Ewa NOWAK

Department of Zoology and Ecology, Institute of Zoology, University of Warsaw, Warsaw

POPULATION DENSITY OF EARTHWORMS AND SOME ELEMENTS OF THEIR PRODUCTION IN SEVERAL GRASSLAND ENVIRONMENTS*

ABSTRACT: The numbers and biomass of earthworms were assessed in five grassland environments differing by the way of their utilization. A comparison of the species composition of the earthworm communities has shown that agricultural activities (mowing, grazing) lead to a decrease in the diversity of the community. There were 9 species present in a reserve meadow and 5 in pastures. The production of the dominant earthworm species, *Allolobophora caliginosa* Sav., in a grazed pasture (of a low primary production) was about 12 kcal/m^2 per year, in a former sheep-fold pasture (with a high primary production) — about 58 kcal/m^2 per year, the turnover being 1.3 and 0.9, respectively. The biomass of the entire earthworm community was found to represent from 0.4% of the organic matter returned to the soil in the grazed pasture, to 2.4% in the former sheep-fold pasture.

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1. THE AIM OF THE STUDY AND DESCRIPTION
OF STUDY AREA

The study represents part of a series of investigations concerned with the productivity of grassland ecosystems.

All meadow ecosystems found under the climatic conditions of Poland are seminatural communities. Depending on the type of agricultural use — pasturing, or mowing — the manner in which man interferes with the dead organic matter economy of the habitats varies. Thus the kind and amount of organic matter available to the soil fauna communities are variable.

The objective of this study was to assess whether the role of the earthworms — one of the most important groups of saprophagous soil organisms — in the economy of the dead organic matter in grassland ecosystems varies with differential grassland utilization.

During the study the numbers and biomass of the earthworms in meadows and pastures were determined, and the production of the population of the dominant species — *Allolobophora caliginosa* (Sav.) in the pastures was analysed.

The investigations were carried out mainly in mountain pastures of the association *Lolio-Cynosuretum cristati* R. T. 1937 (K o c h e v and T r a c z y k 1974), during three growing seasons of the years 1969–1971.

The materials gathered were compared with the results of the less extensive studies carried out in the years 1968–1969 in three lowland meadows. Two of the meadows belonged to the association *Arrhenatheretum medioeuropaeum* (Br.-Bl. 1919) Oberd. 1952 the most frequently encountered association in the lowlands, whereas one meadow belonged to the association *Stellario-Deschampsietum* Freitag 1957 (T r a c z y k 1971).

The pastures covered an area of 100 hectares in a large complex of pastures situated in the Małe Pieniny mountains (part of the Carpathian chain), on a terraced southern slope about 700 m a.s.l.

The soils of the pastures were weakly leached pseudogley brown soils, with a low content of calcium and phosphorus, and a high content of potassium, magnesium and iron. The top soil layer contained 2.13% of well decomposed humus, with the pH of the humus layer being weakly acid (Tab. I) (C z e r w i ń s k i and T a t u r 1974).

The lowland meadows were meadows of the Vistula Valley alluvia near Warsaw. The meadow of the association *Stellario-Deschampsietum* was on moist, rather poor soils of the dark-coloured muck soil type. This was the reserve meadow. The two mown meadows of the association *Arrhenatheretum medioeuropaeum* (designated as MI and MII) were meadows on rich soils of the alluvial gleyed brown soil type. One of these meadows — MII — was characterized by a lower porosity, a higher water-table and lower primary production (a detailed description of the meadows can be found in T r a c z y k 1971, C z e r w i ń s k i 1971).

The above-enumerated habitats were utilized in different ways: grazed, mown, or with no interference by man. The manner of utilization, as well as the quantity of primary production, affected the amount and quality of the organic matter returned to the soil, and thereby the supply of food available to the soil animals.

In the pasture, the amount of organic matter returned was large. It consisted primarily of sheep faeces, that is, material with a higher content of nitrogen and mineral compounds than that found in the vegetable debris. In the pasture environment three habitat types were distinguished, depending on the way of utilization: a grazed pasture (*Pas*), former sheep-fold pasture (*PF*), and a sheep-fold (*F*).

The grazed pasture, referred to also as the pasture (*Pas*) was a habitat where the traditional extensive sheep grazing continued from May until September.

The former sheep-fold pasture (*PF*) and the sheep-fold (*F*) were situated in an area which, in addition to its being used as a grazing area, was used every three years as a sheep-fold[1]. In the first year the part used for penning sheep was found to be greatly damaged by the sheep manure. In the second and third years normal sheep grazing continued in these areas. The former sheep-fold pasture (*PF*) was the area used as a sheep-fold one or two years before the season of research.

The third habitat, referred to as the sheep-fold (*F*), comprised areas that were being used for penning sheep in them during the year of study — it was therefore a considerably changed habitat undergoing rapid succession. The large dose of manure caused changes in the plant association of the penned areas. The percentage of monocotyledonous plants increased and the primary production of the aboveground parts doubled. At the same time the soil microbiological process became activated (C z e r w i ń s k i et al. 1974). The content of C and N in the soil increased and the pH changed towards the basic value — from 5.7 to 6.1 (C z e r - w i ń s k i and T a t u r 1974).

The yearly influx of organic matter returned to the soil varied from habitat to habitat (Tab. I). In the grazed pasture (*Pas*) the lowest influx was recorded — 623 g dry wt/m^2. It consisted of 360 g dry wt/m^2 of sheep faeces (O l e c h o w i c z 1974) and 201 g dry wt/m^2 of dead roots (P l e w c z y ń s k a — K u r a ś 1974). The quantity of vegetable debris was assumed to be equal to the average biomass of the green parts, i.e., 62 g dry wt/m^2 (A n d r z e j e w s k a 1974).

In the former sheep-fold pasture more organic matter was returned to the soil, as much as 781 g dry wt/m^2 (Tab. I). As in the grazed pasture, the amount of manure left here by the grazing sheep was 360 g dry wt/m^2. Dead roots represented 311 g dry wt/m^2, while the green part debris accounted for 119 g dry wt/m^2 (A n d r z e j e w s k a 1974, P l e w - c z y ń s k a — K u r a ś 1974).

The third habitat, referred to as the sheep-fold (*F*), was characterized by a very extensive flow of organic matter to the soil, equal to at least 901 g dry wt/m^2 per year, where the manure constituted 500 g dry wt/m^2 per year. Because this area was not used for grazing during the first year, the entire primary production, equal to about 200 g dry wt/m^2 in green parts, and 201 g dry wt/m^2 in roots (these values have been adopted on the basis of the data given by C z e r w i ń s k i et al. 1974), was returned to the soil.

In the assessment of the quantity of organic matter returned to the soil in the meadows the assumption was made that root production was equal to the production of aboveground parts of plants (T r a c z y k 1968, P l e w c z y ń s k a — K u r a ś 1974). In the association *Stellario-Deschampsietum* the annual supply thus assessed amounted to 390 g dry wt/m^2. In the meadows of the association *Arrhenatheretum* the supply of organic matter was much higher, and despite the fact that 80% of the crop was harvested it amounted to about 500 g dry wt/m^2 per year (Tab. I).

The climate of the foothills pastures is characterized by an average annual total amount of precipitation of about 872 mm, and an average annual temperature of 5.5°–6.0°C (C z e - m e r d a 1966).

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[1] The sheep-folds were enclosures, each of 1,250 m^2 in area, moved over the pasture every 2–3 days. The sheep stayed there overnight. Only 1/3 of the whole pasture was used as sheep-folds each year.

Tab. I. Description of the environments under study

| | Lolio-Cynosuretum cristati | | | Stellario-
-Deschamp-
sietum
reserve
meadow | Arrhenatheretum
medioeuropaeum
mown meadows | |
| | grazed
pasture
Pas | former
sheep-fold
pasture
PF | sheep-fold
F | | M II | M I |
|---|---|---|---|---|---|---|
| Influx of organic
matter to the soil
$(g\ dry\ wt/m^2)$ | 623 | 781 | 901 | 390 | 490 | 500 |
| Cellulose decomposi-
tion rate*
(%/month) | 5.4 | 8.6 | 6.3 | 1.5 | 2.7 | 2.7 |
| C : N** | 9.7 | 8.6 | 9.3 | 18.7 | 10.0 | 9.2 |
| C**
(%) | 2.13 | 2.42 | 2.60 | 4.07 | 6.35 | 2.68 |
| pH in H_2O | 5.7 | 5.5 | 6.1 | 5.5 | 6.5 | 6.1 |

*Jakubczyk (1971) and Jakubczyk (1974).
**Czerwiński (1971), Czerwiński et al. (1974) and W. Walendzik (unpubl.).

The lowland areas, where the meadows under study are situated, differ slightly from the foothills by the average air temperature, and more markedly by precipitation. In the growing season of 1969, when all the above-enumerated habitats were investigated, the differences in average temperature were very small: $13.9^{\circ}C$ — Warsaw (Vistula Valley), $14.0^{\circ}C$ — Nowy Sącz (Małe Pieniny). At that time the total precipitation was 287 mm for Warsaw, and 528 mm for Nowy Sącz. The distribution of precipitation in individual months was similar in both localities.

The assumed season of earthworm activity was the period in which the average monthly temperature of the soil at the depth of 10 cm was equal to, or higher than $0.5^{\circ}C$. In the study areas it lasted from early April until the end of November (240 days).

2. METHODS

2.1. Assessment of numbers and biomass

The numbers of the earthworms were estimated by handsorting of samples 625 cm² in area and 30 cm deep. In each habitat 10 such samples were dug up every month. The soil was sorted by hand 3 times (Axelson et al. 1971). The depth of the pits was determined on the basis of a series of soil samples collected from three 15-cm layers. The number of earthworms in layer I was always found to exceed 80% of the numbers of the whole population, and layers I and II together practically contained the whole population. The species composition of the

earthworms (presence of mobile species *Lumbricus* sp.) was cnecked by three series of formaldehyde samples (R a w 1959, S a t c h e l l 1969). Both types of samples proved to be equally efficient, however the relief of the terrain suggested the choice of the handsorting method.

The summaries relating to the whole macrofauna contain the results from the monthly series of 20 soil cores of 100 cm^2 in area, as only in the small-sample procedure could all the animals of the macrofauna, such as enchytraeids and small dipteran larvae, be thoroughly extracted. It is from these samples that the data on the numbers of cocoons is derived.

The earthworm biomass was determined on the basis of specimens preserved in 75% alcohol. During such a storage for from 7 to 10 months the specimens were found to loose 32% of their weight (N o w a k 1971). The ratio of dry weight to wet weight, as calculated for 55 individuals, was 22%. Using the established ratios the biomass of the animals was calculated, including the contents gut. In the calculation of the caloricity 26% of the weight was subtracted from the dry weight, this quantity being equivalent to the weight of the alimentary canal (S a t c h e l l 1971). The caloricity of 1 g body weight was assumed to be 4.42 kcal (F r e n c h, L i s c i n s k y and M i l l e r 1957).

2.2. A s s e s s m e n t o f *Allolobophora caliginosa* p r o d u c t i o n

Production was only assessed for *Allolobophora caliginosa* in the pasture environment.

The growth rate, fecundity and mortality of the population were determined on the basis of laboratory and field cultures. In laboratory cultures single individuals were weighed and placed in containers, each of 150 cm^3 in capacity, filled with soil taken from the study areas (from the 0–10 cm layer) and kept at about $13°C \pm 1°$. The earthworms were weighed every month, and thus the monthly weight increments were determined. Apart from that, in each of a number of vessels, 1,500 cm^3 in capacity, 10 sexually mature earthworms were reared. The fecundity of these earthworms was checked every month by removing the cocoons.

In the growing season of 1971 (from mid-May until mid-October) field cultures were conducted. Single earthworms were placed in gauze bags of the size 20 cm^2 × 15 cm, filled with soil. Every month a check was made for mortality and weight increase of the individuals. Dead individuals were replaced with new ones. In the pasture that had formerly been used as a sheep-fold (*PF*) 144 individuals (720 weight measurements) were kept in culture, as were 30 individuals (150 measurements) from grazed pasture (*Pas*).

The fecundity of *A. caliginosa* was estimated on the basis of the number of sexually mature individuals and the number of cocoons produced by each sexually mature earthworm in the culture.

Two methods were used for the determination of the death rate of the earthworms: (1) on the basis of the reduction of numbers in the field culture (the reduction occurred without the participation of large predators), (2) on the basis of the consecutive changes in numbers of *A. caliginosa* according to the formula:

$$E = N_{t_1} - (N_{t_2} - \nu_{t_2}) \tag{a}$$

where N_t – density in month t, ν_t – numbers of newly born individuals (i.e. animals weighing 17–47 mg).

The production of *A. caliginosa* was estimated by Allen's graphical method (P e t r u -

s e w i c z and M à c f a d y e n 1970). It was calculated as the sum of the areas under the
straight-line segments of the survivorship curve plotted for the corresponding weight classes.
The following formula was used in the calculations:

$$P = \sum \frac{v_i + v_{i+1}}{2} \ (W_{i+1} - W_i)$$
                                                                                  (b),

where v_i — number of individuals of successive stages (attaining the successive size classes in
time $t_{i...}$); W_i — weight of individuals of the successive stages.

There is no data on the survivorship model of the earthworms in the grazed pasture. For an
approximate estimation of the production in this habitat two methods were used: (1) Allen's
method with the assumption that in the former sheep-fold pasture and in the grazed pasture the
mortality curves are similar, (2) a method based on the knowledge of the growth curve
(V i n b e r g, P e č e n and Š u š k i n a 1965). The course of the first part of the growth
curve for the former sheep-pen pasture had been known. The production was calculated
according to the formula:

$$P = \sum \frac{(W_{i+1} - W_i) \, v_{i+1}}{t_i}$$
                                                                                  (c),

Using data from the literature the author also calculated the respiration of the whole
earthworm community of the habitats studied. The calculations were based on B y z o v a's
(1965) formula on the relationship between size and oxygen uptake of the earthworms. The
results were reduced to an average temperature of the study period, i.e. 11°C, assuming that
Q 10 $\approx$ 2 (on an average about 1.96 according to B o l t o n 1970). Among the many papers
dealing with the respiration in the earthworms B y z o v a's (1965) paper is the one in which
the values of the respiratory rate given for the surface species differ from those for the species
living in deeper soil layers, hence its usefulness in the comparison of earthworm communities. It
was assumed that the energy equivalent of one litre of oxygen is 4.8 kcal (P e t r u s e w i c z
and M a c f a d y e n 1970).

3. RESULTS

3.1. Species composition and dominance
structure of the earthworms

In the grassland ecosystems under study 10 earthworm species were found: *Allolobophora
caliginosa* (Sav.), *A. rosea* (Sav.), *A. chlorotica* (Sav.), *A. georgii* Mich., *Dendrobaena octaedra*
(Sav.), *D. rubida* (Sav.), *Eiseniella tetraedra* (Sav.), *Octolasium lacteum* (Oerley), *Lumbricus
rubellus* Hoffm. and *L. terrestris* L. All these species, except *A. georgii*, are common species.
Three of them: *D. octaedra*, *D. rubida* and *L. rubellus* are placed among the surface species.
They live in the 0—5 cm layer and feed on poorly decomposed litter. In this species group the
author included *L. terrestris* on account of its feeding habits (and the difficulty in identification
of young individuals).

The remainder of the species — soil earthworms — live at a depth of are relatively rare on the
surface. Their food consists of more well decomposed organic matter and mineral parts. This
species group plays an important rôle in the mixing of the soil and accelerating of the micro-
biological processes.

The percentage contribution of the surface earthworms varied from 43% of the population in the reserve meadow to 1% in the former sheep-fold pasture (*PF*). The pH of these habitats, which varies from 5.5 to 6.5, cannot be the factor that limits the distribution of the earthworms (cf. S a t c h e l l 1955). Thus the distribution of this group is probably determined by the type of decomposition of the organic matter. Both the percentage contribution and numbers of the surface earthworms appeared to decrease as the rate of cellulose decomposition in the environment (Fig. 1) increased. This group is, therefore, a characteristic component of ecosystems of a low microbiological efficiency. A similar type of correlation between the occurrence of some of the earthworm groups and the C:N ratio of the soil has been reported by B o u c h é (1971).

In all the habitats considered, except the reserve meadow, the ubiquitous species: *A. caliginosa* and *A. rosea*, were found to be the dominant and sub-dominant species. These species dominate in most grassland environments in Central Europe and in some outside Europe,

Fig. 1. Relationship between the percentage of surface earthworms and the rate of organic matter decomposition

S.–D. – reserve meadow *Stellario-Deschampsietum*, *MI, MII* – mown meadows *Arrhenatheretum*, *Pas* – pasture *Lolio-Cynosuretum*, *PF* – former sheep-fold pasture *Lolio-Cynosuretum*, *F* – sheep-fold *Lolio-Cynosuretum*

regardless of their soil and geographic diversity (B a l u e v 1950, A l e j n i k o v a 1969, V a ł i a c h m e d o v 1969, Z a j o n c 1971), and even in crop-field environments (J o p k i e-w i c z 1972, A t l a v i n y t é 1973), and in some woodland habitats (B o u l a n g é 1968, Z a j o n c 1971). Such a high plasticity of a species is rare.

In the clearly dominant structure of the earthworm community two types of dominance can be distinguished: a relatively uniform structure, and a decidedly dominant one.

(1) In the relatively uniform structure the dominance index (O d u m 1971 after Simpson 1949) varies between 0.21 and 0.30 (Tab. II). The dominant species represents 30–50% of numbers, and the next species comes up to 10–30% of the population. This type of structure is found in all meadow habitats and in the typical grazed pasture, and it occurs in its most typical form in the multi-species reserve meadow of the association *Stellario-Deschampsietum* (dominance index 0.21; Tab. II).

(2) With the decidedly dominant structure the dominance index value is 0.58, and the most numerous species represents over 70% of numbers. This type of dominance structure was found to occur in the sheep-fold environments, i.e. in the former sheep-fold pasture and in the sheep-fold (Tab. II). The density of the species *A. caliginosa*, which is most plastic and which exhibits a wide range of dominance possibilities showed a tenfold increase as a result of the penning-up of sheep.

In the ecosystems discussed there occurred a reduction in the species composition of the earthworm community. The number of species decreased from 9 – in the reserve meadow, down to 5 – in the pastures (Tab. II). The index of variety of species (Margalef 1958 after
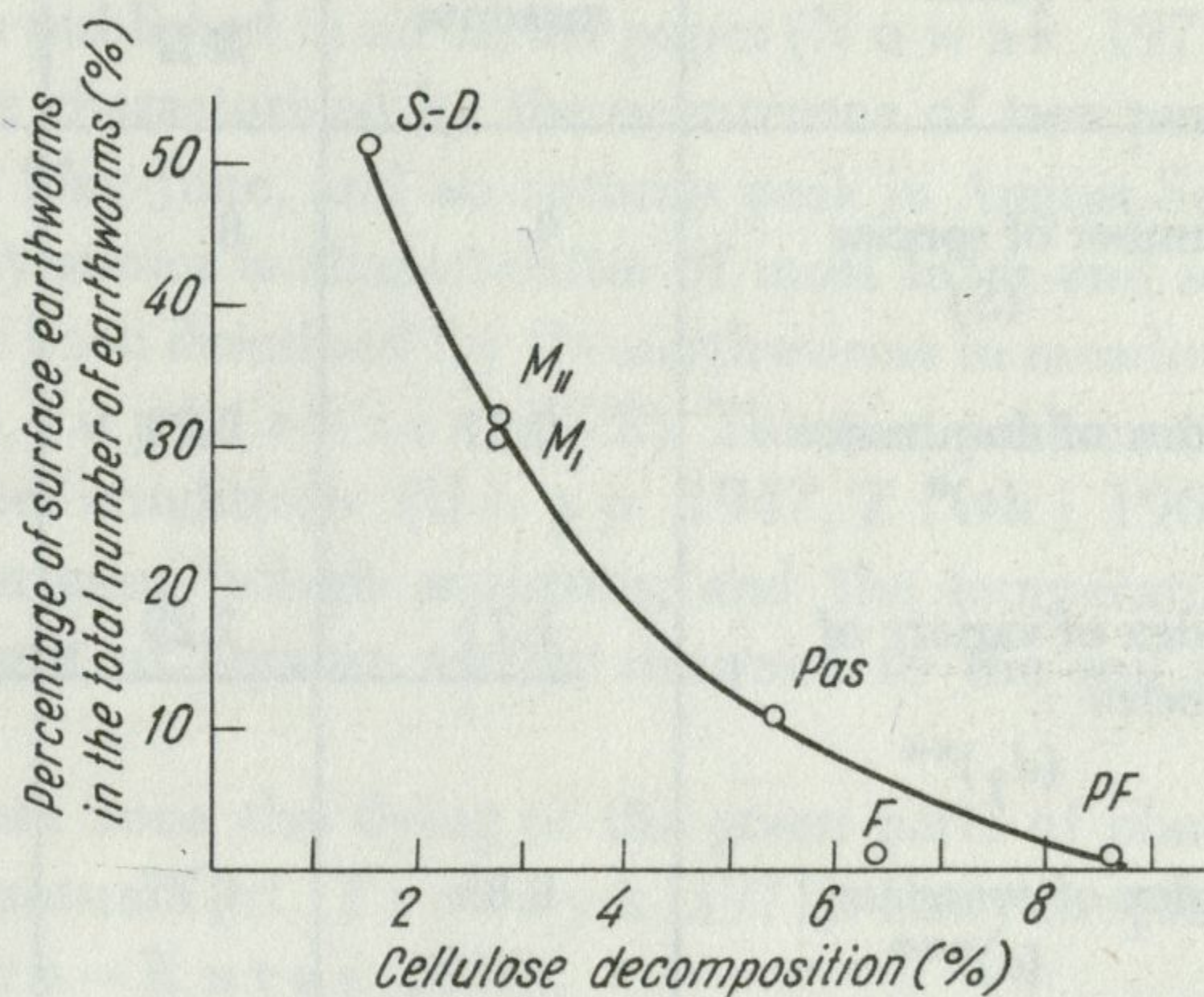
Tab. II. Indices of diversity of the earthworm communities in the environments investigated

Index	Reserve meadow	Mown meadows		Pasture Pas	Former sheep-fold pasture PF	Sheep-fold F
		M II	M I			
Number of species (S)	9	8	6	5	5	5
Index of dominance (c)*	0.21	0.29	0.28	0.30	0.58	0.58
Index of variety of species (d₁)**	1.71	1.29	1.22	0.83	0.62	0.74
Index of evenness (e)***	0.86	0.77	0.82	0.81	0.48	0.65

$*c = \Sigma(n_i/N)^2$ (Simpson 1945 after O d u m 1971).

$**d_1 = \dfrac{S-1}{\ln N}$ (Margalef 1958 after O d u m 1971).

$***e = \dfrac{-\Sigma(n_i/N)\ln(n_i/N)}{\ln S}$ (O d u m 1971 after Pielou 1966).

n_i = percentage of individual species in total numbers, N = numbers.

O d u m 1971) decreased in the following order: the reserve meadow, cultivated meadows, grazed- and penned pastures (Tab. II). This process was parallel to the reduction of the vegetation structure and to the acceleration of the rate of organic matter decomposition (Tab. I).

The utilization of meadows (mowing, grazing) appears to cause a reduction in the species composition not only of the plant community, but also of the animal·community. The pasture is a habitat created as a result of the strong and diverse stimuli afforded by animal grazing. A „time integration of the trophic stimulus", as exemplified by the penning-up sheep, causes a further reduction in the structure (specific and spatial) of the plant community, as well as a lowering of the diversity of the earthworm community (Tab. II).

A characteristic feature is a certain degree of inertia of the earthworm community in the penned habitat in response to the trophic stimulus. During the first months following the penning of·sheep the community still does not undergo reduction. In spite of the drastic changes in the plant community (destruction by the high rate of manure), the evenness index (Pielou 1966 after O d u m 1971) of the earthworm community in the penned habitat appeared to be higher than in the control area, whereas the community that formed a year after the penning was found to be a clearly reduced community (Tab. II).

The type of dominance structure of the earthworm community in the former sheep-fold pastures permits the presumption that relative to the remainder of the grassland ecosystems these habitats are subject to a considerably stronger control by a set of physical and chemical features (in the particular case probably the content of some elements in the soil, the pH etc.).

3.2. Variation in density and biomass of the earthworms

Population dynamics of earthworms were investigated in the pastures. Data on the variation in density of the meadow earthworms has been published in an earlier paper (N o w a k 1971).

Population dynamics of the earthworms are characterized by the occurrence of two peaks during the year: a spring peak which occurs in May-June, and an autumn peak in August-September (Figs. 2–5). This type of population dynamics is characteristic of most litter and soil animals species of the temperate climate and has been described for the earthworms in meadows and fields (H o p p 1947, N a k a m u r a 1968, J o p k i e w i c z 1972). This two-peak course of variations in density is determined by weather conditions (H o p p 1947, Z i c s i 1969) which are at their optimum in spring and autumn. (a high moisture, and the temperature $9-12^{\circ}C$), and also by variations in the amount of organic matter returned to the soil (as suggested by W a t e r s 1955).

In the grassland ecosystems of the temperate zone the dying of the green parts of plants begins in July and increases steadily until late autumn (cf. T r a c z y k 1971). Early in spring (March) the roots begin to die (P l e w c z y ń s k a – K u r a ś 1974).
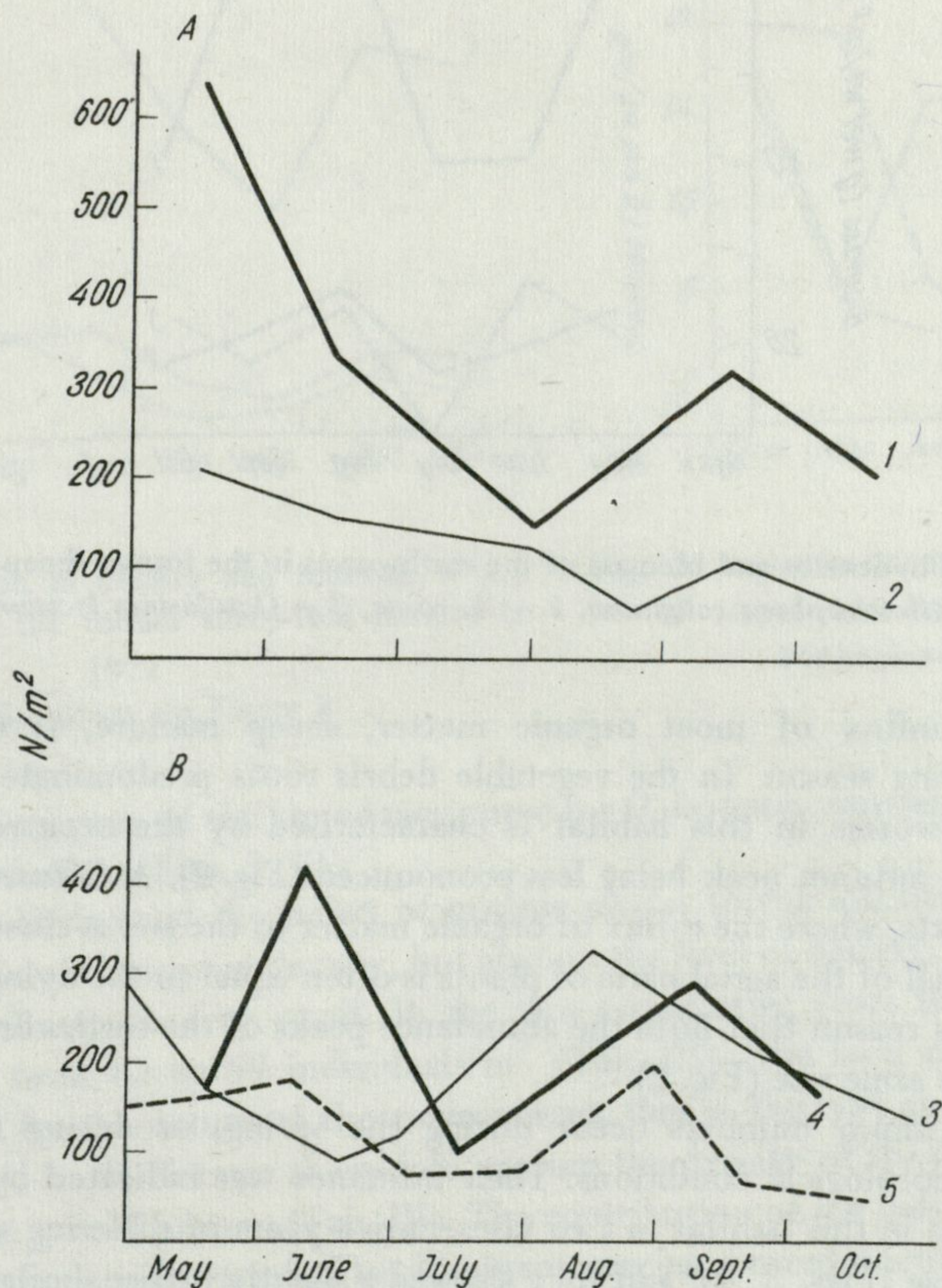

Fig. 2. A comparison of number dynamics of the earthworms in pastures (A) and meadows (B) according to the data for 1969

1 – former sheep-fold pasture, 2 – pasture, 3, 4 – mown meadows MI and MII, 5 – reserve meadow
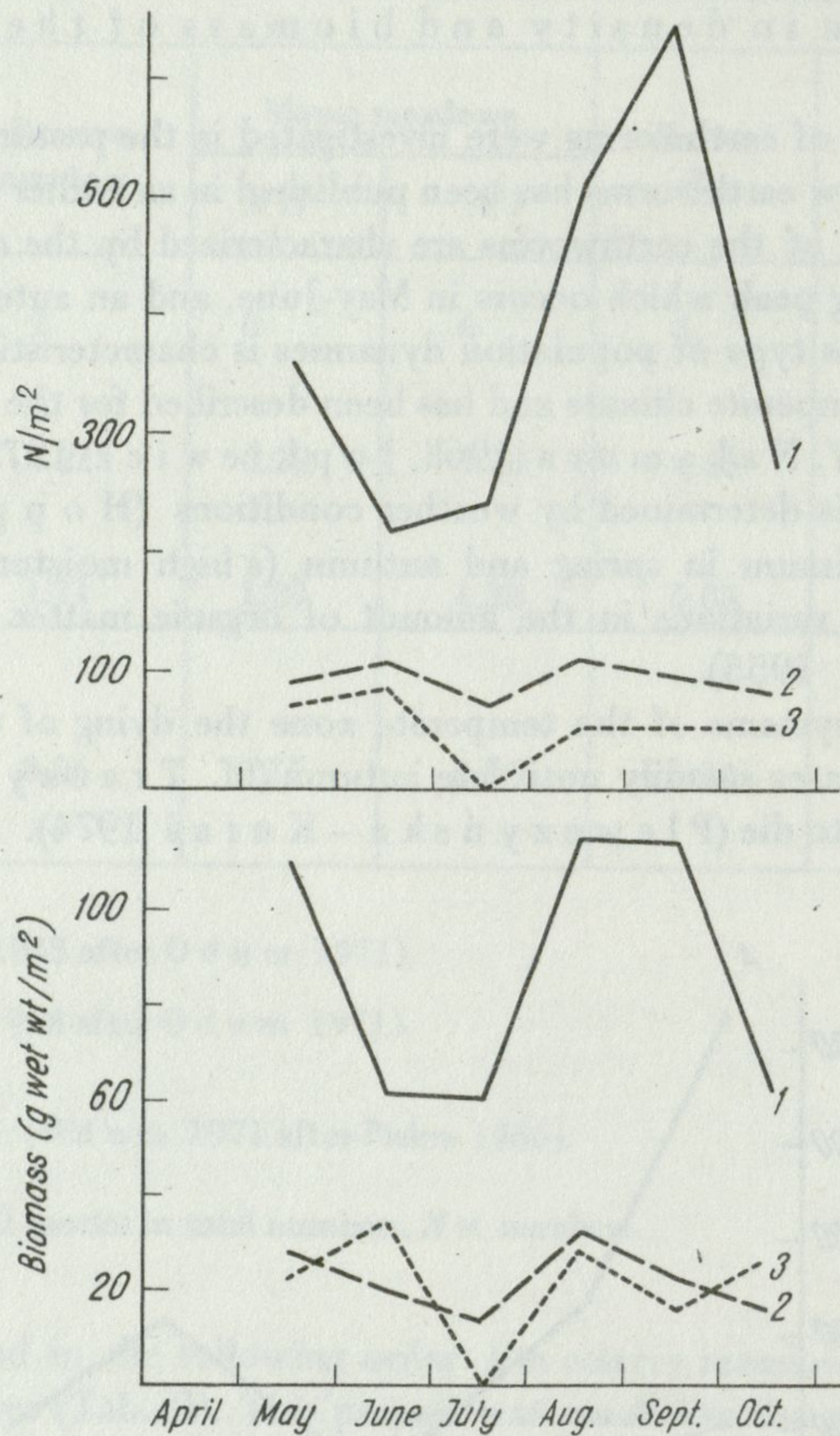
Fig. 3. Variation in density and biomass of the earthworms in the former sheep-pen in 1970
1 — *Allolobophora caliginosa*, 2 — *A. rosea*, 3 — *Octolasium lacteum*

In pastures the influx of most organic matter, sheep manure, is evenly distributed throughout the growing season. In the vegetable debris roots predominate. The variation in density of the earthworms in this habitat is characterised by the occurrence of maximum density in spring, the autumn peak being less pronounced (Fig. 2). A different situation is seen in the meadow habitats, where the influx of organic matter to the soil is closely associated with the season, and the fall of the aerial parts of plants is often equal to the dying rate of the roots. It is probably for this reason that both the abundance peaks of the earthworms in this environment are of about the same size (Fig. 2).

Whether the maximum numbers occur during the spring, or during the autumn peak, depends on the meteorological conditions. Their influence was indicated by the fact that the variations in numbers in this habitat in two consecutive years of differing weather conditions differed in their course (Figs. 3, 4), and they showed a slightly higher similarity in two pasture habitats in the same year (Figs. 4, 5). In 1970, which was a wet year, the most abundant species: *A. caliginosa* and *A. rosea*, attained their maximum density in autumn, whereas in the dry year 1971 the largest numbers occurred in spring. The effect of wheater conditions on the density of the third numerous species *O. lacteum*, which penetrates deeper layers of the soil, is
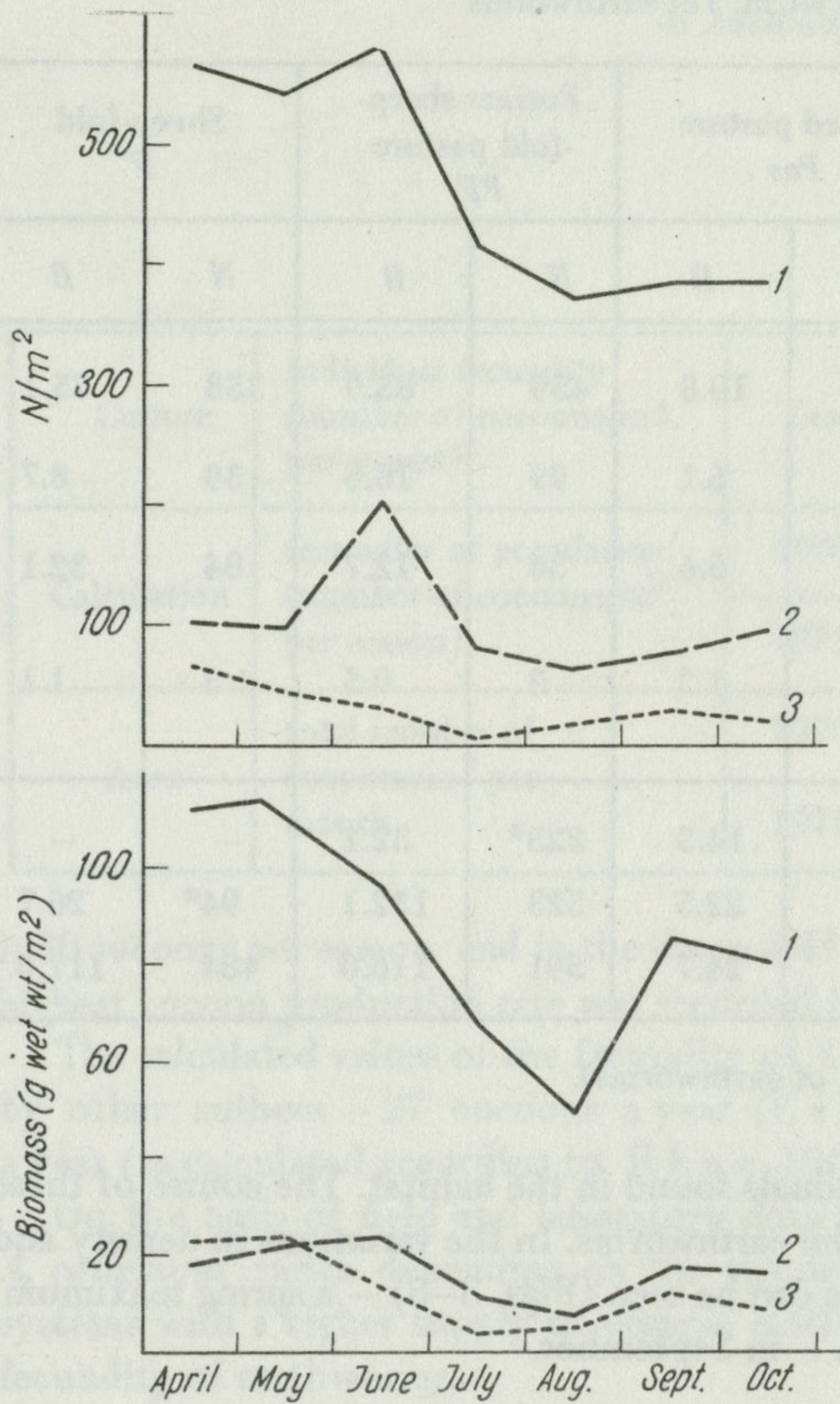
Fig. 4. Variation in density and biomass of the earthworms in the former sheep-fold pasture in 1971
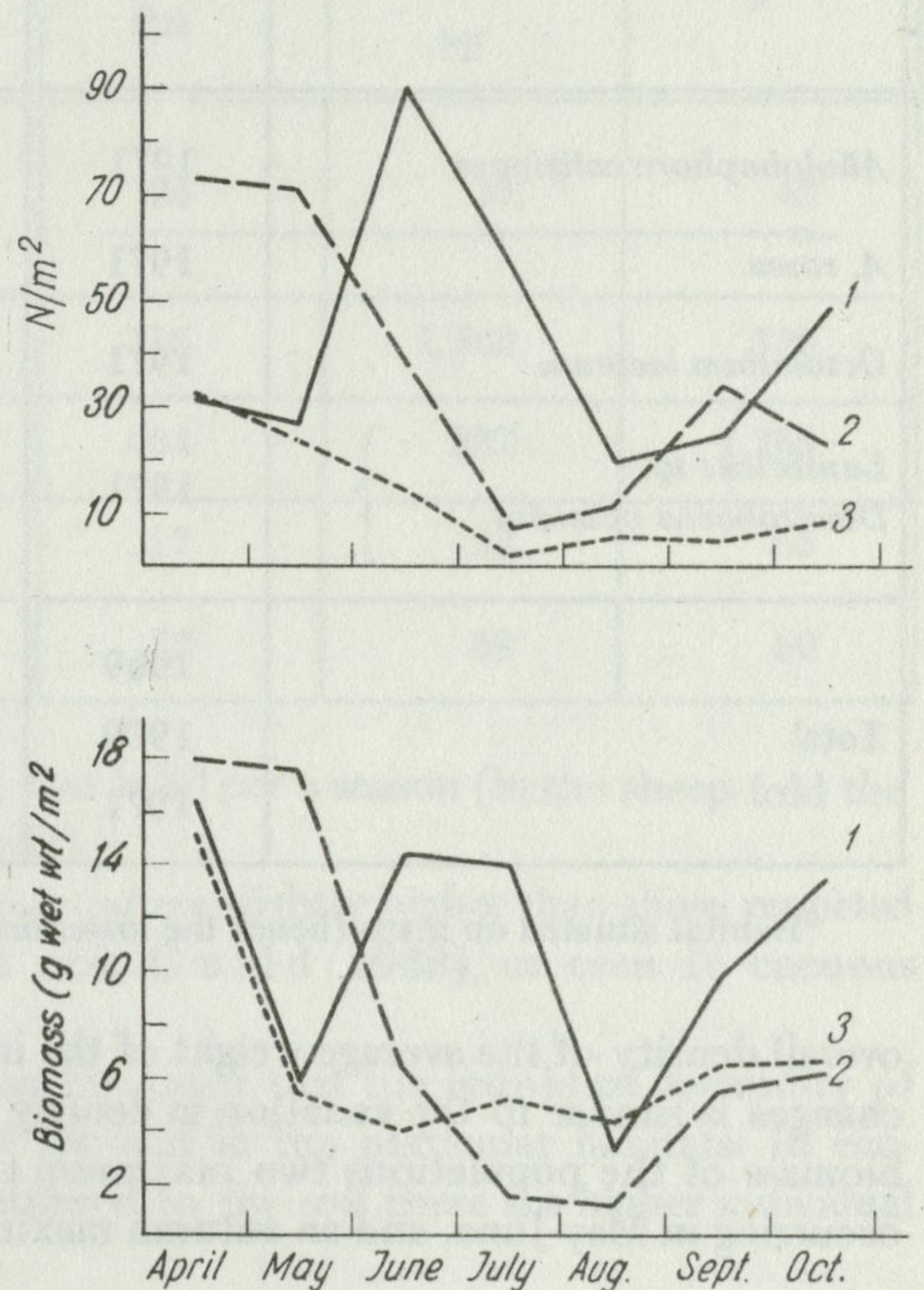For explanations see Figure 3

Fig. 5. Variation in density and biomass of the earthworms in the pasture in 1971
For explanations see Figure 3

less marked. The course of the abundance curve for *O. lacteum* remained unchanged regardless of the year and habitat (Figs. 3—5).

Weather conditions and the influx of organic matter to the soil have an effect not only on the course of the variations in density, but also on the level of density, although in this case the effect of the climate is very small. In the two consecutive years the density in the grazed pasture varied from 83 to 99 individuals/m^2 (Tab. III). The level of numbers is to a larger extent affected by the nature of the environment, that is, the type and quantity of the organic matter supplied. In the former sheep-fold pasture the density of the earthworms was six times as high as in the grazed pasture (Tab. III). The contribution of the individual earthworm species to the increase in density varied. The dominant species showed a tenfold increase in numbers, *A. rosea* and *O. lacteum* — a threefold increase, while the surface species showed a decrease in numbers (Tab. III).

Seasonal variations in the biomass of the earthworms are the resultant of changes in the

Tab. III. The effect of different ways of pasture utilizing on the density (N/m^2)
and biomass (B in g wet wt/m^2) of earthworms

Species	Year	Grazed pasture Pas		Former sheep--fold pasture PF		Sheep-fold F	
		N	B	N	B	N	B
Allolobophora caliginosa	1971	46	10.8	459	85.9	358	75.1
A. rosea	1971	32	6.1	99	16.6	39	8.7
Octolasium lacteum	1971	12	6.6	30	12.7	84	32.1
Lumbricus sp. *Dendrobaena octaedra*	1971	9	1.2	3	0.5	3	1.1
	1969	83	14.5	223*	32.1	–	–
Total	1970	93	22.5	523	132.1	94*	20.7
	1971	99	24.7	591	116.0	484	117.0

*Habitat situated on marls (hence the lower density of earthworms).

overall density of the average weight of the individuals found in the habitat. The course of these changes is similar to the variation in density of the earthworms. In the variations in density and biomass of the populations two maximum values can be seen (Figs. 3–5) – a spring maximum, occurring in May-June, and an autumn maximum – in September.

3.3. Fecundity

The fecundity of the earthworms, as well as the other production parameters, was estimated in the mountain pastures. The fecundity of a population depends on the number of individuals able to reproduce and on individual fecundity.

On the basis of laboratory cultures the individual fecundity of *A. caliginosa*, as indicated by the number of cocoons produced by one mature individual during a year, was found to vary with the soils taken from different habitats. The lowest fecundity was recorded for earthworms from the grazed pasture (26 cocoons per one individual per a season) and the highest in the sheep-fold – 42 cocoons (Tab. IV).

A similar tendency to increase the individual fecundity in the different habitats could be observed during the field studies. The cocoons found during the field investigations in most cases belonged to *A. caliginosa* – the most abundant and at the same time most fecund of all the species present in the pasture (E v a n s and G u i l d 1948). The number of cocoons per sexually mature individual was determined during the maximum abundance of cocoons, that is, when the laying of cocoons exceeded their reduction (April 1971). As indicated by the calculation, in the pasture the average monthly rate of cocoon production was 2.9 cocoons per an individual, i.e. 23 cocoons per individual per season; in the former sheep-fold pasture 3.7, that

Tab. IV. The effect of different ways of pasture utilization on the fecundity
of *Allolobophora caliginosa*

			Grazed pasture Pas	Former sheep-fold pasture PF	Sheep-fold F
Culture	Individual fecundity (number of cocoons/ind. per season)	Year	26	35	42 →
Calculation	fecundity of population (number of cocoons/m^2 per season)	1970	115	1,503	520
		1971	404	327	1,265
Area	total number of cocoons/m^2 per month	1970	17	33	65
		1971	32	69	60

is 30 cocoons per season, and in the sheep-fold 4.7, that is 38 per a season (in the sheep-fold the highest cocoon production rate was recorded for July).

The calculated values of the fecundity of *A. caliginosa* are slightly higher than those reported by other authors — 27 cocoons a year (E v a n s and G u i l d 1948), or even 16 cocoons a year (as calculated according to R h e e 1967)[2].

On the basis of field and laboratory data it may be stated that the individual fecundity of *A. caliginosa* varies depending on the richness of the soil in the particular habitats. In ecosystems with a higher supply of organic matter returned to the soil there is a higher individual fecundity of earthworms.

Thus the individual fecundity is one of the elements which may secure an increase of the earthworm population when the food resources of the habitat increase.

Changes of the other element, the number of sexually mature individuals, which determins the fecundity of the population appeared to be irregular in the environment discussed. A certain regularity could only be seen in the variation of fecundity, peculiar to a particular species. The percentage of individuals able to reproduce is: from 2 to 23% of a population of *A. caliginosa*, from 21 to 42% of an *A. rosea* population, and from 18 to 67% of an *O. lacteum* population (Tab. V). The dominant species had the lowest percentage of individuals able to reproduce and at the same time the highest individual fecundity. These two quantities, each of which may compensate for the other, indicate the existence of differences in the biology of the species. *A. caliginosa* probably passes through a prolonged phase of fast growth and a shortened period of sexual maturity, as compared with the remaining two species. The smallest sexually mature individuals of *A. caliginosa* weighed about 210 mg — the largest ones 650 mg, while in *A. rosea* the sexually mature individuals showed a body-weight range of 54—360 mg, and in *O. lacteum* 40—1,000 mg.

In the dominant species the percentage of sexually mature individuals in a population

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[2] Both values are based on laboratory cultures in which the earthworms reproduced throughout the year.

Tab. V. Percentage of sexually mature earthworms in the populations found in pastures utilized in different ways

Species	Year	Grazed pasture Pas	Former sheep-fold pasture PF	Sheep-fold F
Allolobophora caliginosa	1970	16.0	11.2	11.2
	1971	22.7	2.0	9.4
A. rosea	1970	28.2	41.9	23.0
	1971	32.4	21.2	20.8
Octolasium lacteum	1970	20.0	36.5	18.1
	1971	50.0	65.1	67.3

appeared to be in both years slightly higher in the grazed pasture (Pas) than in the former sheep-fold pasture (PF) (Tab. V). A situation like this may be the result of a higher rate of reduction of adult earthworms in the former sheep-fold pasture, or a lower rate of their attaining sexual maturity. To eliminate the effect of reduction the percentage of sexually mature individuals was calculated in relation to the heaviest individuals that might already become mature, i.e. those weighing more than 210 mg. Mature individuals of A. caliginosa represented 30—39% of the heaviest earthworms in the grazed pasture, and 7—29% in the pasture that had formerly been used as a sheep-fold. One may, therefore, say that in a habitat with a lower density of individuals the possibility to attain sexual maturity is more fully used. Here, a stimulation or inhibition of sexual maturation may become a mechanism controlling the density.

The minimum incubation time for the cocoons of A. caliginosa was estimated at 1.5 months, because after this period under optimum laboratory culture conditions earthworms emerged from 30% of the cocoons. It may be presumed that in the field the time between the laying of the cocoons and the hatching of the young individuals lasts during the growing season at least 3 months. Together with the winter period the incubation time probably lasts 8 months, for this is the time interval between the occurrence of maximum numbers of cocoons (September 1970) and the most abundant emergence of the young (April 1971). An 8-month's incubation time corresponds to the average incubation time reported by S a t c h e l l (1967).

Assuming the incubation time for the cocoons laid in spring and in summer to be 3 months, and that for the cocoons laid in autumn — 8 months, the earthworms that hatched out during the growing season were from the cocoons laid during the time from the beginning of September of the preceding year to the September of the study year. The production of cocoons during the year (Tab. IV), from September 1970 to September 1971, were calculated. The cocoons laid in the latter period hatched in 1971.

In 1971 the average density of adult individuals in the former sheep-fold pasture was $9/m^2$, individual fecundity was 4.4, and thereby the production of cocoons — $327/m^2$ per a year. In the autumn of 1970 very large numbers of adult individuals were recorded, and therefore the average number of adult individuals as calculated per a month for the period from September 1970 to September 1971 was 27 individuals per m^2, and the production of cocoons — $700/m^2$ per a year.

3.4. The growth rate of *Allolobophora caliginosa*

The relevant literature contains only scarce data on the growth rate of the earthworms. The development of these animals takes many years (E v a n s and G u i l d 1948, S a t c h e l l 1967). It has also been known that weather conditions may accelerate or retard their growth (S a t c h e l l 1967, L a v e l l e 1971, E d w a r d s and L o f t y 1972). The growth curves for *L. terrestris* and *D. rubida* have been described by several authors (Michon 1954 after S a t c h e l l 1967, L a k h a n i and S a t c h e l l 1970). For the assessment of the production of the dominant species it was necessary to know the individual growth rate. On the basis of the results from the field culture, kept in the former sheep-fold pasture, this growth was described by the logistic curve equation (Fig. 6)[3].

$$W_t = \frac{kW_1}{W_1 + (k - W_1)\, e^{-k\lambda t}} \qquad (d),$$

where: W_1 — the weight of the hatching earthworms in mg, t — the life span of an individual in months, λ — the growth coefficient equal to 0.0014, k — the limit value of the equation. The growth of the earthworms was determined empirically from the time of emergence (average body weight – 27 mg) until attaining a weight of 360 mg.
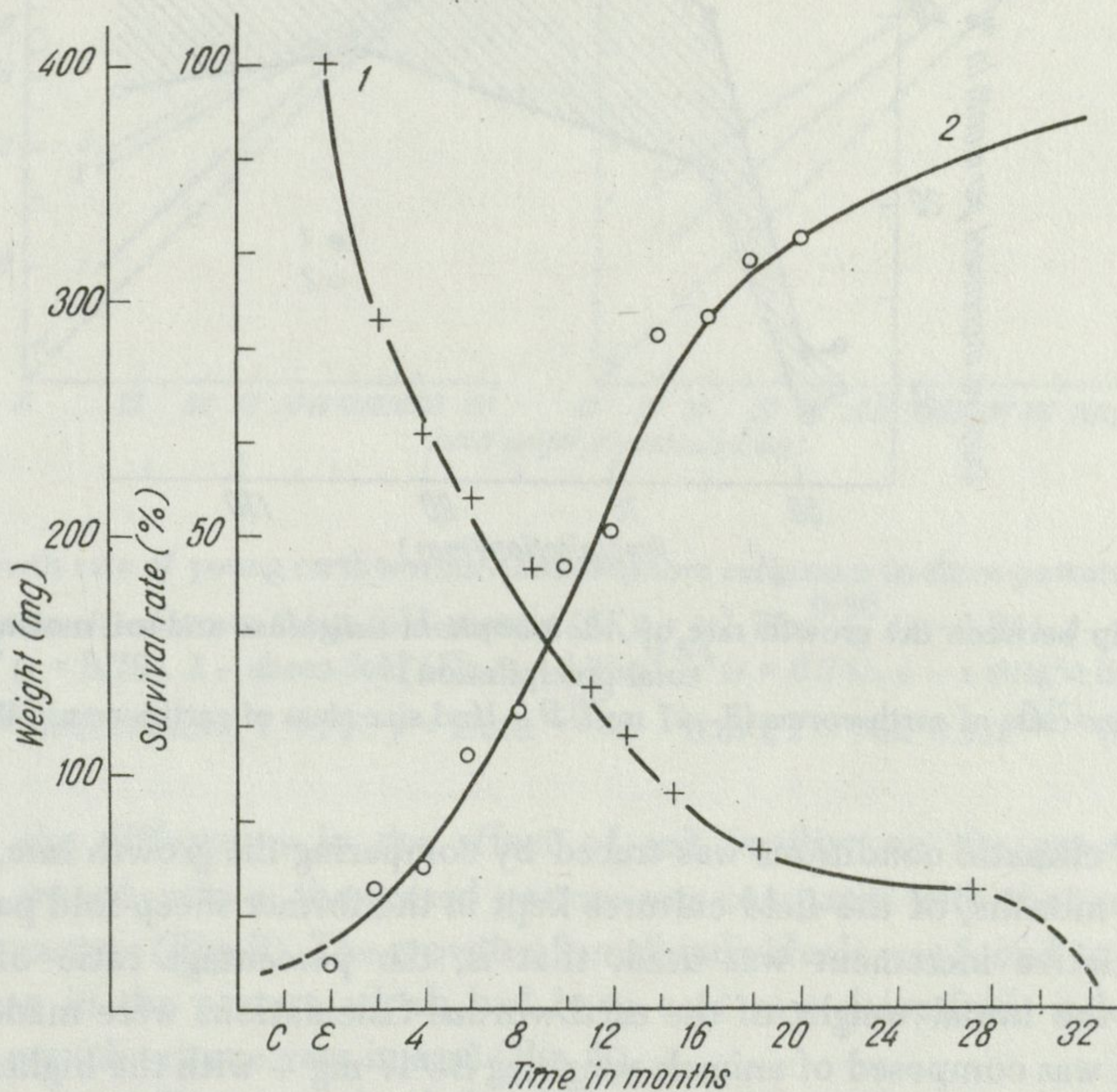

Fig. 6. Growth and survivorship curve for *Allolobophora caliginosa* in the former sheep-fold pasture
1 — survivorship, 2 — growth, C — cocoons, E — time of emergence

According to A v e l (1959) the growth curve of the earthworms is characterized by the occurrence of three phases: I — pre-reproductive — of a fast growth, II — reproductive — with

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[3] The calculations were carried out by J. Józwik, M.Sc., from the Institute of Ecology, Polish Academy of Sciences.

a certain retardation of growth, III — post-reproductive — of a slow growth, and even a decrease of weight. The curve obtained empirically during the present investigations includes growth phase I, lasting till the attainment by the earthworms of a body-weight of about 260 mg (occasionally, sexual maturity is attained by individuals of a body-weight of 210 mg), and phase II during which individuals weighing 260—300 mg attain sexual maturity (Fig. 6). In the former sheep-fold pasture phase II occurred during the second year of the animals' life, that is, after about 60 weeks of growth[4]. According to E v a n s and G u i l d (1948), in culture, sexual maturity is attained within a slightly shorter time, 55—58 weeks.

Earthworms in the first two growth phases, that is, of a body-weight of 360 mg, represented about 90% of the field population. The second part of the curve discussed, covering the growth of the remaining 10% of the population was extrapolated to a maximum, encountered in the field, body-weight — 650 mg.

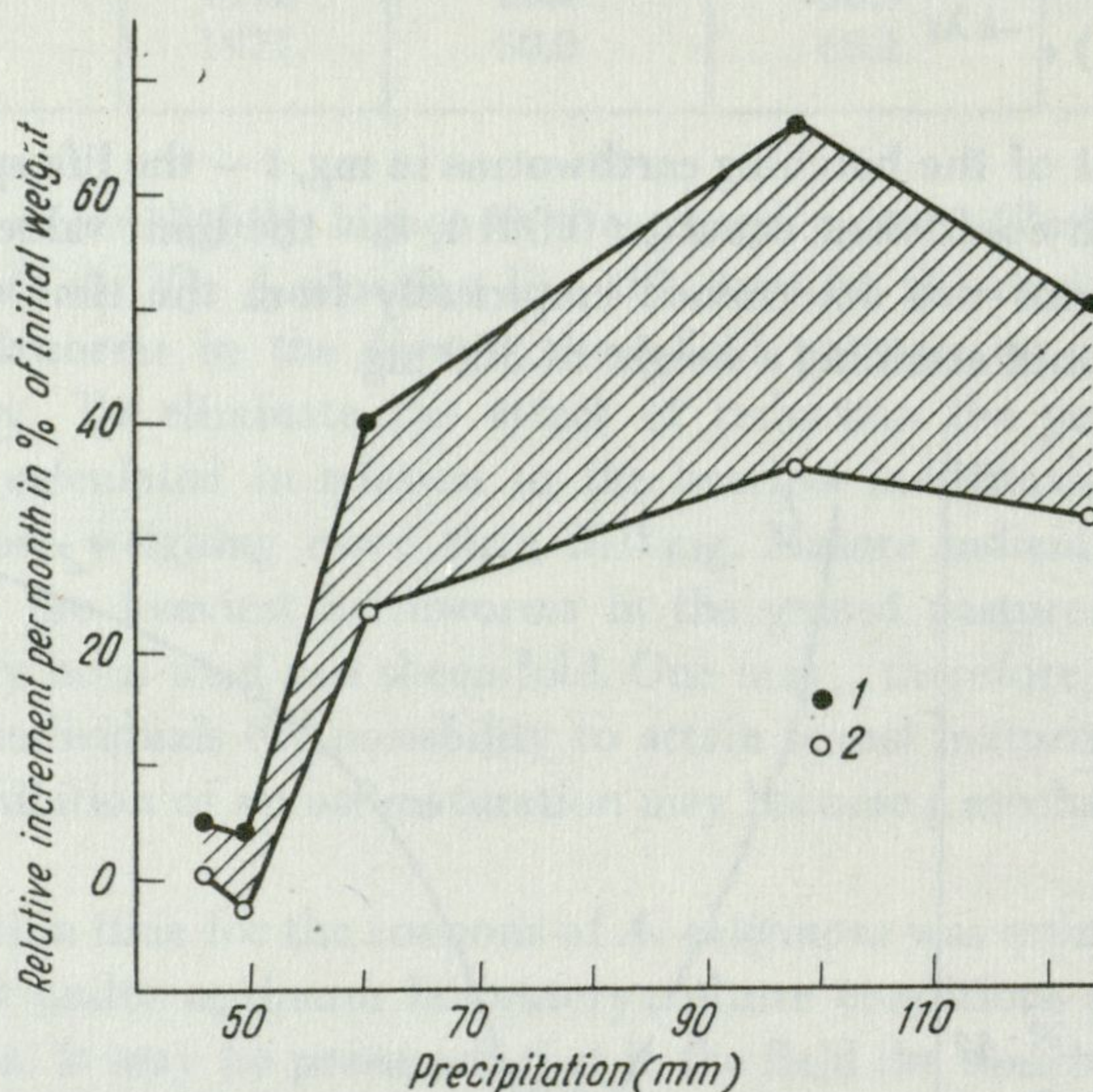The growth rate of animals is affected by factors of two types: climatic and trophic.

Fig. 7. Relationship between the growth rate of *Allolobophora caliginosa* and soil moisture (as measured by total precipitation)
1 — Ist size class of earthworms (8—47 mg), *2* — IInd size class of earthworms (48—247 mg)

The effect of climatic conditions was traced by comparing the growth rate, recorded during five consecutive months, of the field cultures kept in the former sheep-fold pasture (Fig. 7). In this case the relative increment was used, that is, the percentage ratio of the increase in body-weight to the initial weight of the earthworms. Calculations were made for two animal groups: Group I was composed of animals weighing 8—47 mg — with the highest relative weight increment. The number of individuals of the same size class in each months exceeded 25. Group II included earthworms weighing 48—247 mg. The number of cultured individuals of the entire group was over 50.

Although the variation of the quantity of precipitation was too low to calculate correlations, it seems that the total amount of precipitation in individual months is the main factor causing

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[4] In the cultures left to winter over the growth of the individuals was not recorded.

variations in the growth rate (Fig. 7), temperature only playing a modifying role. In 1971 a fast growth of earthworms was observed to continue for three moist months – from mid-May to mid-July, and from mid-August to mid-September. In the period during which a low precipitation was recorded (mid-July to mid-August, and mid-September to mid-October) there was no increase at all, with even a slight decrease in the body weight of the earthworms.

The growth curve described at the beginning has been plotted on the basis of average values illustrating the variable growth rate in the individual months of the growing season. It, therefore, applies to the given environment for the average years the meteorological features of which do not differ from the conditions prevailing in 1971. In very wet years the growth is probably faster. This is indicated by the change of the time of attaining sexual maturity in 1970.
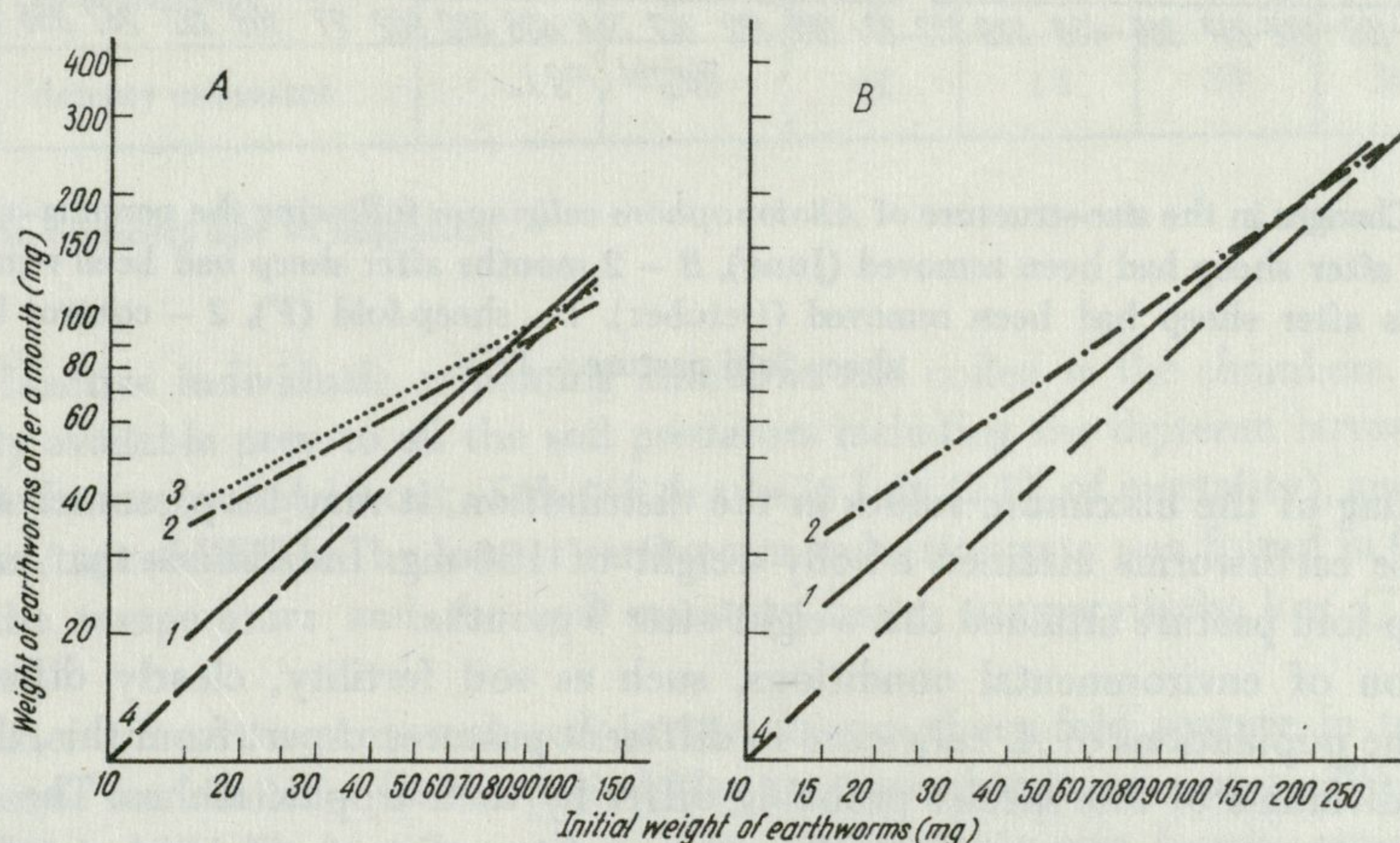

Fig. 8. Growth rate of young earthworms *Allolobophora caliginosa* in three pasture habitats

A – laboratory cultures: 1 – former sheep-fold pasture (PF): $y = 1.75x^{0.90}$ $(r = 0.84)$, 2 – grazed-on pasture (Pas): $y = 8.21x^{0.54}$ $(r = 0.70)$, 3 – sheep-fold (F): $y = 8.96x^{0.54}$ $(r = 0.74)$, 4 – a stright line indicating lack of growth; B – field cultures: $1 - PF$: $y = 2.30x^{0.87}$ $(r = 0.87)$, $2 - Pas$: $6.21x^{0.71}$ $(r = 0.87)$

To determine the differences in the effect of soil fertility on the growth rate of the earthworms their growth rate in the grazed pasture was compared with that recorded for the former sheep-fold pasture (Fig. 8). The growth of small individuals was found to be faster in the grazed pasture than in the pasture which had been used as a sheep-fold; it became equal in weight group 150 mg (about one year in age) (Fig. 8).

This growth rate, peculiar to each of the different habitats, has also been confirmed by laboratory cultures (Fig. 8) in which individuals with a maximum body-weight of 158 mg were kept. The parameters of the curves obtained for the data from the field and from the laboratory were similar. In the laboratory cultures the young earthworms also appeared to grow faster in the soil from the grazed pasture than in that from the former sheep-fold pasture (PF). The highest growth rate of young individuals was seen in the sheep-fold soil (F) (Fig. 8), as confirmed also by the size-class distribution of the earthworms in this habitat (Fig. 9). Judging
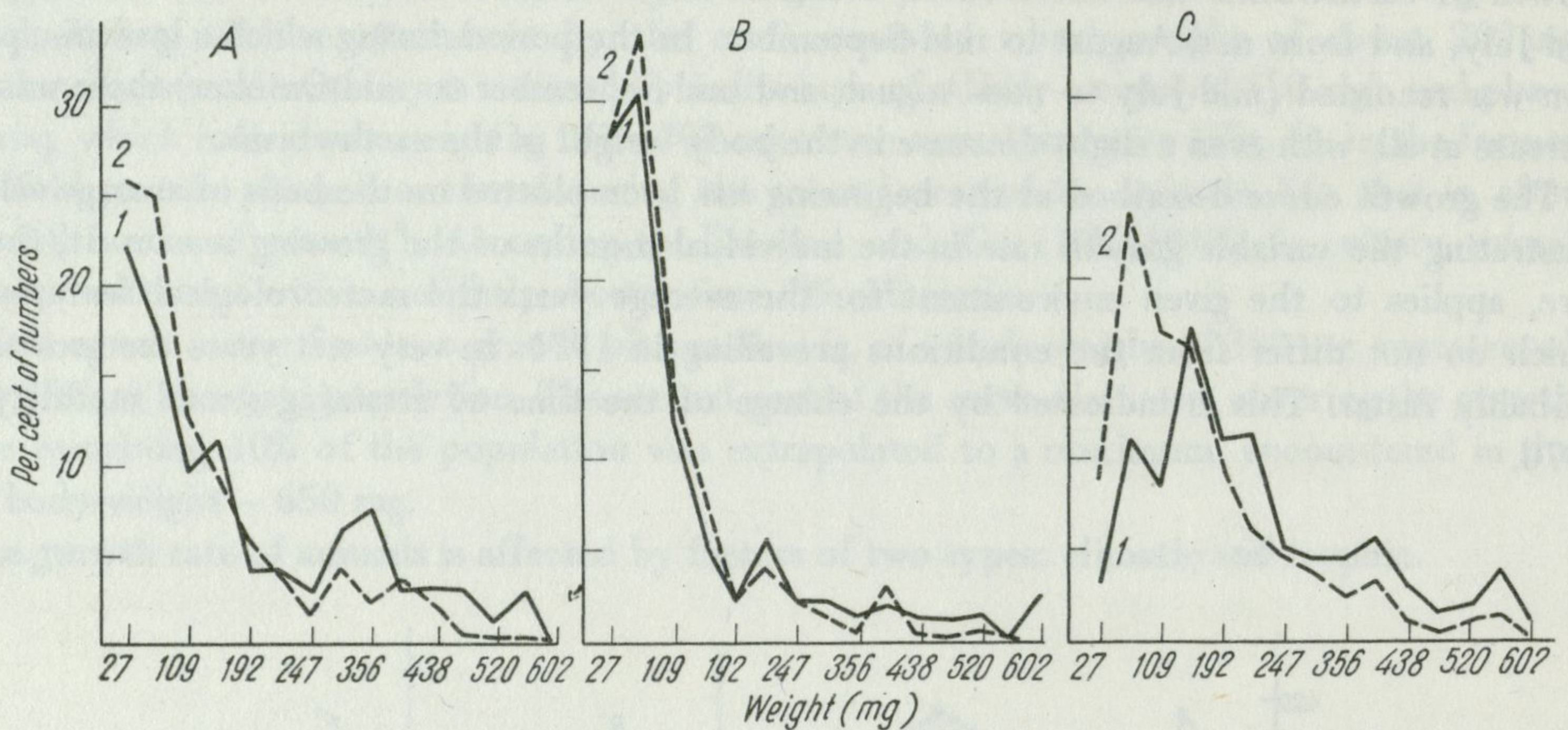
Fig. 9. Changes in the size-structure of *Allolobophora caliginosa* following the penning-up of sheep
A — 2 weeks after sheep had been removed (June), *B* — 2 months after sheep had been removed (August),
C — 4 months after sheep had been removed (October), *1* — sheep-fold (*F*), *2* — control habitat (former
sheep-fold pasture — *PF*)

by the shifting of the maximum values in the distribution, it may be presumed that within 4
months these earthworms attained a body-weight of 150 mg. Individuals that hatched in the
former sheep-fold pasture attained this weight after 9 months.

The action of environmental conditions, such as soil fertility, clearly differentiates the
growth of the populations of *A. caliginosa* in different pastures. Apart from this, the young and
the adult individuals of this species probably differ by their trophic niches. The conditions of
a natural pasture with a poor soil, as well as those of a medium-fertile pasture of a new sheep-
fold with a manure-disturbed balance, favour a fast growth of young earthworms.

3.5. The mortality of *Allolobophora caliginosa* population

In the literature few estimates can be found concerning the actual death rate of an
earthworm population. Examples of such calculations are the studies by L a k h a n i and
S a t c h e l l (1970), and by L a v e l l e (1971 b). The long pre-productive phase in the develop-
ment of the earthworm permits the presumption that under field conditions a low mortality is
the rule. Weather conditions, such as droughts (H o p p 1947, G e r a r d 1967), are
considered to be the main cause of mortality, the role of predators being less important.

Seasonal variations in the reduction of *A. caliginosa* were studied on the basis of the
successive changes in population density in the habitats investigated, and mortality changes in
the cultures in the former sheep-fold pasture. The results of direct field investigations were
similar to those from the field culture. The highest earthworm reduction rate was observed in
July (Tab. VI). This reduction was caused by drought and by predatory dipteran larvae. As
a result of the drought, during the period concerned a high percentage of inactive earthworms
was found. In the culture these individuals represented 8% of the population in July, and 32%,

Tab. VI. Seasonal variations in the reduction of *Allolobophora caliginosa* in sheep-fold habitats (*PF* and *F*) in 1971 (reduction being calculated as a percentage in relation to total numbers during the preceding month N_{t-1})

Habitat	Method	Reduction in %						Average per season
		M	J	J	A	S	O	
Former sheep-fold pasture *PF*	field cultures	–	10	22	13	8	2	19
	density estimates	11	6	32	16	0	2*	13
Sheep-fold *F*	field cultures	–	34	–	–	–	–	–
	density estimates	–	38	42	14	39	30*	28

*Increase in numbers due to migration.

in August. Inactive individuals, remaining immobile and coiled in the chambers, may become a more easily available prey to all the soil predators including the dipteran larvae. In the field culture these larvae caused 10 out of the 42 deaths in July (24% of mortality), and 9 out of the 27 deaths in August (33%). The lowest earthworm reduction rate was found in October (Tab. VI), with the temperature and the soil moisture being comparatively low (7.5°C, 43 mm precipitation).

The number of earthworms reduced in the former sheep-fold pasture in two successive growing seasons was similar — for the period May to September it came up to 306 individuals in 1970, and 341 in 1971, that is to say, the average monthly reduction for this period was 19% in both years.

In the same former sheep-fold pasture the numbers of earthworms reduced during the remaining 8 months (September 1970 to May 1971) was 411, that is, about 10% of the population. Earthworm mortality appears to be higher during the growing season than in winter. The average monthly reduction rate of the earthworms in the culture kept in the former sheep-fold pasture constituted 19% of the population; the same reduction calculated on the basis of the variations in numbers for the entire growing season was 13%, and for the corresponding period — 19% (Tab. VI). In the cultures the reduction seems to be overestimated due to accidental mortality connected with the removal of the earthworms every months. On the basis of the small differences between these two estimates it may be presumed that in the habitat concerned the reduction of individuals is caused mainly by physical factors and predation by dipteran larvae.

The reduction determined for the cultures in the grazed pasture was 9%, and that calculated on the basis of variations in numbers — 22%. In this habitat there probably occurs a strong reduction caused by predators larger than dipteran larvae, eliminated in field cultures.

The difference in the contribution of predators larger than dipteran larvae to the reduction of earthworms in the two habitats is confirmed by the overall density of the epigeic predatory

fauna. In the grazed pasture this density is 59.2, and in the former sheep-fold pasture, besides the food being more abundant there, it is 14.1 individuals/m^2 (Kajak unpublished).

The dominant species appeared to be more intensively reduced in the grazed pasture than in the former sheep-fold pasture, the former habitat having more favourable physical conditions and a stronger predator control. These findings confirm earlier suggestions that animal communities with a clear dominance (this being true of the former sheep-pen pasture) are under a stronger control of the soil physical conditions. As has been revealed by the short-term cultures kept in the sheep-fold, during the first month the reduction rate in cultures is similar to that in the field (Tab. VI). The strong reduction observed during this period may be the result of changes in the physical conditions and not in predation.

As the estimates of mortality obtained for the field culture and those calculated for the former sheep-fold pasture did not differ, a survivorship curve has been drawn for *A. caliginosa* on the basis of the results from the culture (Fig. 6).

The highest mortality – equal to 27% of the population – was recorded for the newly born earthworms. A second increase in mortality up to 21% occurred during the stage of sexual maturation (Fig. 6). In general terms, the survival rate of young individuals (up to 90 mg) and of the oldest ones (from 290 mg) could be described by an equation of the form:

$$N_t = N_o e^{-0.10t}$$

where: N_o – initial population density, and N_t – population density after time t. During the period that preceded the sexual maturation the mortality of the earthworms increased; the survivorship curve was described by the equation:

$$N_t = N_o e^{-0.23t}$$

3.6. The production of *Allolobophora caliginosa* population

Estimated by the graphical method, the production of *Allolobophora caliginosa* in the former sheep-fold pasture in 1971 was 58.4 kcal/m^2 per year, and the ratio of production to the average biomass, that is, the rate of biomass turnover equals to 0.9 (Tab. VII). This means that the average ecological life of the earthworms is over 1 year. For the assessment of the production in the grazed pasture two methods were used: the graphical method, and Winberg's method. According to the graphical method $P = 11.1$ kcal/m^2 per year, and according to Winberg's method $P = 12.0$ kcal/m^2 per year (Tab. VII). The turnover in this habitat appeared to be higher than in the former sheep-fold pasture, and equal to about 1.3.

The biomass turnover of the earthworms is probably higher in a diversified habitat, controlled by predators (pasture) than in a habitat in which both the fecundity and reduction depend primarily on the soil physical conditions (the former sheep-pen pasture).

The above values of earthworm biomass *A. caliginosa* turnover are relatively small. The corresponding value for *L. terrestris* L., a species whose body size is eight times as large, was yet smaller, 0.4 (Lakhani and Satchell 1970), and for the large-sized species *Milsonia anomala* Omodeo, which is subject to a very strong reduction by climatic conditions (Africa), this value was 2.4 (Lavelle 1971a).

The value of respiration of the entire earthworm community of the grazed pasture was estimated at 21.6 kcal/m^2 a year, and that of the former sheep-fold pasture – at 103.4 kcal/m^2 a year (Tab. VII). Due to the similarity of the biomass structure of both communities the

Tab. VII. Comparison of some of the parameters of earthworm production in pasture environments (*Pas, PF*) during the growing season of 1971

a — Allolobophora caliginosa, b — all earthworms

		Grazed pasture *Pas*	Former sheep- -fold pasture *PF*
a	Newborn individuals in % $\bar{N}$	26	11
	eliminated individuals in % $\bar{N}$	22	13
	production in kcal/m^2 per year	11–12	58
	$P/\bar{B}$	1.3	0.9
b	biomass in kcal/m^2	19.1	90.6
	respiration in kcal/m^2 per year	21.6	103.4
	$R/\bar{B}$	1.1	1.1

dissipation of energy by unit biomass ($R/\bar{B}$) of the community in both habitats approximates 1. In both the habitats concerned species of medium body-size predominate — *A. caliginosa* and *A. rosea* Sav., the largest body-size species, *Octolasium lacteum* Oerley, representing a small percentage.

Transferring the data obtained for the dominant species onto the entire earthworm community one may presume that in a habitat with a highly diversified earthworm community of low density there is a higher production and reduction of earthworms.

3.7. The earthworms as the main component of soil macrofauna[5]

One of the simplest, although not universal, measures of the importance of a particular animal group in an ecosystem is its abundance — numbers and biomass, against the corresponding parameters of the remaining components of the ecosystem.

The numbers and biomass of the earthworms in grassland ecosystems (mainly in pastures) attain one of the highest levels among the ecosystems compared (Tab. VIII). In a mixed forest, the richest of all woodland habitats, the average density of the earthworms was 133 per m^2, whereas in the pastures their density was 351 per m^2 (Tab. VIII). Less marked were the differences in the biomass: 64.3 g/m^2 in mixed forests, and 72.7 g/m^2 in the grasslands (Tab. VIII). This was because in the grassland ecosystems there occur abundant small body-size earthworm species. The average body size of a meadow earthworm is 210 mg, in mixed forests — 480 mg, and in the oak forests, where the heaviest species, *L. terrestris*, is abundant the average weight is 670 mg.

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[5] According to v a n d e r D r i f t's classification (1951) plus the earthworms.

Tab. VIII. Numbers and biomass of earthworms in different environment types in Europe

Environment	Number of individuals N/m^2	Biomass g wet wt/m^2	Number of habitats	Authors
Coniferous forests	15 0.8—43	5.9 0.2—17.0	12	Zajonc 1971, Edwards and Lofty 1972
Waste lands	22 14—34	5.9 4.6—8.4	3	Edwards and Lofty 1972
Crop-fields	87 2.3—287	27.1 1.3—76	12	Edwards and Lofty 1972, Jopkiewicz 1972, Atlavinyté 1965, 1973
Beech forests	61 0—356	28.6 0—142	13	Zajonc 1971, Bornebuch 1930
Oak forests	91 0—192	61.6 0—153	17	Zajonc 1971, Edwards and Lofty 1972
Mixed forests	133 5.4—439	64.3 0.9—221.2	15	Zajonc 1971, Edwards and Lofty 1972
Meadows and pastures	351 21—640	72.7 5.5—152	12	Edwards and Lofty 1972, Atlavinyté 1973, Balujev 1950, Bouche unpublished Zajonc 1970, Graff 1971, Nowak present date
Orchards	449 254—848	126.7 63.5—287	3	Edwards and Lofty 1972

A comparison of geographically distant ecosystems seems to indicate that the earthworm biomass is correlated with the factors determining the soil fertility of an ecosystem, e.g. the content of humus in the soil (Kalinowska in press).

In forest ecosystems, where there are fewer earthworms than in the meadows, the biomass of this group generally constitutes 7—75% of the biomass of the soil macrofauna (Bornebusch 1930, van der Drift 1951), while in the grassland ecosystems earthworms come up to over 60% of the biomass (Tischler 1955).

In the earlier-discussed meadow habitats near Warsaw the biomass of the earthworms was above 82% of the soil macrofauna biomass (Nowak 1971), and their numbers, 26—68%. Both in the meadows and pastures the density of earthworms was higher in the fertile ecosystems, i.e. those with a higher primary production and a higher percentage content of carbon and nitrogen in the soil (Tab. I). The difference in the density of the earthworms between the association *Stellario-Deschampsietum* — a poor-soil meadow, and *Arrhenathe-*

retum a rich-soil meadow, was considerable, the earthworms being almost twice as abundant in the latter meadow as in the former one (the differences within *Arrhenatheretum* should be attributed to the varying soil moisture). The earthworm population found in the poor-soil grazed pasture was 5 times as large as that in the fertile former sheep-fold pasture (Tab. IX).

Tab. IX. Density of the macrofauna in the environments investigated

Average densities for two years. From samples of 100 cm^2 in area

Macrofauna groups	Lolio-Cynosuretum cristati				Stellario- -Deschampsietum		Arrhenatheretum medioeuropaeum			
	pastures				reserve meadow		mown meadows			
	grazed Pas		former sheep- -fold PF				M II		M I	
	N/m^2	%	N/m^2	%	N/m^2	%	N/m^2	%	N/m^2	%
Lumbricidae	125	38	659	68	107	26	227	68	138	55
Enchytraeidae	159	48	262	27	224	55	53	16	54	22
Dipteran larvae	22		33		35		11		8	
Coleopteran larvae	6	14	9	5	20	19	27	16	35	23
Other insect larvae	18		7		18		16		14	
Total	330	100	970	100	404	100	334	100	249	100

An increase in the fertility of the habitat caused a more marked increase in numbers of the earthworms than of the remainder of the macrofauna groups. Consequently, in the fertile habitats there occurred a considerable increase in the percentage of the earthworms in the animal community. In the mown meadows and in the former sheep-fold pasture the earthworms represented over 55% of the population, and in the remaining two habitats — 26 and 38% (Tab. IX).

Of the remainder of macrofauna groups *Enchytraeidae* are animals associated with an early stage of organic matter decomposition (the decomposition being in this case ,,incomplete''), as a rule they occurr in acid environments with a litter of the mor type. Therefore, as a dominant, this group is often replaced by the earthworm group, especially soil earthworms, producing the mull type of litter. In the infertile habitats the enchytraeids represented 48—55% of numbers, in the fertile ones — below 27% (Tab. IX).

In the meadows studied the density of insect larvae varied slightly, their proportion ranging from 5 to 23%.

Beetle larvae were found to grow in numbers in the fertile habitats, their density ranging from 6 per m^2 in the grazed pasture, up to 35 per m^2 in the *Arrhenatheretum* meadow (Tab. IX). The tendency to increase was most evident among the herbivorous beetles (*Agriotes* sp., *Curculionidae*). Roots are the basic food of most of these beetles. Their growth in numbers may be connected with an increase in root production.

Due to the above-described dominance of the earthworms in the community of soil macro-fauna most of the macrofauna biomass of the grassland ecosystems is the biomass of the slow turnover group. In fertile environments there is a larger accumulation of earthworm biomass, its turnover being slower — hence the growing importance of the earthworms as a retentive factor.

4. THE ROLE OF EARTHWORMS IN THE ECOSYSTEMS UNDER STUDY

The manifold effect of the earthworms on the environment is the result of their direct biological activity, as well of the microbiological changes caused by their action.

Some of the parameters of the productivity of the earthworm population, such as the quantity of biomass, the rate of biomass turnover, or respiration, may be regarded as a measure of the direct action of the earthworms.

Tab. X. Utilization of energy inflow to the soil (D) by the earthworm community

	Lolio-Cynosuretum cristati			Stellario- -Deschampsietum		Arrhenatheretum medioeuropaeum			
	pastures					mown meadows			
	grazed Pas		former sheep- -fold PF	reserve meadow		M II		M I	
	1969	1971	1971	1968	1969	1968	1969	1968	1969
Energy stored in biomass of earth-worms in kcal/m^2 $\bar{B}$	11.3	19.1	90.6	16.4	19.6	47.5	25.5	21.7	47.4
Respiration in kcal/m^2 in the growing season $\bar{R}$	11.8	21.6	104.4	18.8	28.2	46.7	24.8	26.2	43.3
Contribution of earthworms to organic matter degradation in per cent $\bar{R}/D$	0.4	0.9	2.9	1.1	1.7	1.6	1.1	1.1	1.9
Contribution of earthworms to energy sto-rage in per cent $\bar{B}/D$	0.4	0.6	2.4	0.9	1.0	2.0	1.1	0.9	2.0

The value of the respiration of the earthworms found in the grassland ecosystems under study varied between 0.4% nad 2.9% of the organic matter returned to the soil (Tab. X). The lowest value of respiration was recorded for the grazed pasture, and the highest one for the former sheep-fold pasture being the most fertile of the habitats discussed. In the meadows, the respiration of the earthworms was found to be 1.1—1.9% of the organic matter supplied to the soil (Tab. X).

The quantity of energy utilized by the earthworms for respiration may not be equal to (on account of their body-size) that utilized by the remaining, smaller soil animals with a faster metabolism. For instance, an enchytraeid population with a biomass of 11 g/m^2 dissipates 149 kcal during a year, i.e. 11% of the total energy supply to the soil (O'Connor 1967), and the earthworms with a biomass of 25 g/m^2 in a grazed pasture respire 22 kcal, that is, only 0.4% of the energy supplied to the soil. Earthworm respiration represents 5—7% of the total respiration of the most important saprophagous groups in the pastures (acc. Kajak 1974). It should be noted that the lower the percentage of the earthworms in a soil animal community, the more efficient is the respiratory process. The transfer of dominance from the earthworms to the enchytraeids in the least fertile ecosystem results in a more efficient respiration of the soil animal community.

Due to the abundance of earthworms in grassland ecosystems, as well as to the relatively small body-weight of the individuals, the value of their respiration in these ecosystems is comparatively high. The respiration of the earthworms in meadows exceeds their respiration in crop-field communities. Thereby the contribution of this group to the mineralization of the vegetable debris is higher in grassland ecosystems than in crop-field ecosystems. Calculated according to Jopkiewicz (1972) and Ryszkowski (1972), the value of earthworm respiration in the crop-fields is equal to 0.4% of the primary production remnants returned to the soil, that is, of the order of the lowest value recorded for the meadows.

It seems that in grassland ecosystems a more important role of the earthworms is the storage of energy and not its dissipation. The earthworm biomass accumulated in the habitats under study exceeds the biomass of any other group of invertebrates (Breymeyer 1971, Kajak 1974). This biomass represents from 0.4 to 2.4% of the organic matter returned to the soil (Tab. X). Adopting for the entire earthworm community the biomass turnover rate of the dominant species, equal approximately to 1, we find that the degradation of the previously enumerated organic matter quantities in the ecosystem is delayed by a year.

This retardation of the energy degradation processes (larger biomass quantities, lower turnover rate) is of particular importance in fertile ecosystems, where high intensification of bacterial mineralization may result in a rapid leaching of elements from the ecosystem. The organic matter accumulated by the earthworms may be comparatively easily again returned to the cycle by predators. However, the low mortality (22% of the population in the pasture, seasonal variations from 0 to 32% of the population in the former sheep-fold pasture) indicates that this way of elongating the trophic chains was only utilized to a slight extent in the ecosystems under study.

The ability to retain biomass may be of great importance in the biogene balance of the ecosystems.

The role of earthworms in the circulation of carbon and nitrogen in the three grassland ecosystems was approximately estimated. The following three real values were used: quantity of earthworm biomass, number of casts deposited by them on the surface during the growing season, and the content of mineral elements in the casts. The assessment of the two quantities was the object of earlier studies (Czerwiński, Jakubczyk and Nowak 1974). The

remaining values are similar. The biomass turnover rate was assumed = 1, and the ratio $R/\bar{B} = 1$ (Tab. X). The relative consumption of a given element by the earthworms was calculated as the sum of an approximate value of assimilation (the content of the element in the bodies of the earthworms and its amount respired) and the relative excretion (the difference between the content of the element in the wormcasts and in the same volume of soil).

Tab. XI. Contribution of the earthworms to the cycles of elements in three grassland environments

		Flow of carbon			Flow of nitrogen		
		Arrhenat-heretum medioeuro-paeum mown meadow	*Lolio-Cynosure-tum cristati*		*Arrhenat-heretum medioeuro-paeum* mown meadow	*Lolio-Cynosure-tum cristati*	
			pasture *Pas*	former sheep-fold pasture *PF*		pasture *Pas*	former sheep-fold pasture *PF*
Influx in g/m^2	in organic compounds	226	281	352	8.9 ⎱ 15.3	14.0 ⎱ 57.5	16.2 ⎱ 59.7
	in mineral compounds				6.4 ⎰	43.5 ⎰	43.5 ⎰
Content in earthworm biomass in g/m^2		2.6	1.3	7.4	0.5	0.3	1.5
Enrichment of worm-casts in g/m^2		28.8	16.5	78.4	2.2	1.6	.5.3
Ratio of the relative earthworm consump-tion to the influx in g/m^2		15.0	6.8	26.5	17.6	3.4	11.4

The content of carbon in the dry weight of the litter of the association *Arrhenatheretum* was 45.1% (the analyses were carried out by W. Walendzik). This was assumed to be also the percentage of this element in the litter of the related association *Lolio-Cynosuretum*. The dry weight of manure contained 39.8% carbon (O l e c h o w i c z 1974). As the supply of organic matter was known the amount of carbon returned to the pasture soil every year could be calculated. This amount was 281 g/m^2 carbon, whereas 5,500 g was found to be accumulated in the form of humus in the 0—10 cm layer (Tab. XI). If we assume that the dry weight of the earthworms contains 39.8% carbon (B ò u c h é 1967), then we find that these animals retain 1.3 g carbon for the period of one year. A similar amount of carbon is in the CO_2 production during respiration. Thus the earthworms utilize 0.8% of the carbon returned to the soil. In this habitat the amount of wormcasts was estimated at 780 g dry wt/m^2 per season; the content of carbon in the wormcasts was 4.8% (in the soil — 2.7%). The additional 16.5 g carbon contained in the wormcasts in effect means 28 g/m^2 per season of humic substances added to the soil (C z e r w i ń s k i et al. 1974). On account of the differences in specific gravity between the

mineral and the organic parts of the soil this enrichment should derive from the organic debris and not from an appropriately larger amount of the soil consumed. Relative consumption would amount to 7.8% of the debris, or 0.7% of the top humus soil layer (Tab. XI).

Such is the role of the earthworms in the carbon cycle (or energy flow) in a habitat in which their numbers and biomass are small, and the abundant and highly productive coprophagous fauna utilizes a large part of the organic matter supplied to the surface of the soil (O l e c h o - w i c z 1974).

In the fertile former sheep-fold pasture there is an increase in primary production, and thereby in the amount of carbon supplied to the soil. With the manure and vegetable debris a joint amount of 352 g carbon/m^2 per year is supplied (Tab. XI). The number of wormcasts in this habitat is much larger: $3,534$ g/m^2 per season. Here respiration and storage by the earthworms constitute about 4.2% of the organic matter supplied, and the soil of a former sheep-fold pasture is enriched by 145 g/m^2 humic substances (C z e r w i ń s k i et al. 1974). The relative consumption of the earthworms amounts to 27% of the organic debris, or 2.5% of the humus stored in the top soil layers (Tab. XI).

In the fertile *Arrhenatheretum* meadow carbon is consumed by the earthworms at an intermediate rate — about 15% of the organic matter flowing in (Tab. XI).

A different situation is seen in the case of nitrogen flow through an earthworm population. The role of the earthworms in the cycle of this element is particularly important for two reasons: (1) nitrogen is the element which occurs in grassland ecosystems most frequently in excess, (2) among the many groups of saprophagous the earthworms belong to the group of definite humifiers (K o z l o v s k a j a 1965). The wormcasts of this group are enriched with humified organic matter and at the same time most enriched with mobile nitrogen which is available for plants (B a r l e y and J e n i n g s 1969, K o z l o v s k a j a 1965, E l D u w e i n i and G h a b o u r 1971).

In pastures and in cultivated meadows the main route of nitrogen supply to the soil is via the compounds easily assimilable to plants: mineral fertilizers, sheep urine. Their decomposition depends on the microorganisms. This does not apply to the nitrogen supplied with the organic debris. The decomposition of these substances to a large extent depends on the macrofauna, including the earthworms.

The content of nitrogen in the dry weight of the litter of the association *Arrhenatheretum* was estimated at 1.8% (W. Walendzik unpublished), and in the manure at 2.6% (O l e c h o - w i c z 1974). An additional source of this element is mineral fertilizers — 6.4 g N/m^2, or sheep urine — 43.5 g N/m^2 (O l e c h o w i c z 1974 after Jameson).

If we assume that the nitrogen content in the body of the earthworms is 7.1% dry wt (B o u c h é 1967), the storage of this element in their biomass in the pastures will be of the order 0.4—2.4%, and in a mown meadow as much as 3.3% of the total amount supplied. The relative consumption of nitrogen (stored nitrogen, and that contained in the wormcasts) in the pastures (*Pas* and *PF*) represents 3.4 and 11.8%; in the meadows as much as 17.6% of the amount supplied. At the same time about 6.4% of the decomposed nitrogen becomes changed to forms that are easily absorbed by plants (B a r l e y and J e n i n g s 1969). The remainder is subject to further decay by the microorganisms and animals.

The above-described role of the earthworms in the organic matter cycle has been diminished considerably. The description has not taken into account the organic matter contained in the wormcasts not taken to the surface of the soil, it left out the high content of nitrogen in the mucus and urine excreted, and finally, it has not taken into account the variations in the respiratory activity. In spite of this, in the most fertile of the habitats studied, i.e. in the former

sheep-fold pasture, which was rich in earthworms, 11% of the carbon supplied to the soil, or 42% of nitrogen, passed through these animals, these quantities indicating that earthworms play an important role in the economy of the ecosystems.

The most important aspect of earthworm activity is their effect on all the microbiological processes of the environment. It has been found that the smaller the numbers of the microflora in a habitat, the greater its numbers in the wormcasts (K o z l o v s k a j a and Ž d a n - n i k o v a 1961, C z e r w i ń s k i et al. 1974). The cause of this is the accumulation in the wormcasts of nutrients that easily undergo further decay. In poor habitats such an accumulation strongly increases the microbiological activity. Of particular importance for a further growth of the microflora may be the nitrogen evolution in the alimentary canal of the earthworms (H a r m s e n and v a n S c h r e v e n 1955, K o z l o v s k a j a 1965). It has also been found that in the wormcasts those microorganism groups grow most intensely which are responsible for the course of the decay processes which is slightly different from that actually occurring in the environment. If in the environment processes of a complete mineralization prevailed, in the wormcasts the most intense were the protein-forming processes (C z e r w i ń s k i et al. 1974). This processes cause a retention of the mineral compounds released during the mineralization.

The last feature – a delayed stimulation of the microflora – is of particular importance for the energy and mineral compounds balance, being a control process, a „safety valve" that prevents a complete exhaustion of the mineral resources of the soil.

The grassland ecosystems discussed differ by the quality of the organic matter supplied to the soil and by the predominance of the individual microbiological processes controlled by it in conjunction with the habitat conditions (J a k u b c z y k 1971, J a k u b c z y k 1974, C z e r w i ń s k i et al. 1974). In poor habitats, such as the association *Stellario- -Deschampsietum*, muck-forming processes predominated. A group of great importance for the decay are fungi – microorganisms that cause a slower mineralization than that brought about by the corresponding groups of bacteria. In the fertile former sheep-fold pasture of the association *Lolio-Cynosuretum*, with a high organic matter supply rich in nitrogen, the more efficient bacterial decay predominates.

In the reserve meadows, where the earthworms do not transform much soil microbiological changes are most significant. The nitrogen liberated during the mineralization processes, taking place in the alimentary canal, causes a rapid growth in the activity of the microorganisms, especially of bacteria, and thereby accelerates the processes leading to a complete mineralization (C z e r w i ń s k i et al. in press.). In this habitat with a low availability and a very high rate of retention of the organic matter (T r a c z y k 1968) mineralization appears to be the most important process that makes primary production possible. Acceleration of mineralization occurs not only due to the changes caused in the environment by the earthworm casts, but also due to changes within the entire macrofauna community (i.e.) replacement of the earthworms, slower mineralizers, by the enchytraeids which are more efficient).

The other extreme is the former sheep-fold pasture, a very fertile habitat with the highest level of microflora (J a k u b c z y k 1974). Although the intensity of microbiological processes is in this habitat high, their activation in the wormcasts is lower. In the wormcasts the most intense are the protein-forming processes which retard the full mineralization of the organic matter (C z e r w i ń s k i et al. 1974).

As a result, in the former sheep-fold pasture the most important process, intensified by the earthworms, is the ability to prevent the elements from being washed down the soil profile. This results from the protein-forming process, as well as from the specific wormcast structure, and the earthworm biomass retention rate which is higher than in the other habitats.

5. SUMMARY

In the ecosystems studied 10 of the 15 earthworm species known from grassland habitats in Poland were found. The two main agricultural practices, mowing and grazing, appeared to reduce the species composition and to change the dominance structure of the earthworms. The change consisted of an increase in the density of the ubiquitous species *Allolobophora caliginosa* Sav. The index of diversity of the earthworm community (O d u m 1971) in a reserve meadow was 1.7 and in a former sheep-fold pasture — 0.6 (Tab. II).

The occurrence of the surface earthworms was correlated with the rate of organic matter decomposition (Fig. 1). In habitats with rapid decomposition these earthworms represented a small percentage, and the main role was played by the soil-mixing earthworm group.

In the seasonal variation of numbers and biomass of the earthworms two peaks could be seen — a spring peak and an autumn peak. These increase in number were due to the emergence of young earthworms. The two-peak variation in population size was more marked in meadows with a seasonal supply of organic matter to the soil, and less so in pastures with a continuous inflow of organic matter (Fig. 2).

Individual fecundity of *A. caliginosa* grew with the increasing nutrient supplies in the soil. Calculated for three pastures per season this fecundity was as follows: 26 cocoons in a grazed pasture, 35 in a former sheep-fold pasture, and 42 in a sheep-fold (Tab. IV).

Individual growth rate of *A. caliginosa* is illustrated by the logistic curve (Fig. 6). The growth in individual months depended on weather conditions, mainly on soil moisture (Fig. 7). Variations in the nutrient resources of the environment had a variable effect on the growth rate of the earthworms. Young individuals appeared to grow faster in habitats with the highest and in those with the lowest organic matter supply, i.e. in a grazed pasture and in a sheep-fold (Fig. 8).

The mortality of the dominant species was low — on the average 19% a month during the growing season. High survival rate values were recorded for the youngest and the oldest earthworms; the survival rate was found to decrease during sexual maturation (Fig. 6). The main cause of mortality was the physical conditions and then the predation by dipteran larvae. The remainder of the predators seemed to have a marked effect on the earthworm population of a grazed pasture, and a very low effect on the earthworms of a former sheep-fold pasture.

The production of *A. caliginosa* populations was about $12\,kcal/m^2$ per a year in a grazed pasture, and $58\,kcal/m^2$ per year in a former sheep-fold pasture (Tab. VII). .

The earthworm turnover was low, about 1 (it was slightly higher for the grazed pasture — 1.3, and lower for the former sheep-fold pasture — 0.9).

The earthworms represented 28—68% of the macrofauna of the ecosystems studied (Tab. IX). The numbers, biomass and percentage contribution of this group grew with the increasing fertility of the environment. Parallel with this was a growth of the earthworm contribution to the flow of energy. The ratio of the amount of carbon respired by the earthworms to that returned to the soil during a year was 0.4—2.9% (Tab. X).

Assessed quantitatively, the role of the earthworms varies in meadows of variable nutrient resources. In poor-soil meadows with a deposited layer of organic matter the most important microbiological process stimulated by the earthworms was mineralization. Mineralization is also accelerated as a result of the predominance, in this habitat, of small surface earthworms, and of the dominance in the macrofauna of enchytraeids whose respiration is more efficient than that of the earthworms. In fertile meadows most important is the retardation by the earthworms of the degradation of organic matter, both by storing it in their bodies and stimulating the protein-forming processes.

6. POLISH SUMMARY (STRESZCZENIE)

W badanych ekosystemach występowało 10 z 15 gatunków dżdżownic znanych ze środowisk trawiastych Polski. Dwa główne zabiegi gospodarcze — koszenie i wypas, powodowały uproszczenie składu gatunkowego dżdżownic i zmianę struktury dominacji. Zmiana ta polegała na silnym wzroście liczebności ubikwistycznego gatunku *Allolobophora caliginosa* Sav. Wskaźnik zróżnicowania zespołu dżdżownic (O d u m 1971) malał od 1,7 na łące rezerwatowej do 0,6 na pastwisku koszarowanym (tab. II).

Występowanie dżdżownic powierzchniowych było skorelowane z tempem rozkładu materii organicznej (fig. 1). W środowiskach o szybkim tempie rozkładu dżdżownice te występowały w niewielkim procencie, a główną rolę odgrywała grupa dżdżownic mieszających glebę.

Sezonowe zmiany liczebności i biomasy dżdżownic charakteryzowało występowanie dwóch szczytów — wiosennego i jesiennego. Te wzrosty liczebności powodowane były wylęganiem się młodych dżdżownic. Dwuszczytowość dynamiki liczebności była wyraźniejsza w środowiskach łąkowych o sezonowym dopływie materii organicznej do gleby, a mniej wyraźna na pastwiskach o ciągłym dopływie materii organicznej (fig. 2).

Płodność osobnicza gatunku *A. caliginosa* wzrastała zgodnie ze wzrostem zasobności pokarmowej gleby. W trzech badanych środowiskach pastwisk w przeliczeniu na sezon wynosiła ona: 26 kokonów na pastwisku, 35 na pastwisku koszarowanym i 42 na pokoszarze (tab. IV).

Osobnicze tempo wzrostu *A. caliginosa* obrazuje krzywa logistyczna (fig. 6). W poszczególnych miesiącach wzrost zależny był od warunków klimatycznych, głównie od wilgotności gleby (fig. 7). Zróżnicowanie zasobności pokarmowej środowisk odbijało się w różnym stopniu na tempie wzrostu dżdżownic. Młode osobniki rosły szybciej na stanowiskach o najwyższym i najniższym dopływie materii organicznej, tj. na pastwisku i pokoszarze (fig. 8).

Śmiertelność dominującego gatunku była niewielka — średnio w sezonie osiągała wartość 19% miesięcznej liczebności. Wysoką przeżywalność miały najmłodsze i najstarsze dżdżownice, a w okresie dojrzewania płciowego przeżywalność zwierząt malała (fig. 6). Główną przyczyną śmiertelności były warunki fizyczne; na drugim miejscu można wymienić drapieżnictwo larw *Diptera*. Wydaje się, że pozostałe drapieżce wyraźnie oddziaływały na populację dżdżownic pastwiska spasanego, natomiast minimalnie na dżdżownice pastwiska koszarowanego.

Produkcja populacji *A. caliginosa* wynosiła na pastwisku około 12 kcal/m^2 na rok, a na pastwisku koszarowanym 58 kcal/m^2 na rok (tab. VII). Turnover dżdżownic był niski i wynosił w przybliżeniu 1 (nieco wyższy był na pastwisku spasanym — 1,3, a najniższy na pastwisku koszarowanym — 0,9). Dżdżownice stanowiły 28—68% liczebności makrofauny badanych ekosystemów (tab. IX). Liczebność, biomasa i udział procentowy tej grupy wzrastały wraz ze wzrostem żyzności środowiska. Równolegle z tym wzrastał udział dżdżownic w przepływie energii. Stosunek ilości węgla respirowanego przez dżdżownice do tej ilości, która dopływa w ciągu roku do gleby wynosił 0,4—2,9% (tab. X).

Oceniana jakościowo rola dżdżownic jest odmienna na łąkach o różnej zasobności. Na mało żyznych łąkach z warstwą zalegającej materii organicznej najważniejszym stymulowanym przez dżdżownice procesem mikrobiologicznym było przyspieszenie mineralizacji. Mineralizację tę przyspiesza także przewaga w tym środowisku niewielkich dżdżownic powierzchniowych, a także dominacja w zespole makrofauny wazonkowców o wyższej niż dżdżownice wydajności respiracji. Na łąkach żyznych największe znaczenie ma proces opóźniania przez dżdżownice degradacji materii organicznej — zarówno przez magazynowanie jej w swoim ciele, jak i przez stymulację procesów zbiałczania.

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Paper prepared by J. Stachowiak

AUTHOR'S ADDRESS:
Dr Ewa Nowak
Zakład Zoologii i Ekologii
Uniwersytetu Warszawskiego
ul. Krakowskie Przedmieście 26/28
00—325 Warszawa
Poland