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Original Article

Reproduction and embryonic development in the African freshwater prawn *Macrobrachium macrobrachion* (Herklots, 1851)

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Abstract: The current study aimed to determine parameters and conditions for successful reproduction of *Macrobrachium macrobrachion* (Herklots, 1851) in a controlled medium and describing its embryonic development. A total of 122 adult specimens were collected from the delta of Ouémé River and stored in polyethylene tanks with 1:2 male-female sex ratio. This broodstock was fed on pelleted food (Biomar Efico) once a day. For the embryogeny monitoring, eggs were sampled each hour through the first two days after spawning and then every 2 hours till hatching. Spawning happened at a mean temperature, dissolved oxygen concentration and pH of 27.80±0.56°C, 5.83±0.45 mg/L and 7.41±0.34, respectively. The eggs incubation meantime was 12±1 days with nine main embryonic development stages. Hatching lasted on the average 21.00±1.94 h and led to larvae with a mean size of 2.30±0.90 mm. Mean fecundity was 13062.4±5489.93 eggs and 14715.2±6108 eggs, respectively for the first and second seasons with a highly significant difference between them. The best hatching rates were obtained with salinities equal to 2 and 4‰. The results constitute the first database for larval breeding of *M. macrobrachion* species.

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Introduction

In Benin, the total production of freshwater (Palaemonidae) and marine (Penaeidae) prawns is estimated at 4048.108 tons in 2018 (DPH, 2019). Freshwater prawns of the Palaemonidae family distributed throughout the tropical and subtropical area (Holthuis, 1980). There are more than 220 species of freshwater prawns in the genus *Macrobrachium* (New, 2002). *Macrobrachium macrobrachion* is an important fishery resource along the west coast of Africa, from Senegal (latitude 20°N) to Angola (latitude 16°S) (Holthuis, 1980). It is widely distributed in waterbodies and streams and, especially in the catchments of Ouémé and Mono rivers (Kouton, 2004; Agadjihouèdé, 2006; Adite et al., 2013). *Macrobrachium macrobrachion* and *M. vollenhoveni* are the most valued and their demand is high for local consumption as well as exportation to European Union and other western Africa's countries (Nigeria, Togo, Ghana and Ivory Coast) (Houngbo et al., 2015; Ollabodé, 2019). Therefore, *M. macrobrachion* is subjected to intensive fishing by artisanal fishermen especially during reproduction periods (Koussovi et al., 2019) to satisfy the increasing demand. For example, in Southern Benin, these species are caught by up to 75 and 83% of fishermen, respectively (Ollabodé, 2019).

In this context, it is very important to develop some breeding techniques of *M. macrobrachion* in a controlled area to satisfy human consumption. That will contribute to the development of aquaculture and consequently to the preservation of the species in its natural environment (Poncin and Phillipart, 2002; Rakaj et al., 2019). On the other hand, the development and mastery of the breeding techniques in African freshwater prawn species such as *M. macrobrachion* are also important since none of them is involved in commercial breeding of

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crustacean species worldwide despite its rapid development with a global production reaching 7.9 million tons in 2016 (FAO, 2018). Moreover, given *M. macrobrachion* is a native species, and its production in aquaculture may provide good yields when grown in their place of origin with no effect on habitat conservation (Yamasaki-Granados et al., 2013).

Successful breeding of prawn species depends on the mastery of the reproduction process and the availability of its juveniles for a continuous supply of production farms (Vargas-Ceballos et al., 2018). The mastery of artificially induced reproduction of *M. macrobrachion* constitutes the first step of its breeding process. In fact, this is a key step for improving reproduction yield and juveniles production of fish and crustacean in aquaculture (Philippart, 1995; Montchowui et al., 2011; Rakaj et al., 2019). But, no basic knowledge exists on how the reproductive performance and embryonic development of *M. macrobrachion* respond to hatchery conditions. It is therefore important to work on these beginning stages of the development cycle of *M. macrobrachion* to understand the different phases of their process. Also, such knowledge will be helpful to make easy the management of its broodstock and embryos during the breeding process. These pieces of knowledge may provide an insight into the process of changes, particularly of salinity, needed during these early stages of development. This is the first time such detail embryonic study with all stages, is done on the species. Thus, the current study aims to (1) determine the reproduction parameters (mating time, spawning and fecundity, incubation time, hatching rate and hatching salinity) to evaluate the reproduction performances of *M. macrobrachion* in experimental conditions and (2) describe its embryonic development.

Materials and Methods

Broodstock management and reproduction conditions*:* The broodstock (both sexes) of *M. macrobrachion* were collected from the Ouémé River delta (6°30' and 10°N, 0°52' and 3°05'E) among specimens caught by artisanal fishermen using fish-trap during two successive reproduction seasons (July 2018 and July 2019). Mean total length of the collected specimens was 8.27±0.41 cm for females and 7.98±0.52 cm for males. The sampled prawns were transported in plastic buckets (15 L) in the evening or early in the morning and stored in the hatchery at the School of Aquaculture of the National University of Agriculture (Porto-Novo, Benin).

Before the trial, the broodstock was acclimated and stored in 1 m^3 polyethylene tanks at a density of 60 individuals in 600 L tap water prior chloride-freed and filtered. A 1:2 male-female sex ratio was applied (Koussovi et al., 2019). Each tank was provided with two bubbles blowers connected to an aerator (Resun, 1100 W; 1800 L/min) for permanent water oxygenation. The refuge (hiding-place) was provided to the prawns using punched PVC pipe (10 cm diameter and 30 cm length) put at the bottom of tanks to favour spawning. Photoperiod was settled to 12h light and 12h darkness by the mean of AKT fluorescent lamps with 40 W power in the hatchery.

Prawns were fed on pelleted food Biomar Efico (53% crude proteins, 8% lipids) once a day. Remaining food, dejections and other wastes were daily removed by siphoning. The water temperature and pH were monitored using a multi-parameter (Hanna, HI 99130), while the dissolved oxygen concentration was assessed with digital oximeter Lutron version DO-5509.

The total length (from rostrum till the end of telson) and the weight of female specimens were taken using a sliding calliper Draper with 0.05 mm precision and an electronic scale (Kern 440-33N) with 0.01 g precision, respectively.

Determination of reproduction parameters in captivity: Reproduction parameters of *M. macrobrachion* in captivity were determined for two reproduction seasons. During the trial, control fishing was carried out every 12 hours. Ovigerous females were separated and put in a small floating cage (18x15x10 cm; 2 mm mesh size) to prevent cannibalism and monitor eggs development. The date and time of the spawning were recorded in each

ovigerous female. Floating cages containing ovigerous females were put in other tank (1 m^3) filled with 600L water with continuous aeration till pre-hatching stage (Fig. 1). Each of these females was then transferred at hatching to a 30L bowl containing 10L of water to collect whole larvae and unhatched eggs. Parameters such as incubation and hatching times, fecundity and hatching rate were determined in each ovigerous female. The eggs incubation time was noticed as the time interval between fertilization and hatching and hatching time was calculated as the time interval between the beginning and the end of this process (Willführ-Nast et al., 1993). Absolute Fecundity (AF) is total number of the laid eggs by the female (Willführ-Nast et al., 1993; Nhan, 2009). Hatching rate (HR) was calculated as following: HR = (number of hatched eggs / non-hatched eggs) × 100 (Nhan, 2009; Vargas-Ceballos et al., 2018).

Besides, to determine the optimal salinity for better eggs hatching in captivity, ovigerous females that eggs are near to hatch were selected and transferred to different bowls containing water with different salinity level. Thus, six salinity concentrations (0, 2, 4, 6, 8 and 10‰) were tested in triplicate as previously documented for the *Macrobrachium* species (Bauer and Delahoussaye, 2008; Anger, 2013) especially in *M. macrobrachion* (Koussovi et al., 2019). These salinity levels were obtained by mixing marine water (prior filtered by 10 µm mesh plankton net) with tap water. Salinity was measured by portable ATC refractometer and readjusted in need case.

Monitoring of the embryonic development: For the description of the different embryonic development stages in *M. macrobrachion*, 21 ovigerous females were monitored in the same above-mentioned conditions. The first sample was the freshly spawned eggs. Then, eggs were hourly sampled during the first two days after spawning and every two hours during the following days till hatching. A cluster of eggs was taken from each female put in a 20 mL plastic recipient containing 5 mL of water. The eggs from the taken cluster were then separated using a sterile pincer, counted and observed under Stereo zoom microscope (Kern, OZM 554) at 45× magnification to

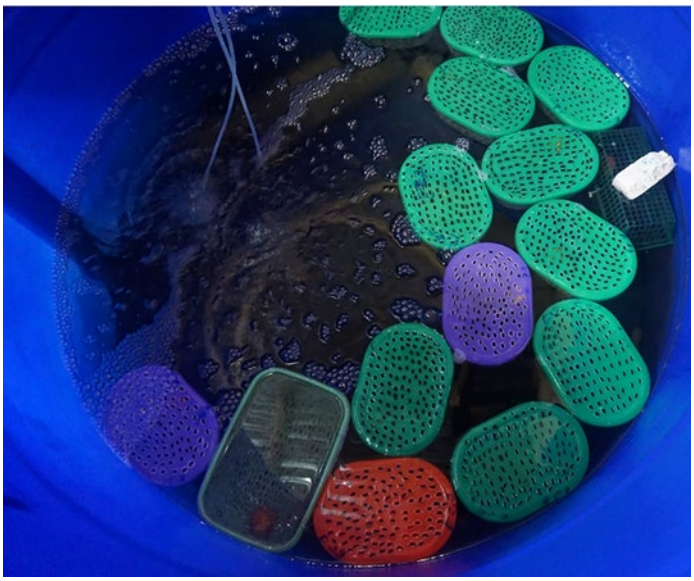

Figure 1. Stocking device of ovigerous females of *Macrobrachium macrobrachion* separated for embryonic development monitoring.

describe their morphological characteristics and identify their development stage. Microscopic observations were made on about 40 eggs for each sampling and some photos were taken with a digital photo device Sony type ILCE-5100 24 megapixels at 45× magnification. Morphological features of embryos were described according to Müller et al. (2003), García-Guerrero and Hendrickx (2009) and Habashy et al. (2012). In addition, the different embryonic development stages were illustrated by drawings realized using Adobe Photoshop CS6 and Adobe Illustrator CC2017. The length (L) and size (H) of the observed eggs were immediately measured to evaluate their volume and follow up the progression from a development stage to another. These measurements were carried out on 30 eggs randomly chosen during each embryonic development stage. For that, eggs were put in petri dish set on millimetre paper and projected on the computer by mean of a "Digital Micro Capture Microscope" Vetus model ESD-50 (Koussovi et al., 2019). Then, the AMCAP version 4.9 software was used for images capture from which the direct measurement of eggs length and height were made by the "Camera Measure" software version 1.0. Eggs volume at each stage was calculated from the formula $V=\pi LH^2/6$ (Odinetz-Collart and Rabelo, 1996; Vadrucci et al., 2007) with L: egg length (long

Figure 2. Eggs colour change in *Macrobrachium macrobrachion* during embryogenic: (a) 7 first days after spawning; (b) from the 8th day after spawning till hatching.

axis) in mm; H: egg height (short axis) in mm; π = 3.14 and V: egg volume in mm^3.

Data analysis: The effect of salinity on hatching and survival rate, eggs volume at each development stage and fecundity were compared among females and seasons using a one-way analysis of variance (ANOVA). The Tukey post-hoc test was used to appreciate differences for each parameter in case of significance (P<0.05) (Zar, 1999; Vargas-Ceballos et al., 2018). Linear regression was carried out to determine the relationship between fecundity and hatching times. Statistical analyses were realized using R software (version 1.1.4456).

Results

Fecundity and eggs characteristics: The mean total length and weight of females collected during the first season were 8.05±0.67 cm and 14.31±3.09 g, respectively while during the second season they were 8.75±0.48 cm and 16.10±1.00 g, respectively. Therefore, the mean length (P<0.001) and weight (P<0.0001) of females from the second survey were quite significantly higher than those of the first survey.

In hatchery conditions (27.8±0.56°C; 5.83±0.45 mg/L and 7.41±0.34 respectively for temperature, dissolved oxygen and pH), a total of 76 females (33 for the first survey and 43 for the second one) of *M. macrobrachion* spawned and incubated eggs in their pleopods till hatching. The mean incubation time was 12±1 days without no significant difference between seasons (P>0.05). Hatching was started at night and lasted on average 21.46±1.94 h for both of seasons with significant variation from a female to another (P<0.05). Mean absolute fecundity was 13062.4±5489.93 eggs and 14715.2±6108 eggs, respectively for the first and second seasons with a highly significant difference between them (P<0.001). Eggs coming from each female underwent synchronic development and hatched a few minutes after the end of the embryonic process.

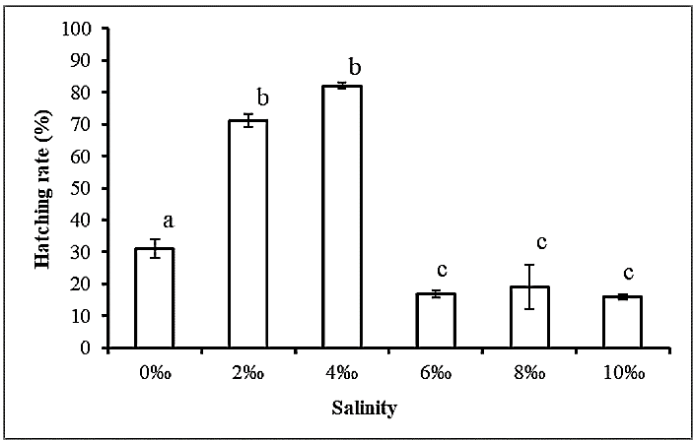

Figure 3. Eggs hatching rate in *Macrobrachium macrobrachion* in relation to salinity levels. Letters show significant differences among treatments (P<0.05).

Concerning the colour of the eggs, two noticeable changes were observed during the incubation period similarly in both of study seasons. During spawning, the fertilized eggs were dark olive coloured and then remained changeless for seven days (Fig. 2a). From the eighth day after spawning till hatching, eggs colour changed to dark grey (Fig. 2b).

Hatching rates: Hatching rate varied significantly (P<0.05) with salinity (Fig. 3). Thus, females incubated in salinity 4‰ presented the highest hatching rate (82%). Nonetheless, this hatching rate did not significantly differ (P>0.05) from that of 2‰ salinity medium (71%). In return, the lowest hatching rates (19, 16.9 and 16%) were obtained in 8, 6 and 10‰ salinity, respectively with no significant difference (P>0.05). The medium with 0‰ salinity led

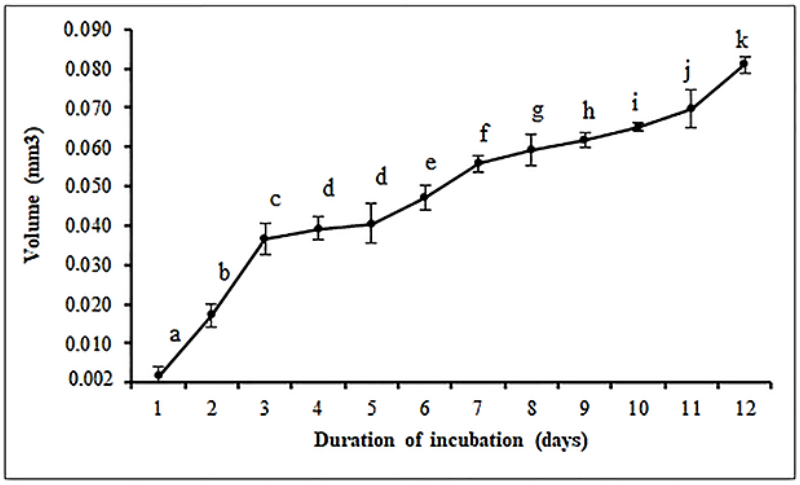

Figure 4. Progression of eggs volume during incubation period in *Macrobrachium macrobrachion*. Letters show significant differences (P<0.05).

to a hatching rate (31%) significantly different from others.

Embryonic development in *M. macrobrachion*: Eggs volume varied significantly from 0.002±0.001 to 0.081±0.031 mm^3 (P<0.05) throughout all the incubation period (Fig. 4). The embryonic development of *M. macrobrachion* is divided into nine different stages characterized by important morphological changes (Figs. 5, 6).

Stage I: Fertilization (00-03 hours): Starting from eggs fertilization, lasted about 3 hours and ended just before the first cell division. Fertilized eggs were almost spherical in shape and include mainly a granulous mass uniform dark olive coloured surrounded with a transparent chorion (Figs. 5a, 6a).

Stage II: Cleavage (03-07 hours): Several cleavage furrows appear in the egg mass, pointing up the formation of the first embryonic cells. Furthermore, a translucid area (germinal disc) set up at one pole of the egg shrinking slightly the egg's inside mass (Figs. 5b, 6b). These changes pointed out the beginning of embryonic development with a slight increase in eggs volume.

Stage III: Blastula (07-27 hours): The translucid area widened progressively without noteworthy morphological changes in the eggs (Figs. 5c, d, 6c, d). Therefore, two parts were noticed inside the eggs namely a light region (translucid area) representing the abdominal part of the developing embryo and a dark olive coloured part corresponding to its cephalic part.

Stage IV: Gastrula (27-126 hours): 27 hours after the fertilization, the light region still increased by contracting the internal mass of the egg mostly in the peripheric part (Figs. 5e, f, 6e, f). This enabled a perfect differentiation of the abdominal region with the appearance of some abdominal segments and the cephalic region taking a «V» form (Figs. 5g, 6g). This stage ended 5 days after fertilization.

Stage V: Nauplius (126-155 hours): A broad black spot appeared in the internal part of the embryo's cephalic region which still decreased because of the abdominal part extension (Figs. 5h, 6h). At 136 hours after fertilization, this black spot, representing a sketch of the embryo's ocular region became more clear (Figs. 5i, 6i). Furthermore, some vitellin reserve vesicles appeared in the peripheric part of the cephalic region.

Stage VI: Post-nauplius with a heartbeat (155-179 hours): The optic region, previously set up, enlarged with a more marked pigmentation (Figs. 5j, 6j). At the abdominal region, the caudal papilla clearly appeared with a rudimentary telson and folded in the direction of the optic region. Furthermore, heartbeats started with 89±18 beats/min on the average. At that time, the remaining content of the egg including mainly the vitellin reserve narrowed because of the development of embryonic structures and took a dark grey colour.

Stage VII: Post-nauplius with eyes individualization (179-216 hours): Eyes individualized from the optic region, enlarged, took an oval form and parted from the cephalic region but still stuck on it at their basis (Figs. 5k, l, 6k, l). The embryo rolled itself up and took a marked «C» form due to the complete making up of

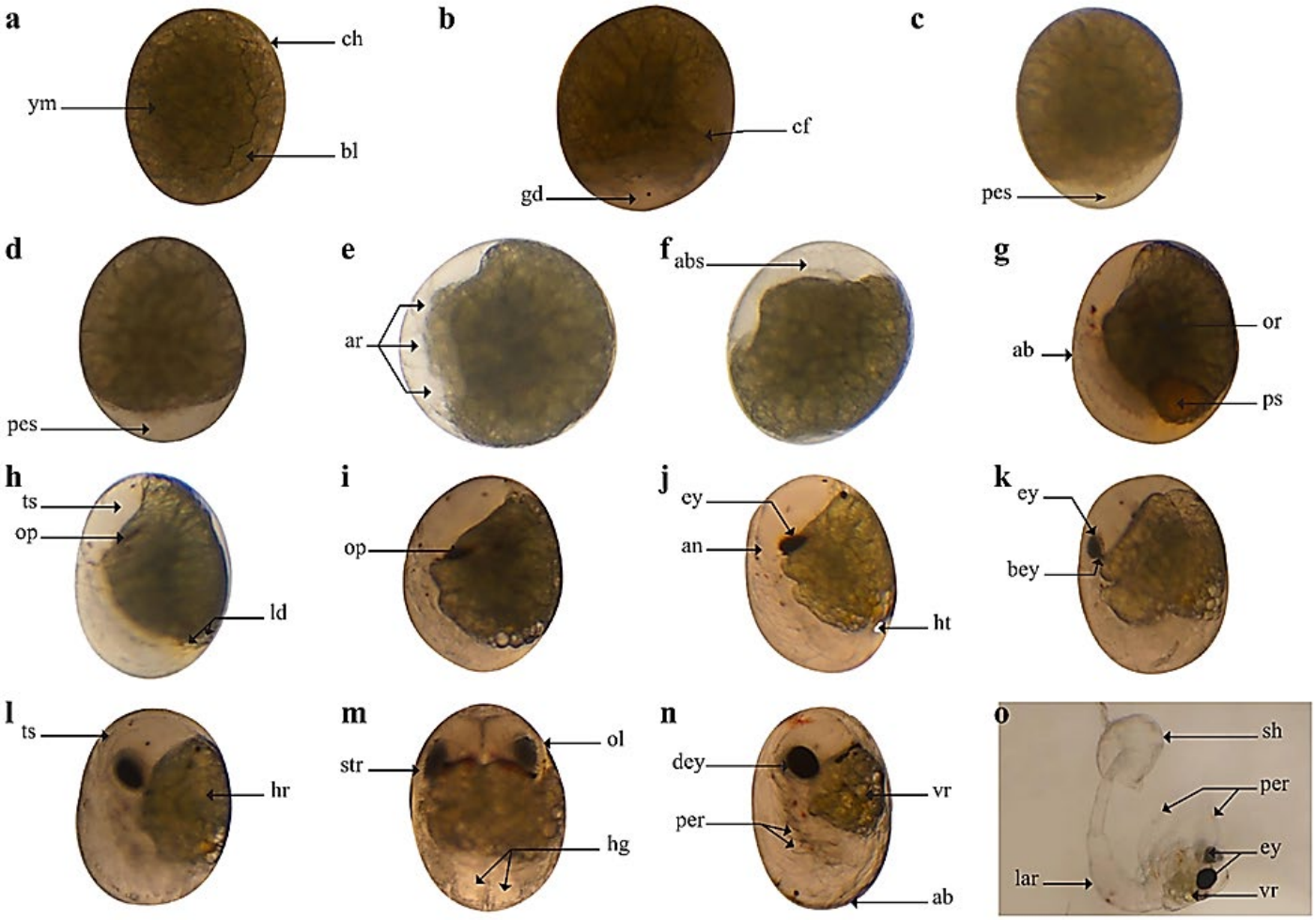

Figure 5. Embryonic development stages in the freshwater prawn *Macrobrachium macrobrachion* (45× magnification). Scale bar = 0.1 mm. a: fertilization; b: cleavage; c: blastula; d: blastula; e: gastrula, making up of blastopores; f: gastrula with increase light region; g: gastrula with distinction of the abdomen; h: nauplius with black spot; i: nauplius with dark black spot; j: post-nauplius with heart beats; k: post-nauplius with eyes pigmentation; l: post-nauplius with oval eyes; m: post-nauplius with eyes condensation; n: pre-hatching; o: freshly hatched larva. ab: abdomen; abs: abdominal segment; an: antennae; ar: abdominal region; bey: base of the eye; bl: blastomeres; cf: cleavage sillon; ch: chorion; dey: developed eye; ey: eye; gd: germinal disc; hg: heart growth; hr: head region; ht: heart; lar: larva; ld: lipid droplet; ol: optical lobe; op: ocular pigment; or: ocular region; per: pereiopods; pes: primitive embryonic structure; ps: perivitellin space; sh: shell; str: streaks; ts: telson; vr: vitellin reserve; ym: yolk mass.

the caudal papilla with a telson quite close to maxillaries. The heart beats increased reaching in average 97±12 beats/min.

Stage VIII: Final post-nauplius with eye condensation (216-264 hours): Eyes diameter increased with an intensification of their colour. Above each eye, some eyelashes appeared (Figs. 5m, 6m). Maxillipeds were well-developed, segmented and overlapped the abdomen. The embryo occupied whole egg space. The vitellin vesicles intensified and were more visible in the cephalic region of the embryo. Besides, heartbeats frequency increased and reached 127±21 beats/min.

Stage IX: Pre-hatching (264-288 hours): The dark grey part located in the cephalothorax (vitellin reserve) was much more reduced (Figs. 5n, 6n). The heart was completely distinct from the vitellin mass and its contractions were more active than during the previous stages. Moreover, some irregular movements such as abdomen contractions were noticed. The uropod (an abdomen part) was clearly segmented with its last segment provided with bristles. The edge of the telson overlapped the rostrum that spread over the head. Embryonic development was completed at this

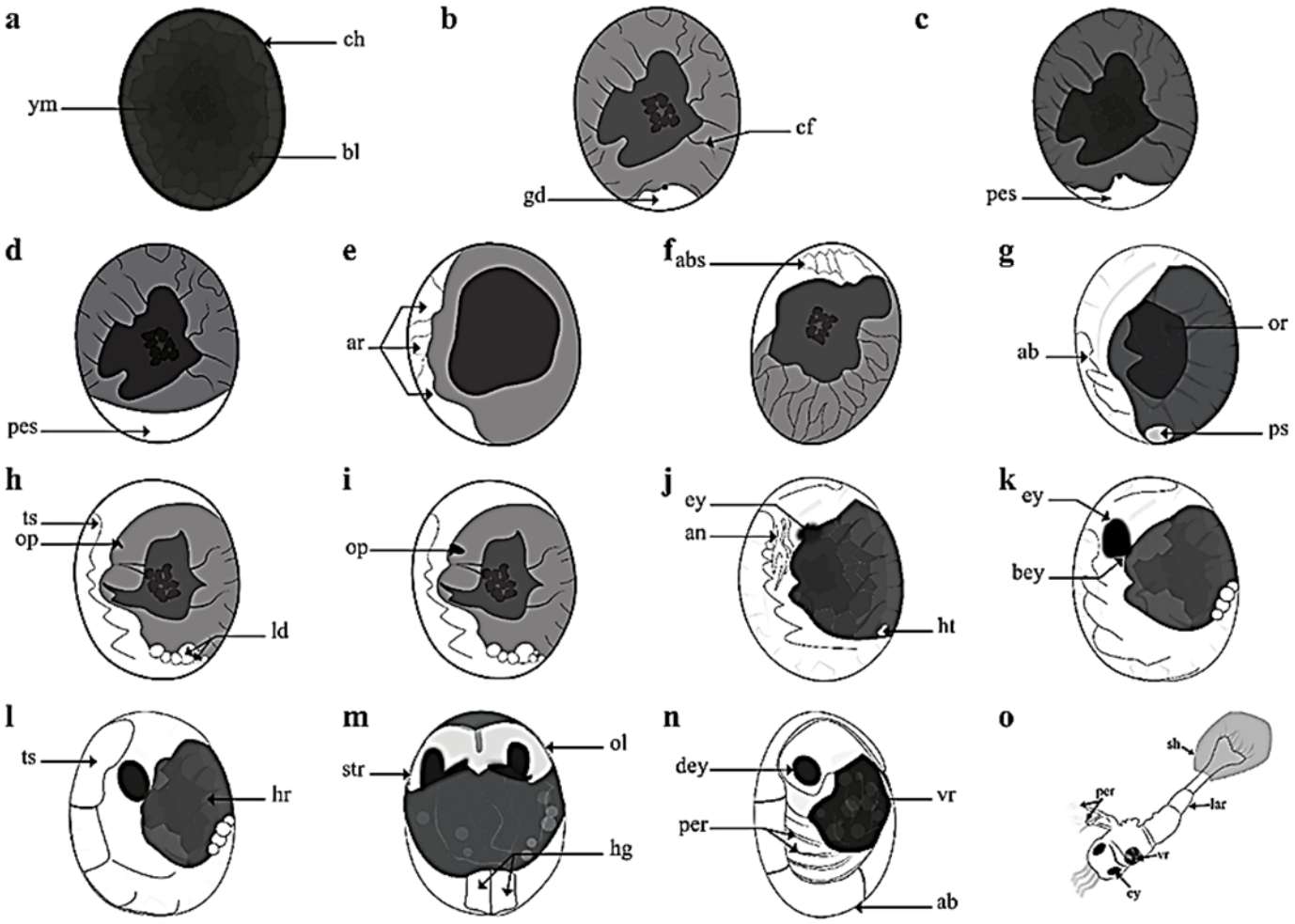

Figure 3. Drawings of the embryonic development stages of *Macrobrachium macrobrachion* (for abbreviations see fig. 5).

stage (12 days after fertilization) leading to the hatching of the egg releasing a new larva (zoe I) (Figs. 5o, 6o).

Discussions

The results of the present study constitute the first data on the reproductive parameters and embryonic development of the freshwater prawn *M. macrobrachion* in captivity. A high fecundity proportional to the size of the female specimen is noticed in *M. macrobrachion.* This fecundity variation can be tied to the age and the reproduction capacity of females (Graziani et al., 1993). However, the fecundity recorded in the females of *M. macrobrachion* was lower than that of most species belonging to *Macrobrachium* genus (Willführ-Nast et al., 1993; Makombu et al., 2014). This is probably due to the small size of *M. macrobrachion* allowing less space in their cephalothoracic cavity to enable the ovocysts growth during ovarian maturation (Koussovi et al., 2019). Besides, the narrowness of the abdomen of *M. macrobrachion's* specimens does not allow the development of a large mass of egg (Koussovi et al., 2019).

The eggs incubation mean time in *M. macrobrachion* (12±1 days at 27.8°C) was shorter than that recorded in other *Macrobrachium* species such as *M. vollenhoveni* (13 to 14 days at 28.15 and 30°C) (Willführ-Nast et al., 1993; Sintondji et al., 2020), *M. rosenbergii* (20 days at 28.5°C) (Habashy et al., 2012), *M. olfersi* (14 days at 26°C) (Müller et al., 2003) and *M. lar* (29 days at 28°C) (Lal, 2012). This is due to the small size of their eggs compared to

those of other *Macrobrachium* species, for instance, *M. lar* (0.072 to 0.133 mm^3) (Lal, 2012), *M. mammillodactylus* (0.044 to 0.099 mm^3) (Cuvin-Aralar, 2014) and *M. vollenhoveni* (0.0455±0.003 to 0.0857±0.002 mm^3) (Sintondji et al., 2020), given the embryonic development duration depends among others on eggs height (Müller et al., 2004). Furthermore, this difference in the eggs incubation time among *Macrobrachium* species can also be due to the temperature of the incubation medium (Habashy et al., 2012; Cuvin-Aralar, 2014).

During the embryonic process, the eggs increased in size leading to their volume increasing as embryos developing. This increasing of eggs volume could be tied to the osmotic absorption of water to ensure cells' mobility (Kobayashi and Matsuura, 1995), the structural organization (Müller et al., 2003) and the biochemical composition of eggs (Cuvin-Aralar, 2014).

As for hatching rates, the best ones were obtained in low-salinity media with 2 and 4‰. These salinities seem to be suitable for embryogeny process in *M. macrobrachion*. This justifies the migration of adult specimens of this species from rivers to estuaries or mouths (Koussovi et al., 2019) as do others *Macrobrachium* species during the reproduction period (Anger, 2013; Bauer, 2013). In return, the lowest hatching rates were noticed in media with pure freshwater (0‰) and at salinities higher than 4‰. This is because these ranges of salinity can stop embryogenic process by causing some physiological damages (Ituarte et al., 2005) leading to their death and/or abortion (Fukuda et al., 2017).

Concerning embryogeny, the results revealed the embryonic development in *M. macrobrachion* includes nine main stages almost based on the same principles as most of *Macrobrachium* species (Müller et al., 2003; Müller et al., 2004; García-Guerrero and Hendrickx, 2009; Habashy et al., 2012; Sintondji et al., 2020). First of all, it is important to notice that eggs of *M. macrobrachion* are filled with yolk which could represent energy source and necessary food for embryo development (Ma et al., 2019). The embryogenesis started with external fertilization eggs (stages I), previously laid and stocked on females' pleopods. Three to twenty-seven hours after fertilization, some furrows started to be established from the outside of eggs. The depression noticed at stage II to III highlighted the differentiation of blastomeres. However, this seemed to represent a holoblastic cleavage mode, in which blastomeres are separated by furrows. But these early cleavage furrows are superficially noticed as in most decapod crustaceans (Anderson, 1973). During the embryonic development of *M. macrobrachion*, the first four embryonic development stages (stage I to IV) leading to gastrula, lasted approximately five days whereas the last five ones (stages V to IX) focusing on the nauplius development and leading to the zoe, lasted up to seven days. This distribution of time is expected because the more complex structures are mostly formed during the stages after gastrulation (Chen et al., 2012; Ma et al., 2019). The development of the nauplius, happening from stage V to stage VIII, was much more focused on the abdominal segments formation and the eyes organization. At stage VI, the egg's content decreased and this can be due to metabolic processes using lipidic and proteinic reserves for the formation of some embryonic structures, including especially the retina differentiation leading to a marked pigmentation of eyes at this stage (Müller et al., 2004; Cuvin-Aralar, 2014). The progressive transformation of the embryo at this level of the embryogeny (stages VI) in *M. macrobrachion* is similar to that happening in most of the decapods (Müller et al., 2000; Müller et al., 2004; Manush et al., 2006). This stage ended by the embryonic heart contraction showing the embryo of *M. macrobrachion* acquired the heart regulation capacity. The heartbeats were more and more frequent during the following stages (VII, VIII and IX) also characterized by an intensification of the motor activity of post-nauplius appendixes as well as a marked development of eyes. Once the embryonic development completed, the egg hatched releasing a zoe similarly to the majority of decapods crustaceans (Yamaguchi, 2001; Pinheiro and Hattori, 2002; Lal, 2012; Sintondji et al., 2020).

Conclusion

In *M. macrobrachion*, the mating, fertilization and embryonic development are happened in freshwater whereas the eggs hatched in low-salinity water. The embryonic development involved nine stages similar to that happening in most of the species belonging to *Macrobrachium* genus with nonetheless some specificities among others eggs colour changes. The salinities for a better hatching rate were 2 and 4‰. The present study reports the results of the first successful reproduction of *M. macrobrachion* in hatchery conditions. These results are therefore useful for further surveys intended to develop techniques for the breeding of *M. macrobrachion* in captivity.

Acknowledgements

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Ethics approval

The research protocol was approved by the Animal Ethics Committee of the School of Aquaculture, National University of Agriculture/Porto-Novo in Benin. Thus, data collection was carried out in accordance with the ethical standards of this institution, and guidelines for the care and use of animals were followed during this study.

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