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Yolk resorption and larval development in the brackish river prawn *Macrobrachium macrobrachion* under laboratory conditions: Perspectives for aquaculture

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Abstract

Macrobrachium macrobrachion is an African native brackish river prawn with a high commercial value. Currently, there is little information on the post-larval production of this species. Two experiments were conducted in the laboratory to develop production techniques for this species. The first experiment analyzed the duration of yolk resorption and the second described the larval stages. Yolk resorption was studied in 240 newly hatched larvae for 24 h based on the reduction in yolk area over time. For larval development stages, six breeding tanks containing 100 L with a density of 50 larvae/L were used. Larvae were fed a combination of *Artemia* nauplii, *Brachionusplicatilis*, and pelleted food (Larviva ProStart, Biomar Efico). The results have shown that the area of yolk reserves varied significantly in the hours after hatching. At 14 h after hatching, each larva resorbed approximately 85% of its yolk reserve, and at 18 h after hatching, each of them still had approximately 6.1%. Twelve larval stages were identified and described in three

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critical stages. *M. macrobrachion* larvae are lecithotrophic and need to start exogenous feeding at 14 h at the earliest and 18 h at the latest after hatching. These results are the first to highlight the potential for mass production of brackish river prawns.

KEYWORDS
critical period, exogenous feeding, *Macrobrachium macrobrachion*, native prawn, point-of-no-return

1 | INTRODUCTION

In terms of crustacean production, *Macrobrachium rosenbergii*, a native of Asia is the first freshwater prawn and the largest farmed worldwide. It has shown rapid growth in this sector, particularly in the last decade (Food and Agriculture Organization [FAO], 2020). *M. amazonicum* is native to South America, is consumed (Agüero-Fernández et al., 2022; De los Santos et al., 2022), and plays a relatively small role in the global production of farmed crustaceans. Despite the diversity of African native freshwater prawn species, comprising approximately 15 species, none of them have been raised in an industrial production system because of the lack of information about the biological and zootechnical aspects of breeding. Most African freshwater prawn species are not suitable for cultivation because of their aggressiveness, small size, and slow growth, which do not allow diversification of prawn species. Nevertheless, there have been a few studies on the reproduction and larval production techniques of the African native prawn *M. vollenhoveni*, conducted in Germany (Willführ-Nast et al., 1993), Cameroon (Makombu et al., 2014), Senegal (Niass & Fall, 2015), and Benin (Gangbé et al., 2016). In addition to *M. vollenhoveni*, which has been used in breeding techniques without success, no other species of freshwater prawns of commercial interest have been explored regarding breeding techniques.

Macrobrachium macrobrachion is a native African brackish river prawn that is widely distributed in lakes, lagoons, and rivers (Willführ-Nast et al., 1993). It is predominantly consumed as a food and condiment in many African countries, especially in rural areas. In Benin, *M. macrobrachion* is exploited and sold in three forms as fresh, smoked, and fried prawns and, therefore, are more profitable and provide an economic benefit (Ollabodé et al., 2021). It contributes 67.2% to the value chains (Houngbo et al., 2015; Ollabodé et al., 2021). According to Koussovi et al. (2019), this species is a suitable candidate for the development of native freshwater prawn aquaculture in Benin to meet demand from local and international consumers. The development of breeding techniques for *M. macrobrachion* is the only option for the sustainable production and conservation of native species. In recent years, *M. macrobrachion* has been studied in Benin for its introduction into aquaculture. These have been multidisciplinary studies on the exploitation (Koussovi et al., 2023), economic performance of value chains (Ollabodé et al., 2021), biology (Koussovi et al., 2019), ecology (Koussovi et al., 2020), and zootechnical parameters related to breeding (Koussovi, Adjahouinou, et al., 2021; Koussovi, Niass, et al., 2021). However, none of these studies have investigated the duration of zoea yolk resorption or the pattern of larval development. According to Jalihal et al. (1993), knowledge of the role of early aquatic species ontogeny and organogenesis is essential for a better understanding of larval dynamics and mechanisms of adaptation to variable environmental conditions. In *Macrobrachium tenellum*, De los Santos et al. (2022) showed that the habitat of origin seems to produce significant differences in enzymatic activity among animals cultivated with different feeds. Therefore, it is important to study the use process of yolk reserves, which are also a source of food for the larvae of *M. macrobrachion*.

The pattern of use of the yolk reserve after hatching varies considerably among prawn species (Evjemo et al., 2001; García-Guerrero, 2010). Some prawn species are prone to massive mortalities at the start of exogenous

feeding during the nonlecithotrophic period (Kailasam et al., 2007; Lal et al., 2014). Studies on the use of yolk reserves in *Macrobrachium* prawn have mainly been conducted at the embryonic level (García et al., 2008; García-Guerrero et al., 2021). There have been relatively few studies on the larval stage, despite the fact that these two phases of ontogenetic development do not occur in similar ways and under the same conditions in *Macrobrachium* species. This suggests that different biological characteristics may have evolved, leading to different biological requirements when using yolk reserves at the larval stage after hatching. According to Anger and Hayd (2009), the yolk reserve observed in *Macrobrachium* larvae is converted into metabolic energy and the chemical precursors needed for the synthesis of new tissues, developmental reconstruction processes, and larval growth. Under these conditions, determining the duration and pattern of use of yolk reserve in *M. macrobrachion* larvae during development becomes a necessity to meet the period of starting exogenous feeding after hatching with precision. This avoids food waste, which is detrimental to larval survival during breeding.

According to De los Santos et al. (2022), studies on the nutrition of wild freshwater prawns are valuable in determining feeding habits and requirements, but they are scarce.

The dietary requirements of the first larval stage may vary inter- and intraspecifically, as well as seasonally or interannually. This depends on energy reserves and essential nutrients stored in the egg yolk, and on larval abilities to synthesize macromolecular nutrients from precursors (Kattner et al., 1994; Staton & Sulkin, 1991). Given the rapid depletion of yolk reserves, the larvae of most marine invertebrates and fish species need to start feeding within a limited time after hatching to avoid starvation. Based on observations of larval herring, Blaxter and Hempel (1963) coined the term "point-of-no-return" (PNR). This critical point within larval development represents a threshold where starved and subsequently fed larvae, which may remain alive for an extended period, cannot recover from previous nutritional stress, and lose their capability to develop further. Paschke et al. (2004) investigated starvation tolerance in *Crangon crangon* prawn larvae and quantified starvation tolerance as median PNR. According to the same authors, the PNR is defined as the time when 50% of the starved larvae have lost the capability to recover after subsequent feeding.

Larvae of the genus *Macrobrachium* develop in distinct stages, exhibiting different morpho-physiological and behavioral characteristics with a change in food requirements during this development (Araujo & Valenti, 2017). Larval development is the most critical phase in decapod crustaceans because high mortality rates are recorded, especially at certain larval stages, whether in a natural or controlled environment (Anger & Hayd, 2009; Yamasaki-Granados et al., 2012). The stages at which larval survival in *Macrobrachium* species is low are called critical stages (Lal et al., 2014). Therefore, it is important to determine the different stages of development for each species of prawn candidate for aquaculture to identify the different critical stages during which special attention must be paid to optimize survival. The objective of the present study was to determine the duration of yolk reserve use and to characterize the different stages of larval development in *M. macrobrachion* to facilitate its production in captivity.

2 | MATERIALS AND METHODS

2.1 | Obtention of *Macrobrachium macrobrachion* larvae

Experiments were conducted with newly hatched larvae (Zoea I) of *M. macrobrachion* from artificial reproduction (Koussovi, Adjahouinou, et al., 2021). Broodstock specimens were collected from the Ouémé River delta (06°39′36″N 02°28′54″E) using traps. The mature specimens selected were immediately placed in two plastic small bags and transported by vehicle between 6 am and 7 am or in the evening after 5 pm to the hatchery of the School of Aquaculture of the National University of Agriculture at Adjohoun (06°41′44″N 02° 28′52″E). The transport lasted for an average of 30 min. For acclimatization, water from the hatchery was gradually added to the transport water to reduce temperature differences. After 3 h of acclimatization, the specimens were transferred to previously prepared storage tanks (2000 L capacity). The water temperature was maintained at 28°C using thermal resistance (RS-399;

12–34°C). PVC pipes 10 cm in diameter and 30 cm in length were placed at the bottom of the tanks to provide shelter for the prawns. The temperature was checked regularly with an oxy-thermometer (AZ8403 dissolved oxygen meter). A male:female sex ratio of 1:2 (male: female) (Koussovi et al., 2019) was selected for loading the broodstock. The prawns were fed once a day with granulated feed (Biomar Efico, France) (53% crude protein and 8% fat).

Females becoming ovigerous were individually placed in small floating cages (18 × 15 × 10 cm; mesh size 2 mm^2) that were put in the storage tanks. Larvae obtained after 12 days of incubation (Koussovi, Adjahouinou, et al., 2021) were used as biological material in the present study.

2.2 | Yolk resorption

To determine the pattern and duration of the use of the yolk reserve in freshly hatched larvae, 80 larvae (Zoea I stage) were isolated and placed in 60-L rearing tanks with three replicates. The rearing salinity was 18 ppt, and the temperature was 28 ± 1°C (Koussovi, Niass, et al., 2021). During the observation period, the mean pH of the water was 8.23 ± 0.15, whereas the mean dissolved oxygen was 7.46 ± 0.36 mg/L. Yolk reserve resorption was monitored based on the reduction in yolk area over time (Sulaeman & R., 2017). Thirty larvae were caught every 30 min and observed under a stereo zoom microscope (Kern, OZM 554). A photograph of each larva was taken using a Sony digital camera (ILCE-5100, 24 megapixels). These images were introduced into the Camera Measure software (Version 1.0) to measure morphometric characteristics (CL: carapace length; d: yolk reserve diameter) (Figure 1a). The measurement accuracy was 0.01 cm. These measurements were used to calculate the yolk reserve area. Given that the yolk surface has an approximately circular form (Figure 1b), the area (Ya) was calculated as $\pi(d/2)^2$.

2.3 | Development stages

2.3.1 | Rearing of larvae

To determine developmental stages, larvae were reared until the completion of metamorphosis. The rearing system consisted of six containers, each with a capacity of 120 L in an air-lift system. Each tank was filled with 100 L disinfected and filtered water at 18 ppt salinity and 28 ± 1°C of temperature (Koussovi, Adjahouinou, et al., 2021). Dissolved oxygen and pH were measured daily using a multiparameter probe (HANNA, HI 99130; Hanna Instruments, Woonsocket, RI, USA) and an oxymeter (DO-5509; Lutron, Taiwan), respectively. For these two parameters, the mean values obtained were 7.65 ± 0.34 mg/L and 7.82 ± 0.51, respectively. Ammonia, nitrite, and nitrate levels were determined using an API kit (5-in-1). The mean values recorded were 0.02 ± 0.00 mg/L, 0.01 ± 0.00 mg/L, and 0.001 ± 0.00 mg/L, respectively. Water aeration was permanent in all the tanks using a mechanical system (RESUN, 1100 W; 1800 L/min; Guangdong, China).

A 60 W fluorescent lamp was suspended above each tank 30 cm from the water surface. The objective was to attract larvae and live prey to concentrate on the column and water surface (Lal et al., 2014). Water quality management was performed by manually renewing 30% of the water each day throughout the breeding period. This renewal was up to 70% if the breeding environment seemed to be too polluted. Excess food, feces, and other waste were siphoned off daily.

2.3.2 | Larvae feeding

Brackish river prawn larvae were fed a combination of rotifers (*Brachionus plicatilis*), *Artemianauplii*, and pelleted food (Larviva ProStart, Biomar Efico, France). The nutritional content of the inert food, according to the manufacturer, is shown in Table 1. The density of live prey in each distribution was 15 individuals/mL for rotifers (Baylon, 2009) and

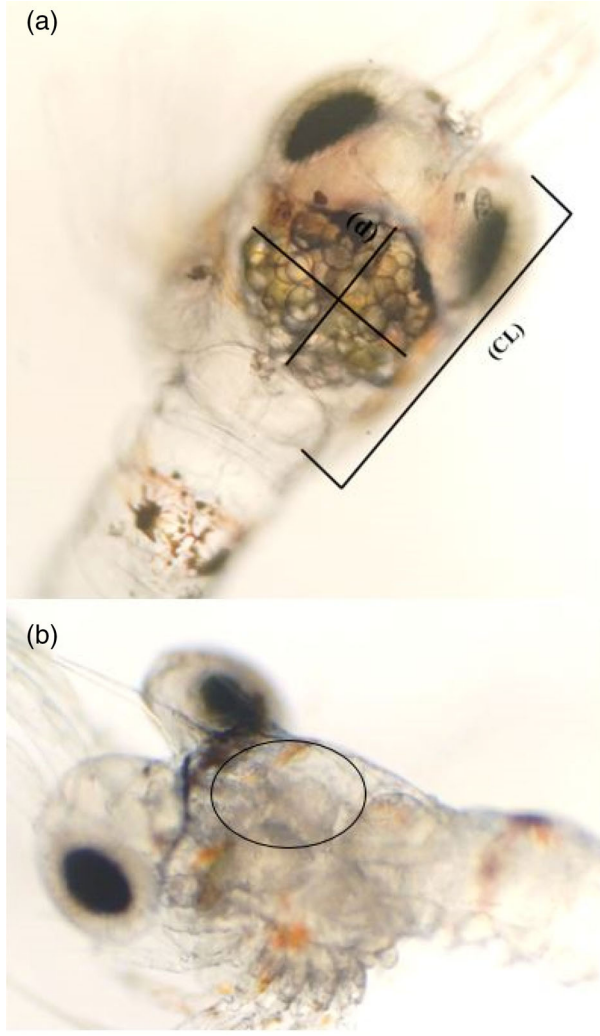

FIGURE 1 Zoeae I of *Macrobrachium macrobrachion*, a, Newly hatched larva showing the morphometric measurements; b, 24-h-old larva (after yolk resorption). CL: carapace length; d: yolk reserve diameter (Scale bar: 5 μm).

5 individuals/mL for *Artemianauplii* (Lal et al., 2014) from Zoea I to Zoea XII. The larvae were fed ad libitum four times a day from 7 am to 7 pm with live prey mixture (Lal et al., 2014; Makombu et al., 2014). For the inert food (300 μm in size), 0.12 g was taken, crushed, and distributed once a day in the afternoon (1 pm) in each tank when the larvae reached the Zoea IV stage. The size of the inert food was selected according to the developmental stage of the larvae in the rearing tanks, using sieves of various mesh sizes.

Production of Artemia *nauplii*

The *Artemia* cyst used was marketed by the company "INVE," which is small and frequently used in studies on prawn larvae (Lal et al., 2014; Makombu et al., 2014; Niass & Fall, 2015). The incubation device consisted of two plexiglass cones of 7 L volume, each according to the hatching procedure indicated by the manufacturer. The number of *Artemia* cysts incubated per day was estimated according to the density of the larvae to be fed. *Artemia* nauplii was harvested after 24 h of incubation. Hatched nauplii were harvested and distributed in rearing tanks.

TABLE 1 Nutritional composition of the inert food according to the manufacturer (Larviva ProStart, Biomar Efico, France).

Ingredients: Fishmeal, krill meal, hydrolyzed fish protein, fish gelatin, lecithin, algae, betaine, yeast extract, DL-methionin probiotics.	
Composition	**Percentage (%)**
Crude proteins	67
Crude lipids	12
Crude ash	11.5
Crude cellulose	0.1
Phosphorus	1.70

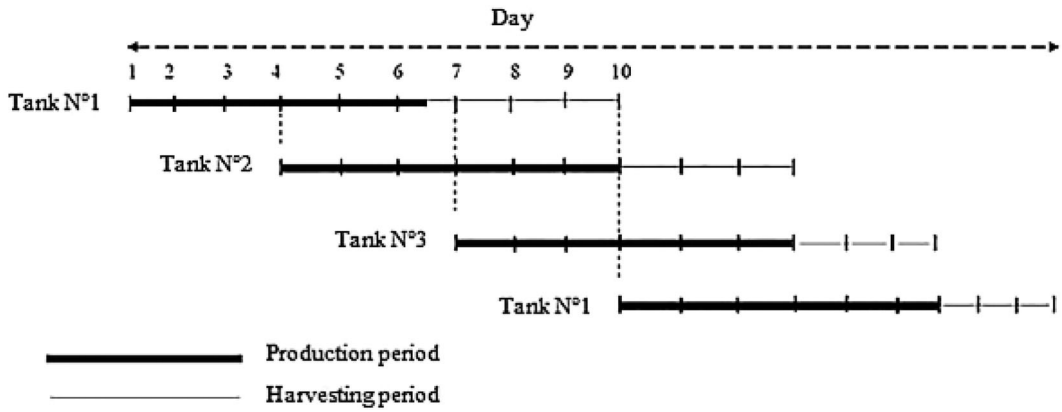

FIGURE 2 Timeline of *Brachionus plicatilis* production.

Production of Brachionus plicatilis

Brachionus plicatilis was isolated from a sample collected from Lake Nokoué (6°25′60″N, 2°270″E). Sampling was performed using a 50-μm mesh plankton net. After harvesting, the samples were placed in a plastic bucket and transported to the laboratory. These samples were examined using a trioccular magnifying glass (Stereo Zoom Microscope, Kern, OZM 554), and the individuals of the rotifer *B. plicatilis* were isolated using a micropipette. Individuals of *B. plicatilis* that had been isolated were introduced into a tank containing 5 L of a phytoplankton culture from the same origin. This culture was subcultured five times at 96 h intervals. Monospecific stock cultures of *B. plicatilis* were then obtained. Three inocula (1 L each) were taken from the stock culture to inoculate three tanks containing 700 L of brackish water (15 ppt). These three tanks were seeded 4 days apart. Fertilization was conducted with a chicken baster (Agadjihouèdé et al., 2010) for rapid multiplication of phytoplankton. After 7 days of production, the density of *B. plicatilis* reached 100–150 individuals/mL. The production from each tank was then harvested from the 7th to the 10th day when a new product was inoculated (Figure 2). This procedure allowed for the continuous production of *B. plicatilis*.

2.3.3 | Development stages monitoring

The development of *M. macrobrachion* larvae was monitored from 8 to 9 am on live larvae. Thirty larvae were sampled from each rearing tank and were used to determine the stages of larval development. Photo-microscopy was conducted using a stereo zoom microscope [Kern, OZM 554 with a Sony digital camera (ILCE-5100, 24 megapixels)]

to determine the characteristics of the larvae at each stage of development. Each developmental stage has been identified by the appearance, development, and complexity of structures such as the rostrum, pereiopods, pleopods, antennae, telson, and uropod. These structures have been used for the morphological description of larvae, as in most *Macrobrachium* species (Ito et al., 2006; Lal et al., 2014; Marco-Herrero et al., 2019; Niass & Fall, 2015) to facilitate the management of larvae in production systems. Larvae were stored in 90% alcohol for larval staging, and the carapace length was determined. The different stages of larval development observed were carefully illustrated with drawings using Adobe Photoshop CS6 and Adobe Illustrator cc2017, from the pictures taken of each stage.

The total length (TL) and carapace length (CL) of the larvae were measured to assess larval growth at each stage of development. For these measurements, larvae were placed in a Petri dish, which was placed on graph paper and screened on a computer using a Micro Capture Digital Microscope (Vetus model ESD-50). AMCAP version 4.9 software was used to capture images that were used to directly measure the total length and the carapace length with the "Camera Measure" software version 1.0.

2.4 | Data treatment and statistical analyses

The survival and growth rates of the larvae were determined. The survival rate was calculated using the following equation:

- Survival (%) = ($\sum$ Final number of larvae × 100)/Initial number of stored larvae

Larval growth was estimated by calculating the Larval Stage Index (LSI), according to Mallasen and Valenti (2006):

- LSI = ($\sum$Si × ni)/*N* with Si = Larval stage, ni = number of larvae observed per larval stage, and *N* = Total number of larvae observed.

The mean yolk area and mean carapace length were compared between hours after hatching and larval rearing time using analysis of variance (ANOVA). A simple linear regression was performed between survival rate and rearing duration to assess the correlation between the two variables. Statistical analyses were performed using Statistica software (version 6.31.100.1190).

3 | RESULTS

3.1 | Yolk resorption

The newly hatched *M. macrobrachion* larvae were transparent with a yolk sac, and the mean carapace length was 0.98 ± 0.1 mm. Lipid droplets of varying sizes formed tightly knit networks (Figure 1a). The use of the yolk reserve varied according to the larvae and was faster at its onset than towards the end of absorption. Yolk area varied significantly between hours after hatching ($p < 0.001$) (Figure 3). Fourteen hours after hatching, each larva resorbed approximately 85% of its yolk. At 18 h after hatching, each still had approximately 6.1% of its yolk reserve. All the larvae completely resorbed their yolk reserves after 24 h (Figure 4). This suggests that larvae of the freshwater prawn *M. macrobrachion* take 24 h to deplete their yolk reserve without any significant increase in carapace length or change in stage ($p > 0.05$).

3.2 | Development stages

3.2.1 | Survival and growth rate

At the end of the study, the survival rate of *M. macrobrachion* larvae was 8%. The rearing duration for newly hatched larvae to metamorphosis into complete prawns was 35 days. High mortality rates were recorded on the third (68.5%), ninth (45.6%), and nineteenth day (21.8%) of rearing. These three periods correspond to Stages II, V, and IX, respectively, and constitute critical periods for larval development in *M. macrobrachion*. Overall, the larval survival rate showed a negative correlation throughout the rearing period, with a coefficient of determination (R^2) of 0.99 (Figure 5).

Growth in *M. macrobrachion* larvae was reflected by an increase in the larval stage index (LSI) value (Figure 5). The larvae showed progressive growth from the first (LSI = 1) to the fifteenth (LSI = 1.49). From Days 15 to

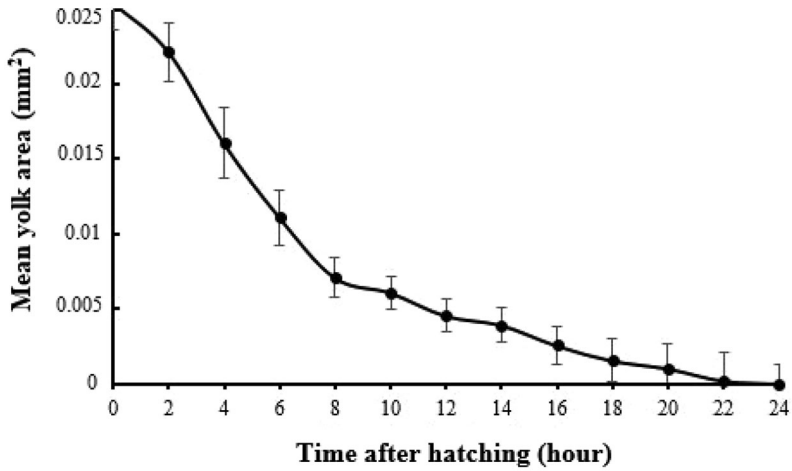

FIGURE 3 Regression of the yolk area in *Macrobrachium macrobrachion* larvae after hatching. Error bars indicate standard deviation, $N = 80$.

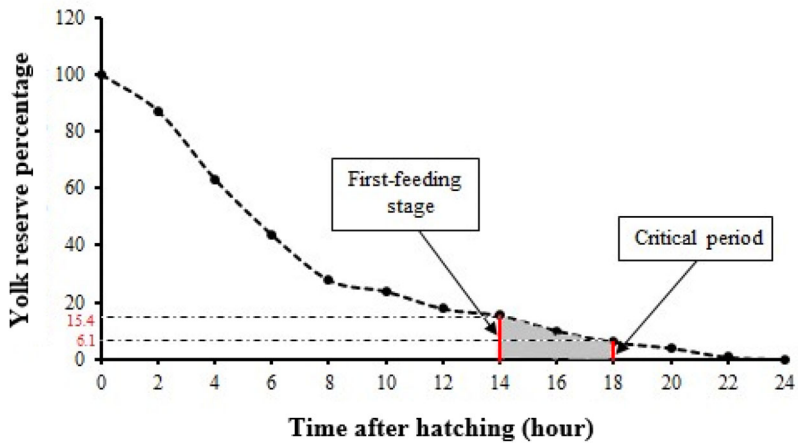

FIGURE 4 Conceptual representation of the "critical period" in *Macrobrachium macrobrachion* larvae.

21, larval growth slowed with a constant value of the larval stage index of 1.52. During this period of slow growth, substantial mortality was observed. From the 24th to the 25th day, exponential growth occurred with the highest LSI of 2.67.

3.2.2 | Molting frequency

Twelve larval stages have been observed in *M. macrobrachion*. The newly hatched larvae were at Zoea I stage and molted 3 days later to reach the Zoea II stage. The second molt took place 5 days later, resulting in stage III Zoea. Ten molts occurred on days 7th, 9th, 11th, 13th, 15th, 19th, 22nd, 26th, 29th, and 35th days after hatching, leading to Zoeae IV, V, VI, VII, VIII, IX, X, XI, and XII (complete metamorphosis). This shows that each molt occurred on average every 2 to 3 days, then every 3 to 5 days until metamorphosis into a full prawn (post-larva), involving an increase in size in the length of the carapace of the larvae (Figure 6).

3.2.3 | Stages of larval development

Twelve (12) stages of larval development were identified in 35 days and described based on morphological descriptions (Marco-Herrero et al., 2019; Niass & Fall, 2015; Yamasaki-Granados et al., 2013).

Zoea-I

The larva has a transparent body with a triangular telson without uropods. The eyes were sessile and located in the anterior cephalothorax. The pereiopods were grouped, folded under the carapace, and were barely visible. The rostrum is short and straight with no rostral spines. The larvae did not have pleopods. Antennas and antennula are present but are poorly developed. Three pairs of maxillipeds were also present (Figure 7-I). At this stage, the larva measures 0.67 ± 0.15 mm in total length.

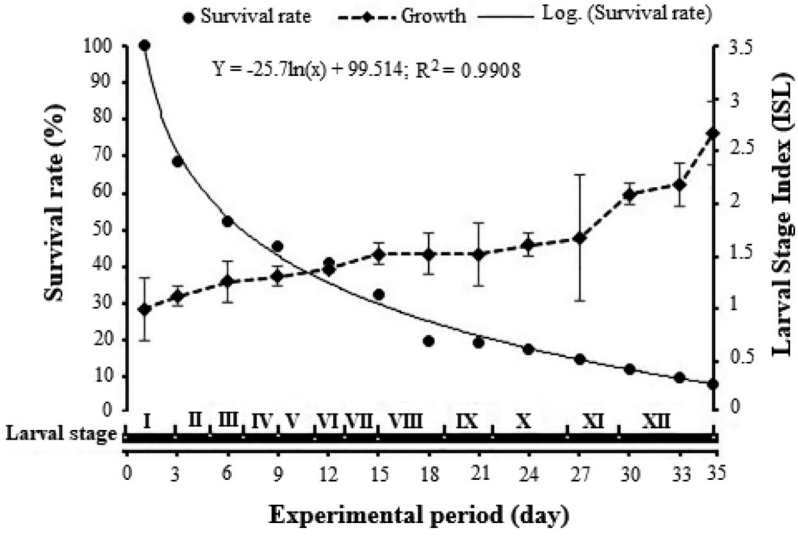

FIGURE 5 Survival (full line) and growth (dash line) of *Macrobrachium macrobrachion* larvae during the 35 days experimental period.

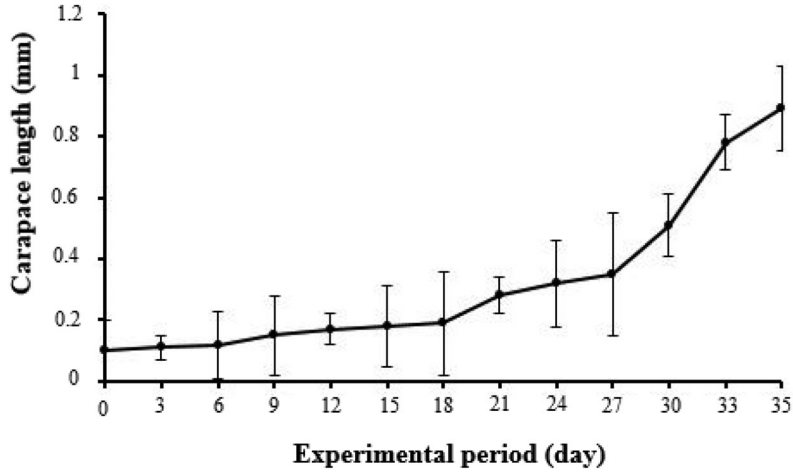

FIGURE 6 Growth (carapace length) in *Macrobrachium macrobrachion* larvae along the experimental period.

Zoea-II

At this stage, the telson had undeveloped uropods. The eyes were larger and the pereiopods were unfolded and more visible than in the previous stage. The rostrum was slightly curved upward from the middle and still had no teeth. Antennal flagella were present but not segmented. An attachment point is formed between the sixth abdominal segment and the telson. There was also a start of cracking at the tail, which initially appeared as a fan with five to seven setae. The first two pairs of pleopods consisted of barely observable buds (Figure 7-II). The larvae average total length is 0.78 ± 0.20 mm.

Zoea-III

The telson was separated from the uropod by a narrower and more concave segment with eight setae on each side. Uropod development was observed, with two clearly visible cracks. The larva had a rostral tooth located immediately behind the eyes. Pereiopods developed and were more visible than in the previous stages. The eyes do not undergo any development at this stage as well as the antennae and antennules. The buds of the first two pairs of pleopods were more visible than those in the previous stage. The flagellum of the antennae split into two at this stage and had 2–3 segments (Figure 7-III). The mean total length of the larvae at this stage was 0.90 ± 0.18 mm.

Zoea-IV

The telson is elongated with the terminal spine. Uropods have exopods and endopods with setae in the form of a fan. The rostrum and eyes were more developed than those in the previous stage. The antennae and antennules had three segments with barely visible setae. Tail cracking is complete with the appearance of small setae. The pereiopods were longer and larger than those in the previous stage (Figure 7-IV). At this stage, the larvae were a total length of 1.25 ± 0.13 mm.

Zoea-V

The telson becomes narrow at the posterior end, becoming triangular from the previous stage, with the uropods having one spine and setae. At this stage, the rostral tooth count decreased from 1 to 2. The antennae and antennules presented more visible and more developed setae than those in the previous stage. The fourth pair of pereiopods was more developed than that in the previous stage (Figure 7-V). The mean total length of the larva was 1.67 ± 0.14 mm.

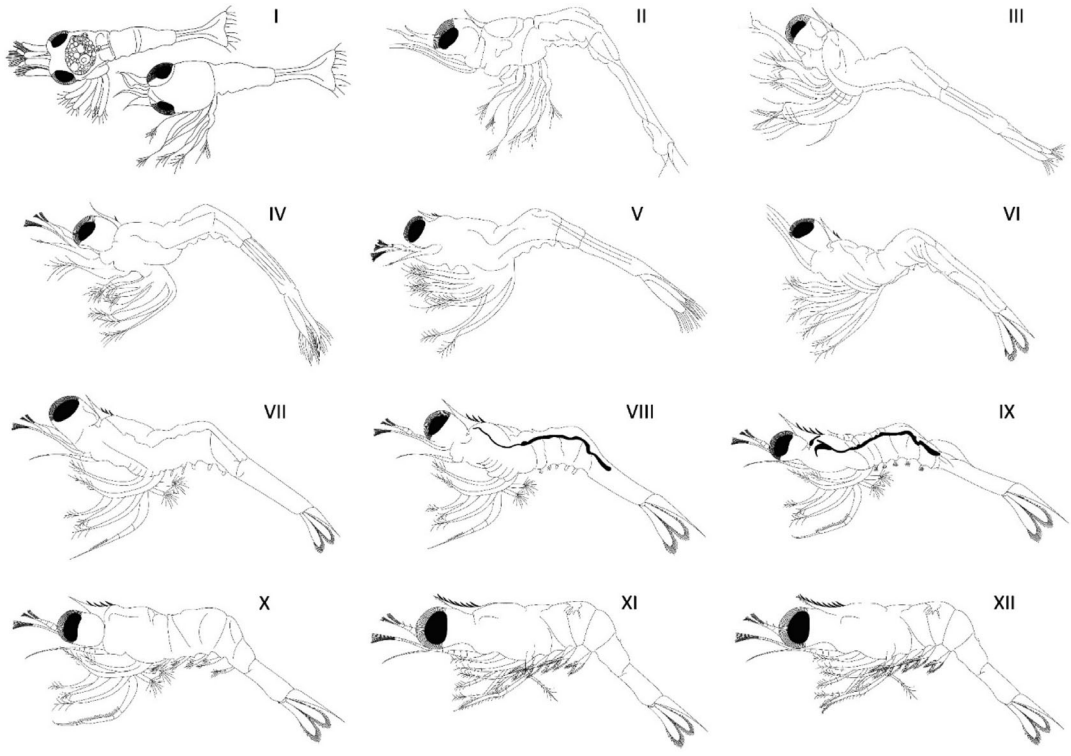

FIGURE 7 Illustration/schematic drawings of the different stages of larval development in *Macrobrachium macrobrachion* (Scale bar: 5 μm).

Zoea-VI

At this stage, the posterior part of the telson is narrower than that in the previous stage, with two pairs of setae. The number of rostral teeth remained the same as that in the previous stage. The antennal peduncle has 2–3 setae with a thorn. The fourth and fifth pereiopods had four and two segments, respectively. The third and fourth pairs of pleopods were present as buds in the abdomen of the larvae (Figure 7-VI). At this stage, the larva measures 2.45 ± 0.22 mm in average total length.

Zoea-VII

The uropods were wider and shorter than those of telson. At this stage, the number of rostral teeth increased from 2 to 3. This stage is marked by the presence of 2–3 setae in the second rostral tooth. The fifth pleopod pair appeared as buds on the abdomen of the larva. Five segments were observed on the antennal flagellum, with one segment on the antennular flagellum (Figure 7-VII). The mean total length of the larva was 2.75 ± 0.35 mm.

Zoea-VIII

The number of rostral teeth was three for some larvae and four for others. The buds of the first, third, and fourth pleopod pairs elongated in most larvae at this stage (Figure 7-VIII). The fifth pleopod pair continued to emerge as a single bud. The second pair of pleopods is elongated and biramous without any seta. The two antennae lengthened and segmented again. At this stage, the larva measures 3.61 ± 0.20 mm in average total length.

Zoea-IX

This stage is marked by five to six rostral teeth for most larvae. All the pleopods were biramous with setae. The antennal and antennular flagella had eight and four segments, respectively. All the pleopods were biramous and had setae (Figure 7-IX). The endopods of the third and fourth pleopods were fully formed, and the buds of the internal appendages began to appear along their internal margins. The mean total length of the larva was 4.25 ± 0.12 mm.

Zoea-X

The number of rostral teeth remained the same as that in the previous stage. The larva presents five pairs of well-developed and biramous pleopods possessing setae that make larval development almost complete. Antenna flagella and antennular flagella carry nine and five segments, respectively. Chelas appeared to form at the ends of the second pair of pereiopods (Figure 7-X). The larva measures at this stage 4.58 ± 0.10 mm an average total length.

Zoea-XI

The number of rostral teeth increased to seven for some larvae and eight for others. Twelve and eight segments were observed on the antennal and antennular flagella, respectively. The internal appendages of the pleopods were completely formed with setae. The chelae of the second pair of pereiopods are larger than those in the previous stage. The basal segment of the fifth pair of pleopods had setae on the rear margin (Figure 7-XI). The mean total length of the larva was 4.92 ± 0.11 mm.

Zoea-XII

The larvae at this stage exhibited the typical morphology of an adult prawn. The number of rostral teeth was eight for some and nine for others. Chelipeds have been extensively developed. Segments of the fifth pair of pleopods had up to nine setae. This stage marks the end of pelagic life and gives way to benthic life (Figure 7-XII). The larva measures 5.18 ± 0.14 mm in average total length.

4 | DISCUSSION

4.1 | Yolk resorption

The results of the present study have shown that *M. macrobrachion* has lecithotrophic larvae with a yolk sac, which is the main source of food during the first hours of larval life. This indicates *M. macrobrachion* larvae do not require exogenous food intake at this stage. Approximately 85% of the yolk reserve was absorbed by the larvae 14 h after hatching, and the entire reserve was absorbed 24 h after hatching. This suggests that the exogenous feeding in the larvae of *M. macrobrachion* needs to start 14 h after hatching at the earliest and 18 h after hatching at the latest to prevent the larvae from having reabsorbed their yolk reserve falling into a critical and irreversible nutritional void (critical period), causing high mortality. This transition period between the depletion of yolk reserves and the switch to an exogenous diet constitutes a critical period in larval life (Rome et al., 2009). High mortality rates are often observed after the first hour of feeding with exogenous food. The supply of exogenous food in quantity and quality of live prey before 18 h after hatching in *M. macrobrachion* larvae, is, therefore, a vital requirement for survival and growth.

The almost complete use of the yolk reserve 18 h after hatching by *M. macrobrachion* larvae could be linked to tissue construction and the establishment of some first organs necessary and useful for the larvae in the first hours of life, but also for the maintenance and proper functioning of these organs. The antennae, pereiopods, pleopods, rostrum, and telson are developed after hatching and used by the larvae. This rapid use of the yolk reserve could also be linked to the energy needs of freshly hatched larvae for locomotion and the development of catching organs. According to Clarke and Gore (1992), the yolk reserve has three potential functions: (1) intervening in the synthesis of new tissues in developing larvae, (2) providing energy for tissue maintenance once they are produced, and (3) providing energy to

freshly hatched larvae before exogenous feeding. These three functions explain the almost total absorption of the yolk reserve during the 18 h after hatching in *M. macrobrachion* larvae. In *M. rosenbergii* larvae, Borisov and Kryakhova (2011) observed that lecithotrophic feeding in Zoea II larvae from 24 h of age is facultative. They noted that Zoea II larvae still have some residual reserves that allow them to survive without external feeding until 96 h of age, which is not the case for *M. macrobrachion*. However, without feeding, these larvae are subject to high mortality and low growth performance. These authors suggested that Zoea II larvae of *M. rosenbergii* need to be fed plankton prey from 24 h of age. However, their study did not report a pattern of yolk resorption in *M. rosenbergii* larvae.

A comparison of the features of *M. macrobrachion* larvae to other species in the literature is currently difficult because studies on the use of yolk reserves in the *Macrobrachium* genus have mostly been conducted at the embryonic level (García et al., 2008; García-Guerrero et al., 2021; Walker et al., 2006). However, these two phases of ontogenetic development do not occur in a similar manner and under the same conditions in the species of *Macrobrachium* genus. The embryonic phase occurs during incubation in freshwater, and the larval phase occurs in brackish water in most freshwater prawn species. This suggests that different biological characteristics may have evolved, leading to different biological requirements when using yolk reserves at the larval stage after hatching.

4.2 | Larval survival

In the present study, the overall survival rate was 8%. Mortalities were recorded from the start to the end of the experiment, with high mortality on the 3rd, 9th, and 19th days after hatching. This high mortality could be from transient nutritional stress or to a diet inappropriate both in quality and quantity because of unsuitable food for feeding *M. macrobrachion* larvae in breeding. According to Yamasaki-Granados et al. (2013), feeding problems are the main cause of poor survival. These authors have suggested that the river prawn *M. americanum* larvae did not have sufficient energy to successfully molt to the next stage because of nonadequate nutrition. Lal et al. (2014) determined the periods during which the survival of larvae of species belonging to *Macrobrachium* genus was greatly affected as critical periods. Consequently, the three periods mentioned (3rd, 9th, and 19th days after hatching) could be qualified as critical periods during the larval development phase of *M. macrobrachion*. These periods correspond to Zoea II, Zoea V, and Zoea IX, respectively, in *M. macrobrachion* larvae. In *M. vollenhoveni*, Makombu et al. (2014) characterized the transition period of larvae from stages V to VI and IX to X as critical periods during larval development because, during these phases, a high mortality rate was recorded. However, the observation of critical periods during the development of the *Macrobrachium* genus is a common phenomenon. During the critical periods, larvae certainly have specific feeding requirements in order to progress to the next stage. This suggests that a high-quality diet should be fed to the larvae during these critical stages and other stages of development to cover the necessary nutritional requirements that can allow them to pass through these different stages in captivity. This was confirmed by Yamasaki-Granados et al. (2013) who suggest that the low survival rate obtained in *M. americanum* larvae is due to the fact that the larvae did not have enough energy to successfully molt. The results of our study do not allow us to confirm that the high mortality rate recorded during the critical developmental phase of *M. macrobrachion* larvae is related to energy requirements or a nutritional defect. Nevertheless, the research of Yamasaki-Granados et al. (2013) and García-Guerrero (2010) showed that feeding is one of the main keys to prawn larval survival, which in fact is defined as the principal index to determine the success or failure of larval cultivation (Daniels et al., 1992). According to Liu et al. (2007), the ontogenetic changes that the larvae of species of the *Macrobrachium* genus undergo throughout their development do not allow them to find foods that meet all the requirements of each larval stage, which causes high mortality (sometimes 100%) in larvae during breeding.

In the natural environment, the larvae of species of the *Macrobrachium* genus have a high mortality rate, and only 0.1% of larvae survive to the post-larval stage after hatching (Bagenal, 1967; Jennings et al., 2006). Although several factors such as predation, water movement keeping some larvae away from food sources, and adequate water quality for larval survival may be the cause of natural death, the survival rate of 8% obtained in the present

study is higher than that reported in the natural environment in the species of *Macrobrachium* genus (< 0.1%) (Bagenal, 1967; Jennings et al., 2006) and that obtained from breeding other species in the same genus. This is the case with *M. lar* where, Lal et al. (2014) reported a survival rate of 0.08%, although this species had undergone several domestication studies (Nandlal, 2010; Sethi et al., 2011; Takano, 1987). This shows that the breeding of *M. macrobrachion* in captivity can be achieved. The survival rate could be improved in the future because this is the first time that this species has experienced captive breeding trials. The objective of the present study was not to determine the appropriate food type and prey density for rearing *M. macrobrachion* larvae. Therefore, determining the appropriate food for the larval phase could further improve the survival of *M. macrobrachion* larvae during production. Survival rates reported in other species of the *Macrobrachium* genus were relatively low during early breeding attempts but improved over time with continued refinement of production techniques (Lal et al., 2014). This is the case, for example, with *M. rosenbergii*, whose early survival rates obtained during metamorphosis for the first time were 16% and 17%, respectively (Ling, 1961). However, the current survival rate of the species is between 60% and 80% in Thailand hatcheries and commercial systems (Valenti et al., 2010).

4.3 | Stages of larval development

Determining the exact number of prawn larval development stages in captivity for mass production is important because it allows effective larval management and more careful monitoring of the critical stages (Anger, 2013; Anger & Hayd, 2009). The number of larval stages depends on the rearing conditions because some molts may not be associated with important morphological changes (Anger, 2006; Anger & Hayd, 2010). Twelve stages were identified in *M. macrobrachion* after 35 days of rearing, which could be linked to favorable rearing conditions. The larvae were reared at a salinity of 18 ppt and 28°C of temperature. According to Koussovi, Niass, et al. (2021), salinity and temperature conditions are the most favorable for the survival and growth of *M. macrobrachion* larvae in breeding, as more than 50% survival at Zoea II has been obtained. Therefore, under these rearing conditions, *M. macrobrachion* larvae could abbreviate or surpass certain morphological changes, shortening the number of stages and duration of larval rearing. According to Jalihal et al. (1993), three types of larval development exist in species of the *Macrobrachium* genus: (1) prolonged or normal development (with 8–20 stages), (2) partially abbreviated development (with two or three stages), and (3) completely abbreviated development (with only one stage). For prawns with prolonged or normal development, the larvae occur at salinities between 10 and 30 ppt and at temperatures varying from 24 to 30°C (Alekhnovich & Kulesh, 2001). This larval development type is characteristic of species that produce many small eggs and hatch small larvae in open water, whose larval development can exceed 3 months with ten or more larval stages (Alekhnovich & Kulesh, 2001). This is also the case for *M. vollenhoveni* (Makombu et al., 2014; Willführ-Nast et al., 1993), *M. lar* (Lal et al., 2014), *M. rosenbergii*, *M. olfersii*, *M. Americanum*, and *M. nilottocum* (Jalihal et al., 1993). Considering the number of stages of development (12 stages) obtained in the present study and the results of Koussovi, Niass, et al. (2021), *M. macrobrachion* can be classified as a freshwater prawn with prolonged or normal development. The number of larval development stages observed and described for species of the *Macrobrachium* genus varies among species. Eleven (Makombu et al., 2014) and 15 (Niass & Fall, 2015) larval development stages have been defined for *M. vollenhoveni*. Nine developmental stages of *M. pantanalense* and nine development stages have been identified and described (Marco-Herrero et al., 2019). Uno and Kwon (1969) and Ling (1967) defined 11 and 13 developmental stages for *M. rosenbergii*, respectively. Therefore, this variation in the number of larval development stages observed in species of the *Macrobrachium* genus and within the same species of prawns could be explained by the different rearing conditions of each species (Williamson, 1982). According to Anger (2001) and Gonzalez-Ortegon and Gimenez (2014), physicochemical parameters, especially salinity and temperature, have a pronounced influence on molt intervals, duration, and the number of larval development stages in the *Macrobrachium* genus. This could be the reason for the differences observed in the number of developmental stages of prawns.

5 | CONCLUSION

This is the first study to examine the rearing of *M. macrobrachion* larvae in captivity. Data obtained from the rearing indicated that *M. macrobrachion* larvae are lecithotrophic and need to begin an exogenous diet based on live foods 14 h at the earliest after hatching (Zoea I) and 18 h at the latest after hatching to optimize their survival rate. Twelve larval stages (Zoea I to Zoea XII) were identified and described in three critical stages (Zoea II, Zoea V, and Zoea IX) of larval development. These results constitute the first database on the duration of yolk resorption and the different developmental stages of larvae in captivity, highlighting the potential for mass production of the species. Nonetheless, further studies are needed to determine a suitable diet for the larvae, which will ensure optimal survival and growth in a large-scale *M. macrobrachion* trading system in Benin and the West African subregion.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Yes, I make my accord for publication the data

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