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THE INFLUENCE OF DRAINAGE ON ENCHYTRAEIDS (ENCHYTRAEOIDEA, OLIGOCHAETA) OF FENS IN THE BIEBRZA ICE-MARGINAL VALLEY

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ABSTRACT: An effect of fen reclaming (mainly drainage) on species composition and structure of an Enchytraeid community has been studied. Contribution of that group of animals to peat mineralization was assessed in relation to other soil saprophages. The studies were carried out in four meadows: one natural and three drained ones. Considerable similarity between communities of enchytraeids occurring in the meadows of different peat origin was found. Moreover, it appeared that agrotechnical management accompanying drainage did not reduce species diversity of those communities. Despite little contribution of enchytraeids to mineralization, they play significant role in soil processes of the examined sites as they exist more successfully than earthworms under unfavourable soil conditions.

KEY WORDS: enchytraeids, community structure, vertical distribution, abundance dynamics, organic matter mineralization

1. INTRODUCTION

The Biebrza River ice-marginal valley is located in north-eastern Poland. It is one of few natural river valleys in Europe encompasses large (117 000 km^2) natural peatlands.

There have not been any faunistic information available on Enchytraeidae occurring in that region of Poland althought quantitative investigation were performed (K a j a k et al. 1985). Evaluation of enchytraeid occurrence in particular regions of Poland as well as faunistic recognition of various environments is incomplete. Composition of enchytraeid species oc-

curring in the soils of peatlands and peaty meadows of north-western Poland was studied by M o s z y ń s k i (1928, 1934) and K a s p r z a k (1977, 1982).

Since the beginning of 20th century some areas of the Biebrza ice-marginal valley had been reclamed and converted into meadows. This consisted in soil drainage, ploughing and sowing of pasture species of grass. Such manipulations may lead to irreversible diversity reduction of natural communities and transformations of the entire ecosystems (C i e - s i e l s k a et al. 1991). Drainage has

initiated rapid soil mineralization: every year over 2 mm of peat is being lost from drained peatlands (K a j a k and O k r u s z k o 1990).

The objectives of this work were:

1) to compare species composition and structure of enchytraeid communities between a natural fen and meadows developed as a result of drainage and management of primeval areas,

2) to evaluate contribution of that group of animals to peat mineralization with respect to alarming intensification of that process in grassland soils.

2. STUDY SITES AND METHODS

The studies were carried out in four sites located in a lower part of the Biebrza river basin and upper part of the Narew river basin in north-eastern Poland. One site was a natural fen on sedge-moss peat (NM), three others comprised meadows on soils drained about 30 years ago and characterized by different peat origin: sedge-moss (M), sedge (S) and alder peat (A). Differences in peat origin results from different water conditions prevailing in the areas considered prior to their drainage. At that time, the driest areas

were overgrown by alder-swamp, whereas the wettest ones – by mosses and sedges. Although the differences are smaller now, moisture sequence remains the same (Table 1). The undrained site NM is not only wet but also periodically flooded. Moisture content in the drained peatlands is decreasing in the order from the M site on sedge-moss peat to the A site on alder peat. Drainage causes that peat-forming process from plant debris is reduced, and mineralization of organic matter begins to dominate, instead. The drier the soil, the

Table 1. Soil moisture contents and levels of ground water table of the examined sites
NM – fen; M, S, A – managed meadows

	April	May	June	July	September	October
Soil moisture (%)						
NM	...*	88.0	...	...	85.1	85.4
M	...	76.5	...	71.3	75.2	73.9
S	...	75.4	...	69.5	70.2	71.7
A	...	69.6	...	47.0	63.7	65.6
Ground water level (cm)						
M	36	...	21	65	39	74
S	40	...	43	85	51	73
A	54	...	70	83	47	59

*No measurements made.

more intensive is process of mineralization. Mineralization measured by the amount of nitrogen released from the drained meadows differed by 2.6-fold (Z i m k a and S t a c h u r s k i 1996), and 15 years earlier – when the rate of carbon release was taken into account – by factor 1.1 (S z a n s e r 1991 a). The soils of the examined sites are slightly acidic with high C : N ratio (Table 2).

Regarding vegetation, the fen (NM) is somewhat uncommon association of Caricetum diandrae. Agrotechnical measures (sowing, fertilization) applied to the meadows altered their primary floristic composition. At present, the sites (A, M, S) are communities from the class Molinio-Arrhenatheretea (Kotowska, personal communication, P a s t e r n a k-K u - ś n i e r s k a et al. 1997).

Preliminary quantitative studies were undertaken in May, July and September 1994, while systematic ones were performed from April to October 1995. Intensive studies comprised the three drained grasslands. To evaluate abundance dynamics, 7 series of samples were taken at monthly intervals. Each series consisted of 15 samples of 10 cm^2 in area and 16 cm deep.

Species composition and community structure were assessed on the basis of two series, each consisting of 20 samples of 20 cm^2 in area and a depth of 16 cm, collected in April and September, i.e. during the periods when the animals occurred in great numbers. Each sample was divided into 4 cm layers and extracted using the method described by O'C o n n o r (1955). Species identification was done on living material consisting of 4445 individuals. Out of this number, 568 individuals were from the NM site, 1162 – from the M site, 1129 – from the S site, and 1586 individuals – from the A site.

To describe enchytraeid communities, the following indices were used:

1) Species richness

$$d = \frac{S-1}{\ln N}$$

where: S – number of species in a sample, N – number of individuals in that sample.

2) Frequency

$$Fr = \frac{N_a}{N}$$

where: N_a – number of samples containing a given species, N – number of samples in a series.

3) Morisita's index of similarity of communities structure (modified by Horn) (H o r n 1966)

Table 2. Site (NM, M, S, A) characteristics

	Site			
	NM	M	S	A
Plant association	Caricetum diandrae	Molinio-Arrhenatheretea		
Peat origin	sedge-moss	sedge-moss	sedge	alder
pH in H_2O	6.3*	6.1*	6	5.4
C : N in soil	...[a]	12.2	12.3	12.4
Mineralization rate in:				
g C m^{-2} year^{-1}	...	524**	655**	692**
g N-NO_3 m^{-2} day^{-1}	...	0.061***	0.081***	0.16***

*M a k u l e c (1991); **S z a n s e r (1991b); ***Z i m k a and S t a c h u r s k i (1996); [a]No measurements made.

$$M = \frac{2 \sum\limits_{i=1}^{s} x_i y_i}{\sum\limits_{i=1}^{s} x_i^2 + \sum\limits_{i=1}^{s} y_i^2}$$

where: x_i, y_i – participation of species i in abundance in X, Y sites, S – total number of species.

4) Shannon-Weaver's index of diversity

$$H' = -\sum\limits_{i=1}^{s} \frac{n_i}{N} \log_2 \frac{n_i}{N}$$

where: n_i – relative abundance of i species, N – relative abundance of the entire community.

Body lengths of the animals were measured with an accuracy of 0.5 mm. Size distribution of individuals was assessed for every sample. Estimation of enchytraeid biomass was based upon the size of individuals and the following conversion factors: $y_1 = 6.22 \, x^{1.55}$, where y_1 – biomass in µg, x – body length in mm, and $y_2 = -62.38 + 20.14 \ln x$, where y_2 – dry weight in µg, x – biomass in µg (M a k u l e c 1983). Mean weights of individuals figured out from the above formulas differ on average by 4% from those calculated from equations for small-sized enchytraeids (A b r a h a m s e n 1973). It

was assumed that carbon content in enchytraeid bodies was 46.3% dry wt, and nitrogen content – 11.4% dry wt (C o u l - s o n and W h i t t a k e r 1978).

To estimate respiration of enchytraeids, methods given by P h i l l i p - s o n et al. (1979) and R ö m b k e (1991) were employed. On the basis of meteorological data an assumption was made that the growing season (i.e. period of mean positive temperatures in a decade) in 1995 was 270 days with the mean temperature amounting to 10.6°C. Regarding the fact that soil temperatures at the depth of 5 cm are by 0.2–4.2° C lower than air temperatures (K a c z m a r e k 1991a), assumed mean seasonal temperature of the soil was 10°C. Enchytraeid respiration was estimated according to the formula: $Q = 33.6^{0.67}$, where Q – respiration in µl of O_2, W – weight of an individual in g of biomass (Nielsen and O'Connor after R ö m b k e 1991). Correction factor for animal activity 1.6 (M a k u l e c 1983) or 2.2 (Standen after M a k u l e c 1983) was assumed to be equivalent to that for temperature $Q_{10} = 1.4 – 2.5$ at 10°C (O'C o n - n o r 1971). When converting respiration into the carbon amount, RQ was assumed to be 0.7 (M a k u l e c 1983).

3. RESULTS

3.1. SPECIES COMPOSITION

When describing species composition of enchytraeids, species from the family Enchytraeidae and one species from the family Propappidae classified formerly to Enchytraeidae, were included.

Twenty four species of enchytraeids were recorded to occur in the soil: 14 species at the fen (NM), and in total 20 species in the three meadows (M, S, A)

(Table 3). Similarity of species composition was considerable – 11 species occurred in each of the three meadows. Eight species were noted to be common for all the meadows and the fen.

Comparing species composition of enchytraeid communities between the fen (NM) and the meadow on sedge-moss peat (M), it appeared that from among 20 species, 9 were common for both habitats

Table 3. Species composition, dominance (D – %) and frequency (F) in the enchytraeid communities of peat soils. NM – fen; M, S, A – managed meadows

Species	Site							
	NM		M		S		A	
	D	F	D	F	D	F	D	F
Propappidae								
Propappus volki Mich.	1.0	0.1						
Enchytraeidae								
M. armatus (Lev)	3.7	0.3						
C. atrata (Bret.)	0.3	*	0.1	*				
C. immota (Knoell)?	0.7	*						
B. appendiculata (Buchh.)					0.2	0.1		
B. fallax Mich.					0.7	0.1		
C. glandulosa (Mich.)	18.3	0.5	0.2	*	0.5	0.1	0.1	*
C. sphagnetorum (Vejd.)	23.1	0.6	3.9	0.5	12.8	0.7	6.5	0.3
M. argentea (Mich.)	25.2	0.7	5.1	0.4	2.8	0.2	0.8	0.1
M. riparia Bret.					0.1	*	0.1	*
E. buchholzi Vejd.	1.2	0.1	0.9	0.2	4.8	0.2	0.8	0.2
F. bisetosa (Lev.)	2.8	0.2	0.5	0.1	0.1	*	4.3	0.6
F. bulboides Niel. & Christ.	0.3	0.1	2.3	0.2	0.4	0.1	0.2	0.1
F. galba (Hoffm.)			0.1	*				
F. leydigi (Vejd.)			0.1	*			0.4	0.1
F. maculata Issel			1.5	0.2				
F. perrieri (Vejd.)							0.1	*
F. ratzeli Eisen			0.4	0.1	0.4	0.1	0.8	0.2
F. striata (Lev.)	0.2	*						
H. heleotropha Steph.			0.8	0.1	0.1	*	0.2	0.1
H. jutlandica Niel. & Christ.			0.2	*	0.5	0.1	0.6	0.1
H. nasuta Eis.	3.9	0.2	0.6	0.2				
H. perpusilla Friend	0.7	0.1	18.2	0.9	40.2	0.9	29.1	0.9
H. ventriculosa d'Udek.	1.4	0.1	3.7	0.5	2.6	0.2	5.2	0.6
Mesenchytraeus sp.	0.4							
Cernosvitoviella sp.	3.7							
Buchholzia sp.					0.1			
Enchytraeus sp.	1.6		6.4		10.0		3.0	
Fridericia sp.	11.3		45.8		23.4		37.6	
Henlea sp.	0.2		9.2		0.3		10.2	
Number of species	14		16		14		14	
Index of species richness	2.05		2.13		1.85		1.76	
Index of diversity	2.04		2.10		1.80		1.69	

*less than 0.01.

and constituted about 45% of species composition.

Species occurring exclusively at the fen included *Propappus volki, Mesenchytraeus armatus, Cernosvitoviella atrata, Fridericia striata* and a questionable species *Cernosvitoviella immota*. All these species prefer very wet or wet habitats. Species occurring exclusively in the meadows were: *Buchholzia appendiculata, B. fallax, Marionia riparia, Fridericia galba, F. leydigi, F. maculata, F. perrieri, F. ratzeli, Henlea heleotropha* and *H. jutlandica*. From among these species *M. riparia, H. heleotropha* and *H. jutlandica* show special preferences for wet environments. Remaining species are tolerant of wide range of soil moisture conditions. The lack of *P. volki, M. armatus* and *C. atrata* in the meadows resulted from the drop in moisture content in comparison with the natural fen (Table 1).

Although the number of species recorded in the examined sites was similar, the index of species richness reached the highest values in case of enchytraeid communities living in the least mineralized soils (sites NM and M) (Table 3).

3.2. COMMUNITY STRUCTURE

The fen was dominated by *M. argentea* (Table 3) constituting 1/4 of the entire enchytraeid community of that site. Considerable participation in enchytraeid numbers of that community was also characteristic of *Cognetia sphagnetorum* and *C. glandulosa*. The dominant species in all the meadows was *H. perpusilla*. Its participation in enchytraeid abundance was the lowest at the M site, while the highest – at the S site. Considerable proportion of specimens from the genus *Fridericia* was found for all the meadows. The only species declining in numbers with the decrease in moisture status of the meadows was *M. argentea*.

Species displaying the highest values of frequency (constant class) at the fen (NM) were *M. argentea* and *C. sphagnetorum*. *C. glandulosa* was an accessory species, and 11 remaining ones were accidental species (Table 3). In the meadow M, *H. perpusilla* was absolutely constant species (eu-constant class), and *H. ventriculosa* – a constant one. Two species: *C. sphagnetorum* and *M. argentea* belonged to accessorial class, and 12 remaining species – to accidental class. *H. perpusilla* was also an absolutely constant species at the S site, whereas *C. sphagnetorum* was a constant species, and 12 remaining ones constituted accidental class. At the site A, the eu-constant class was again represented by *H. perpusilla*, and constant class – by *H. ventriculosa* and *F. bisetosa*. The only accessory species at that site was *C. sphagnetorum*, whereas accidental class included 10 remaining species.

Dominance and frequency indices show that the same species are numerous and constant. Solely at the site A frequency of the species *F. bisetosa*, indicates that, despite its low abundance, it is characteristic and important for that site.

Dissimilarity of enchytraeid dominance structure among the examined sites is reflected by the values of Shannon-Weaver's index of diversity (Table 3). At similar species numbers, the most uniform density distribution producing the highest value of the index took place in case of the M site community (Table 3). The index of species richness enabled to distinguish two groups of communities: the first one included the NM and M sites, while the second one – the S and A sites. The values of that index were sig-

nificantly different for the two groups at p < 0.02. Within-group variation was statistically insignificant for either group. Therefore, enchytraeid communities of the natural fen NM and the meadow of the same peat origin (M) had a rich diversity, whereas communities of the remaining two meadows: S and A were characterized by a poorer diversity.

With a view of assessing similarity of enchytraeid communities, Morisita's index was employed. Its values varied from 0.25 to 0.80 (Fig. 1). Enchytraeid communities are similar among the three cultivated meadows – the index ranges here between 0.61 and 0.80. The fen community is markedly different from those of the meadows. Merely communities of
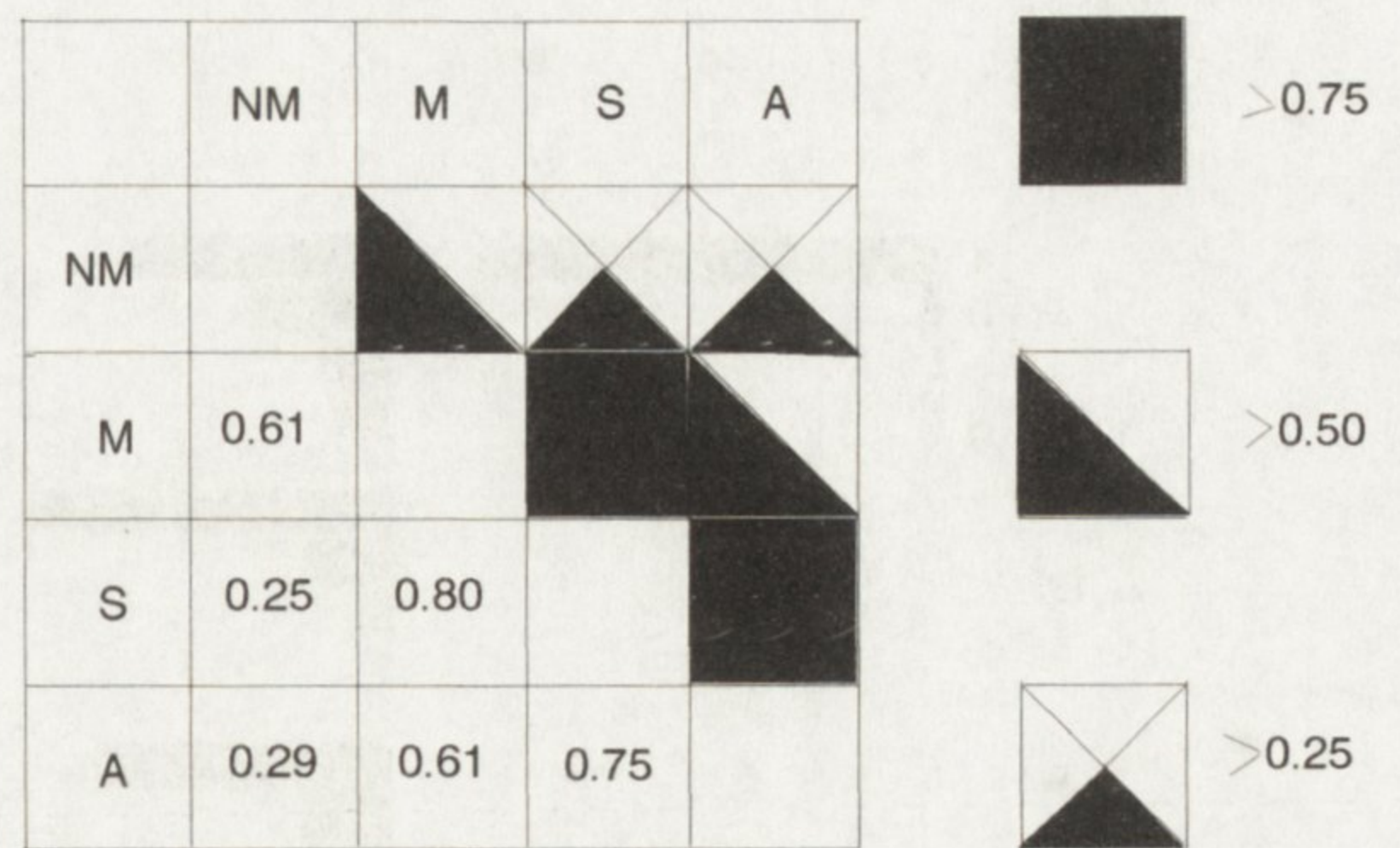

Fig. 1. Similarity of the enchytraeid communities (the diagram contains Morisita's index values) NM – fen; M, S, A – managed meadows

the fen and meadow M, i.e. two sites of the same peat origin, were found to be similar. In this case Morisita's index was equal to 0.61.

3.3. DENSITY

3.3.1. Vertical distribution

A pattern of vertical distribution of enchytraeid communities varies with regard to both site and season (Fig. 2). The seasonal variability coincides with actual moisture conditions in the soil profile. In April and May, from 90% (fen NM) to 33% (meadow A) of all individuals of these communities occurred in the upper soil layer (0–4 cm). During summer (July, August), lower soil layers were colonized more intensively. In autumn (September, October), the majority, i.e. 60–76% of enchytraeids was again concentrated in the upper layer, except the site A, where scarcely 19% of all specimens occurred in that soil layer.

Thus, it is evident that, regarding moisture conditions, substantially different sites NM and A have definitely different patterns of vertical distribution of the animals. At the fen, the upper soil layer is always more numerously populated by enchytraeids, whereas the lowermost one

(12–16 cm) contains from 2 to 7% of the animals. This is the only site where samples can be taken, as usually practised, to a depth of 10 cm without a risk of making any serious error. The least wet site A was characterized by much more uniform distribution of enchytraeids: the upper layer contained 8–58% of individuals, and the lowermost – between 7 and 30% (Fig. 2).

The correlation existing between enchytraeid distribution and soil moisture content of the examined sites may be expressed by the formula:

$$y = \exp (1.92 + 0.30 \ x)$$

where: y – soil moisture in % of water content, x – relative (%) abundance of enchytraeids in the upper (0–4 cm) soil layer.

The correlation coefficient $r = 0.82$ is significant at $p < 0.01$ (Fig. 3). The above formula may be useful in the future when extrapolating population abun-
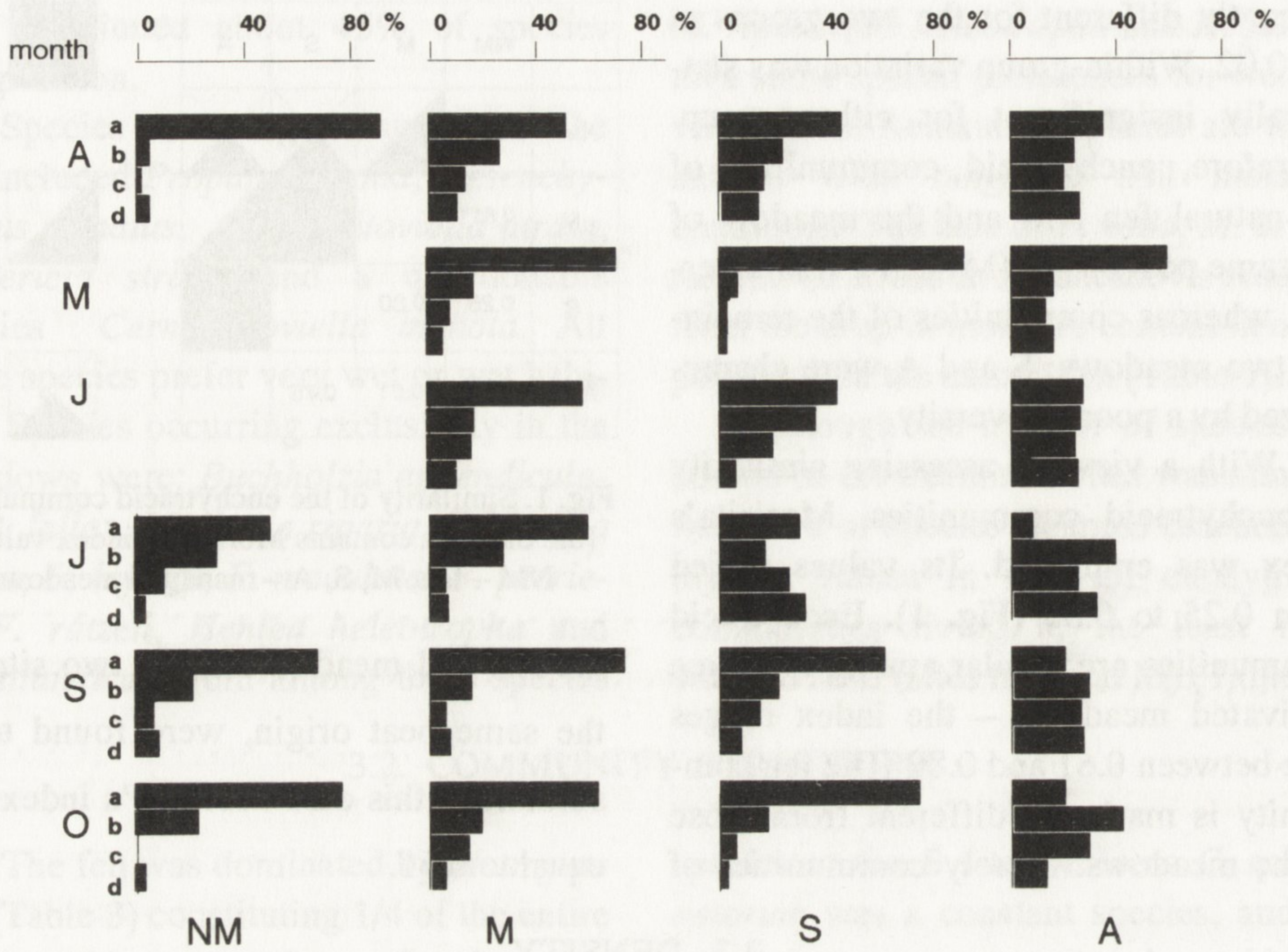
Fig. 2. Vertical distribution of enchytraeids across 4 soil layers
a – 0–4 cm, b – 4.1–8 cm, c – 8.1–12 cm, d – 12.1–16 cm of depth; NM, M, S, A – site symbols
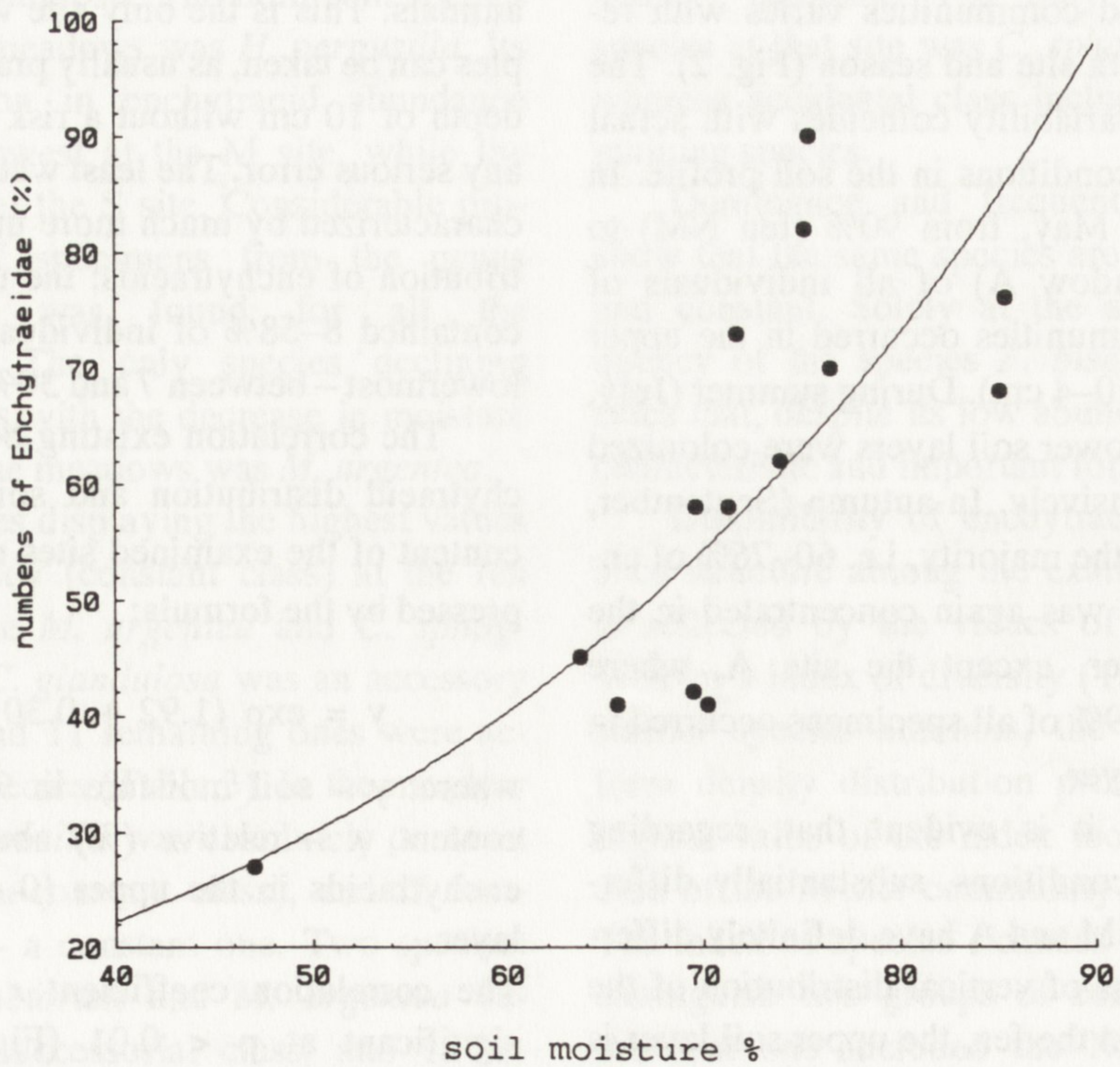

Fig. 3. The effect of soil moisture on enchytraeid occurrence in the surface soil layer (0–4 cm)

dance from the values recorded for various soil depths.

Vertical distribution of the most abundant species was analysed. At the fen NM, the dominant species *Marionina argentea* was the most numerous in solely the surface soil layer, whereas the deeper layers were populated mostly by *C. glandulosa* and *C. sphagnetorum*. All the soil layers of meadow environments were dominated by *H. perpusilla*, though *M. argentea* predominated in another layer (8–12 cm) of the site M.

3.3.2. Seasonal changes in enchytraeid numbers

During the season 1995 mean abundance of enchytraeids was from $10.6 \cdot 10^3$ indiv. m^{-2} at the fen NM to $2.7 \cdot 10^3$ indiv. m^{-2} in the meadow S.

In case of meadows it was possible to compare changes in enchytraeid numbers estimated for three different months and different years between sites of the same types (though not identical). The meadow on alder peat appeared to have the lowest enchytraeid density. Densities found for the two remaining meadow types were ca. 2 times higher (differences significant at p = 0.01) (Table 4).

Seasonal changes in enchytraeid numbers are greater than the between-year variation. The fluctuations at the least wet meadow A ranged between $32 \cdot 10^3$ indiv. m^{-2} in April and $2 \cdot 10^3$ indiv. m^{-2} in August, and at the site S (where the numbers were equally variable) the respective values were $44 \cdot 10^3$ indiv. m^{-2} and $5 \cdot 10^3$ indiv. m^{-2} (Fig. 4a).

Seasonal changes exhibits similar tendencies in all the meadows. There are two peaks in abundance – in spring and

autumn though a time shift is sometimes the case. At the site A, enchytraeids occurred in greatest numbers in April and October, whereas at the other sites – in

Table 4. Mean density of Enchytraeidae $(N \cdot 10^3 \ m^{-2})$ in peat meadows in the period May–September in different sites

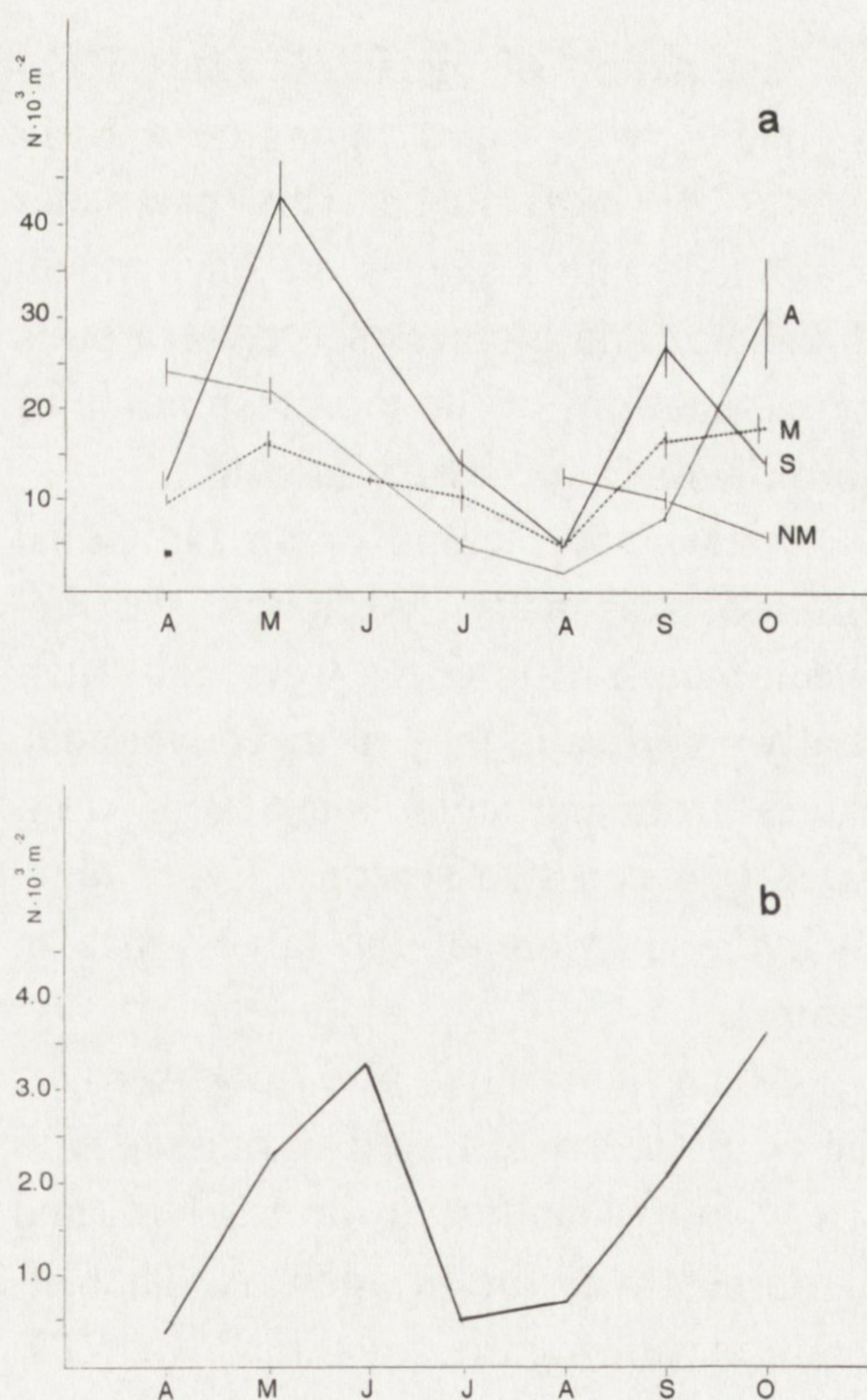| Years	Peat		
	Sedge-moss	Sedge	Alder
1981*	28.5	25.9	9.3
1994	15.4	14.8	6.9
1995	14.6	14.8	7.4

*After Kajak and Okruszko (1990).

Fig. 4. Seasonal changes in density: a – of enchytraeid communities on examined sites NM, M, S, A; b – of *M. argentea* on the managed meadow M

May and September or October (Fig. 4 a). Such a two-peak pattern is characteristic not only of the entire community but also of particular species.

Abundance dynamics of a subdominant species *Marionina argentea* at the site M also shows a tendency to have two peaks. However, the spring maximum does not overlap the peak for the entire community (Fig. 4 b).

Fluctuations of enchytraeid numbers as well as variations in their vertical distribution are in agreement with moisture conditions of the soil (Table 1). In July, when both ground water table and relative moisture content were the lowest, recorded numbers of the animals were small. Moisture contents in peat amounting to 50 and 70% delimit minimal and maximal values beyond which biological activity of the soil is being reduced (S z a n s e r 1991a). In the season 1995, soil moisture dropped below 50% solely in the meadow A. Hence, it seems that occurrence of two peaks in enchytraeid abundance is not a direct effect of summer drought.

3.4. CONTRIBUTION OF ENCHYTRAEIDS TO ORGANIC MATTER MINERALIZATION

Estimation of metabolic rate of enchytraeids was based upon mean body lengths of individuals. This parameter combined with changes in enchytraeid abundance and biomass served as a basis for calculations of the total respiration of the animals in successive months.

Mean body length of an individual differed seasonally. Although the between-month differences were not statistically significant, they recurred when the values from particular sites were compared between two seasons. Every time, enchytraeids were of the largest size in autumn.

Mean individual size reckoned for the whole season differed among the sites – it was the smallest at the fen NM, and the largest – in the meadow A. The differences were significant at the level 0.01, except for the difference between M and S sites. The differences in body size result from the fact that wet environments are preferred by small-sized species and, moreover, juveniles of large-sized species have different numbers (from 33% at the NM site to 28% at the A site when speci-

mens not larger than 2.5 mm are considered).

Enchytraeid biomass at the examined sites was small – from 73 to 277 mg dry wt m^{-2} (Table 5) and differed between the two years of observations, having been always the greatest in case of the site S. The differences in biomass were found to be even more clear-cut than those concerning enchytraeid numbers. The most remarkable between-year variation was observed in the meadow M where biomass ranged from 206 mg dry wt m^{-2} to merely 137 mg dry wt m^{-2}, for the period May-September of 1994 and 1995, respectively. This corresponds to 34–128 mg of C m^{-2} and 8–32 mg of N m^{-2} retained in biomass (Table 5). Thereby, enchytraeids retard element turnover, and thus contribute to inhibition of mineralization process.

For one of the sites – M, respiration rates in successive months of 1994 and 1995 were estimated. The values ranged between 112 ml of O_2 m^{-2} and 414 ml of O_2 m^{-2} in August and May 1995, respectively. Mean annual respiration of enchytraeids was the lowest at the fen NM

Table 5. Biomass and respiration of enchytraeids in 1995 year

	Site			
	NM	M	S	A
Mean length of individual (mm)	2.83	3.58	3.6	4.02
(s.e.)	(0.14)	(0.08)	(0.06)	(0.08)
Mean weight of individual (μg)	31.2	44.9	45.3	53.8
Biomass				
mg dry wt m^{-2}	73	178	277	276
mg C m^{-2}	34	82	128	128
mg N m^{-2}	8	20	32	31
Respiration (g C m^{-2})	1.18	1.78	2.75	2.47

where it amounted to 2.21 l of O_2 m^{-2}, while the highest value – 5.14 l of O_2 m^{-2} was found for the meadow S. These values correspond to 1.18 and 2.75 g of carbon released per m^2 of NM and S sites, respectively (Table 5), thus constituting from 0.3 to 0.4% of carbon pool mineralized annually through microbiological processes.

Nitrogen retention was 32, 31 and 20 mg m^{-2} at the S, A and M sites, respectively (Table 5). These values are equivalent to 40, 19 and 33% of daily mineralized nitrogen.

3.5. PARTICIPATION OF ENCHYTRAEIDS IN SAPROPHAGE BIOMASS

Five groups of soil saprophages including Lumbricidae, Enchytraeidae, and Collembola, saprophagous Acarina and Nematoda, were compared with regard to their biomass among the three meadows (M, S, A). All the sites are dominated by earthworms. Participation of enchytraeids in biomass of the community ranged between 2% in the meadow M to 11.2% in the meadow A (Fig. 5).

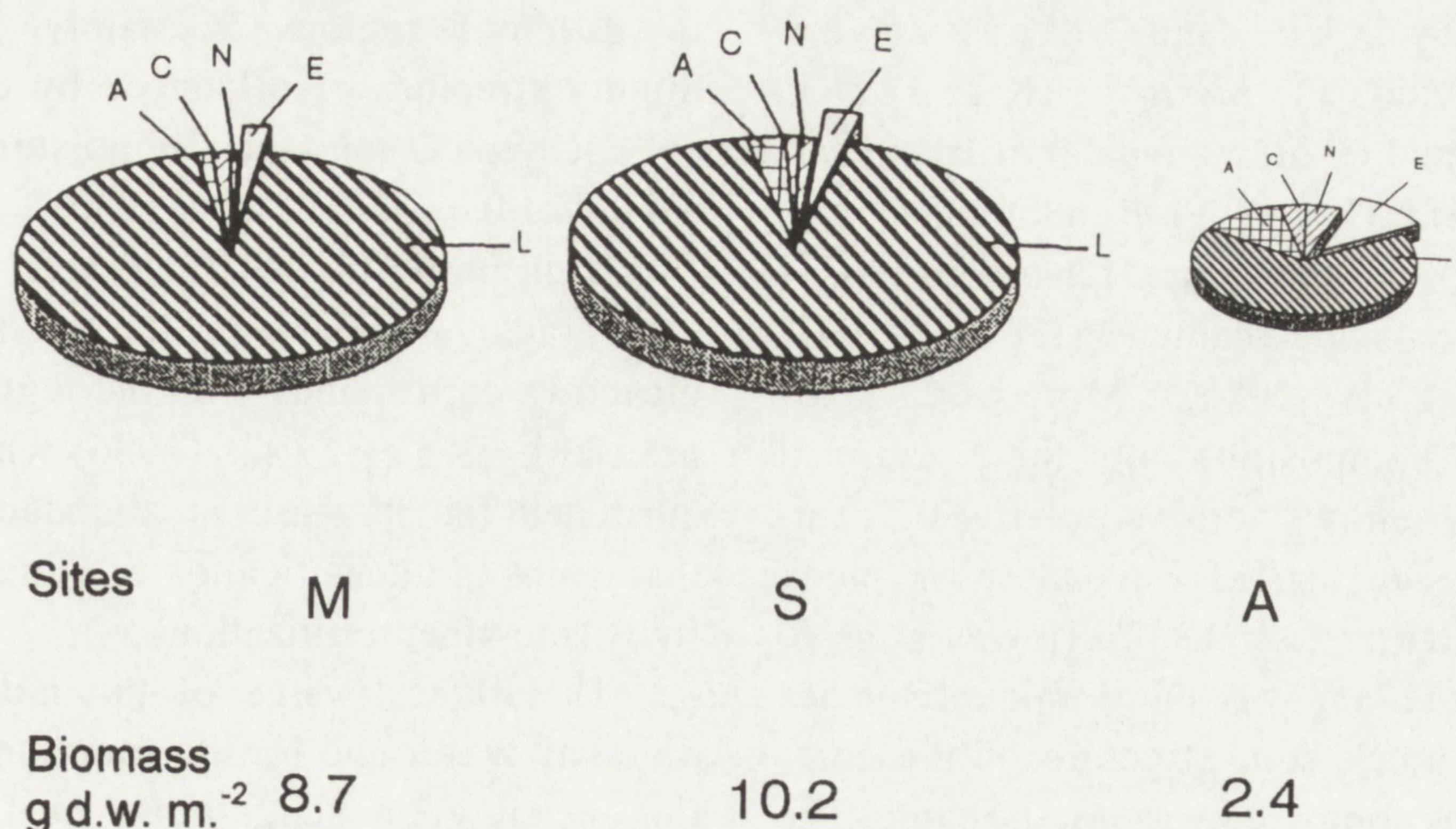Sites | M | S | A

Biomass g d.w. m.$^{-2}$ | 8.7 | 10.2 | 2.4

Fig. 5. Participation of selected saprophage groups in biomass on managed meadows
A – Acarina, C – Collembola, E – Enchytraeidae, N – Nematoda, L – Lumbricidae

An apparent increase in percentage contribution of Enchytraeids in the order of increasing soil moisture is brought about by not only the increase in enchytraeid biomass but also by the drop in earthworm biomass. The respective values of Lumbricidae : Enchytraeidae biomass ratio found for particular sites were as follow: M – 46, S – 34, A – 6, NM – 3. The two smallest values resulted from the drop in earthworm biomass; the biomass being equal to merely 255 mg dry wt m^{-2} at the fen (M a k u l e c 1991), and in the least wet meadow – to 1660 mg m^{-2}, i.e. 5 times less than the values found for the two remaining meadows (Makulec, unpublished data). Enchytraeid biomass at the latter site is comparable to that in the meadow S. Regarding the two groups of similar importance for soil processes, enchytraeids appeared to exist more successfully under critical (minimal and maximal) moisture conditions.

4. DISCUSSION

The list of enchytraeids occurring at the natural sedge-moss fen contains more species than having been recorded in course of former studies. Eleven species have hitherto been evidenced to occur in peatlands of Poland. This number is likely to result from the lack of quantitative studies in the past, which normally have enabled to recognize species composition more completely. Species noticed previously in peatland environments include *Cognetia sphagnetorum*, *Fridericia striata*, *Henlea nasuta*, *H. ventriculosa* (M o s z y ń s k i and M o s z y ń s k a 1957) and *F. bisetosa* (K a s p r z a k 1977), and *C. atrata* typical of Irish peatlands (H e a l y 1979). Remaining species evidenced at the natural fen are also associated with wet habitats (H e a l y 1979, K a s p r z a k 1986). Moreover, taxonomic composition of the examined meadow shows some similarity of communities to that of a meadow on muck soil (K a s p r z a k 1982). However, as *B. appendiculata* was the dominant species in the muck soil, structure of the communities compared was not the same. The differences in species composition and community structure could be brought about by numerous factors like intensity of muck-forming process, land use or geographical position of the meadows.

On the other hand, it seems that the core of enchytraeid communities in peatlands consists of species that have similar environmental requirements and belong to the same genera. P e a c h y (1963) and S t a n d e n (1980) evidenced *C. sphagnetorum* and species from the genera *Marionina*, *Cernosvitoviella* and *Mesenchytraeus* to occur in England. This would suggest alike pattern of community structure in habitats of the same type located in different regions. Certainly, community structure is influenced by different enchytraeid tolerance to moisture and acidity of the soil (H e a l y 1980).

High proportion of *Fridericia sp.* in enchytraeid numbers in the examined meadows corresponds with the regularity noticed by K a s p r z a k (1986) who has attributed the increase in abundance of that genus to intensification of human activity (mowing, fertilization).

The highest value of the index of diversity was found for the community of the meadow on sedge-moss peat (M). Hence, excess moisture in the soil of a peatland NM is likely to reduce fauna diversity. In habitats being affected by

anthropogenic pressure, a temporary increase in biodiversity has frequently occurred that consists in expansion of species having wide range of tolerance to environmental factors. At the same time, species of a narrower tolerance range typical of peatland habitats are being suppressed. In the material presented, almost all species found at the fen and meadows are characterized by wide tolerance range. Therefore, an explanation of the diversity rise at the site M should rather be suspected in the fact that drainage had improved soil moisture conditions. Reduced diversity of enchytraeid communities of the two remaining meadows indicates that overdrying and progressive peat decline has lead to some unification of fauna.

A comparison of similarity between enchytraeid communities shows their structures to be greatly affected by the type of agrotechnical management employed: despite moisture differences, the meadows resemble each other rather than the fen. Peat origin (or ecosystem history) plays also some role, as its influence is still noticeable after 30 years.

Greater abundance of enchytraeids in deeper soil layers observed during summer has commonly been elucidated by increased mortality of the animals in the surface layer or by their migrations deep into the soil profile (S p r i n g e t t et al. 1970, H e a l y 1987, D i d d e n 1993). In the meadows examined, the latter phenomenon took place. This is evidenced by the autumnal increase in enchytraeid abundance being accompanied by body weight increase, not a drop, which could have taken place in case of rapid reproduction.

Mean densities of enchytraeids recorded at the sites examined correspond with the values found formerly for peat meadows of Biebrza river basin and ranging between $6.1 \cdot 10^3 - 7.6 \cdot 10^3$ indiv.

m^{-2} in dry meadows and $13.9 \cdot 10^3 - 56.9 \cdot 10^3$ indiv. m^{-2} in wet ones (W a s i l e w - s k a et al. 1985).

Comparing the results obtained by various authors, D i d d e n (1993) reported enchytraeid densities of meadows and peatlands to be between 1.4 indiv. 10^3 m^{-2} and 145 indiv. 10^3 m^{-2}. Enchytraeid abundance in the examined sites fall within the range of low and moderate levels.

Two-peak dynamics of enchytraeid density has manifold been described (D a s h and C r a g g 1972, K a s p r z a k 1982, P h i l l i p s o n et al. 1979). The seasonal variability in enchytraeid numbers is undoubtedly influenced by fluctuations of soil moisture and temperatures. This is however compensated by ecophysiological adaptations of enchytraeids, such as diapause independent of moisture or temperature fluctuations (apart from facultative diapause), or ability to protect cocoons against overdrying found for some species (D i d d e n 1993, D ó z s a - F a r k a s 1973). Two-peak dynamics of abundance occurring also within other saprophages (earthworms) may be associated with regularities in input and decomposition of organic matter.

Share of enchytraeid respiration in organic matter mineralization was the highest on meadows exhibiting moderate or high rate of mineralization (S and A sites) and amounted to ca. 0.3 and 0.4% of primary production. D i d d e n (1993) reported that this may be as much as 0.3–5.2% depending on habitat: 2% – in a peatland, and 2.8% – in a sedge meadow. Like other soil animals, enchytraeids may play a significant role in nutrient cycling. The role is not however restricted to their contribution to biomass retention or mineralization measured by respiration. A b - r a h a m s e n (1990) revealed that in the presence of *C. sphagnetorum* in mor

humus, nitrogen mineralization increased by 18% due to an additional stimulation of soil microorganisms.

In the examined meadows, enchytraeids contributed less, and earthworms – more to saprophage biomass than it would result from the literature data. A comparison of soil saprophage biomass made by Cragg (1961) between different peatlands revealed that enchytraeids constituted from 68 to 99% of biomass, whereas earthworms – scarcely 1%. Participation of enchytraeids in biomass found for an Irish peatland Glenamoy reached over 40%, and in a peat meadow – about 30%. Earthworms were lacking in that peatland, whereas their contribution in the meadow was about 20%, i.e. less than that of enchytraeids (Moore et al. 1975). The sources of the differences should be suspected in dissimilarity of soil conditions between the sites compared. In Poland, the examined fen is characterized by more favourable moisture conditions and acidity of the soil, and none of the above factors exclude earthworms having been here fairly abundant (Makulec 1991).

Hence, as enchytraeids are more successful than earthworms when coping with critical soil conditions, they play a compensatory role. This is evidenced by a gradual decrease in the ratio of earthworm to enchytraeid biomass with decreasing moisture sequence of the meadows.

It has been found that in case of drained peatlands of the Biebrza valley, intensification of the mineralization process of organic matter is accompanied by reduction in individual body size of numerous mesofauna groups. An increase in % proportion of Collembola and Acarina individuals smaller than 5 mm, and Diptera larvae smaller than 2 mm has been observed (Kaczmarek 1991 b, Kajak and Okruszko 1990). Moreover, mean weight of Nematoda living here has decreased (Wasilewska 1991). The decreasing proportion between earthworms and enchytraeids in the managed meadow M, S and A is in good agreement with the tendency described: the more intensive mineralization, the smaller organisms are involved. However, within the enchytraeid community one can observe the opposite. Mean size of individuals, and consequently such parameters as metabolic rate, growth rate, i.e. indirectly the rate of matter turnover, decrease with increasing rate of organic matter mineralization.

That slightly slower matter turnover brought about by the increase in size (and supposedly – longevity) of enchytraeids, as well as elevated significance in element retention due to the biomass increase – are a measure of real importance of that group of animals in inhibition of peat mineralization process. Thereby, the animals play a significant role in delaying soil degradation in peat meadows subjected to rapid mineralization.

5. CONCLUSIONS

1. Despite number of species at the examined sites was similar, both taxonomic composition and community structure exhibited certain differences. The fen was dominated by *Marionina argentea*, whereas the managed meadows – by *Henlea perpusilla*.

2. Considerable similarity among enchytraeid communities of the three managed meadows indicates that community

structure is greatly affected by the type of agrotechnical management and soil drainage.

3. An influence of peat origin on the communities is still noticeable after 30 years. This is testified by similarity between communities of the fen and the meadow of the same peat origin.

4. Reduced species diversity found in managed meadows accounts for unification of fauna affected by unfavourable conditions (drainage).

5. Correlation between abundance of enchytraeids inhabiting the surface layer of the soil (x) and soil moisture content (y) figured out for all the examined sites was expressed by the formula:

$$y = exp \, (1.92 + 0.03 \, x).$$

6. Contribution of enchytraeids to the mineralization process in the sites studied was low due to relatively small enchytraeid numbers and biomass.

7. Enchytraeids exist more successfully under critical soil conditions, this being testified by a gradual decrease in the ratio of earthworm/enchytraeid biomass with the decrease in soil moisture of the meadows. Thus, the group plays a significant role in delaying soil degradation in dry peaty meadows. Owing to the slower matter turnover and the increase in enchytraeid biomass, their role in element retention and inhibition of peat mineralization is being increased.

6. SUMMARY

Species composition, community structure and changes in densities of enchytraeids in four sites in peatland area of old Biebrza river valley were investigated. One of the sites was a natural fen (NM), the three others included reclamed grasslands (M, S, A) having been managed for 30 years. There are located on peat of different origin and, therefore, of different moisture contents and mineralization rates of organic matter (Tables 1 and 2). The soil of the M site, alike that of the natural fen, originates from sedge-moss peat, S site – from sedge peat, and A site – from alder peat.

The natural fen was dominated by the hygrophilous species *Marionina argentea*, whereas the three managed meadows – by *Henlea perpusilla* (Table 3). The index of diversity allowed to distinguish two groups of communities: NM and M sites having a richer diversity, and S and A sites having a poorer diversity. The meadow communities appeared to be similar to each other, while the fen community remained somewhat specific in that it was akin to

solely the meadow of the same peat origin (Fig. 1).

Vertical distribution of enchytraeids was studied in four consecutive 4 cm soil layers (Fig. 2). It was found to be correlated with soil moisture. This may be described by the formula: $y = exp \, (1.92 + 0.03 \, x)$, where y – enchytraeid abundance in the surface layer of the soil, x – soil moisture content expressed in % (Fig. 3).

Seasonal changes in enchytraeid numbers exhibited a two-peak pattern (Fig. 4). Mean number of enchytraeids in 1995 ranged from $10.6 \cdot 10^3 \, m^{-2}$ at the fen NM to $27.7 \cdot 10^3 \, m^{-2}$ in the meadow S. After recalculation these numbers into biomass, the respective values were 73 and 277 mg dry wt m^{-2} (Table 5).

Contrary to the rate of organic matter mineralization, mean individual size as well as biomass of all enchytraeids of the managed meadows increased from the wet site M to the dry one A, resulting in the increase in importance of that group for element retention.

7. POLISH SUMMARY

Badano skład gatunkowy, strukturę zgrupowań i dynamikę liczebności wazonkowców na czterech stanowiskach położonych w pra-

dolinie Biebrzy (północno-wschodni rejon Polski). Jedno z nich to naturalne torfowisko niskie (NM), 3 pozostałe to łąki zmeliorowane i zagos-

podarowane przed 30 laty (M, S, A). Położone są one na torfach o różnym pochodzeniu i tym samym różnej wilgotności i różnym tempie mineralizacji materii organicznej (tab. 1 i 2). Gleba stanowiska M pochodzi tak jak na torfowisku naturalnym z torfu mechowiskowo-turzycowiskowego. S – turzycowiskowego, A – olesowego.

Na torfowisku naturalnym dominuje wilgociolubny gatunek *Marionina argentea*, a na wszystkich uprawianych łąkach *Henlea perpusilla* (tab. 3). Wskaźnik różnorodności gatunkowej dzieli zgrupowania na dwie grupy: bardziej różnorodnych na stanowiskach NM i M i mniej różnorodnych na stanowiskach S i A. Zgrupowania z łąk uprawianych okazały się podobne do siebie, a zespół z torfowiska zachował pewną specyfikę wykazując podobieństwo tylko do zgrupowania z łąki uprawianej o tym samym podłożu (rys. 1).

Rozmieszczenie pionowe wazonkowców badane było w 4 kolejnych 4 cm warstwach gleby (rys. 2). Wykazuje ono zależność od wilgotności gleby. Korelację tę można opisać równaniem: $y = \exp(1.92 + 0.03\ x)$ gdzie: y – liczebność wazonkowców w górnej warstwie gleby, x – wilgotność gleby wyrażona w procentach (rys. 3).

Dynamika liczebności wazonkowców ma przebieg dwuszczytowy (rys. 4). Średnie liczebności w 1995 roku osiągają wartości od $10.6 \cdot 10^3\ m^{-2}$ na torfowisku NM po $27.7 \cdot 10^3\ m^{-2}$ na łące S, co można przeliczyć na wartości biomasy równe 73 i 277 mg s.m. m^{-2} (tab. 5).

Średnia wielkość osobnika podobnie jak biomasa wszystkich wzonkowców na łąkach uprawianych rosną od łąki wilgotnej M do suchej A, przeciwnie niż tempo mineralizacji materii organicznej, zwiększając tym samym znaczenie tej grupy w retencji pierwiastków.

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