The life cycle of Pseudosida ramosa, Daday 1904, an endemic Neotropical cladoceran.

FREITAS[1], E.C. & ROCHA[2], O.

[1,2] Department of Ecology and Evolutionary Biology, Federal University of São Carlos, Post box 676, 13560-905, São Carlos, SP, Brazil. [1]emanuela@linkway.com.br; [2]doro@power.ufscar.br

ABSTRACT: The life cycle of Pseudosida ramosa, Daday 1904, an endemic Neotropical cladoceran. The life cycle of Pseudosida ramosa was studied considering longevity, fecundity, growth, and the duration of embryonic and post-embryonic development were determined. Organisms collected from Óleo Lake (21°20'–21°55'S and 47°35'– 47°55'W) were cultured at 25 and 30 ± 0.5°C, photoperiod of 12/12 h (light/dark) and fed with Selenastrum capricornutum at 10^5 cell.mL^{-1}. Eight stages were distinguished during the embryonic development. The embryonic development lasted 50 h at 25 ± 0.5°C, and 33 h at 30 ± 0.5°C. Clearly the ambient temperature has a strong influence on the embryonic development of Pseudosida ramosa. For post-embryonic development, the best performance was obtained at 25 ± 0.5°C, since animals attained larger length, higher longevity and showed a tendency to higher total fecundity.
Key words: life cycle, embryonic development, zooplankton, Cladocera, Pseudosida ramosa.

RESUMO: O ciclo de vida de Pseudosida ramosa, Daday 1904, um cladócero Neotropical endêmico. O ciclo de vida de Pseudosida ramosa foi estudado considerando a longevidade, fecundidade, crescimento, e a duração do desenvolvimento embrionário e pós-embrionário foram determinados. Os organismos coletados da Lagoa do Óleo (21°20'–21°55'S e 47°35'– 47°55'W) foram cultivados a 25 e 30 ± 0,5°C, com fotoperíodo de 12/12 h (claro/escuro) e alimentados com Selenastrum capricornutum a 10^5 céls.mL^{-1}. Oito estágios foram diferenciados durante o desenvolvimento embrionário. O desenvolvimento embrionário durou 50 h a 25 ± 0,5°C, e 33 h a 30 ± 0,5°C. Sem dúvida, a temperatura ambiental tem uma forte influência sobre o desenvolvimento embrionário de Pseudosida ramosa. Para o desenvolvimento pós-embrionário, o melhor desempenho foi obtido a 25 ± 0,5°C, já que os animais atingiram um maior comprimento, maior longevidade e mostraram uma tendência de maior fecundidade total.
Palavras-chave: ciclo de vida, desenvolvimento embrionário, zooplâncton, Cladocera, Pseudosida ramosa.

Introduction

Research on the life cycle of zooplankton species is especially important for the study of population dynamics, secondary production, food-chain interactions and ecotoxicology, which is aimed at environmental quality control. In this context, widely distributed cladoceran species, which are readily cultured in the laboratory, are potentially a good choice for environmental indicators to be used in controlled conditions.

Various aspects of the biology of these cladoceran species and their use in assays for environmental quality control have been researched in standard conditions (Adema, 1978). In Brazil, over the last few years, an attempt has been made to study in detail the biology of some species of Neotropical Cladocera, evaluating their sensitivity to various toxic agents and comparing their responsiveness to that of other test-organisms (Fonseca, 1998). A few cladocerans, especially species belonging to the family Daphnidae, have already been investigated and their life cycle recorded in considerable detail, including their developmental times at various concentrations of food and different temperatures, their growth rates and fertility. This is the case for species of Daphnia (Rocha & Matsumura-Tundisi, 1990), Ceriodaphnia (Fonseca, 1998; Fonseca & Rocha, 2004; Rietzler, 1998) and Moina (Böhrer, 1995; Bozelli, 1996; Santos-Wisniewski, 1998).

Species of the family Sididae are an important component of limnetic plankton in São Paulo State, Brazil, occurring in a

wide variety of water-bodies. So far, seven species were recorded (Rocha & Güntzel, 2000). Nevertheless, little is known on the biology or ecology of those sidid species.

In this context, the aim of this study was to collect detailed information on the life cycle of Pseudosida ramosa Daday 1904, a cladoceran species belonging to the family Sididae, by observing a laboratory culture, maintained under controlled conditions. Thus, embryonic and post-embryonic development were studied at two temperatures (25 and 30 ± 0.5°C) and analyzed, considering individual longevity, fecundity, growth and the age and body length of the pre-primipara and primipara instars. Knowledge of these details is essential to establishing criteria to be used in ecotoxicological assays.

Materials and methods

Maintenance of Pseudosida ramosa stock culture

Pseudosida ramosa (Crustacea, Cladocera) was collected from Óleo Lake (21°20' - 21°55'S and 47°35'- 47°55'W), an oxbow lake in Jataí Ecological Station in district of Luis Antônio, São Paulo State, Brazil. Natural water, taken from outdoor experimental tanks at the Federal University of São Carlos, rich in humic compounds, was filtered through a 68 mm plankton net, autoclaved at 120°C for 20 minutes and diluted with five parts distilled water to produce the culture medium. This water was used instead of the water from the lake due to the lake distance (150 km). The medium had a final hardness of 40-48 mg $CaCO_3.L^{-1}$, pH 7.4 ± 0.2 and conductivity about 160 $mS.cm^{-1}$. The cladocerans were fed on an algal suspension of Selenastrum capricornutum at 10^5 $cell.mL^{-1}$, grown in CHU-12 medium. The cultures were maintained in two liters beakers in two incubators, at temperatures controlled at 25 ± 0.5°C and 30 ± 0.5°C, both with a 12hL/12hN photoperiod and light intensity of 2000 lux in the light period. Organisms were acclimatized through several generations for approximately three months.

Embryonic development

Development of Pseudosida ramosa embryos was observed in order to record the main transformations occurring in the developing progeny starting with the deposition of the eggs in the brood chamber of the female, and hence divide the embryonic period into its characteristic stages. In addition, the duration of each stage of embryonic development (in hours) was measured, at 25 ± 0.5°C and 30 ± 0.5°C.

The method used was as follows. Sexually immature females were separated from the culture in plastic beakers of fresh culture medium. When ready to produce eggs (i.e. just before primipara), 60 females were placed individually in small transparent plastic vessels (150 mL) containing the medium. Thirty individuals were maintained as described in the previous section.

On reading sexual maturation, the females were examined each three hours during the first 24 hours, after which they were monitored every hour until the end of development of the eggs. The stages of embryonic development were photographed with a digital camera coupled to a Zeiss optical microscope. To obtain the images of the embryonic stages, a proportion of the females had to be dissected, to allow the eggs to be photographed outside the brooding chamber. In all, 10 females were dissected.

Post-embryonic development

For each culture temperature (25 ± 0.5°C and 30 ± 0.5°C), six neonates were placed individually in 150 mL of medium in small transparent plastic vessels and maintained as described in the section Maintenance of Pseudosida ramosa stock culture.

To monitor the body length of individual females, they were transferred daily to a watch glass using a Pasteur pipette with a large bore at the tip to avoid damaging them. Using a lens and micrometer scale, the total length was measured from the top of the head to the extreme rear end of the animal (end of the carapace). Growth curves were adjusted using the von Bertallanffy equation, as follows (the initial parameter of which was obtained by the Ford-Walford transformation):

$$L_t = L\infty \left[1 - e^{-K(t-t_0)}\right], \text{ where:}$$

L_t = size at a certain time interval t, expressed in mm; L¥ = maximum length,

expressed in mm; K = constant related to the growth rate; e = base of neperian logarithm; t_0 = parameter related to the initial length of individuals at birth (L_0), expressed in days.

To measure fecundity, the number of eggs produced by each female was counted daily. Longevity was obtained by observing the duration of the life cycle from birth of the embryo until death of the female. In addition, the duration of the pre-primipara and the primipara instars and body-length of pre-primipara and primipara were determined from individual growth results.

In order to identify significant differences between longevity, fecundity, individual growth, and the duration of the pre-primipara and the primipara instars and body-length of pre-primipara and primipara, at 25 e 30 ± 0.5ºC, the Mann-Whitney (U) non-parametric test (with the level of significance p=0.05) was employed.

Results

Embryonic development

In the embryonic development of Pseudosida ramosa, temperature had a strong influence on the duration of the embryonic phase of this species; thus, at 25 ± 0.5ºC the embryo needed, on average, 50 hours to complete its development, while at 30 ± 0.5ºC this time was reduced by 34%, to 33 hours, owing to a rise of only 5ºC.

Eight different stages were distinguished, as follows:

Stage I (Fig. 1, A and B): At the moment the eggs are laid in the brood-chamber, they are spherical, becoming ovoid soon after. They have a granular appearance. A little later, two distinct regions appear. The inner region consists of well-defined granules and the outer (clearer) region has finer grains, the two being separated by a membrane corresponding to the "nauplius membrane" described by Murugan & Venkataraman (1977). An outer membrane was also seen, referred to as the chorion by Lebedinsky (cited in Obreshkove & Fraser, 1940). This stage lasted for three hours in females cultured at either 25 ± 0.5ºC or 30 ± 0.5ºC.

Stage II (Fig. 1, C and D): The eggs grew longer at this stage and exhibited pronounced invaginations in the anterior half, precursors of the future cephalic sinus that separates the head from the main body. At the posterior end there was a small constriction, signaling the start of development of the bilateral symmetry plane (Obreshkove & Fraser, 1940; Lei & Clifford, 1974). This stage lasted for five hours both 25 ± 0.5ºC and 30 ± 0.5ºC.

Stage III (Fig. 1, E): The embryo became more elongated and acquired a mushroom-like shape in sagittal section, exhibiting the rudiments of antennae. It is assumed that the outer membrane (chorion) is ruptured and discarded at this stage (although this event has not been observed), as described by Murugan & Venkataraman (1977), since the embryo was apparently enveloped by the nauplius membrane alone. The first signs of formation of the carapace around the body were also seen at this point. This stage lasted for seven hours at both 25 ± 0.5ºC and 30 ± 0.5ºC.

Stage IV (Fig. 1, F): The head became well defined and a swelling appeared at the dorsal side of the cephalic region, representing the first external sign of a brain. An initially single granular mass was observed, which divided in the next stage into two masses that later would develop into the eyes. Antennae with two rami grew longer, attached to the body, and joints appeared. At the posterior end, the post-abdomen began to form. The carapace became more evident. This stage lasted for nine hours at 25 ± 0.5ºC and six hours at 30 ± 0.5ºC.

Stage V (Fig. 1, G): The antennal rami were now fully segmented and acquired small setae. The digestive tract could be seen, as well as appendages that would be the legs. The head was more clearly defined and the dark brown mass inside it differentiated into two equal parts, initiating the formation of eyes. Anterior to these masses was the small, dense spot of the ocellus, seen in perspective. The brain was more developed than previously, but not yet completely so. Both, the carapace and post-abdomen were seen to be more advanced in their development, than in stage IV. The embryo was observed to move inside the brood chamber. The nauplius membrane had probably been discarded at this point. This stage lasted for 15 hours at 25 ± 0.5ºC and only six hours at 30 ± 0.5ºC.

Stage VI (Fig. 1, H): A pair of eyes, with black pigment, was clearly visible. This stage lasted for five hours at 25 ± 0.5ºC and three hours at 30 ± 0.5ºC.

Stage VII (Fig. 1, I): The eyes were larger and the brain fully formed. The post-abdomen acquired terminal claws. This stage lasted for three hours at 25 ± 0.5°C and two hours at 30 ± 0.5°C.

Stage VIII (Fig. 1, J): The pair of eyes and the body of the embryo grew larger. The embryos were released from the brood chamber. They already exhibited swimming movements, but these were slow at first. The carapace was still open, not yet enclosing the body. The eyes did not fuse before the embryo was released, as has been observed in other species, such as Daphnia magna (Obreshkove & Fraser, 1940) and Moina micrura (Murugan, 1975). This stage lasted for three hours at 25 ± 0.5°C and one hour at 30 ± 0.5°C.

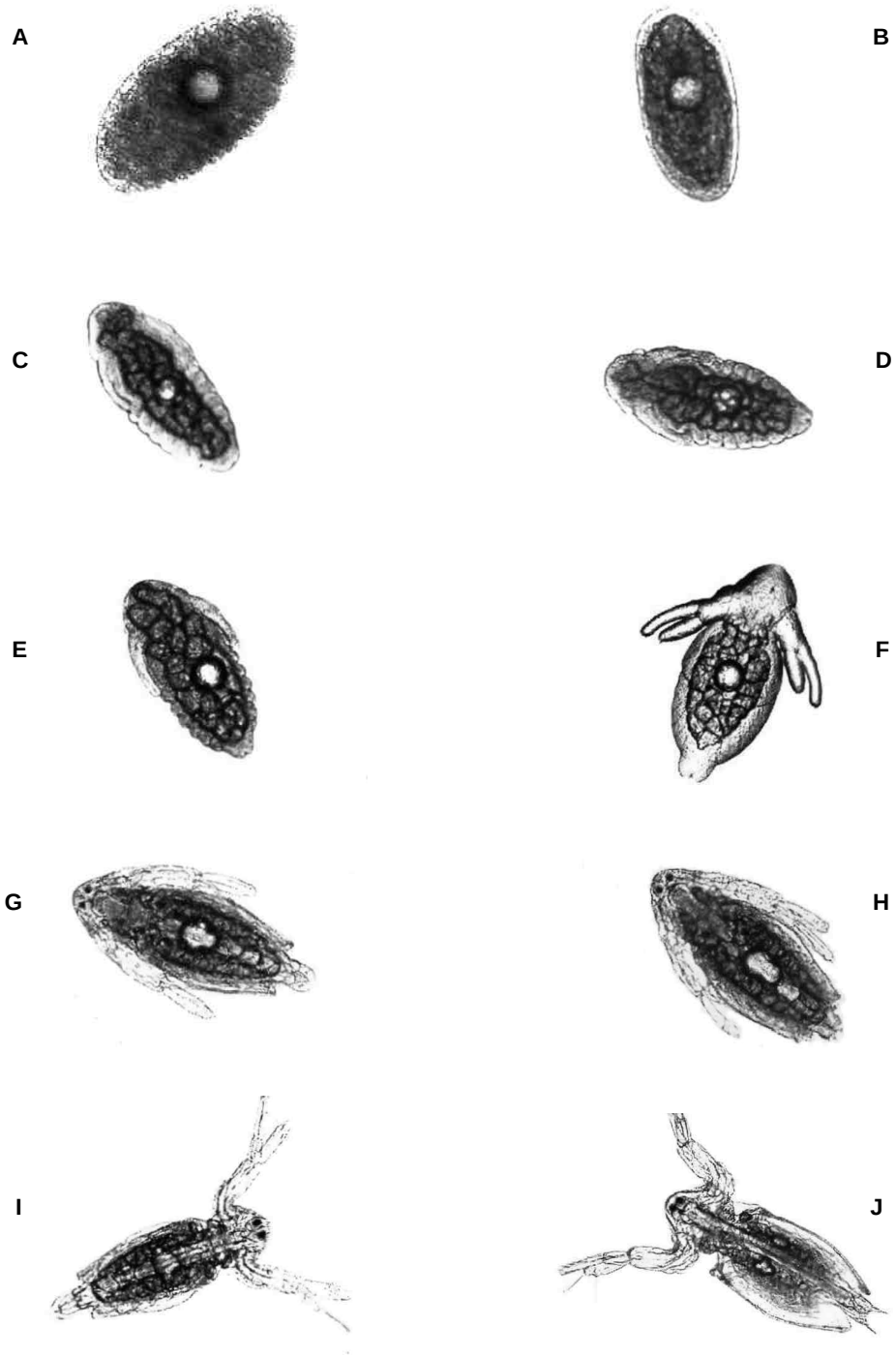

Figure 1: Eight stages distinguished during the embryonic development of Pseudosida ramosa (amplification 50x): A and B – Stage I; C and D – Stage II; E – Stage III; F – Stage IV; G – Stage V; H – Stage VI; I – Stage VII; J – Stage VIII.

Post-embryonic development

Individual growth

Individual growth of these microcrustaceans was analyzed by fitting curves to the daily measurements of the selected individuals, with the help of a computer program. The growth curves for females cultured at 25 ± 0.5°C and 30 ± 0.5°C are displayed in Fig. 2 (A and B). Growth curves can be described by the logistic function, since after a rapid exponential period, there is a reduction in the growth rate, increasing slowly until reaching the asymptotic maximum.

It is clear from the relative steepness of the two curves that the animals cultured at 30 ± 0.5°C (K = 0.19346) grew more rapidly than those at 25 ± 0.5°C (K = 0.09585). Despite the significantly faster growth rate at 30 ± 0.5°C, the females that developed at the warmer temperature died sooner and reached a maximum length (2.16 mm) smaller than that of females cultured at 25 ± 0.5°C (2.49 mm) (U = 213.00, p= 0.0036).

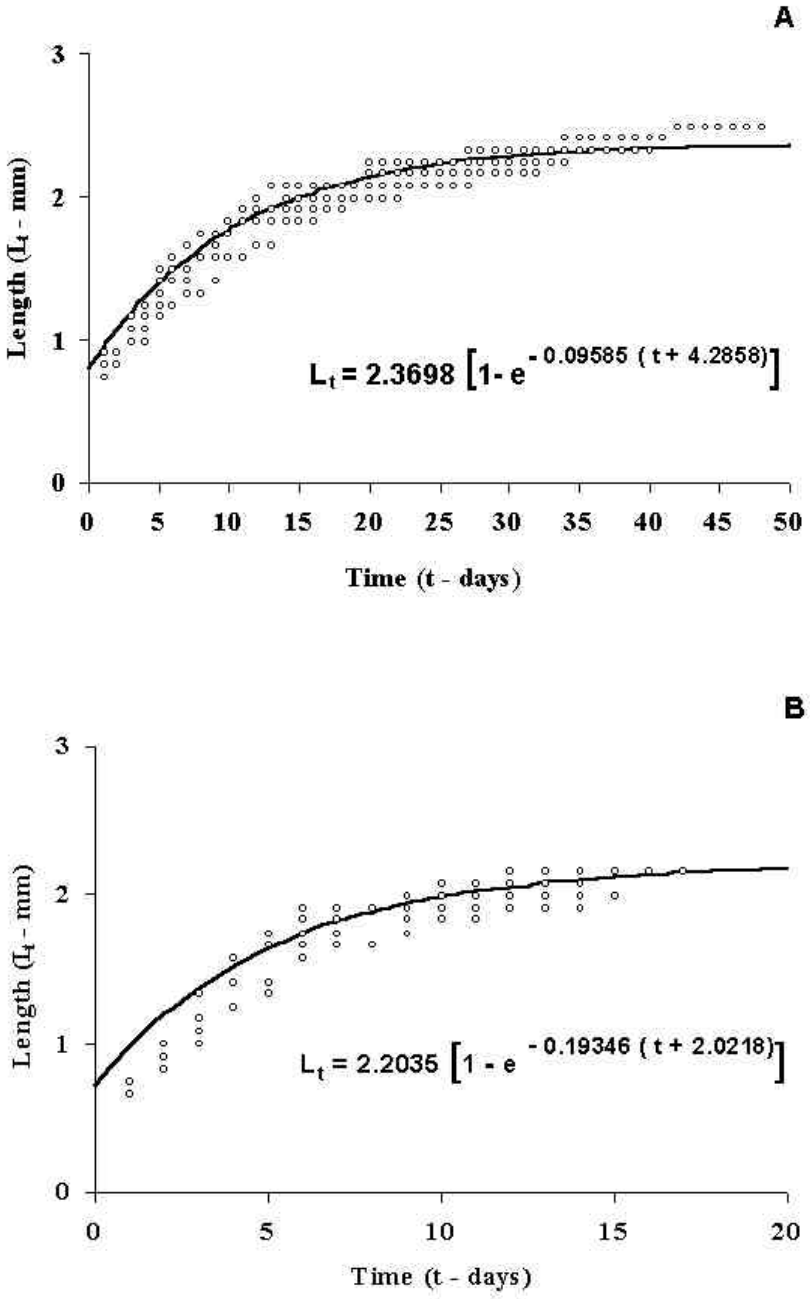

Figure 2: Individual growth curves for Pseudosida ramosa cultured at 25 ± 0.5°C (A) and at 30 ± 0.5°C (B). Points are data from six replicate animals.

Fecundity

Values of the mean fecundity of a female and the mean total fecundity, for six females cultured in the laboratory at 25 ± 0.5°C and 30 ± 0.5°C, can be found in Tab. I.

The daily values of mean fecundity throughout the life cycle of Pseudosida ramosa, recorded during the individual growth test, are plotted in Fig.3.

Note that the highest values of mean fecundity observed were six eggs per female on the 15th day of life and seven eggs on the 34th day, for Pseudosida ramosa grown at 25 ± 0.5°C, and six eggs per female on the 10th and 11th days of life, when cultured at 30 ± 0.5°C.

Table I: Life history data (mean ± standard deviation values) of Pseudosida ramosa raised under controlled laboratory conditions.

Life history parameters	25 ± 0.5°C	30 ± 0.5 °C
Fecundity (eggs.female^{-1})	3.4 ± 1.06	4.3 ± 0.97
Total fecundity (total eggs.female^{-1})	38.8 ± 26.36	27.8 ± 8.11
Longevity (days)	37.1 ± 6.27	14.8 ± 1.17
Duration of pre-primipara (days)	6.67 ± 1.37	4.5 ± 0.54
Duration of primipara (days)	8.34 ± 2.16	5.5 ± 0.54
Pre-primipara length (mm)	1.43 ± 0.04	1.52 ± 0.12
Primipara length (mm)	1.59 ± 0.09	1.64 ± 0.06

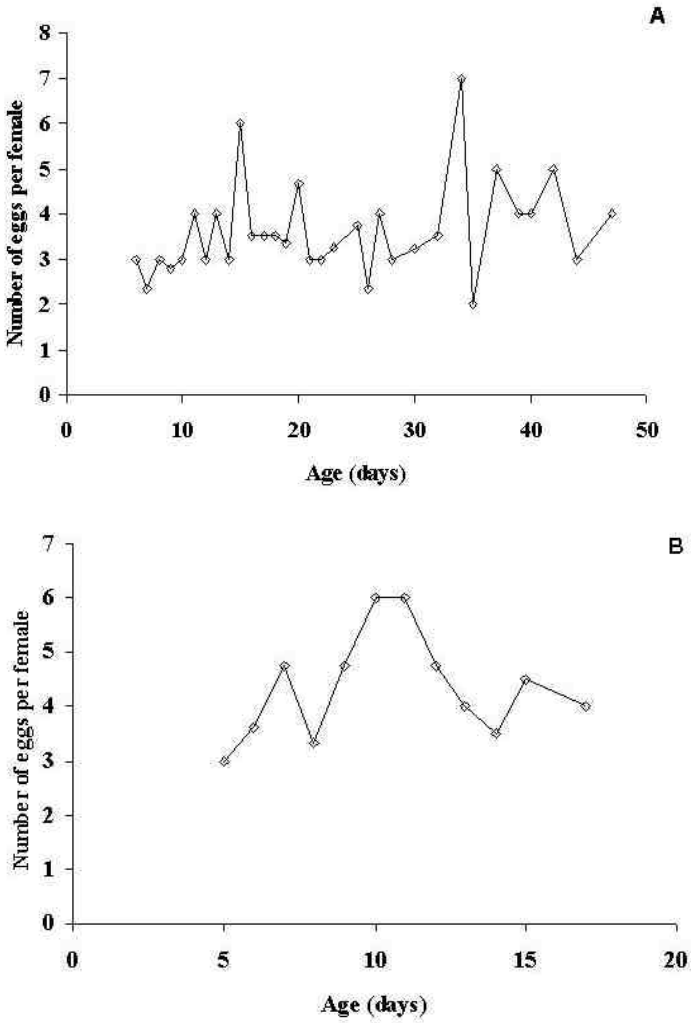

Figure 3: Mean fecundity of Pseudosida ramosa during its whole life cycle, when grown at 25 ± 0.5°C (A) and at 30 ± 0.5°C (B). Points are mean data from six replicate animals.

Longevity

Mean longevity of Pseudosida ramosa at 25 ± 0.5ºC and 30 ± 0.5ºC was recorded during the individual growth experiments, in which growth was observed from the emergence of the neonate until the death of the animal. The resulting data, representing the mean and standard deviation of six replicates, are displayed in Tab. I.

The mean longevity of Pseudosida ramosa at 25 ± 0.5ºC seems to be more than twice as great as that observed at 30 ± 0.5ºC. The longest-living individual at 25 ± 0.5ºC survived for 48 days.

Duration and body-length pre-primipara and primipara

The data on the duration of the pre-primipara and primipara instars and body-lengths of the pre-primipara and primipara in females cultured at 25 ± 0.5ºC and 30 ± 0.5ºC were obtained during the individual growth experiment and are given in Tab. I.

When cultured at 30 ± 0.5ºC, Pseudosida ramosa females reached the post-embryonic instars of pre-primipara ($U = 1.50$, $p = 0.0082$) and primipara ($U = 1.50$, $p = 0.0082$) at younger ages than females cultured at 25 ± 0.5ºC. However, their body-length during pre-primipara instar ($U = 10.00$, $p = 0.2002$) and primipara instar ($U = 12.50$, $p = 0.3785$) showed no significant difference between females grown at 25 ± 0.5ºC and at 30 ± 0.5ºC.

Discussion

Embryonic development of Pseudosida ramosa

On the basis of the present observations, eight stages were recognized in the embryonic development of Pseudosida ramosa. These correspond to the stages reported by Fox (1948) for Daphnia magna and Green (1956) for another ten species of Daphnia. The defining characteristics proposed by these authors for the various stages have been applied to other species, including Daphnia schodleri (Lei & Clifford, 1974), Daphnia carinata and Simocephalus acutirostratus (Murugan & Venkataraman, 1977).

Opinions differ regarding the existence of embryonic membranes in the Cladocera. From the observations of Pseudosida ramosa performed in this study, it is assumed that just two membranes are formed in the developing egg, analogously to those observed by Murugan (1975) and Lebedinsky (cited in Obreshkove & Fraser, 1940) in other cladoceran species. The inner membrane is known as the nauplius or vitelline membrane and attached to it there is an outer membrane called the chorion. Those authors, however, did not indicate the moment when each membrane was discarded. The present observations of Pseudosida ramosa suggest that the chorion was ruptured in stage III and the nauplius membrane in stage V.

It is noteworthy that in Pseudosida ramosa the two composite eyes do not fuse into a single structure before the birth of the neonate, was observed by Obreshkove & Fraser (1940) in Daphnia magna. In the case of Pseudosida ramosa, fusion of the eyes occurred some hours after birth. This fusion is seen as an important characteristic, used by many to point out the last stage of embryonic development. However, in the present study, this final stage was marked by appreciable enlargement of the eyes and of the body. Furthermore, the carapace that encloses the body and appendages in mature animals was not found enclosing the body at the moment of birth.

It is possible that these features of Pseudosida ramosa neonates – the eyes not yet fused and the carapace not enclosing the body – are unique characteristics of the family Sididae. Later, in fact, the composite eyes did fuse into one structure and the carapace closed around the body, enveloping the appendages.

In virtue of its involvement in all life-processes, temperature is one of the outstanding abiotic factors directly acting affecting living organisms, as a controlling, influencing, limiting and lethal factor (Frey, 1947). Goss & Bunting (1983) considered temperature as the main regulator of aquatic ecosystems, affecting growth, development, reproduction, respiration, behavior and, lastly, the survival of aquatic poikilotherms.

It is well known that the time needed for the eggs of planktonic crustaceans to develop is a function of temperature (Bottrell et al., 1976). The present experimental results regarding the embryonic development confirmed that the reproduction of Pseudosida ramosa suffered a strong influence from this factor.

In a general way, these data corroborate the work of Hardy & Duncan (1994), which evaluated the growth and reproduction of Daphnia gessneri, Moina reticulata and Diaphanosoma sarsi, and identified temperature as the dominant factor affecting embryonic development. In the case of Daphnia gessneri, the results showed that the embryonic period was shortened by half when the temperature increased 10°C.

In the present study, it was found that the duration of stages I, II and III did not differ between 25 ± 0.5°C and 30 ± 0.5°C. In fact, in the first three stages, there was no observable difference in the development of the embryos at the two temperatures, this phase taking 15 hours to complete. By contrast, in the following stages (IV to VIII), the influence of temperature on the development of Pseudosida ramosa embryos was quite remarkable, so that the whole period of embryonic development (stages I to VIII) at 30 ± 0.5°C was 34% shorter than at 25 ± 0.5°C. It may be assumed, then, that temperature is an important controlling factor in the embryonic development of this species in its natural environment, given that the Óleo Lake bordering the Mogi-Guaçu River, where the sample of Pseudosida ramosa was collected, is subject to seasonal variations in temperature that include 25 and 30°C.

Post-embryonic development of Pseudosida ramosa

Individual growth

Information on the growth and rates of development of zooplankton species is especially important for the study of population dynamics, secondary production and food-chain interactions (Edmondson & Winberg, 1971).

On most occasions, natural zooplankton populations live under limiting conditions, usually in relation to food. As a result, most species do not achieve their full potential growth and reproduction rates in nature.

A number of studies have also demonstrated that extreme conditions of light, dissolved oxygen, pH and hardness of the water can influence the growth, reproduction and survival of zooplankton. Notwithstanding this, the most important environmental factors are generally the quality and quantity of food and the temperature (Bottrell, 1975; Vijverberg, 1989).

In individual growth experiments, the length of the body is measured at each molt, to obtain growth curves for given sets of conditions.

In the Cladocera, neonates emerge from the brood chamber in the form of miniature adults. There is no metamorphosis during growth and maturation. Growth occurs only after the animal undergoes a molt, while the carapace is still soft, and is characterized by an extremely rapid increase in size (Green, 1956).

In this study the effect of environmental temperature on the growth of individual Pseudosida ramosa was tested. The experimental growth curves reveal considerable differences between growth at the two temperatures. At 25 ± 0.5°C, the increases in length of the developing neonates were slightly smaller than those achieved at 30 ± 0.5°C. In the initial phase of the life cycle, at 30 ± 0.5°C, growth was substantially accelerated until day nine, when the animal reached 1.90 mm, nearly the maximum length (2.16 mm) attained in the life cycle. On the other hand, at 25 ± 0.5°C, there was steady growth throughout most of the life of the animal, which reached a length close to the asymptotic value at around 31 days.

Considering the maximum length reached at the two temperatures, the females cultured at 30 ± 0.5°C reached 2.16 mm at most, while at 25 ± 0.5°C the maximum length was 2.49 mm, or 15.3% greater than that measured at 30 ± 0.5°C.

Lynch (1980) interprets such results as a strategy of distribution of the energy available. In the case, under stressful conditions such as the temperature of 30°C, some species invest more energy in growth in the initial phase of life, rapidly reaching a length very close to the maximum and, from this point, spend most available energy on continuous reproduction throughout almost the whole of the life cycle.

Thus, it can be said that the effect of temperature in the growth-rate arises from its influence on individual metabolic pathways; i.e. it is probably the higher metabolic costs at 30 ± 0.5°C that lead to smaller final sizes and shorter lives, despite the faster early growth-rate. In experiments carried out on Daphnia ambigua, Lei & Armitage (1980) observed that the growth rate increased progressively with rising temperature, between 5 and 30°C.

In the present study, a combination of the 25 ± 0.5°C and a food density of 10^5 cells.mL^{-1} Selenastrum capricornutum allowed better individual growth of the animal species in question than was achieved at 30 ± 0.5°C, with the same concentration of food.

Fecundity

Fecundity is the parameter generally used to estimate the investment made by individuals of a species in reproduction. While the quantity and quality of food are important controlling factors in the growth and reproduction of zooplankton species, temperature also has a crucial role, reflecting directly the energy costs of vital processes.

The fecundity results obtained during the whole life cycle of Pseudosida ramosa revealed that females cultured at 25 ± 0.5°C exhibited a higher fecundity than females maintained at 30 ± 0.5°C ($U = 102.00$, $p = 0.0177$). When the mean total fecundity was examined, it was found that the mean total production of eggs at 25 ± 0.5°C was 38.8 ± 26.36 eggs per female, higher than the value for females cultured at 30 ± 0.5°C, 27.8 ± 8.11 eggs per female. However, due to the large variability in the data at 25 ± 0.5°C, the difference between the two temperatures was not statistically significant ($U = 16.00$, $p = 0.7488$).

In short, the data indicate that when this species was placed in identical conditions of nutrition, varying only the temperature, its reproductive behavior was noticeably altered. The higher mean fecundity observed in Pseudosida ramosa females cultured at 30 ± 0.5°C might be connected with energy distribution, as these animals reached almost their final size in a very short period (half their life cycle) and grew little for the rest of their lives, while those at 25 ± 0.5°C grew constantly throughout most of the experiment. This shows that the females at 30 ± 0.5°C continually invested the energy they acquired in reproduction after day 9th, whereas those at 25 ± 0.5°C, according to the observations both of individual growth and of fecundity, shared the available energy between reproductive activity and somatic growth. Thus, the latter individuals continued growing, albeit in small steps, until they were larger than the maximum size at 30 ± 0.5°C, but reproduced at a lower mean rate.

For the above reasons, it is recommended that cultures of Pseudosida ramosa should be maintained in the laboratory at 25 ± 0.5°C for use in ecotoxicological tests. At this temperature, generally speaking, the females live longer and tend to exhibit a higher mean total fecundity. In the future, it would be interesting to perform experiments at intermediate temperatures, to find an ideal temperature between 25 and 30°C that optimizes the longevity, the mean fecundity and mean total fecundity of this zooplankton.

Longevity

There is a well-known relation between growth and longevity, under conditions of temperature variation: higher temperatures coupled with good nutrition lead to rapid growth and early senescence, whereas a lower temperature with the same food supply leads to a lower growth-rate and longer life (Vijverberg, 1989). Shau & Bercau (cited in Rocha, 1983) mention that the shortening of the life cycle as the temperature increases results from acceleration of the whole cycle, caused by an increase in the metabolic rate.

The present results obtained for the longevity of Pseudosida ramosa show that females grown at 25 ± 0.5°C live 22.3 days longer than those at 30 ± 0.5°C ($U = 0.00$, $p = 0.0039$). Similar relation between longevity and temperature was observed by Rocha (1983), in a study of three species of Daphnia from temperate zone, in which the author evidenced that temperature had a strong effect in daphnid age and maturity.

Schwartz & Ballinger (1980) believe that a shorter life occurring as the temperature increases may be a result of greater stress; in other words, if the rate of reproduction rises, the organism may suffer more physical stress, leading to an earlier death. Evidently, these facts favor the culture of Pseudosida ramosa at 25 ± 0.5°C, which affords greater longevity and hence prolongs its reproductive period.

Development duration and body-length of pre-primipara and primipara

It has also already been mentioned that Shau and Bercau (Cited in Rocha, 1983) attributed the shortened life cycle at higher temperatures to a speeding-up of all the metabolic processes that accelerates the

whole cycle. The present results for Pseudosida ramosa corroborate this hypothesis, in that the females grown at 30 ± 0.5ºC, which had shorter lives, also reached their reproductive age precociously, in comparison with those at 25 ± 0.5ºC.

Nevertheless, comparison of the body-lengths attained at 25 and 30 ± 0.5ºC shows that they did not differ significantly, demonstrating that Pseudosida ramosa individuals need to reach a specific minimum size in order to enter the adult phase, i.e. to be able to reproduce.

Acknowledgements

We are grateful to MSc Timothy J.C. Roberts for translation assistance, to Dr. José Roberto Verani for helping with the curve fitting and to São Paulo State Research Aid Foundation (FAPESP), for financial support (process 04/03228-3).

References

Adema, D.M.M. 1978. Daphnia magna as test animal in acute and chronic toxicity tests. Arch. Hydrobiol., 59:125-34.

Böhrer, M.B.C. 1995. Biomonitoring of zooplankton community at terciary treatment pond at the Liquid Effluent Treatment System of South Petrochemical (SITEL), Triunfo District, Rio Grande do Sul State. São Carlos, UFSCar, 470p (Master Thesis).

Bottrell, H.H. 1975. Generation time, length of life, instar duration and frequency of molting, and their relationship to temperature in eight species of Cladocera from the River Thames, Reading. Oecologia, 19:129-140.

Bottrell, H.H., Duncan, A., Gliwicz, Z.M., Grygierek, E., Herzig, A. & Hillbricht-Ilkowska, A. 1976. A review of some problems in zooplankton production studies. Norw. J. Zool., 24:419-456.

Bozelli, R.L. 1996. The influence of bauxite tailings on the cladoceran populations of lake Batata, Amazonia, Brazil. Int. Rev. Gesamten Hydrobiol., 81:621-634.

Edmondsom, W.T. & Wimberg, G.C. 1971. A manual on methods for the assessment of secondary productivity in freshwaters. Blackwell Scientific Publications, Oxford. 358p.

Fonseca, A.L. 1998. The life cycle of Ceriodaphnia silvestrii (Daday, 1902) and Daphnia laevis (Birge, 1878) (Crustacea, Cladocera) reared under different pH conditions. Verh. Int. Verein. Limnol., 26:1918-1921.

Fonseca, A.L. & Rocha, O. 2004. The life-cycle of Ceriodaphnia silvestrii Daday, 1902, a Neotropical endemic species (Crustacea, Cladocera, Daphnidae). Acta Limnol. Bras., 16:319-328.

Fox, H.M. 1948. The hemoglobin of Daphnia. Proc. R. Soc. B., 135:195-212.

Frey, D.G. 1947. Comparative morphology and biology of three species of Eurycercus (Chydoridae, Cladocera) with a description of Eurycercus macracanthus sp. Nov. Int. Rev. Gesamten Hydrobiol., 58:221-267.

Goss, L.B. & Bunting, D.L. 1983. Daphnia development and reproduction: responses to temperature. J. Therm. Biol., 8:375-380.

Green, J. 1956. Growth, size and reprodution in Daphnia (Crustacea, Cladocera). Proc. Zool. Soc. Lond., 126:173-204.

Hardy, E.R. & Duncan, A. 1994. Food concentration and temperature effects on life cycle characteristics of tropical Cladocera (Daphnia gessneri Herbst, Diaphnosoma sarsi Richard, Moina reticulata Daday): I development time. Acta Amazonica, 24:119-134.

Lei, C.H. & Clifford, H.F. 1974. Field and laboratory studies of Daphnia schoedleri Sars from a winterkill lake of Alberta. Zoology, 9:1-53.

Lei, C.H. & Armitage, K.B. 1980. Growth, development and body size of field and laboratory populations of Daphnia ambigua. Oikos, 35:31-48.

Lynch, M. 1980. The evolution of cladoceran life histories. Q. Rev. Biol., 55:23-42.

Murugan, N. 1975. Egg production, development and growth in Moina micrura Kurz (1874) (Cladocera, Moinidae). Freshwater Biol., 5:245-250.

Murugan, N. & Venkataraman, K. 1977. Study of the in vitro development of the partenogenetic egg of Daphnia carinata King (Cladocera, Daphnidae). Hydrobiologia, 52:129-134.

Obreshkove, V. & Fraser, A.W. 1940. Growth and differentiation of Daphnia magna in vitro. Biol. Bull., 78:428-436.

Rietzler, A.C. 1998. Development times, reproduction and longevity of Diaphanosoma birgei Korinek and Ceriodaphnia silvestrii Daday under natural conditions of feeding. In: Annals of

VII Regional Seminary Ecology. UFSCar, São Carlos. v.3, p.1159-1168.
Rocha, O. 1983. The influence of food-temperature combinations on the duration of development, body size, growth and fecundity of Daphnia species. London, University of London, 337p (Master Thesis).
Rocha, O. & Matsumura-Tundisi, T. 1990. Growth rate, longevity and reproductive performance of Daphnia laevis Birge, D. gessneri Herbst and D. ambigua Scourfield in laboratory cultures. Braz. J. Biol., 50:915-921.
Rocha, O. & Güntzel, A.M. 2000. Crustacea Branchiopoda. In: Ismael, D., Valenti, W.C., Matsumura-Tundisi, T. & Rocha, O. (eds.) Invertebrados de água doce. Biota/ Fapesp, São Paulo. v.4, p.109-120.
Santos-Wisniewski, M.J. 1998. Spatial distribution and secondary production of zooplankton community of the Barra Bonita Reservoir, São Paulo State. São Carlos, UFSCar, 231p (Master Thesis).
Schwartz, S.S. & Ballinger, R.E. 1980. Variations in life history characteristics of Daphnia pulex, fed different algal species. Oecologia, 44:181-184.
Vijverberg, J. 1989. Culture techniques for studies on the growth, development and reproduction of copepods and cladocerans under laboratory and in situ conditions: a review. Freshwater Biol., 21:317-373.

Received: 09 June 2006
Accepted: 20 October 2006