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ENERGY BUDGET OF *TRIBOLIUM CASTANEUM* (Hbst) AT THE POPULATION LEVEL*

ABSTRACT: Production, respiration and assimilation rates were measured with two methods in confined populations of *T. castaneum* (Hbst) developing in the renewed habitat. The populations were started with a small initial number of beetles and developed for 19 weeks under controlled conditions of temperature, humidity and food. All budget elements showed an oscillatory character with a tendency of diminishing oscillations with time. Both methods yielded similar results, the differences being attributed to cannibalism. The net production efficiency, being high at the moment of colonization of the habitat, was found to diminish exponentially with time. Consumption was estimated by assuming that assimilation efficiency was 60%. The instantaneous and cumulative energy budgets of the population developing for four and a half months are given.

Contents

1. INTRODUCTION

There is a great deal of papers in literature dealing with bioenergetics of species. To exemplify this let us mention only the names of several authors and objects of their studies: Hiratsuka (1920) – *Bombyx mori* L., Ivlev (1939) – *Tubifex tubifex* L., Richman (1958) – *Daphnia pulex* Leydig, Klekowski and Shushkina

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(1966) — *Macrocyclops albidus* Jur., K l e k o w s k i, P r u s and Ż y r o m s k a - R u d z k a (1967) — *Tribolium castaneum* Hbst., W h i t e (1968) — *Tracheoniscus rathkei* Brandt, M c D i f f e t t (1970) — *Pteronarcys scotti* Ricker, P r u s (1971, 1972) — *Asellus aquaticus* L., F i s c h e r (1972) — *Lestes sponsa* (Hans.), F i s c h e r and L y a k h n o v i c h (1973) — *Cteropharyngodon idella* Val., C a m p b e l l and S i n h a (1974) — *Sitophilus granarius* (L.), S z w y k o w s k a - R e y (1974) — *Sitophilus granarius* (L.), S i n g h, C a m p b e l l and S i n h a (1976) — *Sitophilus oryzae* (L.).

The majority of these studies were carried out with separate individuals, often reared in isolation and under optimum environmental and food conditions. Such budgets can be referred to as budgets at an individual level.

There is a few papers dealing with bioenergetics of population. We can mention here paper by S m a l l e y (1960) on *Orchelimum fidicinium* Rehn et Hebard. G y l l e n b e r g (1969) has studied the energy flow through a grassland population of *Chorthippus parallelus* (Zett.), S t a c h u r s k a (1970 and in K l e k o w s k i et al. 1972) investigated energy budget of *Dileptus cygnus* Clap. et Lach. and P i l a r s k a (1972)— *Brachionus rubens* Ehr., both in relation to different concentration of food and at the population level. S t ę p i e ń (1970) has elaborated physiological and ecological energy budget of *Rhizoglyphus echinopus* E. et R. H o r n - M r o z o w s k a (1976) has studied the energy budget of a nest of *Formica pratensis* Retzius.

Tribolium castaneum is a species which was rather extensively studied in population aspects such as density, life span, fecundity, mortality, cannibalism, and other features (e.g., P a r k, M e r t z and P e t r u s e w i c z 1961, P a r k et al. 1965, P a r k, M e r t z and N a t h a n s o n 1968). Bioenergetic approach to this species can be found in paper by K l e k o w s k i, P r u s and Ż y r o m s k a - R u d z k a (1967). The energy budget presented there is based on cultures of individuals reared under optimum habitat and food conditions. These studies did not cover consumption, which is especially difficult to assess in flour beetles. Radioisotope methods with ^{32}P also renders some difficulties (D o m i n a s 1975). Nevertheless, with this method consumption was measured in larvae of fifth instar (H. Dominas, R. Z. Klekowski and H. Żyromska-Rudzka — unpublished data) and the budget for this stage is given in paper by P r u s (1975). Similarly, G u p t a and R a d h a k - r i s h n a m u t r y (1971) have measured consumption in larvae of *T. castaneum* and another species using ^{45}Ca-labelled compound as a marker.

An interesting method of assessing assimilation efficiency in *T. confusum* Duv. is that used by B h a t t a c h a r y a and W a l d b a u e r (1970). These authors measured uric acid content in the mixture of food and faeces remaining after feeding *T. confusum* larvae as well as in faeces sorted manually, using enzyme-spectrophotometric method (B h a t t a c h a r y a and W a l d b a u e r 1969). Thus obtained values of consumption, assimilation and assimilation efficiency were compared with the values obtained by manual sorting of faeces from food.

The aim of the present paper was to measure or estimate elements of energy budget as well as production efficiencies in developing populations of *T. castaneum* cl strain (P a r k, M e r t z and P e t r u s e w i c z 1961). It would be interesting to compare the assessed values with the elements and efficiencies of the energy budget for this strain of the species at the individual level, presented by K l e k o w s k i, P r u s and Ż y r o m s k a - R u d z k a (1967).

Calculations were based on formulae reported by I v l e v (1938):

$$C = P + R + F, \qquad A = P + R,$$

where: C is consumption, P – production, R – respiration, F – egestion, A – assimilation. The components of the second equation were only measured which allowed to calculate the net production efficiency acc. to formula: $K_2 = \dfrac{P}{A} \cdot 100$. Consumption was estimated by assuming that assimilation efficiency in *T. castaneum* is similar to that of *T. confusum* and amounts to 60% (after B h a t t a c h a r y a and W a l d b a u e r 1970). Gross production efficiency, $K_1 = \dfrac{P}{C} \cdot 100$, was also estimated.

2. MATERIAL AND METHODS

Elements of energy budget were measured in continuous cultures of 10 populations of *T. castaneum* cI strain. The initial number of young beetles were 4 pairs per vial. The cultures were run in 8 g of standard medium (95% wheat flour "wrocławska" + 5% dry powdered yeast, by weight) in a dark incubator at a temperature of 29°C and relative humidity of 75%. The experiments were run in two series with time delay of two days between them.

Every 7 days respiration of the populations was measured and, on the following day, the populations were removed by sifting from the old medium and the numbers of eggs, larvae, pupae and adults were counted. These stages were weighed to assess living biomass of the population. Dead individuals and exuviae were also weighed and used later for measurement of calorific value and water content. After censusing, the populations were returned to new portions of medium which had been weighed with a high accuracy. The vials with population and habitat were also weighed before starting the population census and after returning the population to a new medium. The cultures and measurements were run for 19 weeks.
census and after returning the population to a new medium. The cultures and measurements were run for 19 weeks.

Two methods were adopted for measuring each budget element.

F i r s t   m e t h o d. Production was calculated from the changes of population biomass in 7-day intervals. Production of a given stage was calculated as the difference between the two subsequent biomass values. Taking into account the different water content in the living biomass of different stages and variations in their calorific values, the energy equivalents of production for various stages were calculated. The total production of living biomass was obtained by summing up the values of production by each stage. Weighing was done with semi-analytical balance to an accuracy of 0.0001 g, after a thorough separation of animals from the medium. Dead individuals and exuviae formed so-called dead production. This part of production and the production of living biomass were added up to form the total production.

Respiration was measured in a Warburg apparatus every 7 days, on a day preceding the population census. This ensured performance of measurements with the least possible disturbance of the population by experimenters. Culture vials were at the same time the respiratory chambers which could be easily connected to the Warburg apparatus. The only disturbance was transferring the culture vials from the incubator to a water bath of the Warburg apparatus. The volume of the culture vial together with that of the respirometer system was about 30 ml. Carbon dioxide was absorbed with 0.5 ml 20% water solution of KOH and, when measuring CO_2 evolution, 0.5 ml 20% water solution of $CaCl_2$ was used.

Measurements were taken from 8:00 to 19:00 hours with oxygen consumption measured in the morning and in the evening, and evolution of CO_2 – at noon. Each of the 3 runs lasted at least 2.5 hours. The obtained results of oxygen consumption were presented as $\mu l\ O_2$/popula-

tion · hr, and then converted into calories/population · 24 hrs, according to the oxy-calorific equivalents based on RQ values which were measured each time.

Assimilation was obtained as a sum of production and respiration, both converted into calories.

S e c o n d   m e t h o d. This method depended on the fact that the population and its habitat formed an isolated system. Any loss in weight of the culture vials holding both population and its habitat can be considered as energy loss for metabolism, or cumulative respiration for a given time (7 days). This part of food which is consumed is either respired, which equals to the above mentioned weight loss, or it is built into population biomass, or egested as faeces to the habitat. Both, increase in biomass weight and egestion of faeces do not affect the total weight of the vial content since they remain in the system in an altered form, but the metabolized energy does affect it.

Similarly, the amount of assimilated food (cumulative energy of assimilation) can be measured as a difference in weight of the habitat which in this particular case is also food at the beginning and in the end of exposure, i.e., after 7 days. The weight of habitat changes only by the weight of the assimilated food, since faeces return to the habitat and are not affecting substantially the total weight of the vial content; substantially, since we are conscious of some slight changes in weights due to different hydration and calorific value of food, biomass, and faeces. Both respiration and assimilation were first calculated in terms of flour weight, and then converted into calories. Production assessed with this method was obtained as a difference between assimilation and respiration.

Calorific value and water content in various developmental stages and in food, necessary for calculation of the biomass production with the first method, and respiration, assimilation, and production with the second method, were accepted after K l e k o w s k i, P r u s and Ż y r o m s k a - R u d z k a (1967). Calorific values of exuviae and dead adults were obtained by combusting these materials in the microbomb calorimeter (K l e k o w s k i and B ę c z - k o w s k i 1973) after assessing their dry matter content.

Pearson's correlation and analysis of variance were the means of statistical operations carried out on the numerical data.

3. RESULTS

The population censusing allowed to describe changes in numbers and biomass of the developmental stages of the population as well as in production, respiration and assimilation of the developing population. All this permitted to calculate an energy budget (without egestion), both instantaneous and cumulative one, for the period of 19 weeks. The net production efficiency (K_2) was also calculated. The complete energy budget (with egestion) and gross production efficiency (K_1) were estimated by accepting an arbitrary value of assimilation efficiency.

P o p u l a t i o n   n u m b e r s. The numbers of larvae, pupae and adults are presented in Figure 1. The larvae were found to appear in the population periodically, every 4 weeks or so. The first peak of appearance is highest due to the minimum egg cannibalism operating in the initial stage of the population development. Further the peaks become smaller and smaller so that the curve for numbers of larvae takes form of an extinguishing oscillation. Changes in numbers of pupae follow those of larvae, showing also an oscillatory character with time shift of about 2 weeks. The numbers of adults, after eclosion of the first peak of pupae, increase to the level of about 120 individuals per vial. Further the recruting of adults is inconsiderable one
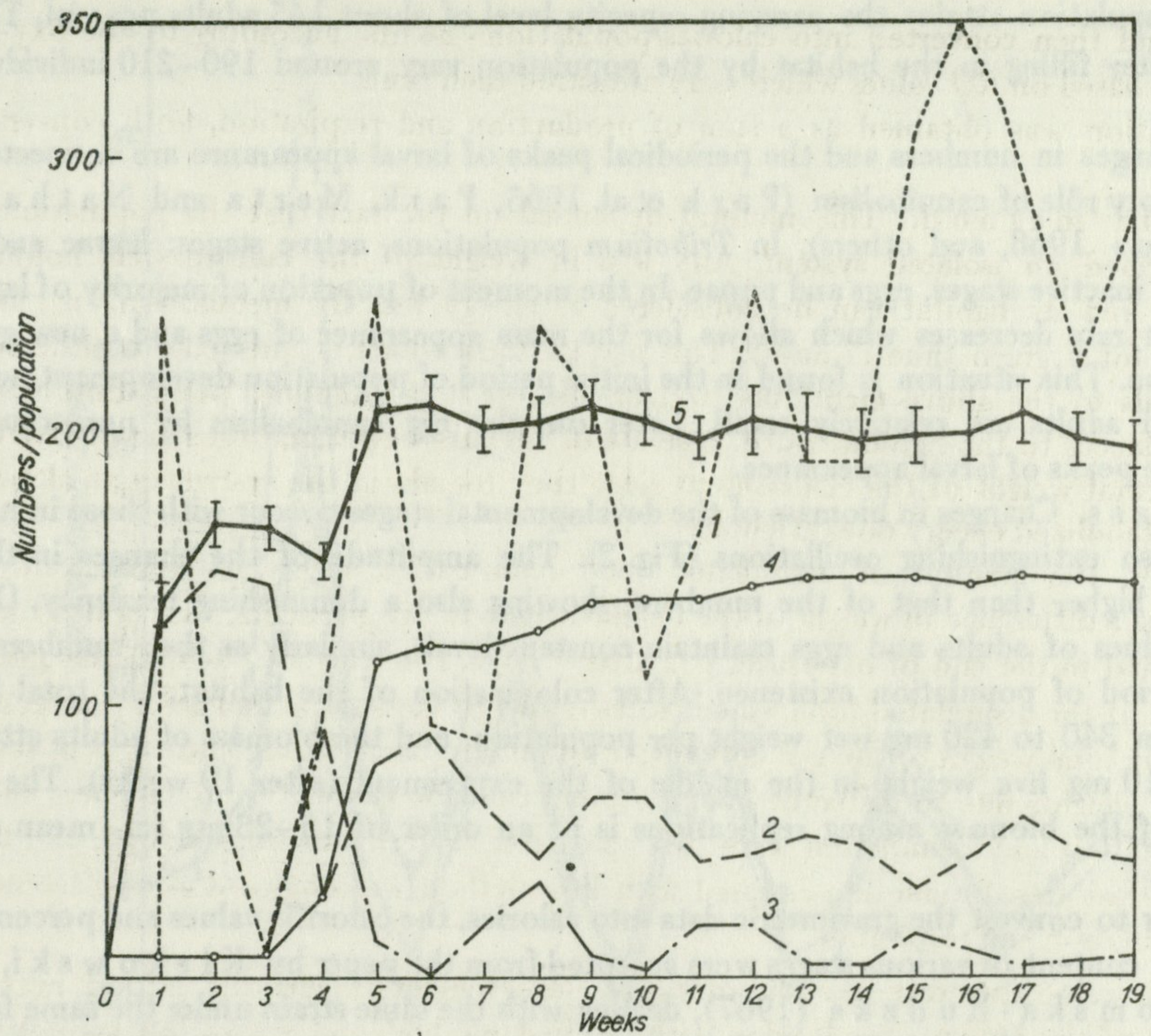
Fig. 1. Numbers of developmental stages in a confined population of *T. castaneum* cI
1 — eggs, *2* — larvae, *3* — pupae, *4* — adults, *5* — total without eggs ± mean error
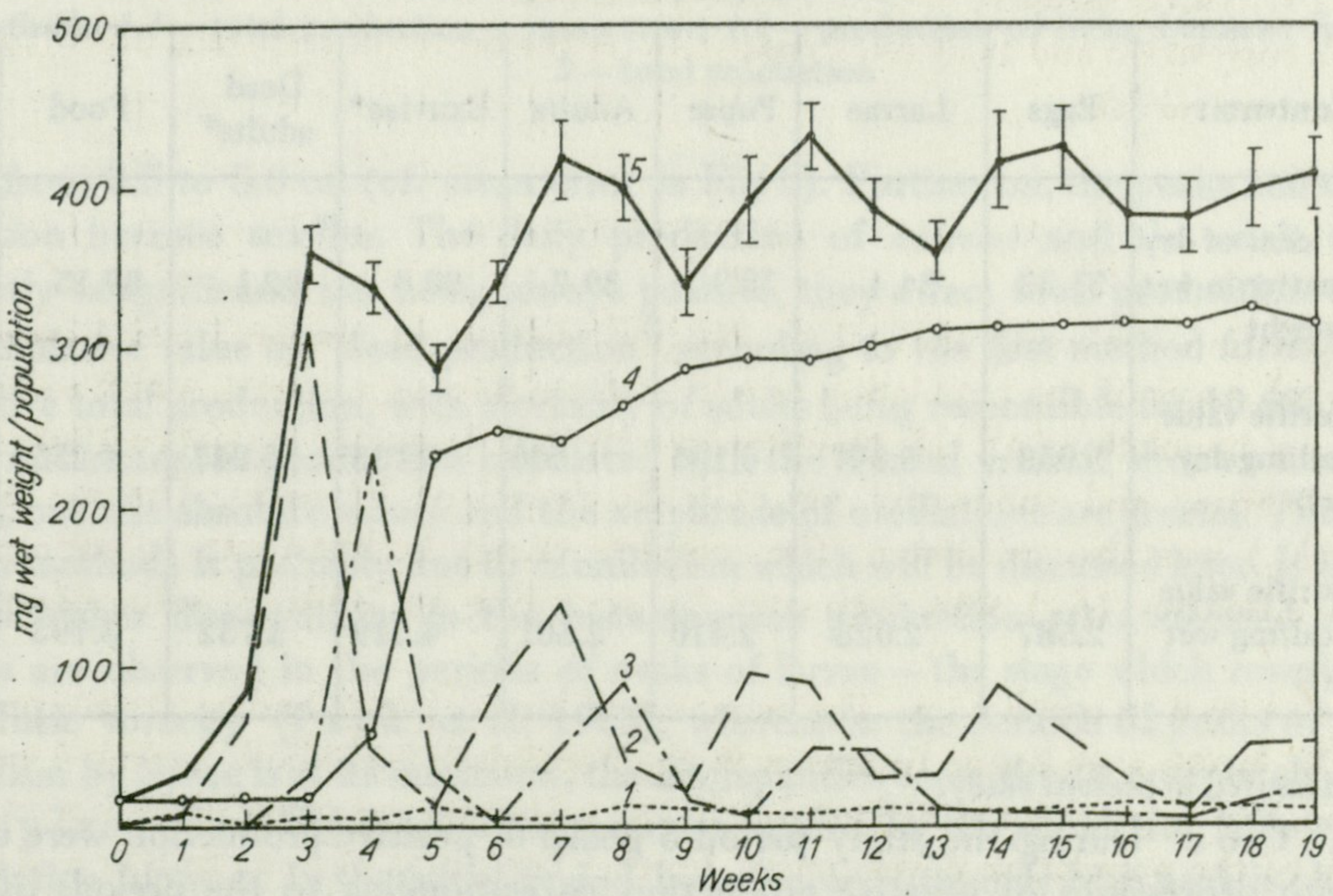

Fig. 2. Biomass of developmental stages in a confined population of *T. castaneum* cI
1 — eggs, *2* — larvae, *3* — pupae, *4* — adults, *5* — total ± mean error

and the population attains the carrying capacity level of about 145 adults per vial. The total numbers after filling in the habitat by the population vary around 190—210 individuals per population.

The changes in numbers and the periodical peaks of larval appearance are connected with the regulatory rôle of cannibalism (P a r k et al. 1965, P a r k, M e r t z and N a t h a n s o n 1968, P r u s 1968, and others). In *Tribolium* populations, active stages: larvae and adults cannibalize inactive stages, eggs and pupae. In the moment of pupation of majority of larvae the cannibalism rate decreases which allows for the mass appearance of eggs and a new group of young larvae. This situation is found in the initial period of population development, when the numbers of adults are relatively small. Later on, the egg cannibalism by numerous adults restricts the peaks of larval appearance.

B i o m a s s. Changes in biomass of the developmental stages concur with those in numbers, showing also extinguishing oscillations (Fig. 2). The amplitude of the changes in the total biomass is higher than that of the numbers, showing also a diminishing tendency. Only the biomass values of adults and eggs maintain constant levels, similarly as their numbers, in the further period of population existence. After colonization of the habitat, the total biomass ranges from 340 to 420 mg wet weight per population, and the biomass of adults attains the level of 310 mg live weight in the middle of the experiment (after 10 weeks). The general variation of the biomass among replications is of an order of 15—25 mg (cf. mean error in Fig. 2).

In order to convert the gravimetric data into calories, the calorific values and percentages of dry matter content of various stages were accepted from the paper by K l e k o w s k i, P r u s and Ż y r o m s k a - R u d z k a (1967), dealing with the same strain under the same food and climate conditions. They are given in Table I.

Table I. Dry matter content and calorific value of developmental stages , exuviae, and food of *T. castaneum* cI (after K l e k o w s k i, P r u s and Ż y r o m s k a-R u d z k a 1967)

Contents:	Eggs	Larvae	Pupae	Adults	Exuviae*	Dead adults*	Food
Per cent of dry matter in wet weight	51.35	34.4	38.9	39.7	88.0	92.1	89.15
Calorific value (cal/mg dry wt)	5.038	5.897	6.195	6.300	5.135	6.247	4.255
Calorific value (cal/mg wet wt)	2.587	2.028	2.410	2.501	4.519	5.752	3.793

*Measured in present study.

P r o d u c t i o n. During the study period 5 peaks of positive production were observed, separated with depressions of negative production, corresponding to the periods of biomass decrease (Fig. 3). The highest production rate was recorded in the initial period of the population existence, reaching value of 90 cal/population · 24 hrs. Variations among replicates
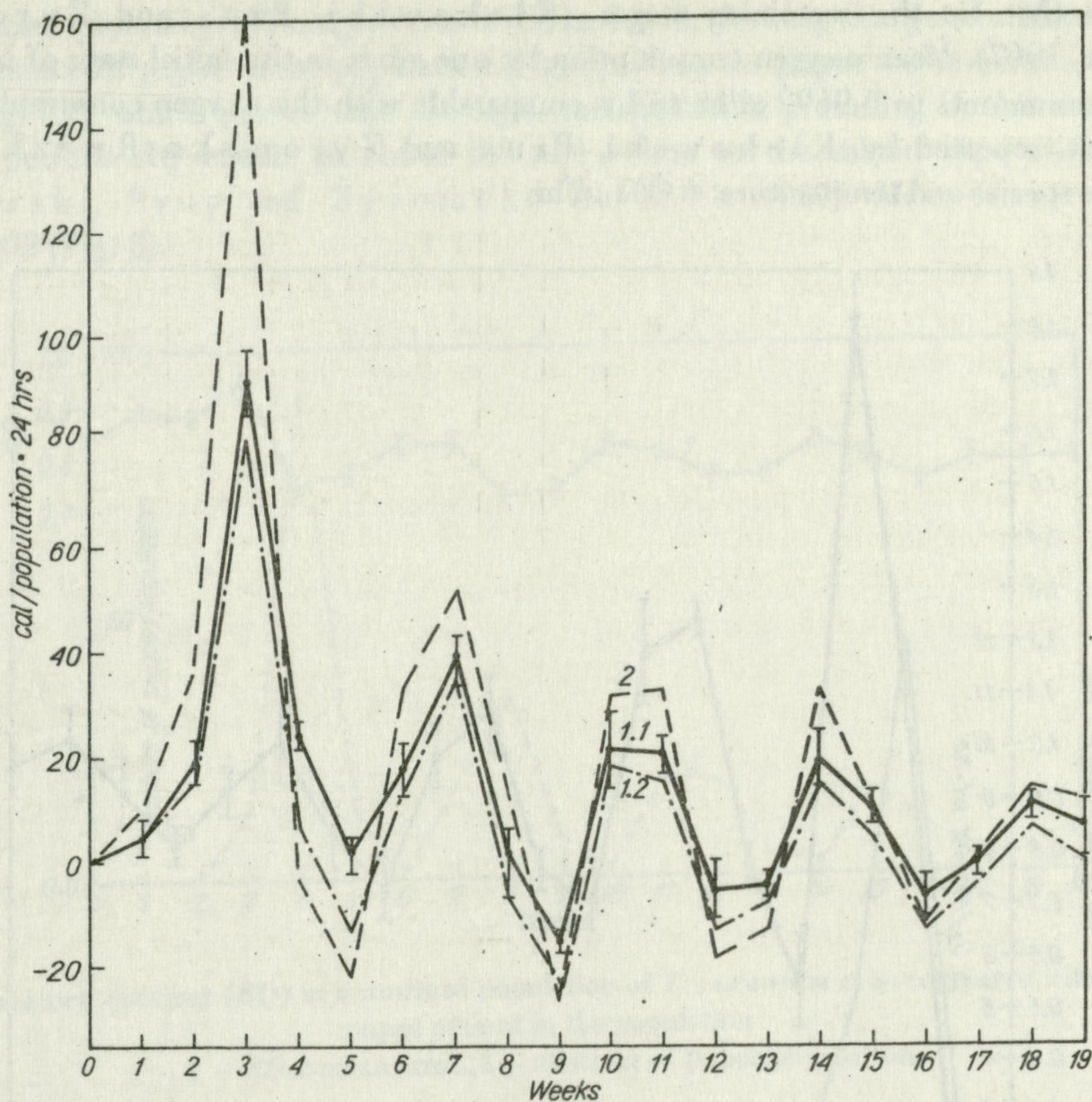
Fig. 3. Production rate in a confined population of *T. castaneum* cI
First method: *1.1* – total production ± mean error, *1.2* – production of living biomass. Second method:
2 – total production

ranged from 0.5 to 5.0 cal (cf. mean error in Fig. 3). Further on, the peaks and depressions of production become smaller. The daily production of exuviae and the adult mortality are apparently insignificant, but being always positive, they affect total production considerably. The cumulative value of "dead production" according to the first method forms 47.5% of the cumulative total production, with mortality of adults being responsible for 10.6%.

The instantaneous production calculated with the second method shows a similar trend of changes, but the absolute values and the amplitude of oscillations are greater. This discrepancy between methods is probably due to cannibalism which will be discussed later. It is noteworthy that the higher discrepancies in the instantaneous production rates assessed with the two methods are observed in the periods of peaks of larvae – the stage which reveals a very high cannibalistic voracity (P a r k et al. 1965), whereas in the periods of peaks of pupae, when cannibalism by larvae is at its minimum, the discrepancies cease almost completely.

R e s p i r a t i o n. The average oxygen consumption by the population follows the changes in population biomass. In the initial period, however, an extremely high peak is observed which may be accounted for by a very intense metabolism of large numbers of fastly growing larvae (Fig. 4). Further oscillations of metabolism are much lower, but they always reflect the changes in numbers of larvae present in the population, since oxygen consumption by larvae is much

higher than that by the remaining stages (K l e k o w s k i, P r u s and Ż y r o m s k a -
- R u d z k a 1967). Mean oxygen consumption by one adult in the initial stage of population
development amounts to 6.9692 μl/hr and is comparable with the oxygen consumption by an
average adult, reported by K l e k o w s k i, P r u s and Ż y r o m s k a - R u d z k a (1967)
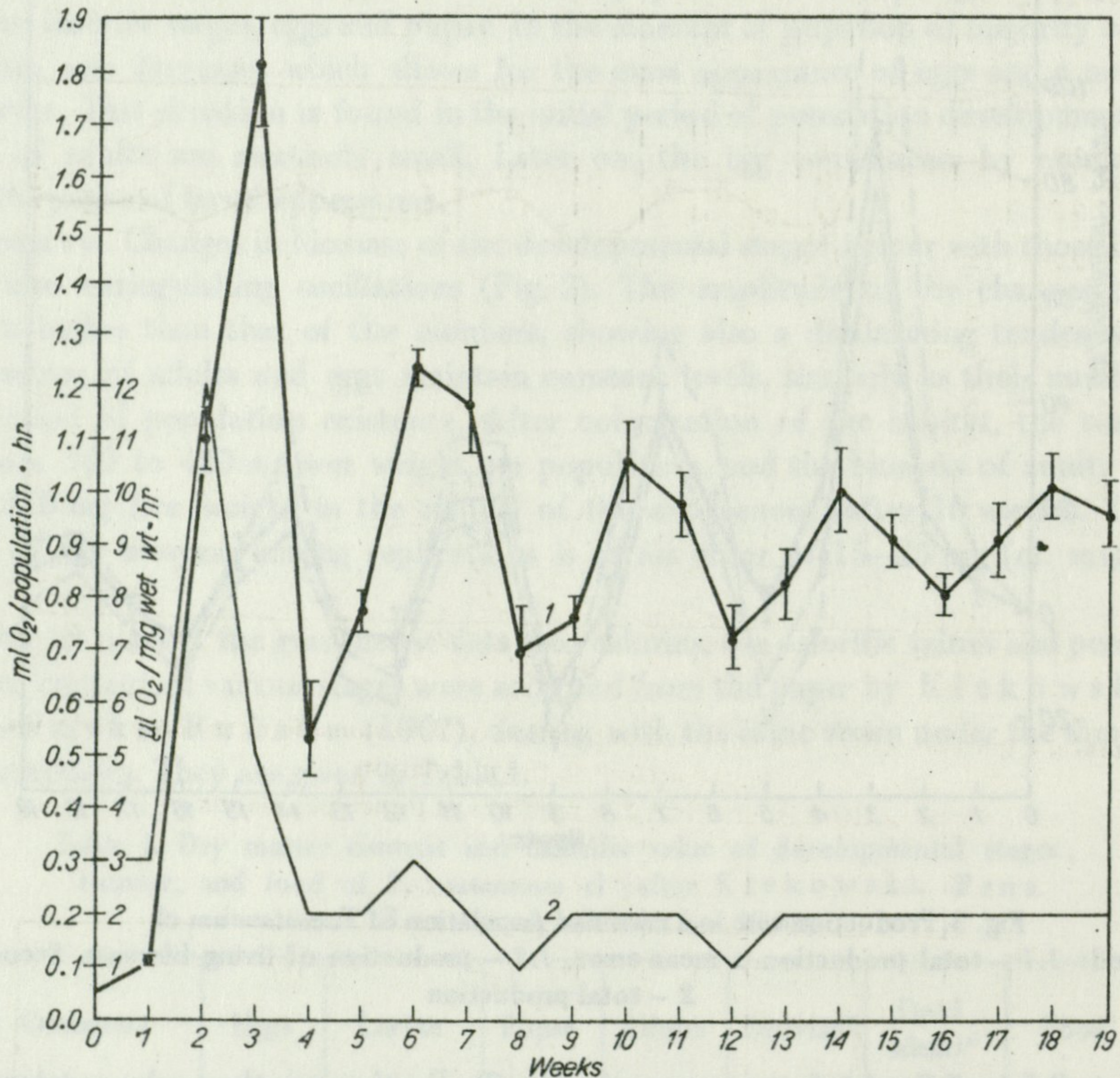for the same species and temperature: 6.801 μl/hr.

Fig. 4. Respiratory rate per population and metabolic rate per mg wet weight of biomass in a confined
population of *T. castaneum* cl
First method: *1* — ml O_2/population · hr ± mean error. *2* — μl O_2/mg wet weight · hr

Respiration of a related species, *T. confusum*, was studied by P a r k (1936). This author
found higher oxygen consumption in adult females than males both in fresh and conditioned
media. Somewhat lower values of respiration rate in *T. confusum* adults than in the present
paper for adults of *T. castaneum* were obtained by O r z e c h o w s k i (1970). However, this
author concludes that the oxygen consumption by separate stages, when summed up for total,
is lower than that measured in all stages kept together.

The oxygen consumption by population of *T. castaneum* cI, after filling in the habitat with
population, amounts to 0.7–1.2 ml O_2/hr with the metabolic rate (per mg living biomass)
ranging from 1.7 to 2.8 μl/mg · hr (Fig. 4). During colonization of the habitat, when the mass
occurrence of larvae was recorded, the metabolic rate was 12.429 μl/mg living biomass · hr
(Fig. 4). General variation of respiration among replications, as expressed by mean errors, is
small (cf. *M.E.* in Fig. 4).

Respiratory quotient (RQ) ranges from 0.722 to 0.949, showing changes correlated with the mass appearance of pupae in the population (Fig. 5). When the pupae are numerous, RQ is low, approaching 0.7, which proves that the lipid metabolism is prevailing in this stage. In the remaining periods RQ equals to about 0.8 and points to the mixed type of metabolism (K l e k o w s k i, P r u s and Ż y r o m s k a - R u d z k a 1967). Mean error ranges from 0.003 to 0.02 (Fig. 5).
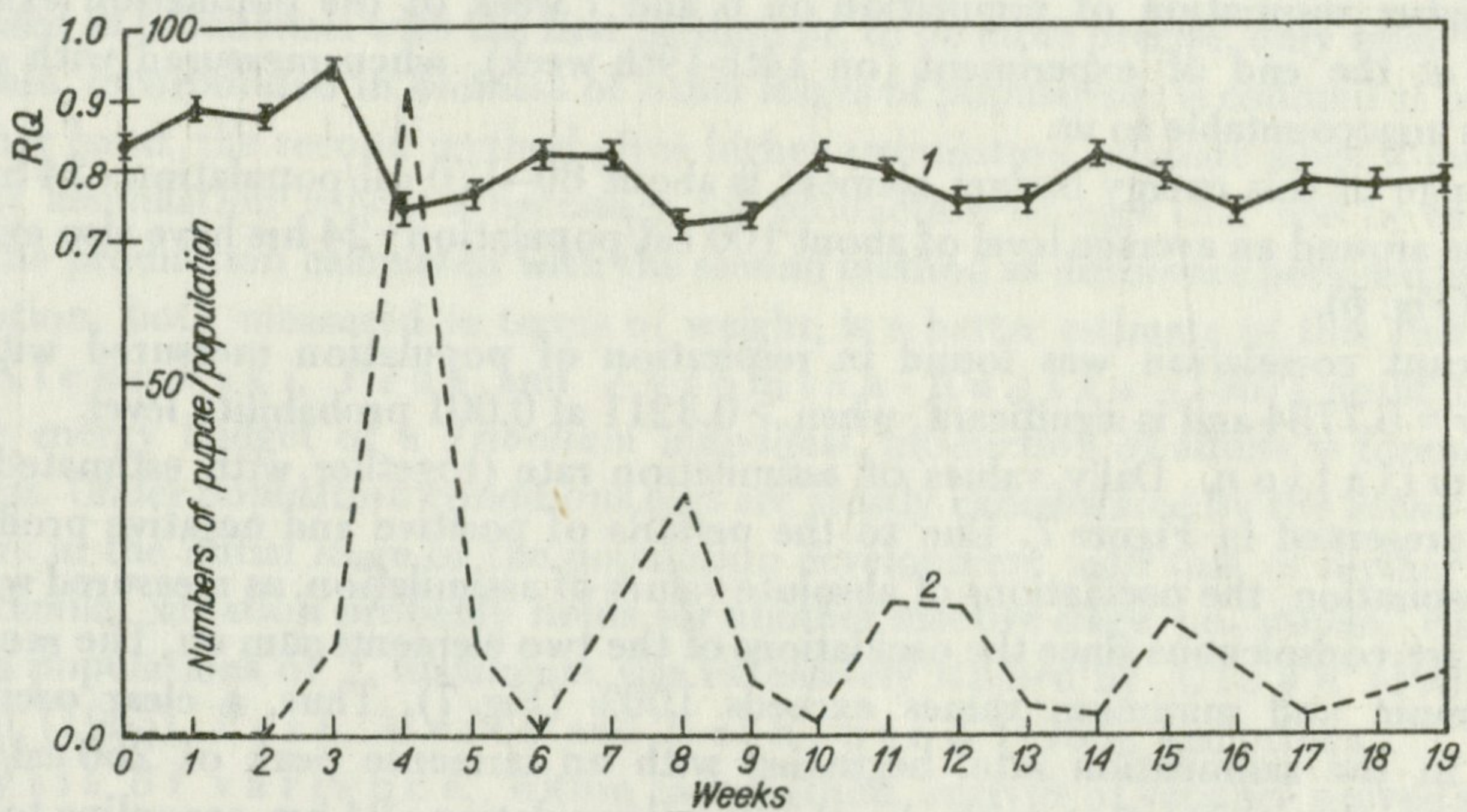
Fig. 5. Respiratory quotient (RQ) in a confined population of *T. castaneum* cI as compared with numbers of pupae present in the population

1 — RQ ± mean error, 2 — numbers of pupae/population

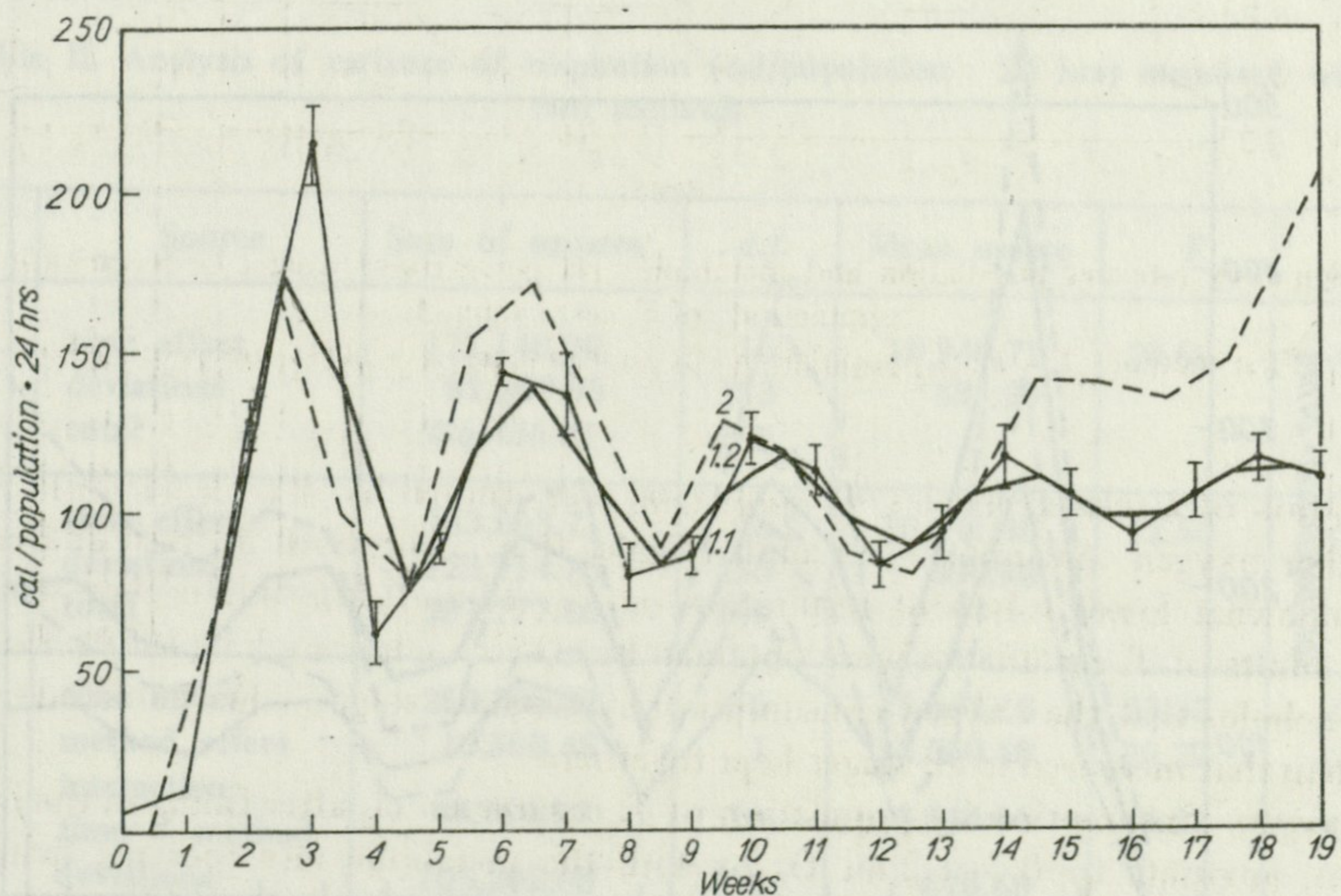Fig. 6. Total respiration in a confined population of *T. castaneum* cI

First method: *1.1.* — instantaneuous averages ± mean error, *1.2* — moving averages of two consecutive measurements. Second method: *2* — averages for 7-day intervals

When converting oxygen consumption into calories, the oxy-calorific coefficients were used, according to Harrow and Mazur (1958).

It is interesting to compare the population metabolism assessed with the two methods (Fig. 6). The courses of the lines are rather similar, with greater similarity found when comparing the line of moving average for the first method with the direct data line of the second method rather than the two direct data lines (Fig. 6). This is comprehendible since the first method gives momentary values of respiration, whereas the second one — averages for 7 days. Higher respiration of population on 6 and 7 week of the population existence and especially at the end of experiment (on 14th-19th week), when measured with gravimetric method, is unaccountable to us.

The range of this energy budget element is about 80–170 cal/population · 24 hrs, and the oscillations around an average level of about 100 cal/population · 24 hrs have also extinguishing character (Fig. 6).

Significant correlation was found in respiration of population measured with the two methods, $r = 0.7754$ and is significant, when > 0.3211 at 0.001 probability level.

A s s i m i l a t i o n. Daily values of assimilation rate (together with estimated consumption) are presented in Figure 7. Due to the periods of positive and negative production and varying respiration, the oscillations of absolute values of assimilation, as measured with the two methods, are conspicuous since the oscillations of the two elements sum up. The range between the maximum and minimum values exceeds 100% (Fig. 7). Thus, a clear oscillation was observed in the assimilation rate, beginning with an immense peak of 260 cal/population · 24 hrs, according to the first method and 330 cal/population · 24 hrs, according to the second method, in the initial period of the habitat colonization. Further on, the oscillations diminish, so that the course of assimilation rate has also the character of extinguishing oscillations around a level of 100 cal/population · 24 hrs since production in the later period of the population existence is very low.
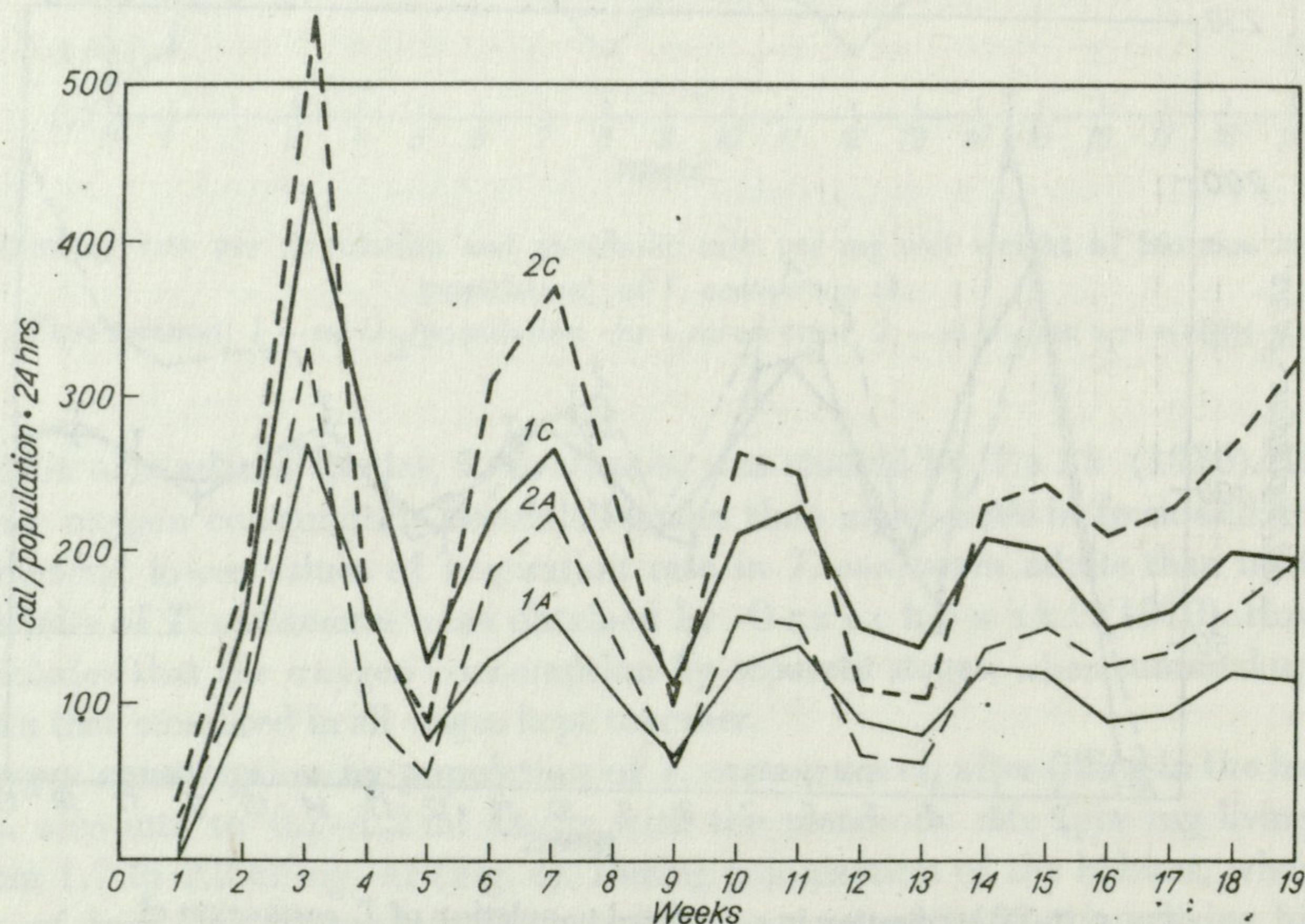

Fig. 7. Assimilation and consumption rates in a confined population of *T. castaneum* cl
1 — first method, *2* — second method, *A* — assimilation, *C* — consumption

Coefficient of correlation calculated for the population assimilation rates measured with the two methods is rather high: $r = 0.8832$ which points to the high similarity of the two line courses. However, the absolute values of the assimilation rate are always higher, when measured with the second method than with the first one.

This difference can be explained by cannibalism operating in the confined population of *Tribolium*. In the first method, assimilation is the sum of production and respiration. It is obvious that such assessed assimilation is underestimated due to underestimated production on account of an intense egg cannibalism. Eggs produced and eaten within the census interval are never counted as production with the first method or, to be more precise, only small fraction of their biomass, incorporated in biomass of other stages of population, is counted as production. On the other hand, the second method gives higher assimilation estimate since it includes also this part of assimilation which is necessary for production of eggs that will be cannibalized later. So, the production calculated with the second method as difference between assimilation and respiration, both measured in terms of weight, is a better estimate of this energy budget element. K l e k o w s k i, P r u s and Ż y r o m s k a - R u d z k a (1967) point to the fact that in the energy budget of a *Tribolium* individual, production of adults is foremost in the form of eggs. Under population conditions eggs are mostly cannibalized by the active stages (cf. egg numbers in the initial stage of the population development with that of further periods in Figure 1). Similar situation probably holds for another inactive stage, i.e., pupae. Cannibalism in confined populations of *T. castaneum* was extensively studied by L l o y d (1965, 1968), P a r k et al. (1965), P a r k, M e r t z and N a t h a n s o n (1968), and others.

A n a l y s i s o f v a r i a n c e. Within each method, analysis of variance proved significant effect of time both on respiration and assimilation (Table II and III, respectively). The significant time, method, and interaction effects were also found in respiration (Table II) and assimilation (Table III), when the analysis of variance was carried out using the whole data (I and II method together).

Table II. Analysis of variance of respiration (cal/population · 24 hrs) measured with two methods

Method	Source	Sum of squares	d.f.	Mean square	F	P
First	time effect	175,148,08	16	10,946.75	20.60	< 0.005
	deviations	81,287.93	153	531.29		
	total	256,436.01	169			
Second	time effect	163,863.71	16	10 241.48	12.65	< 0.005
	deviations	123,914.15	153	809.90		
	total	287.777.86	169			
First and second	time effect	250,306.82	16	15.644.18	23.33	< 0.005
	method effect	13,560.48	1	13,560.48	20.22	< 0.005
	interaction: time × method	88,704.97	16	5,544.06	8.27	< 0.005
	deviations	205,202,08	306	670.60		
	total	557,774.35	339			

Table III. Analysis of variance of assimilation (cal/population · 24 hrs) measured with two methods

Method	Source	Sum of squares	d.f.	Mean square	F	P
First	time effect	629,446.31	18	34,969.24	33.58	< 0.005
	deviations	178,097.58	171	1,041.51		
	total	807,543.90	189			
Second	time effect	935,515.86	17	55,030.34	32.72	< 0.005
	deviations	272,447.67	162	1,681.77		
	total	1,207,963.53	179			
First and second	time effect	1,463,796.02	17	86,105.65	64.28	< 0.005
	method effect	20.052.10	1	20,052.10	14.97	< 0.005
	interaction: time x method	85,187.24	17	5,011.01	3.74	< 0.005
	deviations	434,043.43	324	1,339.64		
	total	2,003,078.79	359			

The significant time effect proves that the observed values of the budget elements tested with the use of the two methods undergo real oscillations. In spite of the significant correlations between the elements measured with the two methods, the absolute values differ, depending on the method used. Thus, one can infer that the energy budgets based on the two methods will also differ in a significant way. Some remedy can be found in using for the energy budget calculation rather moving averages of respiration than the direct values of respiration assessed with the first method, which was the case in preparing this budget. However, the analysis of variance for respiration was carried out on the instantaneous values of respiration measured with the first method, which deviated much more from the corresponding values of respiration obtained by the second method (Fig. 6).

C o n s u m p t i o n. Similarly as production and assimilation, the estimated consumption rate shows 5 peaks of an intense energy flow through the population, altered with the periods of a low consumption rate. The highest consumption rate was observed on the 4th week of the population existence and amounted to about 420 cal/population · 24 hrs (I method) and 520 cal/population · 24 hrs (II method). This peak is connected with very high numbers of large larvae which were fastly growing and intensely feeding. The detailed discussion of this element, due to the hypothetical assimilation efficiency that had to be accepted, seems unnecessary here. The changes in the consumption rate are a mere magnification, sort of a close-up, of changes in the assimilation rate that were already discussed.

I n s t a n t a n e o u s e n e r g y b u d g e t. It consists of production presented in Figure 3 and assimilation and consumption presented in Figure 7. Some numerical data are also given in Table IV. Here we wish only to draw attention to an astonishing convergence in the courses of all budget elements.

C u m u l a t i v e e n e r g y b u d g e t. Such budget for the period of 19 weeks, based on the two methods of measurements, is presented in Figure 8. During the study period, according to the first method the population of *T. castaneum* cI assimilated 15.4 kcal. Of this amount, 1.8 kcal was used for production of biomass and 13.6 kcal — for metabolism. Corresponding values obtained with the second method are the following: assimilation — 18.2 kcal, produc-

Table IV. Instantaneous and cumulative energy budgets of developing population of *T. castaneum* cI, assessed with two methods of measurement

Method	time moment (for week):	Instantaneous (cal/population · 24 hrs)				time interval (weeks)	Cumulative (kcal/population)				production efficiency (per cent)	
		elements					elements					
		P	R	A	$C*$		P	R	A	$C*$	K_2	K_1^*
First	1st	4.753	9.991	14.744	24.57	0–1	0.033	0,070	0.103	0.173	32.2	19.1
	4th	24.277	139.089	163.366	272.27	0–4	0.984	2.745	3.729	6.215	26.4	15.8
	9th	−15.222	83.060	67.838	113.06	0–9	1.293	6.260	7.553	12.588	17.1	10.3
	14th	19.394	105.330	124.724	207.87	0–14	1.651	9.852	11.503	19.171	14.3	8.6
	19th	6.303	112.640	118.943	198.23	0–19	1.795	13.648	15.443	25.739	11.6	7.0
Second	1st	8.648	15.616	24.264	40.40	0–1	0.061	0.109	0.170	0.283	35.6	21.5
	4th	−3.094	99.707	96.613	161.02	0–4	1.454	2.461	3.915	6.525	37.1	22.3
	9th	−26.892	88.924	62.032	103.39	0–9	1.822	6.802	8.624	14.373	21.1	12.7
	14th	32.669	105.483	138.152	230.25	0–14	2.263	10.420	12.683	21.138	17.8	10.7
	19th	11.944	188.810	199.050	333.00	0–19	2.454	15.787	18.241	30.402	13.5	8.1

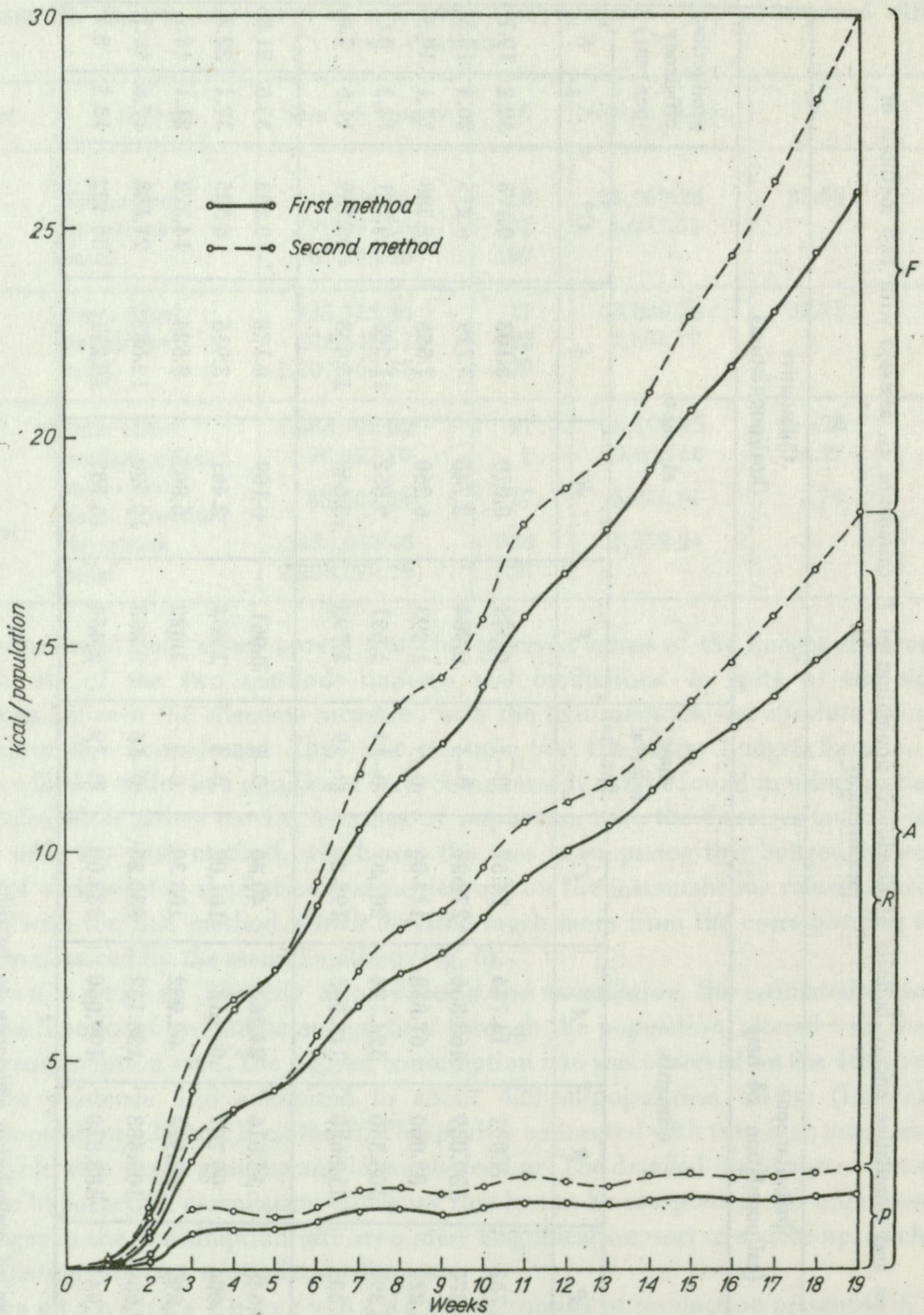*Estimated on assumption of assimilation efficiency to be 60%.

Fig. 8. Cumulative energy budget of a developing confined population of *T. castaneum* cI
P —production, R — respiration, A — assimilation, F — egestion

tion — 2.5 kcal, respiration — 15.8 kcal. The cumulative consumption for this period would be
25.7 kcal (I method) and 30.4 kcal (II method).

When cumulated, the difference resulting from the two methods becomes more conspicuous.

Production efficiencies: K_2 (net) and K_1 (gross). Instantaneous net production efficiency is very variable and ranges from -22.4% to 34.9% (acc. to I method) due to the periods of negative and positive production rates in *Tribolium* populations. Its mean value is 9.19% but has little ecological sense and should not be used for any further calculations.

The net production efficiency can be much better characterized by the cumulative form of this index, when the cumulated production is related to the cumulated assimilation. Such index, based on the two methods, is presented in Figure 9. The production efficiency in the initial stage of population development is highest and amounts to 32.2% of assimilation (I method) and 35.6% (II method), diminishing later exponentially to values of 11.6% (I method) and 13.5% (II method).

In general, the course of this index for the developing population resembles that of an individual male of *T. castaneum* after eclosion (cf. K l e k o w s k i, P r u s and Ż y r o m - s k a - R u d z k a 1967).

If the accepted assimilation efficiency is right, the cumulative gross production efficiency (K_1) would change according to the first method from 19.1% to 7.0%, or from 21.5% to 8.1% according to the second method, after 19 weeks of the population existence. Its course due to the constant assimilation efficiency reflects that of the net production index (Fig. 9).

Chosen numerical data of the instantaneous and cumulative energy budgets resulting from the two methods as well as the cumulative production efficiencies are presented in Table IV. Five time moments, for 1st, 4th, 9th, 14th and 19th week, were chosen arbitrarily.

It is interesting to compare that amount of energy that passed through the population with the total amount of energy comprised in the experimentally restricted habitat. We would like to recall that all populations developed in 8 g of food-habitat (renewed every week) which corresponds to 30.4 kcal. Such amount of energy is consumed by the population within the
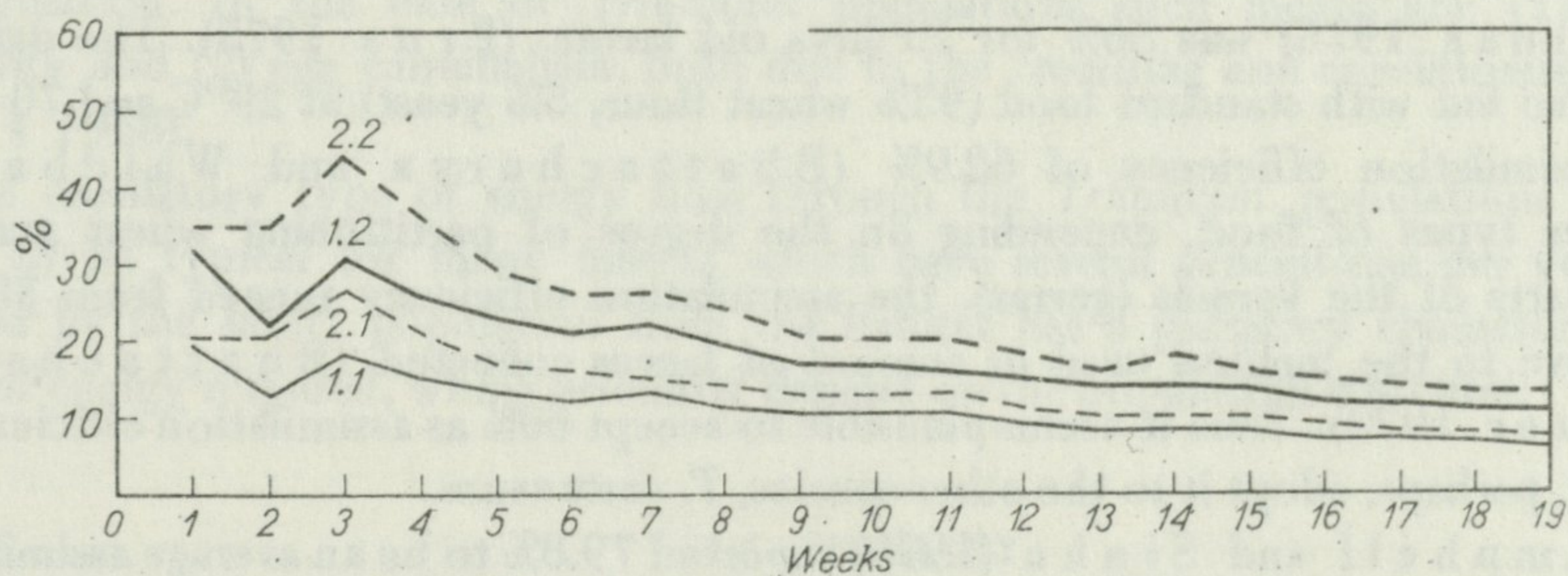

Fig. 9. Cumulative net (K_2) and gross (K_1) production efficiencies in a confined population of *T. casta-neum* cI

First method: *1.1* – K_1, *1.2* – K_2. Second method: *2.1* – K_1, *2.2* – K_2

period of about 4.5 months (II method), or somewhat less (25.7 kcal) according to the first method. This agrees with casual observations which are familiar to anyone who dealt with *Tribolium*. The culture of this species started in 8 g of the standard medium and left over for long in the incubator almost does not contain any medium after several months and the population extincts. This example, although trivial one, is very persuasive and roughly verifies the whole study.

It is worth of mentioning that only about 1/10 of the energy consumed becomes living or dead biomass and about 1/2 is dissipated in the form of respiration. Knowing these proportions it is not difficult to imagine how detrimental *Tribolium* can be to the stocking of flour which is one of the main food components of the human population. However, some reconciliation can be found by realizing that the increasing size of the living habitat in this species has a negative effect on productivity of population. According to Petrusewicz, Prus and Rudzka (1963) larger volume of the habitat yields smaller relative productivity per unit volume.

4. DISCUSSION

These are relationships between elements of the energy budget which deserve discussion rather than the direct data obtained in this study.

Although assimilation efficiency was not ascertained in this paper, it had to be accepted from what is known in the literature in order to calculate the complete budget. In an earlier paper (Klekowski, Prus and Żyromska-Rudzka 1967), dealing with the same strain at the individual level, a value of 46% was accepted according do the data reported by Evans and Goodliffe (1939) for *Tenebrio molitor* L. In recent years, however, new techniques were adopted or invented to assess assimilation efficiency in flour beetles and other granary insects. According to Bhattacharya and Waldbauer (1969); the assimilation efficiency in *T. molitor* larvae seems to be higher by about 7–10% as compared with that reported by Evans and Goodliffe (1939) and amounts to 55.7% (manual sorting of faeces from food) and 52.7% (uric acid method). In another experiment it amounts to 56.3% and 56.4% (manual sorting) or 52.3% and 53.7% (uric acid), depending on the portion of faeces collected (Bhattacharya and Waldbauer 1969).

Assimilation efficiency in *T castaneum* cI strain, when consumption was measured with ^{32}P method (Dominas 1975) was 56% for 10 days old larvae (Prus 1975). The data for *T. confusum* larvae fed with standard food (95% wheat flour, 5% yeast) at 29°C and 70–75% R.H. yielded assimilation efficiency of 62.9% (Bhattacharya and Waldbauer 1970). For other types of food, depending on the degree of partitioning wheat grain or selecting some parts of the kernels (germs), the assimilation efficiency ranged from 58.0 to 59.8%, irrespective to the method used or amount of faeces collected (Bhattacharya and Waldbauer 1970). Thus it seems plausible to accept 60% as assimilation efficiency in *T. confusum* and, perhaps, adopt it to the other species, *T. castaneum.*

Singh, Campbell and Sinha (1976) reported 79.8% to be an average assimilation efficiency in *Sitophilus oryzae* and their explanation for such a high assimilation efficiency in developmental stages of this species was that it results from a high protein or amino acid contents in food (wheat germs and endosperm were mostly consumed).

In *S. granarius* the corresponding value ranges between 70–80% (Campbell and Sinha 1974). However, Szwykowska-Rey (1974) in the same species reared on wheat grain at a temperature of 24.0°C and 75% R.H. obtained much lower values of assimilation efficiency: 31.3% in females and 39.6% in males, and much higher net production efficiencies (36.0% – females and 34.4% – males), as compared with those reported by Campbell and Sinha (1974). Is the difference in temperature the only reason of such high difference obtained in the two studies? Perhaps the results deviate on account of somewhat different spans of life history studies by their authors, or due to the different methods used.

On the other hand, similarly high values of assimilation efficiency as those reported by Campbell and Sinha (1974) and Singh, Campbell and Sinha (1976) were ascertained by Stępień (1970) for an oribatid mite, *Rhizoglyphus echinopus*, reared on rye germs at 25°C and 89% R.H. In active larvae, the assimilation efficiency was 86%, in active protonymphs and tritonymphs it was still over 70%, and in adults – 50–47%. The high assimilation efficiency in this species the author also attributes to a high content of proteins (37.1%) and lipids (7.6%) in the rye germs (Stępień 1970).

We will discuss now the cumulative net production efficiency in *Tribolium castaneum* cI strain. At the population level it decreases from 31.5% (I method) and 41.2% (II method) on the 4th week of population existence to 11.6% and 13.5% (I and II method, respectively) after 19 weeks of population existence. These values are rather different from what might be expected from the individual energy budget of this species (Klekowski, Prus and Żyromska-Rudzka 1967). The K_2 of an average reproducing adult approaches asymptotically value of 46.9% due to an extremely intense oviposition by a female reared in optimal conditions of food and density (one pair per 8 g of flour). The K_2 of a male, on the other hand, during its adult life is decreasing exponentially to zero. This is due to the lack of any noticeable production of this sex in the mature stage (Klekowski, Prus and Żyromska-Rudzka 1967). The similarity in the course of net production efficiency of a developing, confined population and that of an individual male in its adult life results from the fact that in both the cases the producing unit achieves a certain maximum of biomass (maximum weight of an individual and maximum population biomass approaching the level of carrying capacity of the habitat) and later on little or nothing is produced, although energy is continuously consumed, assimilated and respired.

The comparison of the energy budgets calculated at individual and population level proves how difficult and dangerous (because of possible errors) would be to transfer individual energy budgets to population situations especially in insects which have developed special means of self-regulation. In the case of *Tribolium* populations such means are: (1) suppression of fecundity and (2) egg cannibalism, both due to the crowding and conditioning of the habitat (Prus 1968).

The oscillatory type of energy flow through the *Tribolium* populations used as models seems to be typical for many insects which have several generations per year. The energy demand by the insect population from the habitat has a pulsatory character with ebbs and flows of energy required, which primarily depend on the population structure.

5. SUMMARY

The energy budget of *Tribolium castaneum* cI populations, developing in restricted and renewed habitat, was acertained. Two independent methods (routine and gravimetric one) were used to measure production, respiration and assimilation rates during 19 weeks of the population existence. Significant difference (Tables II, III) in budget elements obtained with the two methods is explained by cannibalism operating in *Tribolium* populations. All energy budget elements showed time variations described as extinguishing oscillation (Figs. 3, 7). Cumulative budget, calculated acc. to the first method for 19 weeks of population existence revealed that the population consumed 25.7 kcal (on assuming 60% of assimilation efficiency), out of which 15.4 kcal were assimilated. Of the assimilated energy 1.8 kcal was cumulative production and 13.6 kcal – cumulative respiration. The cumulative net production efficiency was 11.6%. The corresponding values obtained with the second method are the following: C – 30.4 kcal, A – 18.2 kcal, P – 2.5 kcal, R – 15.8 kcal, K_2 – 13.5% (Table IV, Fig. 8).

The course of cumulative net production efficiency showed a tendency to diminish exponentially with time (Fig. 9) and was found to be similar to that obtained in another study (Klekowski, Prus and

Żyromska-Rudzka 1967) for an adult male of this strain. Gross production efficiency, being based on accepted assimilation efficiency, followed the changes of net production efficiency index, diminishing from 19.1 to 7.0% (I method) or 21.5 to 8.1% (II method) after 4.5 months of population existence.

Some general conclusions concerning the energy flow through the insect population are given.

6. POLISH SUMMARY (STRESZCZENIE)

Podano bilans energetyczny populacji *Tribolium castaneum* cI, rozwijającej się w ograniczonym odnawianym środowisku. Użyto dwu niezależnych od siebie metod (standardowej i grawimetrycznej) do pomiarów tempa produkcji, respiracji i asymilacji w czasie 19 tygodni istnienia populacji. Stwierdzono istotne różnice (tab. II, III) w elementach budżetu otrzymanych dwiema metodami, wyjaśniając je zjawiskiem kanibalizmu w populacjach *Tribolium.* Wszystkie elementy bilansu energetycznego wykazały zmienność w czasie, opisaną jako gasnąca oscylacja (fig. 3, 7). Budżet kumulatywny według I metody za okres 19 tygodni istnienia populacji wykazał, że przy założeniu 60% wydajności asymilacji populacja konsumuje 25,7 kcal z czego 15,4 kcal jest asymilowane. Z przyswojonej energii 1,8 kcal stanowi skumulowaną wartość produkcji, a 13,6 kcal – respirację. Kumulatywna wydajność produkcji netto (K_2) wynosi 11,6%. Analogiczne wartości uzyskane na podstawie II metody są następujące: $C - 30,4$ kcal, $A - 18,2$ kcal, $P - 2,5$ kcal, $R - 15,8$ kcal, $K_2 - 13,5\%$ (tab. IV, fig. 8).

Przebieg skumulowanego wskaźnika produkcji netto wykazuje wykładniczą tendencję spadkową (fig. 9) i jest zbliżony do przebiegu analogicznego wskaźnika podanego w innej pracy (Klekowski, Prus i Żyromska-Rudzka 1967) dla dorosłego samca tego gatunku. Wydajność produkcji brutto, oparta na założonej wartości wydajności asymilacji, pokrywa się ze zmianami wskaźnika produkcji netto, zmniejszając się z 19,1% do 7% (według I metody) lub z 21,5% do 8,1% (według II metody) po 4,5 miesiącach istnienia populacji.

Praca zawiera pewne uogólnienia na temat przepływu energii przez populacje owadów.

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