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Development and functional morphology of the mouthparts and foregut in larvae and post-larvae of *Macrobrachium jelskii* (Decapoda: Palaemonidae)

Cristina Pantoja Rocha [a], Adelson Silva de Souza [a], Murilo Maciel [b], Cristiana R. Maciel [b, *], Fernando Araújo Abrunhosa [c]

[a] Graduate Program in Envrionmental Biology, Universidade Federal do Para/IECOS, Campus de Bragança, Al. Leandro Ribeiro S/Nº, Aldeia, Bragança, PA 68600-000, Brazil
[b] Aquaculture Laboratory, Universidade Federal do Para /IECOS, Campus de Bragança, Al. Leandro Ribeiro S/Nº, Aldeia, Bragança, PA 68600-000, Brazil
[c] Carcinology Laboratory, Universidade Federal do Para /IECOS, Campus de Bragança, Al. Leandro Ribeiro S/Nº, Aldeia, Bragança, PA 68600-000, Brazil

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ABSTRACT

The morphology of the mouthparts and foregut of the larvae and post-larvae of *Macrobrachium jelskii* was investigated to determine their functional roles in feeding, in order to understand the larval feeding behaviour and the changes that occur during its development. The mouthparts and foregut of the zoea I and II are morphologically similar, rudimentary and non-functional in feeding. Only in the final larval stage, zoea III, do the external mouthparts and foregut become structurally more complex and thus likely to play a potential role in feeding. Two behavioral trials (point of no return, point of reserve saturation) evaluated the resistance to starvation in zoea I, II, and III. The results indicate that they have sufficient nutritional reserves to permit them to complete metamorphosis without feeding. Overall, our results suggest that the zoea I and II of *Macrobrachium jelskii* engage in obligate lecithotrophy and zoea III in facultative lecithotrophy.

1. Introduction

The prawn species of the genus *Macrobrachium* Bate, 1868 present a variety of strategies of inherent ontogenetic development, ranging from abbreviated to partially abbreviated to extended development (Magalhães and Walker, 1988). A large number of decapod crustacean species found in freshwater habitats have abbreviated larval development. This type of development, which is characterized by two or three stages, is frequently associated with the existence of reserves of nutrients, stored in the egg (Anger, 2001), which allow the animal to complete its larval development, from hatching to metamorphosis, without feed on plankton. This phenomenon is known as endotrophy or lecithotrophy (Anger, 2001).

In the Amazon region, seven *Macrobrachium* species are recorded with abbreviated development – *Macrobrachium aracamuni* (Rodríguez, 1982), *Macrobrachium brasiliense* (Heller, 1862), *Macrobrachium ferreirai* Kensley and Walker, 1982, *Macrobrachium inpa* Kensley and Walker, 1982, *Macrobrachium depressimanum* Pereira, 1993, *Macrobrachium jelskii* (Miers, 1877), and *Macrobrachium nattereri* (Heller, 1862) (Anger, 2013).

M. jelskii is restricted to freshwater environments, and is amply distributed in the continental waters of South America, where it is found in the basins of the Orinoco, Amazonas and Paraguay rivers (Coelho and Ramos-Porto, 1985). This species is found typically in marginal and lentic waters, where it is normally associated with the root systems of aquatic plants (Paiva and Barreto, 1960), which provide feeding resources and shelter for the ovigerous females and for the development of the species' larval stages (Montoya, 2003).

The larval development of *M. jelskii* involves three stages. The duration of each larval period may vary according to the its natural habitat, with a period of 7–15 days being recorded in Venezuela (Gamba, 1980, 1984) and 7–8 days in the Brazilian Amazon basin (Magalhães, 2000).

* Corresponding author. Universidade Federal do Para/IECOS, Campus de Bragança, Al. Leandro Ribeiro S/Nº, Aldeia, Bragança, PA 68600-000, Brazil.
E-mail address: macielufpa@gmail.com (C.R. Maciel).

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Field studies have revealed considerable diversity in feeding behavior related to the type of development, whether long or abbreviated. The feeding behavior of the larvae of *Macrobrachium amazonicum* (Heller, 1862) changes drastically during development, and the larvae do not feed during the first stage (Araujo and Valenti, 2007), when they present obligatory lecithotrophy (Queiroz et al., 2011). In *Macrobrachium rosenbergii* (De Man, 1879), the morphology of the foregut suggests facultative lecithotrophy from stage I onwards, and dependence on exogenous nutrition from stage III (Abrunhosa and Melo, 2002).

Data on the feeding behavior of decapod larvae and post-larvae are normally derived from studies based on the investigation of the supply of different types and densities of nutrients, without taking into consideration the inherent characteristics of the morphology of the digestive tract of the species (Melo et al., 2006). A detailed understanding of the development of the foregut and mouthparts provides important insights into the appropriate nutrients for each larval stage, and can contribute to the development of appropriate rearing conditions, and an increase in survival and growth rates during larval development, especially at the transition between a planktonic and a benthonic lifestyle (Nishida et al., 1990; Minagawa and Takashima, 1994; Abrunhosa and Kittaka, 1997a; Abrunhosa, 1997).

Data on the endotrophic potential of a species, together with those on its functional morphology, may enhance the understanding of the feeding behavior of its larvae. In this context, the present study investigated the functionality of the digestive system of the larvae and post-larvae of *M. jelskii* through a morphological description of the foregut and mouthparts, and evaluated its resistance to inanition through laboratory experiments of the point of no return (PNR) and the point of reserve saturation (PRS).

2. Material and methods

Ovigerous female *M. jelskii* were collected using handnets in a headwater of the Chumucui River (01°06′41.82″ S, 46°48′02.40″ W). In the laboratory, these females were disinfected in a solution of formaldehyde (25 mg/L) and transferred to 15-L hatching boxes with constant oxygenation, freshwater (pH 7.8 ± 0.2) and a mean temperature of 28 ± 0.2 °C. Once hatched, groups of larvae were selected and transferred for rearing.

2.1. Functional morphology of the foregut and mouthparts

Larvae were reared in two 2 L containers having biological filters, a typical closed dynamic hatchery system, with a density of 50 larvae/L. The larvae were fed daily with recently-hatched *Artemia* nauplii. Approximately 15–20 larvae at stages I, II, III, and the post-larval stage were fixed in a 10% formaldehyde solution. The specimens were subsequently immersed in a 5% potassium hydroxide solution (KOH) and heated in a stove at 80 °C for approximately 1 h. The specimens were then washed in distilled water, immersed in a 1:1 solution of 70% ethyl alcohol and glycerine, and then stained with methylene blue 1%.

The specimens were dissected using fine needles under an optical microscope. The foreguts and mouthparts were analyzed, illustrated and photographed with inverted optical microscope equipped with Leica DFC295 aided by a camera lucida, and described based on the terminology of Abrunhosa and Kittaka (1997a) and Abrunhosa et al. (2003).

2.2. Tests of nutritional vulnerability

Larvae from different females were placed in individual 200 mL containers kept in a Bain-marie to maintain a constant temperature regulated by thermostats. The water was changed daily. All the tanks were maintained at a constant temperature of 27 ± 0.2 °C, with continuous and homogeneous aeration, pH of 7.8 ± 0.2, total ammonia-N (NH_4^+, NH_3) and nitrite (NO_2) concentrations lower than 1 mg/L, and a 12:12 h light:dark photoperiod. Mortality and moulting in larval stages were also recorded daily. The experiment trials are described below.

2.2.1. Experimental group I – PNR (point of no return)

For the PNR experiment – the maximum period of starvation prior to the first feeding which will allow the instar to moult to the next instar (Abrunhosa and Kittaka, 1997b) – 90 recently-hatched larvae taken from different females were subjected to an initial period of inanition followed by feeding with *Artemia* nauplii.

The larvae were distributed individually in six treatments, each with 15 replicates. The treatments were: larvae in constant starvation (S); starved for two days (S2); three days (S3); four days (S4); five days (S5) and larvae subject to constant feeding (F).

2.2.2. Experimental group II – PRS (point of reserve saturation)

For the PRS experiment – minimum initial feeding time to allow for the accumulation of sufficient reserves to successfully through larval metamorphosis – 90 larvae (from different females) were subjected to an initial period of feeding with *Artemia* nauplii, followed by the interruption of feeding.

The larvae were distributed individually in six treatments, each with 15 replicates. The treatments were: larvae in constant starvation (S); feeding for two days (F2); three days (F3); four days (F4); five days (F5) and larvae with constant feeding (F).

2.3. Statistical analyses

The experiments were conducted in a completely randomized design. For the analysis of the variation in survival rates and the duration of the intermoult period in the larval stages between experimental treatments (PNR and PRS), the nonparametric Kruskal–Wallis test (H) was used following the verification of the normality (Kolmogorov–Smirnov) and homoscedasticity (Levene's test) of the data. The differences were considered significant when $P < 0.05$.

3. Results

3.1. Mouthparts

The larvae of *M. jelskii* pass through 3 zoeal stage before moulting to juvenile. The mouthpart appendages of stage I and III are described in detail. However, the mouthparts of zoea II are quite similar to zoea I without noteworthy changes, therefore, this structure for the zoea II is not described.

3.1.1. Mandibles

Zoea I – Rudimentary, molar and incisive possess unclearly distinguished showing small denticles (Fig. 1A).

Zoea III – Incisive and molar and process Y-shaped, clearly defined with 2 prominent teeth and denticles on incisive process. Molar process with 2 dentiform terminations associated with small irregularities (Fig. 1B).

Juvenile I – Incisive process with 3 teeth well-developed. Molar process with 3 robust and irregular terminal teeth and one subterminal tooth (Fig. 1C).