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Fecundity and reproductive patterns of the fiddler crab *Uca maracoani* Latreille 1802-1803 in an Amazonian estuary in northern Brazil

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ABSTRACT

In this study, aspects of the reproductive biology of a *Uca maracoani* population from northern Brazil were examined. Ovigerous females monthly captured from December 2013 to November 2015 were measured and dissected to count, collect morphometric data, and classify the eggs. Ovigerous females were encountered throughout the two-year period but were absent during the months with the highest rainfall and lowest salinity, which indicates a seasonal–continuous reproductive pattern. The fecundity varied from of 12,233 to 85,000 eggs per female, and mean was 36,840 ± 3,361 eggs. The egg size increased progressively and significantly over the course of embryonic development. We found a direct relationship between the size of the females and their fecundity, and a clear trend was seen in which the larger females produced more eggs with larger sizes, which increased less in size during embryonic development. The presence of early- and late-stage eggs together in the same ovigerous mass in a considerable number of the ovigerous females suggests multiple spawning. The fecundity of *U. maracoani* is greater than that of other Atlantic fiddler crab species, and its reproductive strategy ensures its survival in the estuaries of the Amazon coast, which are subject to considerable fluctuations in salinity.

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Mangrove; Ocypodidae; reproductive biology; tropical region

Introduction

Brachyuran crabs are one of the most important invertebrate groups found in subtropical and tropical mangrove forests, in terms of the number of species, and their density and biomass (Colpo et al. 2011). In the mangroves of the Amazon coast, fiddler crabs (Brachyura: Ocypodidae) typically occur at very high densities in the intertidal zone of muddy–sandy sediments, where they form an important link in the transfer of energy to both marine and terrestrial habitats, given that they are sediment feeders and are preyed on by many other animals, such as crustaceans, birds, fish, and mammals (Wolff et al. 2000; Koch and Wolff 2002; Koch et al. 2005). Fiddler crabs are also major ecosystem engineers due to their capacity to excavate burrows, which modify the characteristics of the substrate by altering intrinsic biogeochemical processes (Natálio et al. 2017).

Reproduction is the principal mechanism of species continuity and the regulation of population size (Hines 1982). In brachyuran crabs, reproductive patterns result from a complex interaction between environmental factors and biological processes, which includes selective pressures and both inter- and intra-specific variation (Hartnoll and Gould 1988; Mclay and Becker 2015). Fecundity is linked directly to the life history of the species, and permits the compilation of estimates of the reproductive potential of a given species or population and the size of future stocks (Hartnoll and Gould 1988). The understanding of the breeding and spawning patterns of the dominant macrofaunal species is, in turn, essential for the definition of their reproductive biology and community stability (Emmerson 1994).

Numerous methods can be used to estimate crustacean fecundity, which is determined essentially by the number of eggs produced per female during each reproductive cycle (Hartnoll and Gould 1988; Kuris 1990). However, this type of analysis should include not only estimates of the number of eggs, but also of their size, incubation patterns, and seasonal fluctuations in egg production (Del Castillo et al. 2015). Egg size is considered to be an excellent indicator of the investment of energy in embryonic development, and provides important insights into reproductive strategies (Torati and Mantelatto 2008). The fecundity of fiddler crabs is influenced by the age, width, and weight of the female, as well as the mating system and incubation site of the species, together with environmental conditions

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(Christy and Salmon 1984; Salmon and Zucker 1988; Somers 1990). Body size at the onset of maturity and the fecundity of crabs of the family Ocypodidae from temperate and tropical regions may vary considerably due to differences in environmental parameters, such as temperature and the availability of food (Thurman 1985; Bezerra and Matthews-Cascon 2007).

The Brazilian fiddler crab, *Uca maracoani* Latreille 1802–1803, is endemic to the tropical Atlantic coast of South America, ranging from Trinidad and Venezuela to southern Brazil (Wieman et al. 2014). The species occurs continuously along the coast of Brazil, from Amapá (2°N, 38°W) to Paraná (25°S, 48°W). Although a number of studies have focused on the population structure of *U. maracoani* (Koch et al. 2005; Hirose and Negreiros-Fransozo 2007, 2008; Di Benedetto and Masunari 2009; Silva et al. 2016; Azevedo et al. 2017), no published data are available on the fecundity of this species.

The present study investigated aspects of the reproductive biology of an *U. maracoani* population from northern Brazil, including its fecundity, egg size in the embryonic development phases, and the reproductive period. This is the first study to estimate fecundity for *U. maracoani* and results was compared with that of other species of fiddler crab, considering environmental conditions and specific life-history traits.

Materials and methods

Study area

The sampling site was located in an area of mangrove (00° 55′6.37″ S, 047°05′9.8″ W) in the estuary of the Morcego River (Japerica Bay) (Figure 1a), in the municipality of Primavera, northeastern Pará (Brazil). This area is in the upper portion of the estuary, which is a highly fluvial environment.

The study region is dominated by semidiurnal macrotides with an amplitude of approximately 4 m and has a humid tropical climate with a mean annual temperature of 25.5–26.7°C (Souza Filho 2005). Precipitation varies considerably over the course of the year, with a well-marked rainy season extending from January to July, when 90% of the year's precipitation is recorded (Souza Filho et al. 2009). The dry season extends from September to November, with negligible rainfall, which results in an excess of evapotranspiration over precipitation (Souza Filho 2005).

Sample collection and laboratory procedures

Female *U. maracoani* were collected monthly at low tide from a low-lying unvegetated intertidal area (~100 m^2) (Figure 1b) of the Morcego River Estuary between December 2013 and November 2015. Each month, sampling occurred in two 25 m ^{2} areas (equidistant ~10 m) (Figure 1c) in which the crabs were captured manually by two people for 20 min from both the surface of the substrate and burrows (adapted from Mantelato et al. 2005). The ovigerous specimens were preserved individually in 70% ethanol, bagged, and then stored. Samples of surface water were collected during the ebb tide in each sampling occasion to determine salinity levels using a refractometer. Precipitation data were obtained from the local meteorological station in Primavera and were also provided by the Brazilian National Meteorological Institute (INMET).

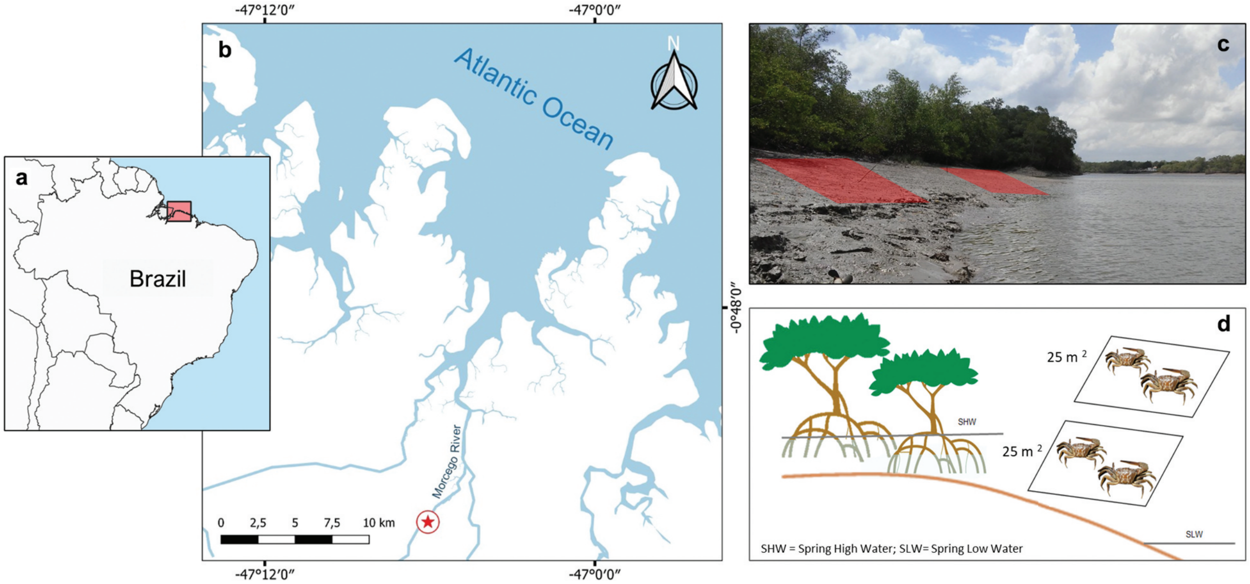

Figure 1. (a-b) Maps of location of northeast coast of Pará state (Brazil) and Morcego River Estuary; and (b-c) figures showing the aspect and layout of sampling areas of *Uca maracoani* crabs.

In the laboratory, the carapace width (CW) of each female was measured, and the values were grouped in 2-mm classes. The pleopods were carefully removed from these females and placed in Petri dishes filled with distilled water after which the eggs were detached by gradually adding a solution of sodium hypochlorite. Once egg-free, the pleopods were separated by gentle stirring in a beaker filled with 100 ml of distilled water. Four 1.5 ml subsamples were then taken using a pipette, and under a dissecting microscope, the eggs were counted and divided into four embryonic developmental stages: I – uniformly distributed yolk, early embryos with no visible blastoderm; II – distinct blastoderm with yolk partially consumed, but embryo still eyeless; III – some yolk remaining, embryo with eyes but no discernible abdominal somites; and IV – embryos near hatching with little or no yolk, large eyes, and the abdomen free from the cephalothorax. This classification was based on the developmental stages described by Yamaguchi (2001a) for *Austruca lactea* (De Haan, 1835), which have been simplified to avoiding the transitional and undefined stages. The total number of eggs in the ovigerous mass was extrapolated from the value obtained for the subsamples (Litulo 2005). A sample of 40 eggs was separated randomly from each female, and the diameter of each egg was measured under a microscope equipped with a calibrated ocular micrometre. To estimate fecundity, 33 ovigerous females carrying only early-stage (I and II) eggs were selected for egg counting.

Data analysis

Breeding intensity was determined by the proportion of adult females found to be ovigerous. The relationship between fecundity and carapace width was evaluated using a linear regression of the log-transformed data. The 'a' and 'b' parameters were estimated by the Gauss-Newton method of least-squares progressive iteration. The significance of the regressions was determined by the value of *F*. The variation in the diameter of the eggs was evaluated using an Analysis of Covariance (ANCOVA), with the carapace width and total number of eggs as the covariates and the stages of embryonic development as fixed factors. Linear regressions were also used to analyse the relationships between egg diameter, carapace width, and brood size (the total number of eggs). Spearman's correlation coefficient was used to evaluate the relationship between biotic (the number of ovigerous females) and abiotic factors (rainfall and salinity).

Results

Reproductive period

A total of 63 ovigerous *U. maracoani* females were collected during the present study. These females had a mean Carapace Width (CW) of 25.1 ± 0.3 mm (range = 19.2–32.3 mm), and were grouped into four size classes (Table 1). The number of ovigerous females collected per month varied seasonally, with larger numbers being obtained during the dry season, when salinity was highest, and a complete absence in months of high rainfall and low salinity (Figure 2). The highest relative frequencies (> 20%) of ovigerous females was recorded in August (2014, 2015), September (2015), and November (2015). The number of ovigerous females collected during the study correlated significantly with salinity ($r = 0.43$; $p < 0.05$) and negatively with rainfall (Spearman's $r = -0.76$, $p < 0.05$).

Fecundity, egg stages, and diameter

Overall, mean fecundity was 36,840 ± 3,361 eggs per female, ranging from 12,233 eggs in a female with a carapace width of 21.8 mm to 85,000 eggs in a large female (CW = 27.8 mm). Larger females presented higher fecundity (Table 1) and the number of eggs correlated significantly with carapace width (Figure 3).

Early- (I and II) and late-stage (III and IV) embryos were found in the same egg mass in approximately one-third of the ovigerous females. The frequency of the later

Table 1. *Uca maracoani*: mean fecundity recorded in ovigerous females from the Morcego River estuary (Brazil) by size class (CW = Carapace Width). *Ovigerous females with early-stage eggs; **all ovigerous females. Tukey's test: < significantly smaller size between eggs of different development stages in females of the same CW class; additionally, different letters (a, b) indicate significantly different between size of the eggs within the development same stage from females of different CW classes.

	Fecundity*		Mean ± SE size (μm) of the eggs in stage**:					
Carapace width (mm)	N	Mean ± SE number of eggs	N	I	II	III	IV	Tukey's test
19–22	5	14,447 ± 866	10	253.5 ± 2.0^{b}	269.3 ± 1.0^{a}	292.7 ± 2.8^{a}	304.0 ± 3.6^{a}	I< II<III≈IV
22–25	8	31,075 ± 5,875	17	260.4 ± 1.3^{ab}	277.9 ± 1.5^{b}	295.8 ± 5.2^{a}	304.4 ± 3.1^{a}	I< II<III≈IV
25–28	20	44,744 ± 3,960	29	260.0 ± 1.1^{ab}	274.8 ± 1.0^{ab}	279.8 ± 2.4^{b}	288.8 ± 2.4^{b}	I< II≈III<IV
>28	0	-	7	267.4 ± 2.2^{a}	277.0 ± 2.5^{ab}	277.8 ± 3.2^{b}	280.8 ± 3.5^{b}	I≈ II≈III<IV
Total	33	36,840 ± 3,361	63	259.7 ± 0.7	274.2 ± 0.7	282.9 ± 1.6	293.3 ± 1.6	

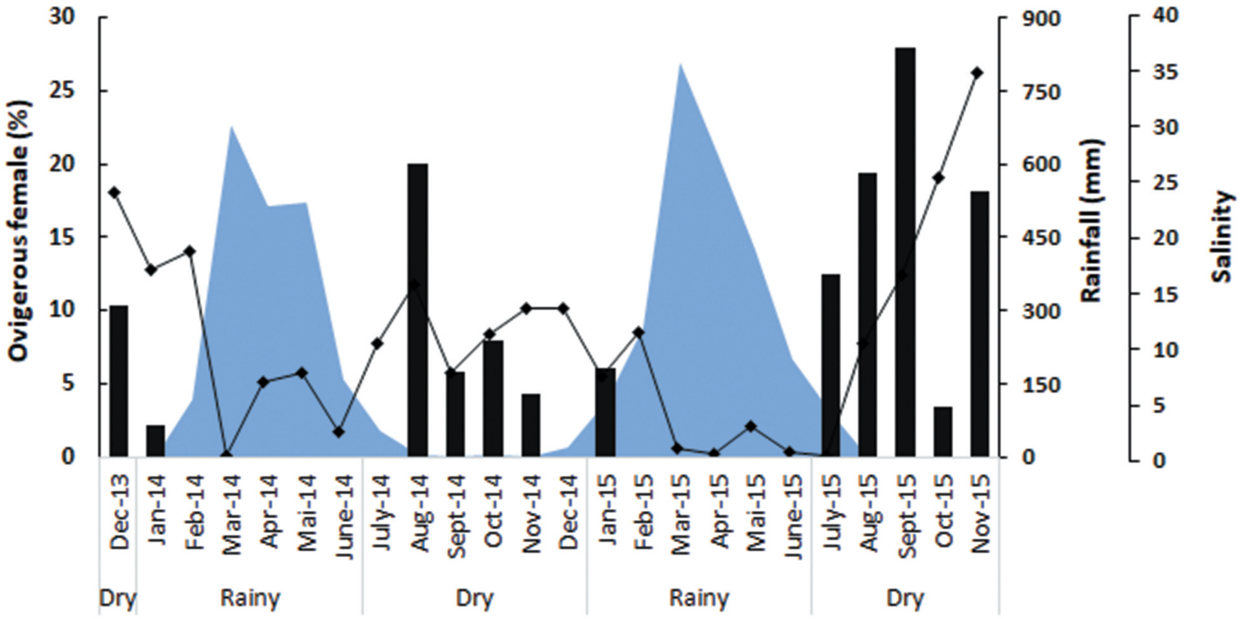

Figure 2. Monthly relative frequency of ovigerous females (bars) of *Uca maracoani*, rainfall (blue area), and salinity (line) recorded during the study period in the Morcego River Estuary (Brazil).

development stages and a reduction in the total number of eggs indicates that spawning occurred over several months, but with greater intensity at the onset of the seasons (January and August) (Figure 4).

The eggs increased in size progressively and significantly (ANCOVA: $F_{3,2515} = 192.8$; $p < 0.01$) over the course of their development, with a mean diameter of 260.7 ± 0.9 µm in stage I, 275.8 ± 0.8 µm in stage II, 283.5 ± 2.0 µm in stage III, and 295.3 ± 1.8 µm in stage IV. Carapace width (ANCOVA: $F_{1,2515} = 4.2$; $p = 0.04$) and the total number of eggs (ANCOVA: $F_{1,2515} = 86.1$; $p < 0.01$) also affected egg size significantly.

Although the eggs increased progressively in size throughout their development, this increase was less significant in the larger females, which had more (and larger) eggs on average (see Table 1). When comparing the

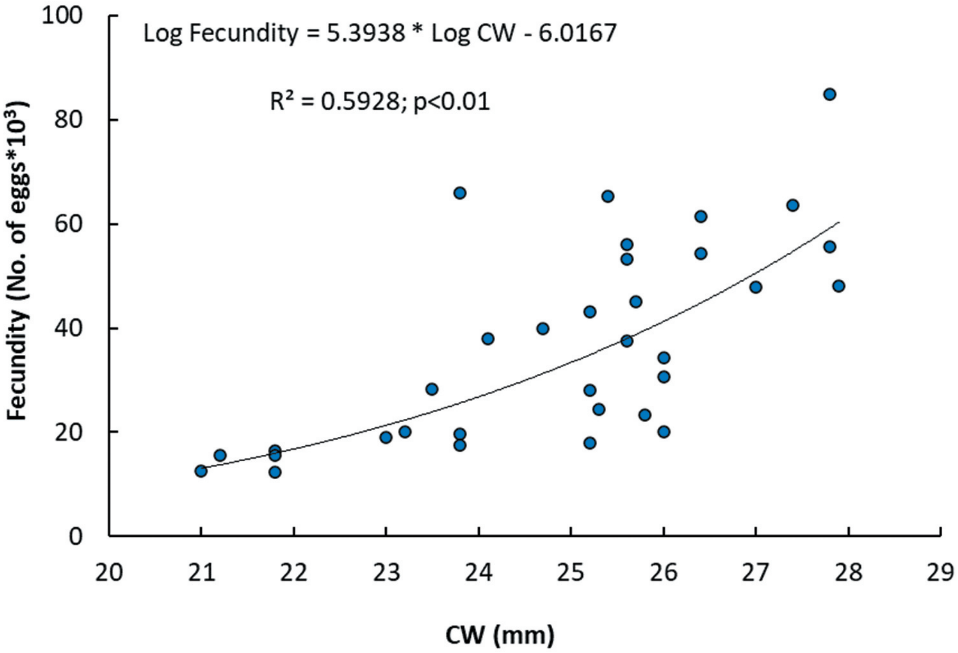

Figure 3. Relationship between the fecundity of the ovigerous females (N = 33) and carapace width (CW) of *Uca maracoani* from Morcego River Estuary (Brazil).

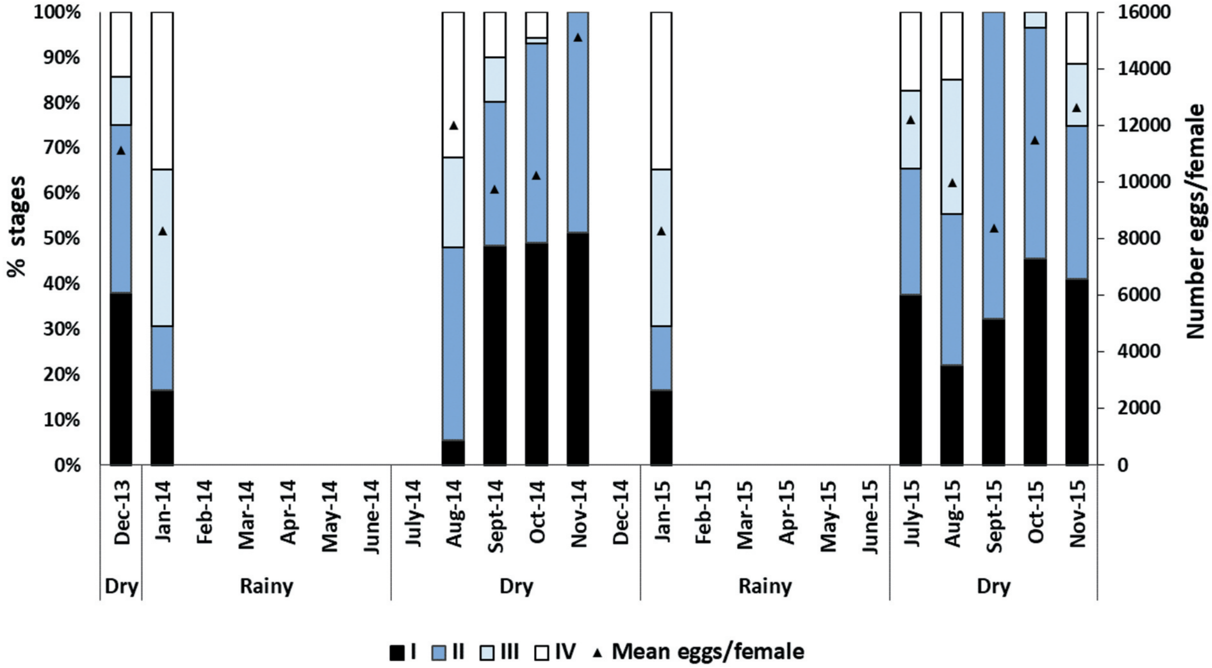

Figure 4. Frequency of the eggs of the difference development stages (I, II, III, and IV) and the mean total number of eggs per female of *Uca maracoani* from the Morcego River Estuary (Brazil).

diameter of the eggs of the same stage in females of different size classes (Table 1), larger females (CW > 28 mm) had early-stage (I and II) eggs of significantly larger diameter than the smaller females (CW = 19–22 mm), while the smaller females (CW = 19–25 mm) had significantly larger late-stage (III and IV) eggs than the larger females (CW > 25 mm).

Given this, the results of the regression analyses indicate that the relationship between female size and egg diameter varies among development stages (Figure 5a). This relationship was positive in the early stages (I and II), but negative in the later stages (III and IV). A similar pattern was found in the relationship between egg diameter and brood size (Figure 5b).

Discussion

The larger proportion of ovigerous *U. maracoani* females collected in the dry season months, and the almost complete absence of reproduction during the rainy season, indicates a seasonal-continuous reproductive pattern. This higher rate of reproductive activity recorded during the dry season is consistent with the pattern observed in other *U. maracoani* population from the Amazon coast (Koch et al. 2005). A continuous reproduction pattern has been proposed for other tropical fiddler crab populations, including those of *U. maracoani*, given that ovigerous females or females with mature gonads are present throughout the year, at similar monthly frequencies (Litulo 2005; Costa et al. 2006; Hirose and Negreiros-Fransozo 2008; Di Benedetto and Masunari 2009). Continuous reproduction in tropical regions is associated with relatively high and stable temperatures and regular circadian cycles, which support high levels of productivity throughout the year (Longhurts and Pauly 1997). In some tropical areas, however, the evidence indicates a seasonal breeding patterns in many crabs, which follows the rainfall cycle closely (Crane 1975; Koch et al. 2005; Torres et al. 2009; Diele and Koch 2010).

On the Amazon coast, the marked annual fluctuations in rainfall and salinity determine a seasonal breeding pattern in fiddler crabs (Diele et al. 2005; Diele and Koch 2010). The number of ovigerous females collected from the estuary of the Morcego River varied according to salinity, reflecting a probable avoidance of spawning during rainy periods, when salinity tends to be lower (with a minimum of zero and mean of 7). In estuarine decapod crustaceans, this pattern is related to larval development, given that the larvae tend to tolerate a narrower range of salinity than the adults (Charmantier 1998), as shown in laboratory experiments of other fiddler crab species. In *Afruca tangeri* (Eydoux 1835), for example, while the adults live in salt marshes with a salinity of 10.8–16.2 in southwestern Spain, larval development is impeded sharply at salinities of below 16 (Spivak and Cuesta 2009). Similarly, while adult *Minuca pugnax* (Smith 1870) tolerate salinity of 5–30, the larvae were unable to moult at a salinity of less than 10 (O'Connor and Epifanio 1985).

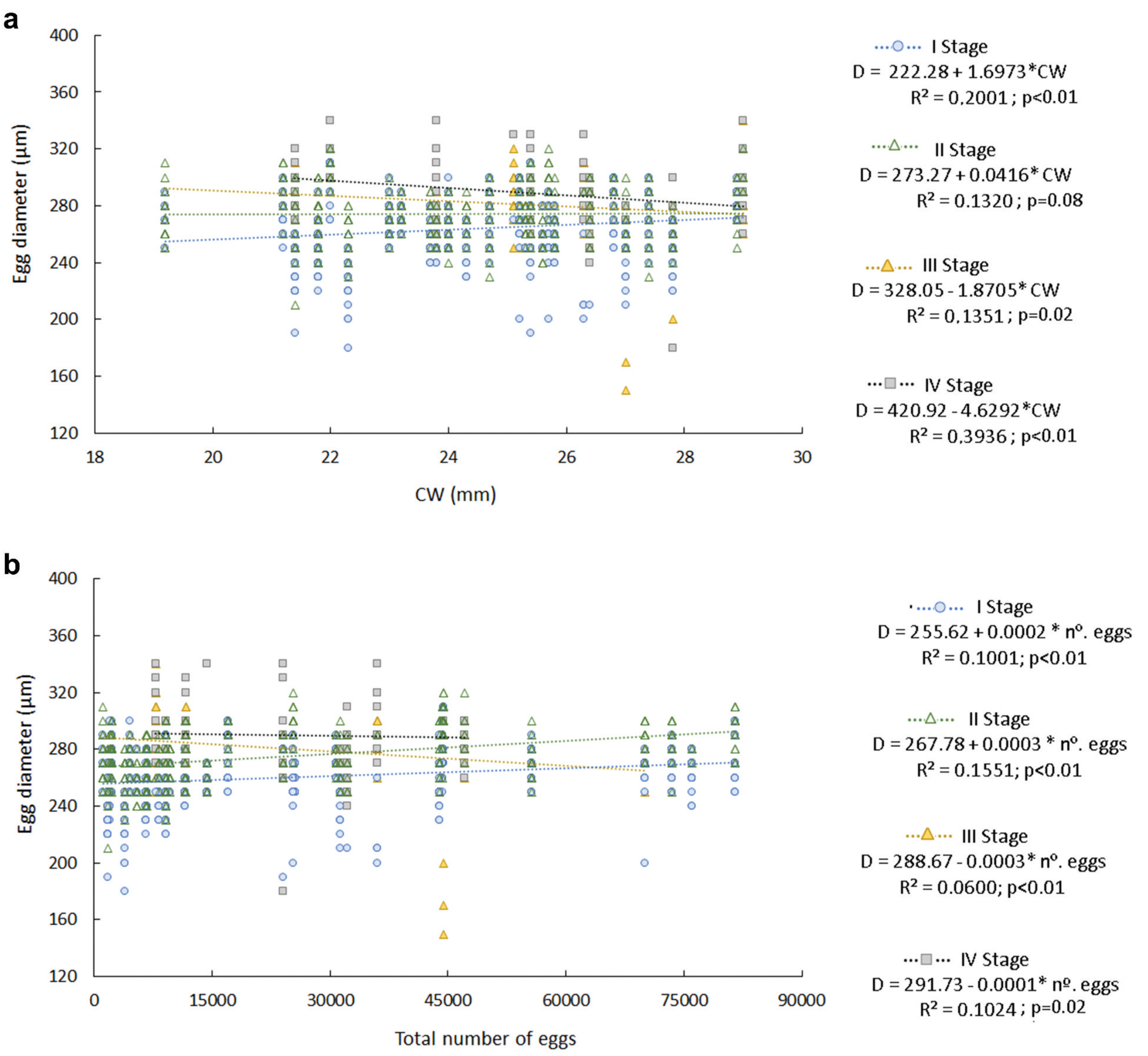

Figure 5. Relationship between (a) egg diameter and carapace width (CW), and (b) between egg diameter and the total number of eggs per female of *Uca maracoani* from Morcego River Estuary (Brazil).

In the mangroves of northern Brazil, where *Minuca vocator* (Herbst 1804) occurs in salinities of 0–39 (Diele and Simith 2006), the larval mortality rate was 100% at extremely low salinity (0–5), with survival increasing at intermediate (10–15) to high (>20) salinity (Simith et al. 2012).

Although no data are available on the salinity tolerance of *U. maracoani* larvae, the adults are considered to be good osmoregulators, even though they prefer meso-eusaline habitats (Thurman et al. 2013, 2017). The hypothesis of a peak seasonal breeding strategy is reinforced by the data on the zooplankton of the neighbouring estuarine system (Marapanim River estuary), which show that *U. maraconi* larvae (zoea I stage) are most abundant in the dry season – in the month of November (Lima et al. 2019).

Uca maracoani showed a higher egg production (mean = 36,840 eggs per female) when compared with other fiddler crab species (Table 2), in which mean broods of between 627 and 31,067 eggs per female have been recorded. The productivity of eggs recorded in *U. maracoani* is likely related to the relatively large size of the species, and the conditions of the environment in which the study population lives. In fiddler crabs, fecundity is closely-related to carapace size, front width, mating strategies, and incubation sites (Salmon and Zucker 1988). Crabs that inhabit the lower intertidal zone in proximity to rivers (Table 2) tend to be larger in size and produce greater quantities of eggs in comparison with terrestrial species or those associated with the upper intertidal zone, such as *Minuca burgersi* (Holthuis

Table 2. Published data on the fecundity of fiddler crab species from different locations around the world. Habitat: TE, Terrestrial; IT-L, low intertidal; IT-H high intertidal; IT-M, middle intertidal. CW = Carapace Width.

Species	Habitat	Study site	Latitude	Mean CW (mm)	Mean fecundity (eggs per female)	Source
Narrow-front group						
Uca maracoani Latreille 1802–1803	IT-L	Morcego River, Brazil	0° S	24.87	36,840	Present study
Austruca annulipes[1] (H. Milne Edwards, 1837)	IT-H	Inhaca Island, Mozambique	26° S	10.87	≈ 1,864	Torres et al. (2009)
Gelasimus vocans [2] (Linnaeus, 1758)	IT-L	Inhaca Island, Mozambique	26° S	18.05	≈ 9,682	Torres et al. (2009)
				24.20	11,045	Litulo (2005)
Austruca iranica (Pretzmann, 1971)	IT-H	Persian Gulf, Qeshm	25° N	12.46	≈6,373	Saeedi et al. (2018)
Broad-front group						
Minuca burgersi [3] (Holthuis, 1967)	IT-H	Barbuda, Leeward Islands	17°N	10.40	1,782	Gibbs (1974)
Minuca virens[4] (Salmon & Atsaides, 1968)	IT-M,L	Tamiahua Lagoon, Mexico	21°N	13.71	≈17,000	Del Castillo et al. (2015)
Leptuca subcylindrica[5] (Stimpson, 1859)	TE	South Texas (USA) and Mexico	26°N	13.40	627	Thurman II (1985)
Leptuca thayeri[6] (Rathbun, 1900)	IT-L	Pacoti River, Brazil	3° S	22.08	21,700	Bezerra and Matthews-Cascon (2007)
		Comprido and Escuro rivers, Brazil	23° S	19.60	31,067	Costa et al. (2006)
Minuca rapax[7] (Smith, 1870)	IT-H,M	Itaipu Lagoon, Brazil	22°S	9.42	4,984	Costa and Soares-Gomes (2009)
Leptuca uruguayensis[8] (Nobili, 1901)	IT-H	Comprido and Escuro rivers, Brazil	23° S	6.60	1,883	Costa et al. (2006)
		Samborombón, Argentine	35° S	10.40	3,339	Cezar (2007)
Minuca vocator[9] (Herbst, 1804)	IT-H,M	Itapanhaú, Brazil	23°S	15.92	10,925	Colpo and Negreiros-Fransozo (2003)
		Indaiá, Brazil	23°S	17.06	19,878	Colpo and Negreiros-Fransozo (2003)
		Itamambuca, Brazil	23°S	20.43	28,290	Colpo and Negreiros-Fransozo (2003)
Paraleptuca chlorophthalmus[10] (H. M.Edwards, 1837)	IT-H	Inhaca Island, Mozambique	26° S	13.74	≈ 2,924	Torres et al. (2009)
Cranuca inversa[11] (Hoffmann, 1874)	IT-H	Inhaca Island, Mozambique	26° S	16.25	≈ 4,449	Torres et al. (2009)

Cited as: [1]*Uca annulipes*; [2]*Uca vocans*; [3]*Uca burgersi*; [4]*Uca virens*; [5]*Uca subcylindrica*; [6] *Uca thayeri*; [7]*Uca rapax*; [8]*Uca uruguayensis*; [9]*Uca vocator*; [10]*Uca chlorophthalmus*; [11]*Uca inversa*.

1967) and *Leptuca uruguayensis* (Nobili 1901), which tend to be smaller and less fecund (Thurman 1985; Bezerra and Matthews-Cascon 2007).

Fiddler crabs have been assigned to two group, based on the size of the front, contrasting broad-front and narrow-front species (Crane 1975; Christy and Salmon 1991). While it is quite clear that these groups are not monophyletic (Shih et al. 2016) and there are oversimplifications, some proposed behavioural generalizations still useful to start evaluating species life history. For example, the males of the broad-front species typically present elaborate courtship displays and mating behaviour, with ovulation and the incubation of the eggs occurring within burrows, when the females stop feeding (Christy and Salmon 1991). In the narrow-front species, such as *U. maracoani*, by contrast, mating is typically brief and occurs on the surface of the substrate, while the eggs may be incubated either inside or outside the burrows and the females generally continue to feed while ovigerous (Christy and Salmon 1984, 1991; Salmon and Zucker 1988). Christy and Salmon (1984) relate burrow mating to the production of large litters, in comparison with the smaller litters of surface breeders. Some fiddler crabs may present an atypical pattern, or may even alternate between these strategies (Salmon 1987; DeRivera and Vehrencamp 2001).

Uca maracoani is one of the largest fiddler crab species and has the greatest biomass (Crane 1975), and typically inhabits the mid- to lower intertidal zone near mangroves on open, unvegetated mudflats in bays and estuaries, or near the mouths of streams (Koch et al. 2005). Santos et al. (2017) suggest that *U. maracoani* preferentially adopts the surface mating strategy, in which mating occurs near the female's burrow. Although we did not quantify occurrence patterns, the ovigerous female *U. maracoani* collected in the present study were encountered on both the surface of the sediment and inside burrows, which indicates that they are active and must be feeding during the incubation period.

There was a direct relationship between carapace width and the total number and size of the eggs of *U. maracoani*. The increase in the number of eggs in the larger individuals is a common pattern in fiddler crabs and other brachyuran crabs in general, and is associated with the morphological and physiological constraints of energy allocation and gonad maturation (Litulo 2005; Bezerra and Matthews-Cascon 2007; Costa and Soares-Gomes 2009; Torres et al. 2009; Del Castillo et al. 2015; Saeedi et al. 2018). The results of the present study also indicate that the eggs of the larger females, which tend to have a larger number of eggs, on average, increase less in size as they mature than the eggs of smaller females, which tend to have smaller broods of smaller eggs. The increase in egg size during embryonic development is typical of fiddler crabs (Gibbs 1974; Yamaguchi 2001a; César et al. 2007; Figueiredo et al. 2008b), and is related to the absorption of water by the egg as the percentage of lipids in the embryo decreases, which facilitates larval release (Wear 1974; Petersen and Anger 1997; Figueiredo et al. 2008b). In the case of the smaller females, which produce a smaller quantity of smaller eggs, more water may be absorbed, contributing to a greater increase in the volume of the ovigerous mass until the release of the eggs.

The mean diameter of the *U. maracoani* stage I (undivided) egg was 259.7 µm, which is within the range of other species of New World fiddler crabs, i.e. approximately 240 µm (Crane 1941; Yamaguchi 2001a). Few species of fiddler crab produce eggs larger than 300 µm, and these larger eggs may be related to small broods and longer incubation periods (Rabalais and Cameron 1983; Yamaguchi 2001a; Figueiredo et al. 2008b). While there are no published data on the incubation period of *U. maracoani*, this period is approximately two weeks in the tropical fiddler crab species for which data are available (Yamaguchi 2001a; Christy 2011; Aguilar et al. 2014).

The presence of early- and late-stage eggs together in the same ovigerous mass as observed in a considerable number of the ovigerous females can indicate embryonic asynchronous development or late fertilization. The asynchronous development of eggs has been mentioned for some fiddler crabs (Aguilar et al. 2014; Anacleto 2018) and others ocypodids (Castilho et al. 2010; Castilho-Westphal et al. 2013). Asynchrony in decapod egg development has been associated with temperature and oxygen availability in the embryo masses, which can exhibit a dramatic contrast between the periphery and the centre (Fernández et al. 2003). Interruption of embryonic development in crabs can also occur because of genetic factors, parasitism/symbionts, and others (Shields and Kuris 1988; Alekseev and Starobogatov 1996; Oh and Hartnoll 1999; Figueiredo et al. 2008a). In relation to fertilization, female fiddler crabs are known to be able to store sperm for long periods, and the eggs do not have to be fertilized and laid immediately after mating (Greenspan 1982; Yamaguchi 1998, 2001b), which may account for the occurrence of multiple broods or piecemeal spawning.

Additionally, fecundity varied considerably among some *U. maracoani* females of similar body size, which may be attributable to individual variation in egg production or the loss (natural or via mechanical abrasion with the substratum) of eggs during incubation (Kuris 1991; Hartnoll 2006; Torres et al. 2009). This result also supports the hypothesis of multiple spawning. Assuming that in the case of multiple spawning, it is expected that the number of eggs would tend to decrease during later spawning, resulting in a wide variation in the number of eggs produced by females in each size class (Adiyodi and Adiyodi 1970; Teixeira et al. 2017). While these reproductive patterns are not well understood in *U. maracoani*, the findings of the present study provide an important preliminary insight into this phenomenon.

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No potential conflict of interest was reported by the author(s).

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