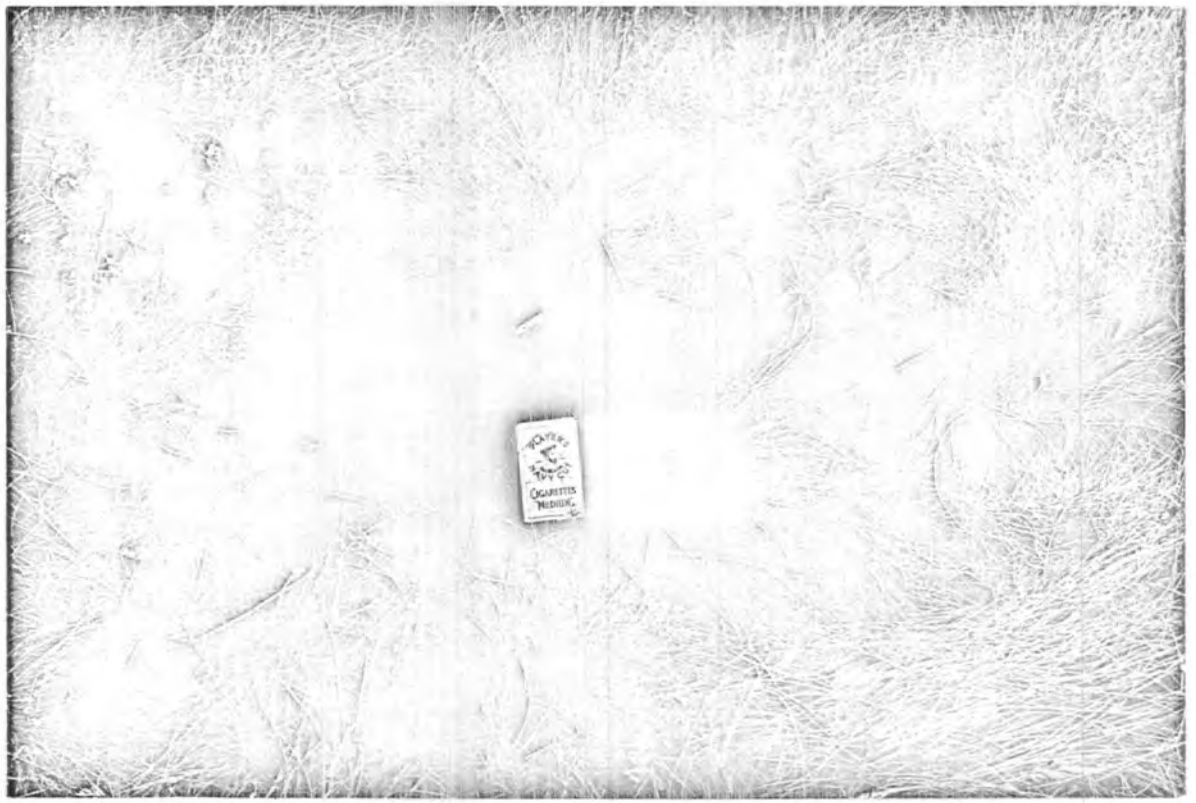


Plate 10. Close up of Juncus 57 area and soil profile.
N.B. vegetation mat and L + F layers, Juncus squarrosus, Deschampsia and Galium flowering.

Table 6. Soil Profile of Bare Peat. (Plates 3 & 4)

A_0 H	(0- 2 cm.)	Black well oxidised crumbly "Calluna type" peat. Somewhat redistributed with many twigs, very slightly humified (H 3) boundary merging
A_0 H	(2-18 cm.)	As above but the peat is plastic and more humified (H 5) boundary merging
A_0 H	(18 cm.)	Brown unoxidised stratified "Calluna type" peat in situ with many twigs, well humified (H 7)

N.B. All layers were waterlogged.

The peat is known to extend to 240 cm. depth and is underlain by gleyed, glacial and solifluction, soils.

Table 7. Soil Profile of Nardus grassland. (Plate 11)

A_0 L	(0- 5 cm.)	Litter mainly composed of very loosely packed living and dead horizontal rhizomes and basal sheaths of Nardus boundary merging
A_0 F + H	(5- 6 cm.)	Fermentation-Humus layer, as above but decaying boundary sharp and wavy
A_1	(6-40 cm.)	Dark brown moist sandy loam fluffy and crumbly with mixed humus (about 20 % dry weight is organic) and abundant fine fibrous roots particularly in upper layers, pH 5·0 boundary merging
B_2	(40-53 cm.)	As above though somewhat leached with common, prominent fine to medium iron mottling with sub-angular stones and boulders (derived from underlying (C) parent sandstone above Single Post Limestone)

N.B. A_0 horizon could be compressed to 3 cm. thickness.
No water in profile pit.

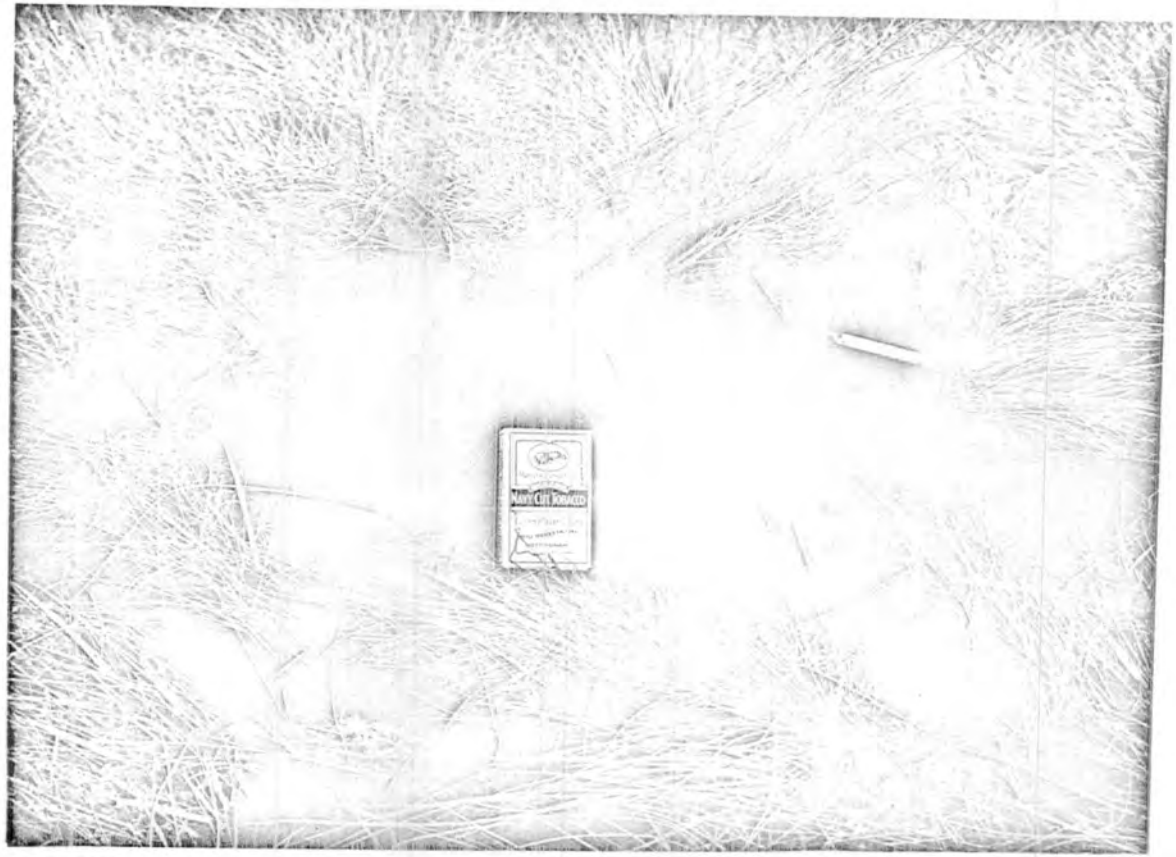


Plate 11. Soil profile of Nardus grassland site.
N.B. very thick vegetation mat and litter.

Table 8. Soil Profile of Alluvial grassland. (Plate 6)

A_1	(0- 7 cm.)	Dark brown black moist silty and sandy soil friable and crumbly with mixed humus (20 % of dry weight is organic) and gravel fragments of shales sandstones, abundant fine fibrous roots boundary merging
A_1	(7-26 cm.)	As above though very stony with stones ranging from gravel fragments to sub-angular boulders of sandstone and limestone, frequent fine roots.

N.B. No appreciably developed horizons apart from A_1 were found.
No water table in profile pit.

(2) CLIMATE OF STUDY AREA

Data available

Manley (1943) gives estimated monthly temperatures (half maximum plus half minimum recorded) for the period 1906-1935 for Moor House based on ten years' records and on comparisons with Newton Rigg (559 ft.) and Durham (336 ft.) over the full period. (Table 9). His rainfall estimates are, however, only based on six years' records and may be rather low.

Since 1953, however, the Nature Conservancy has kept full scale daily meteorological records for Moor House and these are referred to in detail in the present work (Fig. 3). Apart from the normal measurements, work has been carried out (Green 1958) on the amount of water lost by evaporation and transpiration from the surface of the ground. When the evaporation is compared to the precipitation a measure is obtained of the water balance in the soil (excluding drainage effects). This comparison is sometimes expressed as the P/E ratio where P is the precipitation and E the evaporation. Where this ratio falls below one, more water is being lost by evaporation than gained by precipitation.

At Moor House, the Nature Conservancy have obtained the potential evapo-transportation rates by two methods:

(1) computing by a slight modification of Crowe's method (Fig. 3). (This is an improvement on Thornwaite's method 1957.)

(2) observing by using a percolation gauge (evapo-transpirometer) from 1957 onwards (Fig. 3).

It is also possible to measure the amount of actual evaporation

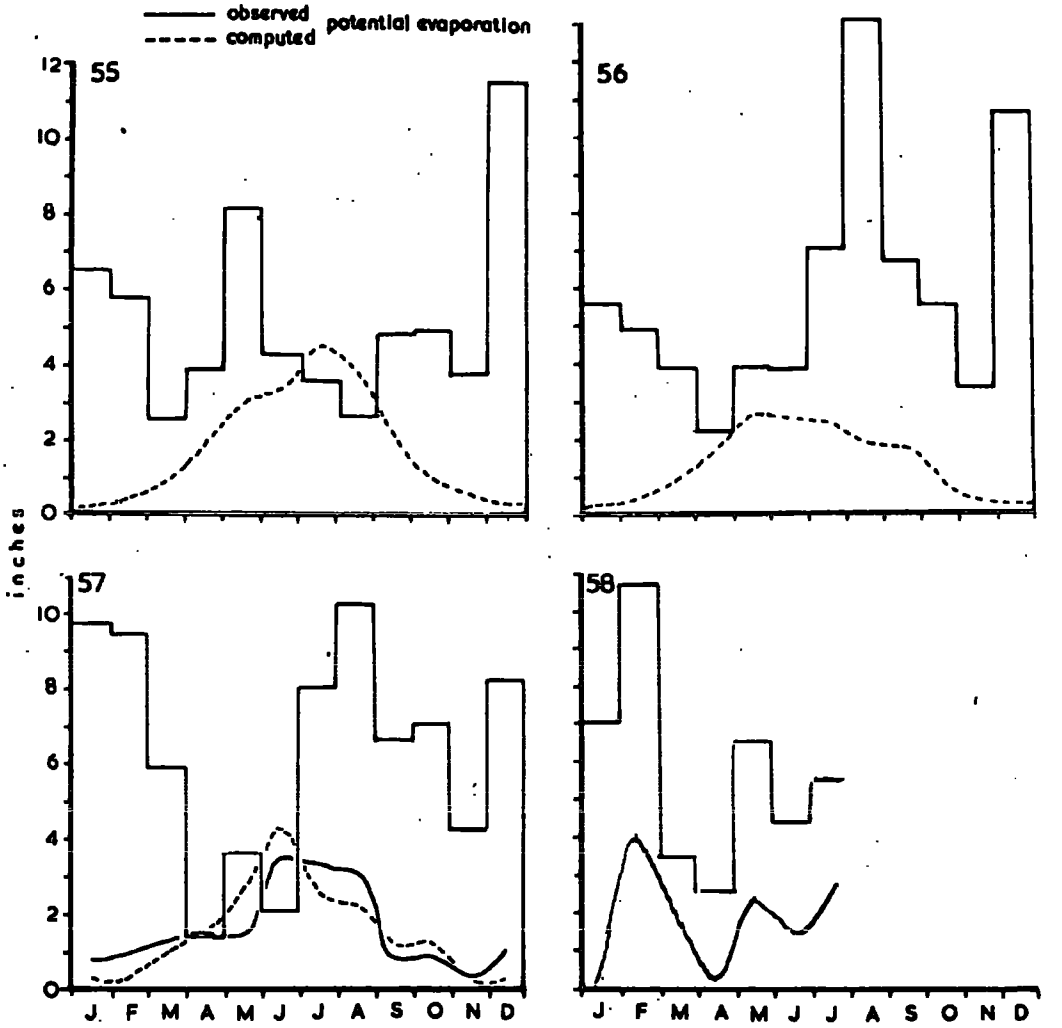


Fig. 3. Rainfall and Evaporation, monthly averages, from Nature Conservancy records.

from run off data obtained from a known catchment-area. The amount of water lost by evaporation and transpiration is the deficit between rainfall and run off. Data of this kind has been collected at Moor House (Green 1958) and the actual evaporation rates are comparable with the observed and computed potential evaporation rates obtained as described above. There are of course errors inherent in the use of these techniques, for example, snow fall and drifting make estimations difficult.

The Climate - General

Table 9 demonstrates, by annual estimates, the colder and wetter conditions experienced at Moor House when compared with lowland stations.

Table 9. Average daily temperatures and annual rainfall at Moor House and two lowland stations

	Average daily air temperatures	Annual rainfall
Moor House (1840 ft.)	42	70
Durham (336 ft.)	47	25
London (27 ft.)	51	23

If evaporation rates are included in the comparison of Moor House with lowland sites then it becomes obvious that in the former area about three times as much water is gained by the soil from the atmosphere (Table 10). Much of this will of course be lost in run-off but the general wetness is reflected in the extensive peat bogs, developed

wherever topographical considerations permitted.

Table 10. Average annual rainfall and potential evaporation for Moor House (1840 ft.) and Doncaster (25 ft.)

Station	Annual Rainfall (P)	Potential Evaporation (E)	P/E
Moor House	70	18·7	4·0
Doncaster	25	17·6	1·3

If we add to this the almost ever present moorland breeze, the low sunshine (3-4 hours daily) and low cloud (6·5 otkas daily) with 80 days of snow, over 150 days of frost and a maximum temperature (ever recorded in the last 4 years) of 76°F we get some idea of the "sub arctic" conditions in the Northern Pennines. Manley (1943) has said that the climate is approximately equal to that of Southern Iceland at sea level.

Seasonal variation in climate

The annual values for climatic factors are useful in the broad assessment of local conditions but it is necessary to consider monthly and often weekly or daily changes to get some idea of seasonal climatic variation when considering its effect on living organisms.

Table 11 gives Manley's estimated monthly air temperature (°F) and the deviations from them for 1955-1957. Manley's rainfall estimates (which are subject to a 10 % error) and the original Moor House potential evaporation computations (although not accurate) are given in Table 12 to give a rough indication of conditions.

Table 11. Estimated average monthly air temperatures at Moor House 1906-1935 (Manley 1936) with the 1955-1958 deviations (Green 1958)

	Jan.	Feb.	Mar.	Apr.	May	June
°F	33.0	32.6	34.1	38.0	44.7	49.4
1955	- 2.8	- 7.9	- 5.9	+ 3.5	- 3.7	- 1.7
1956	- 1.7	- 7.9	+ 1.8	- 1.8	+ 0.1	- 1.1
1957	+ 2.1	- 0.5	+ 7.3	+ 1.3	- 1.2	+ 0.3

	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
°F	52.8	52.3	48.3	42.2	36.4	33.9	41.5
1955	+ 2.8	+ 2.5	+ 1.7	- 0.8	+ 4.0	+ 1.8	- 0.6
1956	- 0.2	- 4.3	+ 2.3	+ 0.9	- 0.7	+ 3.2	- 0.7
1957	+ 0.6	- 0.6	- 2.4	+ 2.3	+ 1.3	+ 0.1	+ 0.9

Table 12. Estimated average monthly rainfall (P) at Moor House (Manley 1943) compared to computed monthly evaporation rates (E) calculated by the Nature Conservancy using Thornwaite's method

	Jan.	Feb.	Mar.	Apr.	May	June
P (ins.)	6.5	6.0	5.7	4.0	3.7	4.0
E (ins.)	0.1	0	0.5	1.2	2.5	3.0

	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
P (ins.)	6.0	7.0	4.5	7.5	6.5	8.5	70
E (ins.)	3.7	3.3	2.4	1.5	0.5	0.5	18.7

It seems then that June to September are the warmest months but that only June, or about that time, is threatened with conditions approaching drying out of the soil. This may be compared with Doncaster

where from April to September evaporation generally exceeds rainfall (P/E <1).

When these average conditions are compared with the climate experienced during the study period (1955-58) the following deviations from average may be noted:-

1955, an exceptionally hot and dry July and August with P/E < 1 - the soil was very dry and observations made at the time showed the peat to be dry and dusty in many places.

a mild November and mild, very wet, December.

1956, a cool and very wet August.

1956-1957, a mild winter.

1957, a dry June with P/E < 1.

PART II

THE BIOLOGY OF ENCHYTRAEIDAE

Some of the general information collected in this study, from observations on living specimens and from the literature is described here. In this connection the author feels indebted to Stephenson's Oligochaeta published in 1930 and now out of print.

The Enchytraeidae are a family of microdril oligochaete worms, remarkably similar to the lumbricids, from their external characteristics, except for their size, being rarely more than 3 cm. long and usually much smaller. The enchytraeids are considered to be more primitive than the earthworms (Christensen & Nielsen 1955). In some ways they are difficult to study anatomically, because of the predominance of immature forms and the absence of hardened parts, or clear stages in their development. This has led to a certain confusion about taxonomical divisions and the study of species from a relatively unworked area has tended to accentuate some of these difficulties. However Ude's key to the family (Dahl 1929) and other sources have made it possible to recognise the general anatomy and the broad taxonomic divisions.

The microscopic examination of worms mounted in water under a coverslip has made it possible to prepare the following descriptions except where other sources are acknowledged.

(1) GENERAL ANATOMICAL DESCRIPTION

The setae are single pointed and straight or sigmoid, arranged in four bundles per segment.

The coelomic cavity, traversed by segmentally arranged septae,

is packed with discoid corpuscles and, in the generative segments, sex cells and gregarine parasites. These coelomic contents move forward and backward with the movement of the animal.

The nephridia are paired segmentally arranged excretory organs, each consisting of a nephrostome, or ciliated collecting funnel, situated anteseptally in the coelomic cavity and leading into a flame-like ciliated tube. This nephridial tube, loosely coiled and embedded in interstitial tissue, forms the post-septal body of the nephridium and subsequently leads to the exterior at the nephridiopore.

The alimentary canal is simple, the oesophagus leading into the intestine in segment 7, the latter forming the greater part of the canal. At the anterior end, however, there is an extrusable pharyngeal plate, well supplied with muscles and evidently used for exploratory purposes (Stephenson 1930). Paired septal pouches are also conspicuous at the anterior end.

The blood system consists essentially of a dorsal vessel which is contractile and collecting in function, and may have local enlargements; it arises from the alimentary sinus in the anterior region and leads forward, connecting by commisural vessels (Stephenson 1930) with the posteriorly directed ventral vessel, which is non-contractile and distributing.

The blood can be colourless, red or yellow, as recognised from the colour of the worm.

The nervous system consists of a dorsally situated brain or bilobed cerebral ganglion leading by a pair of oesophageal connectives to the

ventral nerve cord, which is segmentally swollen into ganglionic enlargements.

The reproductive system is more difficult to observe. The worms are hermaphrodite, testes and ovaries situated in segments 11 and 12 respectively but these were not seen. Oocytes are discharged into the coelom. The sperm funnels which collect the male sex products from the coelom, or in some species from seminal vesicles, are attached anteseptally on the septum between segments 11 and 12; they are ciliated and contractile and connect via the much-coiled vasa deferentia with the protrusable penes in segment 12. The clitellum, a secondary sexual character, is formed by the glandular thickening of the body wall on, or near, the reproductive segments in mature or semi-mature worms. In the genus Enchytraeoides these organs are moved forward to segments 8 and 9. The spermathecae situated in segment 5 are divided into ampulla, diverticula where present and spermathecal duct which connects with the exterior between segments 4 and 5. The spermathecae may be attached to the gut.

(2) DESCRIPTION OF SPECIES FOUND ON THE MOOR HOUSE RESERVE

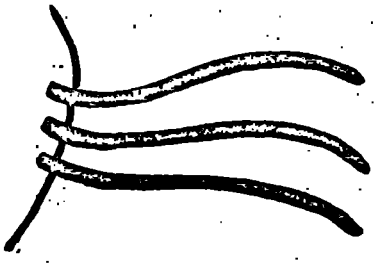
Enchytraeoides sphagnetorum (Vejd.)

A whitish coloured worm often tinged with yellow, thread like and rarely more than 10 mm. long.

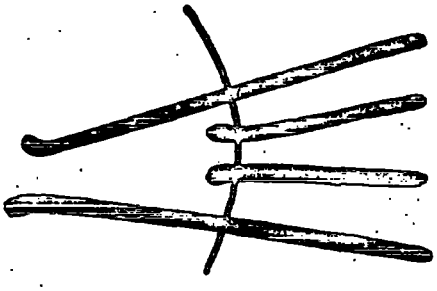
Setae: sigmoid, 3-5 per bundle (Fig. 4).

Lymphocytes: flattened and pointed (Fig. 5).

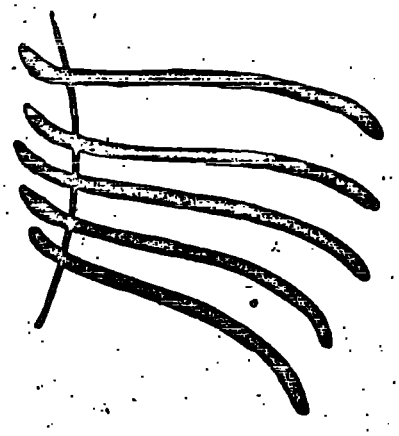
Nephridia: nephridial canal enclosed in much interstitial tissue with small anteseptal region and large postseptal body (Fig. 6).



Enchytraeoides



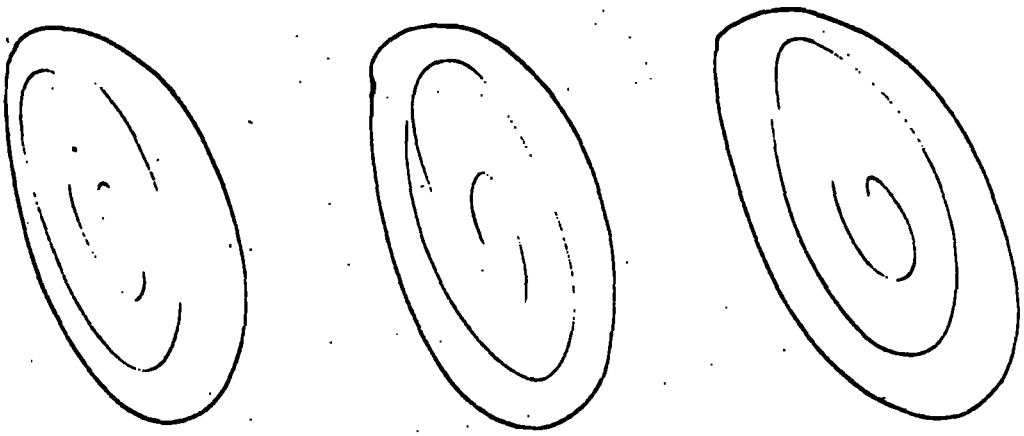
Fridericia



Mesenchytraeus

Fig. 4. Setae of Moor House enchytraeids.

Mesenchytraeus and Fridericia



Enchytraeoides

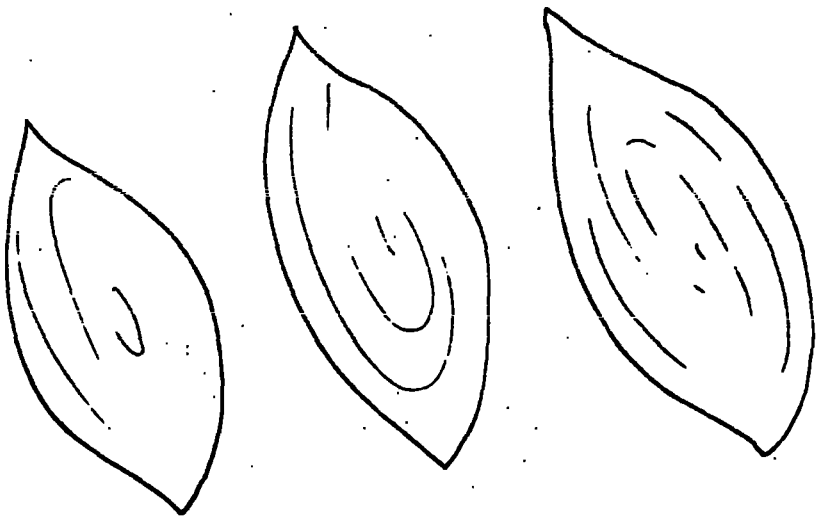


Fig.5. Lymphocytes of Moor House enchytraeids.

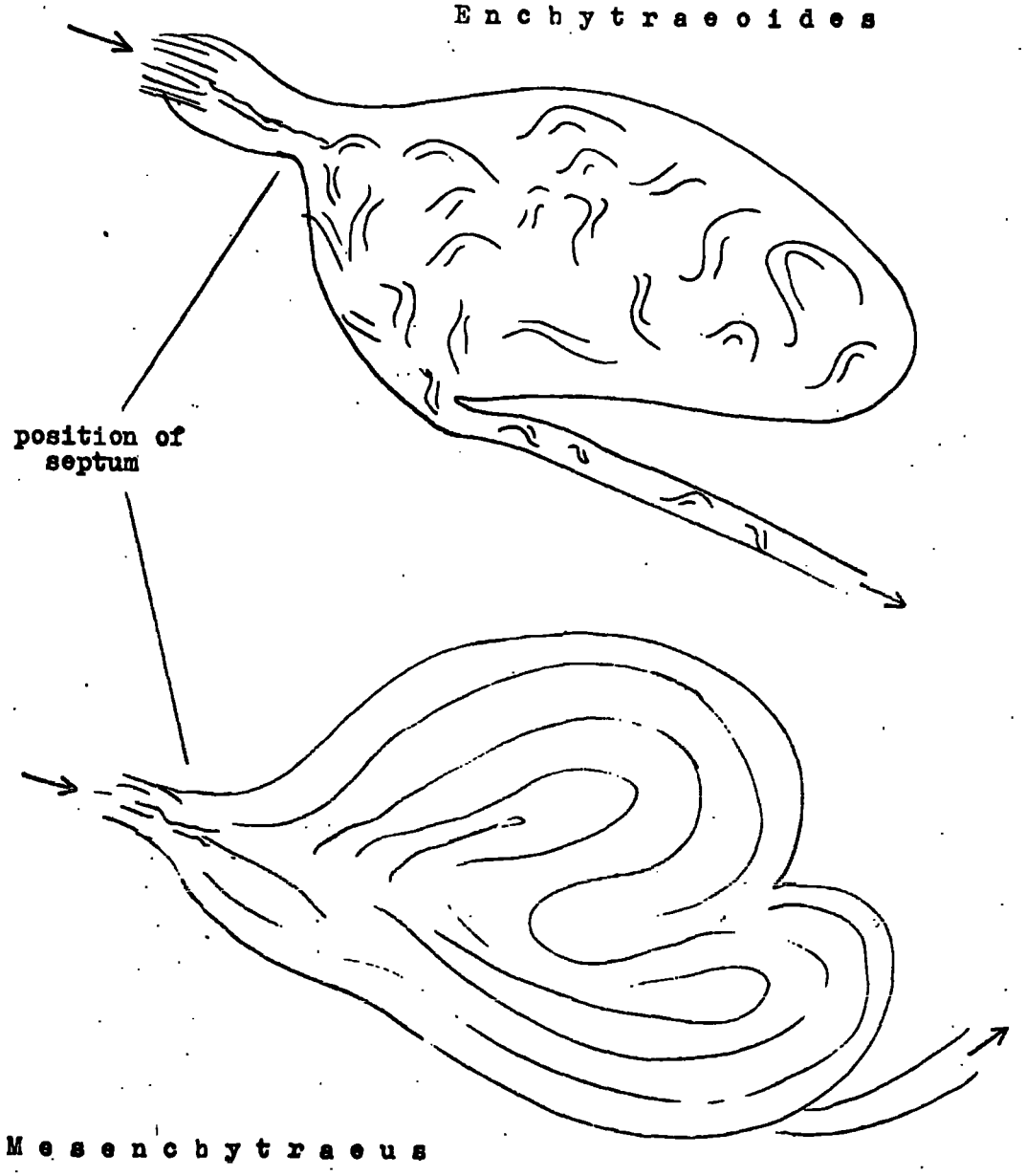


Fig.6. Nephridial types in Moor House enchytraeids.

Oesophagus: merges gradually into the gut in the 7th segment.

Septal pouches: generally 5 pairs.

Blood: yellowish. Dorsal vessel: arises post-clitellially?

Brain: deeply bilobed, longer than broad (Fig. 7).

Spermathecae: no diverticula, ampulla long and pear shaped.

Sperm funnels: not seen in detail.

Clitellum: segments 8 and 9.

Enchytraeoides sp. (separated off from E. sphagnetorum by B. Christensen.)

A small worm below 5 mm. in length, with about 25 segments, considered in this investigation along with E. sphagnetorum.

Setae: highly sigmoid and with nodules.

Spermathecae: not connected to oesophagus.

Sperm funnels: distinctly funnel shaped.

Mesenchytraeus

A distinctly reddish coloured worm, thicker than Enchytraeoides, up to 15 mm. long. (The larger specimens could be identified by the naked eye and so were considered separately in the quantitative work. On inspection these were always found to be mature or semi-mature.)

Setae: sigmoid, 4-6 per bundle (Fig. 4).

Lymphocytes: elliptical but not pointed (Fig. 5).

Nephridia: nephridial tube distinct, not enclosed in much interstitial tissue, with very small anteseptal portion (Fig. 6).

Oesophagus: merges gradually into the gut.

Blood: red. Dorsal vessel: with local enlargements, arises in 13th segment from the alimentary sinus (Fig. 8).

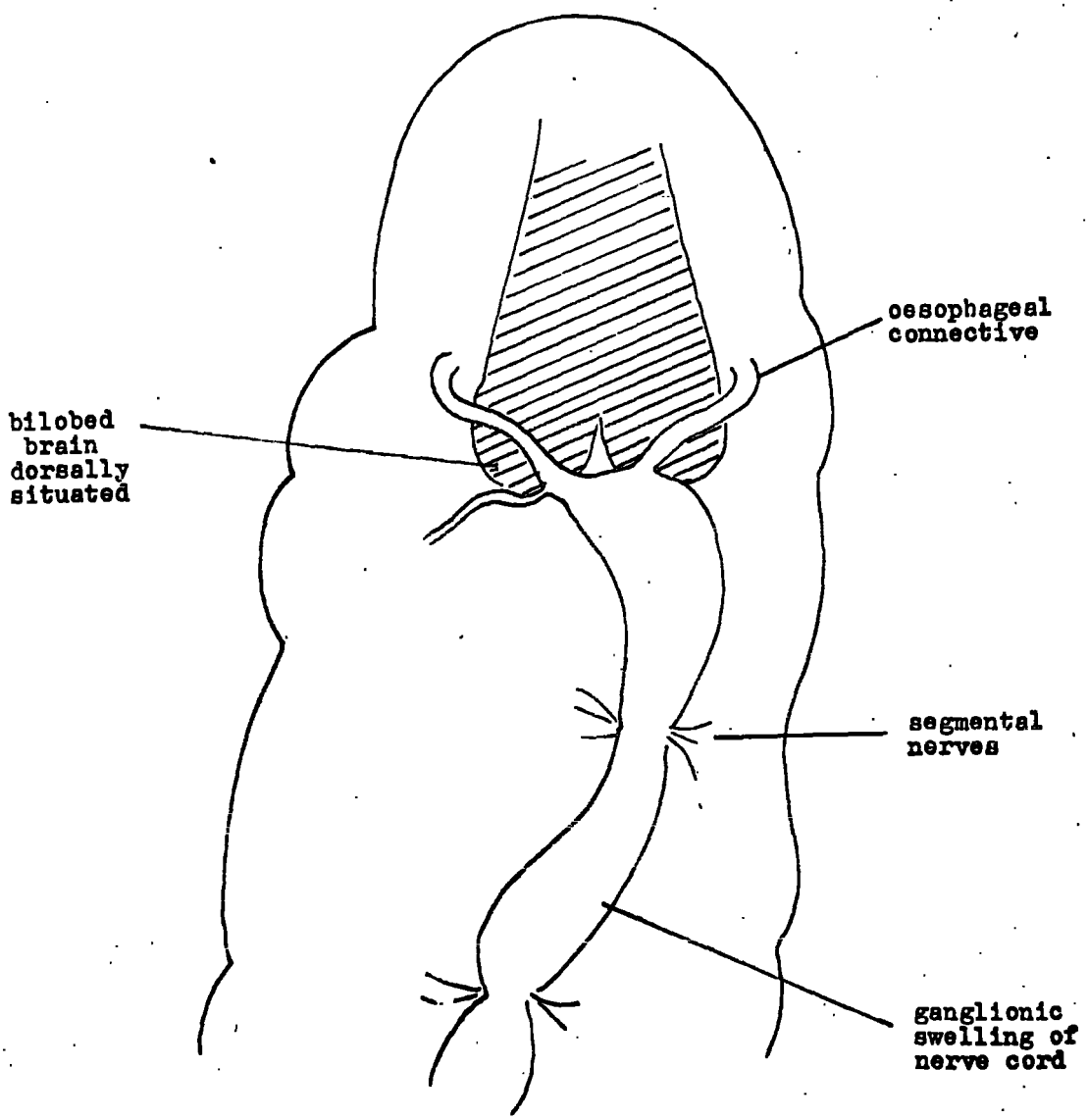


Fig.7.Diagram of nervous system at anterior end of Enchytraeoides.

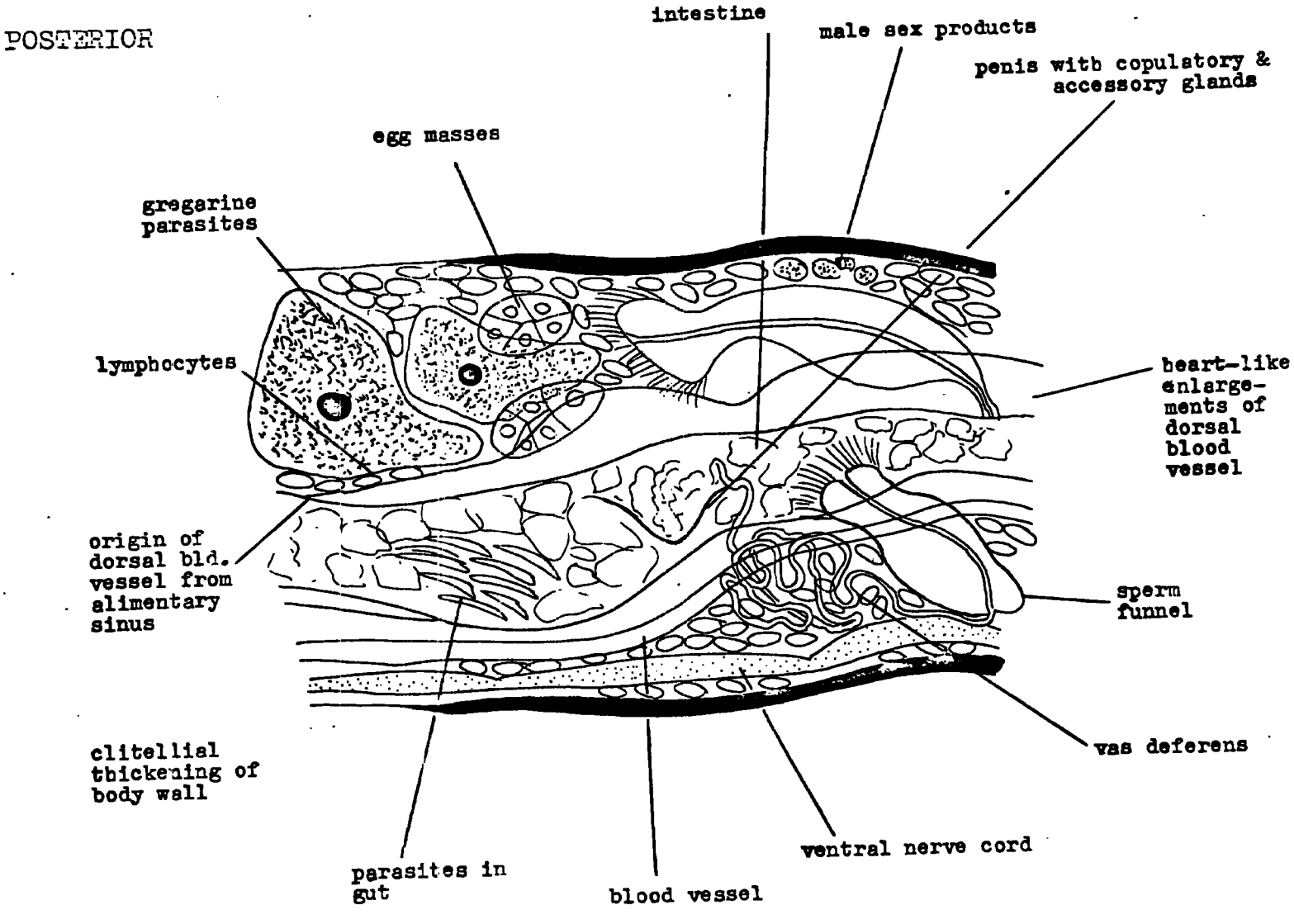


Fig.8. Clitellar region of Mesenchytraeus [illegible].

Brain: hinder end concave, as long as broad.

Spermathecae: no diverticula, receptacle tube shaped, with inverse pear shaped ampulla, extending posteriorly to the 10th segment (Fig. 9).

Sperm funnels: twice as long as broad, in segment 12 (Fig. 8).

Penis: mesenchytraeine type - with copulatory and accessory glands (Fig. 8).

Clitellum: in segments 11-13 (Fig. 8).

Mesenchytraeus 'B'

A large yellowish worm up to 20 mm. long - the colour distinguishes it from Fridericia with which it might be confused.

Setae: sigmoid 6-9 per bundle (Fig. 4).

Lymphocytes: elliptical but not pointed, coloured yellow (Fig. 5).

Nephridia: nephridial tube distinct, not enclosed in much interstitial tissue, very small anteseptal portion (Fig. 6).

Oesophagus: merges gradually into the gut.

Blood: yellow.

Dorsal vessel: arises post clitellially.

Brain: hinder end concave.

Spermathecae: with inversely pear shaped ampulla.

Sperm funnels: three times as long as broad.

Clitellum: in region of segment 12.

Fridericia magna (Friend)

A large and conspicuous white worm up to 32 mm. long. (The larger specimens could be separated off by the naked eye and so were considered

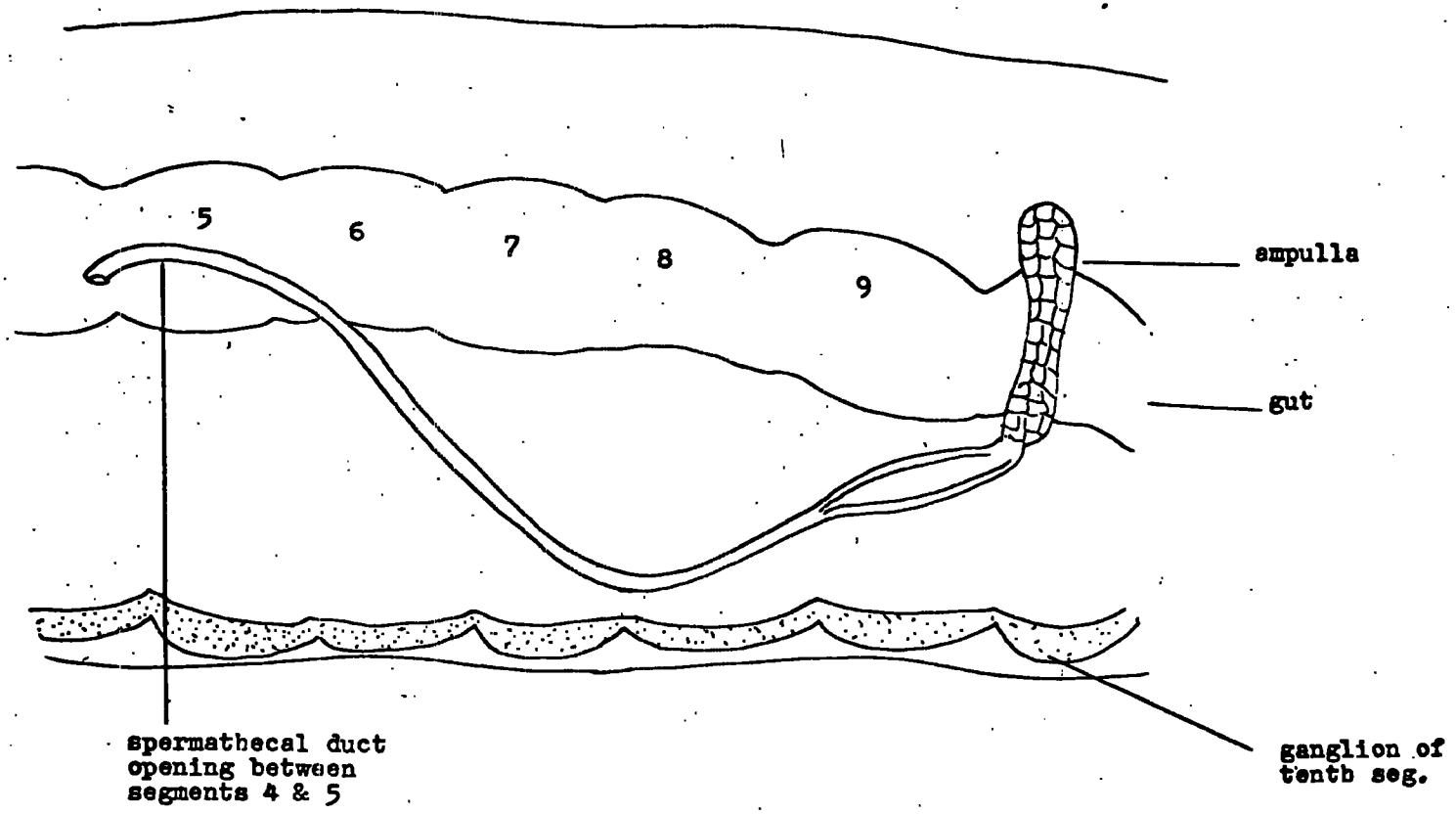


Fig.9.Spermatheca of Mesenchytraeus .

separately in the quantitative work.)

Setae: straight arranged in pairs of varying length (Fig. 4).

Lymphocytes: less transparent than the other species.

Dorsal pores: present and conspicuous.

Nephridia: nephridial canal enclosed in much interstitial tissue, with small anteseptal, and large post septal, body (Fig. 6).

Oesophagus: merges gradually into the gut.

Pepto-nephridia: should be present but not seen.

Blood: colourless.

Dorsal vessel: arises post-clitellially.

Spermathecae: with two diverticula and 'U' shaped ampulla.

Penis: lumbricilline type - simple with no prominent glands.

Clitellum: in region of segment 12.

(3) THE QUALITATIVE DISTRIBUTION OF ENCHYTRAEIDAE

Enchytraeids live in a wide and interesting range of habitats, in decaying organic matter of almost every kind - humus, peat, compost, seaweed, rotting wood and sewage sludge. The soil dwelling enchytraeids are perhaps the most widespread, though less conspicuous than other forms, which may explain their neglect until recent years.

Table 13 shows the dominance of Enchytraeoides at Moor House, with Mesenchytraeus specific to habitats on or at the edge of the peat - the Juncus and Nardus sites. Fridericia which was the dominant genus found by Nielsen in the sandy Danish soils, is only present in the alluvial

soils at Moor House. The preferences shown by these different species agree with the findings of Moszyński (1930), Nielsen (1955a) and O'Connor (1957).

Table 13. Species list of enchytraeids provisionally identified in the present investigation, with approximate percentage composition (by number), from habitats within the Moor House reserve

Species composition		Habitat
Enchytraeoides sps.	90 %	Juncus squarrosus dominant sites
	100 %	Bare peat
	100 %	Calluna moor and associated
dominant species on these areas		Sphagnum and Eriophorum dominant areas
	98 %	Nardus grassland
	75 %	Alluvial grassland
	-	Moss carpets on waterfalls
Mesenchytraeus	10 % ccc	Juncus squarrosus dominant sites Nardus grassland
Mesenchytraeus 'B'	ccc	Juncus squarrosus dominant sites
	2 %	Nardus grassland
	-	Moss carpets on waterfalls
Fridericia magna	25 %	Alluvial grassland and sheep droppings

APPENDIX. MISCELLANEOUS OBSERVATIONS FROM OTHER AREAS

BISHOP'S PARK, BISHOP AUCKLAND, CO. DURHAM

Fridericia perrieri in horse dung.

GLOSSOP, DERBYSHIRE

Enchytraeoides in Eriophorum peat.

CONNEMARA, CO. GALWAY, EIRE**

Enchytraeoides and Mesenchytraeus ?? in Molinia, Sphagnum, Eriophorum and Calluna peat and bog, near Clifden.

Enchytraeus albidus (Henle) in a bank of sea washed peat at Streamstown Bay, Clifden.

DURHAM CO. SCHOOL OF AGRICULTURE, HOUGHALL, DURHAM

Enchytraeus albidus in diseased chrysanthemum stools sent in for examination.

** information obtained from an expedition organised by the Durham University Exploration Society (Peachey 1955).

N.B. In addition to the above records many specimens of Fridericia have been recorded from lowland soils and leaf litter.

(4) THE REPRODUCTIVE BIOLOGY OF THE ENCHYTRAEIDAE

The enchytraeids are hermaphrodite, up to 35 eggs (Ivleva 1953b) may be laid in a single cocoon. The cocoons are small and difficult to see, unless deposited in culture against a glass slide (Christensen 1957). In the present study, a search for cocoons in soil samples has not been successful. It has been reported by Christensen & Nielsen (1955) that the eggs of Enchytraeoides develop parthenogenetically. This is suggested by the high chromosome number (2n = 180 - 200). Recently Christensen (pers. comm.) has suggested that E. sphagnetorum (the dominant species found at Moor House) "reproduces exclusively by fragmentation, followed by complete regeneration, the eggs laid by the exceptional mature worms do not develop". If this is true, then the absence of mature

Enchytraeoides in over 250,000 worms examined.(only a few semi-mature forms were found) is not surprising. Mature Fridericia and Mesenchytraeus were, in proportion to the immature forms, frequently found, the former in the summer months, the latter all the year, but particularly in the colder months.

(5) THE RÔLE OF ENCHYTRAEIDS IN THE SOIL

Many workers have reported the worms to be Humus formers (Friend 1916, Jegen 1920b, Nielsen 1955a). Schaerffenberg (1950) reports that 300 of the worms will take 3 months to eat 3 g. of maple leaf, but that their densities in soil may enable them to exceed earthworms as humus formers (this point is discussed in IV: 8). The present author has noted the finely divided excreta expelled from the worms, while being stored in water. Definition of the term 'humus former' must, however, await further work.

(6) ENCHYTRAEIDS AND OTHER ORGANISMS

In the coelom of the enchytraeids, especially near the reproductive segments, gregarines (Monocystidea) have been found. Ciliates and nematodes were common in the gut.

Nielsen (1955a) mentions Schendyla nemorensis as a predator of enchytraeid worms. The present writer observed substantial numbers of enchytraeid setae in the gut of the tipulid larva Trichyphona immaculata following storage in the same vessel after extraction from the same soil core.

Schaerffonberg and Tendl (1951) maintain that enchytraeids form a significant counterweight against the increase in numbers of plant parasitic nematodes. The enchytraeids are probably indicative of good agricultural practice.

PART III

SAMPLING AND EXTRACTION METHODS

(1) COLLECTION OF SOIL CORES 1956-57

Soil cores, each 7.3 cm. diameter and 42 cm^2 area and 5-6 cm. deep were taken, using a sampler (Fig. 10) consisting of a brass cylinder (A) 25 cm. high, 8·1 cm. internal diameter with a removable rod handle (fitting into B) and a fitted steel cutting edge (C). The cutting edge forms a ledge within the cylinder on which rests an inserted aluminium sample container (D) 7·7 cm. internal diameter. As the sampler is pressed into the ground, the soil core is pushed directly into the container, which is then withdrawn and enclosed in a polythene bag.

The soil cores are therefore kept moist and compact and can easily be withdrawn for extraction. Fifteen pairs of soil cores were taken at random over the sample area.

COLLECTION OF SOIL CORES 1957-1958

It was later decided to use a smaller sample size. A smaller sampler was made, similar to the one previously described with a cutting edge of diameter 3·5 cm. and area 10 cm^2. The soil core was pushed directly into a standard (Metal Box Co.) aluminium tin, 4·3 cm. diameter and 7 cm. depth, which could easily be inserted in the sampler, open end downwards.

Samples were collected from the Juncus 57 site in a stratified random manner.

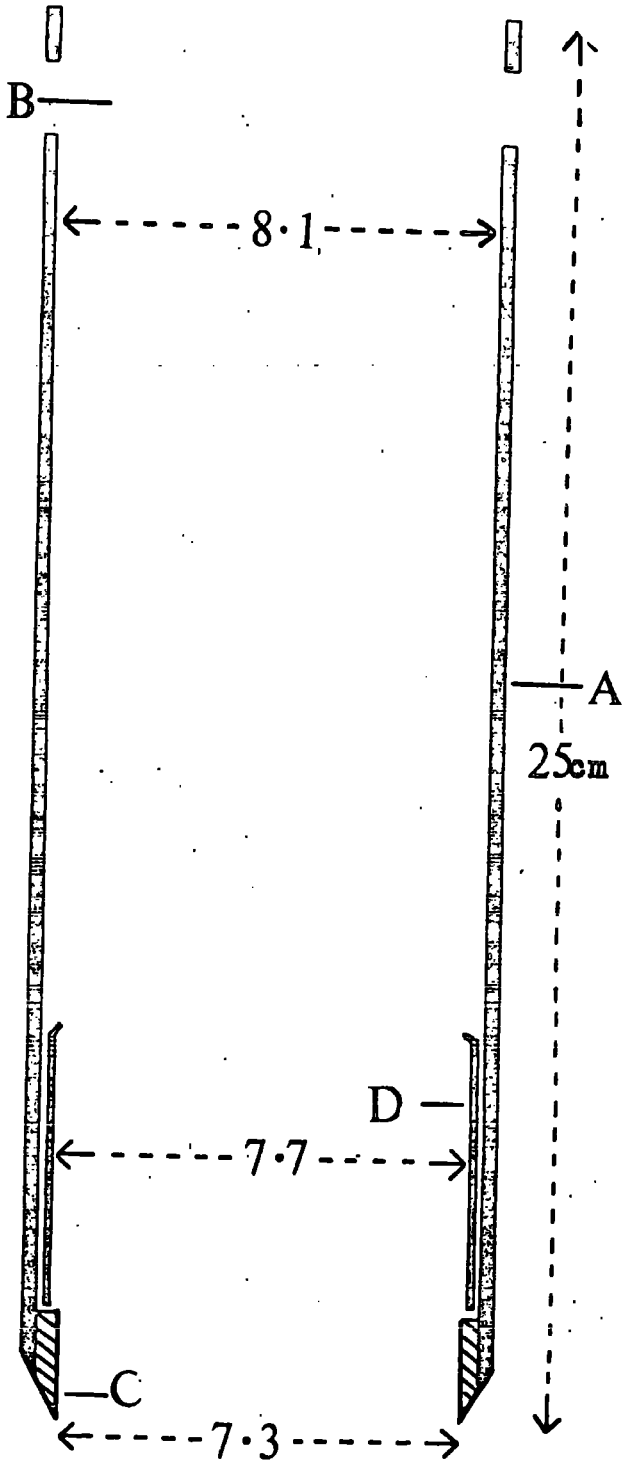


Fig. 10. The soil sampler.

(2) EXTRACTION METHODS.

The hand sorting or mechanical extraction of soil cores dry, in water or magnesium sulphate solution is inefficient and time consuming (Nielsen 1952), and it is necessary to consider methods which repel or attract the animals in such a way that the great majority of them are recoverable in good condition. For this to occur it is desirable to avoid heat paralysis (prolonged exposure to temperatures over 25-30°C) and desiccation, although heat and drying are the basic repellant stimuli for many extraction methods. Drying out is an even more serious threat to enchytraeids than heat so that its use has never been exploited. Overgaard (alias Nielsen) (1947) used modified Baermann funnels for the extraction of nematodes and rotifers from soil and moss. The soil sample was submerged in a funnel filled with water and heat was applied from above, the animals moving away from heat and sinking through the water to the funnel base. Nielsen (1952) and O'Connor (1955) developed this method for enchytraeids but Nielsen (1952) found that the presence of water induces the worms to move upwards - conflicting with the downward heat stimulus. Nielsen (1952) also found that waterlogging made some soils heavy and sticky, impeding the passage of the worms. He therefore developed a new method (Nielsen 1952) involving the application of heat and water from below, the worms being driven upwards into cooled moist gravel, from which they are easily recoverable.

Milne et al (1958) have developed a hot water method for the extraction of tipulids from turves. In principle it resembles the

Nielsen method.

The Nielsen and wet funnel methods have been compared by Nielsen (1952) who found his own method to be more efficient on a Brachypodium grassland in Oxfordshire and O'Connor (1955) who found the wet funnel method more efficient on a coniferous forest soil in North Wales. Both workers (O'Connor 1958) have recently made a comparison of their own methods on a Danish permanent pasture and found no significant difference between the two methods.

Because of these findings it was decided to compare these two methods throughout the sampling year 1956-1957 on four sample areas, using paired soil cores. (In the description of the extraction methods which follows it will be noticed that the degree of heating used was higher than that described by Nielsen and O'Connor. This was because the majority of the samples were from peat which has a lower thermal conductivity than mineral soil and so required stronger heating.)

(3) THE NIELSEN METHOD

Two sets of apparatus, to take in all thirty soil cores, were made, based in detail on the description given by Nielsen (1952), (Fig. 11).

The extraction takes place in specially made glazed earthenware cylinders (A) 14·5 cm. high, internal measure and 7·5 cm. internal diameter. At the base of the cylinder is a hole (B) and the bottom 3 cm. of the cylinder are filled with small stones (C) over which a perforated zinc gauze (D) is kept in position by Plaster of Paris (E). The soil core (F) is placed in its natural vertical position on the ledge

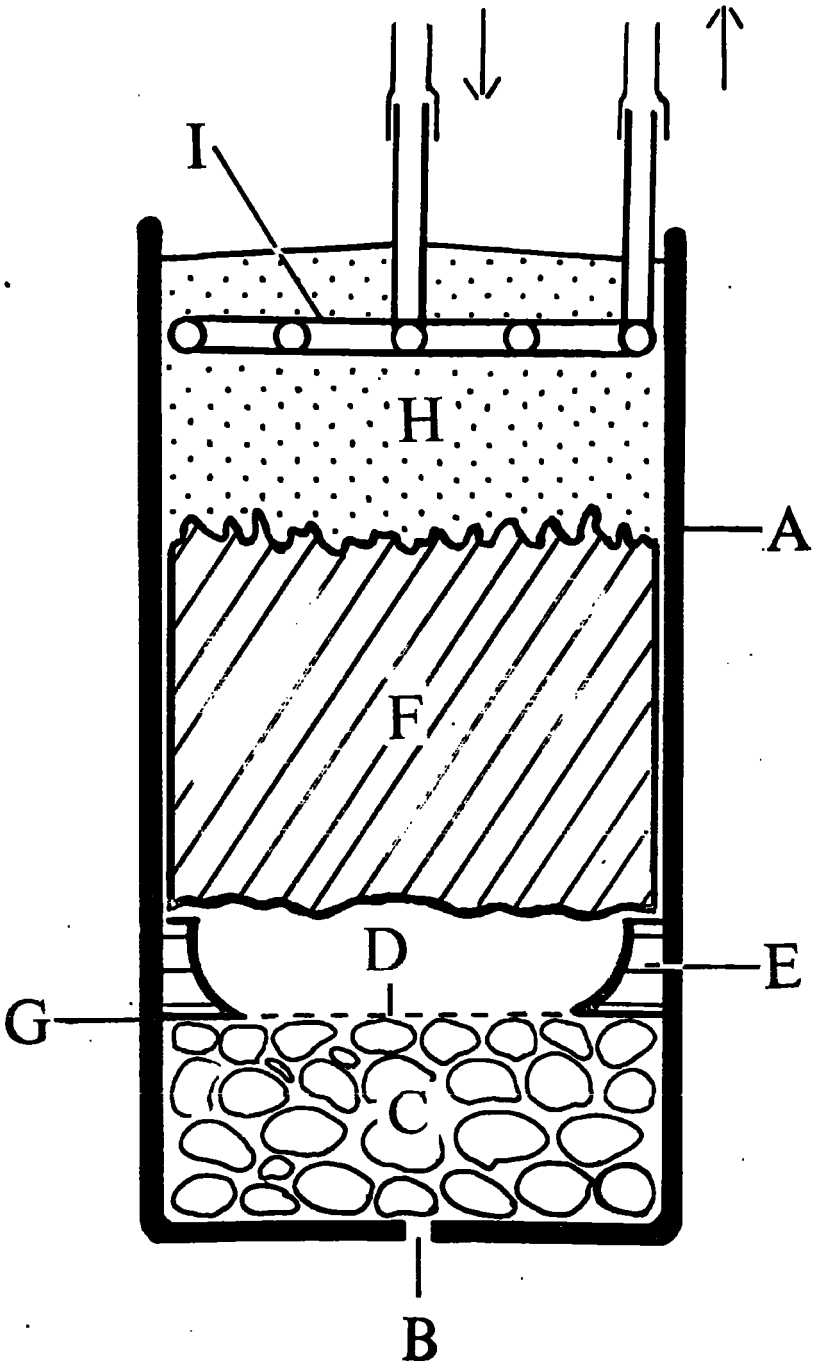


Fig. 11. The Nielsen extractor.

formed by the Plaster of Paris, leaving an air gap between the soil core and the zinc gauze.

Fifteen cylinders are arranged in rows of 3, in an electrically heated and controlled water bath, receiving uniform heating. The water level (G), adjusted to the level of the zinc gauze is prevented from accidentally rising by an overflow pipe.

On top of the sample is placed moist washed fine gravel (>$\frac{1}{8}$ in.) (H) in which is embedded, about 1 cm. from the top of the cylinder, a cooling coil (I) made from copper tube, through which water circulates to keep the gravel cool. The cooling coils have detachable rubber connections to facilitate dismantling.

At the end of the extraction the gravel and the cooling coil are placed in a deep-sided dish and the worms are washed out by manually rotating the water within the dish. The animals, being lighter, separate from the gravel and can therefore be decanted.

The water baths are so controlled that they reach a temperature of 50°C. after two hours and a maximum of 90°C. after three hours (although the temperature may be raised further towards the end of the extraction if required). The cooling system is turned on when the temperature in the top 1 cm. of the sample has reached 20°C. The heating is continued until the temperature in the top cm. of the soil core has been maintained at, or above, 35-40°C. for at least one hour. By this time, usually four to five hours after the start, all the worms will either have moved into the gravel or will have died under extraction conditions. The cooling system is next turned off and the

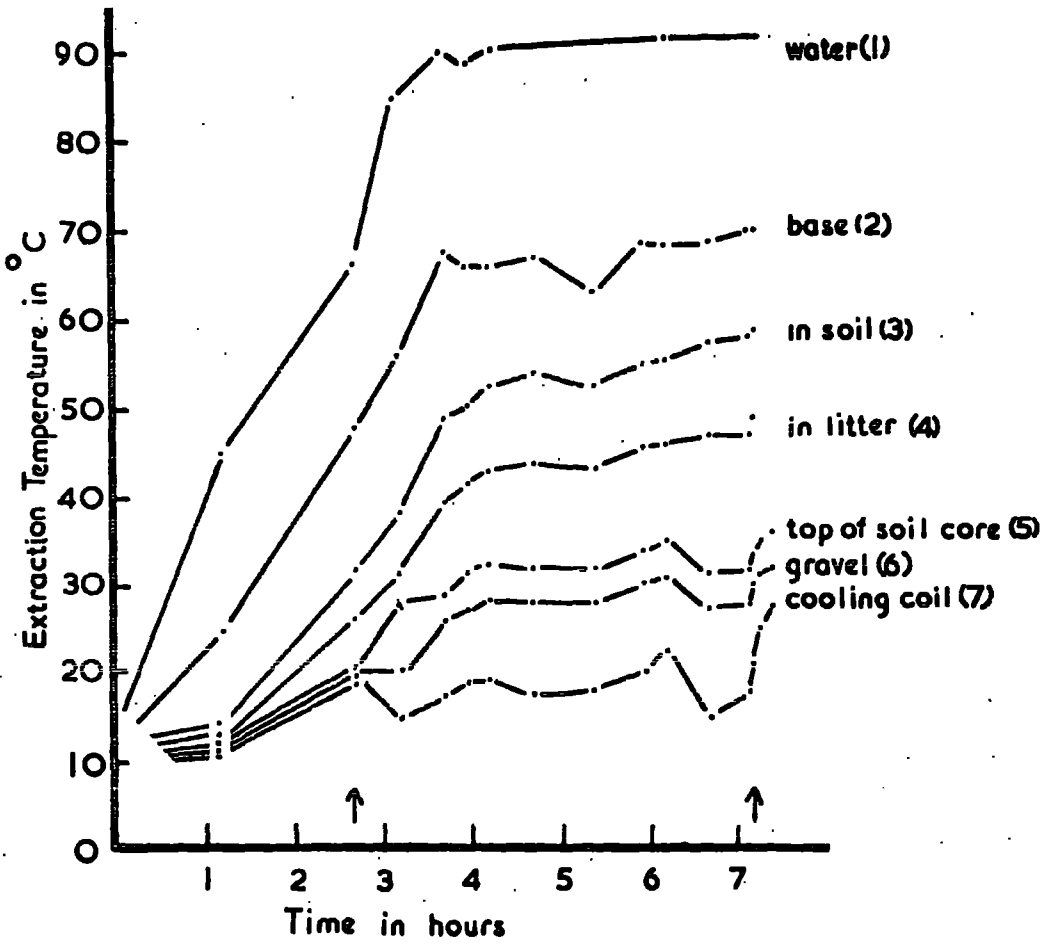


Fig. 12. Heating gradients in the Nielsen extractor.

temperature at the level of the cooling coil allowed to rise from about 15°C. to 22°C., which further concentrates the worms at the top of the gravel before dismantling. Fig. 12 shows the course of heating at various depths in the extraction cylinder, the temperature records being obtained by thermocouple measurements. These show how important the cooling coil is in keeping the top part of the gravel at a consistently low temperature. Because of this the gravel is kept moist as well as cool by condensation of the water vapour and the extracted worms are protected from heat paralysis and desiccation. Nielsen (1952) maintains that during the course of heating a gradient of moisture is established as the steam from the water bath condenses as it reaches the colder soil core.

(4) THE WET FUNNEL METHOD

A full scale battery of 30 extraction units was built according to the dimensions given by O'Connor (1955) (Fig. 13).

Polythene funnels (A), 11 cm. diameter are used resting in a 9 cm. diameter hole in an asbestos board (B). A brass gauze sieve (C), 9 cm. in diameter (with 20 meshes/in.) fits into the funnel at a depth to correspond to the level of the asbestos board (B). The tube of each funnel is closed by a screw clip on a piece of rubber tube (D). The funnels are filled with water to the top (E) and the sample (F) submerged on the sieve (C).

The heat source for each funnel is a 60 watt electric light bulb (G) enclosed in a shade (H), 11 cm. diameter, and 18 cm. high, with the bottom edge splayed out and 0·5 cm. (I) above the top of the funnel.

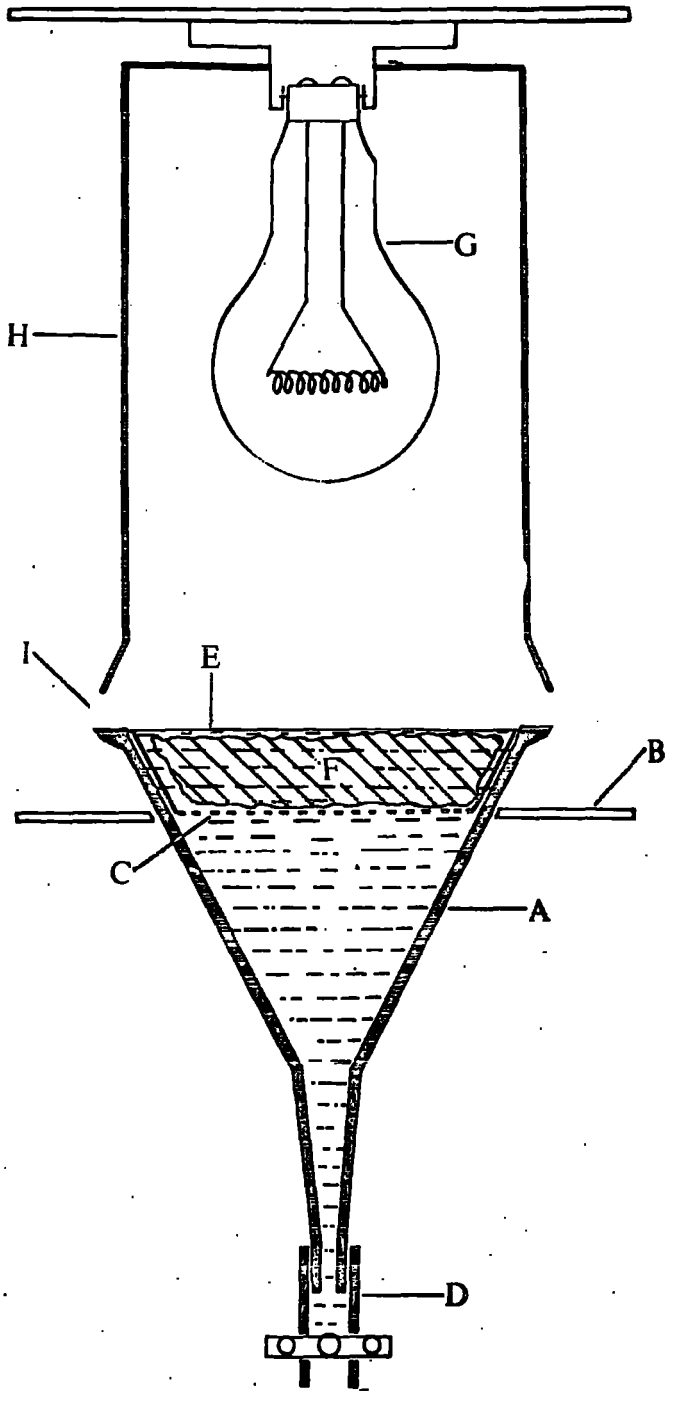


Fig. 13. The wet funnel extractor.

The electric lights are wired in parallel and controlled rheostatically. For convenience the heating units are detachable from the rest of the apparatus.

At the end of the extraction the funnels are allowed to cool, the screw clip (D) is undone and about 90 ml. of water are drawn off with the worms.

The initial temperature of the water in the funnels is in the range 13-15°C., and the top of the submerged sample (E) is raised to 50°C after approximately 3½ hours when heating is discontinued. By this time the bottom of the sample will have slowly reached 45°C. and the worms will either have been driven through the sieve or have died under extraction conditions. Thermocouple measurements were taken to show the heating gradient (Fig. 14).

Precautions were taken to avoid cooling at the edge (I) and the consequent establishment of a lateral gradient. In preliminary experiments a 5°C. drop from centre to periphery of the sample was noted and worms had evidently moved laterally and appeared to be trapped round the circumference. The gap (I) between the funnel and the shade was therefore kept narrow, and draughts avoided by building a shield round the entire apparatus.

Both extractions were carried out at a room temperature between 15°C. and 20°C., or as near as possible to this range.

(5) MISCELLANEOUS TECHNIQUES

(1) Treatment of soil cores

All soil cores were extracted within 72 hours of collection. During storage they were kept at 15°C. Worms from wet soil cores

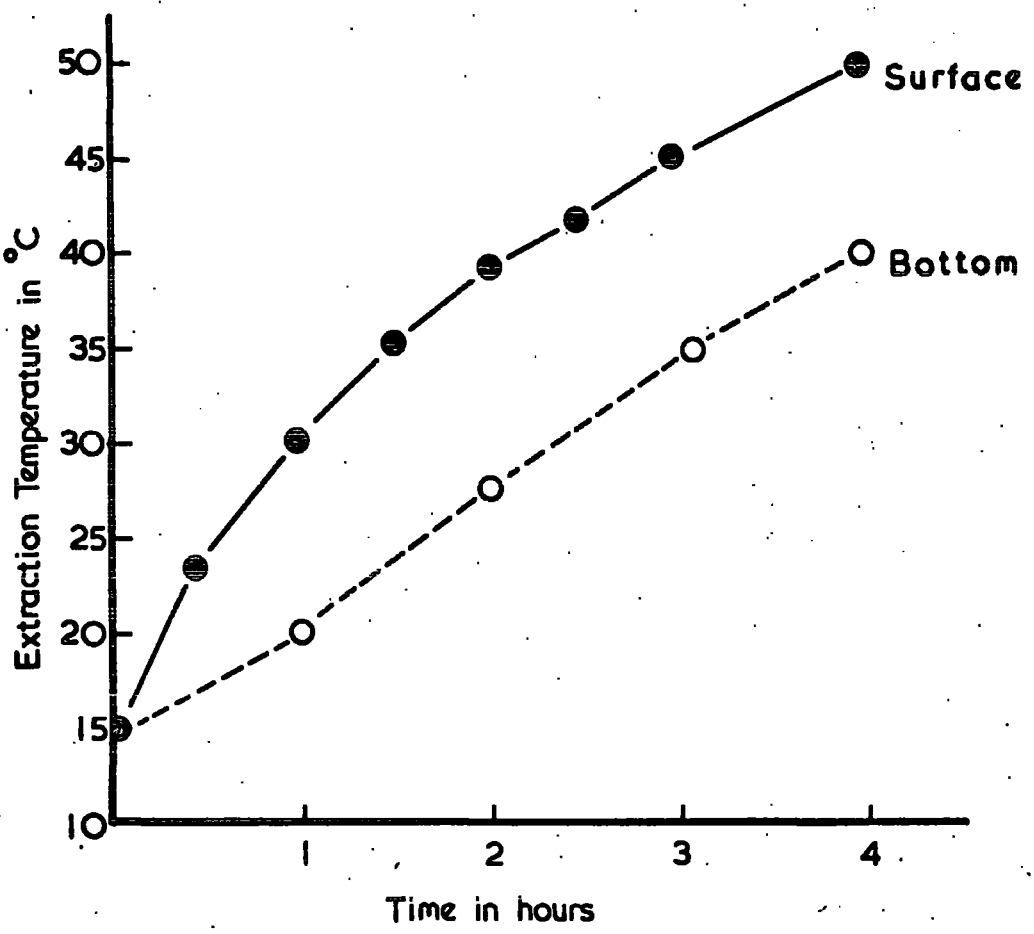


Fig. 14. Heating gradients in the wet funnel.

tended to move out on to the internal surface of the polythene bags and sample containers, these were recovered by rinsing and were added to the extraction material.

One of each pair of samples was extracted by the Nielsen method, the other by the wet funnel method. Soil cores were usually divided into horizontal layers before extraction on account of their bulk.

(2) Treatment of extracted material

After extraction the worms were stored in tap water at 0-5°C., and subsequently counted alive in water against a black background with strong lateral illumination. An electric counter, standardised at intervals, was used to record the numbers.

Other organisms extracted by these methods included tipulid larvae, chironomid and other dipterous larvae as well as planaria and other soil-dwelling animals. The tipulid larvae will be the subject of a separate report.

(3) Weighing technique

Prior to weighing, the worms were stored in clean water until their gut contents had cleared. They were then washed in several changes of water and weighed after draining in 5 batches of randomly selected worms (usually 200 worms per batch). The excess water was easily removed, as the worms tend to form a ball under these conditions which can be transferred to a coverslip for weighing after 'blotting' with filter paper.

(6) COMPARISON OF EXTRACTION METHODS - RESULTS

Preliminary comparisons

During April-May 1956 a preliminary comparison (Table 14) showed

Table 14. Comparison of extraction methods on soil cores (each 42 cm²) taken in sets of three (see text) April-May 1956

Column	(1)	(2)	(3)	(1) with (3)	(1) with (2)	(2) with (3)
Samples	Mean number per soil core Whole	Divided	Divided			
Method	Nielsen	Nielsen	wet funnel	't'	't'	't'
Juncus 56	283	387	528	7·32**	3·01**	5·74**
Bare peat	36	50	51	2·40*	1·63	0·13
Alluvial grassland	31	46	41	1·80	3·06**	1·60
Mesonchytraeus only Juncus 56	5	19	33	7·07**	4·91**	2·93*

* $P < 0.05$. ** $P < 0.01$ (14 degrees of Freedom)

that estimates from whole soil cores extracted by the Nielsen method (Column 1) were significantly lower than the wet funnel estimates (Column 3) on Juncus squarrosus and Bare peat areas. The Nielsen method showed a considerable increase in efficiency when the soil core thickness was reduced by division (Columns 1 and 2). When both methods were compared on divided soil cores (Columns 2 and 3) the differences in estimates were much less, only being significant for the Juncus squarrosus area.

By using the smaller sample size (10 cm²) it was possible in November 1957 to compare both methods using whole samples on a Juncus squarrosus area. The mean value for the wet funnel methods was significantly higher (Table 15).

Table 15. The comparison of extraction methods on paired soil cores (each 10 cm^3 and extracted whole) taken from a Juncus squarrosus area, November 1957.

	Mean number per soil core (thousands/m^2)	Significance
Nielsen method	92	t = 4·36
Wet funnel method	169	P < 0·001

Comparisons throughout 1956-1957

Tables 16-20 give the mean number of worms as extracted by both methods from paired soil cores. In Figs. 15, 16 and 17 these mean values are expressed in terms of relative efficiency of the Nielsen method. Relative efficiency is given by the ratio:

$$\frac{\text{Mean Nielsen estimate}}{\text{Mean wet funnel estimate}} \times 100.$$

Table 16. The comparison of extraction methods on paired soil cores (each 42 cm²) taken from the Juncus 56 area 1956-1957.

Date of sampling	Mean number per soil core		Significance	
	Nielsen method	Wet funnel method	't'	P
28•2	220	351	5.74	0•001
14•3	350	525	5•74	0•001
24.4	387	528	3•33	0•01
12•6	434	514	2•20	0•05
1•7	508	530	0•52	0•70
25•7	780	647	0•93	0•40
9•8	829	654	(2•07 (2•44 (log)	(0•10 (0•05
12•9	786	1039	2•25	0•05
10•10	664	834	3•66	0•01
12•11	565	669	(1•98 (2•20 (log)	(0•10 (0•05
11•12	429	636	4•33	0•001
30•1	487	561	3•17	0•01
4•3	472	559	(1•97 (2•48 (log)	(0•10 (0•05

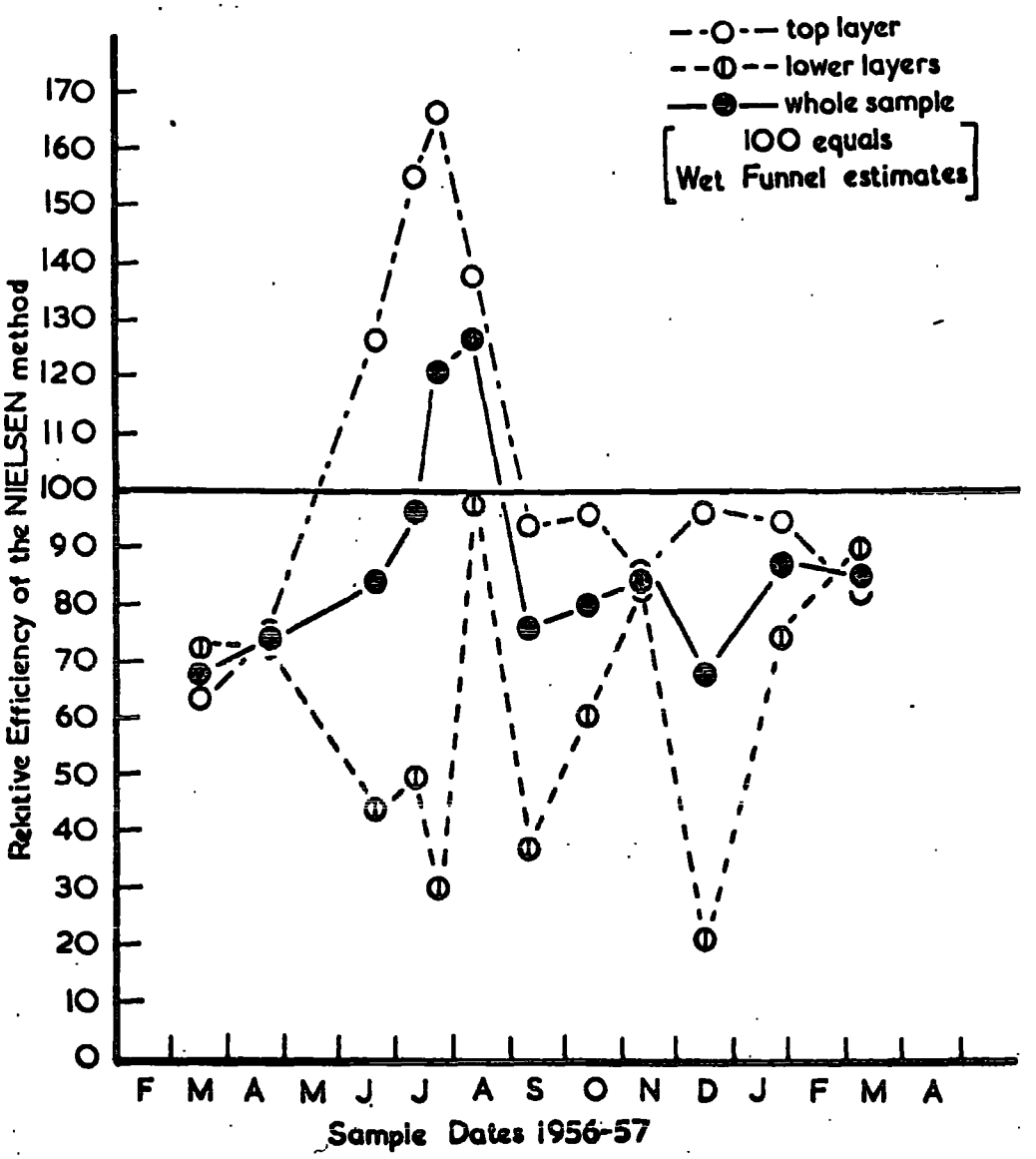


Fig. 15. Relative efficiency of the Nielsen extractor with Juncus 56 samples.

Table 17. The comparison of extraction methods on paired soil cores (each 42 cm²) taken from the Bare peat area 1956-1957.

Date of sampling	Mean number per soil core		Significance	
	Nielsen method	Wet funnel method	't'	P <
23·5	36	51	2·38	0·05
22·8	186	203	0·42	0·70
25·9	116	154	1·38	0·20
1·11	84	117	2·04	0·10
13·3	56	98	4·37	0·001

Table 18. The comparison of extraction methods on paired soil cores (each 42 cm²) taken from Alluvial grassland 1956-1957.

Date of sampling	Mean number per soil core		Significance	
	Nielsen method	Wet funnel method	't'	P <
23·5	31	41	1·80	0·10
30·8	104	89	1·23	0·30
2·10	124	98	3·26	0·01
1·11	113	122	0·80	0·50
4·12	89	110	2·49	0·05
6·2	79	104	2·51	0·05

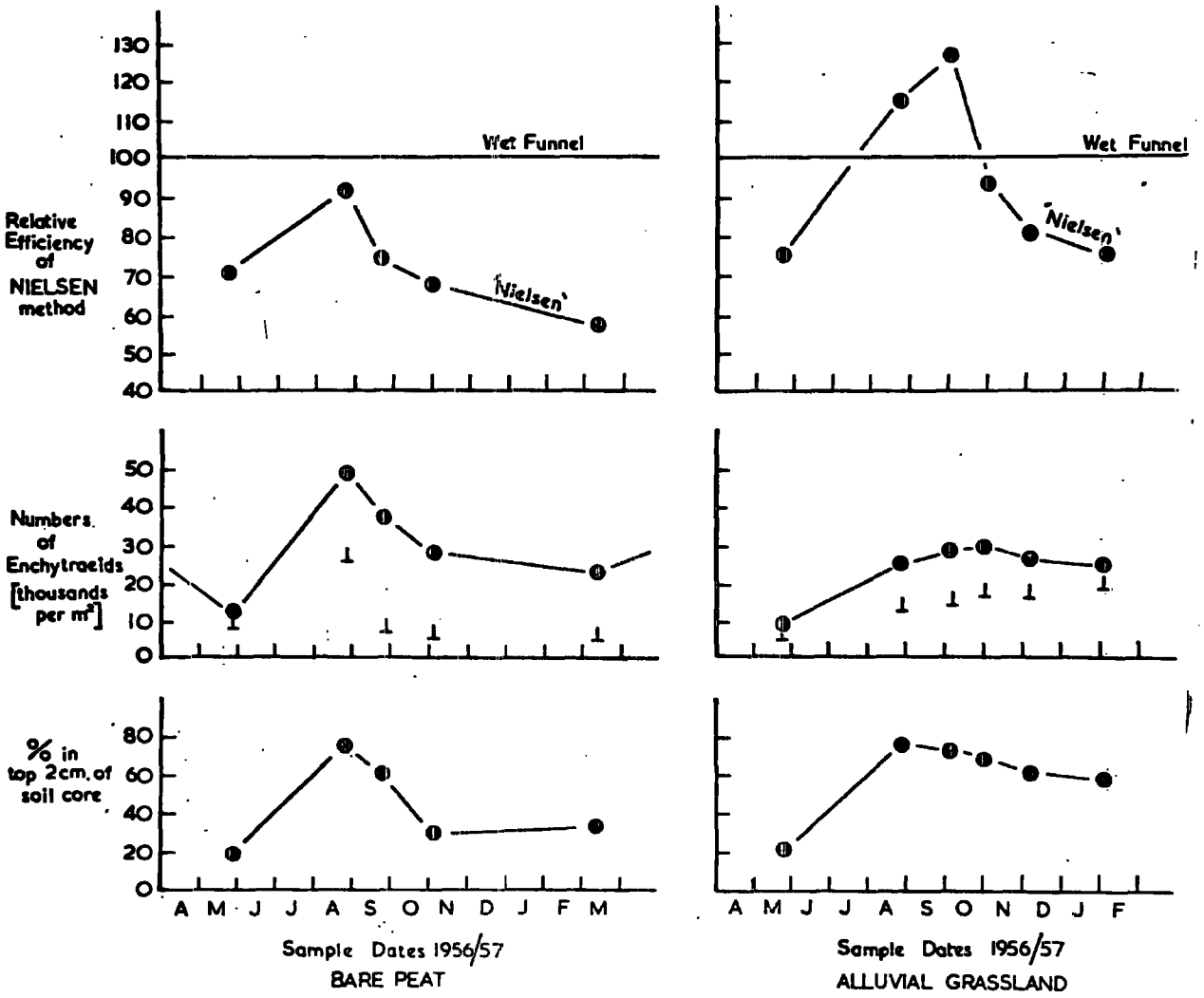


Fig. 16. Relative efficiency and seasonal trends 1956/57.

Table 19. The comparison of extraction methods on paired soil cores (each 42 cm^3) taken from Nardus grassland 1956-1957.

Date of sampling	Mean number per soil core		Significance	
	Nielsen method	Wet funnel method	't'	P <
14•3	88	155	3•10	0•01
5•6	84	51	2•34	0•05
31•7	224	138	3•46	0•01
5•9	239	192	2•24	0•05
18•10	397	405	0•31	0•80
27•11	403	362	1•06	0•40
12•2	447	312	4•42	0•001
11•4	497	518	0•41	0•70

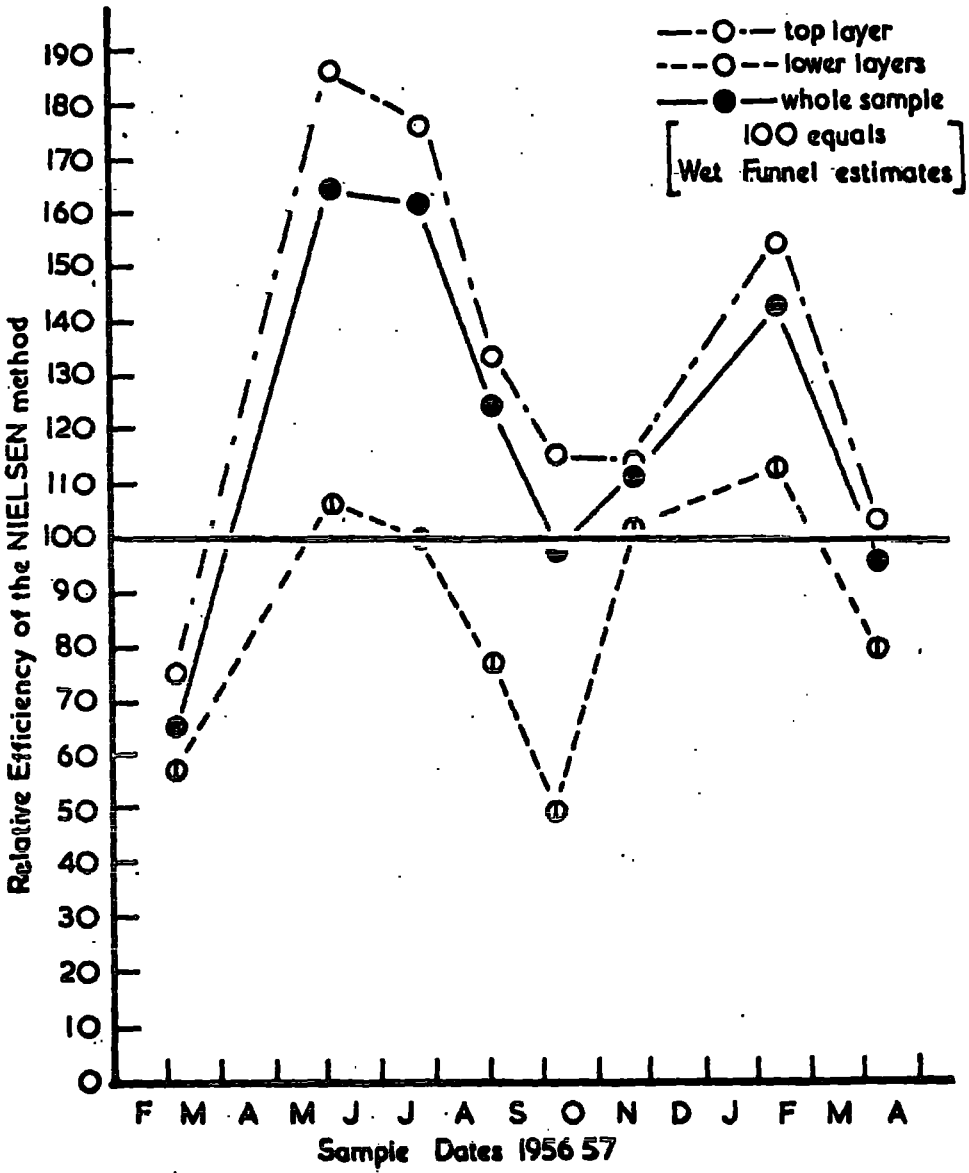


Fig. 17. Relative efficiency of the Nielsen extractor with Nardus samples.

Table 20. The comparison of extraction methods (for Mesenchytraeus only) on paired soil cores (each 42 cm²) taken from the Juncus 56 area 1956-1957.

Date of sampling	Mean number per soil core		Significance	
	Nielsen method	Wet funnel method	't'	P <
14•3	12	21	2•52	0•02
24•4	20	33	2•93	0.02
12•6	12	32	3•89	0•01
1•7	18	30	2•15	0•05
25•7	10	17	3•22	0.01
9•8	12	26	1•76	0•20
12•9	22	37	2•13	0•10
10•10	17	23	2•73	0•02
12•11	19	25	1•89	0•10
11•12	12	21	1•99	0•10
30•1	12	24	3•17	0•01
4•3	16	21	1•17	0.30

(a) Overall differences in relative efficiency

The wet funnel estimates for Juncus and bare peat areas (Table 21, Figs. 15 & 16) were generally higher than the Nielsen estimates. There was less consistent difference between the methods on grassland areas, though the Nielsen method gave higher value for the Nardus area.

Table 21. The overall relative efficiency of the Nielsen method 1956-1957 (wet funnel estimates = 100).

	Relative efficiency of Nielsen method on		
	whole sample	top layer	lower layer
(all species)			
Juncus 56	86	105	57
Bare peat	76	-	-
Alluvial grassland	96	-	-
Nardus grassland	112	123	79
(Mesenchytraeus only)			
Juncus 56	58	80	52
(Fridericia only)			
Alluvial grassland	55	-	-

The wet funnel method gave consistently higher values for Mesenchytraeus and Fridericia considered separately (Tables 20 & 21). Table 22 shows the results of a 't' test carried out on the paired estimates obtained by both methods for these species.

(b) Seasonal variation in relative efficiency

Figs. 15 & 16 show that there was an increase in the relative efficiency of the Nielsen method on July and August sampling occasions (for all areas except Nardus). This coincided with both an increase

Table 22. Comparison of all extraction estimates for Mesenchytraeus and Fridericia 1956-1957

Samples	Mean of mean number per soil core		Significance		
	Nielsen method	Wet funnel method	d.f.	't'	P <
Mesenchytraeus from Juncus 56	15	26	11	8·82	0·001
Fridericia from Alluvial grassland	1·2	2·2	4	5·28	0·01

in the number occurring in the top layer (Figs. 16 & 31) and in the number of Nielsen-extracted worms (Tables 16-18 & 23).

Table 23. The correlation coefficient for relative efficiency of, and numbers extracted by, the Nielsen method 1956-1957

Samples	Value of r	d.f.	P <
Juncus 56	0·638	11	0·02
Bare peat	0·965	3	0·01

(c) The relative efficiency with top and lower layers

The relative efficiency of the Nielsen method for top layer sub-samples was greater (Figs. 15 & 17) than for lower layer sub-samples in all cases (Table 21). It should be remembered however that the lower layer (about 3-4 cm. thick) was extracted whole in the Nielsen extractor, but further subdivided for the wet funnels. The discrepancy in relative efficiency between the top and lower layers may therefore be partly a function of thickness of soil core rather than difference in method. When only the numbers extracted per top layer are compared

for both methods (Table 21) the Nielsen method equals, or excels, the wet funnel method in relative efficiency.

(d) Seasonal variation in relative efficiency with top and lower layers of the sample

Fig. 17 shows that the variations in relative efficiency were similar for both top and lower layers (which were extracted separately). No such correlation existed with the results from Juncus samples (Fig. 15). This may be explained by the lack of a clear zonation between 'litter' and 'soil' which makes a meaningful division of the soil core difficult, whereas the Nardus soil cores could be easily divided.

(e) Relative efficiency and mean weight of worms extracted

The mean weight per worm extracted by the Nielsen method, on the August 1956 sampling occasion for Juncus, was significantly lower than the mean weight obtained from wet funnel extracted worms (Table 24) and since the mean estimate was greater it is concluded that, on this occasion, the Nielsen method extracted relatively more young worms.

Table 24. Differences in mean weight and mean numbers of enchytraeids extracted by both methods from paired soil cores (Juncus 56, August 1956).

	Mean weight** per worm	Mean number* per soil core
Nielsen method	0·209 ± 0·007	817
Wet funnel method	0·246 ± 0·005	626

*P< 0.05. **P< 0·001

DISCUSSION

From the results of the comparison of the two extraction techniques it may be concluded that,

(a) over the whole of the season, the wet funnel method was more efficient than the Nielsen method at extracting enchytraeids from wet peaty soils but there was little to choose between the two methods when tried on grassland samples. When, however, the top layer sub-sample results only are compared the Nielsen method is shown to have been as good as, or better than, the wet funnel method. The lower layer results were shown to be the cause of most of the Nielsen-observed discrepancies.

(b) the efficiency of the Nielsen method was much improved by the division of the soil core into layers which were extracted separately.

(c) the wet funnel method was relatively more efficient at obtaining the larger species - Mesenchytraeus and mature Fridericia. The Nielsen extractor was more efficient in the summer months (June-August) when it extracted more of the younger worms. Seasonal variations in relative efficiency were similar for the separately extracted litter and soil.

In general the wet funnel-extracted-worms were in better condition than the Nielsen-extracted worms, being alive and ready concentrated in the funnel base. At the end of the Nielsen extraction the worms were concentrated in the washed fine gravel from which they were removed by repeated washings. Since the heating gradient was

very much more difficult to control towards the end of the Nielsen extraction there was a tendency for some of the extracted worms to be dead or damaged by the time the washing process was due to be carried out. These damaged worms were often lost in this process especially when the excess washing water was decanted away, as they floated instead of sinking. There was also a loss due to non-recovery from the gravel. The over heating of the worms was partly caused by the uncertainty of ascertaining when all the worms were safely in the gravel. It was always very difficult to get the top of the soil core to the required temperature for expelling the worms without cooking those worms already extracted. Evidently other workers have also found similar difficulties. The cooling system requires very delicate adjustment at this stage - a disadvantage if a mains water supply is used as this is bound to vary in pressure and temperature.

It was also found that draughts and air temperature profoundly affected the establishment of the correct heating gradient particularly in the wet funnel method where, before adequate screening was provided, a 5°C. drop was common at the circumference of the funnels, attracting the worms outwards to the funnel edges where they were subsequently trapped by the warmer layers below.

The labour involved in making these comparisons severely restricted work on the study of the worms themselves and it soon became clear that the main consideration might well be this one of time, where other factors were not important. The Nielsen method required much more attention whilst the extraction was in progress, whereas the wet funnel method was easily managed and produced extracted worms ready for sorting

in a much shorter period of time, with less effort.

From these results and observations the following factors are discussed as relevant:

(a) soil type and soil conditions,

(b) thickness of the soil to be traversed by the animals in the course of extraction,

(c) species composition, age and physiological condition of the animals to be extracted,

(d) the effect of the extraction conditions on the animals,

(e) the labour involved in relation to relative efficiency.

(a) Soil type and soil conditions

The Nielsen method was designed to cope with soil cores taken from mineral soils and has been used extensively by Nielsen (1954, 1955a & b) on the exceptionally sandy soils of the Mols region (Jutland, Denmark). It is not, therefore, surprising to find that the grassland (mineral soil) samples were better suited to this method, whereas the peaty samples were generally best extracted by the wet funnel method, which was designed by O'Connor (1955) for an organic soil.

It is difficult to find out what soil factors influence extraction efficiency, because of the obvious fundamental problems involved such as ease of movement through the soil under extraction conditions. Nielsen (1952) maintains that the advantage of his method lies in the avoidance of waterlogging of the soil, which tends to make some soils, particularly clayey ones, sticky. This objection to submergence could hardly apply to the waterlogged peat samples; indeed it is suggested

that the submergence of the peaty soils helps to increase extractability as they tend to swell and become lighter in texture.

Mention has been made of the difficulty of heating peat in the Nielsen extractor; therefore soil conditions will affect the heating gradient and, as in the present investigation, suitable adjustments will have to be made to the heating arrangement. Nielsen (1952) observed that a moisture gradient was set up in the Nielsen extractor by the condensation of water vapour, rising from the water bath and meeting the cooler soil above. This gradient is supposed to work in conjunction with heat in repelling the worms upwards. It is known that enchytraeids choose optimum soil moistures (Ivleva 1953a) but when extracting naturally wet samples, as in the present work, this gradient can not be of great importance.

(b) Thickness of the soil to be traversed by the animals in the course of extraction

This factor will be influenced not only by the thickness of the soil core placed in the extractor but also by the position of the worms in the soil core. With the additional thickness of gravel, lying immediately on top of the soil core in the Nielsen extractor, it is more difficult to minimise this distance than in the wet funnel apparatus where, after the worms have safely penetrated the sieve, they only have to sink to the base of the funnel. The position of the worms in the soil core has been shown to vary throughout the year and because of the distance effect this variation in distribution will affect the extractability of the worms, especially when soil cores are extracted whole, as with Bare peat and Alluvial samples. This variation will

be reduced when soil cores are extracted as separate layers (as with Juncus and Nardus samples).

The decreased efficiency of the Nielsen method with the lower sub-samples was partly caused by the greater thickness of this layer as extracted in the Nielsen method, it being further sub-divided for wet funnel extraction.

(c) Species composition, age and physiological condition of the animals to be extracted

At this stage it is difficult to advance any reasons for the lower efficiency of the Nielsen extractor with Mesenchytraeus and mature Fridericia although their larger size and deeper distribution might favour the wet funnel method.

The better performance of the Nielsen method with young worms has been shown to be linked with the seasonal rise in efficiency in the summer when the young worms were more abundant. Why young worms should be favoured is not clear, but they may be more sensitive to some extraction condition such as heat or waterlogging which does not affect the older and larger worms.

Further statistical evidence will be given (IV: 3) to confirm the suggestion that the extraction methods tend to be biased in favour of extracting certain 'parts' of the population.

Nielsen (1952) found that under very cold conditions the yield from the extractor drops markedly and attributed this to the inactive condition of the worms, a phenomenon avoided to a limited extent by pre-extraction thawing-out at room temperature for one or two days.

In the present study a similar drop in numbers was encountered in the colder months. However, subsequent winter sampling has been avoided when the soil was hard frozen. This lowered efficiency in winter might be explained by the deeper distribution of the worms at this time which will have the effect of reducing the extractability of the worms present.

That some physiological factor is involved in the variation of extraction efficiency was indicated by the Nardus results, where similar variations occurred with the litter and soil layers extracted separately. Changes in species composition of Enchytraeoides may also be responsible for the efficiency variation.

(d) The effect of extraction conditions on the animals

Nielsen (1952) showed that enchytraeid worms were capable of moving through an 8 cm. column of sand, friable mull and raw humuus in less than 10 min. The present writer has observed worms passing through the sieve in the wet funnel method almost immediately following the start of the extraction. Heating gradients worked out by Nielsen (1952) and O'Connor (1955) adopted in this investigation seem capable of little improvement. Experimental work by Ivleva (1953a) has shown that Enchytraeus albidus when presented with the choice of various temperatures, preferred an optimum of 17°-18°C. This response fits in well with the behaviour of the worms under extraction conditions and demonstrates the importance of the cool 'shelter' for the worms after their extraction.

The fact that most of the worms, particularly those extracted by the wet funnels, remained alive under low temperature storage conditions for up to 2-3 months indicate the satisfactory nature of the heating gradient as far as it affects the worms successfully expelled by it.

Because of the effect of air temperature and draughts on the heating gradients, a constant temperature room would prove ideal for extraction work providing a cooling system was installed to keep the room temperature at 15°-18°C.

(e) The labour involved in relation to relative efficiency

In the preceding paragraphs the shortcomings of the extraction methods have been dealt with in detail, but in practice many of the errors are not as important as they seem, when viewed against the inevitable inaccuracies associated with the whole process from the collection of soil cores to the completed analysis of the data. The major factor may well be the labour involved and on this count the wet funnel method is definitely superior.

These considerations during the first year of sampling (summarised in table 25) led to the following general conclusion: that for the quantitative extraction of soil dwelling Enchytraeidae the investigator requires,

(1) a cheap, easily worked, extraction method which is adaptable to changes in soil core size,

(2) a sample site selected for the suitability of the soil type for the selected extraction method,

(3) a measure of the bias in the extraction technique and of its efficiency compared to some other different and independent method as hand sorting of enchytraeid worms, particularly the smaller ones is so inefficient that its use as a check method is a little pointless,

(4) a measure of the consistency of the technique obtained by suitable replication in sampling and extraction (see IV: 3).

The programme for sampling in 1957-58 was worked out on this basis (IV: 3) using the wet funnel method on Juncus 57. There is no doubt that the Nielsen method could have been used, but the extra effort involved for a brief period of higher efficiency did not justify its acceptance.

Table 25. Summary of comparisons of the extraction methods

	Wet funnel method	Nielsen method
Soil type	better for organic and peaty soils	better for mineral soils
Thickness of soil core to be extracted	should be as thin as possible; more convenient for separate extraction of sub-sample layers	
Species composition and age	better for mature Fridericia, Mesenchytraeus and most Enchytraeoides, [Enchytraeoides Henlea O'Connor 1957]	better for young worms (1-2 mm.) [Fridericia bistosa Nielsen 1955]
Heating gradient	not critical but may be difficult to control in summer without C.T. room	critical difficult to adjust especially cooling system
Condition of the worms after extraction	in water with some debris alive	in washed gravel some may be dead or lost in washing out of gravel

PART IV

THE QUANTITATIVE DISTRIBUTION OF ENCHYTRAEIDAE

Sample data obtained for 1955-58 contains information on the distribution of enchytraeids. An attempt has been made to split up this general distribution into various groups under two arbitrary headings, the first, referring to information obtained from sample unit values, the second, on information obtained from sample mean values as described below.

(a) Sample unit values

(1) SAMPLING DISTRIBUTION, a primarily statistical concept concerning the distribution of sample unit values about the mean. The nature of this distribution has been compared with the expected distribution of sample unit values taken randomly from a theoretical normal population.

(2) MICRODISTRIBUTION, the distribution of the animals in a small plot which is completely extracted. This has been carried out to show the presence of aggregations in a seemingly uniform area.

(3) HORIZONTAL DISTRIBUTION, providing information on the distribution of enchytraeids within the sample site, when sample units were obtained in a stratified random manner.

(b) Sample mean values

(4) VERTICAL DISTRIBUTION, the distribution of the worms with depth.

(5) SEASONAL DISTRIBUTION, the variation in density of enchytraeids in the sample area throughout the year.

(6) ANNUAL DISTRIBUTION, the variation in density from year to year.

(7) AGE DISTRIBUTION, the distribution obtained from weight measurements.

(8) ECOLOGICAL DISTRIBUTION, the differences in density and biomass of the animals from one sample area to another.

(a) SAMPLE UNIT VALUES

These provide information on the statistical requirements of the results, in order to draw the correct conclusion from the sample data. Additional data on the performance of the wet funnel extractor and on the spatial distribution of the animals is also included.

(1) SAMPLING DISTRIBUTION

χ^2 tests

The distribution of most populations sampled is very rarely a normal one. Previous work by both Nielsen (1954) and O'Connor (1957) has shown that the enchytraeid sampling distribution can be expected to be skewed with an excess of sample unit values distributed just below the mean (small negative deviates) and a small excess of values distributed well above the mean (large positive deviates).

Method of study

Information was collected from all the sampling data by arranging the numbers obtained from individual sample units in frequency classes,

whose class marks are numbers of standard deviations from mean values. The sum of their frequencies over the sampling period, expressed on a percentage basis is shown in Figs. 18 & 19 for different sampling areas and extraction methods. The theoretical normal distribution is also shown.

Using X^2 it was decided to compare the discrepancies between

(a) the observed and the theoretical normal distribution (a more refined statistic was also used to separate skew from kurtosis),

(b) distributions obtained by different extraction methods, and

(c) from different sample sites.

For the comparison of the sampling distribution to the normal expectation X^2 was obtained from the formula

$X^2 = \frac{(o-e)^2}{e}$ where (o) is the observed value and (e) the expected (theoretical) value.

For the comparison of the two observed distributions X^2 is given by the formulae

$X^2 = \frac{(a-rb)^2}{r(a+b)}$ where (a) and (b) are the two observed frequencies and $r = Na/Nb$, Na and Nb being equal to the numbers of sample units in each distribution: where these are equal $r = 1$ and $X^2 = \frac{(a-b)^2}{a+b}$. X^2 calculations were of course carried out on numbers, not percentages. Frequency classes of less than 5 were generally grouped.

Results

(a) Deviations from normality

Table 26 shows the comparisons made between the sampling data

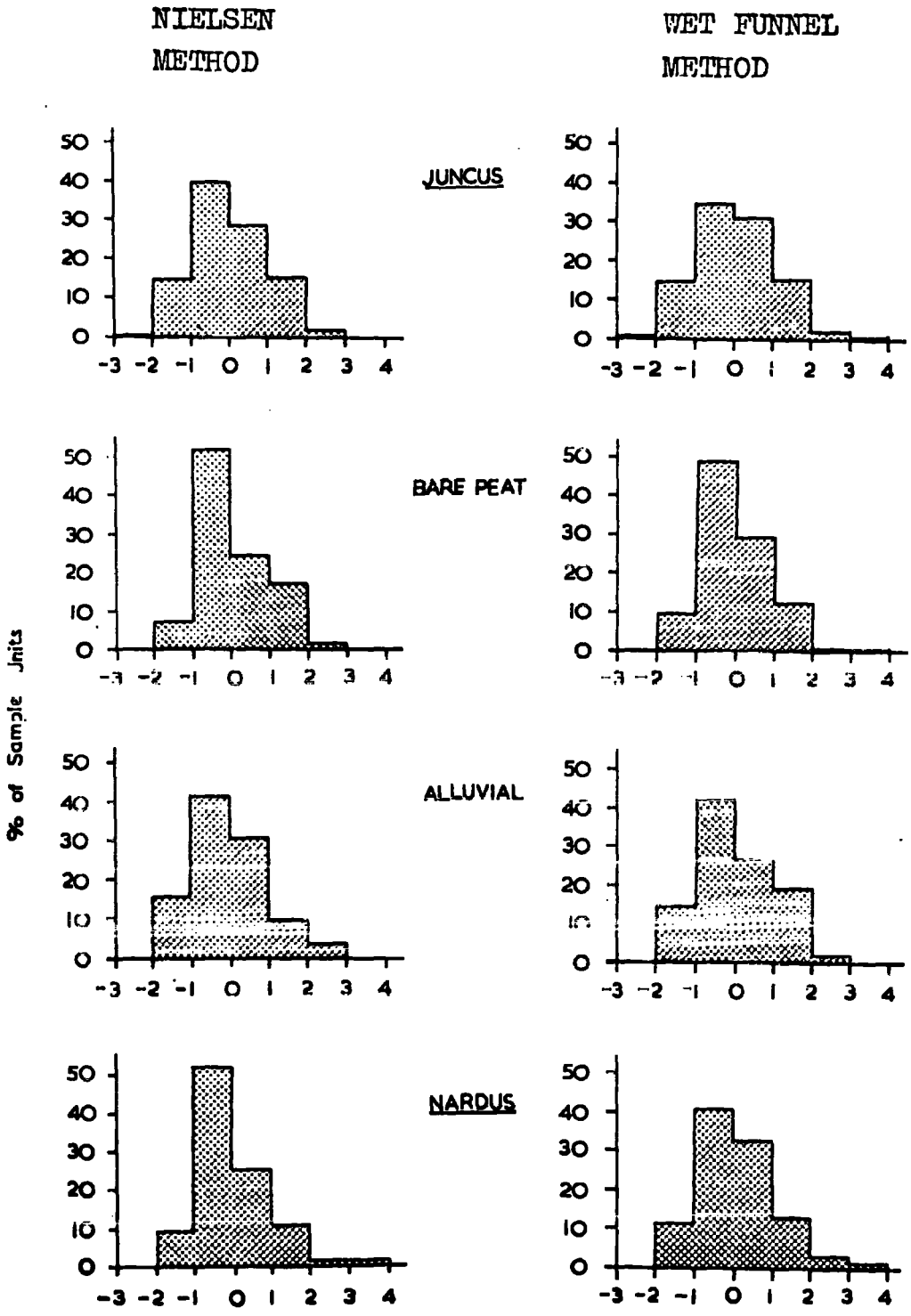


Fig. 18. % distribution of sample unit values.

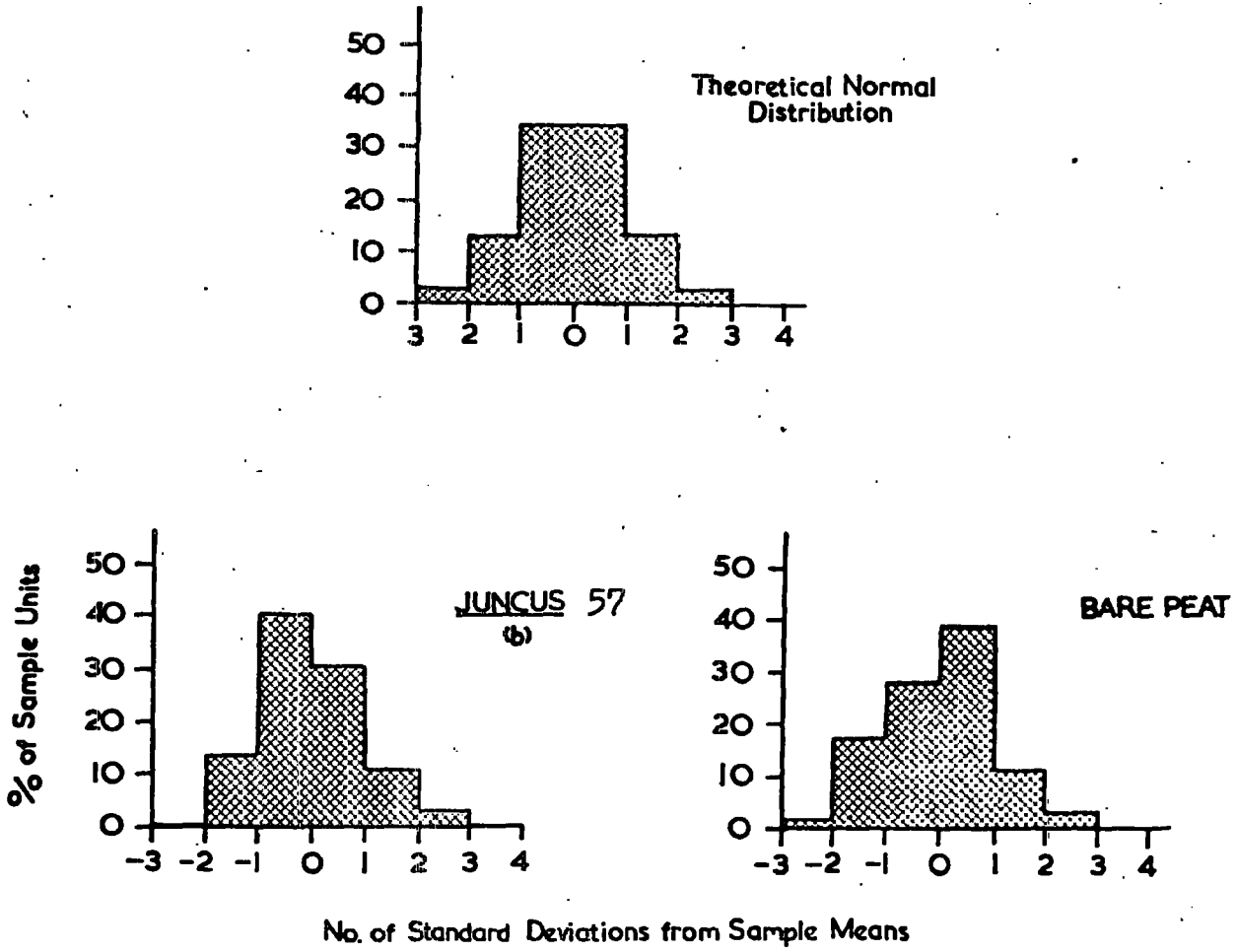


Fig. 19. % distribution of sample unit values.

obtained in this study and published data of Nielsen (1954) and O'Connor (1957), compared to the theoretical normal distribution.

Table 26. % distribution of observations arranged in S.D. classes about the mean

S.D. classes	-2	-1	mean	+1	+2	+3	Number of soil cores
All areas 1956 (Nielsen)	0·2	12·3	45·2	26·7	13·1	2·1	0·4	480
(Wet funnel)	0·4	13·1	39·6	30·2	14·4	1·7	0·6	480
Juncus 57	0·4	13·5	40·1	30·9	11·6	3·4	0·1	735
Previous work (Nielsen 1954)	0·1	11·6	46·5	26·0	11·3	4·1	0·4	2850
(O'Connor 1957)	0·4	15·5	39·4	25·9	15·1	3·7	0	490
Theoretical normal	2·3	13·6	34·1	34·1	13·6	2·2	0·1	-

The X^2 values (Table 27) show that when all the observations from the various sample areas (Fig. 18, Table 26) are considered, significant deviations from normality occurred in the sampling distributions obtained by both extraction methods, with a tendency to greater abnormality for the Nielsen method.

Table 27. Values of X^2 for deviation from normality of the sampling distribution

Sample area	Nielsen extracted	Wet funnel extracted	d.f.	Total number of soil cores
Juncus 56	5·06	0·53	3	195
Bare peat	13·37**	7·14	3	75
Alluvial	2·95	3·85	3	90
Nardus	16·50***	3·55	3	120
All sites 1956-1957	35·65***	14·00*	5	480
Juncus 57	-	28·64***	5	735

* $P<0·02$. ** $P<0·01$. *** $P<0·001$

The sampling distribution (illustrated in Figs. 18 & 19 and Table 26) differed most obviously from normal (Table 27) in the following ways.

(1) Generally there was an excess of negative deviates (Table 28) or skew in the sampling distributions. This skew was greater when sample figures obtained by the Nielsen method were considered,

(2) the most obvious deviation from normality was to be found in the ± 1SD classes. In a theoretical normal distribution the percentage numbers in these two classes should be both equal to 34. An excess of values was however found in the small negative deviate class (-1SD) with consequent inequality of values about the mean, again more pronounced in the Nielsen extracted samples (Table 29),

(3) when the tails of the sampling distribution were compared a small excess of very large positive deviates (>3 SD) and a shortage of large negative deviates (> - 2SD) were conspicuous (Table 30).

Table 28. % numbers of negative deviates

Sample area	Nielsen extracted	Wet funnel extracted samples
All sites 1956-1957	58	53
Juneau 57	-	54
Nielsen Denmark (1954)	58	-
O'Connor N. Wales (1957)	-	55
Theoretical normal	50	

Table 29. % numbers of small negative deviates with their X^2 values for deviation from normality

Sample area	Nielsen extracted samples		Wet funnel extracted samples	
	% small negative deviates	X^2	% small negative deviates	X^2
Juncus 56	40	1·95	35	0·03
Bare Peat	52	7·01**	48	4·23*
Alluvial	42	1·74	41	1·29
Nardus	52	10·76**	40	1·56
All sites 1956-1957	47	17·12***	39	4·12*
Juncus 57	-	-	40	7·75*
Nielsen (1954) Danish results	47	-	-	-
O'Connor (1957) N. Wales results	-	-	39	-
Theoretical Normal	34	-	34	-

* $P < 0.05$. ** $P < 0.01$. *** $P < 0.001$

Table 30. % number of large negative deviates in the +2SD class with their X^2 values for deviations from normality

Sample area	Nielsen extracted samples		Wet funnel extracted samples	
	% large negative deviates	X^2	% large negative deviates	X^2
All sites 1956-1957	0·2	9·09**	0·4	7·36**
Juncus 57	-	-	0·4	11·34**
Normal	2·3	-	2·3	-

*$P < 0.05$. ** $P < 0.01$. *** $P < 0.001$

(b) Comparisons of sampling distributions obtained by different extraction methods

No significant differences exist between the Nielsen and wet funnel distribution - both present a roughly similar picture - however the deviations from normality have been shown to be more severe when the Nielsen samples are considered.

A similar difference is found when the results of Nielsen's (1954) and O'Connor's (1957) data are compared (Table 26)

(c) Comparisons of sampling distributions from different sample areas

Fig. 18 shows that the Nardus and Bare Peat sampling distributions were more asymmetrical than the other distributions. The X^2 values for Nielsen extracted samples (Table 31) were not however significant.

Table 31. X^2 values for the comparison of different sampling distributions (Nielsen method)

Sample area	X^2	d.f.
Nardus-Juncus 56	7·39	4
Juncus 56-Bare peat	5·13	3

(g_1) and (g_2) statistics for skewness and kurtosis

The X^2 tests cannot differentiate between skewness and kurtosis - two ways in which distributions differ from normality. Using the results of preliminary sampling of 75 soil cores on the Juncus 57 sample site a frequency distribution was constructed and from it two statistics, (g_1) and (g_2) were calculated.

(g_1) is the statistic which detects skewness and is given by the formula

$$g_1 = \frac{k_3}{k_2^3}$$ where (k_2) is

the mean square and (k_3) the corresponding statistic for the third power of the deviations from the mean.

(g_2) detects kurtosis and is based on the fourth power of deviation from the mean (k_4). It is obtained from the expression

$$g_2 = \frac{k_4}{k_2}$$

The significance of the values of (g_1) and (g_2) is determined by the estimate of (t) where

$$t_1 = \frac{g_1}{sg_1} \quad t_2 = \frac{g_2}{sg_2}$$

with infinite degrees of freedom, (sg_1) and (sg_2) being the respective standard errors of the values (g_1) and (g_2).

The values of (g_1) and (g_2) are shown in Table 32 for the untransformed and log transformed numbers obtained from 75 soil cores (each 10 cm^3) sampled from Juncus in April 1957.

Table 32. Values of g_1 and g_2 and their significance for 75 sample units from Juncus 57

Data	Test for skewness		Test for kurtosis	
	g_1	t_2	g_2	t_2
Untransformed	+0.564	2.03*	-25.24	46.04***
Log transformed	-0.005	0.02	+ 3.204	5.843***

*$P < 0.05$. ***$P < 0.001$

The positive value of (g_1) for the untransformed data showed that the sampling distribution was skewed with an excess of below - mean values. The negative kurtosis ($-g_2$) indicated that there was an excess of moderate values. The effect of the transformation is to reduce skew (g_1) and kurtosis (g_2)

The relation between mean and standard deviation

The sampling distributions were further studied by plotting mean values against their standard deviations. The standard deviation rose with the mean value (Fig. 20) but at lower mean values the standard mean value was proportionately higher than at higher mean values. This is better shown by using percentage standard deviation or coefficient of variation.

$\%$ S.D. $= \frac{s}{\bar{x}} 100$ where (s) is the standard deviation of the mean value ($\bar{x}$) as shown in table 33.

Table 33. The relationship of mean values and % S.D. (from 15 soil cores each 42 cm^2 area)

Mean	% S.D.
50	55
250	40
750	35

The scatter of the S.D. values is greater at higher densities.

Fig. 21 refers to results using a smaller sample size. Any increase in scatter which may have resulted from using a smaller core was

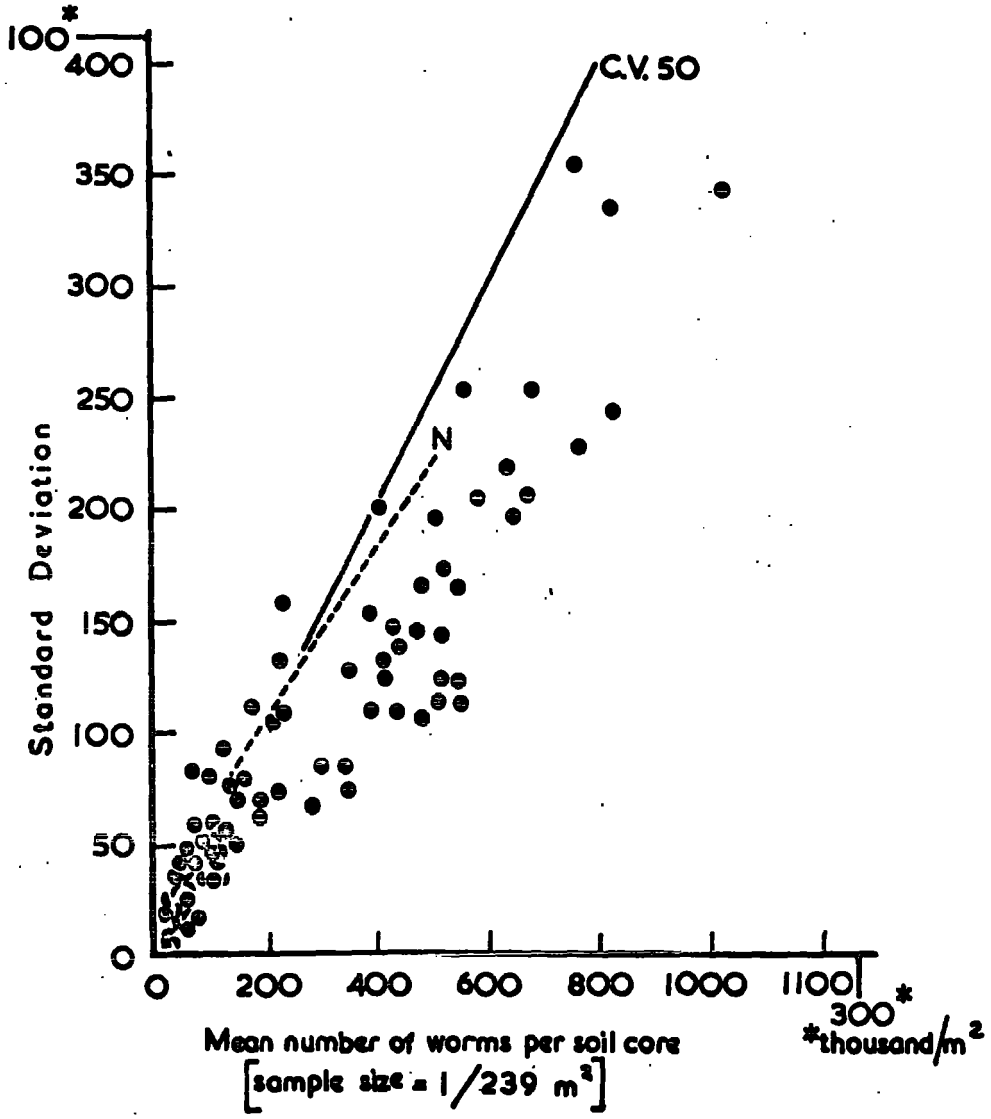


Fig. 20. Mean values and standard deviations, 1956/57.
(N = Nielsen's 1955 results.)

more than offset by taking a greater number of soil cores on each sampling occasion (as indicated in Fig. 21 by open circles representing values for 45 soil cores).

In Fig. 20 the dotted line represents the average trend of Nielsen's (1955a) results from Danish habitats. The 50 % standard deviation line marked on both graphs is approximately equal to O'Connor's (1957) results.

If a detailed comparison is carried out using all the paired sample results from both extractions (Table 34) it will be seen that in general the percentage S.D. was of the same order, though slightly lower for the wet funnel results. If these values are compared to Nielsen's (1955a) on results for similar mean values both sets of figures from the present author's work were generally lower than the Nielsen equivalent.

Table 34. Average % S.D. for results from both extraction methods and the equivalent value obtained by Nielsen (1955a)

Sample area	Nielsen method		Wet funnel method	
	Present work	Nielsen's equivalent	Present work	Nielsen's equivlent
Juncus 56	33	-	28	-
Bare peat	53	64	65	59
Alluvial	48	64	40	62
Nardus	58	51	50	52
Total	54	59	51	57

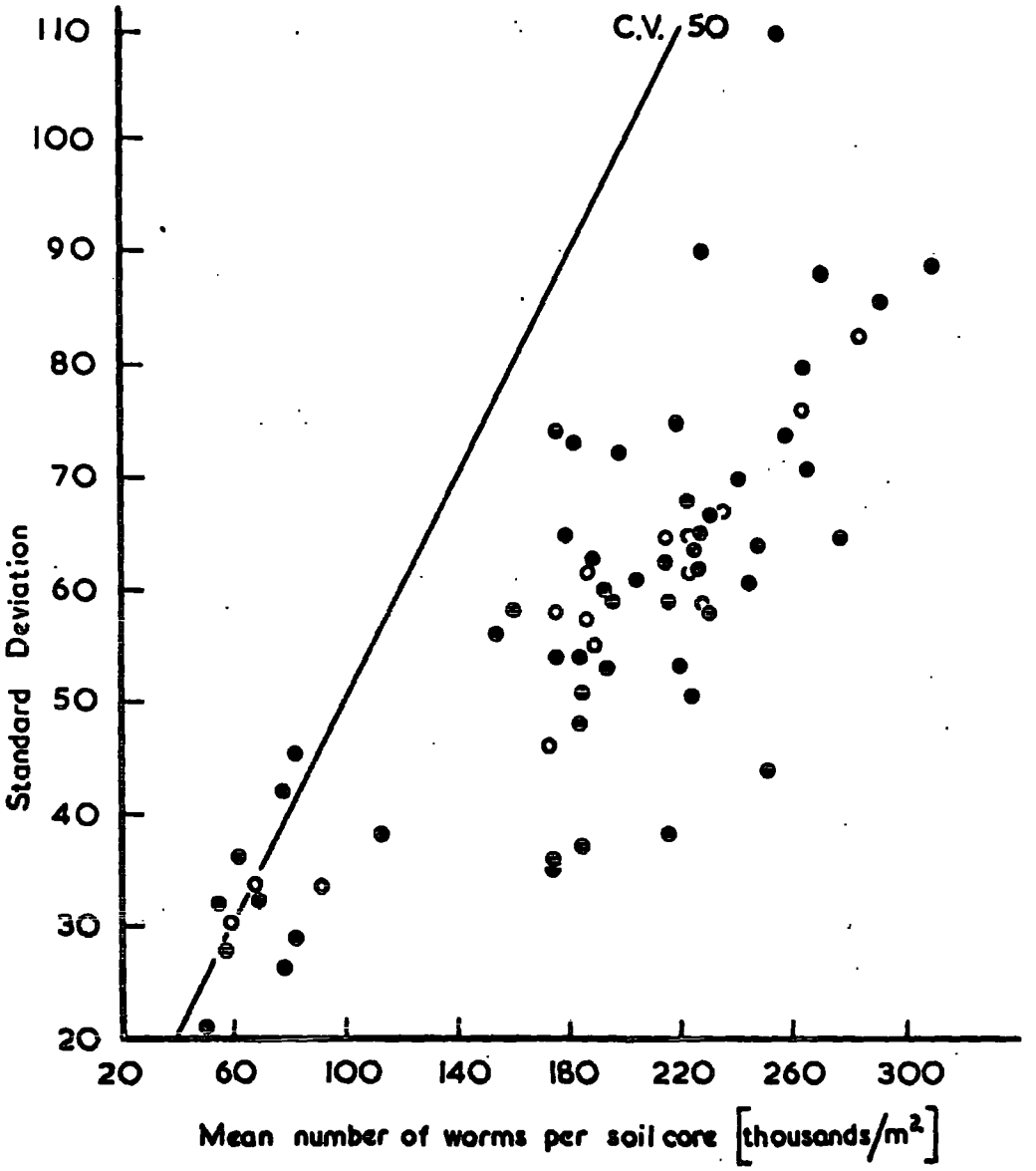


Fig. 21. Mean values and standard deviations of Juncus 57 samples (open circles = 45 sample units, closed circles = 15 sample units).

Discussion

The characteristic excess of small negative and large positive deviates with a resultant negative skew has been shown to be a common feature of almost all the enchytraeid sampling distributions so far recorded. This speaks highly for the extraction methods and sampling procedures used. However the present work has demonstrated that differences, though small, do exist both in the numbers, size (.) and sampling distribution obtained by the two methods - all that can be said at this stage is that if two extractors are not 100 % efficient (and none are) then each will select its own extractable part of the population.

A sampling distribution is of course always anormal in the sense of being finite and having a restricted number of large negative deviates due to the impossibility of sampling a negative number of worms. The excess of large positive deviates, with a resultant inequality around the mean, are attributed to the spatial patterning of the worms in the sample area, to be discussed later. More precisely, the (g_1) and (g_2) statistics showed an excess of moderately placed below-mean values (positive skew and negative kurtosis).

One very practical aspect of anormality is its effect on the statistical tests and significance levels conventionally accepted, though this effect is not considered to be as important as in the earlier days of statistical tests. However, in the present study, it was decided to try the effect of transforming the data, in order to normalise it. The effect of such a transformation is shown (Table 32) by the reduction in value of g_1 (skewness) and g_2 (kurtosis) using the

logarithms of the numbers.

The characteristic relationship of the mean to the standard deviation so typical of sampling distributions like the ones discussed helps in two ways,

(i) to indicate an appropriate transformation, in this case a logarithmic transformation is suitable (Barnes & Bagenal 1951),

(ii) to form a standard against which further values can be checked. By using the relationship for this purpose it has been possible to conclude that in general the Nielsen method gives higher percentage standard deviations than the wet funnel method when both the present work and Nielsen's and O'Connor's results are compared. The lower percentage standard deviations for the Juncus are quite striking. These comparisons are parallel to those made with the normal distribution and the same reasons will apply - that heterogeneity in the efficiency of the extractor or in the sample area is the cause of increase in anormality or variance.

(2) MICRODISTRIBUTION

In recent years much attention has been paid to the spatial distribution of the soil fauna and sampling methods have been designed to determine the form and variation of this arrangement of the members of a soil population.

Microdistribution can be studied in three ways,

(i) from random sampling data. The sampling results are compared to the Poisson distribution to give a measure of the degree of aggregation, or otherwise, to be found in the population studied.

(ii) by the complete enumeration of a small area and the subsequent

mapping and analysis of the numbers obtained. This approach was used by Salt & Hollick (1946) for wireworms and later by Nielsen (1954) and O'Connor (1957) for enchytraeid worms.

(iii) by a method of tie-line sampling, recently described by Hughes (1958). This method combines the advantages of both the preceding ones but avoids the destruction of the sample area (as is necessary for complete enumeration) making possible a repeated study throughout the sampling year.

In this work the first two methods have been used but as the opportunity of the Hughes method has arisen, a comparison has been made between this and a complete enumeration.

(i) Information obtained from random sampling data

Most populations sampled are not randomly distributed. A convenient measure of randomness is given by the coefficient of dispersion (Clapham 1936) which is given by the expression.

$$\frac{\sum (x-\bar{x})^2}{\bar{x}\,(n-1)}$$ where $\sum (x-\bar{x})^2$ is the sum of the squares of the deviations of the individual units (x) from the mean ($\bar{x}$) of all the units (n) making up the sample. It will be noticed that the coefficient is in fact the ratio of variance to mean which is equal to unity when a randomly (Poisson) distributed population is sampled. If the population is overdispersed the coefficient is less than unity, if underdispersed or aggregated, the coefficient is greater than unity. The deviation from unity is significant if it exceeds the value-

$$1 \pm 2\sqrt{\frac{2n}{(n-1)^2}}$$

which for n = 15 samples is 1 $\pm$0·799.

All the sampling figures obtained in the investigation indicated that the populations sampled were highly aggregated, the coefficients of dispersion being significantly greater than unity (Table 35).

Table 35. Some representative coefficient of dispersion from the sampling data 1956-1957

*Mean number	Coefficient of dispersion
50	18
250	40
750	64

* (from 15 soil cores 42 cm² area.)

(ii) Information obtained from complete enumeration data

Aggregations were further studied by the selection of small plots (as vegetationally homogeneous as possible) which were completely sampled and their numbers subsequently mapped. The Nardus, Juncus and Calluna sites (Figs. 22 & 23) sampled in this way revealed aggregations and associated gradients when the values were classified into standard deviations from the mean value. Sources of error such as the inevitable heterogeneity of the vegetation, the difficulty of close sampling and the incomplete removal of the plot owing to the use of a circular soil sampler were eliminated in a subsequent experiment on the Bare peat area. A square plot (32 cm x 32 cm) was selected (Plate 12), having a flat surface completely devoid of vegetation and divided up,

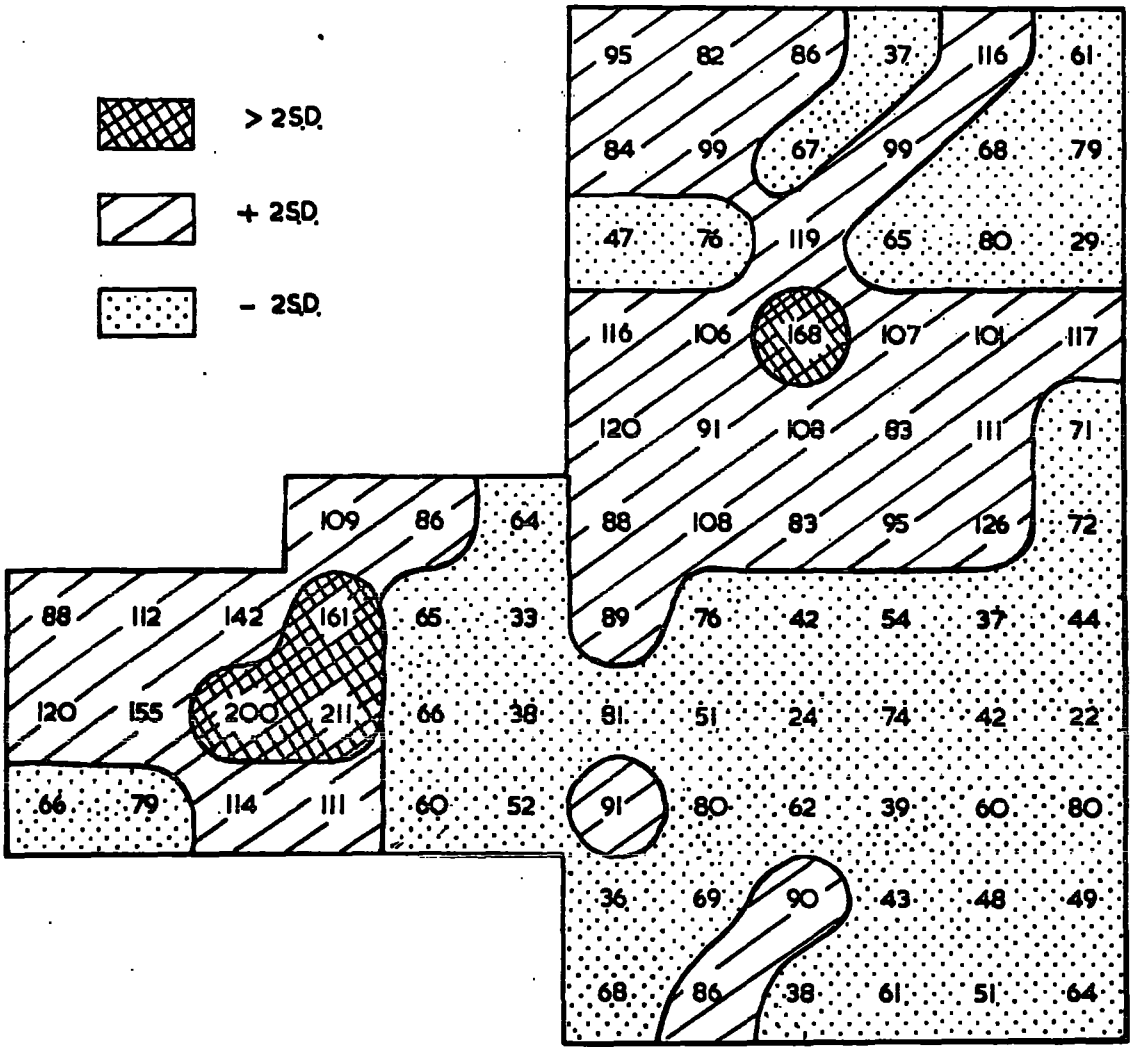


Fig. 22. Density map of Nardus plot (87 x 80cm) with S.D. contours.

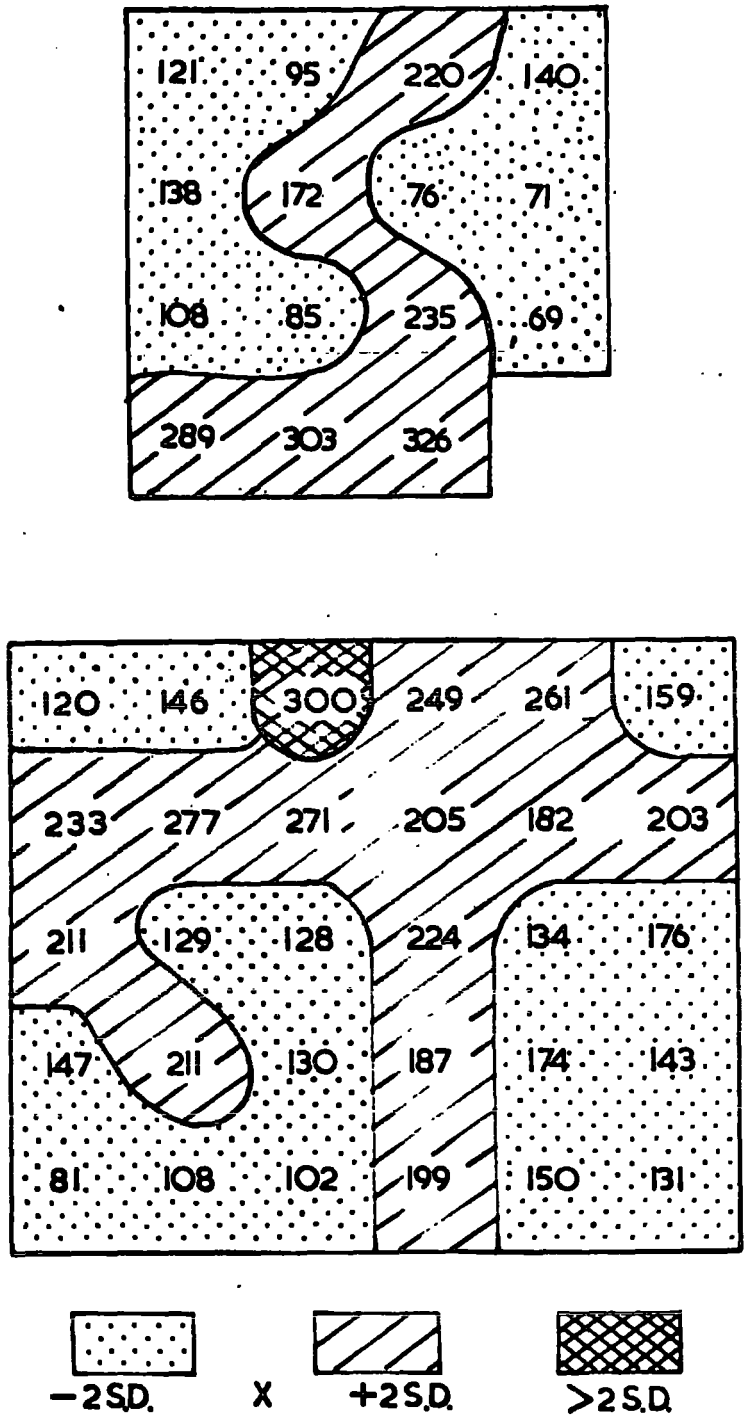


Fig. 23. Density map of Calluna (16 x 16cm), above, and Juncus 56 (37 x 37cm), below.

using a sharp knife into 100 soil blocks 10 cm² in area and 6 cm deep (Plate 13). In this way the entire plot was removed. The soil blocks were randomised into three sets of 30 and one of 10 for extraction. The four extractions gave means of 40, 38, 36 and 31. The numbers obtained per soil block were mapped as shown in Fig. 24. An overall mean of 39, and variance 164 gave a coefficient of dispersion significantly greater than unity. An analysis of variance was carried out on the data (Table 36) and showed that the variation down and along the plot was significant whereas the extraction lots were not significantly different.

Table 36. Analysis of variance for the Bare peat microdistribution plot

Source of variation	$\Sigma(x-\bar{x})^2$	d.f.	Mean square	F	P <
Rows along	3563	9	396	4.3*	0.001
Rows down	4855	9	539	5.8*	0.001
Extraction lots	371	3	124	1.3	
Residual	7259	78	93		
Total	16048	99	162		

In the analysis of wireworm microdistribution plots Salt & Hollick (1946) used the analysis of variance to remove, from the total variance of a plot, a larger component and calculated the coefficient of dispersion for the remainder as well as for the total. If the removal of the larger component reduces the coefficient of dispersion it follows that the aggregation is disproportionately contained within the larger component so removed.

Plate 12. Bare peat microdistribution plot orientated to Fig. 24.

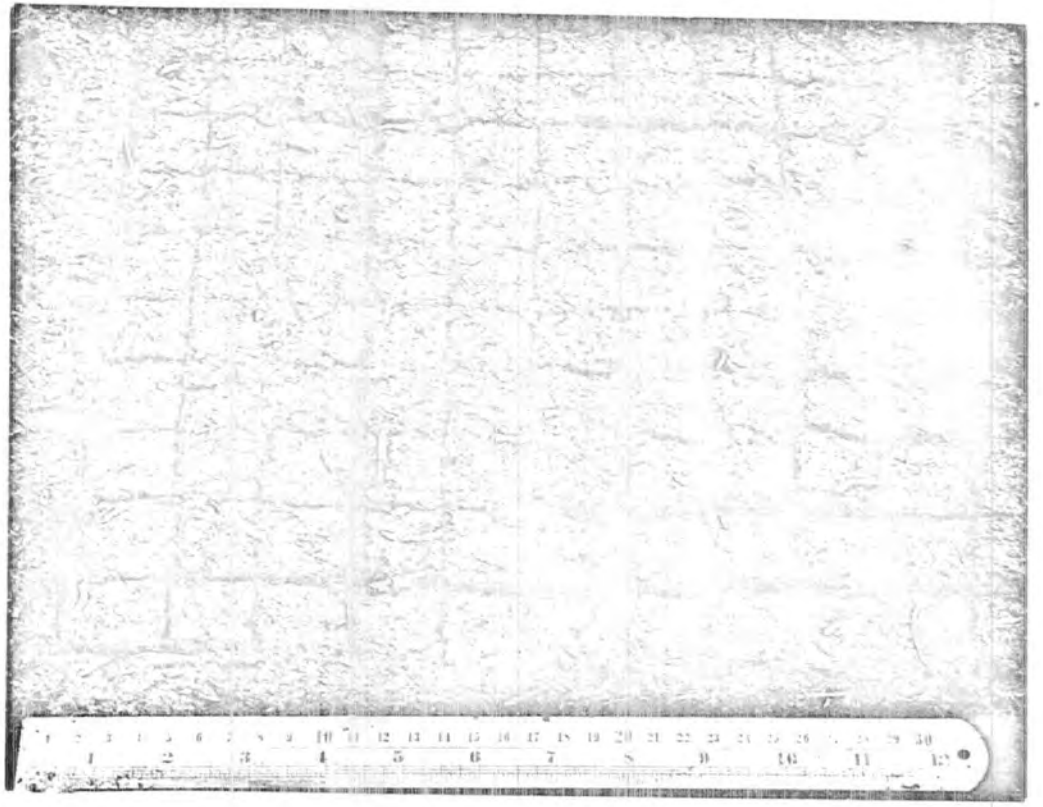


Plate 13. Bare peat microdistribution plot, with soil blocks cut ready for removal.

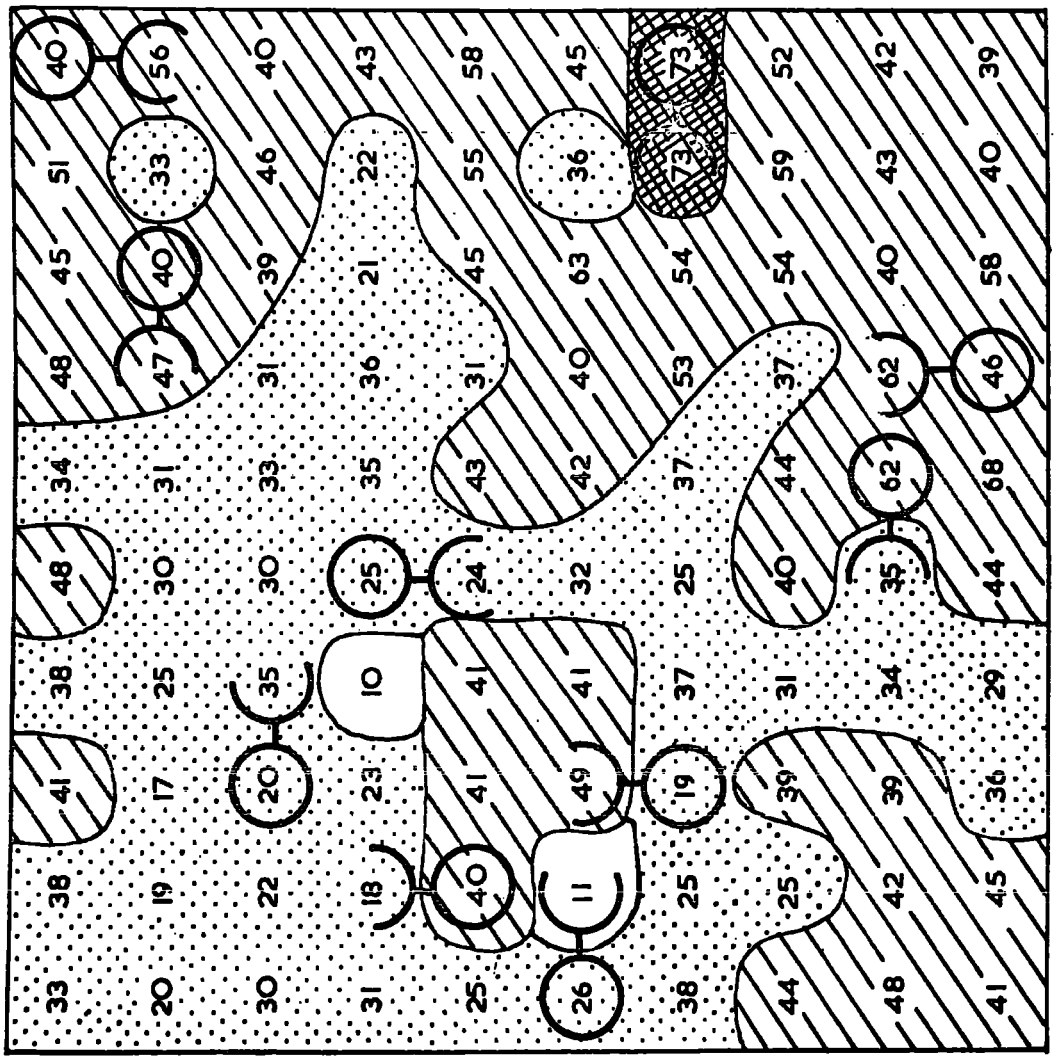


Fig. 24. Density map of Bare peat plot. (S.D. contours as in Fig. 23. Hughes tie-line samples in heavy black circles).

The removal of a larger component for 25 blocks of 4 samples from the Bare peat plot reduced the remainder coefficient by half (Table 37, Fig. 25).

Table 37. Analysis of variance for larger component of the Bare peat microdistribution plot

Source of variation	$\leq(x-\bar{x})^2$	d.f.	Mean square	C. of D.
Larger component	9850	24	409	-
Remainder	6198	75	83	2.1
Total	16048	99	162	4.2

Table 38. The remainder coefficients for the removal of larger components

Component removed		C. of D. for remainder
Size (cm^2)	Number of blocks	
10	100	4.2
40	25	2.1
250	4	2.6
500	2	3.1

The removal of still larger components increased the remainder coefficient of dispersion (Table 38), from which it is concluded that the strongest effect of the aggregation was to be found in areas exceeding the area of one soil block (10 cm^2) but smaller than the area of four grouped soil blocks (40 cm^2). By using contours defined by standard deviation limits (Figs. 24 & 25) it is demonstrated that there were,

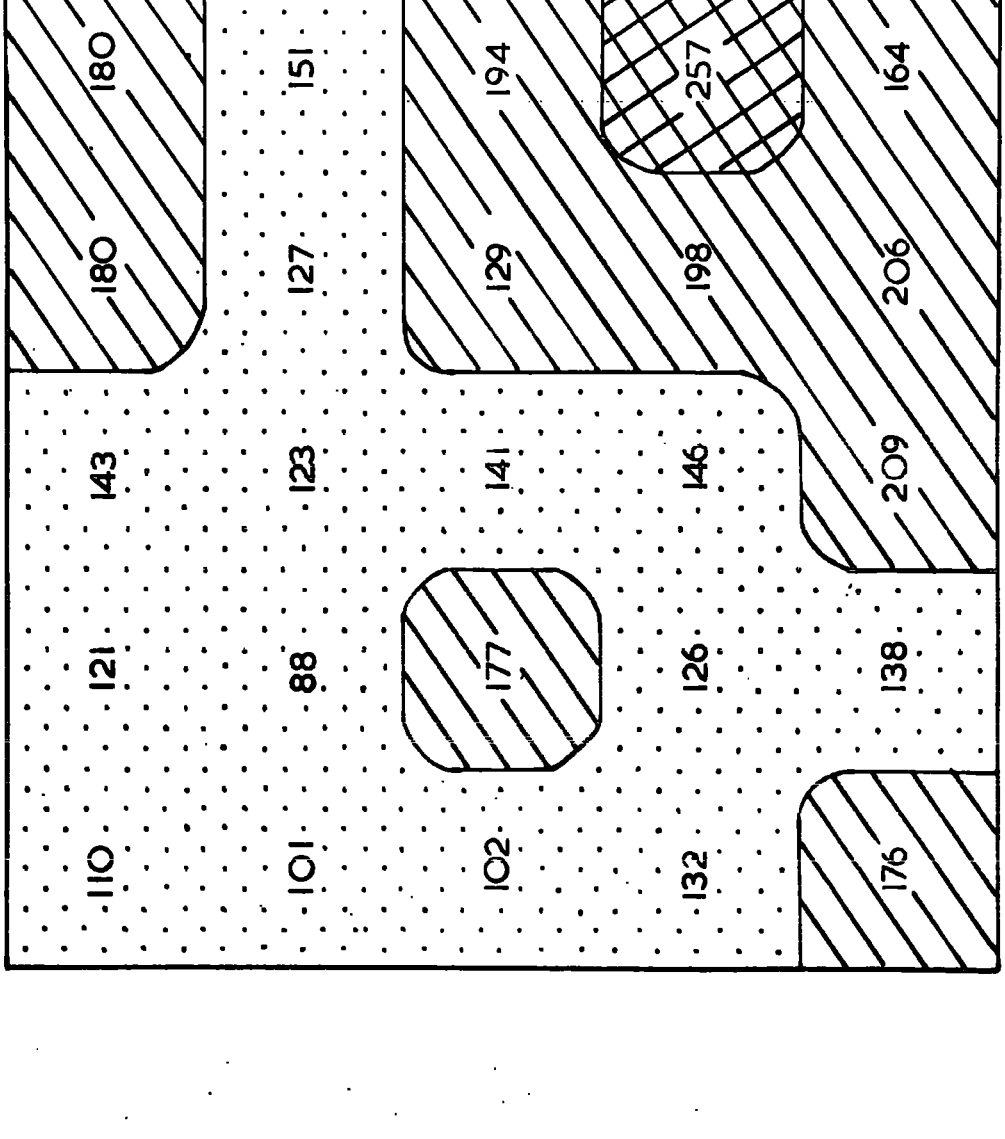


Fig. 25. Density map of larger components of Fig. 24.

(a) one patch of very high density (> 2 S.D.) with 73 worms per soil block,

(b) three or more patches of above mean densities (up to 2 S.D.) with 39 to 62 worms per soil block,

(c) a continuous matrix of below mean values (down to -2 S.D.) with 17 to 38 worms per soil block,

(d) occasional single blocks of low density.

(iii) Information obtained by Hughes (1958) tie-line method

The labour involved and the total removal of the test area are serious drawbacks to the complete enumeration method. Hughes (1958) has described a method of tie-line sampling which enables estimates to be made of aggregation size and number at different density levels without the complete sampling of the selected area. R. D. Hughes has kindly worked out these estimates by selecting, in a random stratified manner, 10 soil block values from the Bare peat microdistribution plot (Fig. 24) and adjacent to each of these another soil block value was taken in a direction changing by 90°. These pairs are said to be connected by a tie-line of length (q) which equals 3·16 cm., since the centres of the soil cores are taken as representative of the density recorded. The sample unit values are divided up into frequency classes (Table 39, Column i) and the frequency (F in Column ii) accumulated (F_a in Column iii) and from this the probability of a random sample unit falling within an aggregate (P_a in Column iv) is calculated. Column v shows the tie-lines and the number of tie-lines that cross the class boundaries. The probability that the tie-line will cross the edge of the aggregate (P_c in Column vi), is calculated directly from the

Table 39. Aggregate system in the Bare peat plot as determined by Mr. R. D. Hughes using the tie-line sampling method. (Hughes 1958)

(i)	(ii)	(iii)	(iv)	(v)	(vi)	(vii)	(viii)
Frequency class	F	F_a	P_a $(1-\frac{F_a}{20})$	Tie-lines and number of crosses	P_c	Mean radius (r)	Number of aggregates (n)
65+	2	20	0	0	0	0	0
65-	2	18	0·10	2	0·2	2·0	8
60-	1	16	0·20	3	0·3	2·7	9
55-	0	15	0·25	3	0·3	3·3	7
50-	3	15	0·25	4	0·4	2·5	13
45-	0	12	0·40	4	0·4	4·0	8
40-	3	12	0·40	3	0·3	5·3	4 - 5
35-	2	9	0·55	3	0·3	7·3	3
30-	1	7	0·65	4	0·4	6·5	5
25-	2	6	0·70	4	0·4	7·0	4 - 5
20-	5	4	0·80	1	0·1	-	-
15-	1	-	(0·95) 0·05				

q = 3·16 cm. (all calculated measurements in cm.)

number of tie-line crosses. The mean radius (r in Column vii) is obtained from the expression

$$r = 4qP_a/\pi P_c$$

and the mean number of aggregates (n in Column viii) in the test area (A) from

$$n = P_o^2 \, A \, \pi / 16 q^2 P_a$$

In table 39 these values are shown for the various densities. The conclusions that can be drawn about the aggregate system are:

(a) the few odd samples above 65,

(b) the discontinuous groups of samples with above (40-) worms,

(c) the more continuous groups with below (40-) worms,

(d) the few small patches of very low density.

Discussion

It has been made clear that the spatial patterning of enchytraeid microdistribution is of a particular kind. The present findings, are remarkably similar to those of Nielsen (1954) and O'Connor (1957). The aggregates consist of high and low density pockets surrounded by more moderately placed values, all in a continuous matrix of low density values.

It will be shown that these aggregations do not seriously affect the statistical tests used in this study, in fact the existence of this spatial patterning, somewhat characteristic for soil enchytraeids has helped to assess the validity of the sampling results, as previously mentioned.

The introduction of sampling methods designed to study aggregation systems, such as the one tried in this work (Hughes 1958) without the destruction of the sample plot should be of some help in pursuing this subject further. Neyman (1957) describes the mathematical theory which will permit us to consider populations as conglomerations of clusters. In the discussion on Neyman's paper Skellam mentions the 'tendency to leptokurtosis perhaps due to variations between organisms in

their powers of diffusion". This may well be the case here, but there are of course other factors, the relative influence of dispersal factors must be balanced against heterogeneity in the sample area of a very local kind, caused possibly by variations in nutrient value, microclimate, biotic factors, toxicity effects and edaphic factors. In order to understand fully the problem of local aggregation much more information on the requirements of the animals is needed. Perhaps larger and more obvious differences require explanation first. It would of course be surprising to find soil animals of this kind distributed in a random manner.

(3) H O R I Z O N T A L D I S T R I B U T I O N

Under the heading of horizontal distribution are grouped the problems of heterogeneity as they effect the validity of sample mean values, whether they are caused by:

(i) density differences, as shown by obvious horizontal gradients within the sample area,

(ii) differences in the performance of the extraction method used, made obvious either by gradients in the number of worms extracted by different extraction units or by differences in the mean estimates obtained from different extraction lots,

(iii) sampling design and statistical analysis.

Preliminary sampling survey on Juncus 57

The sample site measuring 25x3 m (75 m^2) was initially sampled in April 1957 by taking one soil core (10 cm^2) randomly from each m^2 of the selected area. The 75 soil cores so taken were randomised

into two lots of 30 and one of 15 for extraction by the wet funnel technique. The results are given in Table 40.

Table 40. Results of preliminary sampling survey on Juncus 57 sampling site

					Sample block	Sample sub-plots
	Z	Y	X	Total	Mean	Mean
1	193	236	422	851	284	
2	186	188	276	650	217	
a 3	211	218	233	662	221	
4	326	218	312	856	285	
5	282	253	254	789	263	254
6	189	289	355	833	277	
7	165	190	285	640	213	
b 8	148	205	216	569	190	
9	307	245	270	822	274	
10	174	220	218	612	204	232
11	211	183	236	630	210	
12	298	219	118	635	212	
c 13	171	261	185	617	206	
14	301	332	322	955	318	
15	274	256	144	674	225	234
16	243	144	290	677	226	
17	323	243	267	833	277	
d 18	181	142	199	522	174	
19	205	220	125	550	183	
20	187	198	161	546	182	209
21	216	185	244	645	215	
22	162	118	222	502	167	
e 23	204	249	246	699	233	
24	220	195	213	628	209	
25	195	196	191	582	194	204
Total	5572	5403	6004	16979	-	
Sample row Mean	240	216	240	-	226	

The analysis of variance of the data

An analysis of variance was carried out on the data (Table 41),

Table 41. Analysis of variance of all the components in the preliminary survey

Source of variation	d.f.	Sum of squares	Mean square	F
(1) Sample rows	2	7685	3843	1·48
(2) Sample blocks	24	116131	4839	1·87
(3) Extraction lots	2	2539	1270	0·49
(4) Extraction rows	1	560	560	0·22
(5) Extraction blocks	14	43090	3078	1·19
Residual	31	80403	2594	-
Total	74	250408	3384	-

the following components being analysed:

(1) the sample rows (X, Y, Z) along the sample site each 25 m. long and 1 m. wide

(2) the sample blocks (1-25) each 3 m. long and 1 m. wide

(3) the extraction lots whose mean yields are given in Table 42

Table 42. Mean yield per extraction lot

Extraction lot	Number of soil cores	Mean yield
1	30	227
2	30	233
3	15	217

(4) the extraction rows front and back (Table 43)

Table 43. Mean yield per extraction row

Extraction row	Number of soil cores	Mean yield
Front	30	229
Back	45	224

(5) the extraction blocks, or position in the extraction rows (1-15) (Table 44)

Table 44. Mean yield per extraction block

Extraction block	Mean yield
1	223
2	175
3	250
4	261
5	254
6	250
7	215
8	200
9	201
10	205
11	223
12	206
13	203
14	208
15	217

The analysis of variance (Table 41) showed very little evidence of extraction inconsistency or sample area heterogeneity, all the appropriate values of F (except component (2) for sample blocks) were well below significance level and were therefore omitted in a re-analysis of sample components (1) and (2) only (Table 45).

Table 45. Analysis of variance for sample components

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
(1) Sample rows	2	7685	3843	1·46
(2) Sample blocks	24	116131	4839	1·84*
Residual	48	126592	2637	-
Total	74	250408	3384	-

* $P < 0{\cdot}05$

This increased the degrees of freedom attributable to the residual sum of squares and the value of F for soil blocks was made significant at 0·05 level.

Grouping of the 25 sample blocks into 5 sub-plots and comparison of the mean number per sub plot was also analysed. The variance ratio (F)

$$\frac{\text{mean square sub-plots}}{\text{residual mean square}} = 1{\cdot}95$$

(with 4 and 70 degrees of freedom) was not significant.

Validity of the analysis of variance on untransformed data

A final assessment of the values of the variance ratio could only be made if the assumptions underlying the analysis were verified. Of the factors causing most severe distortion in the analysis of variance it was decided to test for anormality and non-additivity.

The test for anormality using the statistics (g_1) and (g_2) has been given. The values of these indicated that the sampling distribution was skewed and kurtosed and that logarithmic transformation helped to

normalise the figures.

Non-additivity, which can be caused by various factors including aberrant observation, proportional effects, interactions and heterogeneous variance can be tested for by using Tukey's (1947) sum of squares for non-additivity with one degree of freedom, given by the expression

$$\sum (x-\bar{x})^2 \text{ non additivity} = \frac{P^2}{\underset{(x-z)}{d^2} \quad \underset{(1-25)}{d^2}}$$

Where P = p.d, (p) being the product of sample block values and (d) the deviations of their means from the grand mean. (d^2) is the appropriate sum of squares of the deviations of means of blocks or rows.

Table 46 shows the values also obtained and the calculations of the variance ratio for non-additivity.

Table 46. Analysis of variance with one degree of freedom for non-additivity

Component	Sum of squares	Degrees of freedom	Mean square	F
Residual	80403	31	-	-
Non-additivity	3992	1	3992	1·57
Remainder for testing	76411	30	2547	-

The values of F for non-additivity were not significant. It can therefore be concluded that the analysis of variance may be affected by the anormal nature of the sampling data, but that in other

respects the data fulfills the assumptions. Cochran (1947) maintains that anormality causes no serious error and that under conditions such as those described above the variance ratio is generally over estimated, making the 5 percent probability level suspect.

In view of the fact that one 5 percent probability had been obtained (from F for sample blocks) it was decided to transform the data and compare the results (Table 47).

Table 47. Comparison of F values for untransformed and log transformed data

Component	Degrees of freedom	F untransformed	F log transformed
(1) Sample rows	2	1·48	0·88
(2) Sample blocks	24	1·87	1·67
(3) Extraction lots	2	0·49	0·42
(4) Extraction rows	1	0·22	0·05
(5) Extraction blocks	14	1·19	1·16

The log transformation was chosen because:

(1) it is advised where mean and variance (Fig. 21) are related (Barnes & Bagenal 1951)

(2) the data under consideration was rendered more normal by transformation

(3) recalculation of the Tukey test for non-additivity on the transformed data gave a non-significant value for F (F = 0·569)

The log transformation reduced the values of F for all components

except sample rows, and removed the 0·05 significance from the F for sample blocks (Tables 47 & 48).

Table 48. Comparison of F values for untransformed and log transformed data. (Sample components only)

	Degrees of freedom	F untransformed	F log transformed
(1) Sample rows	2	1·46	0·86
(2) Sample blocks	24	1·84*	1·64

Discussion

Transformation of sampling data

In previous sections of this work the need for the transformation of the sample unit values has been mentioned. Transformations, particularly the logarithmic variety, have become very popular in recent years and it seems to be assumed that they impart a respectability to data. There is no doubt that, in dealing with aggregated populations, it is necessary to check the validity of the statistical tests used since they are based on certain assumptions about the distribution under study; but it is also possible to go too far in the other direction and end up with an oversensitivity which is of no practical value.

The general effect of the logarithmic transformations (used in this study) is as follows:

(i) they reduce skew and kurtosis, so bringing the data closer to normality which is another way of saying that they reduce the effect of aggregation phenomena.

(ii) they help to clarify the meaning of marginally significant

probabilities. In the comparisons of extraction data, using the paired 't' test, the significant differences were generally improved by transformation (this is of course explained by the reduction in the variability of the sample pair differences).

In the survey on the Juncus 57 site, described above, transformation has been shown to reduce the variance ratio (Tables 47 & 48) values for the sample position components, removing one 5 percent probability level - that for sample blocks. This effect agrees well with Cochran (1947) who maintains that data of this kind need not be transformed for the analysis of variance, provided the 5 percent probability levels are rejected, or treated with suspicion.

The effect of position of the soil core (in relation to the sample site and extraction apparatus) on the sample mean value

In this preliminary survey of the Juncus 57 site, it has been shown that all the components of variation in the analysis based on sample unit position (within the sample site), or extraction position or lot, made no significant contribution to the total variance. The highest value of the variance ratio was found for the sample blocks, though transformation showed this to be inconclusive. It is therefore concluded that:

(i) the sample site was free from obvious horizontal gradients,

(ii) the extraction method was free from obvious inconsistency either between separate extraction lots (which due to randomisation of the soil cores, prior to extraction, could be regarded as replicates) or between extraction units; all the wet funnels behaved in the same way.

Now it is not supposed that all the factors which have been analysed have been proved constant, but rather they have been shown to exercise no measurable effect on the estimate and significance of the sample mean. Errors intrinsic in the sampling methods and extraction technique used were, therefore, considered to be random and the sample mean obtained was regarded as a reasonable estimate of the density of enchytraeids over the Juncus 57 area.

Sampling survey of Juncus 57: 1957-1958

The preliminary survey described had demonstrated the importance of sampling according to a sound experimental design and so it was decided to sample repeatedly in the following way:

(i) the five sub-plots, (a-e in Table 40) each 5x3 m. in size, were divided up into three strata 5x1 m., making 15 strata in all (Table 49). For every 15 soil cores required, one soil core was taken randomly from each stratum. Generally 45 soil cores were collected on each sampling occasion but fewer (15 or 30) were taken when a less detailed indication was required of changes in density or distribution.

Table 49. Stratification of the sample area (Juncus 57) for sampling in 1957-1958

		Sample sub-plot				
		a	b	c	d	e
Sample row	X	3	6	9	12	15
	Y	2	5	8	11	14
	Z	1	4	7	10	13

(ii) the soil cores so taken were randomised for extraction as previously described, each extraction row of 15 funnels containing soil cores randomly arranged but representative of all 15 strata. In this way extraction lots were regarded as sample replicates and the effect of extraction variability within the extractor and between different extractions was analysed.

The sampling design used (stratified random sampling) imposes certain special conditions on the calculation of the sample variance; the mean value, sum of squares, and degrees of freedom are calculated separately for each stratum and then compiled into an average mean value with pooled sums of squares and degrees of freedom (Healy 1958). The absence of conspicuous gradients over the sample area (as determined in the preliminary survey and borne out by the work under discussion) justified, however, the non-pooling of the intra-stratal data. This was very convenient as the analysis of variance of the various components described requires the individual sample unit values to be used.

Sampling survey of the Juncus 57 site (May-November 1957)

(a) All species considered

Sampling data, obtained from 45 soil cores taken on each of 9 sampling occasions during May-November 1957 (Table 50) was analysed for the following components:

(1) sampling occasions,

(2) overall sample sub plot (a-e) mean estimates,

(3) overall extraction lot means

(4) overall extraction row mean yields (Table 51)

(5) overall extraction block mean yields (Table 52).

Table 50. Sample, sub-plot and extraction lot means for the analysis of variance

Date of sampling	Sample means (1)	Sample sub-plot means (6)					Extraction lot means (7)	
		a	b	c	d	e	1	2
Number of soil cores	45	9	9	9	9	9	30	15
15•5	175	167	187	170	147	204	176	172
5•6	91	84	96	100	97	78	80	112
14•6	184	206	180	205	159	173	188	176
25•6	66	54	80	56	72	68	65	67
16•7	175	150	186	199	169	172	187	153
29•7	182	191	169	168	188	193	177	192
13•8	216	254	214	214	180	216	220	207
12•9	221	228	256	215	218	187	219	224
6•11	289	300	301	264	282	294	287	291
Overall means	178	182	185	177	168	176	178	177

Table 51. Overall mean yield per extraction row

Extraction row	Total number of soil cores	Overall mean
Front	270	178
Back	135	177

Components (2) and (3) only give overall information. Variations between sub-plots or extraction lots on the individual sampling

Table 52. Mean yield per extraction block (27 coil cores per block, 3 on each of 9 sampling occasions

Extraction block	Mean yield
1	170
2	160
3	180
4	186
5	180
6	172
7	182
8	166
9	172
10	191
11	180
12	170
13	179
14	177
15	191

occasions were tested by analysing two further components or interactions, a method described by Moroney (1951),

(6) interaction between sample sub-plots and sampling occasions. This component was obtained from the sum of squares of individual sample sub-plot estimates (Table 50) with the sum of squares for components (1) sampling occasions and (2) overall sample sub-plot estimates removed.

Sum of squares for individual sub-plots = 1720877

Sum of squares (1) 1609385

Sum of squares (2) 16118

1625503

less sum of squares for (1) + (2) 1625503

sum of squares for interaction (6) 95374

The degrees of freedom for the interaction are obtained from the product of degrees of freedom for components (1) + (2)

degrees of freedom for interaction (6) = 4 x 8 = 32

(7) the interaction between extraction lots and sampling occasions obtained from the sums of the squares of individual extraction lots less the sum of the squares for components (1), sampling occasions and (3) overall extraction lot estimates removed.

Sum of squares for individual extraction lots 1637015
Sum of squares (1) 1609385
Sum of squares (2) 20
1609405

Less sum of squares for (1) + (2) 1609405
Sum of squares for interaction (7) 27610
Degrees of freedom for interaction (7) = 1 x 8 = 8.

The results of the analysis of variance carried out in the manner described are shown in Table 53.

Table 53. Analysis of variance of the sampling results shown in Table 50

Component	Degrees of freedom	Sum of squares	Mean square	F
(1) Sampling occasions	8	1609385	201173	59·73*
(2) Sample sub-plots (overall)	4	16118	4030	1·20
(3) Extraction lots (overall)	1	20	20	0
(4) Extraction rows (overall)	1	101	101	0
(5) Extraction blocks (overall)	14	28089	2006	0·60
Sample sub-plots (2) and sampling occasions (1)	32	95408	2982	0·89
Extraction lots (3) and sampling occasions (1)	8	27610	3451	1·05
Residual	336	1131658	3368	-
Total	404	2908389	-	-

* $P < 0.001$

F (variance ratio) is 0·1 percent significant for the sampling occasions (1) but all other values are well below significance level.

(b) Mesenchytraeus only

When the results of a similar analysis of variance for Mesenchytraeus only are inspected (Table 54-57) the values of F are 0·1 percent significant for sampling occasions (1) and 5 percent significant for sample sub-plots (2) and interaction (6) between sample sub-plots and sampling occasions. As has already been stated however the 5 percent significance level must be treated with caution.

Table 54. Sample, sub-plot and extraction lot mean values (Mesenchytraeus only) for the analysis of variance

Date of sampling	Sample means (1)	Sample sub-plot means (6)					Extraction lot means (7)	
		a	b	c	d	e	1	2
Number of soil cores	45	9	9	9	9	9	30	15
15·5	4·0	3·7	4·0	4·9	4·3	3·1	4·0	4·0
5·6	3·3	3·1	2·8	4·0	3·9	3·0	3·1	3·9
14·6	2·8	4·0	2·0	3·9	2·1	2·0	3·1	2·1
25·6	2·2	2·0	2·1	3·1	2·4	2·1	2·5	1·4
16·7	2·5	1·1	2·9	3·8	3·5	1·3	2·5	2·7
29·7	2·8	3·2	1·7	3·4	2·5	3·3	3·1	2·3
13·8	2·3	2·5	2·2	2·0	2·8	2·0	2·2	2·6
12·9	2·6	2·3	3·7	1·2	3·9	2·1	2·5	2·9
6·11	2·0	2·4	1·8	1·7	2·5	1·5	1·8	2·3
Overall means	2·7	2·7	2·6	3·1	3·0	2·3	2·8	2·7

Table 55. Mean yield per extraction row. (Mesenchytraeus only)

Extraction row	Number of soil cores	Mean yield
Front	270	2·7
Back	135	2·8

Table 56. Mean yield per extraction block (27 soil cores per block, 3 on each of 9 sampling occasions for Mesenchytraeus only)

Extraction block	Mean yield
1	2·4
2	2·7
3	2·2
4	2·9
5	2·4
6	2·4
7	2·9
8	3·1
9	2·9
10	2·9
11	3·6
12	3·1
13	2·6
14	2·5
15	2·4

Table 57. Analysis of variance of the sampling results shown in Table 54 for Mecenchytraeus only

	Degrees of freedom	Sum of squares	Mean square	F
(1) Sampling occasions	8	142	17·75	4·75**
(2) Sample sub-plots (overall)	4	38	9·50	2·54*
(3) Extraction lots (overall)	1	2	2·00	0·54
(4) Extraction rows (overall)	1	1	1·00	0·27
(5) Extraction blocks (overall)	14	51	3·64	0·97
(6) Sample sub-plots (2) and sampling occasions (1)	32	185	5·78	1·55*
(7) Extraction lots (3) and sampling occasions (1)	8	35	4·38	1·17
Residual	336	1255	3·74	
Total	404	1709		

** P< 0·001. * P <0·05

The comparison of extraction lots using separate analyses for each sampling occasion's data for all species

Because of the large size of the component for seasonal variation encountered in the last analysis there was the possibility that this might have obscured differences in the other factors. Inspection of the extraction lot yields (Table 50) showed that the biggest discrepancy

occurred with the sampling data for 5/6/57 and this was therefore analysed separately (Table 58). The results of this separate analysis showed

Table 58. Analysis of variance for the sample data of 5/6/57

Source of variation	d.f.	Sum of squares	Mean square	F
Extraction lots	1	10492	10492	10·79
Residual	43	41783	972	-
Total	44	52275	1188	-

the mean yields of 80 and 112 to differ significantly. Inspection of the other data (the standard errors already calculated for each set of 15 helped in this assessment, Table 59) suggested no significant differences in yield and the general conclusions of the overall analysis were vindicated.

Consideration of the replicate sets of 15 soil cores

Because of the design of the sampling technique it is possible to consider each of the three sets of 15 cores which make up the 45 sample units taken on numerous sampling occasions through the year 1957 as three replicates. Disposing of all the problems associated with sampling position and extraction efficiency (as these have been shown to be negligible) it is instructive to compare these replicates to see if any further discrepancies in the estimation of density are revealed. Though the replicate means (as already shown under the guise of extraction lots) were remarkably similar this could not be said of the variances of the replicates on some of the sampling occasions (Table 59). The significance of this so called heterogeneity of

Table 59. Replicate sample data 1957

Date of sampling		Replicates of 15 sample units			Total sample	Significance of differences
15/5	Mean	174	178	173	175	n.d.
	S.E.	2	17	2	7	$X^2 = 7{\cdot}05$ *
23/5	Mean	184	198	181	188	n.d.
	S.E.	10	19	19	9	$X^2 = 25{\cdot}6$ **
5/6	Mean	82	79	112	91	$F = 6{\cdot}42$**
	S.E.	8	7	10	5	$X^2 = 1{\cdot}97$
14/6	Mean	184	194	176	184	n.d.
	S.E.	12	14	14	8	n.d.
25/6	Mean	51	79	67	66	$F = 2{\cdot}44$
	S.E.	5	11	9	5	$X^2 = 6{\cdot}34$*
2/7	Mean	59	54	62	59	n.d.
	S.E.	7	8	9	5	n.d.
16/7	Mean	188	185	153	175	$F = 1{\cdot}76$
	S.E.	16	13	15	9	n.d.
29/7	Mean	180	160	192	182	n.d.
	S.E.	14	15	16	8	n.d.
13/8	Mean	223	218	207	216	n.d.
	S.E.	23	10	16	10	$X^2 = 74{\cdot}0$ **
12/9	Mean	218	221	224	221	n.d.
	S.E.	19	18	13	10	$X^2 = 2{\cdot}08$
6/11	Mean	309	265	291	289	n.d.
	S.E.	23	18	22	12	$X^2 = 0{\cdot}9$

* $P < 0{\cdot}05$. ** $P < 0{\cdot}01$.

n.d. - not determined as inspection suggested no significant differences.

variance was crudely tested by Bartlett's test (Snedecor 1956) which compares (a) times the logarithm of the average mean square of the number ('a') of replicates with the sum of the logarithms of the separate mean squares. From the difference in these two values (using corrections for the use of ordinary logarithms and for a slight bias) a value of X^2 is obtained, as follows:

$X^2 = 2{\cdot}3026\ (n-1)\ (a \log s^2 - \Sigma \log s^2)$

Correction factor: $C = 1{\cdot}03$ (for three replicates)

Corrected $X^2 = X^2/C$

Degrees of freedom = 2 (for three replicates).

When heterogeneous variance has been proved, weighted mean squares should be used in determining the variance ratio for testing the significance of sample mean differences. The extent of the heterogeneity was however not great (Table 59) and the only obvious sample difference caused by a difference in extraction yield has already been dealt with and was unaffected by heterogeneity in any case.

Discussion

The overall analysis gives similar results to that obtained by the preliminary survey, except of course that the analysis is dominated by the large and only significant component for seasonal variation. All this data has revealed no obvious error in the sample mean estimates (with the exception of the one occasion of 5/6/57) and no obvious gradient in the horizontal distribution of the enchytraeids in the site.

Heterogeneity was found in the separate variance of replicates though these did not effect the mean values and it is therefore attributed to the effect of the aggregations; the same mean value being obtained from many moderate values (giving a low standard error) or from a wider range of values (giving a high standard error): combining this information with that on the horizontal distribution it may be concluded that the aggregations must have been dispersed randomly over the sample area.

Mesenchytraeus only

This general picture is not quite true when Mesenchytraeus is considered separately because apart from the seasonal variation in numbers the 'F' values for the sample sub-plots both overall and from time to time (interaction) are sufficiently large as to suggest patchiness in the horizontal distribution. This may be explained as follows:

(i) the smaller numbers involved make differences more obvious,

(ii) microscopic observation is required to separate the smaller Mesenchytraeus from the other worms. These are not included in this data, therefore the patchiness may have been caused by variations in age and therefore their chance of recognition throughout the year,

(iii) Mesenchytraeus is a much less generally distributed species than the dominant Enchytraeoides and may be more specific in its requirements and therefore more sensitive to variations in the environment.

(b) SAMPLE MEAN VALUES

The general statistical treatment and significance of the sample mean values has been discussed in connection with horizontal distribution.

Mesenchytraeus and Fridericia are considered separately as well as being included in the total estimates which in practice are estimates of Enchytraeoides.

Apart from the well known preference of soil dwelling animals for the top layers of the soil, previous work on enchytraeid quantitative sampling had demonstrated that 5-6 cm. deep soil cores were enough under normal conditions to give a representative density estimate (Nielsen 1955a). Preliminary sampling, to be described, enabled this procedure to be adopted in the present investigation. Deeper samples (down to a maximum depth of 30 cm.) were taken during conditions of drought and cold, as well as at other times of expected, or observed, flux in numbers - this gave information on vertical distribution. Further evidence of this sort was obtained during the period 1956-1957 by the separate extraction of sub-sample layers, made necessary by the limited capacity of the extractors.

Estimates were obtained in early spring, every year, and it is hoped these will continue to be made.

Results of 0-6 cm. sampling

These samples were taken throughout the period of study in the manner described. Where more than one set of samples were taken (as for the comparison of extraction methods), then the highest estimates were taken as the best (Figs. 26, 27 & 16). Attempts have been made to correlate

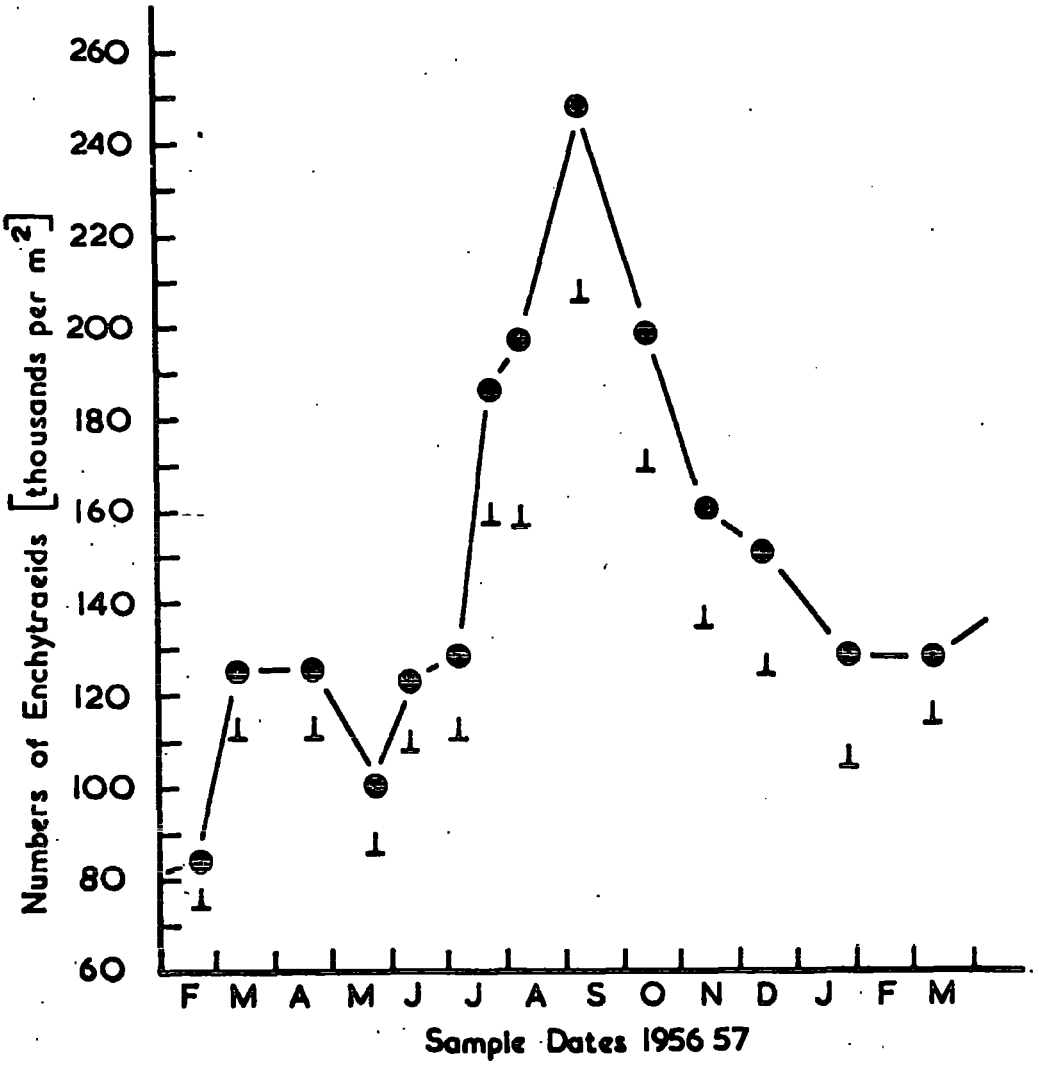


Fig. 26. Estimated numbers of enchytraeids (with -2S.E. limits) in 0-6cm Juncus samples.

some of the 0-6 cm. results with climatic factors, such as rainfall for 14 days previous to sampling and soil temperature on the sampling day (Tables 60-62, Fig. 29).

1956-1957

Significant variations in number throughout the sampling period were found on all sites.

The Juncus 56 estimates (Fig. 26, Table 60) at 126,000 per m^2, in the relatively drier spring, increased with the advent of warmer and wetter conditions to an early September recorded peak of 248,000 per m^2. An autumn, winter decline followed and the numbers had dropped to 134,000 per m^2 by the following spring. A similar variation was observed for the Bare peat sample site (Table 61, Fig. 16).

Table 60. 0-6 cm. sampling data for Juncus 56 and climatic factors 1956-1957

Date 1956-1957	Numbers (thousands/m^2)	Temperature at 30 cm. (°F)	Rainfall for previous 14 days (ins.)
28•2	84	34	2•5
14•3	125	35	3•2
24•4	126	40	0•8
29•5	112	47	0•3
12•6	123	50	1•6
1•7	127	51	1•2
25•7	186	54	1•8
9•8	198	52	4•9
12•9	248	50	2•4
10•10	199	46	4•3
12•11	160	42	1•4
11•12	152	42	4•2
30•1	134	37	5•1
4•3	134	36	3•2

Fig. 27. Estimated numbers of enchytraeids in 0-6cm *Nardus* grassland samples.

Table 61. 0-6 cm. sample data for Bare peat and climatic factors 1956-1957

Date 1956-1957	% top 2 cm.	Numbers thousands/m^2	Temperature at 30 cm. (°F)	Rainfall for previous 14 days (ins.)
23·5	19	12	45	2·6
22·8	74	48	52	7·6
25·9	60	37	53	1·5
11·11	29	28	41	3·2
13·3	33	23	42	1·2

Alluvial grassland peak figures were obtained in October (Fig. 16) but no peak figure was obtained for Nardus samples as the numbers increased right throughout the sampling period.

Mesenchytraeus, considered separately, showed no clear seasonal trends (Fig. 28). Mature Fridericia (Table 62) reached a peak figure in August.

Table 62. 0-6 cm. sample data for mature Fridericia in Alluvial grassland samples

Date 1956-1957	Numbers thousands/m^2
23·5	0
30·8	1·07
2·10	0·68
1·11	0·57
4·12	0·01
6·2	0

Fig. 28. Estimated numbers of Mesenchytraeus in 0-6cm Juncus 56 samples.

1957-1958

Detailed sampling was carried out during this period on Juncus 57 sample area. The sample means obtained here correlated with P/E values evaluated from the previous 14 days rainfall and observed evaporation readings (Fig. 29 and Table 63). It will be seen that the value of the correlation coefficient was improved by suitable transformation of P/E values. Fig. 30 shows the Mesenchytraeus fluctuations considered separately.

Table 63. Correlation coefficient for P/E values and sample means obtained from Juncus 57 samples 1957-1958

P/E data	Value of r	d.f. (n-2)	P <
Untransformed	0·454	20	0·05
Square root transformed	0.602	20	0.01

The correlation was caused by:

(1) a sharp decrease in sample mean values when P/E ratios fell below unity, followed by a recovery when P/E increased beyond unity, as in June, early July and early October 1957.

(2) a general tendency for the highest mean values to be found at the wettest times of the year - 280,000 per m^2 in early November 1957.

Other fluctuations less easily attributed to P/E changes were:

(1) an April-May drop in numbers from 235,000 to 186,000 per m^2, both in 1957 and 1958 (Table 64).

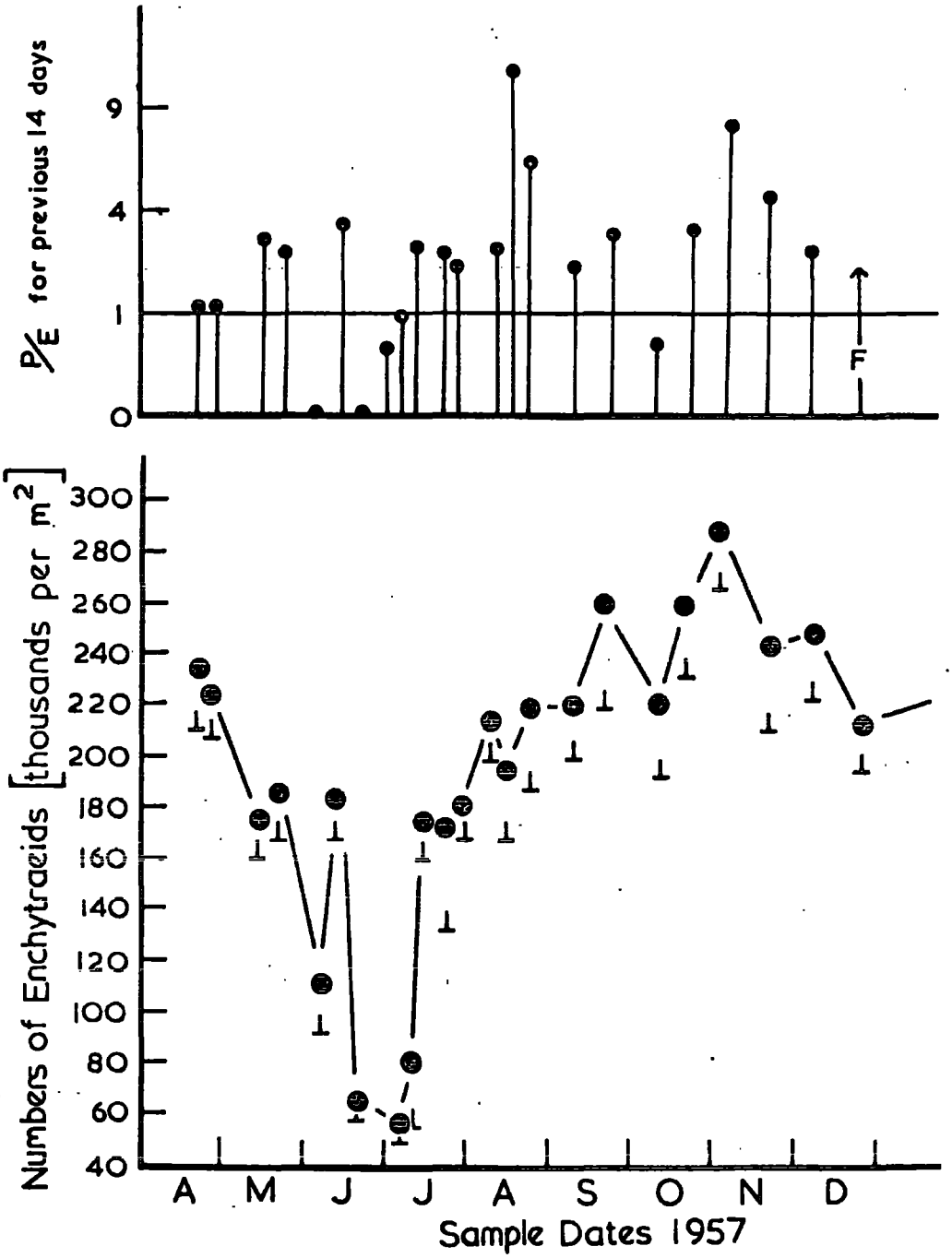


Fig. 29. Estimated number of enchytraeids in 0-6cm Juncus 57 samples and P/E values for sampling occasions.

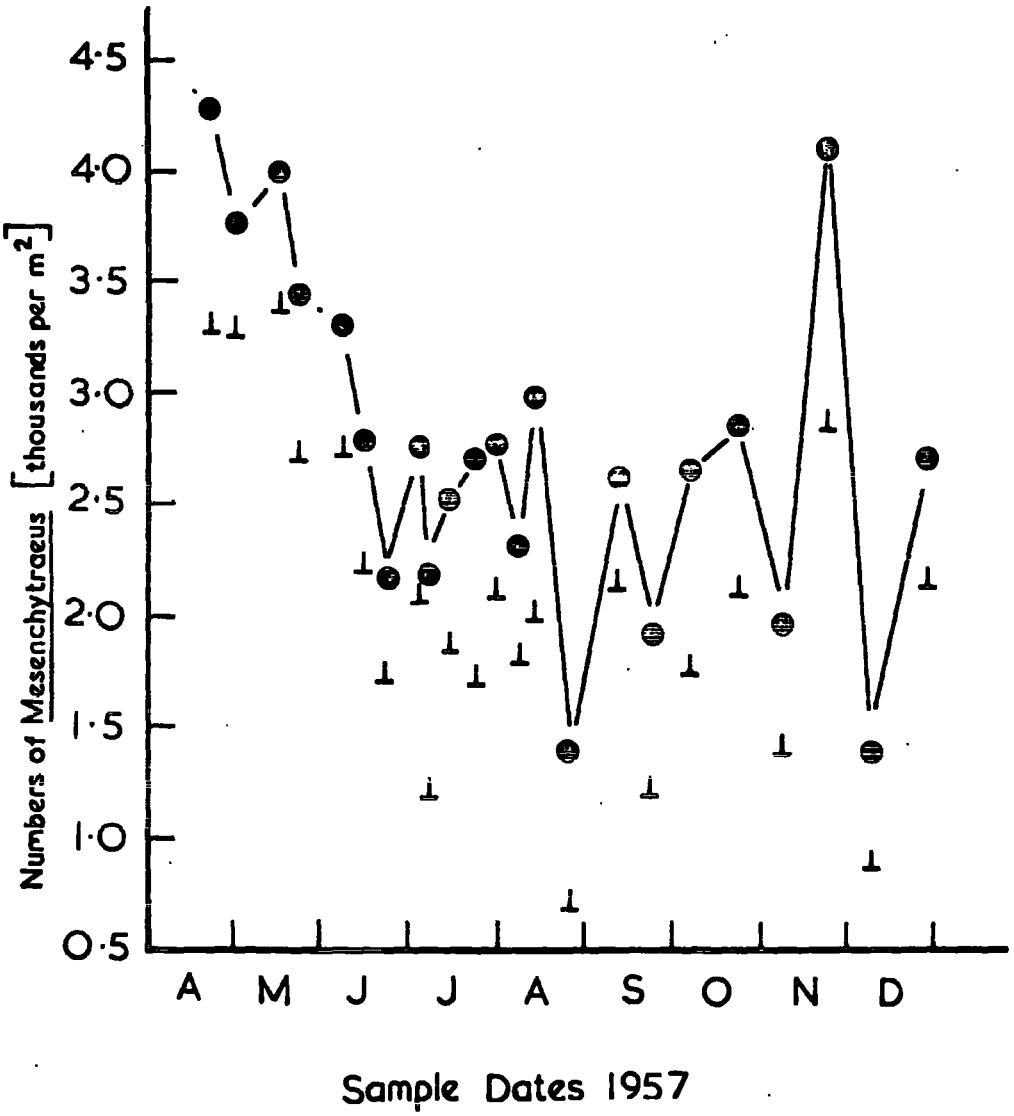


Fig. 30. Estimated numbers of Mesenchytraeus in 0-6cm Juncus 57 samples.

Table 64. Sample data for Juncus 57 obtained in 1958

Date	thousands/m^2	% in top 2-3 cm.
30.4	257	-
15.5	182	85
20.5	182	97
*24.6	158	83
*14.7	183	80

* soil cores 10 cm. deep, otherwise 6 cm. deep. N.B. Sample data, for the last four sampling occasions, obtained from samples taken by Dr. J. C. Coulson for the extraction of small tipulid larvae.

(2) a late December decrease accompanied by the onset of wintry conditions - particularly freezing of the ground, followed by the recovery recorded at the beginning of the spring 1958.

Results of annual 0-6 cm. sampling in spring

Spring estimates taken to be fairly representative of the average annual density obtained for three consecutive years show that the Juncus sites have a fairly constant, average density whereas a pronounced increase occurred in the Nardus area (Table 65). This increase is compared to the P/E values for the preceding August of each year considered.

Table 65. Spring estimates for three consecutive years and computed P/E values for the August preceding each spring

Year	Thousands/m² Juncus 56	Juncus 57	Nardus	P/E for preceding August
1956	126 ± 15	-	37 ± 19	0·7
1957	147 ± 32	227 ± 30	124 ± 21	6·6
1958	155 ± 19	257 ± 58	204 ± 36	4·3

Results of sub-division of 0-6 cm. samples 1956-1957

The necessary sub-division of 0-6 cm. samples, in 1956-1957, for extraction has provided data on the distribution of enchytraeids within this depth.

The top layer, about 2 cm. thick, is mainly composed of litter (L+F) in Juncus and Nardus samples whereas in Bare peat and Alluvial samples it is just $\frac{1}{3}$ of the soil core in which no clear horizons exist.

The best estimates for each layer have been compiled into the last column of figures shown in Table 66 where the number extracted from the top layer is expressed as a percentage of the total number extracted from the 6 cm. deep samples.

When the overall percentage distribution is considered throughout the year it is obvious that enchytraeids were predominantly distributed in the top (litter) layer, where this does not exist - as in Bare peat the percentage occupying the top 2 cm. is much lower. The figure is highest for Nardus grassland where the litter layer is discreet and and easily separable.

Mesenchytraeus and Fridericia showed a deeper distribution with lower percentages in the top layer.

Table 66. Overall % number of worms in top layer of 0-6 cm. samples 1956-1957

Sample area	% in top 2 cm. of sample		
	Nielsen method	Wet funnel method	Best estimates
(All species) Juncus 56	73	60	63
Bare peat	-	43	43
Alluvial grassland	-	59	59
Nardus grassland	81	73	77
Mesenchytraeus Juncus 56	30	21	21
Fridericia Alluvial grassland	-	29	29

When the percentage number extracted from the top layer is considered throughout the year, (Figs. 31 & 16, Tables 67-69), it appears that a summer maximum percentage was associated with warmer and wetter conditions, though this is not clear for Juncus 56 results, possibly due to the difficulty of separating the litter from the peat in these samples. Fig. 16 shows the relationship between high densities and high percentage numbers, in the top 2 cm., for two sample sites.

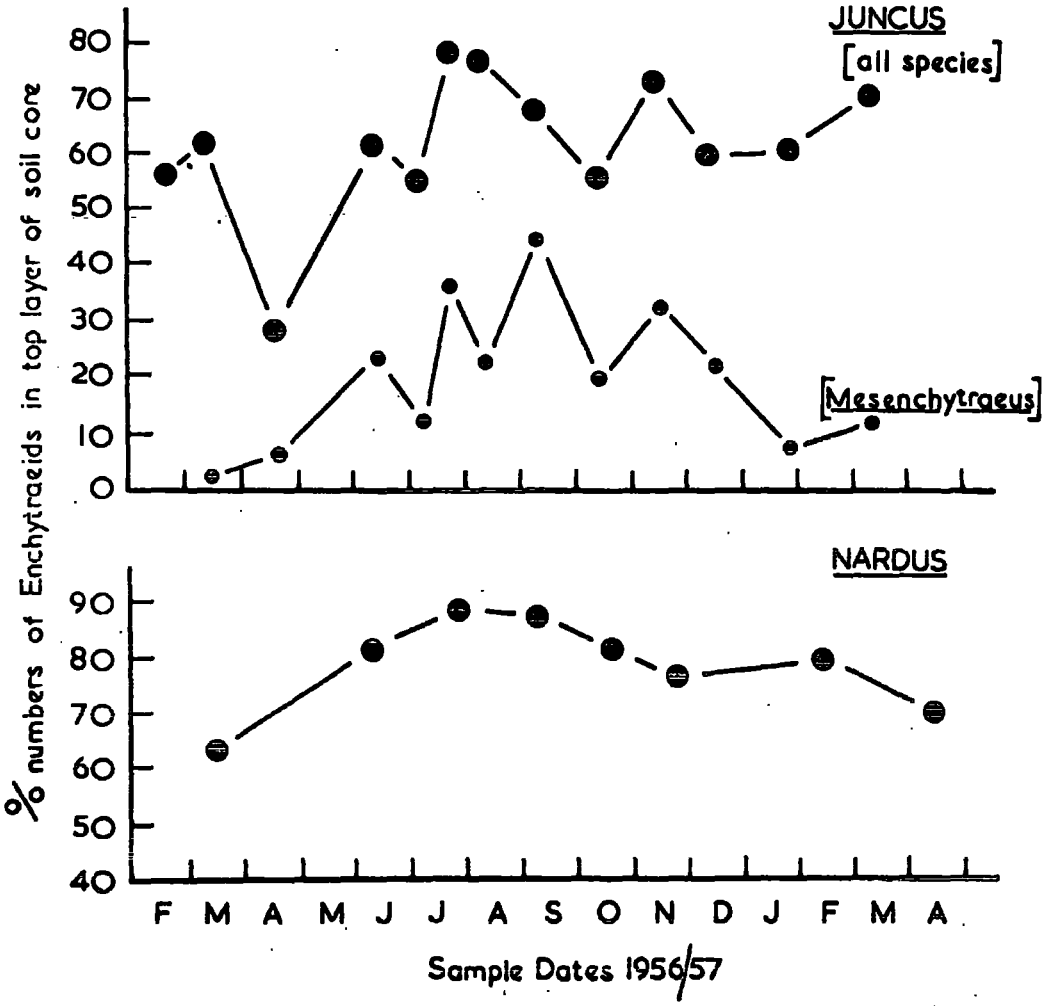


Fig. 31. % number of enchytraeids in top layer of soil cores.

Table 67. % in top 2 cm. of Alluvial grassland samples and climatic factors 1956-1957

Date 1956-1957	% in top 2 cm.	Temp. at 30 cm. (°F)	Rainfall for previous 14 days (ins.)
23·5	21	45	2·6
30·8	76	50	5·5
2·10	72	49	3·7
1·11	67	41	3·2
4·12	60	40	3·0
6·2	56	37	6·5

Table 68. % in top layer of Nardus grassland samples and climatic factors 1956-1957

Date 1956-1957	% in top 2 cm.	Temp. at * 30 cm. (°F)	Rainfall for previous 14 days (ins.)
14·3	63	35	3·2
5·6	81	47	1·2
31·7	88	51	3·6
5·9	87	49	3·7
18·10	81	46	0·8
27·11	76	38	1·7
12·2	79	37	5·1
11·4	69	40	1·7

* correlated with percentage in top layer $r = 0{\cdot}841$ $P < 0{\cdot}01$

Table 69. % of Mesenchytraeus in top later of Juncus 56 samples and climatic factors 1956-1957

Date 1956-1957	% in top layer	Temp. at * 30 cm. (°F)	Rainfall for previous 14 days (ins.)
14•3	2	35	3•2
24•4	7	40	0•8
12•6	24	50	1•6
1•7	13	50	1•2
25•7	37	54	1•8
9•8	23	52	4•9
12•9	45	50	2•4
10•10	21	46	4•3
12•11	33	42	1•4
11•12	22	42	4•2
30•1	8	37	5•1
4•3	12	36	3•2

* correlated with percentage in top layer
$r = 0•687$ $P < 0•02$

In mid-December 1955 a block of peat was divided into sample units and the frozen top 2•5 cm. were extracted separately. Out of a total of 381 worms in the block only 12 were extracted from the frozen layer. This may be contrasted with the high percentage normally extracted under warmer conditions from the top layer.

Results of deep sampling

1955-1957

Preliminary deep sampling in the autumn of 1955 showed that generally over 75 % of the total numbers extracted occurred in the top 6 cm. (Table 70).

Table 70. % vertical distribution of enchytraeids 1955

Sample area	Date	Soil depth	
		0-6 cm.	6-11 cm.
Bare peat	7:10	76	24
Calluna moor	14:10	82	18
	7:11	91	9
Alluvial grassland	30:9	95	5
	14:10	85	15

Sampling on the Juncus 56 area in winter and spring 1956 (Table 71) revealed that over 80 percent of the numbers recorded were from the top 6 cm. of 16 cm. deep samples. However, on the colder winter sampling occasion the percentage numbers of Mesenchytraeus were much lower in the top sample layer.

Table 71. % vertical distribution of enchytraeids in the Juncus 56 sample site 1956

	Date 1956*	0-6 cm.	6-11 cm.	11-16 cm.	Max-Min monthly temp. (°F)
All species	30:1	81	13	6	31
	29:5	90	9	1	45
Mesenchytraeus only	30:1	31	43	26	31
	29:5	94	5	1	45

* P/E on both occasions greater than unity.

On eleven selected sampling occasions, out of a total of 24, deep samples were taken from the Juncus 57 area, down to a maximum depth of 30 cm., although this depth was only sampled where necessary (Table 72, Fig. 32). Over 96 percent of all the worms extracted from 12 cm. deep cores were from the top 6 cm. on all but three of the eleven sampling occasions. The same results were obtained for Mesenchytraeus considered separately.

The downward movement of these soil animals was correlated with a P/E value of less than unity (Table 72). A transformation carried out on these P/E values improved the correlation.

Table 72. % vertical distribution of enchytraeids 1957-1958

Date	Soil layer 0-6 cm.	6-12 cm.	P/E**	
25.6	34 (80)	66 (20)	0·008	Dry soil
2.7	40 (70)	60 (30)	0·443	
9.7 *	48 (64)	61 (40)	0·995	
25.7	98 (100)	2 (0)	2·5	Wet soil
19.8	99 (100)	1 (0)	11·5	
25.9	100 (100)	0 (0)	3·1	
22.10	98 (100)	2 (0)	3·3	
22.11	96 (100)	4 (0)	4·7	
9.12	100 (100)	0 (0)	2·7	
28.12	90 (91)	0 (9)	frozen	
30.4	100 (100)	0 (0)	>1.0	

N.B. Figures in brackets refer to Mesenchytraeus only.

* deep sampling on this occasion showed worms deeper than 12 cm., the percentage of the total population in the top 6 cm. was 39 for all species and 61 for Mesenchytraeus only.

** calculated for the 14 days previous to the sampling date.

$r = 0{\cdot}831$, d.f. = 7, P 0·01.

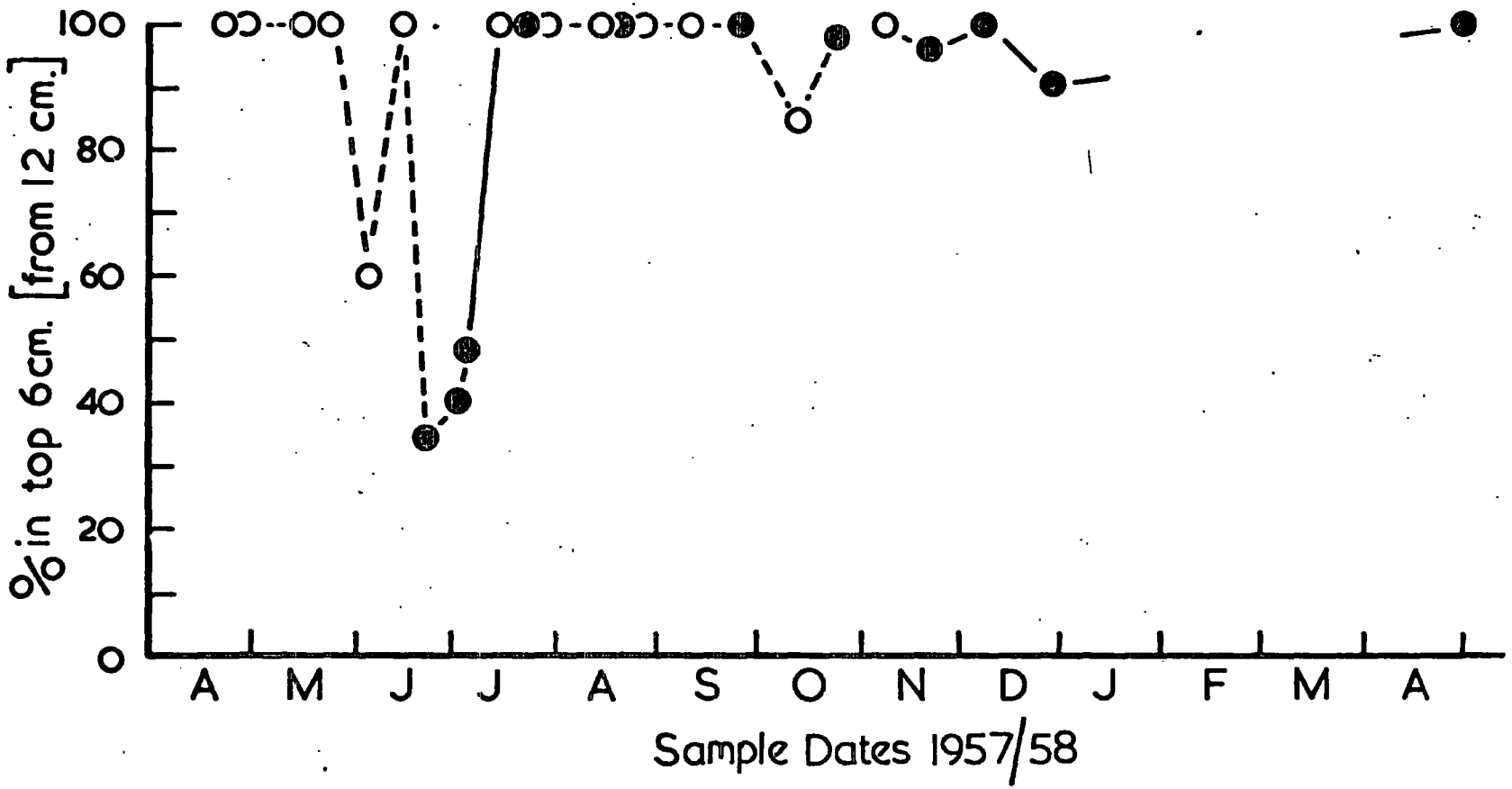


Fig.32. Vertical distribution of enchytraeids in Juncus 57 sample area.

The depth at which worms were found in early July 1957 was about 25 cm.

In 1958 Table 64 shows that from J. C. Coulson's sampling data, high percentages of the numbers extracted occurred in the top 2-3 cm. During this period P/E values were greater than unity, contrasting to the situation in June-July 1957.

(4) VERTICAL DISTRIBUTION

Summary of information collected from sampling data

From the sampling results given it may be concluded that over 50 percent of the enchytraeids extracted from 0-6 cm. samples were present in the litter layer (L+F) where this was present. Mesenchytraeus and Fridericia considered separately were found to prefer a deeper distribution. In Bare peat and Alluvial grassland samples there was less tendency for high percentages of worms to be extracted from the top layer.

The seasonal variation in vertical distribution within the 0-6 cm. sampling depth gave a summer maximum percentage in the top 2-3 cm., particularly in the warmer and wetter August, in many samples this was coincident with an increase in numbers extracted and might be linked with age distribution. When deeper samples were considered it was shown that the normal 0-6 cm. sample depth included most of the worms present except:

(a) under very cold conditions when the top layers of the soil were frozen, particularly with exposed sample areas and with Mesenchytraeus.

(b) under conditions of drought, when P/E values fell below unity as they did in June-July 1957 for the first time since August 1955.

Both these conditions were accompanied by downward movement and a resulting sharp drop in 0-6 cm. sample mean values. Where similar sharp drops in sample means occurred, accompanied by these conditions, but with no deep sample data to demonstrate downward movement, such movement was assumed and estimated (shown by open circles in Fig. 32). Two further occasions when the worms may have been present below the 6 cm. deep samples are suggested - in early June and early October, both during drought conditions. Further, it was assumed that when these conditions were not in operation the population was correctly estimated with 6 cm. deep soil cores. Using this approach in 1958 it would appear that no downward movement, comparable to the previous year, took place, the sample means do not suggest it and the relevant P/E ratios were greater than unity.

Discussion on vertical distribution

The most striking feature of the vertical distribution is the great concentration of the enchytraeids in the topmost layers of the soil. This has also been reported by Nielsen (1955a) and O'Connor (1957) and is fairly true of the soil fauna considered generally. Since sampling has revealed changes in the distribution caused by, or coincident with climatic reverses, two problems require discussion:

(i) what makes the worms move deeper?

(ii) and why do they go back to their former superficial distribution?

The answers to these two questions will help to explain the vertical arrangement of worms in the soil, as well as to link with work on the physiology of these animals.

(i) Downward movement - desiccation

It has been shown that the worms move downwards as the soil dries, presumably they move to avoid desiccation. Ivleva (1953a) has shown that Enchytraeus albidus will actively move from dry soils to wetter ones, provided desiccation is not imminent. Nielsen (1955a & b) did not find any substantial downward movement in Danish soils under very dry conditions, this lack of a clear response being attributed to the absence of a well defined moisture gradient. When the soil moisture was as low as 8 percent the worms studied by Ivleva (1953) rolled up into balls and did not actively prefer increased soil moisture. Perhaps finding local concentrations of slightly increased moisture the worms remain there, as suggested by Nielsen (1955a) rather than reacting to a more general gradient. O'Connor (1957) attributes changes in percentage vertical distribution, under drought conditions, to a decrease in the severity of mortality with depth, rather than to active movement in response to drying out of the surface layers. The discrepancy in the three separate studies on the enchytraeids may again be explained in terms of differences in sample areas.

The Juncus site, where the deep sampling was carried out, was normally very wet. Reference to the soil profile description (Table 5) shows that an impedance to drainage is caused by gleyed soil at 42 cm. Under dry conditions only the surface layers are affected, the underlying

peat will always remain waterlogged or moist. The moisture gradient can therefore be expected to be quite steep at those times of downward movement from the dry litter, fermentation layer and crumbly upper peat to the wetter peats below. This is contrasted to both the Nielsen and O'Connor sample areas the former well drained sandy soils, the latter a silty forest soil with a relatively slight impedance to drainage. More important still is the medium into which the downwardly moving animals penetrate. In the Juncus site this was organic and presumably food-containing, but in the sites sampled by Nielsen and O'Connor the lower (mineral) layers could hardly be expected to contain much organic food material. The same limitations would apply to the grassland areas studied on the Moor House reserve. Considering the annual densities recorded for two and three year periods (Table 65) it would appear that the exceptionally dry summer of 1955 had a much greater effect on the populations of Nardus grassland than on that of Juncus 56 area, either due to the decreased desiccation threat on the moister Juncus site, or because of the avoidance of desiccation by downward movement, as described.

(b) cold

A similar downward movement to that described above has been shown to occur when the site was exposed to freezing conditions, particularly with Mesenchytraeus and with the worms found in the Bare peat. To a considerable extent the thick vegetation mat of Juncus and Nardus prevents the underlying soil from freezing hard, a protection conspicuously absent from the exposed Bare peat. More extensive information is lacking on account of the difficulty of accurate sampling and

extraction as well as the inaccessability of the reserve under severe winter conditions. The milder winters of 1956 and 1957 made the conditions mentioned above rare to sample.

(ii) Upward movement (a) return of wet conditions

The worms moved back to their former distribution, when the drought ended with P/E ratios again greater than unity. Ivleva (1953a) gives the value 21%-22% as the optimum soil moisture, to which Enchytraeus albidus will move from varyingly moistened soils, further increase in soil moisture was injurious. Ivleva explained this as being caused by the filling up of soil pores by water and the consequent disturbance of respiratory facilities, such that the experimental animals moved out, under these conditions, on to the walls of the test apparatus. A similar movement from waterlogged samples was observed during the collection and storage of soil cores in polythene bags 1956-1957. Many of the total worms present in the soil core were obtained by washing the internal surface of the bag. This outward movement from the soil core could take place in less than an hour from collection and only occurred with really wet soil cores. It is suggested that the return of wet conditions and the consequent waterlogging of the peat forces the worms to return to the surface layers, presumably for respiratory reasons.

(b) warm wet conditions

Under warm and wet conditions the percentage numbers occupying the top layer (0-2 cm.) of soil cores extracted, increased considerably. This is partly explained by the increase in density which occurred mainly

in this layer but is also directly related to the climatic factors mentioned, especially the Nardus values. Ivleva (1953a has again shown that Enchytraeus albidus preferred an optimum temperature of 17°-18°C. (about 63°F.). Experience from extraction techniques has shown that temperatures of over 25°C. (75°F.) are lethal if prolonged. During the period of study, temperatures in the soil rarely reached this figure and the upward movement, as described, might be regarded as a positive response to warmer temperatures under wet conditions.

Enchytraeid worms have been shown by other workers to be sensitive to moisture and temperature changes. As Nielsen (1955b) remarks, these two factors cannot really be studied separately in nature. With their lack of cuticle, their permanently moist skin and their restriction to moist habitats, it is not surprising that they are so sensitive to desiccation, and that changes in vertical distribution throughout the year reflect this sensitivity.

(5) SEASONAL DISTRIBUTION

Summary of information collected from sampling data

With the knowledge of vertical distribution, and the effect of changes in it, on the value of 0-6 cm. sample means as estimates of population density, it was possible to separate changes in seasonal distribution from changes in vertical distribution, the former being described as follows:

1955-1956 - a decline in number in the very cold months, which may have been due to mortality or downward movement,

1956-1957 - a period of no, or low, increase in numbers up to July followed by peak populations recorded in August-November,

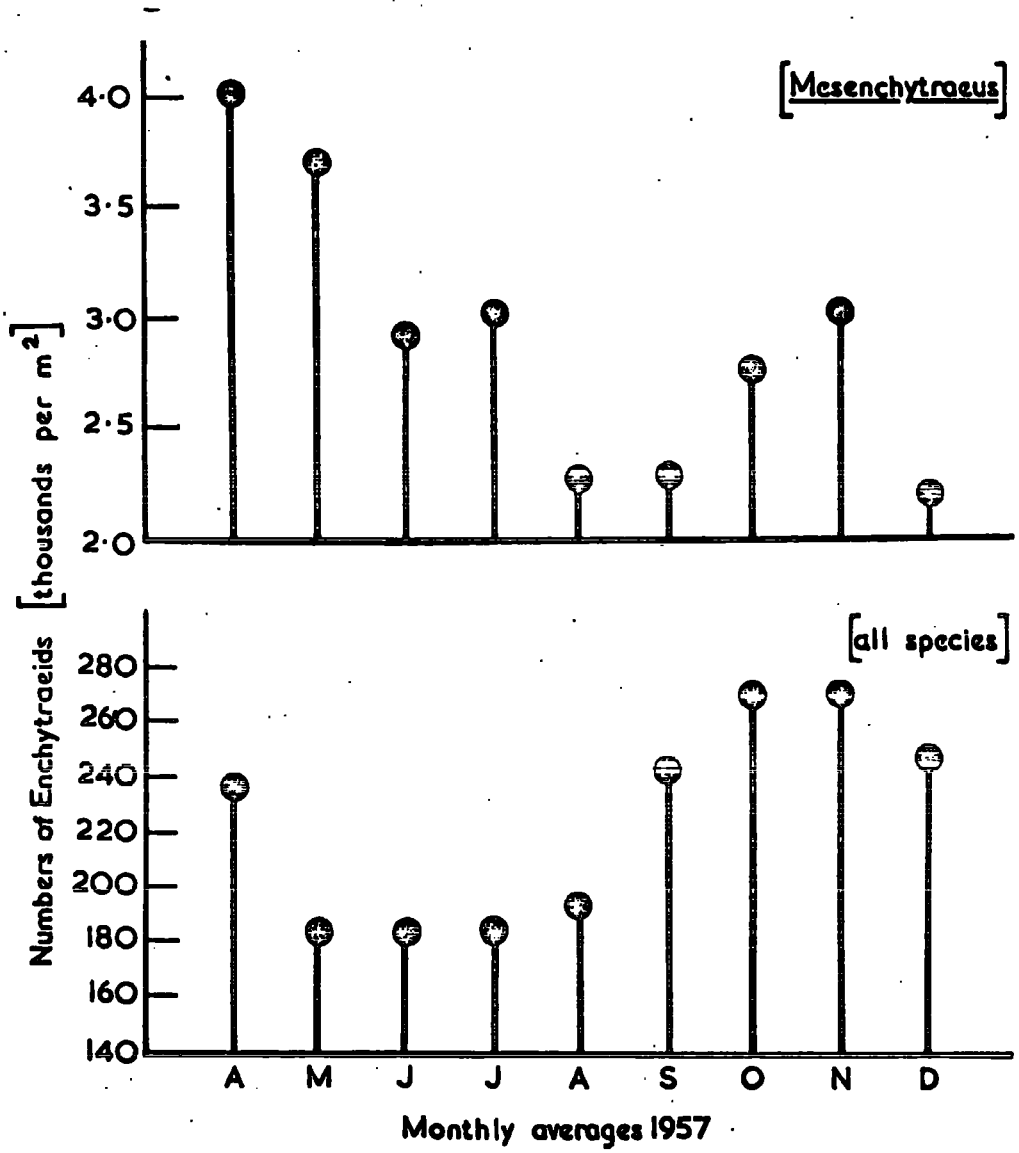


Fig. 33. Estimated density fluctuations of enchytraeids in Juncus 57 sample area.

with an autumn return to the pre-peak density (except with Nardus samples which showed a steady recovery with no peak value),

1957 - an April-May drop in Juncus 57 numbers (as shown by monthly averages Fig. 33) followed by an August increase reaching maximum values in autumn,

1958 - a similar drop in numbers in early spring was recorded.

Fig. 34 shows the correlation between a running P/E mean (over two months) and monthly average density estimates for 1957. Both this and the climatological correlations for 1956 (Tables 60 & 61) show that the greatest increase in numbers started with the wetter and generally warmer months of July and August in both the years 1956 and 1957. The spring and autumn decline in numbers recorded for Juncus 57 and Juncus 56, Bare peat and Alluvial grassland samples respectively was not correlated with any obvious climatic factor. A small decrease in numbers was observed in winter samples.

The result refers really to Enchytraeoides sphagnetorum as this forms the dominant member of the family in the Moor House soils. When the Mesenchytraeus figures are examined separately, it is difficult to discern a trend in the 1956 results. The figures do not represent a complete population estimate as only the older worms were considered. The summer peak of mature Fridericia agrees with Nielsen's (1955a) observations.

(6) ANNUAL DISTRIBUTION

When the annual spring densities for Juncus sites are compared, a remarkable constancy is obtained, over the three years of study (Table 65).

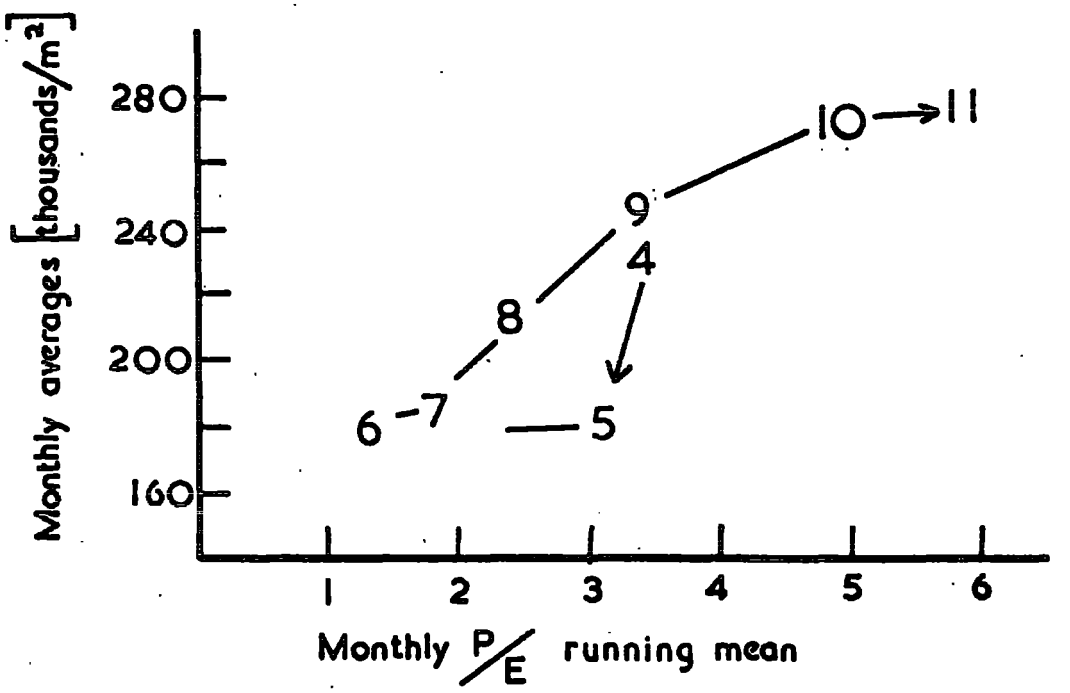


Fig. 34. Correlation between density increase and increasing P/E (4-11 = April - November 1957)

This does not, however, apply to the Nardus site where a spectacular increase in numbers occurred from year to year correlated with the wetter summers of the years 1957 and 1958, as opposed to the very hot and dry July and August 1955. The weather in these months is mentioned as this is the time when the population is most likely to be increasing - if conditions are favourable as they were in 1956 and 1957. A similar increase in density has been recorded from 1956 to 1957 for Alluvial grassland.

(7) AGE DISTRIBUTION

The mean live weight per worm extracted was taken as an indicator of the age distribution of worms when differing sample means were compared.

Seasonal variation in mean weight

A significant drop in mean weight, in 1956 and 1957, of Juncus samples was coincident with the increase in density recorded (Table 73, Fig. 35). This information confirms the reality of the seasonal variation described.

Table 73. The significance of seasonal changes in mean weight per worm from Juncus samples

	Sample area	d.f.	F	P<
All species	Juncus 56	3•24	185	0•001
	Juncus 57	3•19	5•7	0•01
Mesenchytraeus only	Juncus 56	3•16	22•7	0•001

Although the mean weight per worm dropped as the population

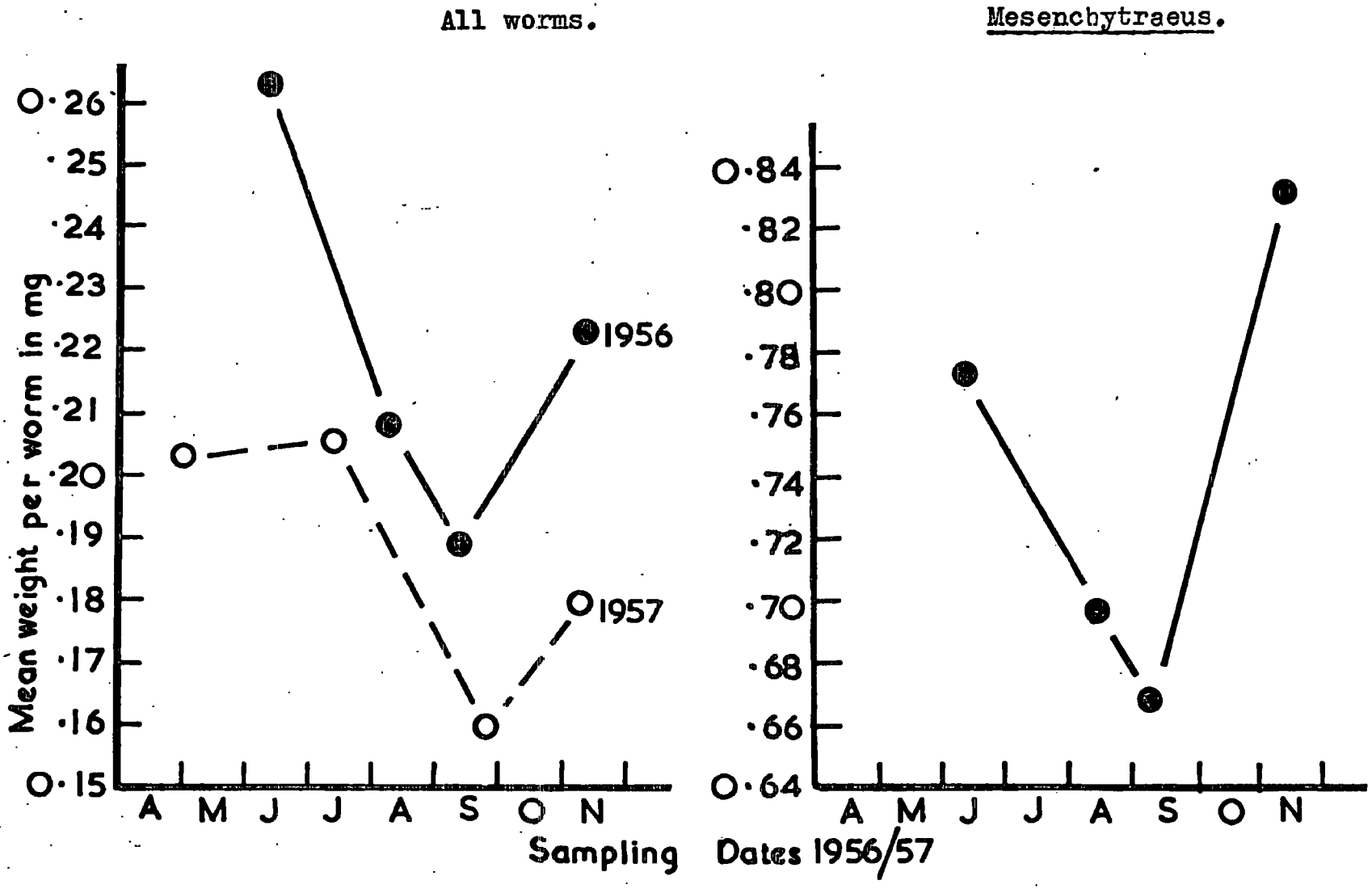


Fig. 35. Seasonal drop in the weight of worms from Juncus sites.

increased, the increase was accompanied by a rise in the value of the biomass (Table 76) which for the Juncus areas was up to 10 g/m² higher at the peak than at minimum densities. It is difficult, however, to assess the validity of this as will be discussed later.

Variations in weight of worms extracted from different depths

It was observed that the young worms were missing from deeper samples and this was confirmed by weighings carried out in July 1957, which showed a statistically significant difference in mean weight between the sample depths, there being more young worms in the top 6 cm. (Table 74).

Table 74. Differences in mean weight per worm (Mesenchytraeus excluded) extracted from different depths

Depth of sample (cm.)	Mean weight per worm (mg.)
0-6	0·174 ± 0·029
6-18	0·224 ± 0·004
F = 17·8 d.f. = 1;5 P 0·01	

Sample site variation in mean weight

When the mean weights per worm for different sample areas are compared at peak density periods they are proportional to the density - the higher the latter the lower the mean weight (Table 75).

Table 75. Mean weights per worm for different sampling areas at peak population periods

Date	Sampling areas	Mean weight per worm	Numbers (thousands/m^2)
11/57	Juncus 57*	0·160	261
9/56	Juncus 56*	0·189	239
11/56	Nardus	0·180	96
8/56	Bare peat	0·211	49
8/56	Alluvial**	0·225	24

*Mesenchytraeus excluded
**Fridericia excluded.

Variation in mean weight from high to low density patches

The mean weight of high density sample unit worms (0·209 mg.) was higher than that (0·164 mg.) of low density sample unit worms. This is the opposite of the expected if it is assumed that high density aggregations contain more young worms. A better method of assessing differences in age structure is required.

Reliability of mean weights

The weighing of live worms is open to objection, because of the indeterminate quantity of water lost or gained by the worms while being prepared for weighing. A far greater source of error in this work was the differential mortality of the worms while awaiting treatment and during preparation. This and the handling difficulties suggest that a larger proportion of the small worms are lost. The mean weights, and therefore

the biomass estimates may be somewhat overestimated. In addition the weight per worm is high, compared to Nielsen's (1955a) and O'Connor's (1957) values.

(8) ECOLOGICAL DISTRIBUTION

Table 76 shows that the densities and biomass were highest for the Juncus sites and least from the Bare peat and Alluvial sites. (The Nardus numbers have since increased.)

Table 76. Live biomass estimates for peak densities

Date	Sample site	Live weight g/m²	Numbers (thousands/m²)
11/57	Juncus 57	53 (2)	289
9/56	Juncus 56	51 (6)	248
11/56	Nardus	17 *	96 *
8/56	Alluvial	15(10)	25
8/56	Bare peat	10	49

N.B. Figures in brackets refer to Mesenchytraeus included in Juncus samples and Fridericia in Alluvial samples.

* Estimated increased to 35 g. (204,000/m²) by following spring.

GENERAL DISCUSSION

Seasonal, annual and age distributions

Violent fluctuations in numbers have been shown to occur, both within and between the years. Although attempts have been made to relate

these fluctuations in numbers (which represent changes in the birth/death ratio) to obvious climatic factors; in the discussion which follows it is painfully obvious that as with most soil animals it is only possible to talk in the most general terms at this stage. This is largely due to the absence of detailed information on the biology, particularly the reproductive biology, of these moorland enchytraeids.

Three aspects of these fluctuations may be considered:

(i) the increase in numbers which occurred in all the sites during the warmer and wetter months of 1956 and 1957 and led to an autumn peak, with the exception of Nardus grassland,

(ii) the return to pre-peak densities which immediately followed the peak (as in 1956, except for Nardus) or occurred in the following spring (as in 1957 and 1958 for Juncus 57) without relation to any obvious climatic change,

(iii) the exceptional rise in Nardus grassland densities in 1956 and continuing through the winter.

The peak densities recorded by Jegen (1920a) and Nielsen (1954, 1955) were preceded by summer minima during unfavourably dry spells. In some areas in 1954 Nielsen found that nearly all the worms had been killed off within a fortnight of the commencement of drought. There was no signifi- record of summer minima at Moor House during the period 1956-1958 because with the exception of the hot and dry July-August 1955 (just before the start of this study) and the dry June of 1957 (when P/E values fell below unity) the last three and a half years at Moor House have been wet and the summers moderately warm. O'Connor did not record summer minima (apart from August 1955) and suggests that the absence of a yearly drought in

N. Wales was responsible for both this and the earlier peak. In the sandy Danish soils studied by Nielsen (1954 & 1955a) drought was an ever-present threat to the worms in the summer. The better protection which the wet peat sites afford has already been discussed in connection with vertical distribution and is connected with the stability of the numbers recorded from these areas from year to year. The increase of Nardus estimates following the summer of 1955 suggests that in mineral soil sites at Moor House (and possibly in exposed peat sites) a summer minimum density occurs under adverse climatic conditions. It is not argued that the worms in the Juncus sites never die of desiccation but simply that this factor cannot be of great importance in affecting their abundance.

There was some drying out of the Juncus site in June-July 1957 but this only affected the vertical distribution. It is suggested that the later in the summer-autumn period the drought occurs, the more lethal its effect, for as the summer advances there will be more young worms present. Young worms have been shown to occupy the top-most layers of the soil. From the deeper distribution of worms in the drought of 1957 it was found that the larger worms were relatively more abundant with depth. Perhaps the young worms cannot penetrate the deeper layers and are therefore more sensitive to climatic adversity, although a differing physiology may well be the explanation.

No obvious climatic factor, it has been mentioned, can be named to explain the return to pre-peak values, for if the Nardus densities can increase through a Moor House autumn and winter (as they did in 1956-1957) then climate cannot explain drops in density, in the Juncus sites.

Density change

For some years now the possible mechanisms of population control have been the subject of prolonged debate and speculation. The most important differences of opinion are based on the relative influence of 'density dependent factors' (factors which operate in relation to the density level) and 'density independent factors' (factors which operate regardless of the density level).

The so called 'competition school' maintains the exclusiveness of density dependent factors in the ultimate fixing of density levels, though density independent factors may determine the population density level at which the appropriate density dependent factor operates. This approach is grounded in the early parasite-host population studies (Lotka 1925, Thompson 1927-1930) or in the laboratory studies of animals competing for a limited food supply (Gause 1935). It is also a deduction from the ideas of Darwin & Malthus, particularly the latter's classical idea of exponential increase leading to over-population and starvation. The logistic curve (Verhulst 1844), the competition curve (Lotka 1925), the idea of Gause's hypothesis and the mathematical theory of Nicholson & Bailey (1935) are all generalisations of this approach. Nicholson (1954a & b, 1957) has redefined the theory and the density factors are renamed in terms which indicate their action on the numbers of animals.

The 'climatic school' (Bodenheimer 1938) has come into its own recently with the work of Davidson & Andrewartha (1948) on field populations of Thrips imaginis and with the publication of 'The distribution and abundance of animals' (Andrewartha & Birch 1954). Density independent factors such as climate are seen to be the most important, acting

through the heterogeneity of the environment to control the distribution and abundance of animals (Andrewartha 1957, Birch 1957).

It is interesting to note the different origins of the two approaches reflecting as they do the great difficulty of laboratory and field synthesis. The problem is further aggrevated by the over generalisation of specific examples of control mechanisms, together with the difficulties over the meanings of the words used in the theory.

Many attempts have been made to reconcile the two approaches but one seems to achieve a real synthesis. Reynoldson (1957) using data on fluctuations in the numbers of field populations including E. albidus in the Huddersfield sewage beds, has suggested that the importance of density dependent control varies with the general physical favourability of the environment. This approach may help in the present study. In the wet peat Juncus sites, physical favourability may be considered to be high, as the worms are more protected from desiccation than in dryer mineral soils. There is no evidence that climate has been a dominant factor here, as return to pre-peak values have occurred at the same time as the numbers in the dryer Nardus mineral soil site have gone on increasing. It has been argued that the Nardus area suffered heavily from the drought of July-August 1955; from this and from the description of the sample area, it becomes obvious that when compared with the wet organic Juncus sites, the Nardus area is physically less favourable. Since the beginning of this study the numbers in the Nardus site have increased greatly, a reduction will presumably occur and when it does it will be much more likely to be a climatic reverse than in the Juncus sites. The continuation of climatic favourability may, however, permit the worms to be

controlled by density dependent factors as in the Juncus sites where the yearly action of such factors is put forward to explain the autumn and spring drop in numbers. What these factors are, is not known at the present time.

Where density independent control is suggested, as with the Nardus grassland and Nielsen's sandy soil populations, in the form of desiccation threat, Reynoldson maintains that such control does not lead to the extinction of the population because of the natural heterogeneity of the environment and variations in the degree of exploitation of it by the population. In this latter connection, Reynoldson sites the aggregations of enchytraeids as evidence of this phenomenon.

Differences in density between sample areas

Birch (1957) puts forward the proposition that the laws which govern the distribution of animals are the same as those governing their abundance.

The Juncus sites were shown to be the most favourable for enchytraeids when compared with the Nardus and other sites. This can be related to the desiccation threat already discussed, but in the explanation of the much lower densities in Bare peat and Alluvial grassland sites, other factors must be involved. In both these sites there is little, or no litter layer - and enchytraeids seem to be concentrated in the L+F soil profile zones in areas where they are present. Organic matter is not in itself sufficient, for there is no shortage of peat on the Bare peat site, however, no freshly decaying increments of plant material and no mineral supply are available to animals living in the surface layers. The Juncus sites provide optimum conditions apparently lacking in both Bare peat and

Alluvial grassland areas.

The distribution of enchytraeids in relation to some other soil animals

In comparing the biomass estimates of the present work to those of other workers there is risk that the comparisons may be biased by the errors inherent in the weighing methods used for live animals as already mentioned.

With all these limitations in mind a very approximate picture of the biomass distribution of three groups of soil animals has been compiled from published work, the present study and also by interpolation (Fig. 36) for 8 habitats arranged in order from the most mineral to the most organic as follows:

1 - Pasture, data from Svendsen (1957), Nielsen (1955a) and Nielsen (1955a) for the earthworms, nematodes and enchytraeids respectively.

2 - Peaty Alluvium (Alluvial grassland) data from Svendsen, Banage (biomass estimated from density) and Peachey.

3 - Coniferous forest soil, data from Nielsen and O'Connor (1957).

4 - Calluna heathland, data from Nielsen.

5 - Nardus grassland, data from Banage and Peachey.

6 - Juncus squarrosus moor, data from Banage and Peachey.

7 - Calluna bog, data from Banage and Nielsen or Peachey.

8 - Bare peat, data from Banage and Peachey.

There is sufficient data and sufficient difference to show quite clearly the ecological relationships of these three groups of animals. The

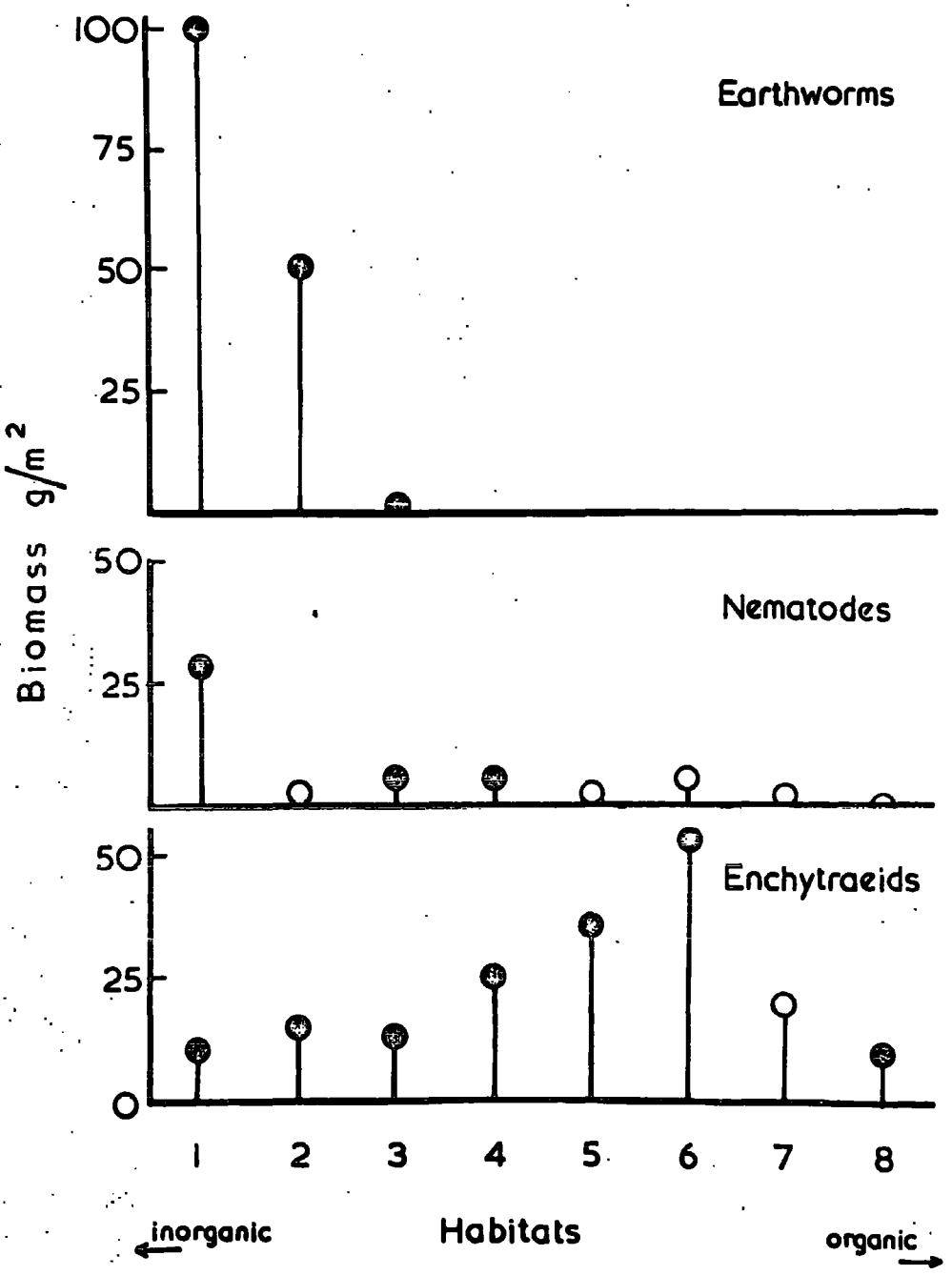


Fig. 36. Live weight biomass estimates (see text).

earthworms and nematodes are predominantly inhabitants of mineral soils, (though specialised nematodes and earthworms such as Bimastus eisoni and Dendrobona octahedra (Svendsen 1957) can exist under acid conditions) as conspicuous members of the fauna. The enchytraeids reach their maximum numbers in habitats containing moist organic material of the right kind. The peak in Juncus squarrosus habitats suggests that the enchytraeids need some mineral requirements as well, which this habitat can supply in quantities that cannot be found in the deeper peats. In the Juncus areas and to a lesser extent in the other moorland habitats (apart from the earthworm inhabited limestone and alluvial soils (Svendsen 1957) the enchytraeids may be regarded as the dominant 'worms' present as members of the permanent soil fauna. It is difficult to compare them to the arthropods as these are greatly different in their manner of life and are generally more difficult to sample and study.

Nielsen (1955c) states "In general distribution, the Enchytraeidae differ very much from their close allies, the earthworms. The latter family is particularly abundant in the rich mull soil while in the raw humus, at least in Denmark only Dendrobena octahedra occur in appreciable numbers.... The Enchytraeidae are also very different from free living nematodes which prefer the mull sites while they [the enchytraeids] seem to resemble more the oribatid mites in attaining their greatest density in soils of the mor type." The present study has confirmed this and has helped to complete the broad picture of enchytraeid distribution in 'mor soils'.

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