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ENCHYTRAEIDAE (OLIGOCHAETA) OF FOREST ECOSYSTEMS

I. DENSITY, BIOMASS AND PRODUCTION*

ABSTRACT: In the two-year studies, the species composition was determined and the changes in density and biomass were analysed for Enchytraeidae inhabiting four forest ecosystems. In all these ecosystems Cognettia sphagnetorum accounted for 68 to 98% of the total density and for 71 to 98% of the total biomass of this group. Production of the dominant species and of the species sexually reproducing was estimated. In general, C. sphagnetorum produced biomass of an energy content ranging from 17.3 to 94.4 kJ · m^{-2} · $year^{-1}$, depending on the season and plant community. The P : B ratio for this species varied from 2.4 to 3.8.

KEY WORDS: Forest, soil, Enchytraeidae, soil invertebrates, production.

C o n t e n t s

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1. INTRODUCTION

The stream of energy flowing through a population is a frequently used index of the role of animals in an ecosystem. This method enables us to recognize the main pathways of energy flux, to estimate the ecological efficiency, and it also is a good starting point for experimental studies.

In contrast to other saprophages, there are no such analyses for enchytraeids. The studies carried out so far have mostly been concentrated upon the numbers and biomass of this group in different ecosystem types (Nielsen 1955, O'Connor 1957, 1963, Springett 1963, Abrahamsen 1969, 1970, 1972, Möller 1969, Dash and Cragg 1972, Dozsa-Farkas 1973b). Few papers deal with the respiratory metabolism of free-living populations (Nielsen 1961, O'Connor 1963, Persson and Lohm 1977, Phillipson et al. 1979). So far only one author has estimated population production of two enchytraeid species inhabiting blanket bog soil (Standen 1973).

In view of such a poor state of knowledge, it seemed to be reasonable to estimate the contribution of this group of saprophages to energy transformation within an ecosystem. High densities and biomass of enchytraeids in most of their habitats suggest that this is an important group, so it cannot be neglected in the studies on energy budget of both soil and the whole ecosystem.

2. STUDY AREA

The study was carried out from May 1976 to May 1978 in four forest associations of the Kampinos National Park, such as a flood-plain ash-alder carr - Circaeo-Alnetum (Oberd. 1953), an oak-hornbeam forest - Tilio-Carpinetum (Traczyk 1962), a pine-oak forest - Pino-Quercetum (Kozłowska 1926), and a pine forest - Vaccinio myrtilli-Pinetum (Kobendza 1930). The first three ecosystems were located close to each other on a 4-ha island surrounded with a bog alder forest, while the pine forest covered a wide dune belt at a distance of about two kilometres northwards. All these communities grow in the ice-marginal valley of the Vistula on alluvial deposits of a texture of loose sands (Czerwiński, Roo-Zielińska and Czerwińska 1974). The basic characteristics of these ecosystems are set in Table I.

The ash-alder carr covered the soils dominated by rich muck black earth with very good water relations. Due to a high level of the accumulation of carbon and nitrogen in the biomass of plants and heterotrophs, and also because of a rapid litter decomposition and small C : N ratio in soil and litter, this community belongs to the richest ones.

The pine-oak and pine forests, in contrast to the ash-alder forest, were very poor in nutrients, the C : N ratio in litter was low, the decomposition rate of litter was slow, the litter was poor in nitrogen. They covered podzolic soils with a low water table so that top soil layers were seasonally overdried, particularly in summer. The oak-hornbeam forest occupied an intermediate position in this series.

The field studies were regularly continued in the period from May 1976 to May 1978. The material collected over this period was classified to two periods not coinciding with the calendar year. The first period extended from May 1976 to the end of April 1977. It has been called period I. The second period, called period II, extended from May 1977 to early May 1978. This division is based

Table I. Some characteristics of the forest ecosystems under study

Characteristics	Circaeo-Alnetum	Tilio-Carpinetum	Pino-Quercetum	Vaccinio myrtilli-Pinetum	Author
	black earths	brown soils	podzolic soil moderately podzolized	podzolic soil moderately gleyed	Traczyk and Traczyk (1965), Czerwiński, Roo-Zielińska and Czerwińska (1974)
pH_{H_2O} in soil layer 10 cm deep	5.5	4.0	4.1	3.9	author's data
Mean water table in cm	32	59	105	-	J. Matuszkiewicz (unpublished data)
Leaf fall biomass in g per m^2	413.0	280.5	273.8	227.2	Zimka and Stachurski (1976)
Energy content of leaf fall in kJ per m^2	8120.7	5357.0	5365.8	4877.6	
N content in leaf fall in g per m^2	9.79	2.79	2.49	1.32	
C : N of leaf fall	20.0	47.4	53.0	86.9	
C : N of soil	12.6	11.5	7.7	7.7	Stachurski and Zimka (1975)
Coefficient of litter decomposition	1.2	0.7	0.5	0.2	
Dehydrogenase activity in µl H per 10 g of soil from 0-5 cm layer	337	271	129	64	K. Chmielewski (unpublished data)
Urease activity in mg N per 100 g of soil from 0-5 cm layer	31.2	19.7	16.9	17.2	

on the natural rhythm of processes occurring in these ecosystems, and on seasonal changes in climatic conditions, especially in humidity. The sum of precipitation in the growing season from April to October was 272.8 mm in period I and 554.2 mm in period II. The study was conducted during the growing season and in autumn--winter period. Winter samples were taken because enchytraeids are frost tolerant (D o z s a - F a r k a s 1973a), and because temperatures above zero centigrades are frequent in winter in the top soil layer, particularly under a deep snow cover.

3. METHODS

3.1. Density

Sampling was made every two months, on the average. Each time 30 soil cores 10 cm deep and 100 cm^3 in volume were taken. A total of 1530 soil cores were taken, from which almost 52 thousand individuals were collected.

The O'C o n n o r (1955, 1962, 1971) method was applied to extract enchytraeids. The funnels 15 cm in diameter were used for 4-hour periods. The temperature of the samples gradually increased by about 45°C. All the individuals were removed, counted and preserved in acetic acid with an admixture of orcein. Then they were put on slides in glycerol with acetic acid for microscopic examination. The N i e l s e n and C h r i s t e n s e n (1959) key was used to identify enchytraeid species.

The specimens of the dominant species, Cognettia sphagnetorum, were classified to four categories: whole worms - denoted by K, worms regenerating tail fragments - denoted by P, worms regenerating head fragments - T, and worms regenerating both head and tail fragments - denoted by S. In all cases, the regenerating segments and all the body segments were counted.

The total density of enchytraeids per m^2 was calculated from the formula

$$\bar{N} = \frac{1}{n} \sum_{i=1}^{i=n} N_i \cdot 10^3 \qquad (1)$$

where $\bar{N}$ stands for density, N_i is the number of individuals per sample, and n is the number of samples.

3.2. Biomass

To estimate the biomass of enchytraeids, the relationship between the weight of live worms and the body length of preserved specimens was used (Fig. 1). This is a statistically significant relationship at 0.01 level, and it is of the form

$$y = 6.22 \cdot x^{1.55} \quad (2)$$

where y is the live body weight in µg, x is the body length of preserved specimens in mm.

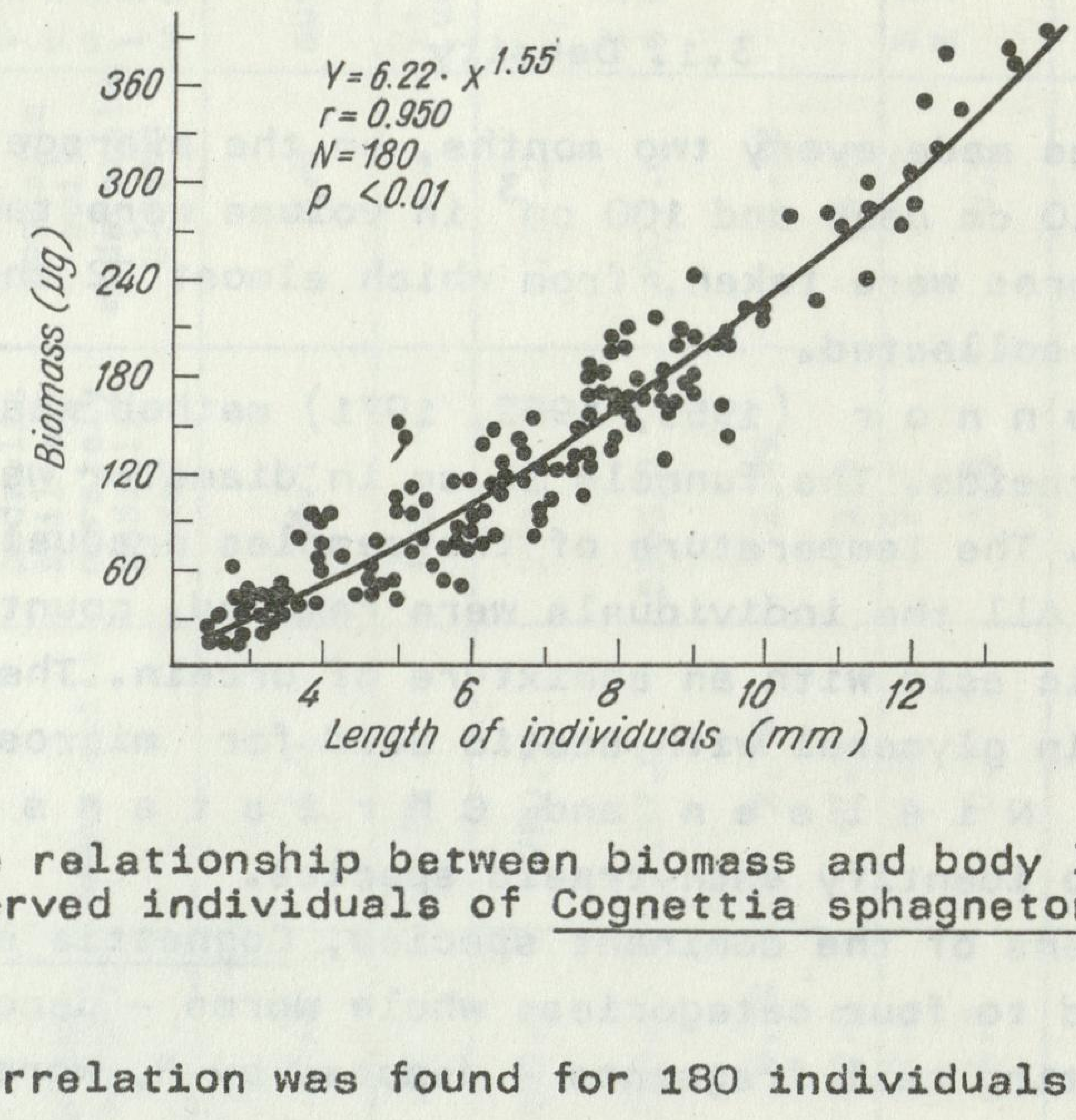

Fig. 1. The relationship between biomass and body length for preserved individuals of Cognettia sphagnetorum

This correlation was found for 180 individuals of Cognettia sphagnetorum weighed to the nearest µg and the body length of which was measured. These worms were preserved in the way described in the preceeding section.

The body length of enchytraeids was measured to the nearest 0.1 mm under a stereoscopic microscope. On each date of sampling, worms from 10 samples were measured, which makes a total of more than 14 thousand specimens.

The biomass of the enchytraeid community per m^2 was calculated from the formula

$$\overline{B} = (\overline{N}_K \overline{X}_K + \overline{N}_P \overline{X}_P + \overline{N}_T \overline{X}_T + \overline{N}_S \overline{X}_S + \overline{N}_I \overline{X}_I) \cdot 10^{-3} \quad (3)$$

where $\bar{B}$ denotes the biomass of enchytraeids in $mg \cdot m^{-2}$, $\bar{N}_K$, $\bar{N}_P$, $\bar{N}_T$, $\bar{N}_S$, and $\bar{N}_I$ are densities of particular categories of Cognettia sphagnetorum denoted by K, P, T, S and of the other species denoted by I; $\bar{X}_K$, $\bar{X}_P$, $\bar{X}_T$, $\bar{X}_S$, and $\bar{X}_I$ stand for the mean body weight of different categories of Cognettia sphagnetorum and other species in μg.

To express the biomass of enchytraeids in energy units, it was assumed that 1 g of dry tissue is an equivalent to 23784 J (S t a n d e n 1973).

Dry weight and then the energy content of the total community was calculated from formula (3), with the difference that the mean body weight has been expressed in μg dry weight. The dry body weight was calculated from the formula

$$y = -62.38 + 20.14 \cdot \ln x \tag{4}$$

where y is dry body weight in μg and x is wet body weight in μg.

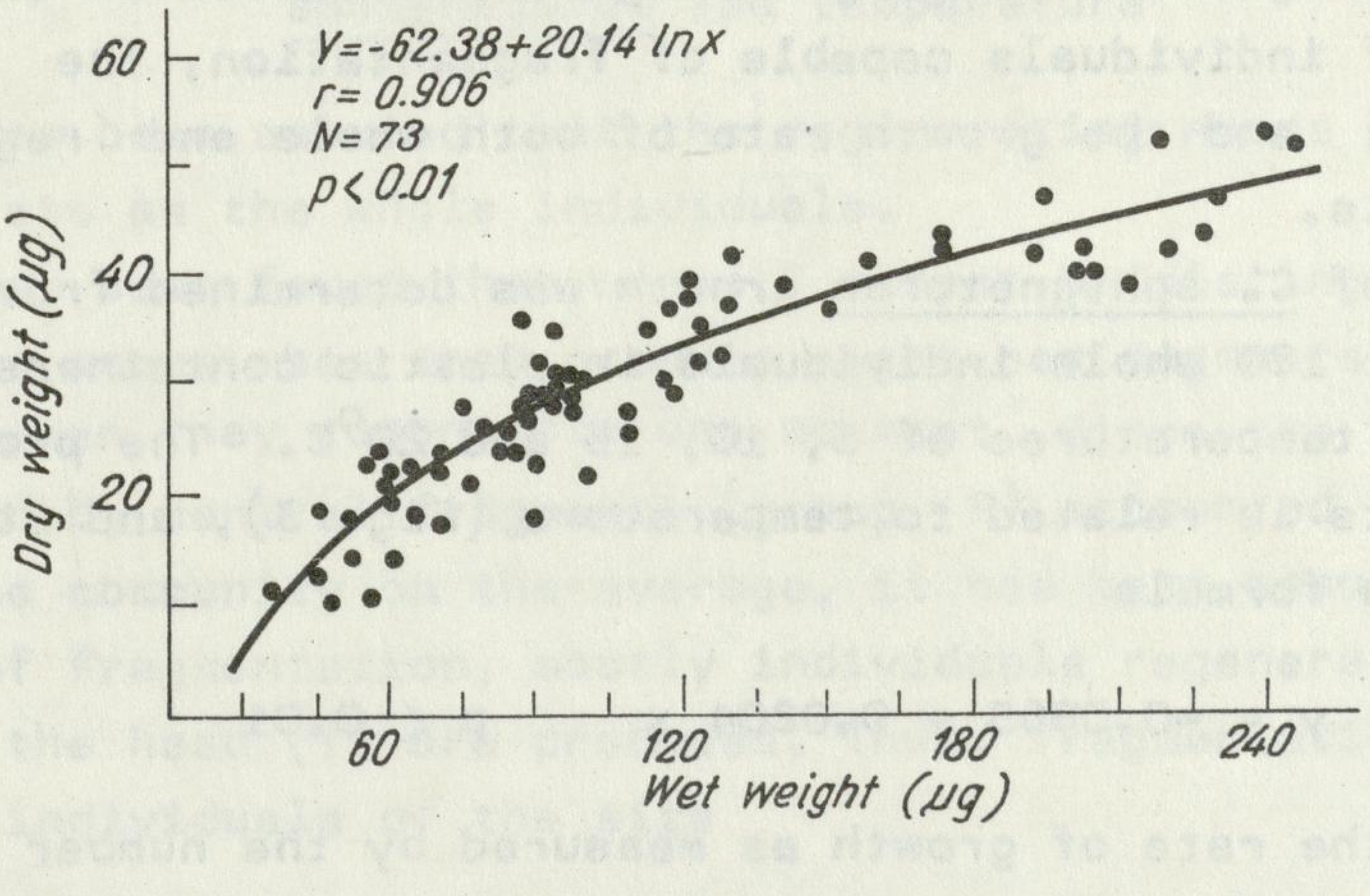

Fig. 2. The relationship between dry and wet body weights

This correlation was obtained for over 70 specimens of Cognettia sphagnetorum. They were kept for two days before weighing in containers with wet filter paper on the bottom to reduce the possible error due to the content of alimentary canal. After weighing they were dried at 85°C and weighed again (Fig. 2).

3.3. Production

To estimate production, formulas developed by Petrusewicz and Macfadyen were used (M a c f a d y e n 1967, P e t r u s e w i c z 1967, P e t r u s e w i c z and M a c f a d y e n 1970):

$$P = \Delta B + E \quad \text{or} \quad P = P_g + P_r \tag{5}$$

where P is the total population production, ΔB is an increase in population biomass, E is elimination, P_g is production due to individual growth, and P_r is production due to population reproduction.

Since enchytraeid communities consist of the species sexually reproducing in addition to the dominant species reproducing by fragmentation, distinct methods were used to estimate production.

To estimate the production of C. sphagnetorum, the procedure developed by S t a n d e n (1973), slightly modified, was used. According to this procedure such variables are needed to estimate the number of organisms passing through a population in unit time as the size of individuals capable of fragmentation, the rate of fragmentation, and the growth rate of both whole and regenerating individuals.

The rate of C. sphagnetorum growth was determined from cultures of about 180 whole individuals in plastic containers filled with soil, at temperatures of 5, 10, 15 and 20°C. The production of new segments is related to temperature (Fig. 3), and it may be described by a formula

$$y = -0.0865 + 0.0204\,x \qquad p < 0.01 \tag{6}$$

where y is the rate of growth as measured by the number of segments per day, and x is temperature.

The cultured enchytraeids differed in their original sizes but this had no noticeable effect on the rate of growth. This is indicated by the b values close to zero in the formulas

$$y = 0.0257 + 0.0004\,x \text{ at } 5^{\circ}C,\ r = 0.170 \tag{7}$$

$$y = 0.1714 - 0.0017\,x \text{ at } 10^{\circ}C,\ r = -0.359 \tag{8}$$

$$y = 0.1666 - 0.0005\,x \text{ at } 15^{\circ}C,\ r = -0.121 \tag{9}$$

$$y = 0.3688 - 0.0015\,x \text{ at } 20^{\circ}C,\ r = -0.195 \tag{10}$$

where y is the rate of growth (number of segments per day) and x is the body size as expressed in the number of segments.

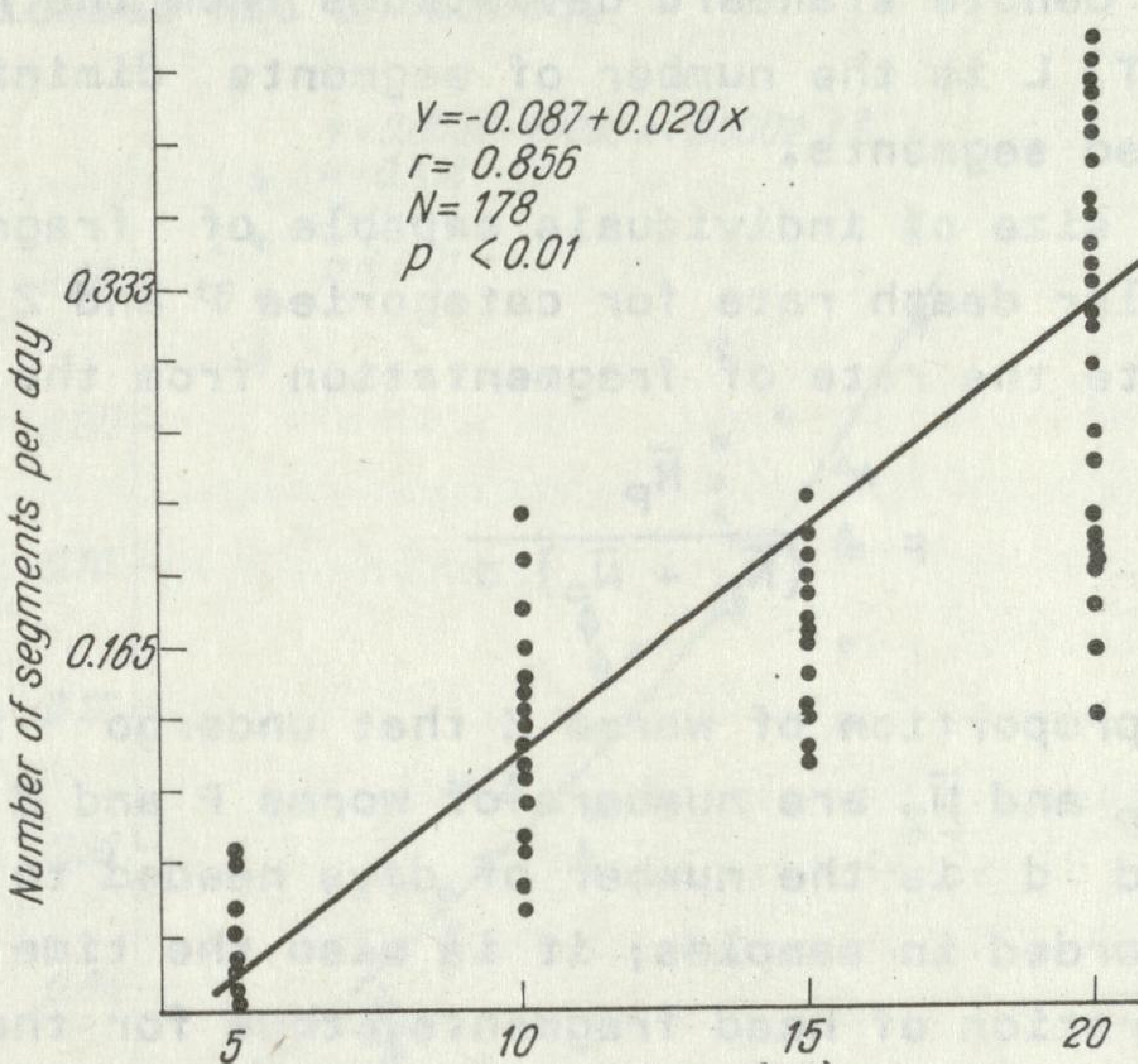

Fig. 3. The relationship between the growth rate of Cognettia sphagnetorum and temperature

It has been assumed that the regenerating worms have the same growth rate as the whole individuals.

It has been found that worms T cannot be distinguished from the whole worms when they produce eight new segments, worms of the group P when they regenerate one segment. Since the individuals represented by central fragments (group S) accounted for 2-5% of the whole community on the average, it has been assumed that as a result of fragmentation, mostly individuals regenerating the tail (P) and the head (T) are produced. Thus, fragmentation mostly occurs in individuals of the size

$$L_Z = L_P + L_T \quad (11)$$

where L denotes the number of segments diminished by the segments already regenerated.

Taking into account the scatter of the number of segments in regenerating individuals, and assuming that the longer the head fragments, the longer should be the tail fragments and conversely, the size of individuals capable of fragmentation has been calculated from the formula

$$(L_P + \delta_P) + (L_T - \delta_T) < L_Z < (L_P - \delta_P) + (L_T + \delta_T) \quad (12)$$

where δ_P and δ_T denote standard deviations from the mean body size of worms P and T, L is the number of segments diminished by already regenerated segments.

Knowing the size of individuals capable of fragmentation and assuming a similar death rate for categories P and Z, it is possible to estimate the rate of fragmentation from the formula

$$F = \frac{\bar{N}_P}{(\bar{N}_Z + \bar{N}_P)\ d} \quad (13)$$

where F is the proportion of worms Z that undergo fragmentation over one day, $\bar{N}_P$ and $\bar{N}_Z$ are numbers of worms P and Z at the time of sampling, and d is the number of days needed to produce all the worms P recorded in samples; it is also the time needed for a complete regeneration of head fragments, thus for the transition to the category K of whole individuals. The analysis of the material collected shows that this corresponds to the production of a single segment. Consequently d was calculated as the sum of increases on successive days prior to sampling (taking into account mean daily soil temperatures) till the total increase was equal to one segment.

From the mean temperature in period d and the rate of fragmentation on particular days of sampling can be calculated from the formula

$$y = -0.0038 + 0.0055\ x + 0.0002\ x^2,\ R = 0.938,\ p < 0.01 \quad (14)$$

where y stands for the rate of fragmentation F, and x is temperature (Fig. 4).

Equations (6), (12) and (14) were used to estimate the number of enchytraeids that can be produced in the population in the periods between sampling dates.

The yearly elimination rate can be calculated from the formula

$$E = \sum_{i=1}^{i=K} (\bar{N}_o - \bar{N}) \cdot i \quad (15)$$

where $\bar{N}_o$ is the expected density, $\bar{N}$ is the real density, and K is the number of days on which the number of enchytraeids was estimated. By multiplying the calculated value of E by the mean body weights of C. sphagnetorum in successive study periods, the elimination of biomass was obtained.

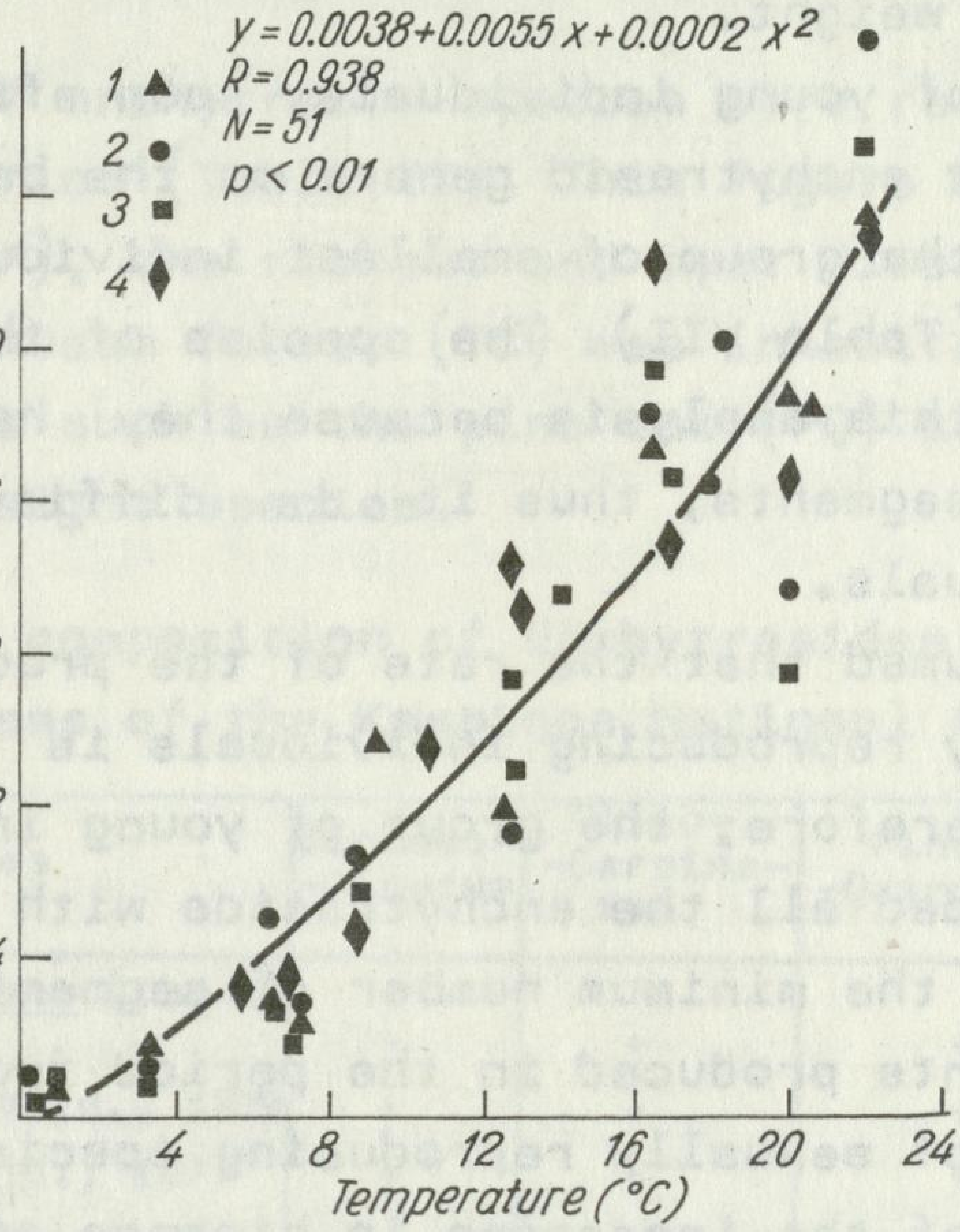

Fig. 4. The relationship between the rate of fragmentation (F) and temperature
1 - Circaeo-Alnetum, 2 - Tilio-Carpinetum, 3 - Pino-Quercetum, 4 - Vaccinio myrtilli-Pinetum

To calculate the production of sexually reproducing species, detailed data are needed on the rate of growth, longevity, number of cocoons produced, and survivorship of young and adults. The present knowledge of this subject is exceptionally poor. An additional difficulty is that in most cases young individuals can be identified only to genus. For these reasons it is very difficult to estimate production, and only very rough estimates can be obtained.

The elimination of individuals and biomass from the population of the species characterized by sexual reproduction has been calculated from the formula developed by Petrusewicz and Macfadyen (1970)

$$E = \bar{N}_{t_n} - (\bar{N}_{t_{n+1}} - V)\frac{\Delta\bar{x}}{2} \qquad (16)$$

where $\bar{N}_{t_n}$ and $\bar{N}_{t_{n+1}}$ denote the densities of enchytraeids on successive sampling dates, V is the number of young individuals, that hatched from cocoons in the period from t_n to t_{n+1}, and $\Delta\bar{X}$ is a change in mean body weight.

The body sizes of young individuals, soon after hatching, were determined for eight enchytraeid genera on the basis of the number of segments in the group of smallest individuals selected from the whole material (Table VII). The species of the genus Achaeta were excluded from this analysis because they have no visible boundaries between segments, thus it is difficult to determine the size of individuals.

It has been assumed that the rate of the production of new segments in sexually reproducing individuals is the same as in C. sphagnetorum. Therefore, the group of young individuals (V in formula (16)) included all the enchytraeids with the body size smaller or equal to the minimum number of segments increased by the number of segments produced in the period from t_n to t_{n+1}.

The production of sexually reproducing species has been calculated as the sum of the increases in biomass of eliminated individuals, survivors from t_n to t_{n+1}, and young hatched from cocoons in the same period:

$$P_g = (\bar{N}_{t_n} + \bar{N}_{t_{n+1}} - V)\ \frac{\Delta\bar{X}}{2} + V\bar{X}_V \qquad (17)$$

where P_g is the production due to individual growth, $\bar{N}_{t_n}$, $\bar{N}_{t_{n+1}}$, and V have the same meaning as in formula (16), and $\bar{X}_V$ is the mean body weight of young in time t_{n+1}.

These calculationst include the production do no of cocoons and eliminated young individuals.

The production of C. sphagnetorum was calculated from formulas (5) and (15). This method neglects the production due to individual growth, and it can be used when the body weight at hatching does not differ much from the body weight of adults (Petrusewicz and Macfadyen 1970). C. sphagnetorum meet this condition since individuals produced as a result of fragmentation are smaller by half, on the average, from whole individuals capable of fragmentation (Table V).

4. RESULTS

4.1. Species composition and dominance structure of enchytraeid communities

A total of 17 enchytraeid species were recorded during the two-year study period (Table II). This figure was found for the ash-alder carr (CA), the richest and most diversified plant community. The oak-hornbeam forest (TC) was inhabited by 11 species. The poorest ecosystems such as the pine oak (PQ) and pine (VmP) forests supported merely eight species.

Table II. Species composition of Enchytraeidae in four forest ecosystems of the Kampinos National Park

Species	Circaeo--Alnetum	Tilio--Carpine-tum	Pino--Quercetum	Vaccinio myrtilli--Pinetum
Achaeta camerani (Cogn.) 1899	+	+	+	+
A. bohemica (Vejd.) 1879	+	+	+	+
A. eiseni (Vejd.) 1877	+	+	+	+
Bryodrilus ehlersi Ude 1892	+	+	+	+
Buchholzia appendiculata (Buch.) 1862	+	+		
B. fallax (Mich.) 1887	+	+		
Cognettia glandulosa (Mich.) 1888	+			
C. sphagnetorum (Vejd.) 1877	+	+	+	+
Enchytraeus buchholzi (Vejd.) 1879	+	+	+	+
Enchytronia parva Niel. et Christ. 1959	+	+		+
Fridericia bisetosa (Lev.) 1884	+	+		
F. callosa (Eis.) 1878	+			
Fridericia sp.	+			
Hemienchytraeus bifurcatus Niel. et Christ. 1959	+	+	+	+
Henlea nasuta (Eis.) 1878	+			
H. perpusilla Friend 1911	+			
Mesenchytraeus pelicensis Niel. et Christ. 1959	+			
Total	17	11	8	8

Therefore, there is a close relationship between the species diversity of enchytraeids and the richness of the habitat. The species diversity of this group is reduced with decreasing site and biocoenotic richness. The same process has been found by G ó r n y (1975a) and K a s p r z a k (1975) in relation to single ecosystems. K a s p r z a k (1975) has recorded 25 enchytraeid species in an oak-hornbeam forest and G ó r n y (1975a) only seven species in an oligotrophic pine forest of the Kampinos National Park.

This regularity is also confirmed by data of foreign authors. A b r a h a m s e n (1972) recorded only two species in an extremely dry pine forest (Cladonio-Pinetum), N u r m i n e n (1967) recorded four species in a similar forest, while D o z s a-F a r k a s (1973b) found 21 species in a rich oak forest.

Among the enchytraeids of the ecosystems under study, a group of seven species can be distinguished which were common to all the four communities, thus they showed a high ecological tolerance. A group of six species occurred only in the ash-alder carr, which implies that they require permanently humid and rich habitat. The dominant species, Cognettia sphagnetorum, belongs to the former group.

The ash-alder carr, a very rich community in the gradient of study ecosystems, supporting a highly diversified enchytraeid community, was characterized by a relatively low dominance of C. sphagnetorum (Table III). On the average, this species accounted for 68% of the number and 74% of the biomass of the total enchytraeid community. At the same time the proportion of the dominant species in this community was most variable, ranging from 41 to 88% of the number and from 50 to 95% of the biomass of all enchytraeids. This fact is mostly related to the phenology of other species, showing sexual reproduction and temporarily rather abundant.

In the other three plant communities, the dominance of C. sphagnetorum was very high, generally more than 80%, and the range of its variability was much smaller. The highest average proportion of this species for the two study years was found in the pine forest. On some dates of sampling this was the only species occurring in this habitat. A similar phenomenon was recorded by A b r a h a m s e n (1972) in five types of pine forests of the order Cladonio-Vaccinietalia in Norway. According to this author, the proportion of C. sphagnetorum was 95-99% of the total enchytraeid community.

Table III. Mean contribution of Cognettia sphagnetorum to the number and biomass of enchytraeid communities

Study periods and variables compared		Circaeo-Alnetum	Tilio-Carpinetum	Pino-Quercetum	Vaccinio myrtilli-Pinetum
I	% N	68.2 ± 13.0 (46.0-88.1)	95.5 ± 2.4 (91.7-99.1)	93.5 ± 4.9 (82.1-97.3)	90.4 ± 11.0 (66.2-98.0)
	% B	76.6 ± 13.8 (50.3-95.1)	97.1 ± 2.5 (91.8-99.8)	94.9 ± 3.7 (86.5-98.4)	94.4 ± 7.2 (78.2-99.1)
II	% N	68.1 ± 19.3 (41.6-85.8)	94.0 ± 4.8 (86.2-98.2)	89.2 ± 6.0 (83.4-95.9)	98.6 ± 1.8 (95.5-100)
	% B	71.4 ± 17.1 (50.3-92.2)	95.3 ± 3.7 (90.8-99.3)	90.8 ± 5.4 (82.7-96.6)	98.9 ± 1.0 (98.6-100)
$\bar{x}$ I, II	% N	68.1	94.8	91.3	94.5
	% B	74.0	96.2	92.8	96.6

In the season characterized by poor moisture conditions (period I), the dominance of C. sphagnetorum was the highest in the oak-hornbeam forest. In the two poorest ecosystems, the overdrying of the top soil layer was followed by a heavy reduction of the dominant and, consequently, by an increase in the proportion of species generally occurring in deeper layers, mostly of the genus Achaeta.

In general, all the communities were dominated by C. sphagnetorum, which is of great ecological importance. Due to its way of reproduction, this species can rapidly and precisely respond to all important changes in the soil habitat. Under suitable food and moisture conditions its number can increase many times, retaining much energy and large amounts of nutrients.

No anabiosis of the type known in Lumbricidae (Górny 1975b) was found in enchytraeids. Probably their ability to migrate into deeper soil layers is also very limited. Therefore, most individuals die when the soil is overdried (Springett, Brittain and Springett 1970). The restoration of their biomass and numbers is realized by the dominant. The standing crop of other species increases due to the hatching of young from the cocoons deposited earlier, which takes more time.

4.2. Density of enchytraeids

The density of enchytraeids largely varied both over the growing season and from one study period to another (Figs. 5-8). In period I, the highest density was noted in the ash-alder carr, the richest most humid habitat. It was 25.5 thousand individuals per m^2, on the average. In the other habitats the densities were lower, and they dropped with decreasing soil moisture and fertility (Table IV). The average values were 20.8 thousand individuals per m^2 for the oak-hornbeam forest, 18.3 thousand for the pine-oak forest, and 16.8 thousand for the pine forest.

In period I (dry), the highest densities recorded in most of the study ecosystems occurred in May-June, in autumn and in winter. Only in the alder-ash carr there was no decrease in number in summer, even a maximum of almost 40 thousand individuals being reached at that period.

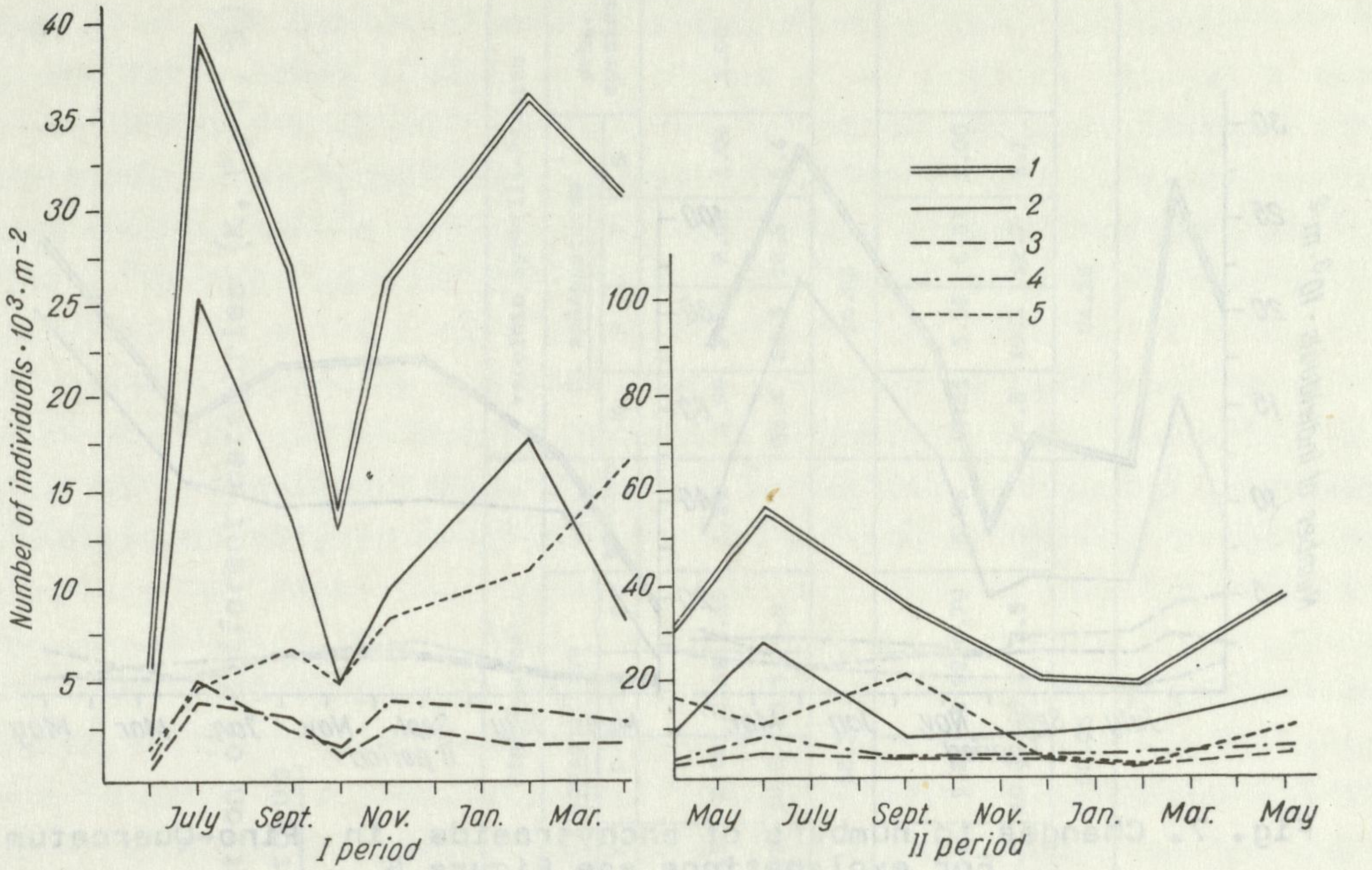

Fig. 5. Changes in enchytraeid numbers in Circaeo-Alnetum
1 - total enchytraeids, 2 - whole individuals (K) of Cognettia sphagnetorum, 3 - head fragments (P), 4 - tail fragments (T), 5 - other species

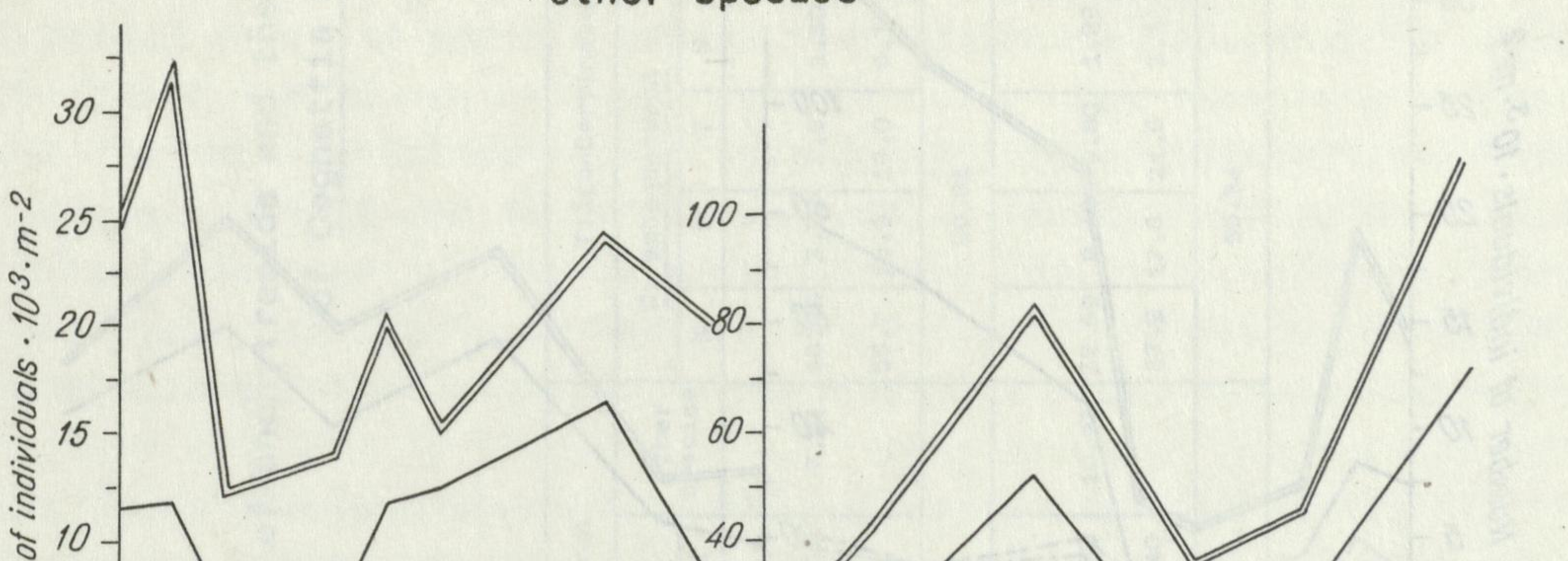

Fig. 6. Changes in numbers of enchytraeids in Tilio-Carpinetum
For explanations see Figure 5

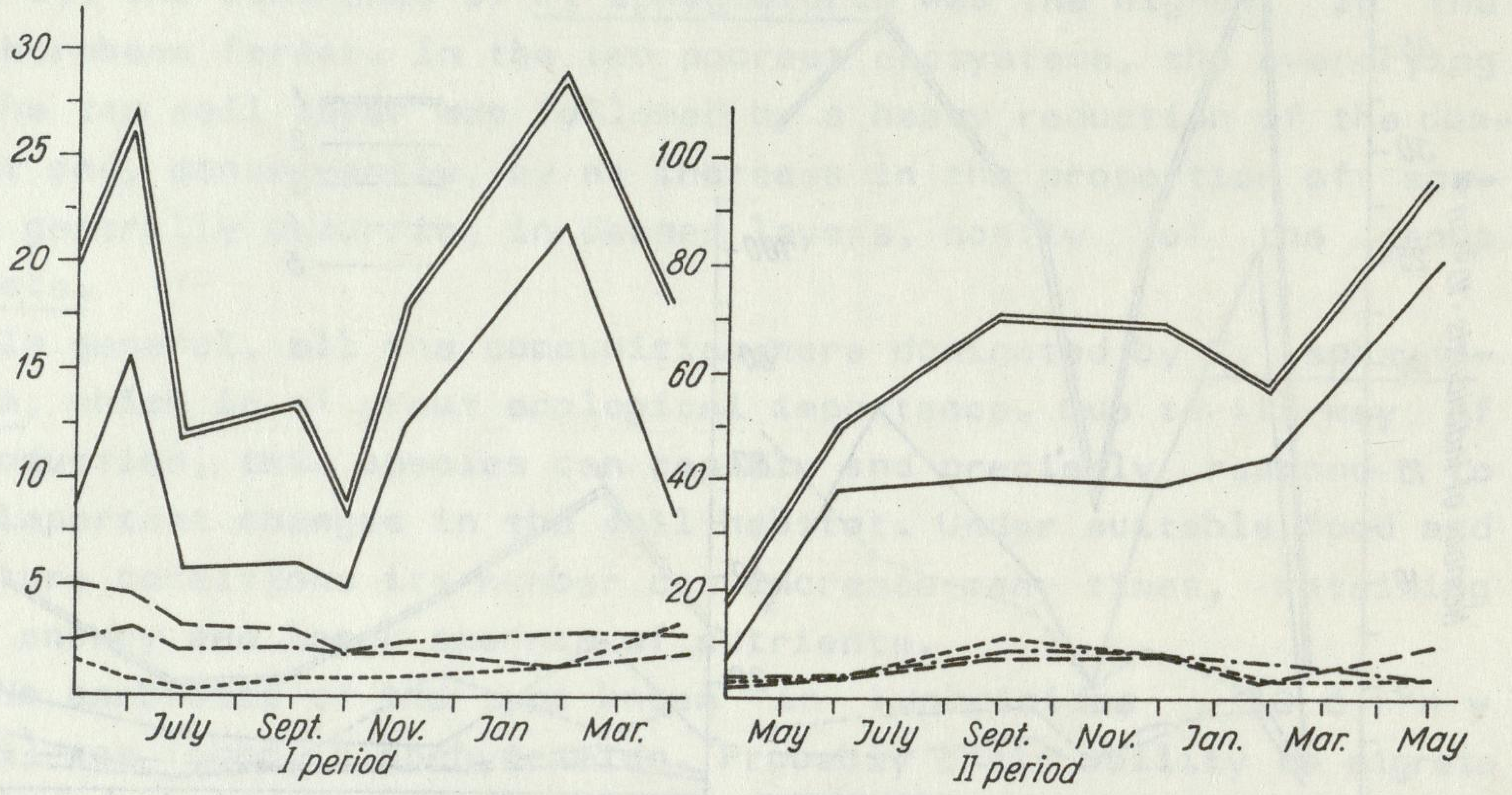

Fig. 7. Changes in numbers of enchytraeids in Pino-Quercetum
For explanations see Figure 5

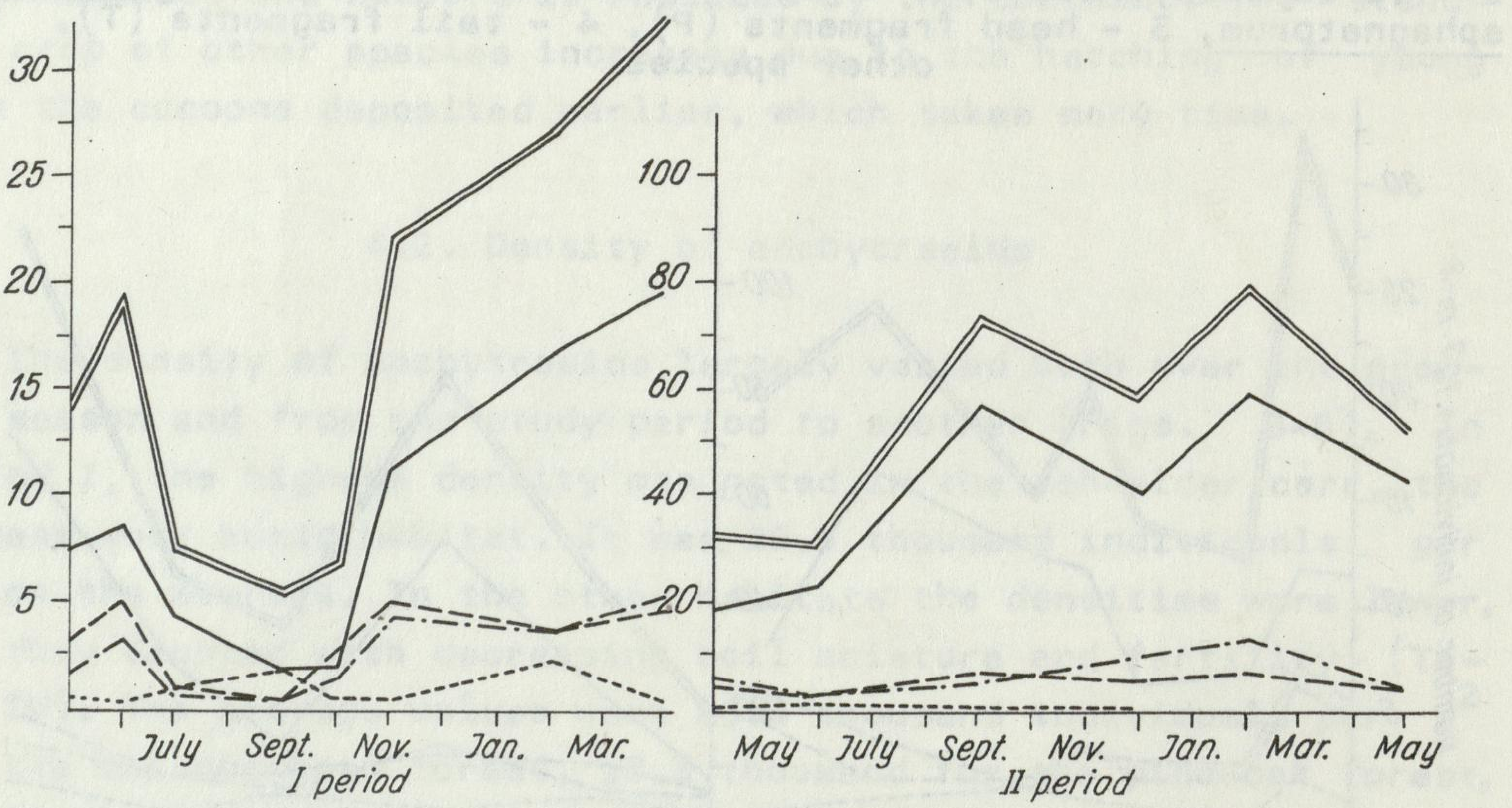

Fig. 8. Changes in numbers of enchytraeids in Vaccinio myrtilli-Pinetum
For explanations see Figure 5

Table IV. Mean densities of enchytraeids and the proportion of different categories (K, P, T, S) of <u>Cognettia sphagnetorum</u>

Study periods and variables compared		Circaeo-Alnetum					Tilio-Carpinetum					Pino-Quercetum					Vaccinio myrtilli-Pinetum				
		C. sphagnetorum				other species	C. sphagnetorum				other species	C. sphagnetorum				other species	C. sphagnetorum				other species
		K	P	T	S		K	P	T	S		K	P	T	S		K	P	T	S	
I	$\frac{\bar{N} \cdot 10^3}{m^2}$	11.82	2.25	3.01	0.62	7.83	10.90	3.76	3.87	1.30	0.96	10.52	2.96	2.51	1.16	1.19	8.99	3.18	2.60	1.06	1.00
	%	63.3	13.6	19.0	4.0		55.7	18.9	19.0	6.3		58.9	18.8	15.5	6.8		55.4	21.3	16.8	6.4	
	$\bar{x}$	25.54					20.81					18.34					16.83				
II	$\frac{\bar{N} \cdot 10^3}{m^2}$	12.57	3.60	4.89	1.50	10.93	32.69	9.40	9.80	1.29	3.14	42.26	5.81	5.92	0.79	5.86	40.61	5.36	6.83	1.00	
	%	54.0	17.1	22.5	6.40		57.2	17.8	21.8	3.1		74.2	10.8	12.5	2.5		74.6	10.3	12.7	2.3	
	$\bar{x}$	33.50					56.34					60.65					54.32				

In period II (wet), the changes in densities did not follow such a regular pattern as in period I. A highest density of about 111 thousand individuals per m^2 was reached in the oak-hornbeam forest early in May of 1978. The highest mean densities occurred in the pine-oak forest, where 60.6 thousand per m^2 were noted, than there was the oak-hornbeam forest with 56.3 thousand per m^2 and the pine forest with 54.3 thousand per m^2. In all the ecosystems, the mean densities in period II were from 1.3 (ash-alder carr) to 3.3 (pine-oak forest) times higher than in period I. In all the habitats, except for the ash-alder carr, even the lowest density recorded in period II was higher than the peak density in period I. Relative changes in densities were rather low, and no distinct spring and autumn maxima were found. A slight reduction in number was recorded in winter of 1977, mostly in December. This was related to low temperatures and absence of snow cover. The densities in the ash-alder carr in period II were the lowest as compared with those in the other habitats, this being an opposite situation to that in period I.

In all the samples taken over the study period, four categories of C. sphagnetorum could be distinguished. The whole enchytraeids (K) were most abundant. The density of this group in period I reached a highest mean value of 11.8 thousand per m^2 or 63.3% of the total population of this species in the ash-alder carr. The lowest density of almost 9 thousand per m^2 or 55.4% of the population was recorded in the pine forest (Table IV). The densities in the oak-hornbeam and pine-oak forests had intermediate values of 10.9 thousand and 10.5 thousand per m^2, that is 55.7 and 58.9% of the population, respectively.

In period II the average density markedly increased and the proportion of whole individuals changed. Only in the ash-alder carr, where the mean numbers slightly increased, the proportion of whole worms in the C. sphagnetorum population was reduced. In the pine forest, the mean density increased 4.5 times, and as a result this category reached more than 74% of the dominant population. In the oak-hornbeam and pine-oak forests, the average density increased less, three and four times, respectively.

Since whole individuals largely predominated the enchytraeid community, the changes in the density of this category in the two study periods were parallel to changes in the total density, and they show the regularities described at the beginning of this section (Figs. 5-8).

The numbers and proportions of the individuals regenerating various body parts followed different patterns.

During period I the highest densities of forms regenerating their heads or tails were observed in May-June. A distinct summer reduction in their number was recorded in the oak-hornbeam and dry pine forests. In the other communities they maintained a relatively stable level, showing only small fluctuations. The mean number of enchytraeids regenerating the tail (P) ranged from 2.2 thousand (ash-alder carr) to 3.7 thousand per m^2 (oak-hornbeam forest), and those regenerating the head (T) from 2.5 thousand (pine-oak forest) to 3.8 thousand per m^2 (oak-hornbeam forest). In general, in period I the regenerating individuals accounted for 32.6% (ash-alder carr) to 38.1% (pine forest) of the C. sphagnetorum population.

In period II, the density of regenerating individuals increased. This increase was most pronounced in the oak-hornbeam forest and the smallest in the ash-alder carr. Mean numbers of category P ranged from 3.6 thousand per m^2 (ash-alder carr) to 9.4 thousand (oak-hornbeam forest), and the mean numbers of category T ranged from 4.9 thousand per m^2 (ash-alder forest) to 9.8 thousand (oak-hornbeam forest).

The way of reproduction of C. sphagnetorum, described in section 3.1, quarantees the production of an equal number of P and T individuals as a result of fragmentation. There are differences, however, in the size of regenerated parts. This size is much greater for category T, thus it can be expected that this category will be more abundant in samples.

In period I, mean numbers of enchytraeids regenerating the head were higher as compared with those regenerating the tail only in rich, wet habitats (ash-alder carr and oak-hornbeam forest) (Table IV). In the poor and dry pine forest and in the pine-oak forest an opposite situation was observed - individuals regenerating tail outnumbered those regenerating the head.

In period II, the individuals regenerating the head outnumbered those regenerating the tail in all the ecosystems. This situation was maintained over the whole sampling period (Figs. 5-8).

When the data for two years are compared, a considerable effect of soil moisture can be found. The sums and distribution of precipitation can be a good index of soil moisture. In 1977 the sum of precipitation was twice of that in 1976, and it reached 554 mm. G ó r n y (1975b) provided a good evidence for the effect of water conditions on enchytraeids. He compared the numbers of these animals in a pine-spruce forest on watered and non-watered plots, and found that the mean densities in the 0-5 cm layer on the watered plots was three times of the densities on the control plot.

Good soil moisture conditions were mostly responsible for a high increase in the density of enchytraeids in period II, as compared with period I, in all the four ecosystems. Favourable soil moisture also enhances the survival of regenerating C. sphagnetorum. The evidence for this is provided by the fact that category T outnumbered category P in period II in all the ecosystems and also in period I in the ash-alder carr and oak-hornbeam forests.

Since enchytraeids do not migrate deep into soil, each moisture deficiency is followed by their high mortality and a reduction in their total numbers (G ó r n y 1975b, S p r i n g e t t, B r i t t a i n and S p r i n g e t t 1970). This process was observed in the summer of period I. Of the four ecosystems under study, the density of enchytraeids did not decrease only in the ash-alder carr, which was permanently wet.

Minimum numbers of enchytraeids in summer were also recorded by N u r m i n e n (1967) in a pine forest, and by P e r s s o n and L o h m (1977) for abandoned fields.

In addition to moisture deficiency, another factor accounting for an increased mortality of enchytraeids in low temperature, particularly when soil is not covered with snow and temperature drops suddenly. Such a case took place in December of 1977, and it caused a decrease in the total density of enchytraeids in the ash-alder, oak-hornbeam, and pine forests.

A reduction of the density of enchytraeids in winter was found in many soils of forest ecosystems (O' C o n n o r 1957, N u r m i n e n 1967, D a s h and C r a g g 1972, H u h t a - in press) and also in soils of meadows (N i e l s e n 1955, P e r s s o n and L o h m 1977).

To sum up, it can be stated that the density of enchytraeids decreases along the gradient from rich to poor habitats. At the same time abiotic conditions in soil, particularly water relation, are of great importance to the occurrence of these saprophages. In the periods of high precipitation, the density increases in all the habitats, and to the highest degree in oligotrophic communities.

4.3. Mean body weight and size

Mean body weight of enchytraeids shows distinct changes depending on the season and plant community. In the two study years the range of these changes was relatively small in rich ecosystems such as the ash-alder carr, where the body weight ranged from 45.7 to 75.4 µg, or the oak-hornbeam forest, where it varied between 44.7 and 85.4 µg. In poor habitats, seasonally overdried, such as the pine-oak and pine forests the variability was higher, ranging from 41.9 to 90.2 µg and from 32.5 to 86.4 µg, respectively (Figs. 9-12).

Mean body weights were similar for four ecosystems and two study years, and they varied between 54.0 and 67.0 µg (Table V). Other authors generally report higher values, this being caused not only by differences in the species composition of enchytraeid communities but also by the application of different methods for body weight measurements. Close to the present results are the values obtained by Phillipson et al. (1979) for a beech woodland (72 µg) and by O'Connor (1957) for a Douglas-fir plantation (80 µg), as calculated here from their data on the total density and biomass.

In all the ecosystems and study years, the heaviest individuals occurred in winter, and the lightest predominated in summer.

This regularity is particularly distinct for the group of whole C. sphagnetorum and is certainly related to the way of reproduc-

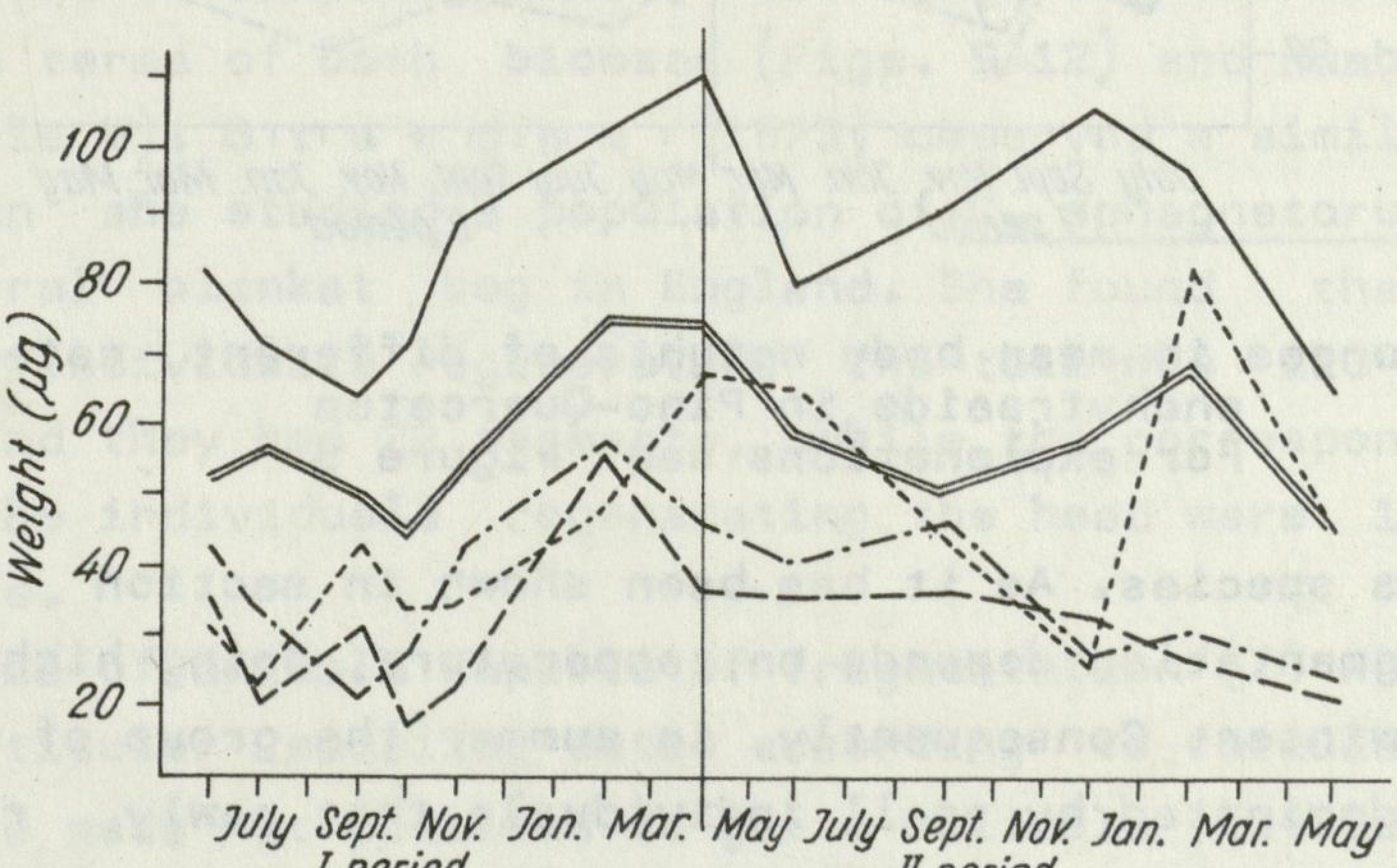

Fig. 9. Changes in mean body weights of different categories of enchytraeids in Circaeo-Alnetum
For explanations see Figure 5

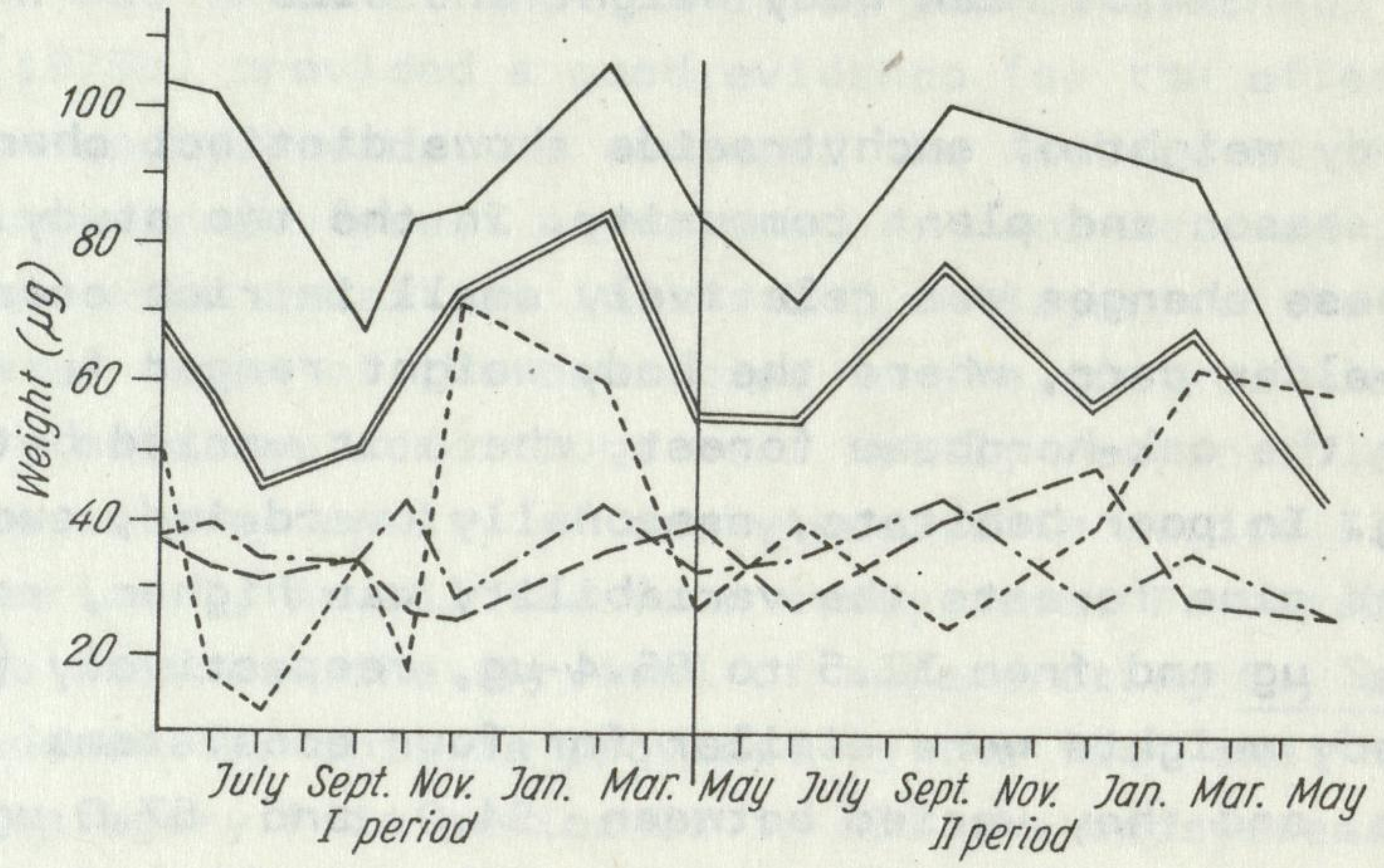

Fig. 10. Changes in mean body weights of different categories of enchytraeids in Tilio-Carpinetum
For explanations see Figure 5

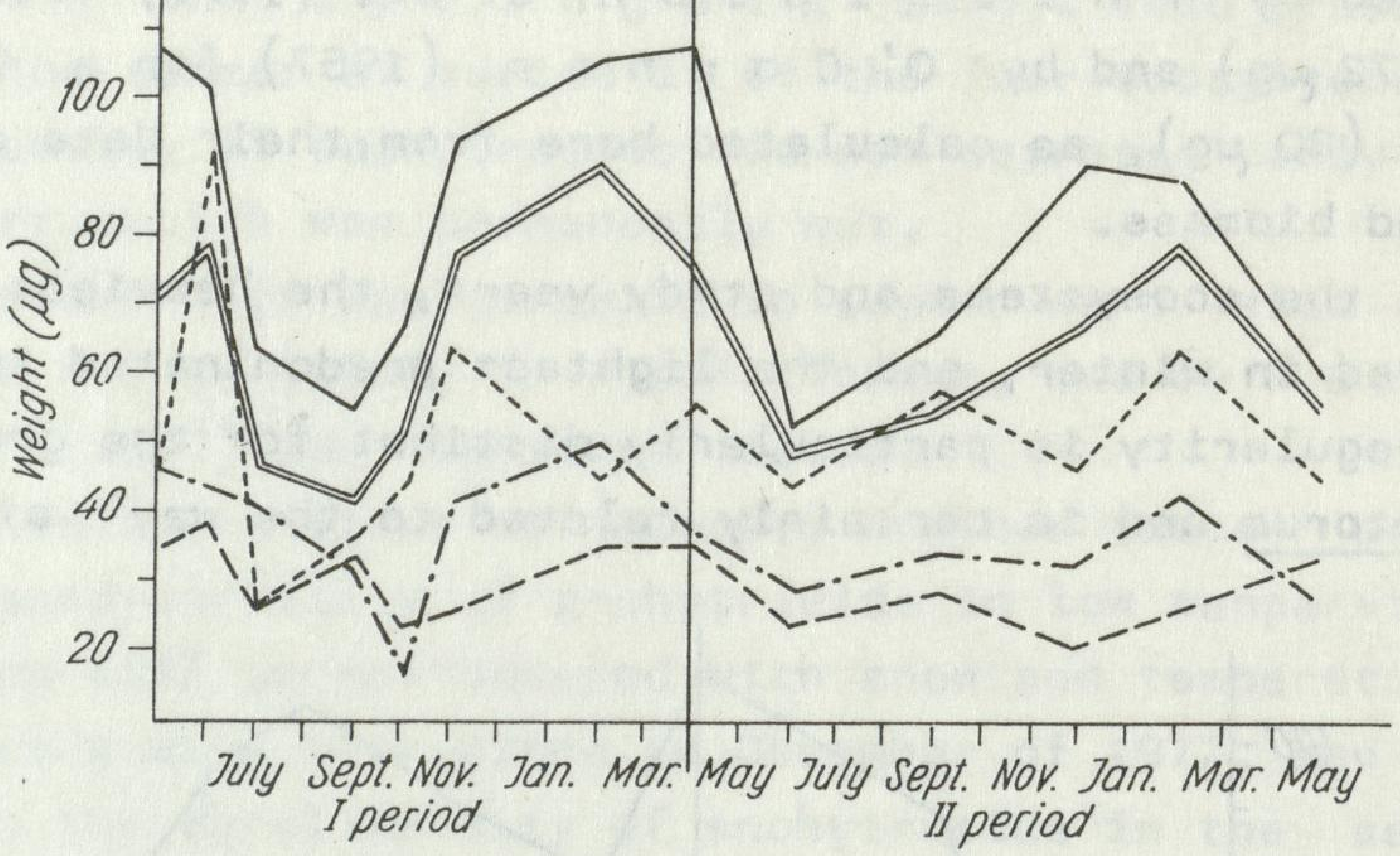

Fig. 11. Changes in mean body weights of different categories of enchytraeids in Pino-Quercetum
For explanations see Figure 5

tion in this species. As it has been shown in section 3.3, the rate of fragmentation depends on temperature, being high in summer and low in winter. Consequently, in summer the group of whole worms will be predominated by small individuals that newly regenerated the lacking segments, while in winter large individuals, reaching and exceeding the size of forms capable of fragmentation, will be most abundant.

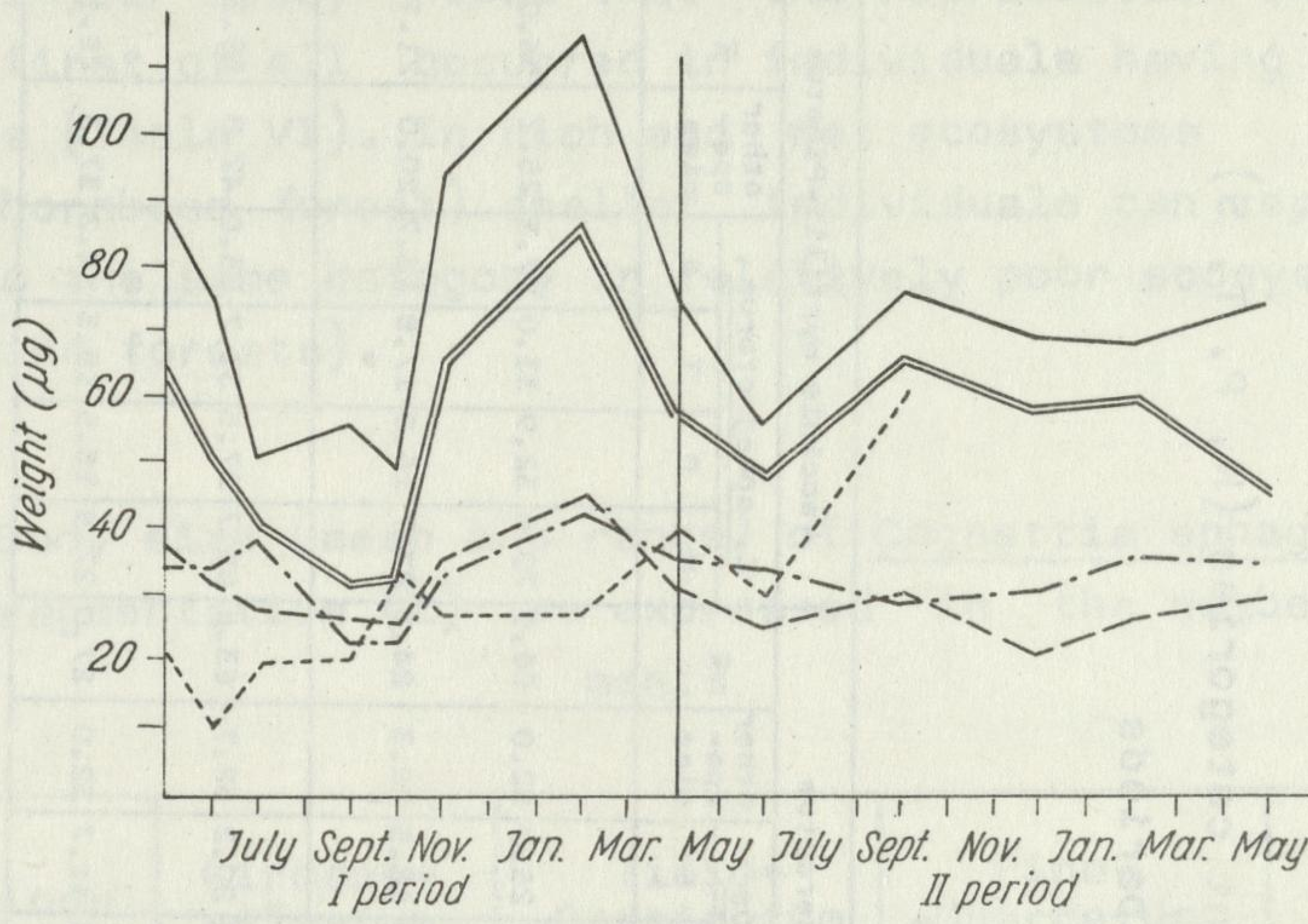

Fig. 12. Changes in mean body weights of different categories of enchytraeids in Vaccinio myrtilli-Pinetum
For explanations see Figure 5

Enchytraeids regenerating the head or the tail, in contrast to whole individuals, did not show distinct and regular changes in the mean body weight over the study periods. Their body weight was reduced 2-2.5 times as compared with the whole individuals.

The enchytraeids regenerating tail segments (P) were smaller than those regenerating the head (T) in all the ecosystems for the two study periods (Table V). This was recorded on a considerable number of sampling dates, and concerned the body size expressed in terms of both biomass (Figs. 9-12) and number of segments (Table V). S t a n d e n (1973) observed a similar regularity when she studied a population of C. sphagnetorum inhabiting a natural blanket bog in England. She found that the body weight of individuals regenerating the tail was 110 µg on the average and they had 22 segments, while the corresponding figures for the individuals regenerating the head were 130 µg and 25 segments.

The size of animals capable of fregmentation (Z) was determined on particular sampling dates according to formula (14). Such a procedure made it possible to get a reliable estimate of the sizes of C. sphagnetorum most frequently subject to fragmentation. An assumption is needed here that the mortality and the efficiency of extraction are similar for both small and large forms of the two categories of regenerating enchytraeids.

Table V. Mean body size and number of segments in different categories (K, P, T, S) of Cognettia sphagnetorum in two study periods

Study periods and variables compared		Circaeo-Alnetum						Tilio-Carpinetum						Pino-Quercetum						Vaccinio myrtilli-Pinetum					
		C. sphagnetorum				other spe-cies	$\bar{x}$	C. sphagnetorum				other spe-cies	$\bar{x}$	C. sphagnetorum				other spe-cies	$\bar{x}$	C. sphagnetorum				other spe-cies	$\bar{x}$
		K	P	T	S			K	P	T	S			K	P	T	S			K	P	T	S		
I	body weight in µg	84.7	32.1	39.2	16.1	40.7	58.6	90.9	33.6	37.4	23.2	42.3	62.2	88.3	32.0	40.2	25.0	52.0	66.9	70.6	32.9	33.0	27.3	25.2	54.0
	number of segments	28.2	14.7	17.0	8.0	21.6	23.2	29.7	15.5	17.4	11.5	23.7	23.4	31.2	16.1	19.1	12.5	28.3	24.8	27.7	16.0	17.8	15.7	20.0	21.9
II	body weight in µg	92,0	32.3	36.5	30.4	56.2	60.4	82.3	35.7	34.5	24.4	42.7	59.7	77.7	28.7	35.7	20.2	52.7	63.6	69.7	27.5	33.7	25.0	42.8	56.3
	number of segments	30.5	14.7	17.5	11.6	24.5	23.7	29.1	15.5	17.1	11.2	25.2	23.7	30.6	15.6	19.3	11.7	32.0	27.0	27.9	15.5	18.5	14.3	37.3	25.1

The two-year study showed that the reproduction through fragmentation first of all occurred in individuals having from 29 to 37 segments (Table VI). In rich and wet ecosystems (ash-alder carr, oak-hornbeam forest) smaller individuals can reproduce, as compared to the same category in relatively poor ecosystems (pine-oak and pine forests).

Table VI. Body size (mean and range) of Cognettia sphagnetorum capable of fragmentation (Z) as expressed in the number of segments

Study periods	Circaeo-Alnetum	Tilio-Carpinetum	Pino-Quercetum	Vaccinio myrtilli-Pinetum
I	31.6 29.4-33.9	32.9 31.2-34.7	35.2 33.1-37.3	33.9 32.6-35.3
II	32.1 30.1-34.3	32.6 30.4-34.9	34.9 32.3-37.5	33.9 31.6-36.2

From the point of view of biomass and energy economy in a population, the fragmentation of larger individuals is advantageous because it enhances the survial of both groups of regenerating individuals. It is of particular importance in the case of tail segments. The large number of these segments enables these animals to move in soil, and, in addition, when the new mouth is being formed these segments provide more material and energy for the regeneration of lacking segments.

Sexually reproducing enchytraeids form multispecies communities in the study esosystems, the composition of which depends not only on the site but also on the season. This variability together with differences in the biology of particular species account for the fact that no distinct regularities were found in changes of the mean body weight for this enchytraeid category.

Maximum mean body weights of individuals sexually reproducing were found in different periods of the year. In winter for the oak-hornbeam forest, in winter and spring for the ash-alder carr, in autumn for the pine forest, and early in summer for the pine-oak forest (Figs. 9-12).

Generally, the periods distinguished were characterized by a high proportion of large individuals, which were sexually mature and often had a distinct clitellum. The largest individuals represented such species as Henlea nasuta, Fridericia bisetosa and F. callosa (Table VII). Relatively little enchytraeids belonged to Hemienchytraeus bifurcatus, Enchytraeus buchholzi and Enchytronia parva.

Table VII. Mean body sizes of sexually mature and young of some enchytraeid species

Species	Mature individuals		Young individuals	
	number of segments	biomass (µg)	number of segments	biomass (µg)
Bryodrilus ehlersi	40.7 ± 8.3	148.6 ± 37.1	16.8 ± 2.6	16.1 ± 9.5
Buchholzia appendiculata	32.0 ± 2.8	82.4 ± 1.7	15.1 ± 3.2	18.7 ± 7.7
Enchytraeus buchholzi	23.4 ± 2.6	48.0 ± 17.2	15.2 ± 3.4	15.1 ± 7.9
Enchytronia parva	25.1 ± 3.3	55.9 ± 23.1	15.1 ± 2.7	13.5 ± 5.7
Fridericia bisetosa	54.6 ± 6.6	319.5 ±166.1	13.4 ± 3.6 (both species)	18.9 ± 9.0 (both species)
F. callosa	38.2 ± 3.7	161.5 ± 63.8		
Hemienchytraeus bifurcatus	23.7 ± 4.1	42.6 ± 30.2	13.6 ± 2.7	10.6 ± 4.9
Henlea nasuta	55.5 ± 7.7	542.0 ±168.8	22.5 ± 0.7	94.0 ±91.6
Mesenchytraeus pelicensis	-	-	13.3 ± 4.2	11.8 ± 5.0

4.4. Total biomass of enchytraeid communities

Changes in the total biomass over the study period generally followed the same pattern as the changes in density. This is a result of the fact that biomass firstly depends on density and to a lesser extent on the mean body weight (Figs. 13-16).

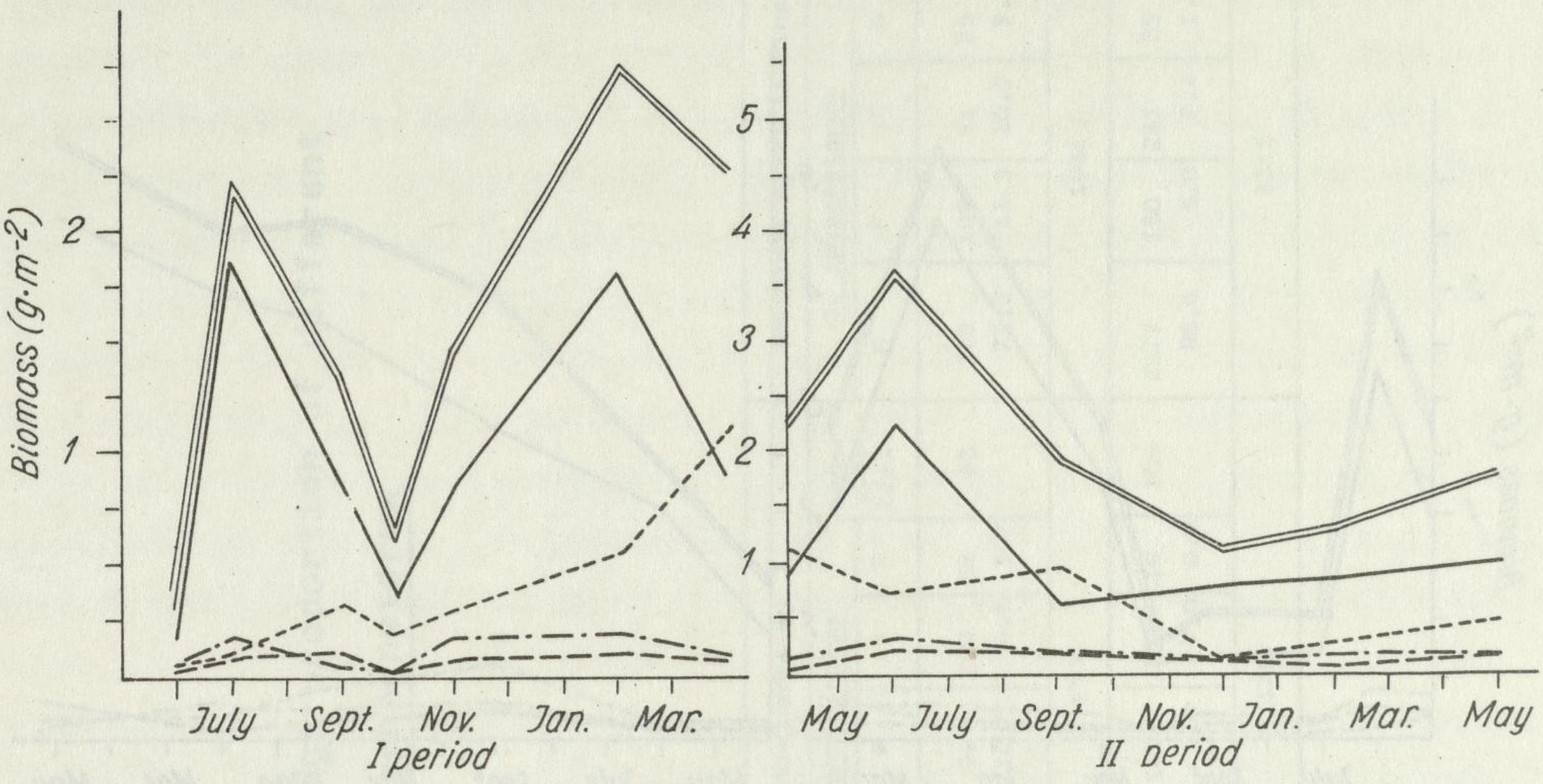

Fig. 13. Total biomass of different categories of enchytraeids in Circaeo-Alnetum
For explanations see Figure 5

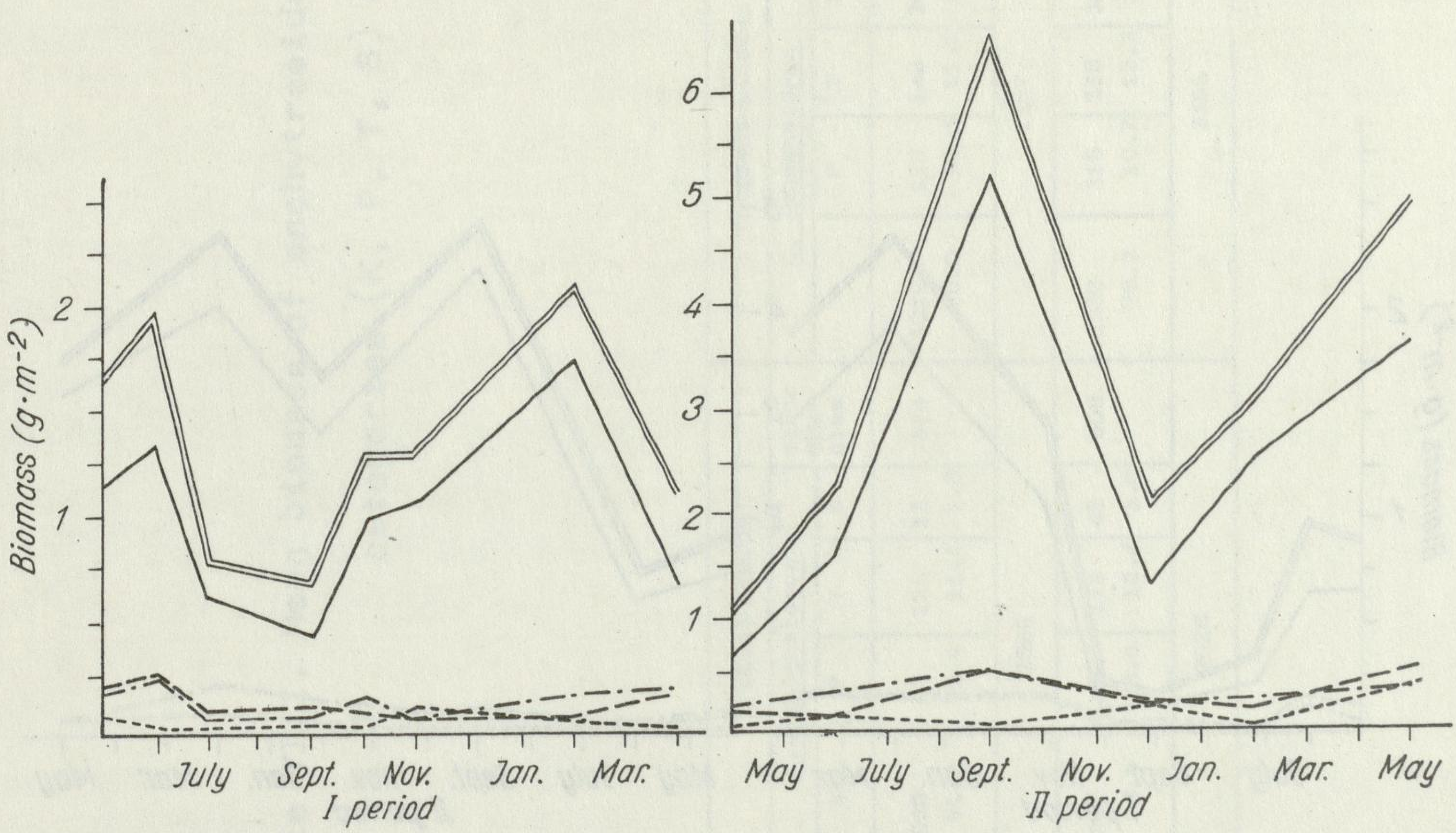

Fig. 14. Total biomass of different categories of enchytraeids in Tilio-Carpinetum
For explanations see Figure 5

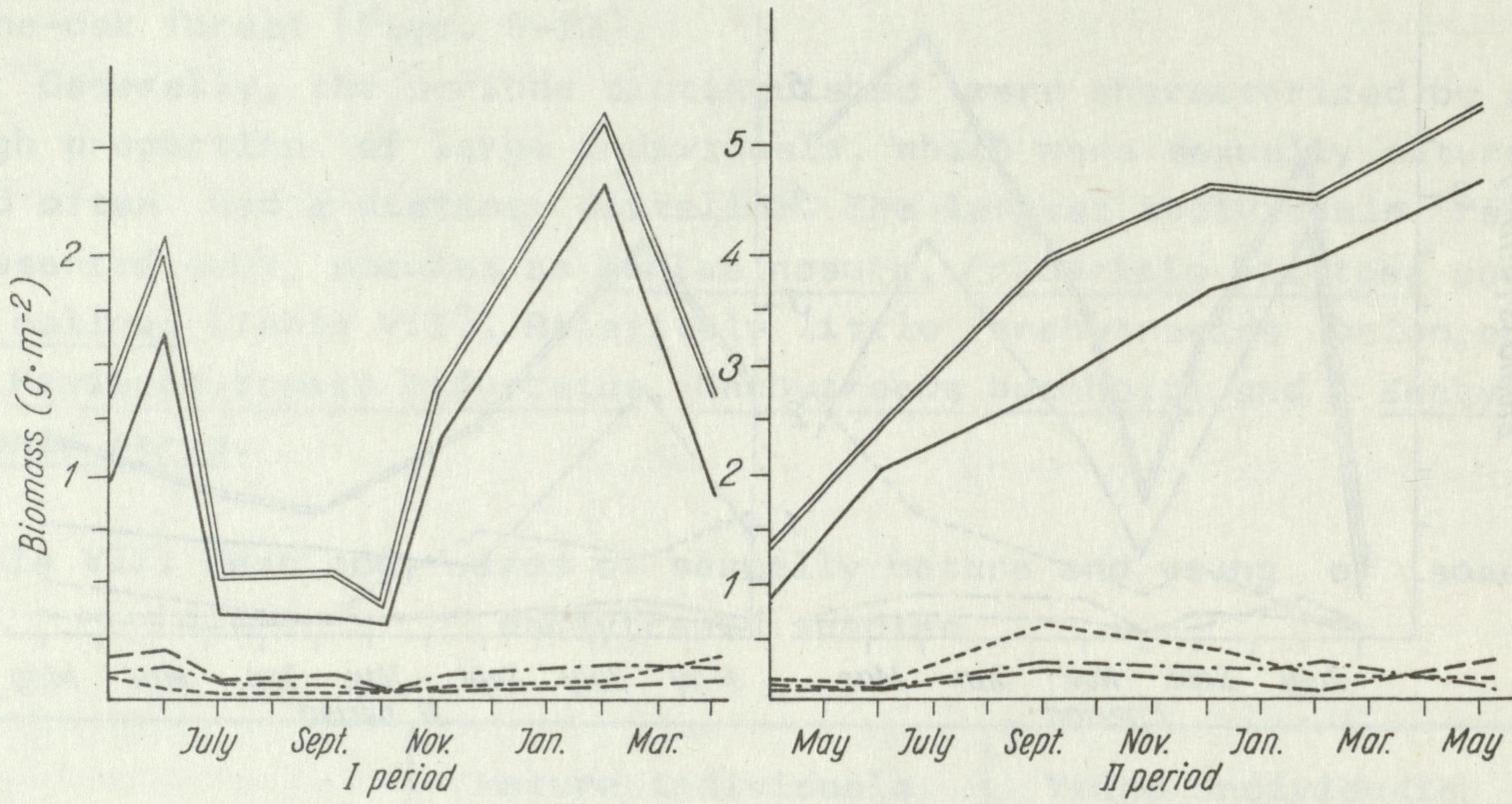

Fig. 15. Total biomass of different categories of enchytraeids in Pino-Quercetum
For explanations see Figure 5

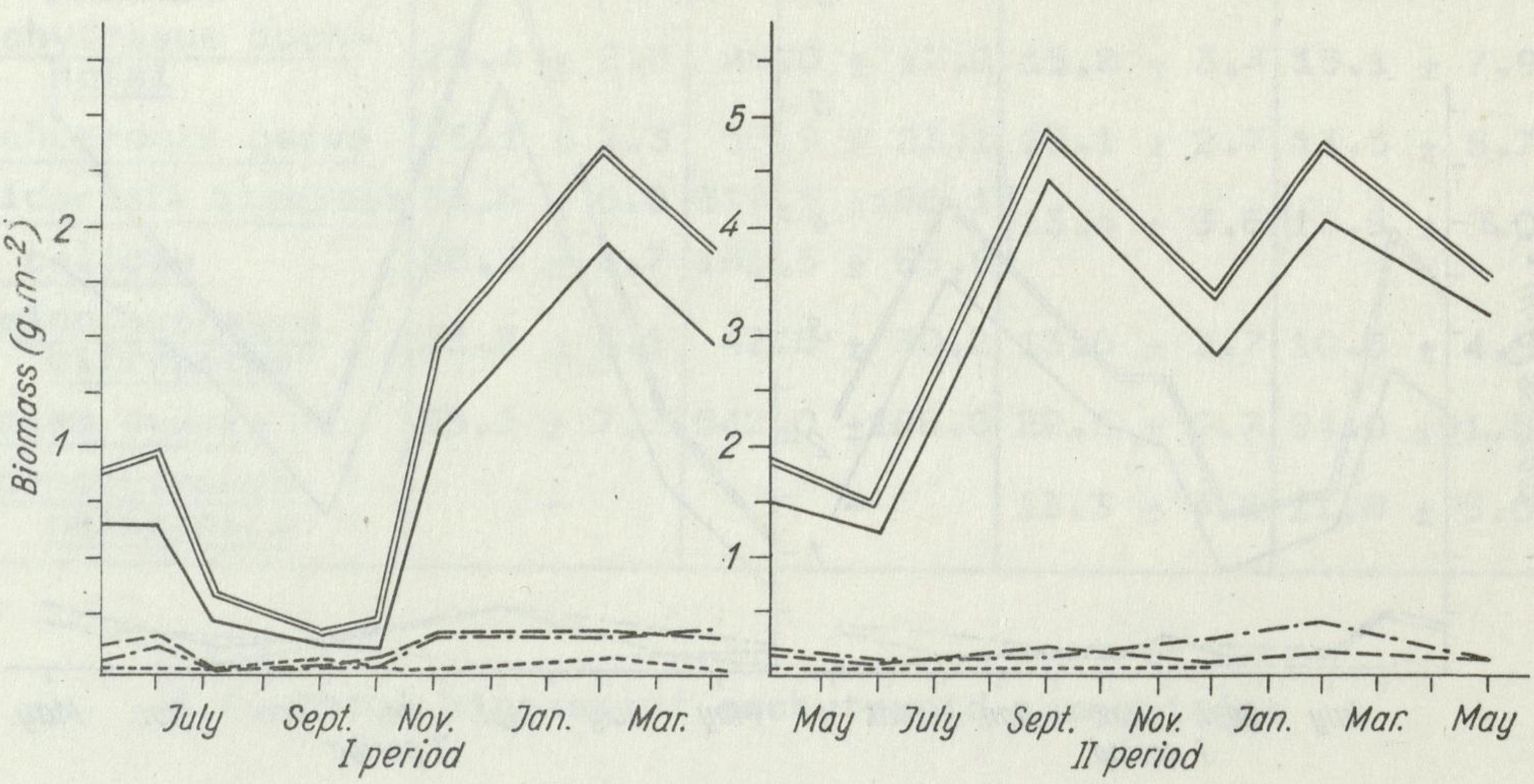

Fig. 16. Total biomass of different categories of enchytraeids in Vaccinio myrtilli-Pinetum
For explanations see Figure 5

Table VIII. Mean biomass of enchytraeids and percentage proportion of different categories (K, P, T, S) of Cognettia sphagnetorum

Study periods and variables compared		Circaeo-Alnetum					Tilio-Carpinetum					Pino-Quercetum					Vaccinio myrtilli-Pinetum				
		C. sphagnetorum				other species	C. sphagnetorum				other species	C. sphagnetorum				other species	C. sphagnetorum				other species
		K	P	T	S		K	P	T	S		K	P	T	S		K	P	T	S	
I	$\bar{B}$ per m^2 (mg)	988	68	121	13	374	1019	129	148	30	39	1004	98	105	32	63	776	109	91	29	25
	%	81.0	6.4	11.4	1.0		76.0	10.4	11.2	2.4		77.5	10,0	9.6	2.7		73.2	13.3	10.0	3.3	
	$\bar{x}$	1565					1367					1304					1031				
II	$\bar{B}$ per m^2 (mg)	1087	116	173	42	608	2532	318	338	30	147	3014	165	210	18	309	2877	150	231	25	26
	%	76.0	8.5	12.4	3.0		75.7	10.7	12.3	1.2		81.2	5.0	7.0	0.8		86.6	5.0	7.4	1.0	
	$\bar{x}$	2028					3366					3718					3311				

In period I, a highest mean biomass of 1565 mg per m^2 occurred in the ash-alder carr, while a lowest mean biomass of 1031 mg per m^2 was recorded in the oligotrophic pine forest. In the oak-hornbeam and pine-oak forests intermediate values of 1367 and 1304 mg per m^2, respectively, were recorded (Table VIII).

In all the ecosystems, mean biomass in period II was higher than in period I from 1.3 times (ash-alder carr) to 3.2 times (pine forest). It reached a highest value of 3718 mg per m^2 in the pine-oak forest, and a lowest value of 2028 mg per m^2 in the ash-alder carr. A similar pattern was followed by changes in density, and it was related to the improvement in soil moisture conditions.

Like total numbers in period I, also the mean biomass generally reached minimum values in the period from July to October and maximum values in winter (Figs. 13-16).

In period II this situation was largely changed. The lowest biomass occurred in December (ash-alder carr) or in early spring and winter (oak-hornbeam and pine forests) and the highest biomass was in summer.

Identical changes were characteristic of the biomass of the whole C. sphagnetorum, and this was related to a large proportion of this group in the enchytraeid community (Table VIII).

There are few papers dealing not only with densities but also with biomass of enchytraeids. This is caused by the necessity of using indirect thus labour-consuming methods for body weight determination.

Relatively high mean enchytraeid biomass was found in coniferous forests. A highest value of 10.79 g per m^2 is given by O'Connor (1963) for a Douglas-fir plantation in North Wales. The lowest mean enchytraeid biomass was found by Kitazawa (1971) for two types of subalpine coniferous forests in Japan (1.16 and 1.13 g per m^2) and Huhta and Koskiennemi (1975) for three pine forests in Finland (1.7, 0.95 and 0.9 g per m^2). Intermediate standing crops (calculated on the basis of only 2-4 sampling dates) are given by Abrahamsen (1972) for very poor cladonia-coniferous forests in Norway. The mean biomass ranged in these ecosystems from 1.82 to 5.23 g per m^2.

In broad-leaved forests, the mean biomass of enchytraeids is less variable than in coniferous forests. A highest mean biomass of 3 g per m^2 was found for an aspen woodland in Canada (D a s h and C r a g g 1972). A lower value of 2.45 g per m^2 was found for a temperate deciduous forest in Japan (K i t a z a w a 1971). An even lower value of 1.908 g per m^2 was found for a beech woodland in England (P h i l l i p s o n et al. 1979).

Against this background, the mean enchytraeid biomass found in the present study for coniferous forests and, in particular, for oak-hornbeam and ash-alder forests are relatively high, especially in the study period II (more humid).

4.5. Production and elimination of biomass in enchytraeid communities

Since the contribution of C. sphagnetorum to the total density and biomass of enchytraeid communities was high, its biomass production was the highest as compared with the other species.

In period I, the highest production of C. sphagnetorum was recorded for the pine-oak and oak -hornbeam forests (Table IX). The annual production in these ecosystems was 31.5 and 32.1 kJ per m^2. The other plant communities were characterized by a smaller enchytraeid production. In the ash-alder carr it was 25.6 kJ per m^2 and in the pine forest 17.3 kJ per m^2.

A similar regularity was found for the elimination of the biomass produced by the dominant species. In the oak-hornbeam forest more than 35 kJ per m^2 passed from C. sphagnetorum to other trophic levels and in the pine-oak forest 33.0 kJ per m^2. The rate of elimination was lower in the pine forest and in the ash-alder carr, where it reached 10.1 and 19.5 kJ per m^2,respectively.

In period II, the increase in density and total biomass of C. sphagnetorum was accompanied by an increased production of biomass. This was most pronounced in the poorest community, thus in the oligotrophic pine forest. In this ecosystem the biomas production of C. sphagnetorum was five times of that in period I, and it reached 87.3 kJ per m^2. A similar value, but a less distinct increase as compared with period I, was observed in the pine-oak and oak-hornbeam forests. In these communities, the annual pro-

Table IX. Production and elimination of Cognettia sphagnetorum in two study periods

Study periods and variables compared		Circaeo-Alnetum			Tilio-Carpinetum			Pino-Quercetum			Vaccinio myrtilli--Pinetum		
		ΔB	E	P	ΔB	E	P	ΔB	E	P	ΔB	E	P
I	ind. $\cdot 10^{3} \cdot m^{-2} \cdot year^{-1}$	10.00	37.32	47.32	-4.35	66.97	62.62	-3.95	62.20	58.24	18.17	22.64	40.80
	$g \cdot m^{-2} \cdot year^{-1}$	0.89	2.46	3.35	-0.53	4.42	3.88	-0.14	4.17	4.03	0.97	1.27	2.24
	$kJ \cdot m^{-2} \cdot year^{-1}$	6.11	19.55	25.66	-3.60	35.08	31.48	-0.92	33.03	32.15	7.20	10.13	17.29
II	ind. $\cdot 10^{3} \cdot m^{-2} \cdot year^{-1}$	14.24	72.82	87.06	85.30	112.46	197.76	78.55	121.63	200.19	19.31	160.88	180.19
	$g \cdot m^{-2} \cdot year^{-1}$	0.16	4.73	4.89	3.53	6.88	10.42	3.99	7.85	11.85	1.67	9.62	11.30
	$kJ \cdot m^{-2} \cdot year^{-1}$	1.04	37.64	38.68	24.66	54.88	79.55	31.86	62.50	94.37	10.50	76.78	87.29

duction of C. sphagnetorum was 94.37 and 79.55 kJ per m^2, respectively.

It follows from this that C. sphagnetorum, the most abundant species in the study ecosystems, will play the most important part in moderately rich ecosystems such as the oak-hornbeam and pine-oak forests. In the years with high precipitation its role in the retention and transfer of energy and nutrients will increase also in very poor pine forests, where it can reach the level similar to that in the oak-hornbeam and pine-oak forests.

The biomass produced by sexually reproducing species is small as compared with C. sphagnetorum production. Only in the ash-alder carr, where the species composition is most diversified, production of this group of enchytraeids is of some importance. In period I its production reached 11.9 kJ per m^2. In the other three plant communities it was much lower - from 1.3 to 2.7 kJ per m^2 in the oak-hornbeam and pine forests, respectively (Table X).

Table X. Elimination and production of enchytraeid species sexually reproducing, in two study periods

Study periods and variables compared		Circaeo-Alnetum E	Circaeo-Alnetum P	Tilio-Carpinetum E	Tilio-Carpinetum P	Pino-Quercetum E	Pino-Quercetum P	Vaccinio-myrtilli-Pinetum E	Vaccinio-myrtilli-Pinetum P
I	$g \cdot m^{-2} \cdot year^{-1}$	0.57	1.67	0.22	0.19	0.27	0.39	0.22	0.24
	$kJ \cdot m^{-2} \cdot year^{-1}$	4.06	11.93	1.59	1.38	1.92	2.76	1.59	1.67
II	$g \cdot m^{-2} \cdot year^{-1}$	3.24	2.57	0.21	0.61	1.33	1.35	0.14	0.12
	$kJ \cdot m^{-2} \cdot year^{-1}$	23.15	18.38	1.50	4.35	9.54	9.63	1.00	0.83

In period II, the production of biomass increased, particularly in the pine-oak forest (3.5 times) and in the oak-hornbeam forest (more than 3 times). The only exception was the pine forest, where the production dropped, reaching 0.8 kJ per m^2. Like in period I, the highest production of this enchytraeid group, that is 18.3 kJ per m^2, was recorded for the ash-alder carr.

The total biomass produced by the enchytraeid communities in period I ranged from 37.6 kJ per m^2 for the ash-alder carr to 18.9 kJ per m^2 for the pine forest. In period II, the production of living tissues considerably increased in all the ecosystems, and most distinctly in the pine forest. The highest production was recorded in the pine-oak forest, and it was 104 kJ per m^2.

5. DISCUSSION AND CONCLUSIONS

The rate of fragmentation is of a key importance to the biomass production and elimination in C. sphagnetorum. Practically, it is not possible to determine this parameter by field or laboratory experiments. This would need a permanent control at short time intervals of a large group of individuals, the age structure of which, as expressed by the number of segments, would correspond to the actual age structure of the population. In similar studies, S t a n d e n (1973) analysed the rate of fragmentation for a group of C. sphagnetorum made up of more than 42 segments in a laboratory experiment. Her results are much lower than those obtained in this paper. The discrepancy may result from differences in the methods applied, but also from the differences between C. sphagnetorum populations.

C h r i s t e n s e n (1959) examined the histological aspect of the regeneration of segments in C. sphagnetorum. The fragmentation of an individual is preceded by a distinct tissue transformation. A band of rapidly dividing cells is formed. These cells grow towards the body cavity with peritoneum till they touch the wall of the alimentary canal. Head fragments (P) regenerate the region of the anus, and at the same time one segment is produced. Tail fragments (T) are subject to more complex transformations leading to the formation of a new brain, septal glands, and terminal part of the dorsal blood vessel. Prior to the formation of a few first segments, these individuals are not active and they do not take food. This may be the reason why individuals P outnumbered category T in samples.

The rate of segment regeneration depends on temperature, S p r i n g e t t (1970) has found that the complete regeneration of tail parts takes 76 days at 5°C and 56 days at 10°C.

S t a n d e n (1973) reports a much higher growth rate. She found that the complete regeneration of tail segments covered 26 days at 10°C and 17 days at 15°C. She has also found that the regeneration of head (P) takes less time, 12 and 13 days, respectively, at the same temperatures. On the basis of examination of a large group of individuals, it has been assumed in the present paper that fragments P become indistinguishable from the whole individuals after the regeneration of one segment. Using the known rate of growth (Fig. 3), it is easy to calculate that this process takes some 9 days at 10°C and some 5 days at 15°C. Thus, the regeneration rate is higher from that recorded by S t a n d e n (1973) in laboratory experiments. This may have an effect on the estimates of elimination and production - the latter may be overestimated. However, the elimination of individuals, calculated in this paper, had negative values in some periods (autumn-winter period). This may be due to an immigration, but also indicates that the rate of growth and fragmentation found here is rather consistent with actual values.

Production of C. sphagnetorum was calculated from formula (5). This method does not take into account the production due to individual body growth, and it can be applied only when the body weight at hatching approaches the body weight of adults (P e t r u s e w i c z and M a c f a d y e n 1970). C. sphagnetorum meet this condition due to their way of reproduction - the individuals produced by fragmentation are smaller by half, on the average, from the whole individuals capable of fragmentation (Table V).

Table XI. Biomass turnover (P : B) in Cognettia sphagnetorum populations in two study periods

Study periods	Circaeo-Alnetum	Tilio-Carpinetum	Pino-Quercetum	Vaccinio myrtilli-Pinetum
I	2.93	3.34	3.67	2.44
II	3.83	3.46	3.70	3.67

The P : B ratio is a good index of the population productivity (Table XI). In C. sphagnetorum P : B varied from 2.44 to 3.83 depending on the study period and plant community. In the year of optimum water relations, this index was higher than in the preceding period for all the ecosystems. On the basis of the two-year study, a P : B of 3.0-3.7 can be considered as characteristic of the population of <u>C. sphagnetorum</u>. S t a n d e n (1973) reports P : B values of 1.19 and 0.77 for two study years, respectively. These are very low values as the author herself stresses. P h i l l i p s o n et al. (1979) found a value of 4.93 for a multispecies enchytraeid community of a beech forest. It should be noted that in this case production was calculated from a known respiration, using the formulas developed by M c - N e i l l and L a w t o n (1970) for short-lived poikilotherms ($\log P = 0.8262, \log R = 0.0948$).

An ability to increase biomass more than three times over a year shows that <u>C. sphagnetorum</u> is a good energy converter, capable of transferring large resources to other trophic levels. A great advantage of this species is the way of reproduction. Fragmentation enables it a rapid recovery after seasonal soil overdrying in summer and also in spring as the temperature increases. According to S p r i n g e t t (1970), in permanently wet peat soils the number of <u>C. sphagnetorum</u> was maintained at a stable level over the growing season, which implies that the emigration and mortality were balanced by reproduction and immigration.

Summing up the results of this paper, it may be stated that:

1. The species composition of enchytraeid communities is simplified with decreasing biocoenotic and site richness. A total of 17 enchytraeid species have been recorded (Table II). This figure is typical of the Circaeo-Alnetum, the richest and most stable community. In poor ecosystems such as the pine forest, the number of species is reduced almost by half, eight species being recovered there.

2. The decrease in the number of species was coupled with a growing dominance of <u>Cognettia sphagnetorum</u>. Depending on the plant community or the study period, this species on the average accounted for 68-98% of the total number and for 71-98% of the total biomass of enchytraeids (Table III). Due to its asexual reproduction, this species is capable of rapid and precise responses to all important changes in the soil habitat. Under favourable food and moisture conditions its biomass can increase many times, large amounts of energy and nutrients being retained.

3. In the ecosystems with a high matter and energy flow, mean densities and biomass of enchytraeids are higher. At the same time the effect of soil moisture is important. In period I, the densities and biomass declined in parallel to the deterioration of trophic conditions in a plant community, and in particular to the reduction in leaf fall, rate of litter decomposition, dehydrogenaze activity, and soil C : N. Along this gradient, the mean density ranged from 25.5 thousand per m^2 for the ash-alder carr to 16.8 thousand per m^2 for the pine forest (Table IV), and the biomass varied from 1.56 to 1.03 g per m^2, respectively (Table VIII). The highest densities and biomass over the year were found in early spring and also in autumn and winter (Figs. 5--8 and 13-16). Improved water conditions in period II accounted for an increase in the total density and biomass for all the ecosystems and most effectively in coniferous forests. The highest densities and biomass of enchytraeids were noted in the pine--oak forest, reaching 60.6 thousand per m^2 and 3.7 g per m^2, and the highest ones in the ash-alder carr, reaching 33.5 thousand per m^2 and 2.0 g per m^2. No distinct seasonal peaks of density and biomass were noted.

4. Cognettia sphagnetorum reproduce by fragmentation of a small group of whole individuals which are made up of 29-37 segments (Table VI). The rate of fragmentation and also the rate of growth as measured by the number of segments increased with temperature. Most frequently, fragmentation occurs in the region of segments 14-16, and it gives individuals mostly representing the head and the tail. Also a small number of middle fragments are produced. In these groups, the individuals regenerating the tail (P) are always smaller from those regenerating the head (T). The mean weight of the former varied in relation to the plant community and study period from 27 to 36 μg, and that of the latter category varied from 33 to 40 μg (Table V). Individuals P become indistinguishable from the whole individuals after the regeneration of one segment, individuals T after the regeneration of eight segments, while middle fragments after the regeneration of nine segments.

5. The highest production of C. sphagnetorum was recorded in the oak-hornbeam and pine-oak forests (Table IX). In period I, it was 31.5 and 32 kJ per m^2, respectively. In the period with high precipitation, the production of this species increased 2-4

times, and for the same ecosystems it was 79.5 and 94.4 kJ per m^2, respectively. The production of C. sphagnetorum in the ash-alder carr and in the pine forest was lower than in the oak-hornbeam and pine-oak forests over the two study periods.

6. P : B of C. sphagnetorum population ranged from 2.44 to 3.83, depending on the forest community and study period (Table XI).

6. SUMMARY

The study was carried out in four plant communities of the Kampinos Forest, such as the ash-alder carr (Circaeo-Alnetum),oak-hornbeam forest (Tillio-Carpinetum), pine-oak forest (Pino-Quercetum) and pine forest (Vaccinio myrtilli-Pinetum) (Table I). The materials collected for over two years were classified to two periods not coinciding with the calendar year. Period I extended from May, 1976 to the end of April, 1977. Period II extended from May, 1977 to the beginning of May, 1978.

To estimate the density of enchytraeids, a series of 30 soil cores 100 cm^3 in volume were taken in regular intervals. O'Connor's method was used to extract the animals. A total of about 52 thousand individuals were collected.

Live body weight was estimated on the basis of its relation to the body length of preserved specimens (Fig. 1). All individuals from 10 soil cores on each sampling date were measured, a total of 14 thousand individuals being analysed.

The dominant species in all the ecosystems was Cognettia sphagnetorum, the species reproducing by fragmentation. It accounted for 68-98% of the total density and for 71-99% of the total biomass of enchytraeids (Table III). Four categories of C. sphagnetorum individuals were distinguished in the samples: regenerating the tail (P), regenerating the head (T), regenerating both the head and the tail (S), and whole individuals without detectable signs of regeneration (K).

The production of both C. sphagnetorum and the species sexually reproducing was estimated. The production of the dominant species was calculated on the basis of the number of individuals that could be produced in the population during the period between sampling dates. It depends on the number of individuals ca-

pable of reproduction and also on the rate of growth and fragmentation. The body size of enchytraeids that can fragment was calculated from formula (12). It has been found that only a small part of the whole individuals, with a body size of 29-37 segments, is subject to fragmentation (Table VI). The frequency of fragmentation depends on ambient temperature (Fig. 4). The growth rate of whole C. sphagnetorum individuals was examined at 5, 10, 15 and 20°C (Fig. 3). It has been assumed that the growth rate of regenerating individuals is the same as whole ones. Enchytraeids of the category P pass to the category of whole individuals after the regeneration of one segment, those of the category T after the regeneration of eight segments, and the category S after the regeneration of nine segments.

The data obtained made it possible to estimate the number of individuals that could be produced in the period between sampling. The production of biomass was obtained as a product of this number and the mean body weight.

Over the two-year study period, 17 enchytraeid species have been recorded. All of them occurred in the ash-alder carr. In the coniferous forests the number of species was reduced by half, eight species being recorded there (Table II).

C. sphagnetorum predominated in all the forest communities by number and by weight. In some periods this species accounted for 100% of the community. Generally, in period I the density dropped from 25.54 thousand per m^2 in the ash-alder carr to 16.83 thousand per m^2 in the pine forest (Table IV). In period II, the density increased in all the ecosystems, and most markedly in the coniferous forests. This increase was related to an improvement in soil water conditions as a result of heavy precipitation. In that period an average of 29.52 thousand per m^2 were recorded in the ash-alder carr, 38.57 thousand in the oak-hornbeam forest, and 39.49 thousand per m^2 in the pine-oak forest.

Similar regularities were found for the biomass of enchytraeids (Table VIII). In the first year the biomass decreased from 1565 to 1031 mg per m^2 along the gradient from the ash-alder carr to the pine forest. In period II, the highest mean biomass, like the highest density, occurred in the pine-oak forest, where it reached 3718 mg per m^2, and the lowest one was recorded in the ash-alder carr, where it was 2028 mg per m^2. Also seasonal changes in density and biomass were similar (Figs. 5-8 and 13-16).

In period I, the highest standing crop was noted in May-June, in autumn, and in winter. In period II, no so characteristic of saprophages spring and autumn peak numbers and biomass were noted.

C. sphagnetorum populations mostly consist of whole individuals without detectable regeneration. They accounted for about 54 to 74% of the total density and for 73-87% of the total biomass, depending on the study period and plant community. The other groups were less abundant, and their proportions did not exceed a few per cent.

Mean body weight of enchytraeids, including whole C. sphagnetorum individuals, is subject to very regular changes (Figs.9-12). The heaviest individuals occur in winter and the lightest in summer. This fact is due to fragmentation, which is intense in summer and negligible in periods with low temperatures.

Most of the enchytraeid production in the forest ecosystems under study was due to C. sphagnetorum. The species showing sexual reproduction produce very little biomass. In the oak-hornbeam, pine-oak and pine forests, the production of this group varied from 0.83 to 4,35 kJ $\cdot$ m^{-2} $\cdot$ year^{-1}. Only in the ash-alder carr they produced as much as 11.93 kJ $\cdot$ m^{-2} $\cdot$ yr^{-1} in period I and 18.38 kJ $\cdot$ m^{-2} $\cdot$ yr^{-1} in period II (Table X).

The dominant species produced biomass the energy value of which ranged from 17.29 kJ $\cdot$ m^{-2} $\cdot$ yr^{-1} in the pine forest to 32.15 and 31.48 kJ $\cdot$ m^{-2} $\cdot$ yr^{-1} in the pine-oak and oak-hornbeam forests, respectively (Table IX). In period II, the production increased in parallel to density and biomass. The increase was most distinct in the pine forest (87.29 kJ $\cdot$ m^{-2} $\cdot$ yr^{-1} and in the pine-oak forest (94.37 kJ $\cdot$ m^{-2} $\cdot$ yr^{-1}).

The comparison of mean biomass and production shows that C. sphagnetorum can multiply its biomass many times over the year. P : B varied for this species from 2.44 to 3.83, depending on the ecosystem and study period (Table XI).

7. POLISH SUMMARY

Badania prowadzono w czterech zespołach leśnych Puszczy Kampinoskiej: w łęgu (Circaeo-Alnetum), grądzie (Tilio-Carpinetum), borze mieszanym (Pino-Quercetum) i borze sosnowym (Vaccinio myrtilli-Pinetum) (tab. I). Materiały zebrane w ciągu przeszło

2 lat rozdzielono na 2 okresy, które nie pokrywają się z latami kalendarzowymi. Pierwszy okres trwał od maja 1976 do końca kwietnia 1977 r. Drugi od maja 1977 do początków maja 1978 r.

Dla oceny zagęszczenia pobierano każdorazowo 30 prób glebowych o objętości 100 cm^3. Wazonkowce ekstrahowano metodą O'Connora. Ogółem zebrano ok. 52 tys. osobników.

Żywą biomasę osobników oceniano na podstawie jej zależności od długości ciała zwierząt konserwowanych (rys. 1). Pomiarami objęto wazonkowce z 10 prób podstawowych w każdym terminie. Zanalizowano w ten sposób 14 tys. wazonkowców.

Gatunkiem dominującym we wszystkich ekosystemach jest rozmnażający się przez fragmentację gatunek Cognettia sphagnetorum. Stanowi on 68-98% zagęszczenia i 71-99% biomasy Enchytraeidae (tab. III). W próbach gatunek ten reprezentują 4 kategorie osobników: regenerujące tylną część ciała (P), regenerujące głowę (T), odtwarzające zarówno głowę jak i tył ciała (S) oraz osobniki kompletne bez widocznej regeneracji (K).

Oceniono produkcję C. sphagnetorum oraz gatunków rozmnażających się generatywnie. Podstawą obliczeń produkcji dominanta była liczba osobników, które mogły być wytworzone przez populację w okresie między terminami pobierania prób. Zależy ona od liczby osobników zdolnych do rozrodu oraz od tempa wzrostu i fragmentacji. Rozmiary wazonkowców podlegających podziałom określano według wzoru (12). Stwierdzono, że fragmentacji podlega niewielka część osobników kompletnych o rozmiarach 29-37 segmentów (tab.VI). Częstość podziałów jest zależna od temperatury otoczenia (rys. 4). Zbadano tempo przyrostu osobników kompletnych C. sphagnetorum w temperaturach 5, 10, 15, 20°C (rys. 3). Przyjęto w obliczeniach, że szybkość przyrostu osobników regenerujących jest taka sama jak okazów kompletnych. Wazonkowce kategorii P przechodzą do osobników kompletnych po wytworzeniu jednego segmentu, kategoria T - 8 segmentów, kategoria S odbudowuje 9 segmentów.

Uzyskane dane pozwalają oszacować liczbę osobników, jaka mogła być wytworzona w okresie ograniczonym terminami pobierania prób. Mnożąc tę liczbę przez średni ciężar osobników w poszczególnych kategoriach otrzymano produkcję biomasy.

W toku 2-letnich badań stwierdzono występowanie 17 gatunków Enchytraeidae. Liczba ta jest charakterystyczna dla zespołu łęgowego. W ekosystemach borowych liczba gatunków jest 2-krotnie mniejsza i wynosi 8 gatunków (tab. II).

We wszystkich zespołach leśnych, zarówno w zagęszczeniu jak i w biomasie, przeważa C. sphagnetorum. W niektórych terminach gatunek ten stanowi 100% zgrupowania. Ogółem w I okresie badań średnie zagęszczenie maleje od 25,54 tys. na m^2 w łęgu do 16,83 tys. na m^2 w borze sosnowym (tab. IV). W następnym roku zagęszczenie wzrasta we wszystkich ekosystemach, a najsilniej w borach. Zmiany te są związane z poprawą warunków wodnych gleby w wyniku intensywnych opadów. W tym okresie w łęgu stwierdzono średnio 29,52 tys. na m^2, natomiast w grądzie i borze mieszanym odpowiednio 38,57 i 39,49 tys. na m^2.

Podobne prawidłowości wykazuje również biomasa wazonkowców (tab. VIII). W pierwszym roku, w gradiencie od łęgu do boru sosnowego, biomasa maleje od 1565 do 1031 mg na m^2. Również w II okresie badań analogicznie do zagęszczenia największa średnia masa żywa Enchytraeidae została stwierdzona w borze mieszanym - 3718 mg na m^2, najniższa w łęgu - 2028 mg na m^2. Również zmiany sezonowe zagęszczenia i biomasy są podobne (rys. 5-8, 13-16). W I okresie badań najwyższe stany biomasy rejestrowano w maju--czerwcu oraz jesienią i zimą. W II okresie brak, tak typowych dla saprofagów, maksimów wiosennych i jesiennych liczebności i biomasy.

Przeważającą część populacji C. sphagnetorum tworzą osobniki kompletne, bez widocznej regeneracji. Stanowią one w zależności od okresu badań i zespołu roślinnego ok. 54-74% zagęszczenia i 73-87% biomasy. Pozostałe grupy są mniej liczne i udział ich nie przekracza kilku procent.

Średni ciężar osobnika Enchytraeidae ogółem, a także kompletnych okazów C. sphagnetorum zmienia się w sposób bardzo regularny (rys. 9-12). Najcięższe okazy występują w miesiącach zimowych, najlżejsze latem. Fakt ten należy wiązać ze zjawiskami fragmentacji - intensywnej latem, znikomej w miesiącach o niskiej temperaturze.

Przeważającą część produkcji Enchytraeidae w badanych ekosystemach leśnych realizuje C. sphagnetorum. Gatunki o rozrodzie generatywnym wytwarzają znikomą ilość biomasy. W grądzie, borze mieszanym i borze sosnowym produkcja tej grupy kształtuje się na poziomie od 0,83 do 4,35 $kJ \cdot m^{-2} \cdot rok^{-1}$. Znaczącą ilość biomasy produkują te gatunki jedynie w łęgu - 11,93 $kJ \cdot m^{-2} \cdot rok^{-1}$ (I okres) i 18,38 $kJ \cdot m^{-2} \cdot rok^{-1}$ (II okres) (tab. X).

Gatunek dominujący produkuje biomasę o wartości energetycznej od 17,29 kJ $\cdot$ m^{-2} $\cdot$ rok^{-1} w borze sosnowym do 32,15 i 31,48 kJ $\cdot$ m^{-2} $\cdot$ rok^{-1} w borze mieszanym i grądzie (tab. IX). W następnym roku, równolegle ze wzrostem zagęszczenia i biomasy, rośnie produkcja - najwyraźniej w borze sosnowym (87,29 kJ $\cdot$ m^{-2} $\cdot$ rok^{-1}) i borze mieszanym (94,37 kJ $\cdot$ m^{-2} $\cdot$ rok^{-1}).

Porównując średnią biomasę i produkcję stwierdza się, że w ciągu roku C. sphagnetorum jest zdolna kilkakrotnie wytworzyć istniejącą w terenie biomasę. P : B tego gatunku zmienia się w różnych ekosystemach i latach badań od 2,44 do 3,83 (tab. XI).

8. REFERENCES

1. A b r a h a m s e n G. 1969 - Sampling design in studies of population densities in Enchytraeidae (Oligochaeta) - Oikos, 20: 54-66.
2. A b r a h a m s e n G. 1970 - Statistical analysis of population density data of soil animals, with particular reference to Enchytraeidae (Oligochaeta) - Oikos, 21: 276-284.
3. A b r a h a m s e n G. 1972 - Ecological study of Enchytraeidae (Oligochaeta) in Norwegian coniferous forest soils - Pedobiologia, 12: 26-82.
4. C h r i s t e n s e n B. 1959 - Asexual reproduction in the Enchytraeidae (Olig.) - Nature, Lond. 184: 1159-1160.
5. C z e r w i ń s k i Z., R o o-Z i e l i ń s k a E., C z e r w i ń s k a K. 1974 - Gleby rezerwatu Grabowy w Puszczy Kampinoskiej /Soils of the "Grabowy" reservation in the Kampinos Forest/ - Phytocoenosis, 3: 17-43.
6. D a s h M. C., C r a g g J. B. 1972 - Ecology of Enchytraeidae (Oligochaeta) in Canadian Rocky Mountain soils - Pedobiologia, 12: 323-335.
7. D o z s a-F a r k a s K. 1973a - Some preliminary data of the frost tolerance of Enchytraeidae - Opusc. Zool. 11: 95-97.
8. D o z s a-F a r k a s K. 1973b - Saisondynamische Untersuchungen des Enchytraeiden-Besatzes im Boden eines ungarischen Quercetum petraeae cervis - Pedobiologia, 13: 361-367.
9. G ó r n y M. 1975a - Metody zoocenologicznej oceny wazonkowców (Enchytraeidae) drzewostanów sosnowych o zróżnicowanej okrywie gleby /Procedures of zoocoenological appraisal of

Enchytraeidae in pine stands with diverse soil cover/ - Polskie Tow. Glebozn., Pr. Kom. Nauk., Kom. Biol. Gleby (III), Warszawa, 16: 83-97.

10. G ó r n y M. 1975b - Zooekologia gleb leśnych /Zooecology of forest soils/ - Państwowe Wydawnictwo Rolnicze i Leśne, Warszawa, 311 pp.

11. H u h t a V. (in press) - Mortality in enchytraeid and lumbricial populations caused by hard frosts (In: Proc. Symp. Adaptations of Animals on Winter Conditions - Moscow 17-21 April 1978) - Moskva.

12. H u h t a V., K o s k i e n n e m i A. 1975-Numbers,biomass and community respiration of soil invertebrates in spruce forests at two latitudes in Finland - Ann. Zool. Fenn. 12: 164--182.

13. K a s p r z a k K. 1975 - Wazonkowce (Oligochaeta, Enchytraeidae)zespołu grądowego (Querceto-Carpinetum medioeuropeum Tx. 1936) w Wielkopolskim Parku Narodowym /Enchytraeidae (Oligochaeta) in the forest association Querceto-Carpinetum medioeuropeum Tx. 1936 in the National Park of Great Poland/ - Fragm. faun. 8: 115-128.

14. K i t a z a w a Y. 1971 - Biological regionality of the soil fauna and its function in forest ecosystem types (In: Productivity of forest ecosystems, ecology and conservation, Ed. P. Duvigneaud) - UNESCO, Paris, 485-498.

15. M a c f a d y e n A. 1967 - Methods of investigation of productivity of invertebrates in terrestrial ecosystem (In: Secondary productivity of terrestrial ecosystems (principles and methods), Ed. K. Petrusewicz) - Państwowe Wydawnictwo Naukowe, Warszawa-Kraków, 383-412.

16. M c N e i l l S., L a w t o n J. H. 1970 - Animal production and respiration in animal populations - Nature, Lond. 225: 472-474.

17. M ö l l e r F. 1969 - Ökologische Untersuchungen an terricolen Enchytraeiden Populationen - Pedobiologia, 9: 114-119.

18. N i e l s e n C. O. 1955 - Studies on Enchytraeidae. 5. Factors causing seasonal fluctuations in numbers - Cikos, 6: 153-169.

19. N i e l s e n C. O. 1961 - Respiratory metabolism of some populations of enchytraeid worms and free living nematodes - Oikos, 12: 17-55.

20. N i e l s e n C. O., C h r i s t e n s e n B. 1959 - The Enchytraeidae. Critical revision and taxonomy of European species - Nat. jutl. 8-9: 1-160.
21. N u r m i n e n M. 1967 - Ecology of enchytraeids (Oligochaeta) in Finnish coniferous forest soil - Ann. Zool. fenn. 4: 147-157.
22. O'C o n n o r F. B. 1955 - Extraction of enchytraeid worms from a coniferous forest soil - Nature, Lond. 175: 815-816.
23. O'C o n n o r F. B. 1957 - An ecological study of the enchytraeid worm population of a coniferous forest soil - Oikos, 8: 161-199.
24. O'C o n n o r F. B. 1962 - The extraction of Enchytraeidae from soil (In: Progress in soil zoology, Ed. P. W. Murphy) - Butterworths, London, 279-285.
25. O'C o n n o r F. B. 1963 - Oxygen consumption and population metabolism of some populations of Enchytraeidae from North Wales (In: Soil organisms, Eds. J. Doeksen, J. van der Drift) - North-Holland Publishing Company, Amsterdam, 32-48.
26. O'C o n n o r F. B. 1971 - The enchytraeids (In: Methods of study in quantitative soil ecology: population, production and energy flow. IBP Handbook No. 18, Ed. J. Phillipson) - Blackwell Scientific Publications, Oxford-Edinburgh, 83-106.
27. P e r s s o n T., L o h m U. 1977 - Energetical significance of the annelids and arthropods in a Swedish grassland soil - Ecol. Bull. No. 23: 1-212.
28. P e t r u s e w i c z K. 1967 - Suggested list of more important concepts in productivity studies (definitions and symbols) (In: Secondary productivity of terrestrial ecosystems (principles and methods), Ed. K. Petrusewicz) - Państwowe Wydawnictwo Naukowe, Warszawa-Kraków, 51-58.
29. P e t r u s e w i c z K., M a c f a d y e n A. 1970 - Productivity of terrestrial animals - Blackwell Scientific Publications, Oxford-Edinburgh, 189 pp.
30. P h i l l i p s o n J., A b e l R., S t e e l J., W o o d e l l S. R. Y. 1979 - Enchytraeid numbers, biomass and respiratory metabolism in a beach woodland - Wytham Woods, Oxford - Oecologia (Berl.), 43: 173-193.
31. S p r i n g e t t J. A. 1963 - The distribution of three species of Enchytraeidae in different soils (In: Soil organisms, Eds. J. Doeksen, J. van der Drift) - North-Holland Publishing Company, Amsterdam, 414-419.

32. S p r i n g e t t J. A. 1970 - The distribution and life histories of some moorland Enchytraeidae (Oligochaeta) - J. anim. Ecol. 39: 725-737.
33. S p r i n g e t t J. A., B r i t t a i n J. E., S p r i n g e t t B. P. 1970 - Vertical movement of Enchytraeidae (Oligochaeta) in moorland soils - Oikos, 21: 16-21.
34. S t a c h u r s k i A., Z i m k a J. R. 1975 - Leaf fall and the rate of litter decay in some forest habitats - Ekol. pol. 23: 103-108.
35. S t a n d e n V. 1973 - The production and respiration of an enchytraeid population in blanket bog - J. anim. Ecol. 42: 219-245.
36. T r a c z y k H., T r a c z y k T. 1965 - Charakterystyka fitosocjologiczna terenów badawczych Instytutu Ekologii PAN w Dziekanowie Leśnym (Puszcza Kampinoska) [Phytosociological characteristics of the research areas of the Institute of Ecology, Polish Academy of Sciences at Dziekanów Leśny (Kampinos Forest near Warsaw)] - Fragm. flor. geobot. 11: 547-562.
37. Z i m k a R. J., S t a c h u r s k i A. 1976 - Vegetation as modifier of carbon and nitrogen transfer to soil in various types of forest ecosystems - Ekol. pol. 24: 493-514.