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The importance of feeding in the larval development of the ghost shrimp *Callichirus major* (Decapoda: Callianassidae)

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ABSTRACT

The present study investigated whether the callianassid *Callichirus major* shows a lecithotrophic behaviour during larval development. Two experiments were carried out. In the first experiment, larvae were subjected to an initial period of feeding, while in the second they were subjected to an initial period of starvation. In Experiment 1, 80% of *C. major* larvae succeeded moulting to juvenile stage in treatment with larvae fed every day. In the treatments with larvae fed for 1, 2 and 3 days there was total mortality before they reached the megalopal stage. In Experiment 2, zoea larvae showed more resistance when subjected to an initial period of starvation in which larvae starved for 1, 2 and 3 days and had survival rates of 100, 60 and 80%, respectively. But, a delay in the development duration of the zoeal stages was observed. Total mortality was observed for larvae reared in the treatment with entire starvation. The results suggest that zoeal stages of *C. major* are not lecithotrophic.

Key words: *Callichirus major*, callianassidae, feeding, lecithotrophic behaviour, starvation.

INTRODUCTION

The callianassid *Callichirus major* (Say 1818) inhabits the western Atlantic, from North Carolina to Florida, Gulf of Mexico, Venezuela and Brazil (Rio Grande do Norte, Pernambuco and Bahia to Santa Catarina States) (Melo 1999). In the present study, the occurrence of this species in Brazil is also extended to the Pará State, northern-Brazil.

This burrowing shrimp species is found in sandy beaches with density varying from 0 to 20 individuals/m^2 and with highest mean density of 6.07 individuals/m^2 in the northeastern of Brazil (Botter-Carvalho et al. 2002, 2007). This species presents a cryptic behaviour living individually in deep galleries in the intertidal zone, generally below mean water tidal level (Frankenberg et al. 1967, Rodrigues and Shimizu 1997). In northern-Brazil studies on this species are scarce, principally in the estuaries of the bragantine region (northern of Pará State).

The callianassid shrimps plays an important role in soft-sediment intertidal benthic habitats as they promote the bioturbation, which directly influence in the chemical (Aller et al. 1983, Waslenchuk et al. 1983, Ziebis et al. 1996, Bird et al. 2000) and physical properties of the sediments (Suchanek 1983, Suchanek and Colin 1986). These organisms significantly enhance the sediment turnover, organic matter and nutrient cycling (Waslenchuk et al. 1983, Branch and Pringle 1987, Ziebis et al. 1996, Webb and Eyre 2004) and redistribute the metals and contaminants (Suchanek et al. 1986, Abu-Hilal et al. 1988). Furthermore, they cause alteration on the structure of benthic bacterial and faunal communities (Berkenbusch et al. 2000, Dworschak 2001). In addition, the burrows and gallery system of *C. major* are important because they provide a favourable micro-

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habitat for associated fauna (Berkenbusch and Rowden 2003), such as the crab *Austinixa bragantina* sp.nov. recorded in northern-Brazil (Coelho 2005).

The species *C. major* is also an important economic resource due to its large use as live bait by fishermen on the several coastal areas world-wide (Wynberg and Branch 1994, Borzone and Souza 1996, Souza and Borzone 2003, Contessa and Bird 2004, Skilleter et al. 2005).

The early larvae of *C. major* were obtained by Rodrigues (1976) under laboratory conditions in which three zoeal stages were obtained. Later, the complete larval development was accomplished by Strasser and Felder (1999a) in two populations of *C. major* reared in the laboratory: one originated from the Gulf of Mexico and the other from Florida Atlantic. The Florida Atlantic specimens passed through 4 or 5 zoeal stages before they reached the decapodid stage (= megalopa), while specimens of the Gulf population almost always developed through 4 zoeal stages and rarely have 3 or 5 zoeal stages (Strasser and Felder 1999a).

Relatively few studies are available on the biology and ecology of the Callianassidae family, mainly those related to their larval biology and ecology. For larvae of *C. major*, Strasser and Felder (1998, 1999b, c) showed that success of settlement and burrowing activity is reached by availability of specific stimulus from adult habitat in the culture, such as sandy substratum and cues emitted by conspecific adults.

Larviculture is recognized as an important instrument to reveal aspects of crustacean biology. But, for larval culture success the food and the feeding regime of the larvae are considered important. The addition of living food in the culture tanks may be prejudicial to larvae in the case of lecithotrophic species. The use of *Artemia* nauplii may deteriorate water quality, causing damage to the larva health due to the liberation of nitrogened substances (Abrunhosa and Kittaka 1997a). Thus, evidence of complete or facultative lecithotrophy in larvae of decapods is favourable in the culture systems, decreasing mortality and improving larval production.

Few scientific studies have been accomplished on feeding and nutritional aspects for larvae of the Callianassidae family. Thus, little is known regarding lecithotrophy in larvae of callianassids. Nates and McKenney Jr. (2000) studied the ontogenetic changes in biochemical composition of the *Lepidophthalmus louisianensis* larvae during development and showed that larvae of this species present lecithotrophy. Thessalou-Legaki et al. (1999) observed that *Callianassa tyrrhena* subjected to an initial treatment of starvation succeeded in the complete larval development until the megalopal stage due to their yolk reserve. However, when given, the larvae were observed feeding on *Artemia* nauplii. These facts suggested that larvae of *C. tyrrhena* have a facultative lecithotrophic development. However, the reduced number of setae and spine in the mouthparts and an under developed foregut suggests a complete larval lecithotrophy in the ghost shrimp *L. siriboia* (Abrunhosa et al. 2006), despite their becoming a feeding animal after metamorphosis into megalopal stage.

On the other hand, observations of the morphological features of the foregut of zoea larvae and megalopa of the *C. major*, which are specialized with some rigid structures, strongly indicated that this species does not have lecithotrophic behaviour (Melo M.A., unpublished data). In addition, Strasser and Felder (1998) observed that the megalopal stage of *C. major* has weak mandibular structures and they are less adapted for capture and chewing of prey. Furthermore, a reduction in feeding behaviour in the megalopal stage of *C. islagrande* was also observed by these authors. Thus, a specific stage that fed less or that did not have a feeding activity might delay the development by means of extending the intermoulting period. The present study investigated the effect of starvation on larvae of *C. major*, in order to support the observations reported by the above cited authors.

MATERIALS AND METHODS

Ovigerous females of *C. major* were collected at Ajuruteua beach, Bragança City (northeast of Pará State, Brazil) with a hand-operated vacuum suction device ('yabby-pump') (see Hailstone and Stephenson 1961, Manning 1975) and transported to the laboratory in a plastic recipient with seawater (salinity 25) and sandy substratum. In the laboratory, the females were placed individually in aquariums (capacity of 10L) with aeration and sand homogeneously distributed on the bottom.

All females spawned at the same time in the laboratory. After hatching, the larvae of all females were

mixed and they were placed individually in small recipients (polyethylene, 150 mL). Only the active swimming larvae with strong positive phototropism were chosen for cultures in both experiments described further on. Temperature, salinity and pH of the culture water were recorded daily. The larvae were reared in a salinity of 25, temperature 27 to 29.5°C and pH 8.1 to 8.4. The larval development was monitored daily in both experiments with mortality and moults being recorded.

The *C. major* larvae were submitted to two experiments where they were individually reared:

Experiment 1 – Zoea I larvae of *C. major* submitted to an initial period of feeding. Four treatments were performed with 10 larvae/treatment, in which they were fed with newly hatched *Artemia* sp. nauplii (at a density of approximately 2 nauplii/ml) for 1 day only (Treatment 1), 2 days (Treatment 2) 3 days (Treatment 3) and every day (Control treatment), respectively.

Experiment 2 – Zoea I larvae of *C. major* submitted to an initial period of starvation. Four treatments were performed with 10 larvae/treatment, in which they were submitted to an entire period of starvation (i.e. they were not fed – Control treatment) and starved for 1 day only (Treatment 1), 2 days (Treatment 2), 3 days (Treatment 3), respectively.

In Experiment 1, after feeding periods the larvae were reared in the absence of food. On the contrary to this experiment, in Experiment 2, after starvation periods the larvae were reared in the presence of food. In both experiments, the duration of the larval experiment cultivation was about 15 days. This experimental design was performed to study the importance of feeding in each larval stage of *C. major*. By means of this model it was possible to verify the effects of the presence and/or the absence of food in the survival and development duration throughout the larval cycle in *C. major*. It also allowed to show if the larvae are feeding animal, or not, during the early period of larval development. It further demonstrated if and how the presence and/or the absence of food affects the duration of each larval stage. In each experiment we have mixed larvae from different females. This procedure has several advantages including: (a) it avoids culture of larvae originating from females with weakened health and nutritional or stress condition which many times may not be observed during the collection in the field; and (b) it diminishes the effects of intra-specific variability, which naturally occurs in the broods.

Statistical Analyses

All statistical analyses followed standard techniques (Sokal and Rohlf 1995). The data analysis of larval duration of each larval stage (in both feeding and starvation experiments) was calculated in order to verify whether the larval period was affected when the larvae were submitted to different starvation or feeding regimes. For the statistical data analysis of larval duration, the non-parametric *Kruskal-Wallis* (*H-test*) was used after the data was checked for normality and homogeneity of variances (*Shapiro-Wilk's* and *Levene's test*, respectively). *Post hoc* test was performed with *Mann-Whitney U-test* for multiple comparisons among treatments (including control treatment) according to the respective experiments. Significant differences were considered when $P < 0.05$.

RESULTS

Experiment 1: Larvae Submitted to an Initial Period of Feeding

Survival

1. Larvae of *C. major* fed every day (Control treatment): The larvae fed daily obtained moulting success into megalopal stage with a survival rate of about 80% (Fig. 1). The complete zoeal development was about 8 to 10 days (Fig. 1).

2. Larvae of *C. major* fed for 1 day (Treatment 1): In the treatment T2, 50% of the larvae moulted to zoea V, although they were quite weakened and lived until the 15th day of the experiment (Fig. 1). No success of moulting to megalopal stage was observed.

3. Larvae of *C. major* fed for 2 days (Treatment 2): In this treatment, 90% of larvae moulted to zoea IV (Fig. 1). Living larvae were observed until the 13th day of the experiment (Fig. 1). No larvae succeeded in moulting to megalopal stage.

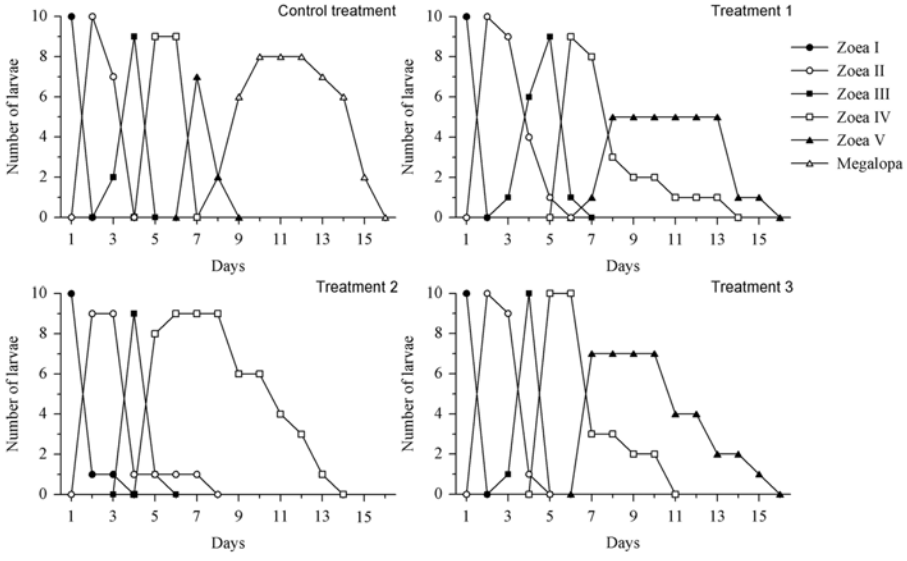

Fig. 1 – Number of surviving larvae of each stage during cultivation of *Callichirus major* submitted to an initial period of feeding. Control treatment: larvae were fed every day; Treatment 1: larvae were fed for 1 day only; Treatment 2: larvae were fed for 2 days; Treatment 3: larvae were fed for 3 days.

4. Larvae of *C. major* fed for 3 days (Treatment 3): In this treatment, 70% of the larvae reached zoea V (Fig. 1). Living larvae were observed until the 15th day of the experiment (Fig. 1). No larvae succeeded in moulting into megalopal stage.

Larval duration

The different feeding periods did not result in significant differences ($P > 0.05$) in the duration of all zoeal and megalopal stages among feeding treatments (Fig. 2). For zoea I stage, the the duration ranged from 1 day recorded in the treatment in which *C. major* larvae were fed for 1, 3 days and every day, to 1.20 ± 0.63 days, observed in the treatment with larvae fed for 2 days (Fig. 2).

For zoea II stage, the durationranged from 1.78 ± 0.44 days, observed in treatment with food offered every day, so 2.30 ± 0.95 days, recorded in the treatment in which food was available for 1 day only (Fig. 2).

For zoea III stage, the duration ranged from 1.10 ± 0.32 days, recorded in the treatment in which food was added for 3 days, to 1.60 ± 0.70 days, observed in the treatment with larvae fed for 1 day only (Fig. 2).

For zoea IV stage, the duration ranged from 1.80 ± 0.45 days, recorded in the treatment in which *C. major* larvae were fed for 1 day only, to 2 days, observed in the treatment with larvae fed for 3 days and every day (Fig. 2).

For zoea V and megalopa stages, the duration was 2.00 ± 0.76 days and 5.00 ± 1.20 days, respectively, in treatments with food offered every day (Fig. 2).

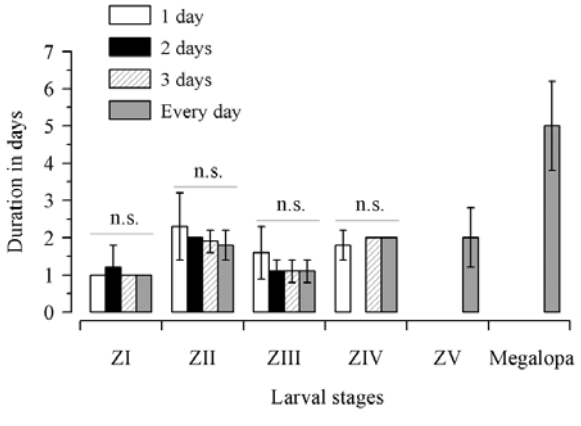

Fig. 2 – Zoeal and megalopal stage duration (in days, average ± standard deviation) of *Callichirus major* submitted to an initial period of feeding. Larvae were fed for 1 day only (Treatment 1); Larvae were fed for 2 days (Treatment 2); Larvae were fed for 3 days (Treatment 3); Larvae were fed every day (Control treatment). n.s. = non significant differences among treatments. ZI–ZV = zoeal larval stages.

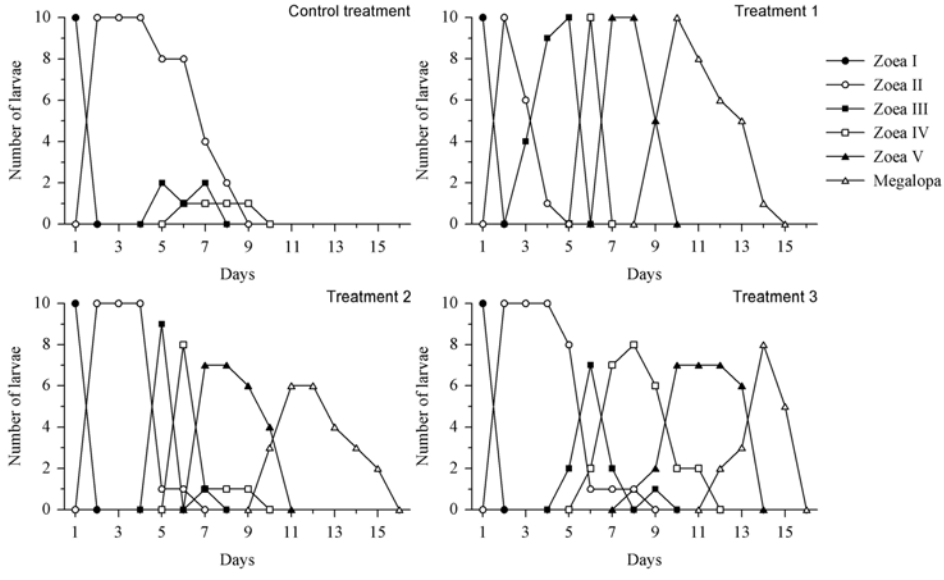

Fig. 3 – Number of surviving larvae of each stage during cultivation of *Callichirus major* submitted to an initial period of starvation. Control treatment: larvae were submitted to entire starvation; Treatment 1: larvae were starved for 1 day only; Treatment 2: larvae were starved for 2 days; Treatment 3: larvae were starved for 3 days.

Experiment 2: Larvae Submitted to an Initial Period of Starvation

Survival

1. Larvae of *C. major* submitted to entire starvation (Control treatment): In this treatment about 10% of the larvae succeeded in moulting to zoea IV, and survived until the 9th day of the experiment (Fig. 3). The total duration of this treatment was 9 days (Fig. 3).
2. Larvae of *C. major* starved for 1 day (Treatment 1): 100% of the larvae reached the megalopal stage (Fig. 3). The complete zoeal development until megalopa was 9 to 10 days (Fig. 3).
3. Larvae of *C. major* starved for 2 days (Treatment 2): 60% of the larvae succeeded in moulting to megalopal stage in a period of 11 days (Fig. 3). The complete zoeal development was about 10 to 11 days (Fig. 3).
4. Larvae of *C. major* starved for 3 days (Treatment 3): 80% of the larvae succeeded in moulting to megalopal stage in a period of 14 days (Fig. 3). The complete zoeal development was about 12 to 14 days (Fig. 3).

Larval duration

The duration of zoea I stage was 1 day in all starvation treatments (Fig. 4). Significant variation only started from zoea II (Fig. 4). For this stage, the duration was significantly distinct among starvation treatments ($H = 23.54$; $d.f. = 3$; $P < 0.05$; Fig. 4). The smallest significant duration ($P < 0.05$) was observed in treatment with *C. major* larvae starved for 1 day (1.70 ± 0.67 days) and the largest significant duration ($P < 0.05$) in treatments in which food was absent for 3 days (4.10 ± 1.10 days) and every day (4.67 ± 1.53 days) (Fig. 4).

As in the previous stage, the duration of zoea III stage, also showed a significant distinction among starvation treatments ($H = 19.26$; $d.f. = 3$; $P < 0.05$; Fig. 4). The smallest duration (1 day) was recorded in treatments in which *C. major* larvae were starved for 2 days and every day (Fig. 4). For this stage the duration was significantly larger ($P < 0.05$) in treatment with *C. major* larvae starved for 1 day (2.30 ± 0.67) (Fig. 4).

For zoea IV stage, the duration was significantly different among starvation treatments ($H = 18.72$; $d.f. = 3$; $P < 0.05$; Fig. 4) with the smallest significant duration ($P < 0.05$) recorded in treatment with *C. major* larvae starved for 1 and 2 days (1 and 1.13 ± 0.35 days, respec-

tively) and the largest significant duration ($P < 0.05$) in treatment without food for 3 days (2.67 ± 1.00 days) (Fig. 4).

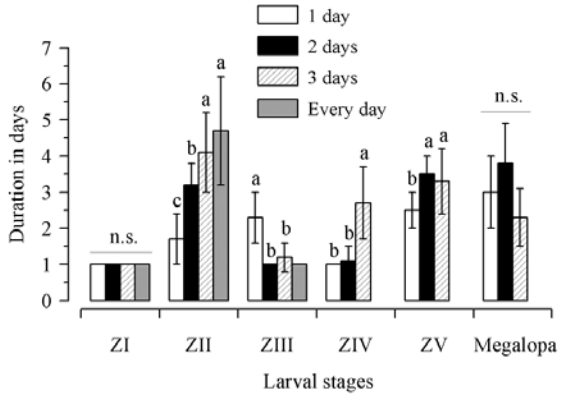

Fig. 4 – Zoeal and megalopal stage duration (in days, average ± standard deviation) of *Callichirus major* submitted to an initial period of starvation. Larvae were starved for 1 day only (Treatment 1); Larvae were starved for 2 days (Treatment 2); Larvae were starved for 3 days (Treatment 3); Larvae were submitted to entire starvation (Control treatment). n.s. = non significant differences among treatments. ZI–ZV = zoeal larval stages.

In the zoea V stage, the duration was also significantly different among starvation treatments ($H = 5.95$; $d.f. = 3$; $P < 0.05$; Fig. 4). The smallest significant duration ($P < 0.05$) was recorded in the treatments with *C. major* larvae starved for 1 day (2.50 ± 0.53 days) and the largest significant duration ($P < 0.05$) in treatments in which larvae stayed for 2 and 3 days without food (3.50 ± 0.55 and 3.33 ± 0.87 days, respectively) (Fig. 4).

On the contrary to zoeal stages (except zoea I) the megalopal stage did not show significant variation among starvation treatments ($H = 5.52$; $d.f. = 3$; $P > 0.05$; Fig. 4). This stage showed the smallest duration (2.33 ± 0.82 days) in treatment in which *C. major* larvae were starved for 3 days and the largest duration (3.80 ± 1.10 days) in treatments with larvae starved for 2 days (Fig. 4).

DISCUSSION

The species *Callichirus major* has a long larval development compared with other species of the Callianassidae family comprising of 5 zoeal and a megalopal stage. The results of the present study corroborates with those obtained by Strasser and Felder (1999a) which showed that population of *C. major* from Atlantic develop through 4 or 5 zoeal and one megalopal (decapodid) stage. In contrast, population of *C. major* from the Gulf of Mexico usually may develop through 4 zoeal stages and rarely via 3 or 5 zoeal stages (Strasser and Felder 1999a). The species *C. islagrande* presents the same pattern in its development passing from 4 to 5 zoeal and a megalopal stages (Strasser and Felder 2000). On the contrary, *C. tyrrhena* has only 2 zoeal and a megalopal stage (Thessalou-Legaki et al. 1999) while *Lepidophthalmus siriboia* has 3 zoeal and a megalopal stage (Abrunhosa et al. 2005). The abbreviated development observed in these species, is probably not only related to the availability or still to the quality of food, but also may be involved with genetic basis or environmental life pattern. This will be investigated in future studies.

Crustaceans with prolonged larval development need an external supply because they hatch with a yolk reserve insufficient to reach the megalopal stage. Studies accomplished with larvae of the decapod crab *Sesarma curacaoense* have demonstrated a short larval cycle (abbreviated development) for this species, which may complete their development without food. But, in such conditions, an extended intermoulting period is observed in the second stage indicating that they have facultative larval lecithotrophy (Anger 1995).

For the Callianassidae family, facultative lecithotrophic behaviour was observed in the species *C. tyrrhena* (Thessalou-Legaki et al. 1999). Studies on biochemical composition of the callianassid *L. louisianensis* have revealed that larvae of this species are adapted for a lecithotrophic life (Nates and McKenney Jr. 2000). Furthermore, it is possible that independence of food or even the combination of feeding activity with yolk reserve enhances the larval energy for a faster development in the plankton. Thus, the species might present a reduced number of larval stages. The larval development of *C. major* is not independent of food and perhaps for this reason their larval cycle is prolonged with many stages. However, quantity and quality of food can be important to accelerate development until post-larval stage. Further studies will verify whether the type of food (quality) affects the larval development duration of this species.

The results of the present study have demonstrated clearly that the nutritional reserve of *C. major* is sufficient

to pass through larval stages without external food, but it is not sufficient to complete its larval development into megalopal stage. For other crustaceans, external food is necessary even in the first larval stage for successful moulting. Some species such as *Homarus americanus* and lobsters of the genus *Jasus* have failed in moulting to the second stage when food is not available or there is insufficient in the culture tank (Abrunhosa and Kittaka 1997a, b). First larvae of mangrove crab *Ucides cordatus* and king crab *Paralithodes camtschaticus* have success in moulting to the second stage when submitted to starvation but high mortality is observed (Abrunhosa et al. 2002).

Many methods are used for studies on feeding behaviour of crustacean larvae observing culture experiments. However, investigations of morphological characteristics of larvae, specifically in the digestive system (mouthparts and foregut), were extensively studied and found important for identification of suitable feeding at different stages of the larvae in order to develop feeding strategies in the mass culture system (Nishida et al. 1990, Abrunhosa and Kittaka 1997a, b, Abrunhosa 1997, Melo M.A., unpublished data, Abrunhosa et al. 2006). Studies on larval foregut and outer feeding appendages of *C. major* have revealed that they are much more morphologically specialized when compared to that of *L. siriboia*. This fact strongly suggests that larvae of *C. major* are adapted to feed on diversified planktonic organisms (Melo M.A., unpublished data). The present study corroborates with this result, in which zoeae of *C. major* are incapable of reaching the megalopal stage if food is not available in the culture.

The results indicate that culture of *C. major* larvae submitted to an initial period of feeding did not show a significant difference in the development period of zoeal stages among treatments. However, when larvae are submitted to an initial period of starvation, the larval development is seriously affected and a prolonged zoeal larval period occurs during treatments. Thus, *C. major* has fastest larval development when food is present, indicating that *C. major* is not lecithotrophic.

The total zoeal duration ranged from 8 (recorded in the control treatment from Experiment 1, where larvae were fed daily) to 14 days (observed in the treatment 3 from Experiment 2, where larvae were starved for 3 days) in those treatments that favoured the complete larval development. These results strengthen the importance of available food. A faster development in the plankton provided by feeding activity relatively enhances the chances of *C. major* in complete successful larval life. Furthermore, a prolonged larval development might result in an increased risk of predation and energy spent in the plankton environment (Morgan 1995). Therefore, food is necessary to enhance the survival to the next stage, besides accelerating the development. In addition, the duration of larval stages could also be affected by abiotic factors such as temperature and salinity. Further studies are needed to test if, besides the availability of diverse types of food, these factors also affect the larval development of *C. major*. These studies would be important for a better understanding of the biologic and ecologic aspects of this species.

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RESUMO

O presente estudo investigou se o callianassid *Callichirus major* apresenta um comportamento lecitotrófico durante o desenvolvimento larval. Dois experimentos foram realizados. No primeiro experimento, larvas foram submetidas a um período inicial de alimentação, enquanto no segundo elas foram submetidas a um período inicial de inanição. No experimento 1, 80% das larvas de *C. major* mudaram com sucesso para o estágio de juvenil no tratamento com larvas alimentadas diariamente. Nos tratamentos com larvas alimentadas por 1, 2 e 3 dias, houve uma mortalidade total antes de alcançarem o estágio de megalopa. No experimento 2, as larvas zoés mostraram mais resistência quando submetidas a um período inicial de inanição. Nos tratamentos nos quais as larvas estiveram em inanição por 1, 2 e 3 dias, as taxas de sobrevivência foram 100%, 60% e 90%, respectivamente. Porém atrasos na duração do desenvolvimento dos estágios de zoés foram observados. Houve mortalidade total para as larvas cultivadas no tratamento com ausência constante de alimento. Os resultados sugerem não existir um comportamento lecitotrófico nas zoés de *C. major*.

Palavras-chave: *Callichirus major*, Callianassidae, alimentação, comportamento lecitotrófico, inanição.

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