EKOLOGIA POLSKA (Ekol. pol.)	44	1–2	3–18	1996

Paweł BIJOK

Laboratory of Ecophysiology of Invertebrates, Institute of Ecology,
Polish Academy of Sciences, Dziekanów Leśny (near Warsaw), 05–092 Łomianki, Poland

COST OF MAINTENANCE AND PRODUCTION IN FLOUR BEETLES *TRIBOLIUM CASTANEUM* HBST. AND *T. CONFUSUM* DUVAL – INTRAPOPULATION DIVERSITY

ABSTRACT: Two species of *Tribolium* and their two phenotypic groups were compared in terms of rate of respiration and production of body biomass and eggs. Intraspecies differences are greater than interspecies ones. The 7-instar groups expend relatively more energy on maintenance while 6-instar ones expend more on growth and reproduction. That indicates different life strategies in the two groups. The intrapopulation diversity improves plasticity of the species.

KEY WORDS: *Tribolium*, metabolism, production efficiency, life-strategy, intrapopulation diversity.

1. INTRODUCTION

Bioenergetical and population investigations of *Tribolium* beetles (Prus 1976, Bijok 1986), as well as of other stored product insects (Howe 1961), showed strong intrapopulation diversity in respect of the number of larval instars, developmental rate and body weight. Two clearly distinct phenotypic groups: arbitrarily called 6- and 7-instar groups can be distinguished within populations of both allied species: *Tribolium castaneum* and *T. confusum*. The groups show different models of individual development. The 6-instar individuals develop faster but obtain lower weight than the 7-instar ones.

Recent studies in Poland have examined the differences between the two *Tribolium* species and between 6- and 7-instar groups of each one. The attributes examined include female fecundity, weight and hatchability of eggs (Prus and

Prus 1987, Prus et al. 1989), reproductive effort (Prus et al. 1995) and the relationship between the duration of embryonic and postembryonic development (Bijok 1992). The results showed that differences between phenotypic groups within both species are of a very similar kind to that which occurs between two species. *T. castaneum* along with lower body weight has higher fecundity and higher reproductive effort than *T. confusum*. The same refers to 6-instar groups of both species when compared with 7-instar ones. These differences suggest different life strategies in two phenotypic groups within population.

The aim of the presented investigation is to extend the studies mentioned above with an analysis of maintenance expenses – level of metabolism in larval and adult stages, and rate of production of body tissues in juveniles and offspring production (eggs) in adult females. That gives the answer whether the distribution of available energy and efficiency of production differs in phenotypic groups within examined species.

2. MATERIAL AND METHODS

One strain of each species: cI – *T. castaneum* and bIV – *T. confusum* were used in this study. Both species originated from the group of genetic strains selected by Park et al. (1961), brought from the Chicago University and reared in Poland since early 60-ties.

All experiments were carried out in standard condition of 29° C, 75% relative humidity, dark incubator, in culture medium consisting of 95% of wheat flour and 5% of backer's yeast (by weight). Before the experiments the culture medium was conditioned in incubator to obtain adequate temperature and humidity.

Newly hatched larvae (no more than two hours old) were placed separately in 5cm spherical respiration chambers, single larva in each chamber together with an amount of 1g of culture medium. Respiration assays was done starting from 4-th day of larval life every second day, and since eclosion respiration measurements combined with reproduction assays have been performed in 3 day interval, as adopted for *Tribolium* by Park et al. (1961). Respiration chambers were connected with constant pressure volumetric microrespirometers (Klekowski 1975). Chambers were darkened with aluminium foil to run respiration measurements in standard light conditions. Second arms of respirometers were connected with compensation chambers, also filled with the same quantity of culture medium. Respirometers were placed in water bath and after 1 hour required for thermal balance of the system measurements of oxygen uptake were run for about 5 hours. After that the chambers were disconnected from respirometers. Animals were separated from medium by sifting through fine mesh, weighed on microbalance with 1 g accuracy, placed into chamber with a fresh portion of medium and left in incubator till the next respirometric measurement. Newly emerged pupae were weighed and their sex was determined by examining size and shape of genital lobes (Sokoloff 1972). Newly eclosed adults were mated into pairs. Each pair was kept in a chamber together to let the individuals develop a full reproductive activity. A male was separated from female and placed in it's own chamber only for the time of respiration measurements. In order to distinguish between males and females when separating, the males were marked with nitrocellulose paint at their elytra just after their eclosion. Eggs laid by a female were separated from medium using a fine mesh sieve and their number was determined just after the end of respiration measurement. Males and females were then placed back together into their common chambers.

Distinguishing between 6- and 7-instar individuals was performed on the basis of differences in weight and time of pupae emerging. Each pupa emerging was presented by a point at time/weight scale. The points produced two clouds clearly distinct for 6- and 7-instar group (Bijok 1989a).

Calculation of energetic equivalent of respiration was performed using table of oxycalorific equivalent for corresponding respiratory quotient (RQ) values (Harrow and Mazur 1958). RQ values in animals of respective age and developmental stage were derived from papers by Klekowski et al. (1967) and Bijok (1989b). Production of body biomass of growing larvae (exuviae production ignored as incomparably small) has been assessed on the basis of weight increments and calculated in energy units using values of calorific equivalent of 1 mg body biomass measured by Klekowski et al. (1967) and Bijok (1989b). Production in adult females has been assessed assuming that practically all production in this stage is that of eggs. Mean energy equivalents of 1mg of eggs were derived from paper by Prus et al. (1995) using correction factor for flour coating on egg surface (Bijok, unpublished). Index of instantaneous net production efficiency K_2i (K_2i= Production/Assimilation, Duncan and Klekowski (1975) have been calculated from determined Respiration/Production ratio according to general equation of energy balance:

$$C = F + U + A$$
$$A = R + P \text{ (urine ignored)}$$
$$K_2i = P/A$$
$$K_2i = 1/(R/P + 1)$$

(Letters stand for instantaneous values of: C – consumption, F – faeces, U – urine, A – assimilation, R – respiration, P –production).

Total number of 13 individuals of *T. castaneum* (5 of 6-instar- and 8 of 7-instar group) and 14 of *T. confusum* (10 of 6-instar- and 4 of 7-instar group) have been examined.

Student t-test for the difference between paired samples have been used for inter- and intraspecific comparisons of the mean values in subsequent ages (juvenile) and time since eclosion (adults).

3. RESULTS

The course of changes of respiration rate during development of two *Tribolium* species (Fig. 1) can be divided into three periods characteristic for holometabolic insects:

1) The period of fast increase of respiratory metabolism during larval development. Oxygen consumption in the last phase of larval development exceeds value of 20 μl h^{-1} in *T. castaneum* and 25 μl h^{-1} in *T. confusum*.

2) Decrease of this value in pupal stage illustrated by U-shaped curve (Edwards 1953). The value reaches its minimum generally in the middle of pupal stage – about 1 μl h^{-1} in *T. castaneum* and below 2 μl h^{-1} in *T. confusum.*

3) An increase in young adult individuals which leads to more or less stable state on the level depending on sex and species.

Very characteristic phenomenon in the first period is a temporary decrease of respiration level, approximately in the middle of larval stage.

One can observe a constant decline in oxygen consumption per unit weight in immature stages (larvae, prepupae and pupae) (Fig. 2). Despite some fluctuations this value is highest in youngest larvae examined and decreases to approximately 1 μl O_2 mg^{-1} h^{-1} fresh wt. at inactive pupae. Both within *T. castaneum* and *T. confusum* 7-instar individuals show higher respiration rate in relation to body weight than 6-instar ones. The differences between mean values are statistically significant at $p < 0.05$ (Table 1). The value for 7-instar *T. castaneum* looks to be a bit higher than for 7-instar *T. confusum* but the between-species differences are not supported by Student t-test. Such difference is significant when metabolism per gain body weight is compared (Fig. 3). That value gives an idea about oxygen uptake that corresponds to a unit of biomass production. It shows also a between groups difference which however only in *T. castaneum* is statistically significant.

Energy share between metabolism and production of body tissues (production of exuviae ignored) in growing larvae is presented in Fig. 4 as R/P ratio calculated in energy units. That can be easily transformed to an index of instantaneous net production efficiency (K_2i = Production/Assimilation – Duncan and Klekowski 1975) often used in bioenergetical studies (Fig. 5). The middle period of larval development (around 10th day) is characterised by highest R/P ratio. It reaches over 12 in *T. castaneum* and over 8 in *T. confusum.* The production efficiency is then lowest at this stage and equals approximately 10%. At the later stages R/P ratio goes down. In prepupa (stage preparing to pupation) and pupa production has negative values indicating loss of body biomass for the cost of maintenance in non-feeding animals so R/P ratio becomes close to –1 in that stages. In 7-instar groups of both species R/P ratio is higher – (production efficiency is lower) than in 6-instar groups however in *T. confusum* that difference can be stated at $p < 0.1$ only. The value for 7-instar *T. castaneum* is higher than for 7-instar *T. confusum.*

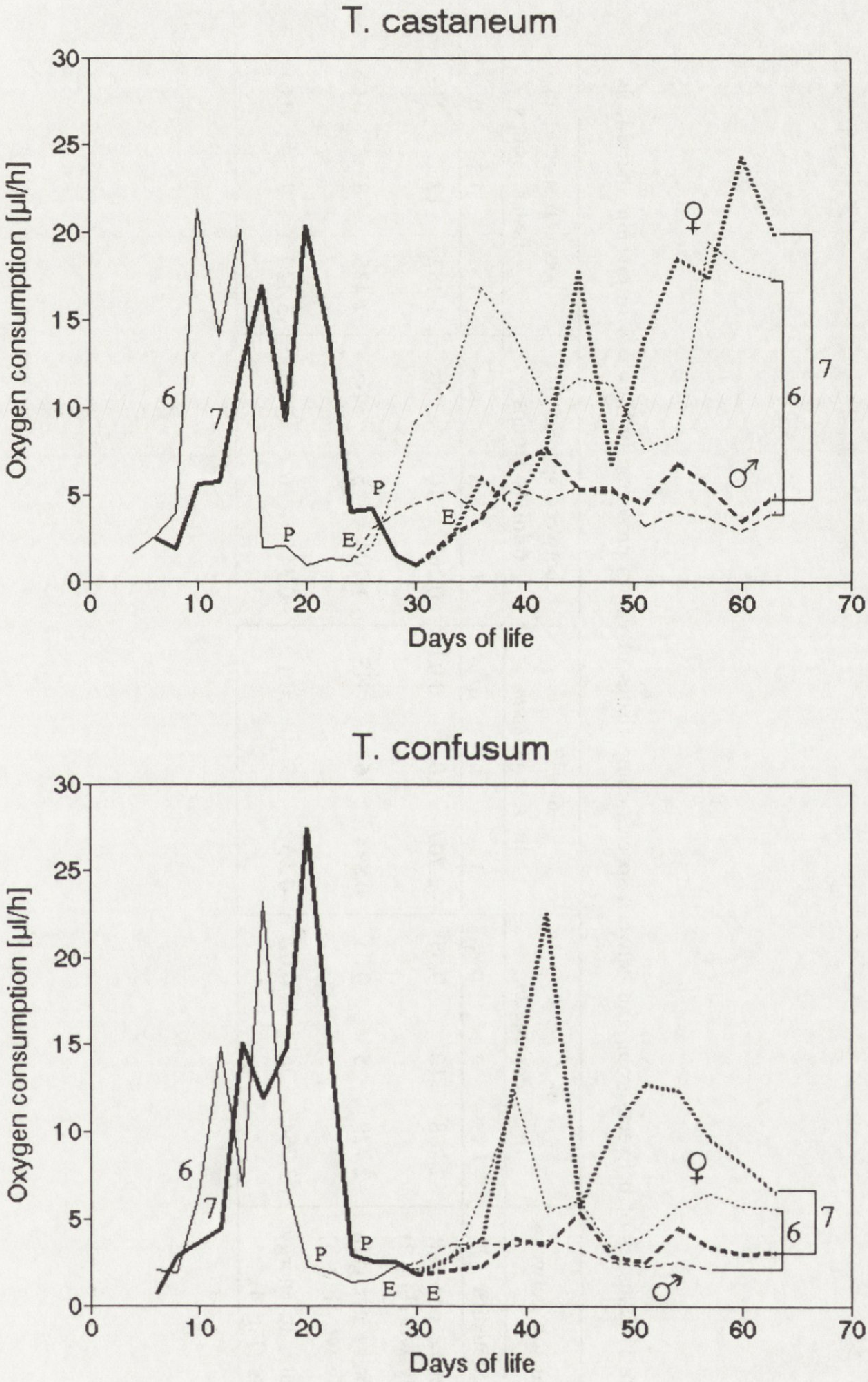

Fig. 1. Oxygen consumption in two *Tribolium* species. Mean values for two phenotypic groups, since eclosion for phenotypic groups and sexes
6, 7 – phenotypic groups, P – pupation, E – eclosion

Table 1. Statistics of between-group and between-species comparisons of values presented in Figs 2–4 in juvenile individuals

Comparison between:	6- / 7- in *T. castaneum*			6- / 7- in *T. confusum*			between-species in 6-instar groups			between-species in 7-instar groups		
Statistics	t	n	$p <$	t	n	$p <$	t	n	$p <$	t	n	$p <$
O_2 uptake per unit body wt. (Fig 2)	–2.268	10	0.05	–2.707	10	0.05	–0.265	10	Ns	1.182	12	NS
O_2 uptake per gain body wt. (Fig 3)	–2.729	5	0.05	0.894	6	NS	–1.204	5	NS	2.435	8	0.05
R/P ratio in energy units (Fig 4)	–3.764	6	0.02	–1.952	7	0.1	–0.344	6	NS	3.420	9	0.01

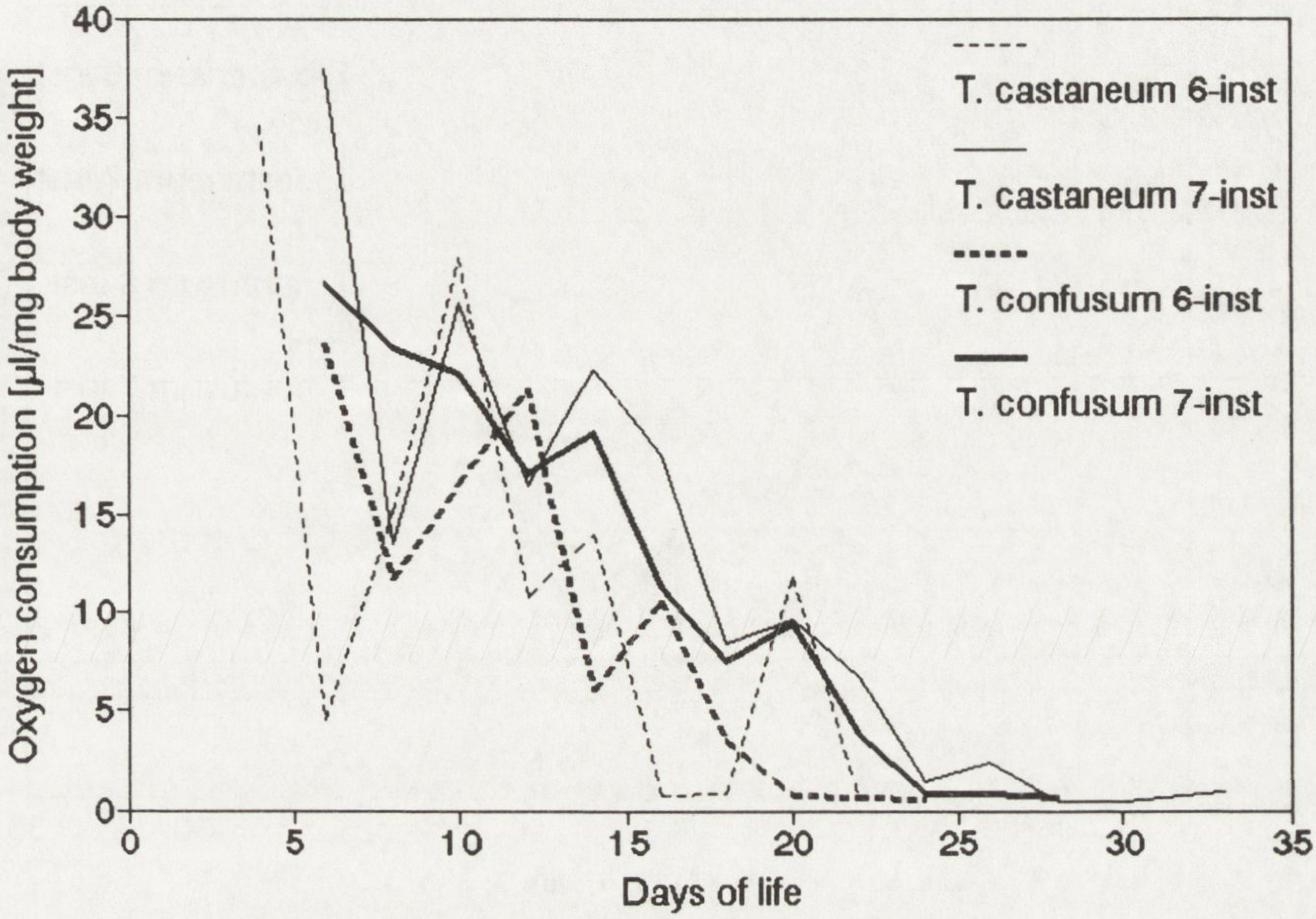

Fig. 2. Oxygen consumption per unit body weight in juvenile stages of two *Tribolium* species and their 6- and 7-instar phenotypic groups

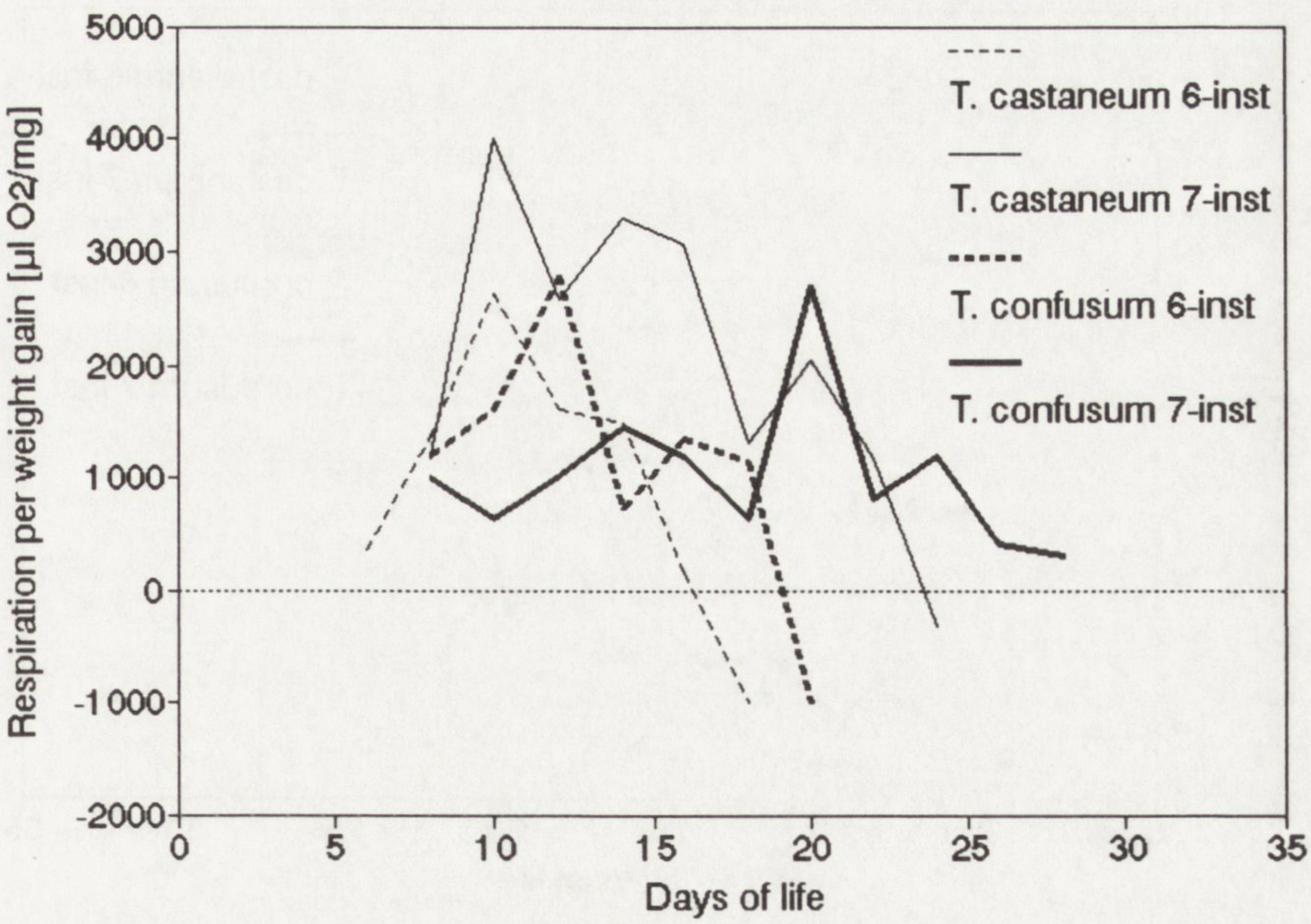

Fig. 3. Oxygen consumption per gain body weight in juvenile stages of two *Tribolium* species and their 6- and 7-instar phenotypic groups

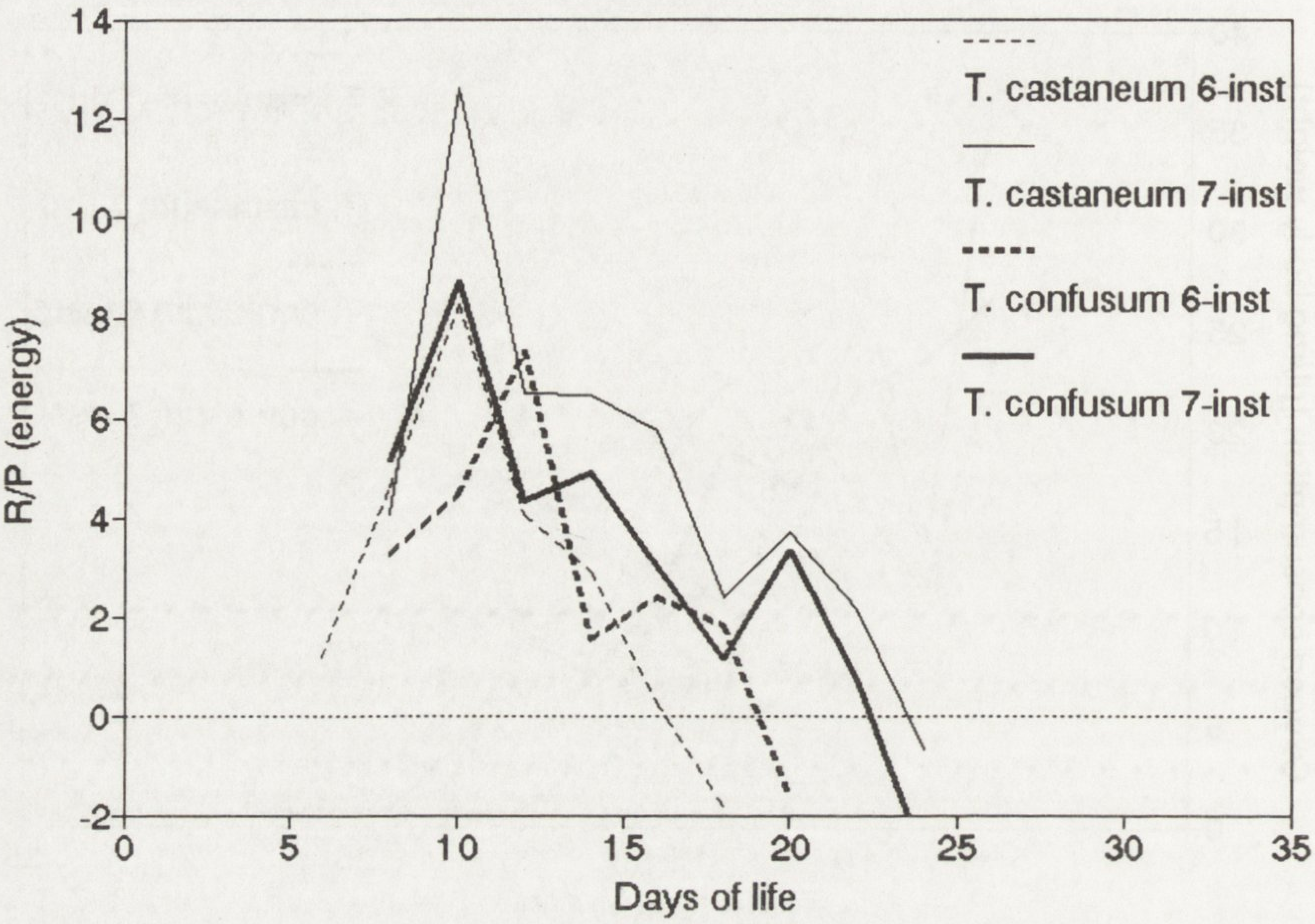

Fig. 4. Respiration/production ratio in energy units in juvenile stages of two *Tribolium* species and their 6- and 7-instar phenotypic groups

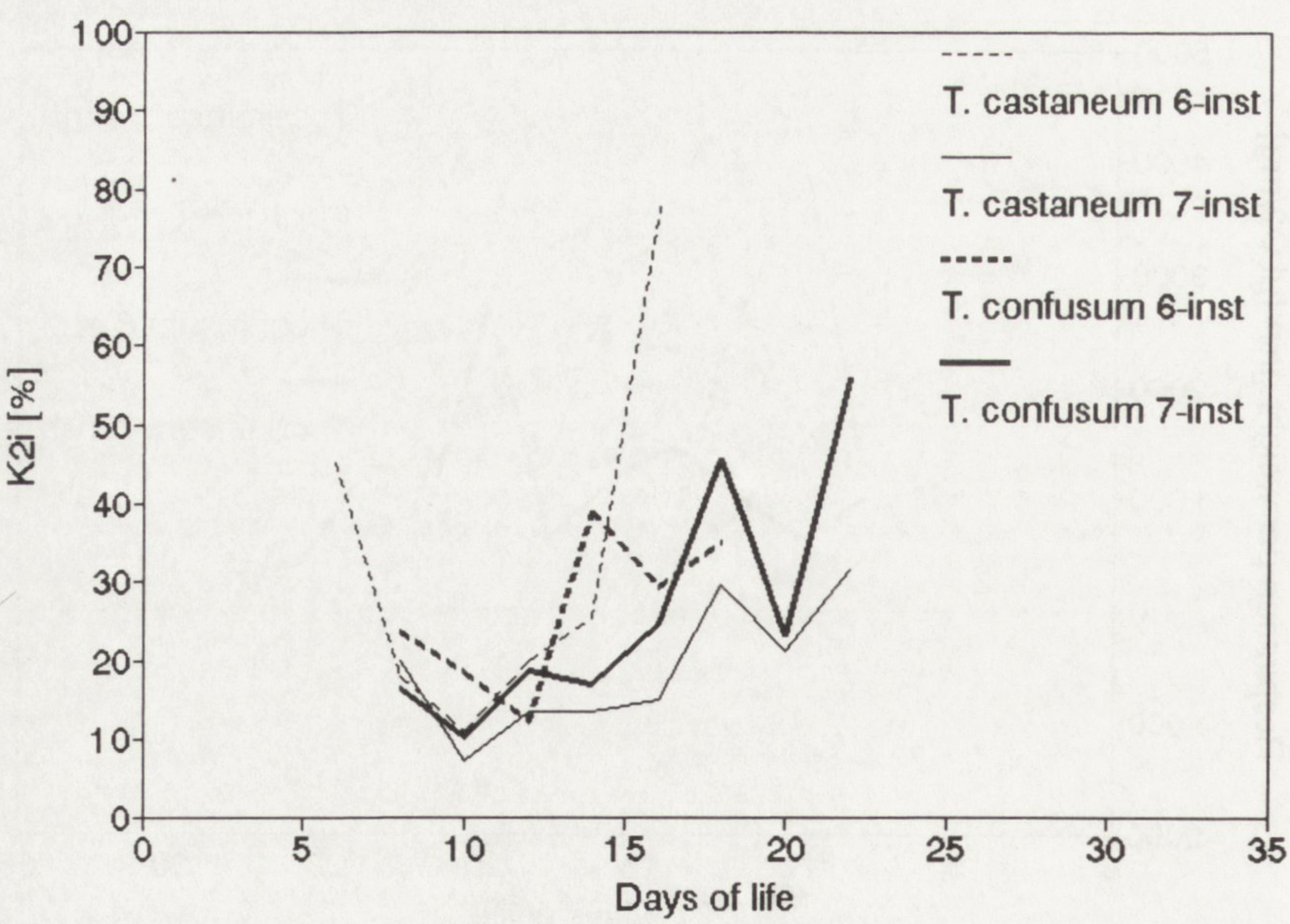

Fig. 5. Index of instantaneous net production efficiency $K_{2}i$ in juvenile stages of two *Tribolium* species and their 6- and 7-instar phenotypic groups

Adult life is characterised by a very changeable level of respiratory metabolism in these species (Fig. 1) – especially in females that value shows high fluctuation. Oxygen uptake rises progressively since eclosion as reproductive activity increases. The value reaches an average level which in females is more or less similar to that of older larvae but is about 3 times higher than that of adult males.

The two examined species are different in respect of fecundity. *T. castaneum* females lay twice as much eggs as those of *T. confusum* (Fig. 6). Differences between phenotypic groups are also to be seen, especially within *T. castaneum* where 6-instar females lay clearly more eggs than 7-instar ones.

The mean oxygen uptake by a female calculated per one egg laid by it was presented in Fig. 7. Lines representing 7-instar females lie above respective lines for 6-instar ones. The differences, especially in the first half of examined period, are however to weak to give significance (Table 2). Differences between phenotypic groups become significant at $p < 0.05$ when analysing energy share between living expenses and reproduction is illustrated by R/P ratio calculated in energy units (Fig. 8). That value has been calculated using calorific equivalent of eggs (P r u s at al. 1995) and assuming that in adult females practically all production is that of offspring. Basing on R/P ratio the index of instantaneous net production efficiency K_2i is also presented in Fig. 9. Seven-instar females show higher R/P ratio (lower K_2i) than 6-instar ones. Between-species differences are less sharp and equivocal than within-species ones.

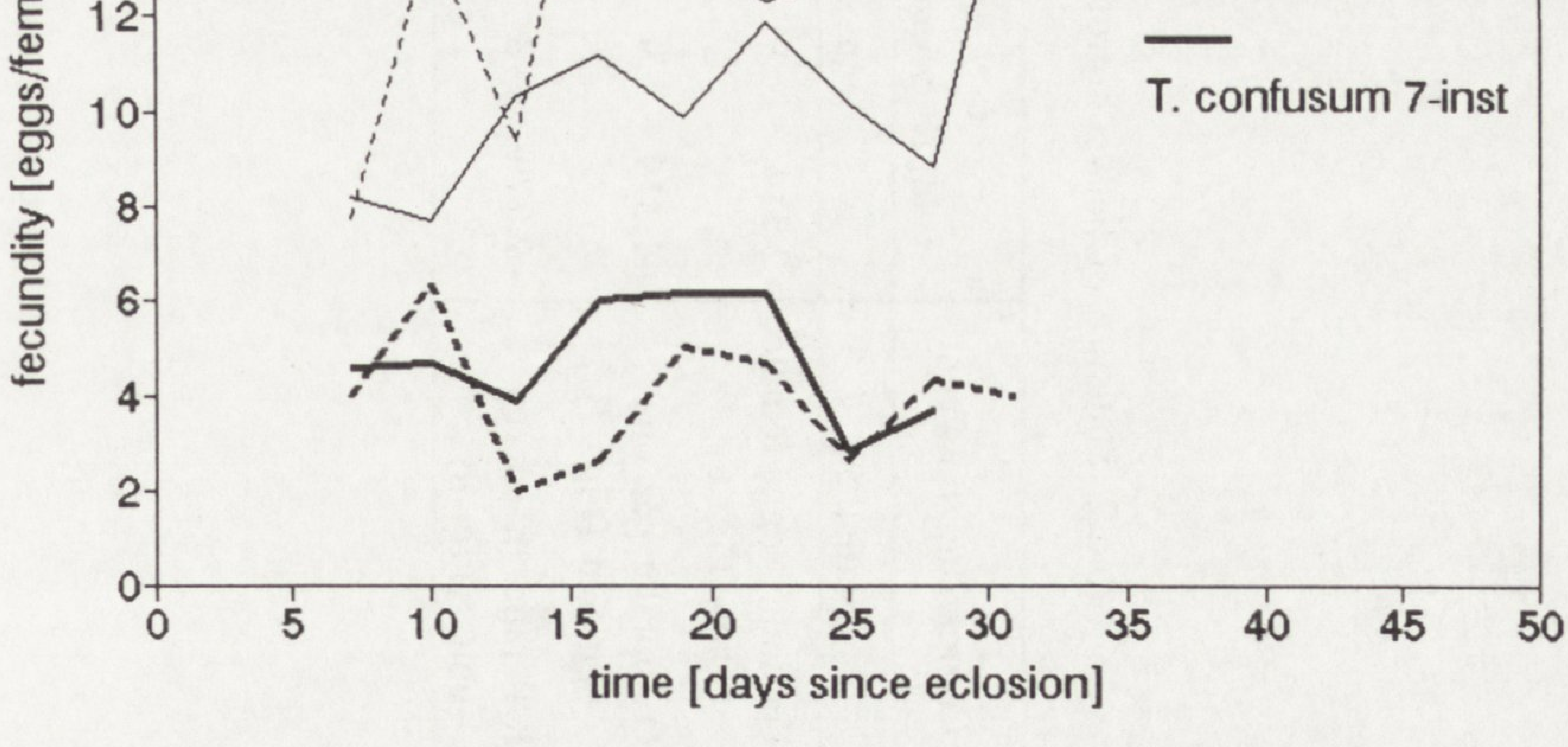

Fig. 6. Fecundity of females of two *Tribolium* species and their 6- and 7-instar phenotypic groups

Table 2. Statistics of between-group and between-species comparisons of values presented in Figs 6–8 in adult females

Comparison between:	6- / 7- in *T. castaneum*			6- / 7- in *T. confusum*			between-species in 6-instar groups			between-species in 7-instar groups		
Statistics	t	n	p <	t	n	p <	t	n	p <	t	n	p <
Fecundity eggs/female · day (Fig. 6)	2.314	9	0.05	–1.428	8	NS	8.364	9	0.001	9.445	8	0.001
O_2 uptake per one egg lied (Fig. 7)	–1.319	9	NS	–1.266	7	NS	–1.987	9	0.1	–1.862	8	0.1
R/P ratio in energy units (Fig. 8)	–2.379	8	0.05	–2.946	6	0.05	–0.620	9	NS	0.125	8	NS

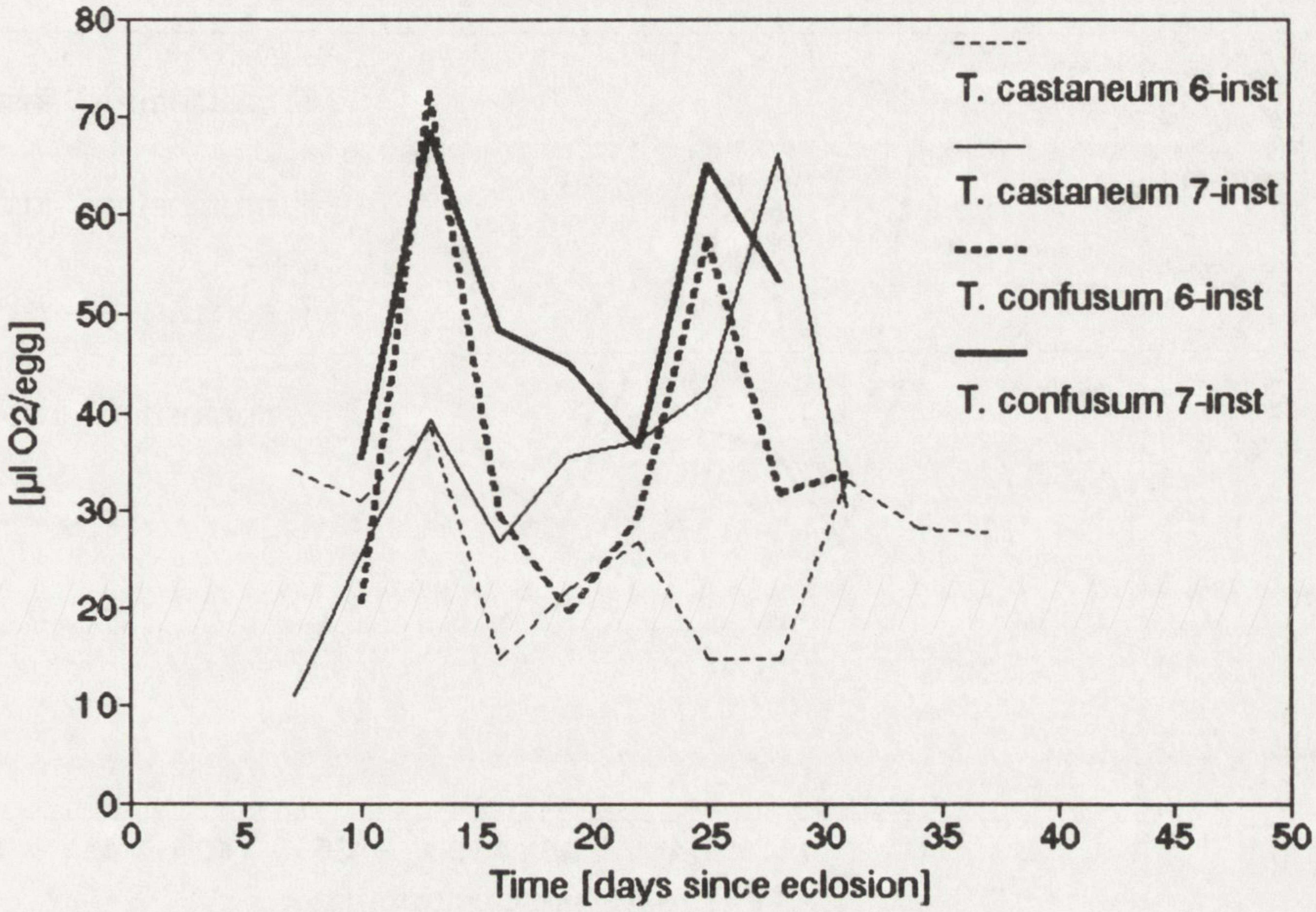

Fig. 7. Oxygen consumption calculated per one egg produced by females of two *Tribolium* species and their 6- and 7-instar phenotypic groups

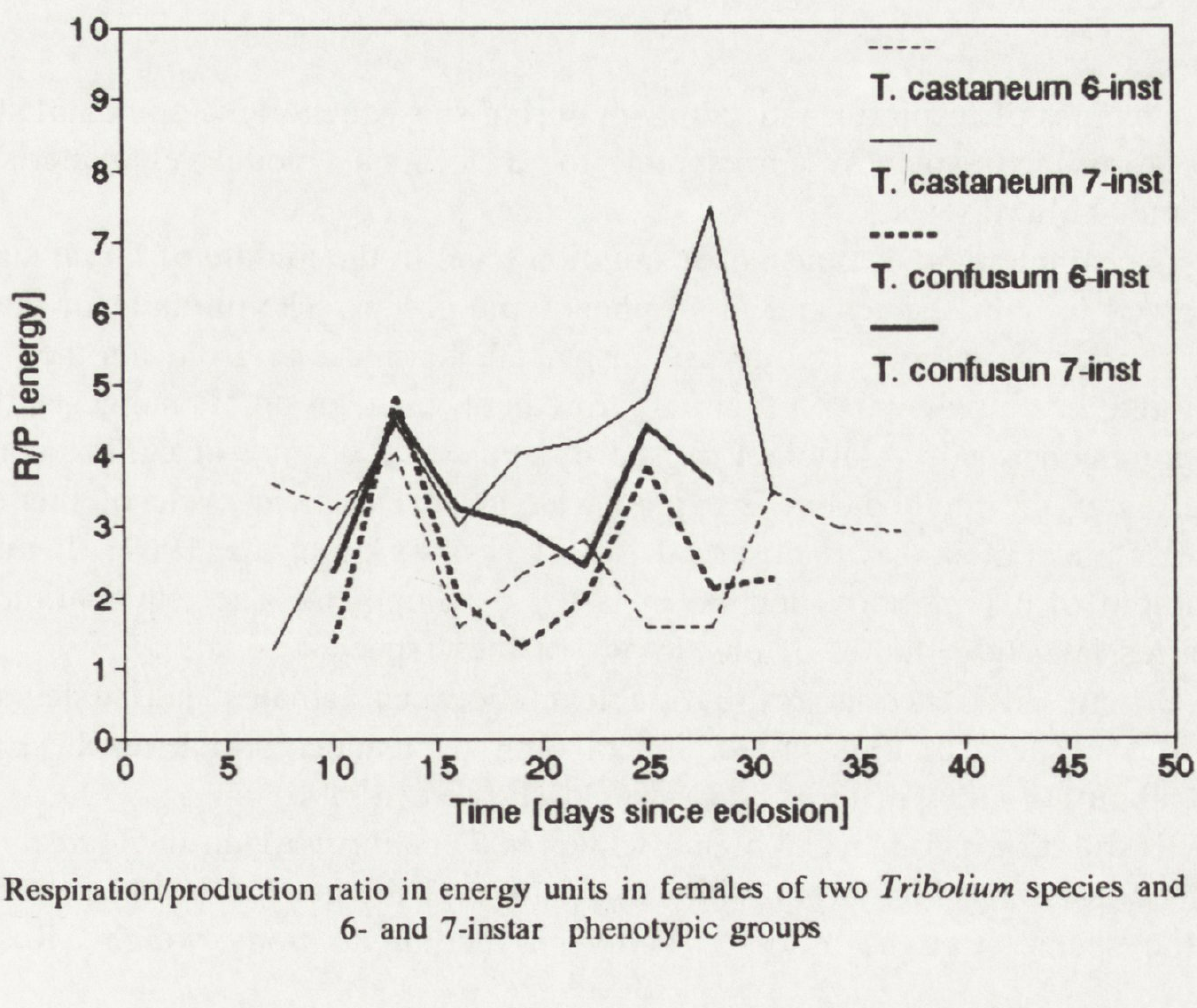

Fig. 8. Respiration/production ratio in energy units in females of two *Tribolium* species and their 6- and 7-instar phenotypic groups

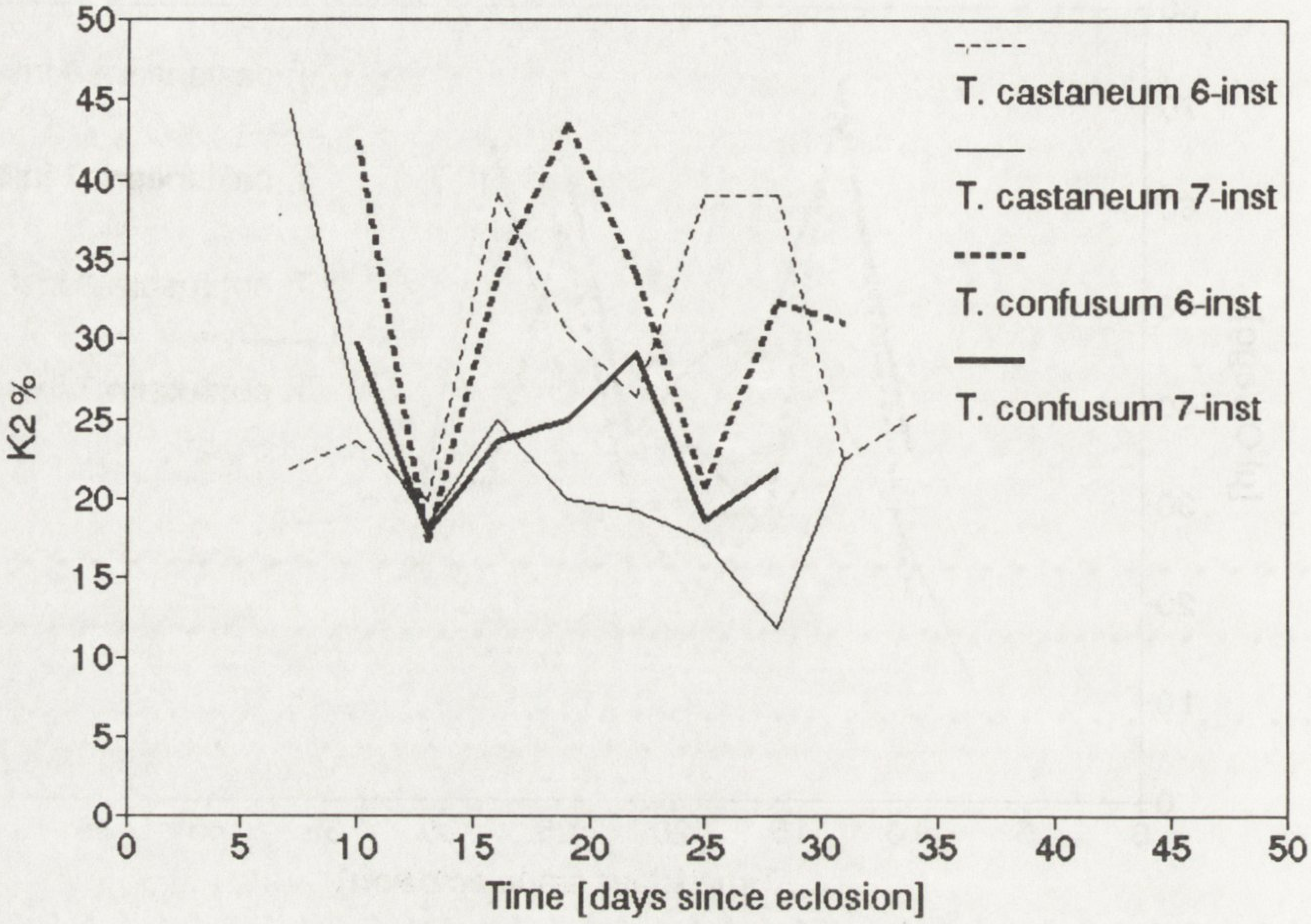

Fig. 9. Index of instantaneous net production efficiency K_2i in females of two *Tribolium* species and their 6- and 7-instar phenotypic groups

4. DISCUSSION

Changes of respiratory metabolism during subsequent developmental stages of two examined species correspond to a general model characteristic for holometabolic insects.

A characteristic decrease of respiration level in the middle of larval stage was observed in both species and in all phenotypic groups. The minima for the longer and shorted developing group are displaced in time one from another so they occurred in similar stage of larval growth of each group. It suggests that this phenomenon is not an artefact caused by accidental change of culture conditions or error of the method, but is a regularity in development cycle of this species. Similar phenomenon was observed by Klekowski et al. (1967). It may be a symptom of a temporary decline in larval development. The explanation of this requires intensive studies of physiology of these species.

Strong difference in respiration level between females and males is quite obvious because of high production of eggs by females which reaches, per one day, about 17–20% of their body weight (Bijok 1989b).

Respiration rate reaches higher values in *T. confusum* than in *T. castaneum* as in species having higher body biomass. However the general level of metabolism of the species can be assessed better in relation to body weight. Results on respiration per body weight suggest that *T. castaneum* is the species of a bit higher metabolic activity than *T. confusum*. That implies higher locomotoric activity of the species which helps in seeking for new habitats. That is associated with flight ability in *T. castaneum* (Dawson 1977) which is not stated in *T. confusum*.

Presented results on metabolism per produced biomass (Fig. 3 and 7) and R/P in energy units (Fig. 4 and 8) show however stronger within species differences than between species ones. In almost all cases 7-instar individuals show higher oxygen requirements and higher R/P ratio than 6-instar ones. That means that 7-instar individuals expend relatively more of available resources for their maintenance than do 6-instar ones. 6-instar individuals expend more on growth and reproduction what is also confirmed by findings by Prus at al. (in press). The index of net production efficiency K_2i illustrates well energy share of production in growing (Fig. 5) and adult (Fig. 9) individuals.

The organism can acquire limited amount of resources necessary for two processes so that an increase of one of them must cause a decrease of the second one (Stearns 1992). In *Tribolium* laboratory cultures the limiting factor can be only the rate of ingestion and digestion because food resources (flour) are practically unlimited. Digested energy and material can then be expend on cost of maintenance: standard and active metabolism, and production: body production in larvae (growth) and generative production in adults (eggs). The distribution of energy between these two costs is different in 6- and 7- instar groups. That may suggest a kind of physiological trade-off. High investment in production means fast growth of individuals and high reproduction rate that give as the result high rate of population increase. On the other hand high metabolism is often connected with reaction on stress and can be related with survival in unfavourable environmental condition. Some resisting mechanisms require additional energy expenditure. Elevation of metabolism has been reported as related with reaction to toxins in invertebrates (Klekowski and Opaliński 1993) but it can also be an effect of response to overcrowding or other stress.

Distribution of energy between maintenance and production, as it has been shown, is different in 6- and 7-instar groups of *Tribolium* beetles. This result indicates different life strategies accomplished by these two phenotypic groups coexisting in populations of both *Tribolium* species.

The 6-instar group is more production-oriented, it invests more in quick production of the body and offspring. Having faster development as well as higher fecundity (Prus et al. 1989) causes higher "r" of the population, assures its rapid growth in optimal conditions. That is a "coloniser type": a group that is responsible for rapid filling available space when the species finds a new, unoccupied habitat e.g. uninfested store-room.

The 7-instar group is more resistance-oriented, it invests more in parents survival than in offspring production. Its lower fecundity is however less dependant on parents aging (Prus et al. 1989). They are bigger and expending more energy on their own maintenance. They have better resistance to both: interpopulation factors as competition overcrowding stress and external ones as bad food conditions, presence of pesticides (Prus 1989) etc. That is a "dweller type": a group responsible for survival of the population in unfavourable conditions when, for example, the population has limited space for life and habitat deteriorates.

The existence of both groups simultaneously in *Tribolium* populations (Howe 1961, Prus 1976, Bijok 1986) can be very advantageous for the species. Presence of two groups of different strategy improves the species' plasticity, let it react on abundance of food with a boom in population increase and on bad conditions with high resistance.

5. SUMMARY

In two species of flour beetles: *T. castaneum* and *T. confusum* intrapopulation diversity have been found manifesting itself in existing of so called 6- and 7-instar phenotypic groups differing in terms of developmental time and body weight (Prus 1976, Bijok 1986). The two species and their phenotypic groups were compared according to maintenance expenses (metabolism) and efficiency of production of body tissues in larvae and of eggs in adult females. The comparisons were made in order to find out whether the distribution of available energy and efficiency of production differs in phenotypic groups within examined species.

Constant pressure volumetric microrespirometer (Klekowski 1975) was used to determine oxygen consumption by insects. Microbalance was used for gravimetric assessment of changes in body biomass.

Changes of respiratory metabolism during subsequent developmental stages of two examined species correspond to a general model characteristic for holometabolic insects (Fig. 1): rapid increase in larval stages, decline in inactive prepupa and pupa, increase in adult. Reproducing females have c.a. 3 times higher metabolism than males. An exception from a general model is a characteristic temporary decrease in respiration level, approximately in the middle of larval stage. *T. castaneum* seams to have higher level of metabolism per unit weight and show higher fecundity (Fig. 6) than *T. confusum*. Intraspecies differences are however much stronger than interspecies ones. 7-instar groups (particularly of *T. castaneum*) show higher respiration per unit weight (Fig. 2, Table 1) and produced biomass (Figs 3, 7 and Table 2) and higher respiration/ /production ratio in energy units (Fig. 4 and 8) than 6-instar ones. That means that they expend relatively more of available resources for their maintenance, when 6-instar ones expend more on growth and reproduction. That is also illustrated by the index of instantaneous net production efficiency K_{2i} (Figs. 5 and 9).

High investment in production gives rapid population increase. High metabolism is often connected with reaction to stress and conditions survival in unfavourable environmental conditions.

The existence of the two groups of different life strategy simultaneously in *Tribolium* populations can be very advantageous for the species: improves the species' plasticity, let it react on abundance of food with a boom in population increase and maintain high resistance in bad conditions.

6. POLISH SUMMARY

U dwu gatunków trojszyka: *T. castaneum* i *T. confusum* stwierdzono zróżnicowanie wewnątrzpopulacyjne przejawiające się istnieniem t.zw. grup 6- i 7-stadialnych różniacych się czasem rozwoju i ciężarem ciała (Prus 1976, Bijok 1986). Dwa gatunki i ich grupy

fenotypowe zostały porównane pod względem metabolizmu i wydajności produkcji: ciała u larw, a jaj u dojrzałych samic. Porównania zostały przeprowadzone w celu stwierdzenia czy dystrybucja dostępnej energii i wydajność produkcji różni się w grupach fenotypowych badanych gatunków.

Do pomiarów zużycia tlenu użyto mikrorespirometrów wolumetrycznych (Klekowski 1975). Pomiary zmian biomasy przeprowadzono metodą grawimetryczną przy użyciu mikrowagi.

Przebieg zmian tempa metabolizmu w trakcie rozwoju dwu badanych gatunków odpowiada ogólnemu modelowi dla owadów z przeobrażeniem zupełnym (rys. 1): szybki wzrost w stadiach larwalnych, spadek na czas nieaktywności (przedpoczwarki i poczwarki) i wzrost u owadów dorosłych. Rozmnażające się samice wykazują ok. 3 razy wyższy metabolizm niż samce. Odstępstwem od ogólnego modelu był charakterystyczny chwilowy spadek poziomu oddychania mniej więcej w połowie okresu larwalnego.

T. castaneum wydaje się mieć wyższy poziom metabolizmu w przeliczeniu na jednostkę ciężaru i wykazuje wyższą płodność (rys. 6) niż *T. confusum*. Jednakże różnice wewnątrzgatunkowe są znacznie wyraźniejsze niż międzygatunkowe. Grupy 7-stadialne (szczególnie u *T. castaneum*) wykazują wyższe oddychanie na jednostkę ciężaru ciała (rys. 2, tab. 1) i wyprodukowanej biomasy (rys. 3 i 7, tab. 2) i wyższy stosunek respiracja/produkcja w jednostkach energii (rys. 4 i 8) niż 6-stadialne. Oznacza to że przeznaczają proporcjonalnie więcej dostępnych zasobów na koszty własnego utrzymania, podczas gdy 6-stadialne więcej na wzrost i reprodukcję. Ilustruje to dobrze indeks chwilowej wydajności produkcji netto K_2i (rys. 5 i 9).

Duży wydatek energii na produkcję daje wysokie tempo przyrostu populacji. Wysoki metabolizm jest często związany z reakcją na stres i warunkuje przetrwanie w niekorzystnych warunkach środowiskowych. Równoczesne istnienie dwóch grup o różnej strategii życiowej w populacji *Tribolium* może być bardzo korzystne dla gatunków: poprawia plastyczność i pozwala reagować szybkim przyrostem populacji na obfitość pokarmu, a zachować wysoką odporność w złych warunkach środowiska.

7. REFERENCES

1. Bijok P. 1986 – On heterogeneity in bIV strain of *Tribolium confusum* Duval – Ekol. pol. 34: 87–93.
2. Bijok P. 1989a – A set of methods for distinguishing between "6- and 7-instar individuals" in *Tribolium* populations - Tribolium Inf. Bull, San Bernardino, USA. 29: 56–59.
3. Bijok P. 1989b – Energy budget and production efficiency of *Tribolium confusum* Duval in the developmental cycle – Ekol. pol. 37: 109–133.
4. Bijok P. 1992 – Relationship between time of embryonic and postembryonic development and weight in two species of *Tribolium* beetles – Ekol. pol. 40: 213–223.
5. Dawson P. S. 1977 – Life history strategy and evolutionary history of *Tribolium* flour beetles – Evolution, 31: 227–229.
6. Duncan A., Klekowski R. Z. 1975 – Parameters of energy budget (In: Methods for ecological bioenergetics, Eds. W. Grodziński, R. Z. Klekowski, A. Duncan) – IBP-Handbook No 24, Blackwell Sci. Publ., Oxford – London-Edinburgh-Melbourne, 97–147.
7. Edwards G. A. 1953 – Respiratory metabolism (In: Insect physiology, Ed. K. D. Roeder) – John Wiley and Sons Inc., New York, 96–146.
8. Harrow B., Mazur A. 1958 – Textbook of biochemistry – Saunders, Philadelphia.
9. Howe R. W. 1961 – Developmental time and weight in *Tribolium castaneum* – Tribolium Inf. Bull, San Bernardino, USA. 4: 21–22.
10. Klekowski R. Z. 1975 – Constant pressure volumetric microrespirometer for terrestrial invertebrates (In: Methods for ecological bioenegretics Eds W. Grodziński, R. Z. Klekowski, A. Duncan) – I.B.P. Handbook No 24, Blackwell Sci. Publ., Oxford-London-Edinburgh-Melbourne, 212–225.

11. Klekowski R. Z., Opaliński K. W. 1993 – Metabolizm energetyczny [Energetic metabolism] (In: Bioenergetyka ekologiczna zwierząt zmiennocieplnych [Ecological bioenergetics of poikilotherm animals] Eds R. Z. Klekowski, Z. Fischer) – Polska Akademia Nauk, Wydział II Nauk Biologicznych, Warszawa, pp. 35–82.
12. Klekowski R. Z., Prus T., Żyromska-Rudzka H. 1967 – Elements of energy budget of *Tribolium castaneum* (Hbst.) in its developmental cycle (In: Secondary productivity of terrestrial ecosystems, Ed K. Petrusewicz) – Państwowe Wydawnictwo Naukowe, Warszawa-Kraków, Vol. 2, 859–879.
13. Park T., Mertz D. B., Petrusewicz K. 1961 – Genetic strains of *Tribolium*: Their primary characteristics – Physiol. Zool. 34: 62–80.
14. Prus M. 1989 – Development time and survival in 6- and 7-instar groups of *Tribolium castaneum* Hbst. and *T. confusum* Duval under the effect of Tricalcium phosphate – Tribolium Inf. Bull, San Bernardino, USA. 29: 85–94.
15. Prus M., Prus T., Bijok P. 1995 – Lipid content and energetic equivalent as a measure of reproductive effort in two species of *Tribolium* – Ekol. pol. 43: 217–225.
16. Prus T. 1976 – On heterogeneity in cI strain of *Tribolium castaneum* Hbst – Tribolium Inf. Bull, San Bernardino, USA. 19: 97–104.
17. Prus T., Bijok P., Prus M. 1989 – Autecological features of strains: *Tribolium castaneum* Hbst cI and *T. confusum* Duval bIV – Ekol. pol. 37: 97–107.
18. Prus T., Prus M. 1987 – Phenotypic differentiation of *Tribolium castaneum* Hbst. cI strain – Tribolium Inf. Bull, San Bernardino, USA. 27: 89–95.
19. Sokoloff A. 1972 – The biology of *Tribolium* with special emphasis on genetic aspects. Vol. I – Oxford University Press, 300 pp.
20. Stearns S. C. 1992 – The evolution of life histories – Oxford University Press, Oxford-New York-Tokyo, 249 pp.

(*Received after revising January 1996*)