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Research Article

Red mangrove crab *Ucides occidentalis* (Ortmann, 1987) (Brachyura: Ocypodidae): complete embryonic development under laboratory conditions

John Ramos-Veliz[1], Oreste Gainza Roche[2], Diego Cumbicos Ortega[2] & Mireya Pozo-Cajas[3]
[1]Centro de Aguas y Desarrollo Sustentable, Escuela Superior Politécnica del Litoral, Guayaquil, Ecuador
[2]Instituto Superior Tecnológico El Oro, Machala, Ecuador
[3]Facultad de Ciencias Naturales, Universidad de Guayaquil, Guayaquil, Ecuador
Corresponding author: Oreste Gainza Roche (ogainzar@gmail.com)

ABSTRACT. The red crab *Ucides occidentalis* (locally called "guariche") is widely distributed along Ecuador's coastline and is the most important crustacean fishery exploited by local coastal communities. However, a lack of information on the species' reproductive cycle has hindered conservation and sustainable management initiatives. Here we documented for the first time the complete embryonic development of *U. occidentalis*, based on its morphological traits. Thirteen ovigerous females were collected in the field, maintained in captivity, and fed with leaves and tender mangrove propagules. Egg samples were taken every 12 h and analyzed under the microscope to evaluate embryonic development. *U. occidentalis* eggs had eight different embryonic stages, which maintained their spherical shape during the entire developmental. The eggs were relatively small and uniform in size. The tenuous heart beating of the precursor coincided with the formation of chromatophores in stage V and became more frequent at stage VIII, just before hatching. The incubation period lasted 15 days. Despite the rapid development, the increase in egg size and volume was not uniform during sequential stages.

Keywords: *Ucides occidentalis*; embryonic development; embryonic stages; hatching; mangrove; Ecuador

INTRODUCTION

The red crab *Ucides occidentalis* (Ortmann, 1987) is widely distributed along the coastline of the Pacific coast of the Americas, from around the Espiritu Santo Island, Baja California, Mexico, to the mangrove-dominated coastline of San Pedro Piura, Peru (Alemán & Ordinola 2017). This crab typically inhabits mangrove wetlands by making partially interconnected burrows in the forest soil (García-García 2017) and feeds on senescent and freshly fallen mangrove leaves from the canopy. Depending on the population density and spatial distribution, *U. occidentalis* can remove significant amounts of leaves, thus increasing the recycling of organic matter within the forest (Mora 2015).

U. occidentalis is the most commercialized crab species in Ecuador (Cruz et al. 2003, Alava et al. 2015, Zambrano & Solano 2018), although there are fishing periods (March) when its capture is prohibited from warranting their reproduction. This species can also spawn outside of that period from January to April (rainy season) (Cedeño et al. 2012, Zambrano 2019) when females are not targeted for capture as an additional measure to promote a sustainable harvest.

Despite the economic importance of this crab species for local consumption and commercialization in Ecuador's coastal communities, there is a lack of information about the biological cycle. The current information mainly focuses on the fishery's commercial performance (Solano & Moreno 2009, Moreno & Ruiz 2010, Solano et al. 2010, Zambrano & Solano 2018). The scarcity of life cycle information makes this fishery susceptible to negative impacts, as has been the case of *Ucides cordatus*, which has the same economic relevance in Brazil. Populations of this crab species underwent a 98% decline due to overexploitation, human impacts such as habitat contamination, and lethargic crab disease (Ferreira et al. 2009, Da Silva et al. 2012). As a result, natural *U. cordatus* populations

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have been restocking since the 2000s, but that measure was associated with a high economic cost (Orélis-Ribeiro et al. 2017). This situation should be avoided in the case of *U. occidentalis* due to the potential social and economic costs.

A program of artificial reproduction of *U. occidentalis* for repopulation in natural environments or commercial cultivation may be required shortly because of the impact of human activities in the mangroves of the Ecuadorian coast (Carvajal & Alava 2007). This requirement may face the reality that there is no information about the embryonic or the larval development phases of *U. occidentalis*. Recently, Schuiteman et al. (2019) described the zoea 1 of the species, but no additional information is available to support the species' implementation of induced artificial reproduction.

Crustaceans tend to be sensitive to different factors during embryogenesis (Lee 1995, Spivak et al. 2016), and both the number of stages and the duration of embryonic development are highly variable. *U. occidentalis*, as other crab species, display sexual dimorphism: females have a rounded abdomen with four pairs of pleopods with fine setae, while males have a triangular pleon covering a pair of pleopods modified for reproduction (Zambrano & Meiners 2018). After copulation, females stay in their burrows, covering them with sediment, and the eggs develop attached to their pleopods (Solano & Moreno 2009). The female remains in the shelter until hatching and the eggs are released into the water during tidal flooding. Fertility is estimated to vary between 12,847 and 3,845,792 eggs per female (Cedeño 2013).

Information about the red crab's biological cycle is required to identify possible temporal reproductive patterns and is valuable to improve decision-making in fisheries management (Martelli et al. 2016). A key reproductive process to elucidate is the identification of the different stages that the organism undergoes during its ontogeny, including the appearance of morphological structures during each stage (Moriyasu & Lanteigne 1998). In general, the brachyuran embryonic development has been widely studied for different species (Munehara & Shimazaki 1999, Bas & Spivak 2000, Amaro & Hattori 2003, García-Guerrero & Hendrickx 2004, 2006, Sarker-Moniruzzaman et al. 2009, Soundarapandian & Tamizhazhagan 2009, Fuentes et al. 2010, González-Pisani et al. 2013, Ikhwanuddin et al. 2016, Martelli et al. 2016). The most used classification of embryonic stages in brachyurans and anomurans is proposed by Boolootian et al. (1959). This scheme is based on the relative proportion of yolk compared to the animal pole and the differentiation of certain embryonic structures.

Although there are advances in our understanding of the embryogenesis of *U. occidentalis* by comparing and contrasting developmental stages with the Atlantic congeneric species *U. cordatus* (Coello et al. 2015), despite its economic and ecological importance, there is, however, no information on the ontogeny of *U. occidentalis*. Therefore, given the knowledge gaps in the biology and reproduction of *U. occidentalis*, the objective of this study was to describe its embryonic development and determine the duration of the incubation period under controlled laboratory conditions.

MATERIALS AND METHODS

Specimen collection

The reproduction of *Ucides occidentalis* in Ecuador is seasonal and associated with the rainy season (Zambrano & Meiners 2018, Alemán-Dyer et al. 2019, Zambrano 2019). The present study collected samples after the beginning of the rainy season (February 2020), when females with recently extruded eggs were captured in mangrove forests. The sampling sites were located within the boundaries of mangrove management concessions granted to local communities (Fig. 1). Technicians from the "Instituto Superior Tecnológico El Oro" (ISTO El Oro) and local crab fishers collected 13 *U. occidentalis* females with recently extruded eggs directly from their burrows. All females collected were marked on the carapace for identification and transported back to the ISTO El Oro laboratory in black plastic containers to control luminosity and humidity levels and reduce animal stress.

Laboratory incubation conditions

The crabs collected in the field were placed individually in plastic containers (57.6 cm long, 44 cm wide, 32 cm high; volume: 39.20 L) and then covered with a fiberglass screen (12 mm mesh); a 24 cm long PVC pipe (diameter: 10.2 cm) was placed inside the container to provide a place for the crabs to hide and reduce animal stress. The containers were exposed to good ventilation, spacing, and low luminosity. The crabs were fed daily with green and senescent mangrove leaves and propagules. Water (water level of 12 cm) inside the container was replaced every day (70%) during the incubation period; water was previously filtered, passing through a 5 and 1 μm filtration system and a UV lamp (15 watts and 0.22 A). The salinity was maintained at 16, and the average temperature varied between 26 and 28°C, reflecting field conditions (Ruperti et al. 2015). The settings were those recommended by Rodrigues & Hebling (1989) and Schuiteman et al. (2019).

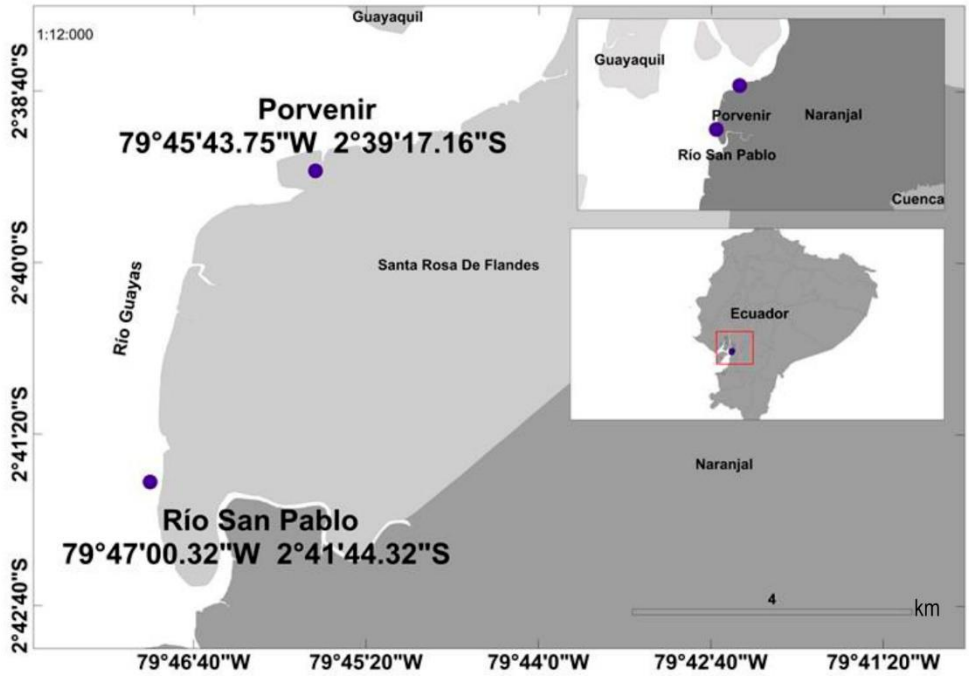

Figure 1. Location of sample sites of *Ucides occidentalis* in the mangrove area concessioned to the associations of crab fishers "Río San Pablo".

Laboratory data collection

Upon arrival at the ISTO El Oro, where the ovigerous females were maintained, each *U. occidentalis* female was marked on the carapace for identification and reared in an individual 39 L plastic container. Egg samples were taken every 12 h using tweezers. Eggs were observed under the microscope to illustrate the developmental stage manually. Additionally, the embryo's heartbeats were counted as soon as they were perceptible by direct observation under the microscope; the heartbeat was considered an indicator of the beginning of stage V and the embryo's physiology development (Samuel & Soundarapandian 2009). The eggs were measured using a digital camera attached to the microscope. The egg volume was estimated using $V = \frac{4}{3}(\pi r^2)$ (Pinheiro & Hattori 2003), where r was the radius and π was the ratio between the circumference and the diameter. Differences in egg size were determined using the average volume at the end of each stage, while the yolk percentage was obtained by the ratio between the yolk size and the egg size multiplied by 100. The biometric variables were compared among the different embryonic stages using the one-way variance (ANOVA) test (Fisher 1992), with a 95% confidence level, followed by a Tukey's post hoc comparisons test (Tukey 1949). Both tests were performed in RStudio (RStudio Team 2020), version 1.4.1106.

RESULTS

Two eggs were hatched from the original thirteen crabs, while the remaining females produced non-viable or undeveloped eggs. Average dimensions (± standard deviation, SD) for each stage are shown (Table 1).

Description of the embryonic development

Illustrations of the embryonic development of *Ucides occidentalis* (stage I-VIII) are shown (Fig. 2).

Stage I (day 1). Eggs are centrolecithal, showing a uniformly bright yellow color indicating yolk components; the shape is spherical without divisions or internal development. The average diameter of the eggs was 215.17 ± 8.69 µ, the volume was 52.20×10^5 μ^3, while the percentage of yolk about the total volume was 100%.

Stage II (days 2-3). The internal division forms small droplets of yolk grouped by similar size; the egg becomes a morula with a dark orange coloration close to brown; no apparent development of structures or tissue. The average diameter of the eggs was 221.17 ± 6.55 µ, the volume was 56.65×10^5 μ^3, while the percentage of yolk with the total volume was 90.0%; the increase in egg size was 6.0%; no heartbeats were observed.

Table 1. Monitoring of different measures during the embryonic development of viable eggs of *Ucides occidentalis*. SD: standard deviation, bpm: beats per minute. Significant differences are indicated by different superscript letters within the same column ($P < 0.05$).

Stage	Diameter Mean ± SD (μ)	Volume ($10^5 \times \mu^3$)	Egg yolk (%)	Size increase (%)	Embryo heartbeat (bpm)
I	215.17 ± 8.69^{a}	52.20^{a}	100.0	-	-
II	221.17 ± 6.55^{ab}	56.65^{ab}	90.0	6.00	-
III	230.61 ± 13.38^{b}	64.70^{b}	80.0	9.44	-
IV	250.17 ± 15.58^{c}	82.73^{c}	72.0	19.56	-
V	260.31 ± 10.52^{d}	92.25^{d}	66.0	10.14	72^{a}
VI	250.45 ± 9.39^{cd}	82.40^{cd}	54.0	-9.86	108^{b}
VII	272.16 ± 5.36^{e}	105.41^{f}	42.3	21.71	190^{c}
VIII	274.67 ± 8.84^{e}	108.55^{f}	30.8	2.51	233^{d}

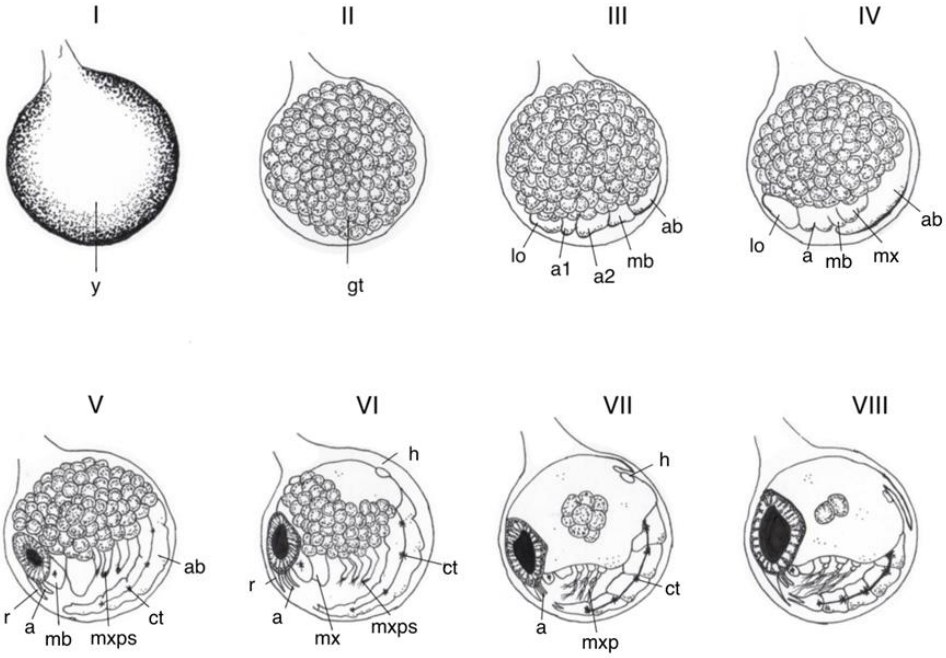

Figure 2. Illustration of the embryonic development of *Ucides occidentalis* under controlled laboratory conditions, showing the development of the main structures: a: antennule-antenna, a1: antennule primordium, a2: antenna primordium, ab: abdomen, ct: chromatophores, gt: yolk droplets, h: heart, lo: optic lobe, mb: mandible, mx: maxillula-maxilla, mxps: maxillipeds 1-2-3, r: rostrum, y: yolk.

Stage III (days 4-5). Yolk droplets become larger and fewer; transparent outbreaks of tissue begin to appear conspicuously in the ventral position of the embryo; appendages develop as evaginations where the following structures are differentiated: antennule - antenna and mandible, between the ocular and thoracic-abdominal process. The average diameter of the eggs was 230.61 ± 13.38 μ, the volume was 64.70×10^5 μ^3, while the percentage of yolk about the total volume was 80.0%; the increase in egg size was 9.4% and no heartbeats were observed (Table 1).

Stage IV (days 6-7). Morphological structures develop and can be differentiated; the ocular region is further developed, acquiring its typical shape but without any pigmentation; start of the formation of the maxillula-maxilla and maxillipeds; yolk drops remain of the same size as in the previous stage but occupy approximately 70% of the egg volume. The average diameter of the eggs was 250.17 ± 15.58 μ, the volume was 82.73×10^5 μ^3, while the increase in egg size was 19.6%; no heartbeats were observed (Table 1).

Stage V (days 8-9). The ocular formation acquires an oval shape with pigmentation in the central part; the abdominal region occupies more space than in the previous period with the beginning of metamerization; cephalic appendages (antennule, antenna, maxilla, and

first maxilliped) are fully developed; buds of maxillipeds 2 and 3 appear. Yolk drops maintain the same size but are reduced in number, allowing better observation of the primordial appendages in the ventral embryo region; small chromatophores can be seen in the abdomen area and certain cephalic appendages; the heartbeat begins. The average diameter of the eggs was 260.31 ± 10.52 μ, the volume was 92.25×10^5 μ^3, while the percentage of yolk about the total volume was 66.0%; the increase in egg size was 10.14%, and 72 bpm (beats per minute) were observed (Table 1).

Stage VI (days 10-12). An increase in the size of the ocular lobes pigmented in black can be appreciated; the number of yolk drops is low, leaving the shell of the embryo uncovered in the dorsal part, where the heartbeats become noticeable; the abdomen presents a complete metamerization with one chromatophore in each segment; cephalic appendages show the development of setae. The average diameter of the eggs was 250.45 ± 9.39 μ, the volume was 82.40×10^5 μ^3, while the percentage of yolk about the total volume was 54.0%; egg size decreased by 9.7%, and 108 bpm were observed (Table 1).

Stage VII (days 13-14). The embryo is occupying all the space; dorsal spines and the rostrum primordium are noticeable; the nervous system beats are continuous, and the yolk drops are well reduced in numbers remaining in the central-dorsal part of the embryo, leaving the embryo carapace uncovered; appendages are segmented, and the abdomen has a small furca. The average diameter of the eggs was 272.16 ± 5.36 μ, the volume was 105.41×10^5 μ^3, while the percentage of yolk about the total volume was 42.3%; the increase in egg size was 21.7%, and 190 bpm were observed (Table 1).

Stage VIII (days 15 to hatching). By day 15, the eyes are completely pigmented, and the embryo carapace is exposed; only a few yolks drops remain. The heart grows in size, and the beats become more frequent and continuous; the abdomen and the furca are more developed with visible chromatophores; the dorsal spine of the carapace reaches the distal part of the first abdominal segment, the rostrum reaches the distal dorsal part of the furca. Hatching of the embryos begins on the 19th day. The average diameter of the eggs was 274.67 ± 8.84 μ, the volume was 108.55×10^5 μ^3 (Table 1), while the percentage of yolk about the total volume was 30.8%; the increase in egg size was 2.5%, and 233 bpm were observed (Table 1).

The average egg diameter, egg volume, and bpm are presented in Table 1. The increase in egg size and volume was not uniform by sequential stages. ANOVA and Tukey's *post-hoc* test indicated that egg volume was significantly different ($P < 0.05$) between sequential grouped stages I-III, IV-VI, and VII-VIII. The number of bpm from stage V to stage VIII was a good indicator of the evolution of physiology, pointing to significant differences ($P < 0.05$) between stages (Table 1).

DISCUSSION

The present study provides the first detailed description of the embryonic development of the mangrove "red crab" *Ucides occidentalis* under laboratory conditions. This information is required to reproduce the species under cultivation conditions and for its preservation in mangrove areas.

The identification of eight stages of embryonic development for *U. occidentalis* is in agreement with similar results obtained for *U. cordatus* (Amaro & Hattori 2003). Other crabs inhabiting mangrove habitats also showed from eight to nine stages, including *Goniopsis pulchra* and *Aratus pisonii* (García-Guerrero & Hendrickx 2004) as well as *Eurypanopeus canalensis* and *Panopeus chilensis* (García-Guerrero & Hendrickx 2006). Given the similarity in the number of stages, the presence of relatively few stages may be typical for brachyuran mangrove crabs; however, non-estuarine crabs can have more than nine periods or stages (Stevens 2006, Zeng 2007, Fuentes et al. 2010, Aguilar et al. 2014, Ikhwanuddin et al. 2016).

One distinct feature during embryonic development was a shift in coloration from an orange tone to a dark brown color. This color change is similar to that reported for *Uca cumulanta*, which belongs to the same family as *U. occidentalis* (Aguilar et al. 2014). This color shift is probably due to the appearance of pigmented structures such as eyes and chromatophores (Sarker-Moniruzzaman et al. 2009) or the absorption of the yolk by the embryo (Soundarapandian & Tamizhazhagan 2009). Independently of the mechanism, this distinct coloration change could be a feasible way to identify the degree of egg development (González-Pisani et al. 2013).

In contrast to Amaro & Hattori (2003), who studied the embryology of *U. cordatus*, which completed development within 19 days, embryonic development in *U. occidentalis* lasted 15 days in our experiments carried out under controlled laboratory conditions. This difference in the duration might be the result of salinity differences during the incubation period. Salinity differences influence embryonic development of brachyurans in estuarine environments (Spivak et al. 2016); crabs have a faster ontogeny at low salinities since the embryos can resist osmotic variations thanks to the presence of an external membrane (Bas & Spivak 2000, Fuentes et al. 2010). However, this membrane has low functionality during the first stages but

becomes more functional as embryos develop (Glas et al. 1997). Unfortunately, in the case of *U. occidentalis*, it is unknown under what conditions this membrane can support different osmotic concentrations.

U. occidentalis eggs were spherical throughout their development, a pattern similar as reported for the crab species *Eurypanopeus canalensis* and *Panopeus chilensis* by García-Guerrero & Hendrickx (2006). In contrast, *U. cordatus* eggs were slightly elliptical in the early stages (Amaro & Hattori 2003) with an average diameter of 390 to 540 µm, while average embryo diameter during the incubation period of *U. occidentalis* varied between 215.17 and 274.67 µm. This morphological difference might represent an adaptation by *U. occidentalis* to increase the egg number per female as the total number depends principally on female size and egg volume (Hines 1982, Munehara & Shimazaki 1999, Amaro & Hattori 2003, Figueiredo et al. 2008).

There is no information on the temperature effect on the duration of the *U. occidentalis* embryonic cycle. The duration of embryonic development can vary between species at different temperatures (Amaro & Hattori 2003). For instance, it can last one year at 5.7 ± 1.6°C for *Erimacrus isenbeckii* (Munehara & Shimazaki 1999) or only 19 days at 27 ± 1.0°C in the case of *U. cordatus* (Amaro & Hattori 2003). Although we were able to obtain some information at incubation temperatures ranging from 26-28°C, further experiments under a wider range of temperatures, especially within the seasonal temperature range observed in the red crab natural habitats along Ecuador's coastal zone, are needed to determine the influence of this variable on embryonic development of *U. occidentalis*.

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