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PRODUCTIVITY INVESTIGATION OF TWO TYPES OF MEADOWS IN THE VISTULA VALLEY

IX. PRODUCTION AND CONSUMPTION OF FIELD LAYER SPIDERS

(Ekol. Pol. 19:197–211). In this paper the production and consumption by spiders of the field layer was compared with that of two groups of dominant insects – the leafhoppers and adult *Diptera*. The dynamic of production of six dominant spider species and consumption of three populations of web spiders was analyzed. The probable total production and consumption of all spiders occurring in this stratum has been calculated on the basis of these data.

On natural meadow the consumption of spiders was greater than the production of the two mentioned groups of insects, while on cultivated meadows it was very small when compared with the insect production. Elimination coefficients for insects appeared to be several times lower in cultivated than in natural meadows which seems to be connected with a very low density of spiders in that habitat.

INTRODUCTION

Studies on production and consumption were undertaken as one of possible methods for the evaluation of the role of the definite group of organisms in an ecosystem. They permit a comparison between the quantity of energy used by the given group with that provided by the production of groups belonging to lower trophiclevel. This paper presents an attempt at a comparison of the consumption of spiders representing one of the dominant predatory groups, and the production of two dominant insect populations – the prey of spiders.

The paper discusses the spiders which mainly penetrate the field layer. Spiders of that stratum depend very much on the vegetation since plants provide an indispensable substrate for fixing webs, coccoons and bulding shelters.

Studies were carried out in three meadow communities quite differentiated in respect to the number of spiders.

1. In a glade in Kampinos National Park situated within a forest not cultivated for several years nor subjected to any other treatment; in patches of the association *Stellario-Deschampsietum* (Traczyk 1966). From its geographic name – Strzeleckie Meadows– symbol SM or an expression a natural meadow is used.

2. In two cultivated meadows of the *Arrhenatheretalia* type (Traczyk 1970) mown twice a year situated north of Warsaw in the vicinity of Kazuń village (the symbols K I and K II).

In the natural meadow the abundance of field layer spiders was many times higher (the average 52 individuals per m^2 during the growing season) as compared with other meadows (average 4.4 individuals per m^2 in K II and 0.64 per.m^2 in K I). Similarly the biomass of spiders on the natural meadow was much higher (Tab. I).

Comparative data on spiders inhabiting field layer in natural and cultivated meadows (mg dry matter per m^2)

Tab. I

		Natural meadow SM	Cultivated meadow K II
Numbers per m^2		52	4.4
Biomass		78.3	5.2
Production per growing season	dominant. species	279	not calculated
	all species	316	not calculated
Consumption per growing season	dominant web species	1617	not calculated
	all species	2482	54
Coefficient of insect elimination	*Diptera**	87	49
	*Homoptera Auchenorrhyncha ***	121	25

* After Olechowicz 1971, ** After Andrzejewska 1971.

On the natural meadow 6 spider species prevailed: *Theridion bimaculatum* (L.), *Tibellus maritimus* (Menge), *Singa hamata* (Clerck), *Singa heri* (Hahn), *Araneus quadratus* (Clerck), *Cheiracanthium erraticum* (Walck). They provided jointly 90% of the number and 87% of the biomass of all spiders occurring in the field layer.

In the cultivated meadow this group of species occurred mainly in the unmown margins. There are periods when the vegetation of these-meadows is very high even higher than in the natural meadow, but due to frequent changes in the environment, the cultivated meadows are inhabited mainly by species for which the turf layer provides the main area of penetration. From among species dominant in SM there occurred: *S. hamata*, *Th. bimaculatum*, and *T. maritimus*, but they comprised only 8% of the number of spiders connected with the field layer. *Xysticus cristatus* (Clerck) and *Linyphia pusilla* (Sund.) were relatively the most abundant species of this group (jointly 54% of the total number).

PRODUCTION

On the basis of two year studies (1967, 1968) the production i.e. biomass increment of six species dominant in SM, was evaluated.

Estimation of production was based on determining increment in weight of the average individual throughout its development and on simultaneously determining the changes in the density of individuals of the particular stages (Nees, Dugdale 1959, Winberg, Pečen, Šuškina 1965, Hillbricht-Ilkowska, Patalas 1967).

In the estimation of numbers and age composition of spiders the quadrat technique was used. It consists in a careful examination of plants in 10 frames on an area of 0.25 m^2 each and the recording of the number, age stages and the species composition of spiders. Such tests were repeated at weekly intervals during the period from May till October.

Each month the material was dried and weighed immediately after collection in order to determine the changes in weight of each species. All weight data were expressed in mg of dry weight.

In order to determine the density of spiders still in coccoons larger patches of meadow were searched – 10 patches with the dimensions of 20 × 0.5 m. Tests were repeated at 3 weeks intervals. On each occasion a portion of coccoons found was collected for the identiffication of the species, number of eggs or juvenile individuals and for the determination of their dry weight.

The fact that the most intensive increment in individual weight occurs at the end of life, at the stage of fertilized females is very characteristic and common for all the studied spider species. The weight of a female due to egg development increased two to four times in a fortnight and in some species, in a month period (Fig. 1–6). Daily increments in weight amounted from 0.3 mg (*S. heri*) to several mg (6.1 – *A. quadratus*) per individual. Even the increment

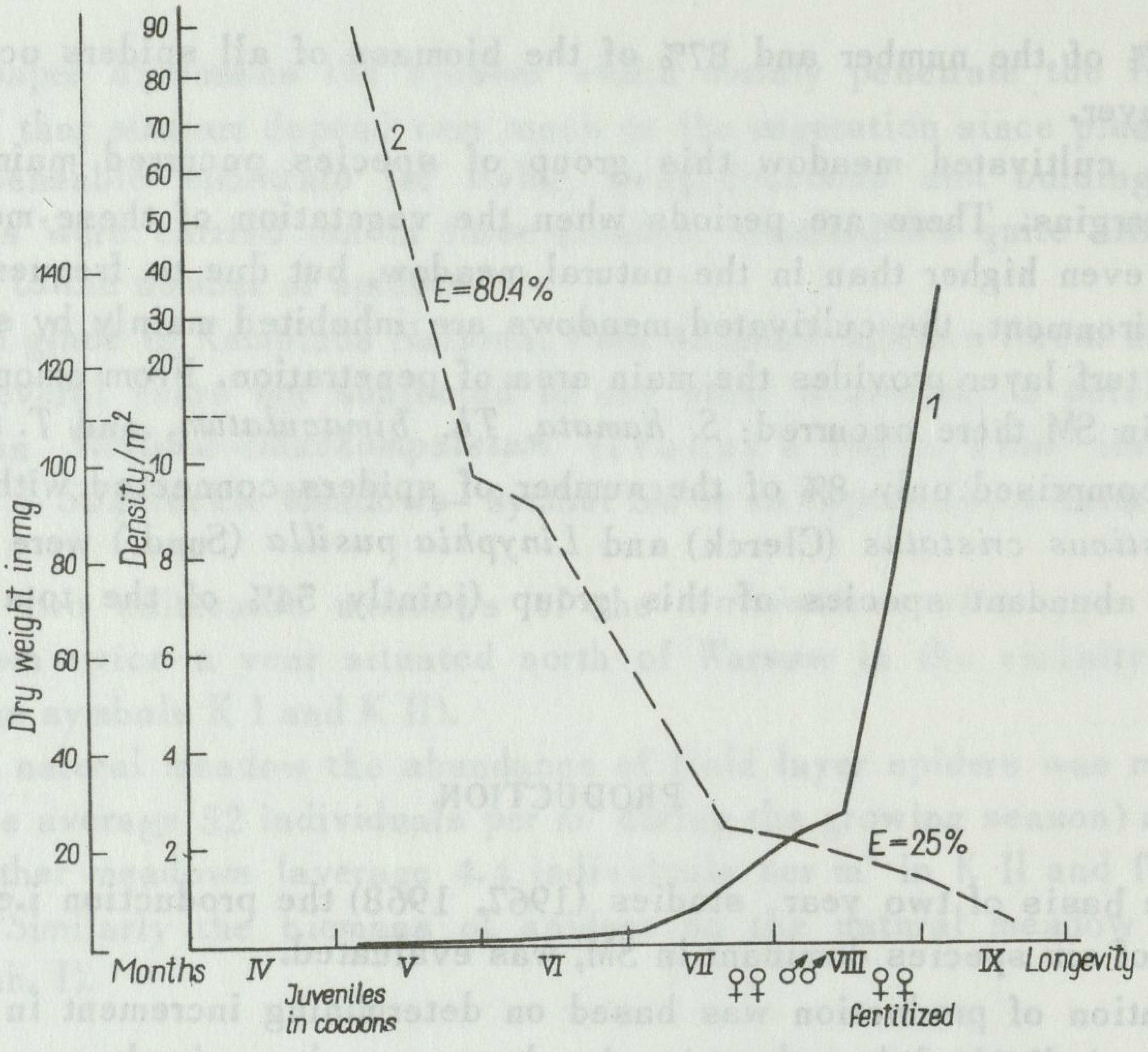

Fig. 1. Changes in body weight of an individual and changes in density of successive stages of *Araneus quadratus*

1 — dry weight in mg, *2* — density per m², *E* — elimination (per cent)

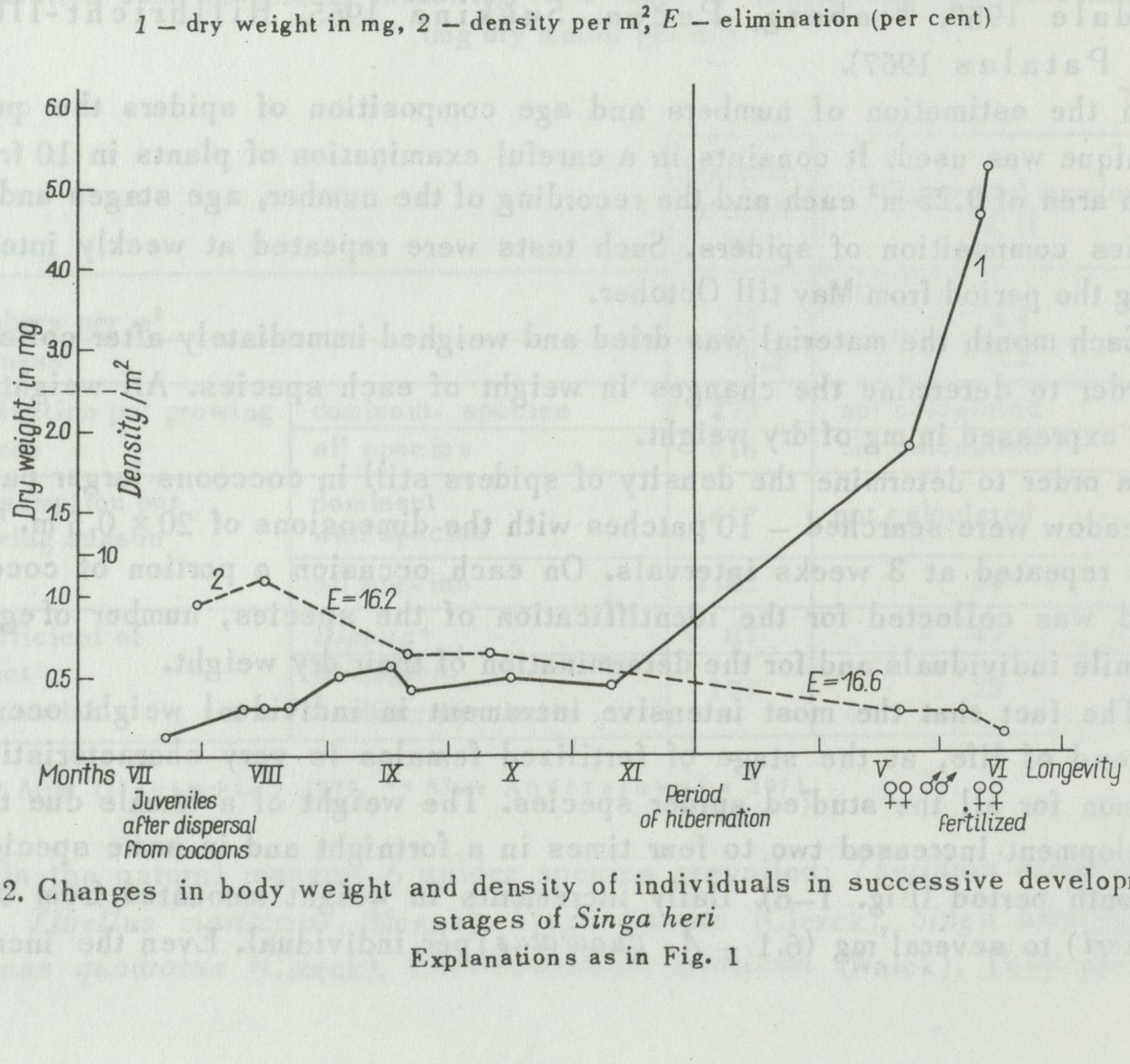

Fig. 2. Changes in body weight and density of individuals in successive developmental stages of *Singa heri*

Explanations as in Fig. 1

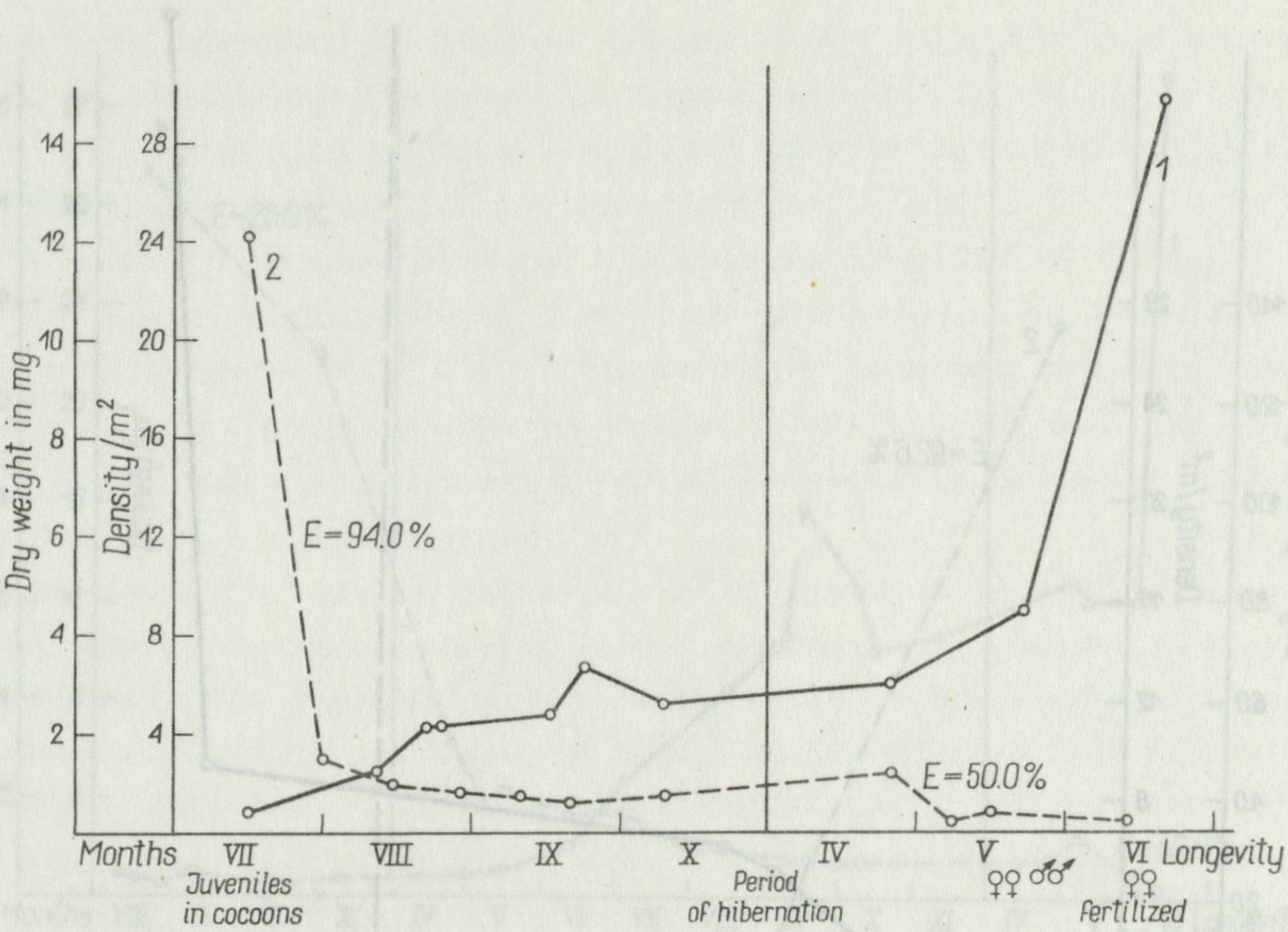

Fig. 3. Changes in body weight and density of individuals in successive developmental stages of *Singa hamata*

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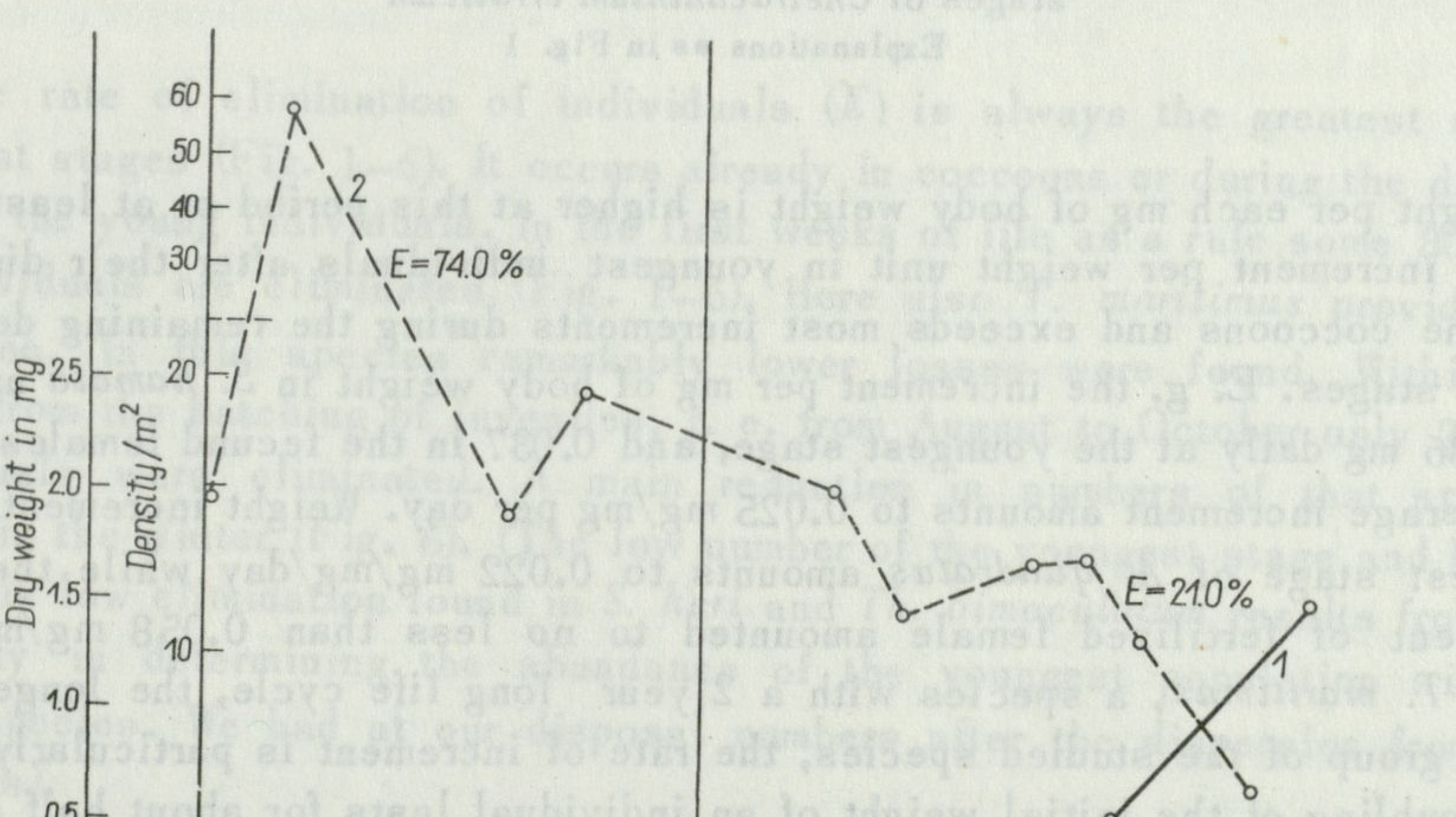

Fig. 4. Changes in body weight and density of individuals in successive developmental stages of *Theridion bimaculatum*

Explanations as in Fig. 1

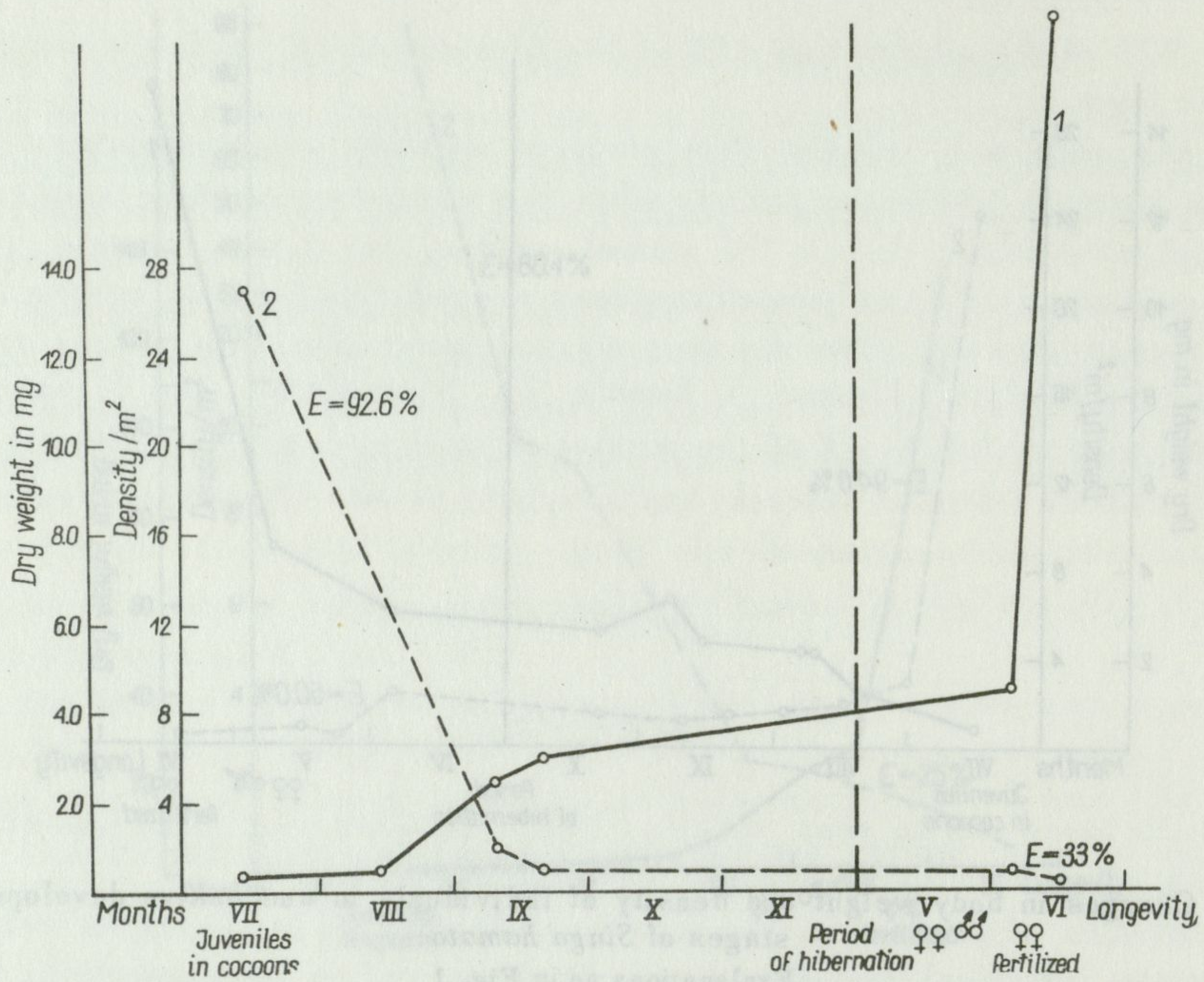

Fig. 5. Changes in body weight and density of individuals in successive developmental stages of *Cheiracanthium erraticum*
Explanations as in Fig. 1

of weight per each mg of body weight is higher at this period or at least equal to the increment per weight unit in youngest individuals after their dispersal from the coccoons and exceeds most increments during the remaining developmental stages. E. g. the increment per mg of body weight in *S. hamata* amounts to 0.036 mg daily at the youngest stage, and 0.037 in the fecund females, while the average increment amounts to 0.025 mg/mg per day. Weight increment at the youngest stage of *A. quadratus* amounts to 0.022 mg/mg/day while the daily increment of fertilized female amounted to no less than 0.058 mg/mg/day.

In *T. maritimus*, a species with a 2 year long life cycle, the longest one in the group of the studied species, the rate of increment is particularly slow. The doubling of the initial weight of an individual lasts for about half a year. It is only after this period that increments become more intensive (Fig. 6). At the final phase of life they are very high and amount to 0.047 mg/mg/day, while on the average – being only 0.021 mg/mg/day. The highest rate of growth was found in *A. quadratus* the species with the shortest life cycle (May-September). The weight of a hatched individual is doubled after already several days and the average daily increment in body weight amounts to no less than 0.044 mg/mg.

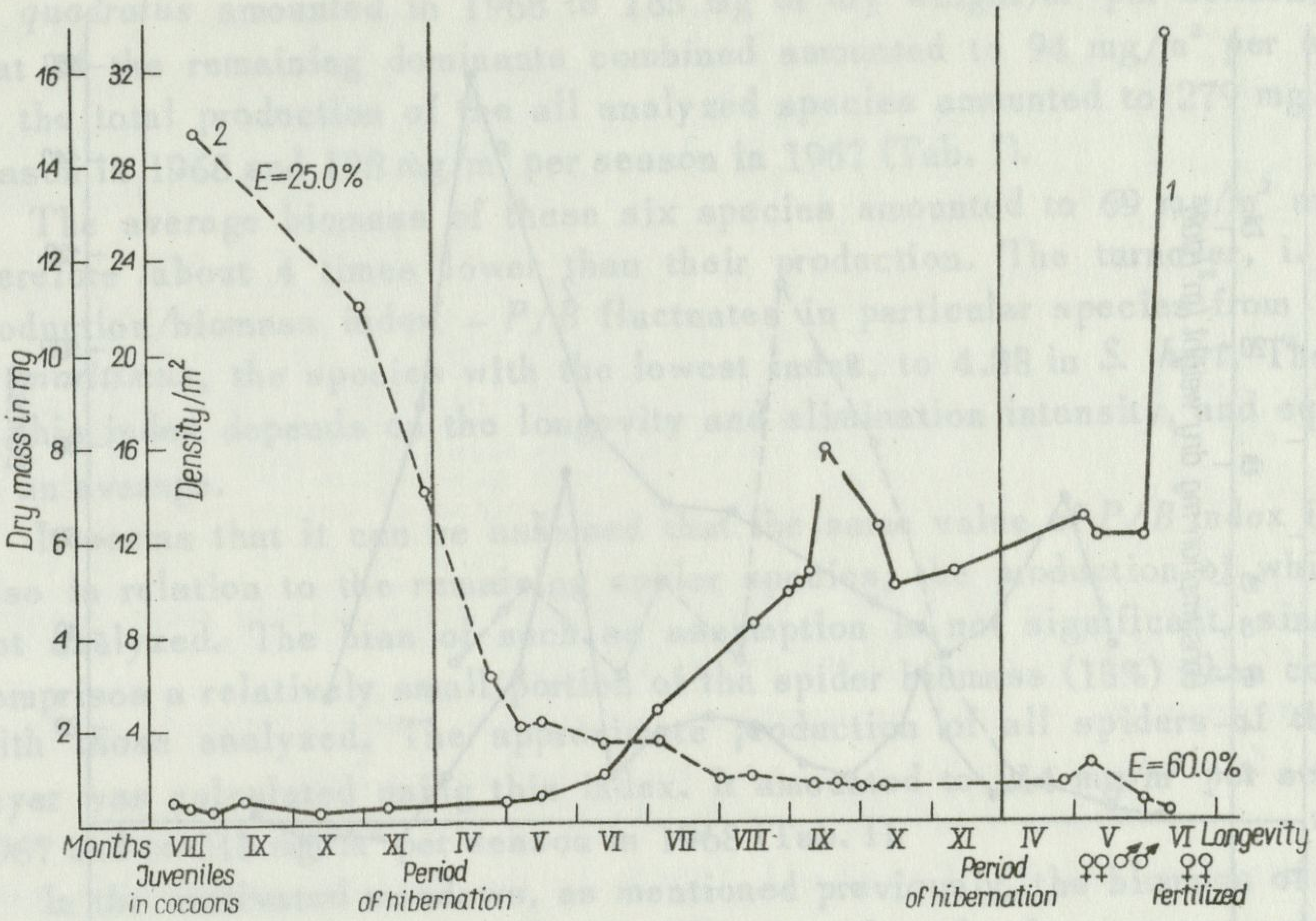

Fig. 6. Changes in body weight and density of individuals in successive developmental stages of *Tibellus maritimus*

Explanations as in Fig. 1

The rate of elimination of individuals (E) is always the greatest at the youngest stages (Fig. 1–6). It occurs already in coccoons or during the dispersion of the young individuals. In the first weeks of life as a rule some 80–90% of individuals are eliminated (Fig. 1–6). Here also *T. maritimus* provided an exception. In this species remarkably lower losses were found. Within the period from the hatching of juveniles, i. e. from August to October only 25% of individuals were eliminated. A main reduction in numbers of that species occurs in the winter (Fig. 6). (The low number of the youngest stage and hence relatively low elimination found in *S. heri* and *Th. bimaculatum* results from the difficulty in determining the abundance of the youngest population size of these species. We had at our disposal numbers after the dispersion from the coccoons).

From among the species dominant in this meadow only one – *A. quadratus* has a life cycle beginning in spring and completed in the autumn of the same year. August is the period of egg development in females and in September – the forming of coccoons which hibernate takes place (Fig. 1). The hatching period of the five remaining species occurs in July or in August (Fig. 2–6), immature stages hibernate and in spring (May-June) the copulation and the forming of coccoons takes place.

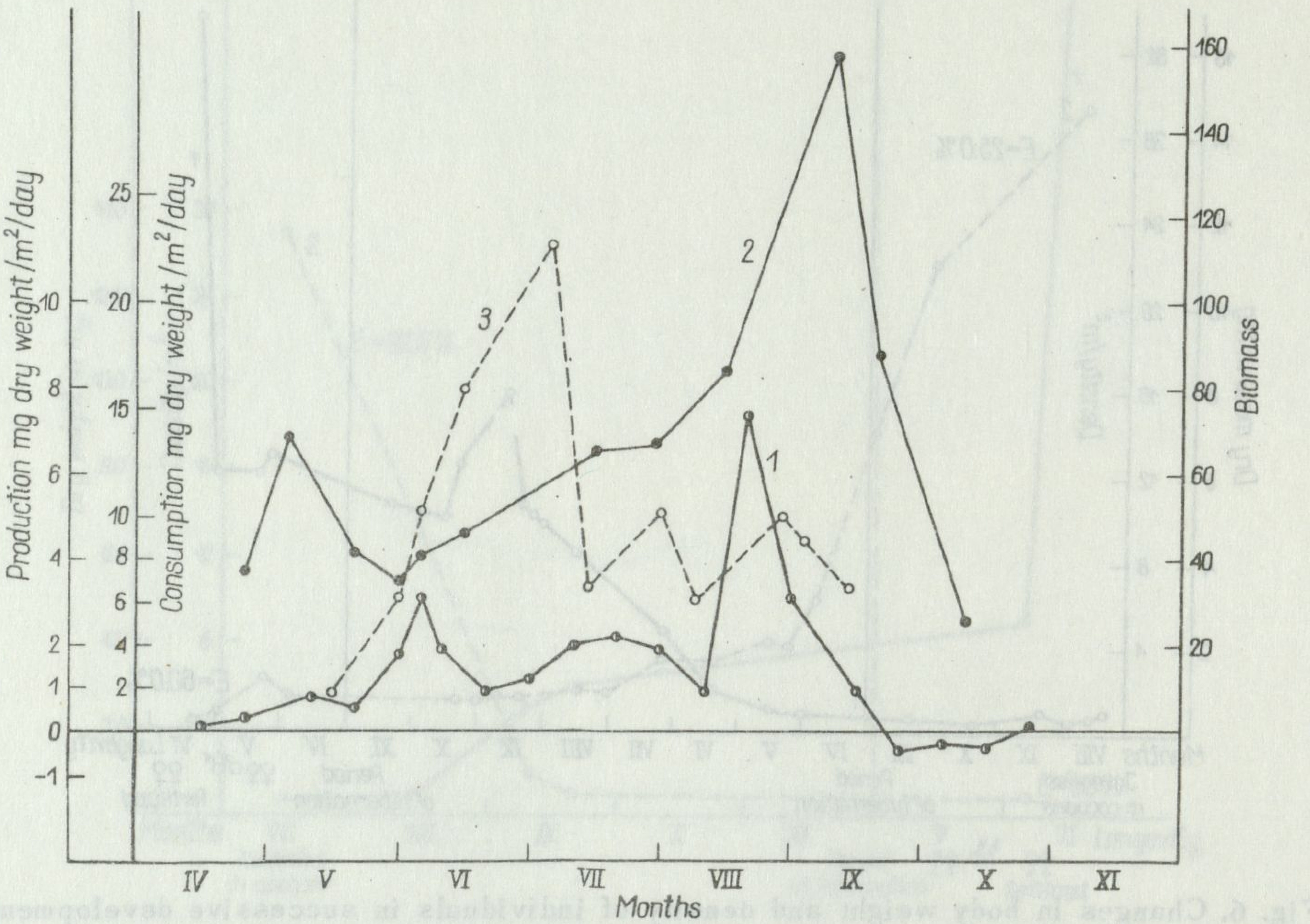

Fig. 7. Changes in production, biomass, and consumption throughout the season (1968)
1 – production of 6 dominant species, *2* – biomass of 6 dominant species, *3* – consumption by *Araneus quadratus* + *Singa heri* + *Singa hamata*

The dynamic of the production is characterized by two periods of maximum increments. One of them occurs between May and June, the other – between August and September (Fig. 7). These two periods of maxima are characteristic by the intensive growth in the weight of the females. The spring peak corresponds to the occurrence of fertilized females of the five studied species. Although the population size of spiders is low at this period, nevertheless the increment in body weight in individuals are sufficiently intensive to maintain a rather high total production – 3 mg/m^2 per day (Fig. 7). The other period of maximum production coincides with the intensive growth of body weight of *A. quadratus* females as well as great abundance and rather high increment in weight of juvenile individuals of the five remaining species following their dispersion from the coccoons (Fig. 7). Production in the latter peak is higher than in the former and amounts to 5 mg/m^2 per day.

In the autumn, until the end of September, there occurs a process of reduction in the biomass of hibernating populations (Fig. 7).

The species *A. quadratus*, in spite of its shortest lasting activity has decidedly the greatest annual production. The production of this species almost doubles the total production of the five remaining dominants. The production of

A. quadratus amounted in 1968 to 185 mg of dry weight/m² per season, while that of the remaining dominants combined amounted to 94 mg/m² per season. So the total production of the all analyzed species amounted to 279 mg/m² per season in 1968 and 198 mg/m² per season in 1967 (Tab. I).

The average biomass of these six species amounted to 69 mg/m² and was therefore about 4 times lower than their production. The turnover, i. e. the production/biomass index – *P/B* fluctuates in particular species from 2.35 in *T. maritimus*, the species with the lowest index, to 4.88 in *S. heri*. The value of this index depends on the longevity and elimination intensity, and equals 4, as an average.

It seems that it can be assumed that the same value of *P/B* index is valid also in relation to the remaining spider species, the production of which was not analyzed. The bias of such an assumption is not significant, since they comprises a relatively small portion of the spider biomass (13%) when compared with those analyzed. The approximate production of all spiders of the field layer was calculated using this index. It amounted to 214 mg/m² per season in 1967 and to 315 mg/m² per season in 1968 (Tab. I).

In the cultivated meadows, as mentioned previously, the biomass of spiders was very low, a few mg per m² only. The size of production was not calculated. The youngest developmental stages were hardly ever found in these meadows. In the face of changes in the environment brought about by mowing the breeding of numerous species takes place not in these maedows, but probably in the shrubs surrounding them. The ratio between the density of juveniles and adult individuals in these meadows was 1 : 5, while in SM – 1 : 1. Thus the production here depends mainly on weight increment for only certain groups of size. The ratio between production and biomass is therefore probably lower here than in the meadows previously discussed.

CONSUMPTION

The number of prey captured by web spiders of species *A. quadratus*, *S. hamata*, and *S. heri* was estimated. The method of direct collection of insects suspended in several scores (50–100) of marked spider webs in meadow was applied. The procedure and part of the results were described in previous papers (Kajak 1965a and b, 1967, Kajak, Olechowicz 1970, Kajak, Olechowicz, Pętal in press).

The observations of the number of preys in the webs were carried out twice a day with about one hour interval. The first time the composition of insects in the webs was recorded, the second time – preys were collected. On the basis of the difference between the first and second record it was estimated how many insects were caught in an hour. All day observations of the webs showed that spiders catch, on the average, during about 9 hours of the day. Knowing the number and weight of prey captured in the webs during a day and the density of spiders, the daily amount of food captured by the population was calculated. This quantity is greater than the actual consumption, because the remainders and food refused by the spiders were included.

The experiment was designed to estimate the consumption of juvenile individuals of *S. heri* and *T. maritimus* the food of which is difficult to obtain in the field. The experiment was carried out during 1.5 month – from mid-August to the end of September. Spiders were reared by three in 12 dcm³ (20 × 20 × 30 cm) cages and were fed adult *Diptera* and *Homoptera* of known weight. There were 3 experimental series with 4 replications each supplied with different number of insects – 5, 10 or 15 – every third day. Alive insects were counted and remnants collected and weighed every third day.

In experiments – food consumption of spiders was estimated, while – amount of food captured in the webs was determined in the field.

The results obtained in rearing *S. heri* are in the general agreement with the results obtained by Turnbull (1962) in the feeding experiments with another web spider – *L. triangularis* (Clerck). The daily food consumption of *S. heri* in experimental conditions corresponds to maintenance rate of feeding of *L. triangularis* in the same size (II and III developmental stage).

The food consumption increases considerably with increasing food supply in all feeding experiments with web spiders – *S. heri*, *A. quadratus* (Kajak, Stejgwiłło-Laudańska 1968) and *L. triangularis* (Turnbull 1962). Food consumption of *S. heri* in experimental conditions was lower than in the field (Tab. II). One of the possible reasons may be, that food supply was lower in an experiment than in the field, or that this species uses food inefectively the large proportion of it being left as remnants.

Comparison of the daily consumption of *Singa heri* in experiment and in field
(Individuals weighing 0.3 – 0.6 mg of dry weight were taken)

Tab. II

Experiment		Field
number of preys offered every 3 days	average consumption mg/mg	average quantity of food in webs mg/mg
5	0.021	
10	0.045	0.48
15	0.095	

Food rations obtained in experiments with another species – *T. maritimus* turned out to be three times smaller than those of web spider. It seems that species with a longer life span feed less intensively than those attaining a similar size within a shorter time. The fact reported by many authors (Bonnet 1930, Turnbull 1962, Kajak 1967, Miyashita 1968) of the prolongation of life in individuals along with a decrease in the quantity of food offered seems to confirm this principle.

On the basis of two years field data on the quantity of food captured in the webs of the three spider species the average quantity of food taken daily per biomass unit of spiders of various size was calculated (Tab. III). Material collected from 950 webs was used for these calculations. The amount of food captured daily comprises from 18 to 39% of individual weight, depending upon the size of the spider. Although the range of variability of these average data is wide, they allow to estimate roughly the amount of food taken by all spiders living in the analyzed ecosystem.

Mean quantity of food caught in webs of various size

Tab. III

Mean dry weight of spiders in mg	0.1–0.4	0.5–1.0	1.0–3.0	3.0–20.0
Daily quantity of food captured (mg of dry weight per mg dry weight of spider biomass)	0.39 ±0.115	0.37 ±0.127	0.26 ±0.106	0.18 ±0.145
Number of measurements used in the calculations	213	87	297	355

Up to now, there are only very scarce informations about spider consumption, especially about their consumption in a field. As a result from my previous data (Kajak 1967) average amount of food captured by *A. quadratus*, one of the greatest species living in that meadow (average weight of individual – 29 mg) works out to 0.8 mg per mg of weight and out to 0.13 mg in *A. cornutus*, species of average weight 6.8 mg.

In laboratory experiments Breymeyer (1967) found for *Trochosa ruricola* that its daily consumption comprises from 3 to 12% of the weight of the individual. According to Turnbull's (1962) experiments the daily food requirement of *L. triangularis* consists of 11–26% of its body weight. So daily consumption fluctuate about several per cent of the body weight when large spiders are concerned (*T. ruricola*, *A. quadratus*) and from dozen up to about thirty per cent when smaller species are analyzed (*S. heri*, *S. hamata*, *A. cornutus*, *L. triangularis*).

It has been assumed that determined relations between consumption and body weight may be used for the rough calculation of the consumption of all spiders in the field layer. The known average biomass of individual species was multiplied by adequate food ration per weight unit and by the number of days in a season with weather conditions making possible the spider hunting. On the basis of the results obtained in an experiment it was assumed that the food requirement of species with a multiannual life span is per weight unit 3 times lower than in species with only an annual life span.

Acceptating the numerous assumptions, e.g. that average amount of food captured in all species with similar dimensions is equal and that multiannual species consume considerably less — is of course a great but unavoidable simplification in order to estimate the total consumption of very diverse species. The consumption by three species, for which accurate data were available, amounted to 1618 mg/m² per season, approximate consumption calculated for all species amounted to 2482 mg/m² per season in 1968 and to 3244 mg/m² in 1967 (Tab II).

The amount of food captured by spiders depends on the intensity of emergence of *Diptera* — their main food component as well as the webs size and predator activity (Kajak 1967, Kajak, Olechowicz 1970, Kajak, Olechowicz, Pętal in press) The seasonal dynamic of the consumption depends on the situation at the given moment. E.g. in 1967 the course of the curve was strongly affected by a short intensive emergence of flies from the *Bibionidae* family occurring in August. Daily amount of food captured amounted then in the three web-spinning species to 56 mg/m². In 1968 the highest rate of food captured occurred at the beginning of July (22 mg/m² per day) (Fig. 7) as an effect of already less intensive emergence of flies from the *Cecidomyidae* and *Sciaridae* families (Olechowicz 1971). If the same rate of feeding considered valid on cultivated as on the natural meadows, it appers that e.g. in K II the amount of food captured by spiders during a season amounts to only 54 mg/m². This is such a small quantity as to compare with insect production there, that the role of spiders in insect reduction on these cultivated meadows is practically negligible.

DISCUSSION

According to data previously published (Kajak, Olechowicz 1970, Kajak, Olechowicz, Pętal in press) web spiders eliminate from 25% to 40% of adult *Diptera* produced in Strzeleckie Meadows. In the cultivated meadows of Kazuń the biomass of spiders was so small that their influence upon *Diptera* abundance is negligible.

The production of two insect groups dominating in the meadow and often contributing to the diet of spiders was estimated, namely the production of adult *Diptera* and that of *Homoptera-Auchenorrhyncha* (Andrzejewska 1971, Olechowicz 1971). The total production of these two insect groups in SM amounted in 1968 to 1497 mg/m^2 per season and was thus lesser than the amount of food captured by spiders (2482 mg/m^2 per season) this year (compare Andrzejewska 1971, Olechowicz 1971). Certainly the diet of spiders also includes other groups of insects whose production has not been estimated, e.g. the diet of web spiders includes: *Thysanoptera*, *Hymenoptera*, *Acridoidea*, *Aphidoidea*, and others (Kajak 1965a, b), nevertheless the statement that the consumption by spiders exceeds the production of two groups of insects dominating in the field layer convincingly shows the importance of this group of predators in the natural ecosystem.

The question has thus arisen if the rate of elimination of insects is different on cultivated and natural meadows. The ratio of the number of insects produced to the mean density of insects per the same unit of area was used as an elimination coefficient:

$$f(E) = \frac{V}{\overline{N}}$$

where V – number of insects produced per growing season, $\overline{N}$ – mean density of insects.

The smaller the ratio, the smaller the proportion of produced animals survive.

The elimination coefficient of this group of *Diptera* which is most often caught in webs (*Chironomidae*, *Cecidomyidae*, *Sciaridae*) is about twice in meadows with a large number of spiders (87 – SM, 49 – K II). The coefficient of the elimination of leafhoppers is almost 5 times higher in the meadow where number of spiders is greater (SM – 121, K II – 25).

Higher values of the coefficients of insect elimination in a habitat with a great number of spiders makes it possible to assume that the elimination caused by the latter is a significant factor affecting the population size of insects in an environment.

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BADANIA PRODUKTYWNOŚCI DWÓCH TYPÓW ŁĄK W DOLINIE WISŁY IX. PORÓWNANIE PRODUKCJI I KONSUMPCJI PAJĄKÓW PIĘTRA ROŚLINNOŚCI

Streszczenie

Zasadniczym celem pracy było porównanie produkcji i konsumpcji pająków z produkcją dwu najliczniejszych, w tym samym środowisku, grup owadów — dorosłych muchówek i skoczków.

Szczegółowo prześledzono przebieg produkcji sześciu gatunków dominujących — *Araneus quadratus* (Clerck), *Singa heri* (Hahn), *Singa hamata* (Clerck), *Theridion bimaculatum* (L.), *Cheiracanthium erraticum* (Walck), *Tibellus maritimus* (Mange). Łączna produkcja tych gatunków wynosiła 198 mg/m²/sezon w roku 1967 i 279 mg/m²/sezon — w roku 1968. Obliczono także dla tych gatunków współczynnik rotacji $\frac{P}{B}$ (przeciętnie wynosi ok. 4), który posłużył do określenia przybliżonej wartości produkcji wszystkich pająków górnego piętra roślinności (tab. I). Gatunki, u których produkcja została obliczona jedynie na podstawie biomasy — stanowią tylko 13% biomasy wszystkich pająków tego piętra.

Najintensywniejszy przyrost ciężaru i produkcja zachodzą w stadium dorosłych samic w fazie rozwoju jaj (fig. 1–6), natomiast ubywanie młodych osobników w ciągu pierwszego miesiąca po rozejściu się z kokonów wynosi najczęściej ok. 90%. Niższe wartości stwierdzono u gatunku o dwuletnim cyklu życiowym (*T. maritimus*) i tam, gdzie trudno jest ściśle określić zagęszczenie jaj (*Th. bimaculatum*, *S. heri*).

Została też określona ilość pokarmu łowionego w sieci przez 3 gatunki — *A. quadratus*, *S. heri* i *S. hamata*, głównie w oparciu o dane zebrane w terenie. Dane z dwóch lat otrzymane z trzech gatunków posłużyły do obliczenia przeciętnego, dobowego zapotrzebowania pokarmowego przy różnych rozmiarach ciała (tab. III). Na podstawie tego zapotrzebowania wnioskowano o przybliżonej ilości pokarmu, łowionego w ciągu sezonu także przez inne gatunki pająków.

Na łące rezerwatowej, nie użytkowanej, konsumpcja pająków przekraczała wartość produkcji dwu dominujących grup owadów (*Homoptera* i imago *Diptera* — 1497 mg/m²/sezon). Nieznacznie przewyższała tę wielkość nawet konsumpcja trzech dokładnie analizowanych gatunków (1618 mg/m²/sezon), a tym bardziej łączna konsumpcja wszystkich pająków tego piętra (2482 mg/m²/sezon). Na łąkach użytkowanych (K I i K II) pająki, jako zwierzęta ściśle uzależnione od roślinności, nie znajdują odpowiednich warunków i są nieliczne (tab. I). Wielkość konsumpcji jest tam oczywiście także stosunkowo bardzo niewielka w porównaniu z wielkością produkcji owadów, która na obu typach łąk była mniej więcej jednakowa (tab. I).

Warto podkreślić, że przy podobnej produkcji obu grup owadów przeciętna ich liczebność na łąkach użytkowanych jest z reguły kilkakrotnie wyższa, co wskazuje, że na łąkach tych ginie stosunkowo mniej owadów. Prawdopodobnie przyczynia się do tego mała liczba pająków w tych środowiskach.

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