STUDIES ON THE EFFECT OF TEMPERATURE ON THE DEMOGRAPHIC PARAMETERS OF *ACHIPETRIA HOLOMONENSIS* (ACARI, ORIBATIDA)

BY G. P. STAMOU *

SUMMARY : The effect of constant temperature conditions on *Archipteria holomonensis* demographic parameters has been studied in laboratory.

The experiment shows that 15-20°C is the optimum temperature for rearing *Achipteria holomonensis* in laboratory. At low constant temperatures mortality of all life stages was minimum, while spermatophores and oviposition were not recorded. Development did not advance at all and animals hardly moved at 10°C or remained even inactive at 5°C. Fungal hyphae cause mortality in *Achipteria holomonensis* only at high temperatures (20 and 25°C), while predation by Insecta Staphylinidae and Acari Rhodacaridae as well as relative humidity above 70 % and inundations don't affect the parameters of this species.

RÉSUMÉ : L'effet des températures constantes sur les paramètres démographiques d'*Achipteria holomonensis* fut étudié en laboratoire.

Les expériences réalisées ont montré que la température optimale pour élever *Achipteria holomonensis* en laboratoire est située entre 15 et 20°C. A la température de 5 et 10°C la mortalité est minimale, alors que la production des œufs et des spermatophores est nulle. Le développement est presque arrêté. Les animaux restent inactifs à 5°C ou presqu'immobiles à 10°C. Le développement des champignons dans les cellules d'élevages entraîne une mortalité seulement aux températures plus élevées (20 et 25°C), tandis que la prédation par les Insectes Staphilinidae et par les Acariens Rhodacaridae, ainsi que l'humidité relative au dessus de 70 % et l'eau en excès n'affectent pas les paramètres démographiques de cette espèce.

INTRODUCTION

Achipteria holomonensis Cancela da Fonseca and Stamou, is the most abundant oribatid mite in the litter layers of an oakwood in Mt Holomon (Halkidiki, Greece). Among the abiotic factors governing its population dynamics, temperature seems to be the most important one (STAMOU 1981). In a previous paper (STAMOU *et al.*, 1981) we provided information concerning demographic parameters of *A. holomonensis*, estimated at room temperature conditions varying between 20° and 25°C. Never-

* Division of Ecology, Department of Biology, University of Thessaloniki, 540 06 Thessaloniki, U.P.B. 119 - Greece.

thless, this information is only of general interest, since temperature in the experimental fild varies between 0 and 17°C (STAMOU, 1981). Therefore, it was necessary to study the behaviour of *A. holomonensis* at a temperature range below 20°C in order to analyse its behaviour in the field. Naturally, estimation of demographic parameters of oribatids made at standard temperature conditions deviate from those made at fluctuating ones (LEBRUN, 1977) ; however, these estimations can be used as a basis describing general tendencies of their behaviour with reference to temperature and furthermore, to estimate demographic parameters at fluctuating temperature conditions (HADJIBIROS, 1977 ; STAMOU, 1986).

In this paper we studied the influence of constant temperatures (5, 10, 15, 20 and 25°C) on the demographic parameters of *A. holomonensis*. In addition, we provide some further information concerning the effect of predation, humidity and inundation on these parameters in order to complete our study.

MATERIALS AND METHODS

Experimental materials as well as methods used in order to culture *A. holomonensis* in laboratory are described in a previous paper (STAMOU *et al.*, 1981). During this experiment, animals collected in the experimental field during July 1978, were introduced with proper food supply in culture pots at 15 and 25°C. Cultures were daily observed under stereomicroscope and the newly emerged individuals (after ecdysis) as well as eggs oviposited by adults, were removed and put in other culture pots, either singly or by two, three, four or five specimens. By this way a good number of new cultures containing animals whose age was approximately known (by 24 h) were obtained. Demographic parameters of each life stage of *A. holomonensis* were recorded in these cultures. The eggs oviposited in adult cultures were separately reared as well as larvae emerged from these eggs.

Development of fungal hyphae is always a serious problem in culturing oribatids. So, GRANDJEAN (1948), suggests that failure of oribatid cultures is due to individuals immobilisation among hyphae or to their toxic activity. LEBRUN (1974), observed immobilisation of *Damaeus onustus* C. L. Koch and *Damaeus clavipes* Hermann larvae. Notice that these species feed voraciously on fugal hyphae at high temperatures (25°-26°C). CANCELA DA FONSECA (1975), too, reports strong attack of *Damaeus verticillipes* Nicolet immatures by fungal hyphae, so that ecdyses were prevented or, whenever they happened, the newly appeared individual had anomalies, particularly in legs. It seems that the effect of hyphae on mycetophagous species is less important due to their ability to control their development (ROCKETT and WOODRING, 1966). In order to control the development of fungal hyphae in the cultures of *A. holomonensis*, three, five or ten adult individuals of the family Oppiidae were introduced in cultures containing the specimens of *A. holomonensis*. The cultures were stored at 5, 10, 15, 20 and 25°C constant temperatures. The rates of demographic parameters were compared with those recorded after cultures without specimens of Oppiidae by using t-test.

During this experiment possible predators of oribatids (species of the families Rhodacaridae : Acari, Mesostigmata, and Staphylinidae : Insects, Coleoptera) were kept in culture without food supply for 5-10 days. After that they were introduced in cultures containing immatures *A. holomonensis* and stored at 15, 20 and 25°C constant temperatures. The effect of predators on *A. holomonensis* was monitored daily at about the same time for a period of 10-15 days under stereomicroscope. Experimental design provided that the rate of natural mortality was to be subtracted from the rate of the recorded total mortality so that the rate of predation could be calculated.

To study the effect of humidity on *A. holomonensis* demographic parameters, cultures were stored in plastic pots at 60, 70, 80, 90 and 100 % relative humidity and at 15, 20 and 25°C constant temperatures. Air humidity was controlled by KOH solutions in distilled water (BUXTON and MELLANBY, 1934). The cultures were daily observed and the data were analysed by using the analysis of variance technique. In addition, a number of individuals, all, of the same life stage, was placed on the bottom of

vessels containing water. These vessels were stored at 5 and 25°C for 30 days. The rate of mortality was recorded daily and it was compared with the one determined in control cultures (t-Test).

Results and discussion

1. Culturing of *A. holomonensis* at high constant temperatures.

1.1 High temperatures and demographic parameters of juvenile life stages.

Cultures of *A. holomonensis* were regularly developed at 15, 20 and 25°C standard temperature conditions. On the contarary, at 5 and 10°C constant temperature, they were not developed at all. In Table 1 demographic parameters of juvenile *A. holomonensis* recorded at 15, 20 and 25°C, are given. As it can be seen, the duration of development of immature life stages of *A. holomonensis* increases from larva to tritonymph at all three temperatures (notice the exception of larva's development time at 25°C). Above behaviour cannot be considered as a general one for oribatids. However, this is reported for *Camisia segnis* Hermann (Grandjean, 1950), *Camisia spinifer* C. L. Koch (Sengbusch, 1958), *Tectocepheus velatus* Michael (Murphy and Jalil, 1964), *Hermania scabra* C. L. Koch (Jalil, 1965), *Nothrus palustris* C. L. Koch (Lebrun, 1968), which comprise a small part of oribatids whose life cycle is known. According to Lebrun (1970a), the duration of life cycle of species belonging to an homogenous taxonomic group can be related to the body dimensions of each species. Within one species, namely *A. holomonensis*, it seems that the duration of development of each life stage can be related to its dimensions too — notice that body dimensions of *A. holomonensis* increase with life stage — at least at 25°C where complete data exist. The same seems to happen also in the case of *N. palustris* (Lebrun, 1968).

The values of the coefficient of variation of the duration of development determined for immature life stages at 15, 20 and 25°C are low, ranging between 5.8 and 35.8. They approximate to low values which were calcualted in laboratory cultures for three species of Galumnidae : *Galumna nervosus*

Table 1. — Demographic parameters of immature life stages of *Achipteria holomonensis* at standard temperature conditions (15, 20 and 25°C). Mean duration of development (l_x), coefficient of variation (CV%), number of observations on which above determinations have been based (n), as well as mortality (m) are given.

Life stage	n	l_x (days)	CV% (s/x̄.100)	m (% ind.week^{-1}
15°C				
Egg	11	32.27	12.4	1.8
Larva	17	48.14	20.9	3.2
Protonymph	16	50.17	14.9	5.2
Deutonymph	14	77.50	7.1	6.0
Tritonymph	—	—	—	—
20°C				
Egg	16	20.50	5.8	11.4
Larva	17	36.00	14.7	4.3
Protonymph	17	40.50	8.7	11.1
Deutonymph	15	66.20	8.0	5.0
Tritonymph	—	—	—	—
25°C				
Egg	16	31.00	14.0	18.1
Larva	14	28.50	35.8	8.2
Protonymph	15	40.60	11.8	10.6
Deutonymph	14	69.00	9.4	6.8
Tritonymph	14	91.00	7.7	3.8

* Tritonymphs accomplish their development at 15 and 20°C. demographic parameters at these temperatures were not recorded because of the long duration of their development.

Berlese, *Galumna longipluma* Berlese and *Galumna eliminatus inthacensis* Jacot (Sengbusch, 1954) while these are lower compared with values of the coefficient of variation which are reported for developmental life stages of *N. palustris* at 18-20°C (Lebrun, 1970a), eggs and larvae of *D. onustus* and *D. clavipes* in the temperature range from 10 to 28°C (Lebrun, 1974) and the developmental stages of *Oppia nitens* C. L. Koch at 20°C (Sengbush and Sengbush 1970). High variability in development time of *C. segnis* life stages is also observed by Grandjean (1950). Sengbush (1954), suggests that the variability in duration of development must be attributed to deviations of culturing temperature conditions from the optimum ones. If this is valid, the optimum culture temperature for *A. holomonensis* is about 20°C, since coefficients of variation of the development time recorded at 20°C for almost all immature life stages is lower than the ones recorded at 15°C. On the other hand, it is possible

to take into consideration only the duration of development in order to determine the optimum temperature for culturing oribatids. Considering duration of development of immature life stages of *A. holomonensis*, 20°C seems to be the optimum temperature too, while the highest limit for rearing *A. holomonensis* in laboratory seems to be about 25°C. Analogous observations have been made by LEBRUN (1974) concerning rearing of eggs and larvae of *D. clavipes* and *D. onustus*.

Mortality of all immature life stages of *A. holomonensis* increased from 15 to 25°C (deutonymphs between 15 and 20°C are excluded). This is in agreement with observations made by LEBRUN (1974) in eggs and larvae of *D. clavipes* and *D. onustus*. Mortality recorded for juveniles at 25°C is high. In general it is higher than that calculated for juveniles belonging to three species of Galumnidae (SENGBUSCH, 1954) and *T. velatus* (MURPHY and JALIL, 1964) reared at 25°C, as well. Furthermore, mortality of eggs and larvae of *A. holomonensis* determined at 20°C is superior than that calculated for eggs of *D. clavipes and D. onustus* (LEBRUN, 1974) at the same temperature; yet this is lower than mortality reported for the eggs of these species at 26°C. High mortality has also been reported by JALIL (1965) for larvae *H. scraba*, by HARTENSTEIN (1962c) for eggs *Protoribates lophotrichus* Berlese and by SAICHUAE *et al.* (1972) for immature life stages of *Northrus biciliatus* C. L. Koch.

High mortality recorded at high temperatures (20 and 25°C) of the immobile life form (egg) and the form of low mobility (tritonymph) should be partly attributed to the observed infection by hyphae of these life stages of *A. holomonensis* similar to those observed by CANCELA DA FONSECA (1975) in immatures *D. verticilipes*. Hyphae attacked the less active individuals especially tritonymphs, which remained immobilized for the longest time period. On the other hand, mortality rates recorded at high temperatures for mobile life forms (larva, protonymph and deutonymph) as well as mortality recorded for all juvenile life stages at 15°C must be considered as natural, since such infections have not been observed; notice that at 15°C hyphae were not well developed in culturing vessels. Contrary to what ROCKETT and WOODRING (1966) reported about *Ceratozetes jewlli* Rockett and Woodring, at 20 and 25°C no effect of hyphae on the mean duration of eggs and larvae development has been observed. Yet, no effect of hyphae has been recorded on the mean duration of development of later instars.

1.2. Temperature and demographic parameters of adults.

Survivorship of adults *A. holomonensis* was determined at 15, 20 and 25°C (Table 2), but, as the coefficient of variation calculated at 20 and 25°C is high, only results obtained at 15°C were taken into consideration.

The longevity of adults *A. holomonensis* is high. In general, the duration of life cycle of *A. holomonensis* is of the longest one compared to that of other oribatids, e.g. at 25°C it exceeds 262.5 days, which is reported for *N. palustris* by LEBRUN (1970a).

Data concernig survivorphip of adults *A. holomonensis* at 15°C were simulated by a logistc curve (Fig. 1). The greatest number of adults *A. holomo-*

TABLE 2. — Demographic parameters of adult *Achipteria holomonensis* at standard temperature conditions (15, 20 and 25°C). Mean time of survival (l_x), coefficient of variation (CV%), fecundity recorded in the two-month (August-September) period (f), as well as number of observations on which above determinations have been based (n) are given.

Temperature °C	n	l_x (days)	CV% (s/x̄.100)	f (eggs.ind.$^{-1}$.week^{-1}	CV% (s/x̄.100
15	60	140.61	7.4	0.113	35.2
20	60	109.26	22.3	0.118	47.6
25	60	97.34 (357.44)[1]	37.9	0.112	85.1

1. The total duration of the life cycle of *Achipteria holomonensis* recorded at 25°C standard temperature conditions, is given in parenthesis.

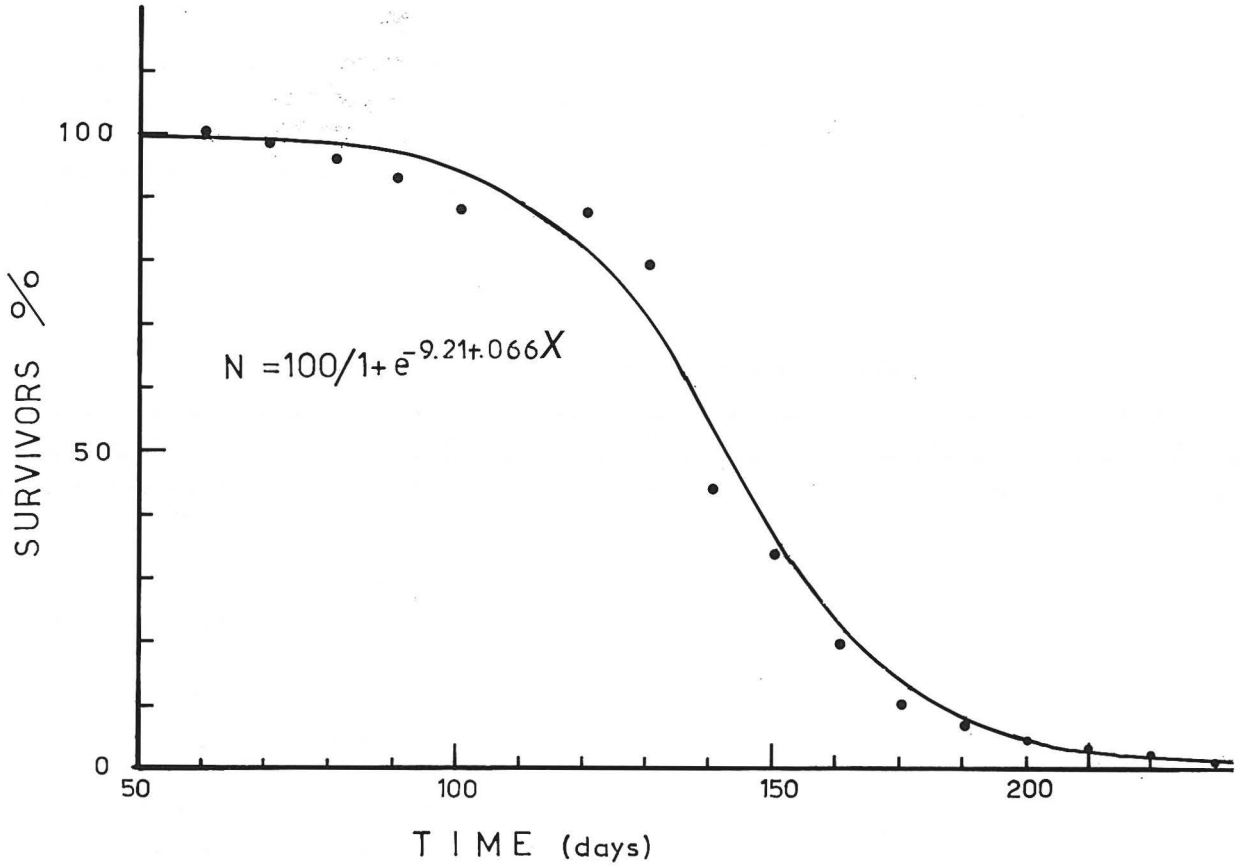

FIG. 1 : Survivorship curve of adults *A. holomonensis* at 15°C constant temperature. Data concerning survivors percentage (N) with time (X) were simulated by a logistic model.

nensis dies in a short time period (between 100 and 180 days), while a small number survives for a longer period. This behaviour of adults *A. holomonensis* seems to be analogous to that of *Neoribates gracilis* Travé (TRAVÉ and DYRAN, 1971), but it is not in agreement with observations made by LEBRUN (1970b).

Survivorship curve at 15°C from laboratory cultures approximates the phenological curve which was derived from census data (STAMOU, 1981). In *A. holomonensis* case the rate of mortality at a constant temperature of 15°C seems to coincide with the one exhibited in the field under fluctuating temperatures. It seems that at 15°C constant temperature, mortality is realised at the same rate as the mean rate it is realized in the field. Above statements appear to contrast observations made by LEBRUN (1970b), who reported that the mean longevity of *N. palustris* is shorter in semi-natural conditions than in laboratory ones.

Oviposition in cultures of adult *A. holomonensis* took place from July to March. The greatest number of eggs in cultures was observed in a short two-month time period (August-September), while during the remaining time period adults lay eggs rather accidentally. It is remarkable to notice that mass mortality of adults (late October-January) takes place somewhat later than when oviposition is practically over.

Temperature influences fecundity of *A. holomonensis*. Highest rate of oviposition in August-September period was observed at 20°C (0.118 eggs.

ind^{-1}.week^{-1}) while at 15 and 25°C it was 0.113 and 0.112 eggs.ind^{-1}. week^{-1}, respectively. These rates are lower than the ones recorded in cultures of *A. holomonensis* stored at room temperature varying between 20 and 25°C (STAMOU *et al.* 1981). In any case above estimations cannot be considered as unbiased, since coefficient of variation varies from 35 % at 15°C to 85 % at 25°C.

2. Culturing of *A. holomonensis* at low constant temperatures.

In Table 3 we present some observations on the behaviour of *A. holomonensis* cultured at low constant temperatures (10 and 5°C).

As it can be seen there is a temperature limit when rearing *A. holomonensis* at standard tempera-

TABLE 3. — Observations on the behaviour 36A. holomonensis at low constant temperature.

Life stage	Phases of life stage	Nb. observ.	Treatment	Observations
Egg	Just laid at 15°C	6	Stored at 5°C for 42-123 days	No evidence of development. Inactive
			↓	
			Transferred and stored at 10°C for 40-68 more days	No evidence of development. Hardly moved.
			↓	
			Transferred and stored at 15°C	Larvae emerged in 17-20 days
Egg	Ready to hatch at 20°C	3	Transferred and stored at 0°C for 10 days	No hatching
			↓	
			Transferred and stored at 5°C for 10 more days	No hatching
			↓	
			Transferred at 20°C	Larvae emerged in a few days
Larvae	Just emerged at 20°C	8	Stored at 5°C for 108 days	No evidence of development. Inactive.
			↓	
			Transferred and stored at 15°C	Protonymphs emerged in 17-20 days
Larvae	Just emerged at 20°C	6	Stored at 10°C for 126 days	No evidence of development. Hardly moved.
			↓	
			Transferred and stored at 15°C	Protonymphs emerged in 15-19 days
Protonymphs	Just emerged at 20°C	12	Stored at 5°C for 48-128 days	No evidence of development. Inactive.
			↓	
			Transferred and stored at 10°C for 31-42 more days	No evidence of development. Hardly moved.
Protonymphs	Immobilized and even swollen at 20°C	6	Transferred and stored at 5°C for 30 days	No ecdysis
			↓	
			Transferred at 15°C	Four hatched in 5-9 days and two died
Deutonymphs	While hatching at 15°C	3	Transferred and stored at 5°C for 10 days	No hatching
			↓	
			Transferred at 15°C	Ecdysis fulfilled in a few hours

ture conditions, between 10-15°C, over which development can be completed. Similar behaviour is exhibited by *Oppia nodosa* Hammer (BHATTACHARYYA *et al.*, 1978) : It was regularly developed at constant temperatures higher than 16°C, while at 8°C it remained immobile.

It is remarkable to notice that at 15°C the development of immatures previously stored at lower standard temperatures is accomplished in a 15-20 days time interval. This time period is much shorter than mean development time of any immature life stage regularly cultured at 15°C. In order to interpret this phenomenon, we have to suggest the following : It does not seem possible that development is performed at low rates when animals are kept at low temperatures. Our point is that individuals at low temperatures display a sort of quiescence, preserving their aptitude to respond rapidly to any temperature change. So, *A. holomonensis* can exploit increase of temperature in order to accomphish a part of its life cycle when transferred at room temperature for observation under stereomicroscope. The aptitude of *A. holomonensis* to respond rapidly to temperature changes is also emphasised by the fact that immobilised specimens at 5°C begin to move immediately when they are transferred at room temperature. Similar suggestions for oribatids have also been made by TARMAN (1973) an LEBRUN and VAN RUYMBECKE (1971). Development arrest of soil inhabitants at low temperatures has frequently been reported (EITMINAVICIOUTE, 1959 ; HAARLØV, 1960 ; LEINAAS, 1983). Yet, HARTENSTEIN (1962b), reports a particular case of temperature shock. What really happened is that larvae *Metabelba montana* Kulsz., emerged from eggs acclimatized at low temperatures in the field, were unable to develop at high temperatures in laboratory. Such a temperature shock was not observed in the case of *A. holomonensis*.

Quiescence seems to be the physiological adaptation stratergy of *A. holomonensis* towards regular short-term diurnal fluctuations of temperature or random changes happening in the field. In quiescence, *A. holomonensis* can overwinter with no high rates of mortality, while in cases of temporary temperature increases it is able to accomplish part of its development.

Physiological adaptations, like the one shown by *A. holomonensis* towards temperature, are exhibited by Acari to other environmental parameters, as well. For instance, CANCELA DA FONSECA (1975), observed immobilisation of *Hermania gibba* C. L. Koch as a response to drought,while HAZAN *et al.* (1973), observed inhibition of egg production in *Tetranychus cinnabarinus* Boisduval at 100 % relative humidity.

The behaviour of *A. holomonensis* at low standard temperature conditions does not coincide with census data (STAMOU, 1981). As a matter of fact, maximum density of *A. holomonensis* in the field is recorded in winter. In addition to that, *A. holomonensis* is regularly developed in this period, when temperature in the field is much lower than the temperature limit determined for *A. holomonensis* at constant temperatures. In general, progress in oribatid development is possible at low temperatures in the field. Indeed, *T. velatus* shows a two-year duration of life cycle in a region covered by snow for about eight months a year (SOLHØY, 1976). Furthermore, populations of oribatids are active under snow coverage and air temperature of about –35°C (MCBRAYER and CROMACK, 1980). LEBRUN (1977), observed that eggs of *D. onustus* in semi-natural cultures show shorter development time than the ones cultured at constant temperatures in laboratory. Above considerations indicate that development of oribatids at standard temperature conditions deviates from that recorded at fluctuating ones. The same has also been demonstrated for respiration behaviour of *A. holomonensis* (STAMOU, 1986). This behaviour of Oribatids raises the problem of parameters estimation at fluctuating temperatures in the field, a problem discussed by STAMOU (1986).

3. The effect predators.

Among mesofauna taxa, Rohdacaridae and Staphylinidae are considered as intensive predators of immature oribatids. For instance, LEBRUN (1970 b), reports high values of predation of *Pergamasus* sp. on juveniles *N. palustris* (4-8 g of prey/predator/day). However, no predation on a *A. holomonensis* has been observed, at least under the condition of this experiment. On the contrary, sometimes the number of predators appeared decreasing in the

cultures. This can be attributed to predators cannibalism similar to that reported by BHATTACHARYYA (1962). HARTENSTEIN (1962a) recording predation of two species of Parasitidae on oribatids, concluded that predation rate depends on the hardiness of prey exoskeleton. Besides, LEBRUN (1970b), has observed that *Permagasus* sp. does not affect mature individuals of *N. palustris* having hard exoskeleton. In the case of *A. holomonensis* we consider that the hard exoskeleton of anomalous relief, even that of immatures, seems to prevent predation by Rhodacaridae and Staphylinidae.

4. The effect of inundations and humidity.

According to LEBRUN (1970b), inundations cause death to oribatids due to asphyxia. However, in individuals of *A. holomonensis* placed on the bottom of vessels containing water, no increase of mortality was recorded. Immobilisation of immatures and even ecdysis happened regularly at 25°C. Furthermore, it is remarkable to notice that mortality of tritonymphs at 25°C equals zero, while in the control cultures stored at the same temperature, overall mortality rate was about 50 %. This difference can be attributed to the fact that immobilized tritonymphs were not attacked by hyphae.

According to VANNIER (1978) relative humidity below a critical level causes mortality to oribatids. This critical level depends on species, life stage and temperature conditions. In the case of *A. holomonensis*, relative humiditiy above 70 % does not seem to affect *A. holomonensis* demographic parameters, while relative humidity lower than 70 % causes mortality to all developmental stages at all temperatures. It seems that humidity operates on demographic parameters (especially mortality) in a YES-NO mode.

Another observation, which unfortunately was not quantified, is also remarkable, that is, immatures in cultures with relatively desiccated subtrate showed an acceleration of their development towards immobilisation, whenever the substrate was saturated again. This is contrary to the observation reported by CANCELA DA FONSECA (1975), for *H. gibba* C. L. Koch, that this species is immobilised under conditions of drought, while it begins moving again when humidity increases.

CONCLUSIONS

1. There is a temperature limit between 10 and 15°C, below which development and reproduction of *A. holomonensis* are not possible at standard temperature conditions.

2. Duration of development of juvenile life stages of *A. holomonensis* at 15, 20 and 25°C increases in relation to their dimensions.

3. Taking upon consideration mortality, the optimum temperature for rearing *A. holomonensis* in laboratory is about 15°C, while examining duration of development, egg production and variability of development time of juveniles, optimum temperature is about 20°C.

4. Egg production takes place in a short time period (August-September), while mass mortality of adults is observed a little after the end of oviposition.

5. Thermal behaviour of *A. holomonensis* stored at standard temperature conditions in laboratory is different from that in the field.

6. Behaviour of *A. holomonensis* at low temperatures could be considered as a physiological adaptation to overwintering. That is *A. holomonensis* manages to survive in Winter, remaining inactive when temperature decreases, while it exploits even the lightest increase of temperature to accomplish a part of its life cycle.

7. Predation of Staphylinidae and Rhodacaridae on the life stages of *A. holomonensis* is prevented by the hardiness of their exoskeleton.

8. Relative humidity above 70 % as well as inundations are not limiting factors for the development of *A. holomonensis*.

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