



Influence of environmental patterns on the population structure and secondary production of the fiddler crab *Uca maracoani* (Latreille) in the Amazon mangroves

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ABSTRACT

Uca maracoani is a fiddler crab found in estuaries along the western Atlantic coast, with a notable preference for euhaline environments. This study aimed to analyze the population structure and dynamics of this species in an estuary on the North Coast of Brazil, specifically in an area of the upper estuary where seasonal rainfall fluctuations result in significant changes in salinity. Monthly crab samples were taken from December 2013 to November 2015, together with measurements of environmental variables, such as water and climate parameters. The population maintains a balanced sex ratio; however, males are generally larger, with lower mortality rates and longer lifespans than females. Reproduction is continuous but mainly takes place in the dry season when salinity levels are higher (above 12‰). Higher crab densities have been observed during the rainy season when, despite lower salinity levels (below 10‰), the conditions for survival (food availability and milder climate) seem to be more favorable. The estimated average annual biomass and production for the population were 2.62 g AFDM m⁻² and 5.43 g AFDM m⁻² year⁻¹, respectively, characterized by a high turnover rate (P/B = 2.10 year⁻¹). Our results suggest that *U. maracoani* has thriving populations in the Amazon coast's mangroves, benefiting from the vast muddy intertidal zone and the high organic content delivered by the estuaries.

1. Introduction

The fiddler crab (Ocypodidae) is a well-known group of brachyuran crabs characterized by marked sexual dimorphism. Males have one hypertrophied cheliped, while females have chelipeds of similar size (Crane, 1975). Often found in estuarine habitats like salt marshes and mangroves, these crabs are key species due to their abundance and role in ecosystem engineering (Kristensen, 2008). In Amazon estuaries, fiddler crabs rank among the most important prey in the mangrove food web, converting a substantial portion of bacterial production into food for larger predators (Wolff et al., 2000). They can account for almost 90% of total intertidal benthic macrofauna production in Amazon mangroves (Koch and Wolff, 2002).

Salinity is considered a key ecological parameter affecting the distribution of aquatic species due to its high variability in marine coastal ecosystems (Anger, 2003). Salinity fluctuations can alter the metabolic rate of decapod crustaceans during their ontogeny, leading to physiological and behavioral changes. These alterations impact survival, development, morphology, and growth, consequently affecting biomass and secondary production (Guerin and Stickle, 1997a, 1997b; Anger, 2003; Anger et al., 2008; Shock et al., 2009; Simith et al., 2012). In the evolutionary history of fiddler crabs, salinity has been a significant driver of osmoregulatory evolution, thus forming the functional basis for habitat diversification (Faria et al., 2017). The osmoregulatory ability demonstrates substantial variance amongst fiddler crab species, reflected in the salinity of their osmotic niches (Faria et al., 2017;

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Thurman et al., 2017). Moreover, intraspecific variations amongst fiddler crab populations suggest this characteristic is an ecophenotypic attribute, as demonstrated in the more widely distributed species (Thurman, 2002; Thurman et al., 2017).

Uca maracoani (Latreille, 1803) is the largest species of fiddler crab in Brazil, found in intertidal areas near mangroves, on open mud flats, and along estuaries. The species is distributed along the western Atlantic coast of South America, stretching from the Gulf of Paria (eastern Venezuela and Trinidad) to southern Brazil (Paraná, Brazil) (Thurman et al., 2013). *U. maracoani* displays a preference for meso-euhaline habitats, however, occurring in salinity under 5‰ (Thurman et al., 2013). Laboratory observations suggest that adult *U. maracoani* cannot express survival mechanisms under hypo- or hyperosmotic conditions (Thurman et al., 2017). Field studies focusing on the population structure of *U. maracoani* have been conducted in polyhaline and mesohaline zones of subtropical estuaries (di Benedetto and Masunari, 2009; Hirose and Negreiros-Fransozo, 2007, 2008; Machado et al., 2021), however, scarce data from tropical areas are available (Silva et al., 2016; Azevedo et al., 2017). Concerning the population dynamic parameters and production, data are available from only one population in North Brazil (Koch and Wolff, 2002; Koch et al., 2005). Thus, comparisons serve as a valuable strategy for identifying differences between populations and understanding the environmental and biological limitations that shape them.

U. maracoani is an abundant species in the intertidal zone of Amazonian estuaries, areas significantly influenced by high river discharge and rainfall regimes. These conditions create two distinct seasonal periods and result in a marked variation in salinity (Koch and Wolff, 2002). Specifically, estuarine environments in Northeast Pará range from oligohaline (salinity 0–5‰) to euhaline (salinity \approx 35‰) conditions within a single year (Silva et al., 2011; dos Santos et al., 2019). As such, these estuaries offer ideal areas for analyzing the salinity-related ecological patterns of this species. This, in turn, facilitates comparisons with the life history traits of other populations along

the Atlantic coast.

The study aimed to investigate the structure and population dynamics (growth, mortality, and secondary production) of *U. maracoani* in an estuary on the North Coast of Brazil, specifically in an area of the upper estuary where salinity reaches zero during the rainiest months (dos Santos et al., 2019). Given that *U. maracoani* is a meso-euryhaline species, we hypothesized that this Amazonian population experiences lower densities during the rainiest periods and expected a positive relationship between crab densities and estuary salinity. Furthermore, we assume that biomass and production have this would follow the same relationship to salinity.

2. Material and methods

2.1. Sampling

This study was conducted on the Japerica Bay Estuary, located in Primavera Municipality, Pará State, on the Brazilian Amazon coast (Fig. 1). The local climate is equatorial humid with an annual mean temperature of 26–27 °C and a mean annual precipitation (a 30-year record) from 2300 to 2800 mm (Moraes et al., 2005). Precipitation varies considerably over the year, with well-marked rain season (>500 mm/month) from February through April and a drier season (<100 mm/month) from September through November (Amanajas and Braga, 2012). The region is dominated by semidiurnal macrotides with an amplitude of 4–7 m (Araújo da Silva et al., 2009).

One low intertidal area (100 m²) of the mangrove was established in the zone of the upper estuary sector (0°55'44.1"S 47°06'03.7"W), on the Morcego River, in which crabs were collected from December 2013 through November 2015. For each month, all crabs were manually sampled in two quadrants of 25 m² each (see Aviz et al., 2022). The crabs were collected from the surface of the sediment; furthermore, all visible burrows were excavated to search for crabs. In parallel with the crab sampling, three samples of surface water were collected on the ebb

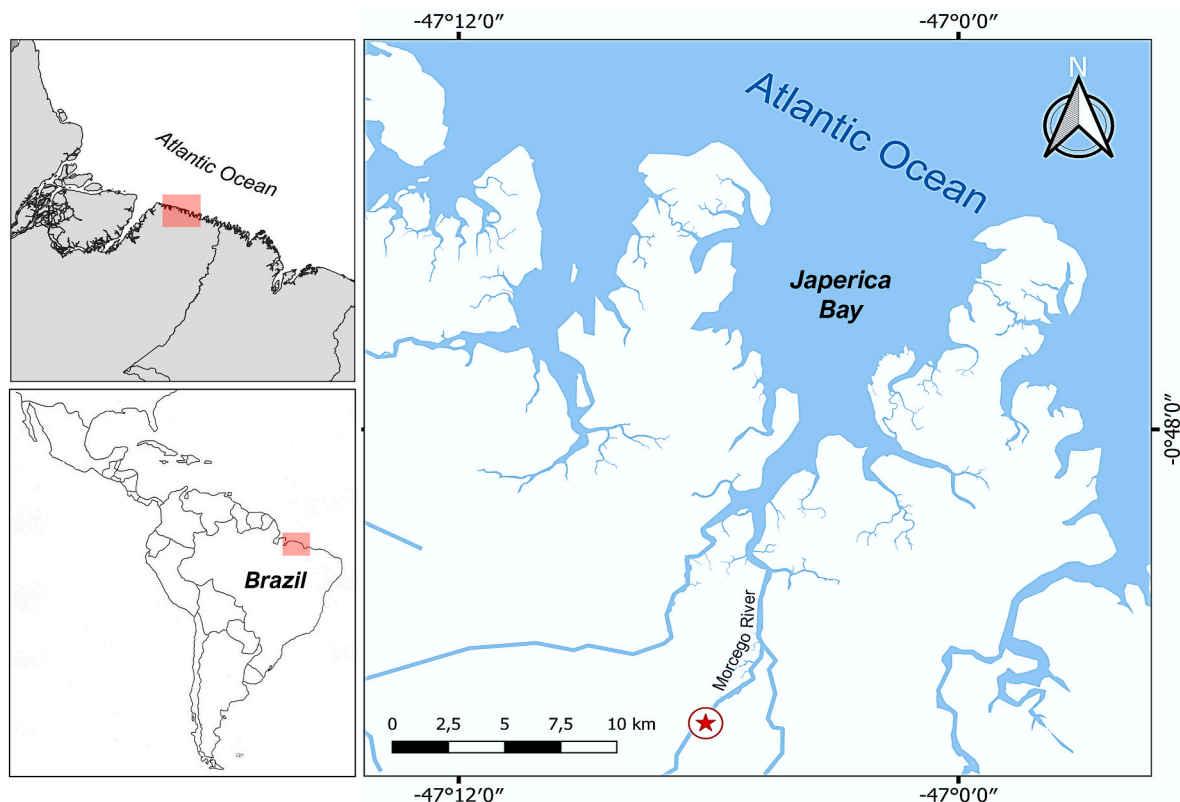


Fig. 1. The location of the Japerica Bay Estuary, Amazon coast of northern Brazil. The red rectangles and the red star indicate the location of the study area.

tide to determine salinity levels using a refractometer and in situ measurements were taken of pH, electrical conductivity, dissolved oxygen, and temperature, using a multiparameter equipment (Hach HQ40D). Precipitation, air temperature, and solar insolation data were obtained from the local meteorological station in Primavera and were provided by the Brazilian National Meteorological Institute (INMET).

2.2. Laboratory procedures

In the laboratory, the sex (by examination of the number of pleopods, presence of gonopodium, and heterochely), and biometric measurements (carapace width, CW) of each specimen were determined. To obtain ash-free dry body mass, used to estimate the mass-width body relationship, individuals (71 males; and 73 females) were dried at 70 °C for 48 h (dry mass, DM). The dried mass was burnt in a muffle furnace for 5 h at 550 °C (ash mass, AM). Ash-free dry mass (AFDM) was calculated by subtracting ash mass from dry mass.

Voucher specimens were deposited in the carcinological collection of the Goeldi Museum in Belém, Brazil (catalog numbers: MPEG 003258–003281).

2.3. Statistical analysis

2.3.1. Population structure

The sex ratio was analyzed using Chi-square for the study period to test for significant deviation from the hypothesized 1:1 ratio. The sex ratio was also analyzed for each month, and for each carapace width class. Differences in mean CW between sexes was assessed using a *t*-test for unequal variances, for the study period.

For seasonal comparisons of crabs abundance, four periods were established based on the accumulated precipitation data: Dry-Rainy Transition (DRT) periods (December to February), with a mean of 164 mm/month; Rainy periods (March to May), with a mean of 594 mm/month; Rainy-Dry Transition (RDT) periods (June to August), with a mean of 85 mm/month; and Dry periods (September to November), with a mean of 1.2 mm/month. Analyses of two-factors variance (ANOVA) were used to compare abundances (total, males, non-ovigerous females, and ovigerous females) between year (each cycle of 12 sampling; two levels, fixed and orthogonal) and season periods (four levels, fixed and orthogonal), with a posteriori comparison based on the Tukey tests. Prior to application of the ANOVA, the data were evaluated for normality (Shapiro–Wilk test) and homoscedasticity of variance (Levene's test).

Multiple regression was used to identify the potential of the environmental variables measured and modeled in the present study to explain the temporal variability observed in the abundance of crabs. A stepwise forward procedure was used to determine the subset of environmental variables (salinity, pH, electrical conductivity, dissolved oxygen, water temperatures, and solar irradiation) that best explained the observed variation, using the minimum Akaike Information Criteria (AIC) values (Tabachnick and Fidell, 1996). Before the regression, the degree of collinearity between environmental variables was estimated using Pearson's correlation coefficient, and any strongly correlated variables ($r \geq 0.8$) were excluded from all subsequent analyses.

All the analyses were run in the R software (version 3.3.0), and a level of significance of $p = 0.05$ was used.

2.3.2. Population dynamics

Monthly width-frequency distributions were grouped into 5 mm CW size classes and used to estimate growth parameters. The ELEFAN I (Electronic Length Frequency Analysis) routine of the FISAT II package (FAO-ICLARM Stock Assessment Tools) was employed for this analysis using the generalized von Bertalanffy growth function (VBGF: Pauly and Gaschütz, 1979). This function is given by: $L_t = L_\infty(1 - e^{-k(t-t_0)})$ where L_t is the carapace width at time t (mm); L_∞ is the asymptotic carapace width attained by the species; K is the curvature parameter; and t_0 is the

theoretical age at zero width. In this study $t_0 = -0.07$ year was based on the time of development of larvae of other Amazonian crab fiddlers (Simith et al., 2012), as there are no data on *U. maracoani*. The growth index phi prime (ϕ'), defined as $\phi' = 2\log_{10}(L_\infty) + \log_{10}K$ (Pauly and Munro, 1984), was employed to measure growth performance. The instantaneous mortality rate (Z) was calculated by the single negative exponential model using the width-converted catch curve method (Pauly et al., 1995) of the FISAT program (Gayaniolo et al., 1996). Life span was estimated using the width representing the 99th percentile of the population, $L_{99\%}$ (Sparre et al., 1989).

The relationship between carapace width and ash-free dry mass (AFDM) was estimated by the power function $M = a \cdot CW^b$, where M is the ash-free dry mass per individual (g AFDM), CW is the carapace width (mm), and a and b are constants. Biomass (B) was calculated annually and monthly from the density of population categories (males and females) multiplied by body mass obtained from the mass-width relationship. Annual production (P) was estimated using the mass-specific growth rate method from the width-frequency distribution obtained from all pooled samples, the width-mass relationship, and the von Bertalanffy growth function parameters (Brey, 2001). Monthly production was also estimated. The turnover rate (P/B) was calculated by the ratio between somatic production (P) and mean biomass (B). As with abundance, ANOVA tests were also used to examine the variation of the crab biomass and production between years and season periods.

3. Results

3.1. Environmental data

Climatic variables exhibited a strong seasonal pattern during the sampling two years (Fig. 2). The rainy months were characterized by higher rates of rainfall (680–808 mm/month) and lower solar irradiation (127.1 ± 16.1 kW/m²) (\pm SD) and by lower values of air temperatures (25.9 ± 0.1 °C) and salinity (3.3 ± 1.3 ‰), ranging between 0 and 8.5‰. In contrast, rainfall (0–4 mm/month) was practically absent in the dry months, and the highest irradiation (270.8 ± 4.9 kW/m²), salinity (20.4 ± 4.6 ‰), ranging between 12.5 and 39.3‰, and temperature (27.1 ± 0.2 °C) values occurred. In general, the transitional periods (RDT and DRT) exhibited intermediate values of these variables. The water-dissolved oxygen did not show clear seasonal patterns (Fig. 2), though minimum values (1.7 and 2.8 mg/L) were observed in the transitional periods, while the maximum values occurred in both the rainy (8.6 and 8.7 mg/L) and dry (8.7 mg/L) periods. The water pH was often neutral to slightly alkaline (7–8.5), except for September/2014 (Dry), when it had a slightly acidic pH (6.2) (Fig. 2).

3.2. Population structure

A total of 3036 crabs were collected, of which 48.6% were males and 51.4% were females (49.3% non-ovigerous, and 2.1% ovigerous) (Table 1). Males were ($t = 8.46$; $p < 0.01$; $n = 3036$) larger than females, with CW of males ranging from 3.2 to 36.2 mm and the CW of females ranging from 2.9 to 32.7 mm. The CW of ovigerous females ranged from 15.2 to 32.3 mm.

The overall sex ratio was 0.9: 1 (males: females), which did not deviate ($\chi^2 = 2.43$; $p = 0.12$; $df = 1$) from the expected (1:1). However, the population was female-dominated during some months (Fig. 3). Females predominated in the smallest (0–3 mm) to mid-size classes (15–29 mm), whereas males predominated in the largest size classes (>29 mm) (Fig. 3).

Variance analysis revealed that only seasonal periods had effects on the crab's density (males, non-ovigerous, and ovigerous females) (Table 2). No difference was found among the years, and interactions between factors (periods x years) were also not identified (Table 2). Both crab groups (total, males, and non-ovigerous females) were more abundant in the rainy period than in other seasonal periods (Table 2).

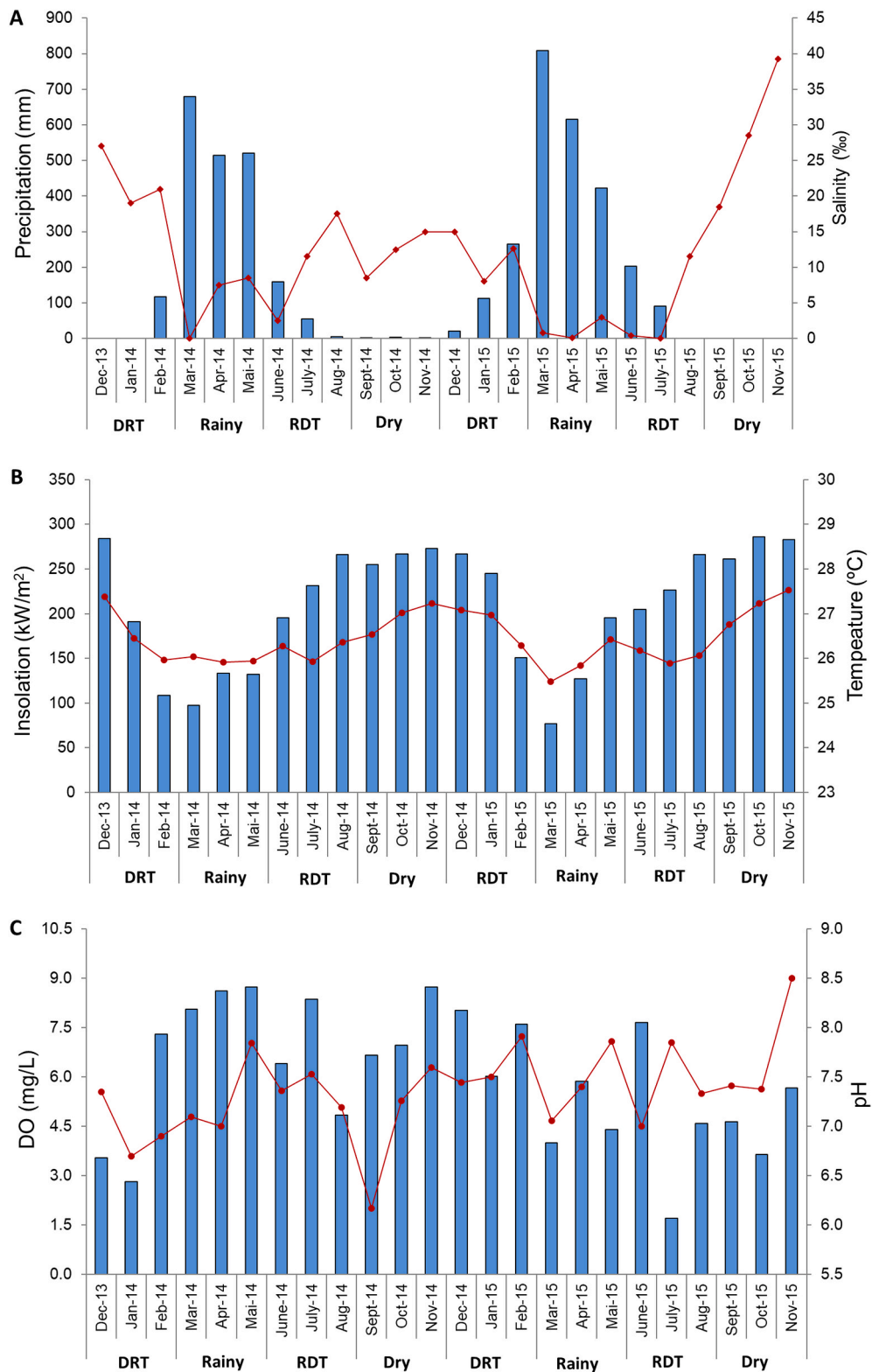


Fig. 2. Environmental characteristics recorded between December 2013 and November 2015. A: Rainfall (bars) and salinity (line); B: Solar irradiation (bars) and water temperature (line); C: Water dissolved oxygen (bars) (OD) and pH (line). Seasonal periods: Dry-Rainy Transition (DRT); Rainy; Rainy-Dry Transition (RDT); Dry.

Conversely, ovigerous females were more abundant in the dry period and absent in the rainy period (Table 2).

The best-fitting regression models to explain the abundance of crabs included water salinity and solar irradiation (Table 3). Salinity was related negatively to the crabs' total abundance, as well as to the

abundance of male and non-ovigerous female crabs (Fig. 4A and B). In contrast, a positive relationship between salinity and ovigerous females' abundance was observed (Fig. 4C). Solar irradiation was related negatively to the crabs' total abundance (Fig. 4D).

The monthly variation in the distribution of the size classes (Fig. 5)

Table 1
Uca maracoani, descriptive statistics for each demographic category.

Category	N	Relative abundance (%)	(CW mm)	
			Min-Max	Mean ± SD
Males	1475	48.6	3.2–36.2	22.4 ± 7.3
Females	1561	51.4	2.9–32.7	20.4 ± 5.9
Non-ovigerous	1498	49.3	2.9–32.7	20.2 ± 6.0
Ovigerous	63	2.1	15.2–32.3	24.9 ± 2.8
Total	3036	100	2.9–36.2	21.4 ± 6.7

N = number of crabs; CW = carapace width; SD = standard deviation.

indicates the recruitment of juveniles throughout the year and fluctuations in the size structure of the population. Nevertheless, the recruitment of juveniles appeared to be more intense in the rainy season, from March to May (Figs. 5 and 8).

3.3. Population dynamics

The asymptotic carapace width (L_{∞}) of the von Bertalanffy growth function (VBGF) (Fig. 5) and curvature parameter (K) of males (L_{∞} : 38.35 mm CW; K: 1.48 year⁻¹) was higher than that of females (L_{∞} : 34.20 mm CW; K: 1.30 year⁻¹). No seasonal oscillation in growth was

observed in this population, i.e., C = 0. The growth index, phi prime (ϕ'), of males (ϕ' : 3.33) was higher than that of females (ϕ' : 3.18). The instantaneous mortality rate, Z, of males (Z: 2.91 year⁻¹) was lower than that of females (Z: 3.51 year⁻¹) (Fig. 6), while, conversely, the life span of males (1.77 years) was longer than that of females (1.55 years).

3.4. Mass-width relationship and secondary production

The relationship between carapace width (CW) and ash-free dry mass (g AFDM) was strong for both sexes (males: $y = 0.00001x^{3.460}$; n = 71, $r^2 = 0.96$, $p < 0.01$; females: $y = 0.00006x^{3.564}$; n = 73, $r^2 = 0.96$; $p < 0.01$). The body mass of males of *U. maracoani* was higher than that of females (ANCOVA, $F_{1, 141} = 4.09$, $p = 0.04$).

The mean annual biomass population was 2.62 g AFDM m⁻², 2.82 and 2.41 g AFDM m⁻² in the first and second years, respectively. The mean annual population production was estimated at 5.43 g AFDM m⁻² yr⁻¹ (year 1: 5.46 AFDM m⁻² yr⁻¹; and year 2: 5.40 g AFDM m⁻² yr⁻¹). The P/B ratio was 2.08 yr⁻¹ for the population (year 1: 1.94 yr⁻¹; year 2: 2.24 yr⁻¹).

The mean biomass and secondary production have higher estimates for males (1.65 g AFDM m⁻²; 3.49 g AFDM m⁻² yr⁻¹) than for females (0.97 g AFDM m⁻²; 1.94 g AFDM m⁻² yr⁻¹). The P/B ratio was 2.12 year⁻¹ for males and 2.01 yr⁻¹ for females. The highest production occurred around the 18–28 mm (females) and 18–32 mm (males) size classes. Because only males were observed within size classes from 34 to

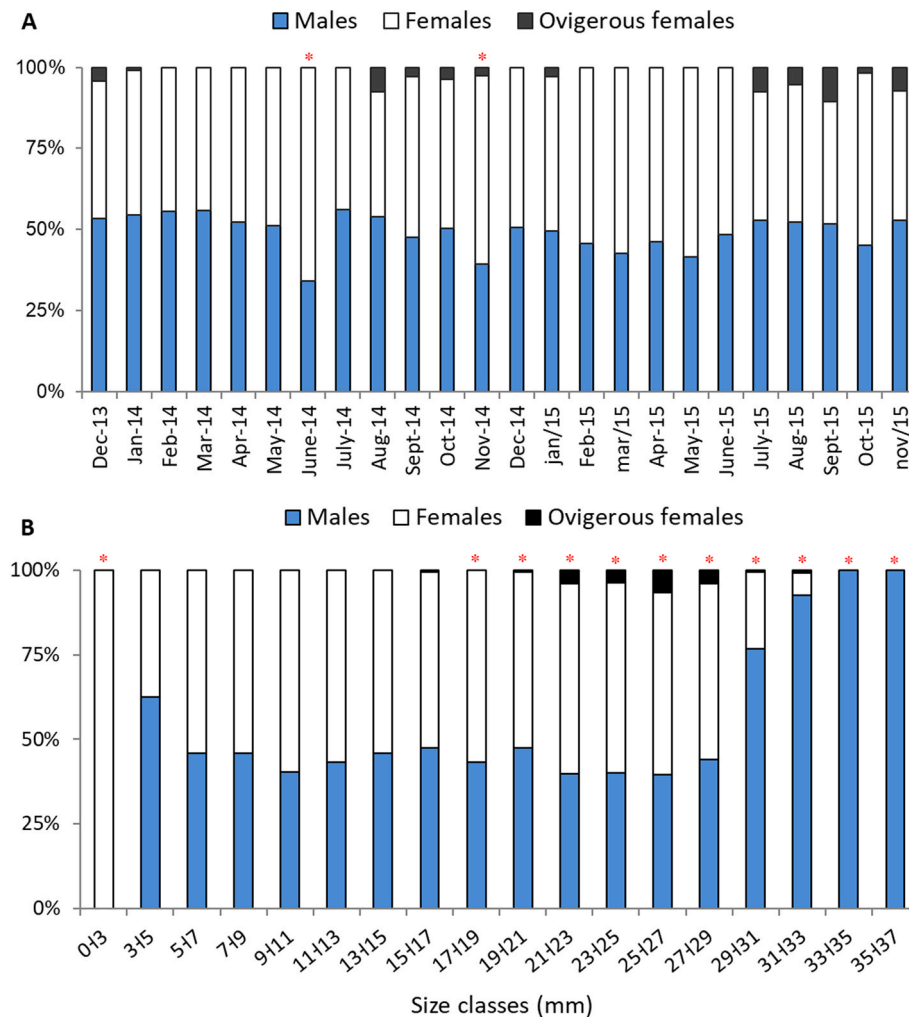


Fig. 3. (A) Percentage of males, females, and ovigerous females in each month, (B) Percentage of males, females, and ovigerous females in each size class (CW, mm) of *Uca maracoani* crabs. Asterisks indicate significant deviation from a ratio of 1:1.

Table 2

Mean density (ind./25 m² ± SE) for population of *Uca maracoani* crabs. NO = non-ovigerous. ANOVA results, *p < 0.01. Letters a, b and c indicate significant results in Tukey's test. Seasonal periods: Dry-Rainy Transition (DRT); Rainy; Rainy-Dry Transition (RDT); Dry.

Year	Total	Males	NO-Females	Ovigerous females
Year 1	61.9 ± 5.2	30.8 ± 2.9	30.1 ± 2.8	1.0 ± 0.3
Year 2	64.6 ± 4.6	30.7 ± 2.0	32.3 ± 3.1	1.6 ± 0.5
Periods				
TDR	56.8 ± 6.5 b	29.3 ± 3.8 b	26.3 ± 2.7 b	1.1 ± 0.5 b
Rainy	85.3 ± 7.8 a	40.6 ± 4.0 a	44.7 ± 4.5 a	0.0 ± 0.0 c
TRD	53.1 ± 6.0 b	25.3 ± 2.5 b	26.3 ± 4.2 b	1.4 ± 0.5 b
Dry	57.9 ± 2.1 b	27.7 ± 1.7 b	27.5 ± 2.1 b	2.8 ± 0.7 a
ANOVA				
Year (F _{1,40})	0.22	0.02	0.43	1.34
Periods (F _{3,40})	6.46*	5.02*	6.78*	5.86*
Year*Periods (F _{3,40})	1.94	2.35	2.19	2.21

Table 3

Best-fit models of the stepwise multiple linear regression of the data on the *Uca maracoani* population and the environmental variables.

(A) TOTAL DENSITY - F _(2,45) : 11.59, p: <0.01, Adjusted R ² : 0.52				
N = 48	Beta	Standard error of Beta	t	p
Intercept			0.63	0.52
Salinity	-0.51	0.13	-3.98	<0.01
Solar irradiation	-0.28	0.13	-2.12	0.04
(C) MALES DENSITY - F _(1,46) : 4.21, p: <0.05, Adjusted R ² : 0.29				
N = 48	Beta	Standard error of Beta	t	p
Intercept			13.88	<0.00
Salinity	-0.44	0.13	-3.32	<0.01
(D) NO-FEMALES DENSITY - F _(1,46) : 8.70, p: <0.01, Adjusted R ² : 0.39				
N = 48	Beta	Standard error of Beta	t	p
Intercept			7.69	<0.01
Salinity	-0.40	0.14	-2.94	<0.01
(D) OV-FEMALES DENSITY - F _(1,46) : 5.62, p: <0.01, Adjusted R ² : 0.35				
N = 48	Beta	Standard error of Beta	t	p
Intercept			-0.47	0.64
Salinity	0.28	0.13	2.14	<0.05

OV = ovigerous; NO = non-ovigerous.

36 onward, all the secondary production estimated based on larger-sized individuals is attributed to males (Fig. 7).

No effects of the year and seasonal period factors on the variation in biomass and secondary production were identified (Supplementary Material). The biomass and production peaks of males and females occurred in both the dry and rainy seasons, followed by population density fluctuations (Fig. 8). The lowest estimates of these variables occurred in transitional months.

4. Discussion

Our results indicate that *Uca maracoani* maintains a well-established population in mangroves of the Japerica Bay, despite significant environmental variations mainly driven by seasonal changes in precipitation. The study population presents a balanced sex ratio, aligning with those recorded in other *U. maracoani* populations along the Brazilian coast (Table 4). This finding diverges from the common trend of male-biased sex ratios in fiddler crab populations (reviewed in Johnson, 2003). Male-biased *U. maracoani* populations have been identified along the Brazilian coast (Table 4). Typically, in crustaceans, primary sex ratios (larvae and juveniles) are even, skewing only during growth and development (Johnson, 2003; Ewers-Saucedo, 2019). Factors such as differential growth and mortality, as well as distinct habitat use between males and females, can generate a sex ratio bias (Johnson, 2003; Ewers-Saucedo, 2019). Our results demonstrate that the sex ratio maintains a 1:1 balance until the carapace width reaches approximately

20 mm. Upon attaining this size, differences in the sex ratio of crabs become apparent, with males predominating in the largest size classes. This trend of shift in sex ratio with size class concurs with reports for other fiddler crabs (Spivak et al., 1991; Johnson, 2003).

In the current study, males were larger than females a common finding among fiddler crab species (Crane, 1975). As they grow larger, males enhance their odds of success in courting females and in intra-specific combats (Christy and Salmon, 1984). Conversely, the reproductive investment of female crabs tends to be high, potentially limiting the energy available for growth (Hartnoll, 2006). Additionally, the growth of the female body is constrained due to their inability to molt while incubating eggs, leading to smaller sizes compared to males (Hartnoll, 2006). The larger size of *U. maracoani* males is also by their higher growth performance, lower mortality, and longer lifespan (Table 5), which enable them to grow larger than females.

The mean and maximum sizes of crabs in our study fall within the range of values recorded along the Brazilian coast (Table 4). However, as expected, the maximum sizes were observed at higher latitudes (23°S). Low temperatures and the duration of the growing season primarily limit the geographical distribution of fiddler crabs at higher latitudes. Generally, we can expect longer lifespans and slower growth rates towards the distribution limits (Crane, 1975; Koch et al., 2005). This latitudinal effect also appears to influence species' maturity. One of the smaller ovigerous females of *U. maracoani* (15.2 mm CW), for instance, was recorded in Japerica Bay (Table 4), suggesting that tropical populations reach sexual maturity earlier. At lower latitudes, higher

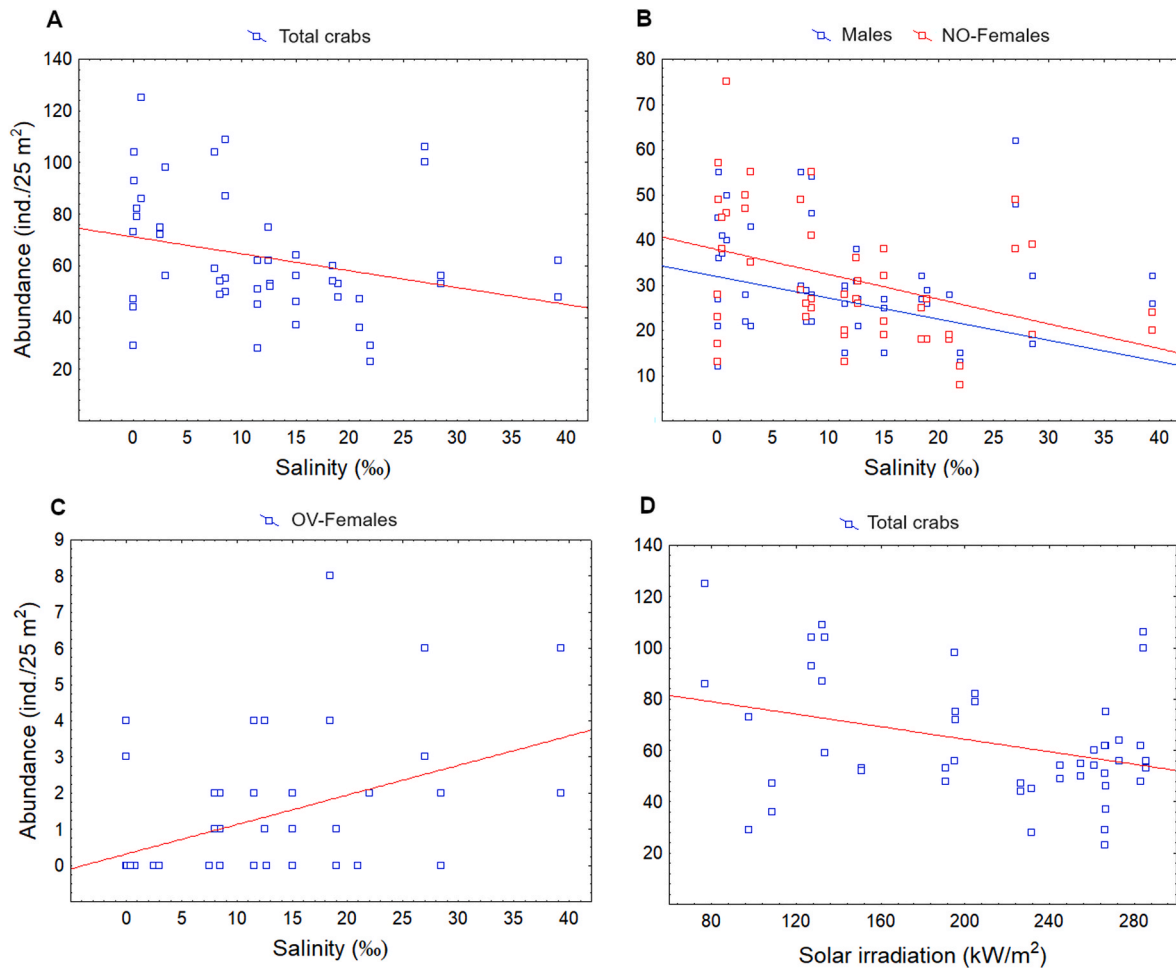


Fig. 4. Relationships between *Uca maracoani* abundance and environmental variables: salinity and crabs density (A: total; B: males, and non-ovigerous females; C: ovigerous females); solar irradiation and crabs density (D).

temperatures tend to accelerate metabolism, reducing the amount of oxygen available for growth per unit of time and leading to earlier sexual maturity (Pauly, 1981; Audzijonyte et al., 2019).

The proportion of ovigerous females found in Japerica Bay was low (2% of total females captured), similar to studies on other *U. maracoani* populations, regardless of sampling techniques (e.g., Di Benedetto and Masunari, 2009; Azevedo et al., 2016; Silva et al., 2016; Machado et al., 2020). Ovigerous females likely remain more sheltered (at the bottom of burrows or in closed burrows) due to their higher vulnerability (Macia et al., 2001). However, the presence of ovigerous almost the entire year in Japerica Bay indicates a continuous reproductive pattern, as is also expected in tropical crab populations, including that of *U. maracoani* (Litulo, 2005; Hirose and Negreiros-Fransozo, 2008; di Benedetto and Masunari, 2009). Continuous reproduction in tropical regions is associated with high stable temperatures and regular circadian cycles, which support a high level of productivity throughout the year (Longhurst and Pauly, 1997).

The *U. maracoani* population abundance demonstrated a negative relationship with increased salinity, contradicting our initial hypothesis. This is likely due to the higher density of crabs observed during the rainiest months, probably following recruitment peaks. Therefore, we believe that due to their ability to tolerate low salinity (<5‰), the crabs can take advantage of the higher organic availability that the Amazonian estuaries carry during the rainy season (Smith and Demaster, 1996), as well as reduced solar irradiation rates. Fiddler crab species, throughout tidal cycles, are exposed to high temperatures and risk desiccation, potentially leading to dehydration and metabolic stress,

which may result in mortality or decreased performance (Jimenez and Bennett, 2007; Allen et al., 2012; Principe et al., 2018; Levinton, 2020). This situation becomes even more critical when discussing species residing in open mud flats, like *U. maracoani* (Crane, 1975; Koch et al., 2005).

Our results indicate that while *U. maracoani* is commonly identified as a euryhaline species in scientific publications (Thurman et al., 2013; Faria et al., 2017), stable populations thrive in the oligohaline (0–5‰) to euryhaline (>30‰) estuarine waters of the Amazon coast's mangroves throughout the year. These findings seem to contradict laboratory observations, which infer that adult *U. maracoani* cannot generate survival mechanisms under hypoosmotic conditions and thus promptly die in situations of low osmolarity (Thurman et al., 2017). It is crucial, however, to consider that the salinity within the burrow was not measured and might surpass that of the main creek water, a phenomenon documented in multiple studies on different mangrove crab species (Thongtham and Kristensen, 2003; Araújo and Calado, 2011). For instance, Araújo and Calado (2011) recorded tenfold higher salinity levels inside *Ucides cordatus* (Linnaeus, 1763) burrows compared to the creek water during the rainy season. Moreover, the behavioral responses of crabs could ensure survival under low salinity. Fiddler crab species, for example, might retreat deeper into burrows or actively block their entrance with sediment at the end of low tide periods to maintain optimal habitat conditions (de la Iglesia et al., 1994; Ribeiro and Iribarne, 2011; Fusi et al., 2015; De Grande et al., 2018). By only examining the salinity inside *U. maracoani* burrows in a Northeast Brazil mangrove, Araújo et al. (2012) noted 2.7‰ salinity in the upper layer

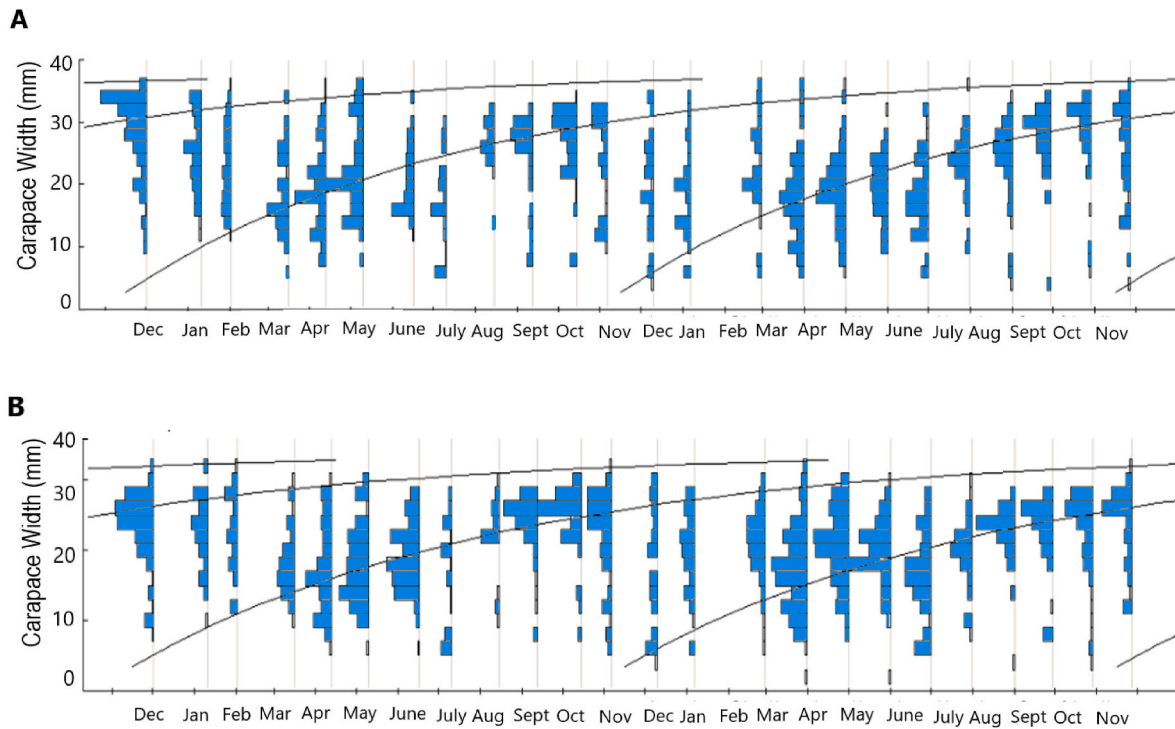


Fig. 5. Frequency distribution of carapace width and growth curves of von Bertalanffy for *Uca maracoani* males (A) and females (B).

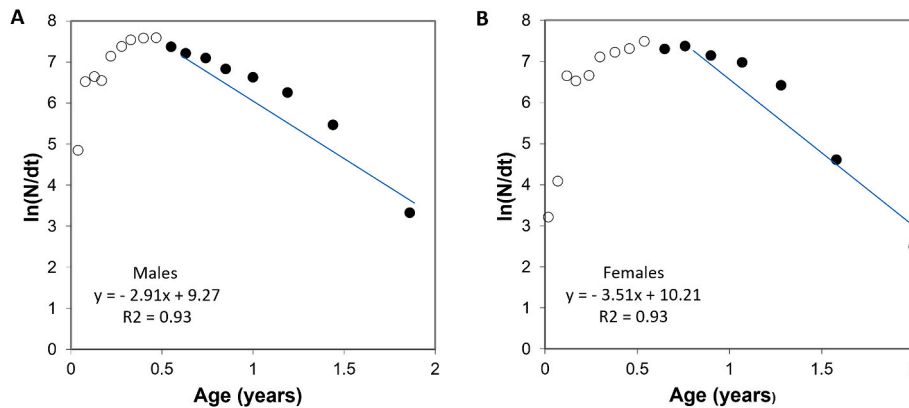


Fig. 6. Results of the width-converted catch curve of *Uca maracoani* males (A) and females (B). Instantaneous mortality rate ($Z = -$ slope of regression line). Open circles were not used to fit the linear model.

and 12.0‰ in the lower layer during the rainy season.

In any case, considering the wide geographic distribution of *U. maracoani*, which includes overcoming oceanic currents and freshwater barriers, we expect environmental acclimation (Thurman et al., 2013, 2017). Macrophysiological studies have proven that, although the intraspecific osmoregulatory traits of tropical fiddler crabs from different Atlantic locations are quite similar, lethal osmotic concentrations vary among conspecific populations. These variations appear to be ecophenotypic (Thurman, 1985; Thurman et al., 2010, 2017; Faria et al., 2017). *U. maracoani*'s populations have demonstrated significant morphological divergence along Brazil's coast without concurrent genetic variation. This divergence most likely arises from phenotypic plasticity driven by environmental differences (Wieman et al., 2014). However, further studies are necessary to determine whether genetic and molecular mechanisms are responsible for the diversification of these crabs' osmoregulatory capabilities.

Despite the negative trend of population density with increased salinity, the positive correlation between the density of ovigerous

females and salinity confirms that *U. maracoani* has greater reproductive success in higher-salinity water. An analysis of fecundity and the frequency of ovigerous females suggests that *U. maracoani* likely avoids spawning during the rainy periods along the Amazon coast when salinity tends to be lower, with a minimum of zero and a mean of 7 (Aviz et al., 2022). The hypothesis of a seasonal peak breeding strategy is supported by data from the zooplankton of the neighboring estuarine system (Marapanim River estuary), which shows that *U. maracoani* larvae (zoea I stage) are most abundant in the dry season (Lima et al., 2019).

Regarding the secondary production of *U. maracoani*, the higher value in males results from their greater biomass. Besides a larger carapace size, the major cheliped is a significant sexual morphological trait in male fiddler crabs, accounting for 13–30% of an adult's body mass (Swanson et al., 2013). Notably, the growth rate of this cheliped is higher in adults than in juvenile males (Araújo et al., 2012; Colpo et al., 2022). In addition to higher biomass, males also exhibit a faster rate (K value) at which the crab approaches the asymptotic width and the asymptotic width (L_{∞}) compared to females. Higher biomass is linked to

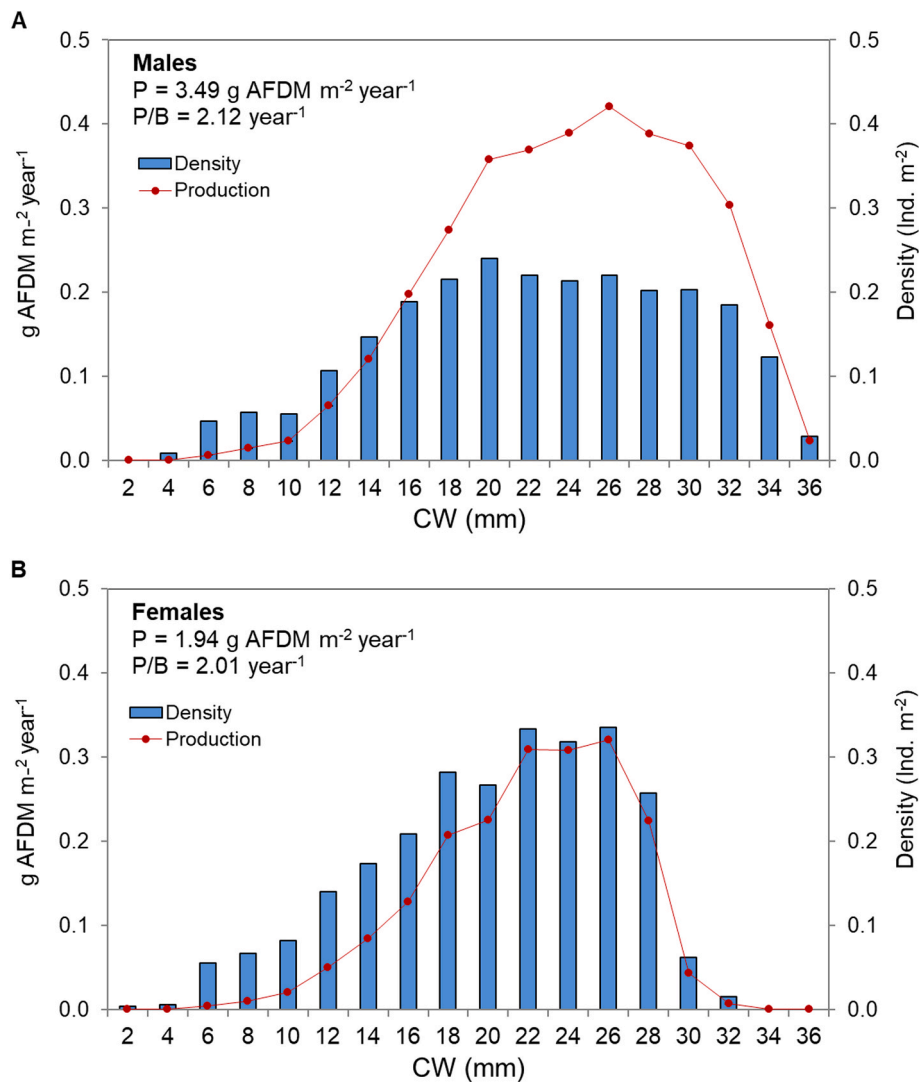


Fig. 7. Annual distribution of density and production of males (A) and females (B) across *Uca maracoani* carapace width classes.

faster growth, which consequently leads to higher production in males. Intermediate individuals contribute more to population production than either smaller or larger individuals of both sexes. This high contribution from this size class group is due to its high density associated with substantial G values, which exponentially decrease towards larger individuals. Peaks of production and biomass for both males and females occur in both dry and rainy seasons, mirroring population density fluctuations. During the rainiest months (April and May), when recruitment peaks, smaller individuals elevate their contribution to production due to their rapid growth.

The growth parameters estimated for *U. maracoani* are similar to those obtained for other Amazonian population from the Caeté Estuary (Koch et al., 2005) (Table 5). However, the growth and mortality rates at Japerica Bay were substantially lower than those estimated in the Caeté Estuary. Additionally, the P/B of *U. maracoani* from Japerica Bay was lower than the estimates for this species and other fiddler crabs in the Caeté Estuary (Tables 5 and 6). This could potentially be attributed to the oligohaline conditions and significant variations in salinity throughout the year in Japerica Bay (Table 4).

To enhance the chances of survival, plasticity in response to environmental variation impacts species fitness. This is the outcome of selecting an optimal pattern for energy allocation between maintenance, reproduction, and somatic growth (Caswell, 1983; Donelson et al., 2019). Although estuarine crabs exhibit strong osmoregulatory

capacity, comprehensive long-term growth experiments demonstrate that the energy remaining for somatic growth is halved or more at lower salinities (Guerin and Stickle, 1997a, 1997b). Thus, the extended additional energy expenditure due to subtle, sublethal effects of salinity might dictate growth, particularly for animals already living outside their optimal salinity (Guerin and Stickle, 1997a, 1997; Gillikin et al., 2004). The research focused on oxidative stress in crabs (*U. cordatus*) and oysters (*Crassostrea gasar* (Adanson, 1757)) from Japerica Bay revealed that seasonal changes in environmental conditions modulated biomarkers (in gills and muscles). Antioxidant defenses were highest during the rainy season, indicating that both species seem to be better physiologically adapted to high-salinity conditions (dos Santos et al., 2019, 2021).

Alternatively, the differences in methods utilized (Munro plot, Munro, 1982) by Koch et al. (2005) for estimating von Bertalanffy growth parameters may have resulted in higher K values for *U. maracoani* at the Caeté Estuary. This, in turn, may have led to increased mortality and P/B in this population. Although our dataset did not permit obtaining growth parameters using more reliable methods such as age-length keys, the growth curves we established appear to correctly track the modal progression of carapace width for both males and females in both study years (Fig. 5).

In terms of interspecific evaluations on secondary production, the turnover rate (P/B) is most suitable for comparison of production due to

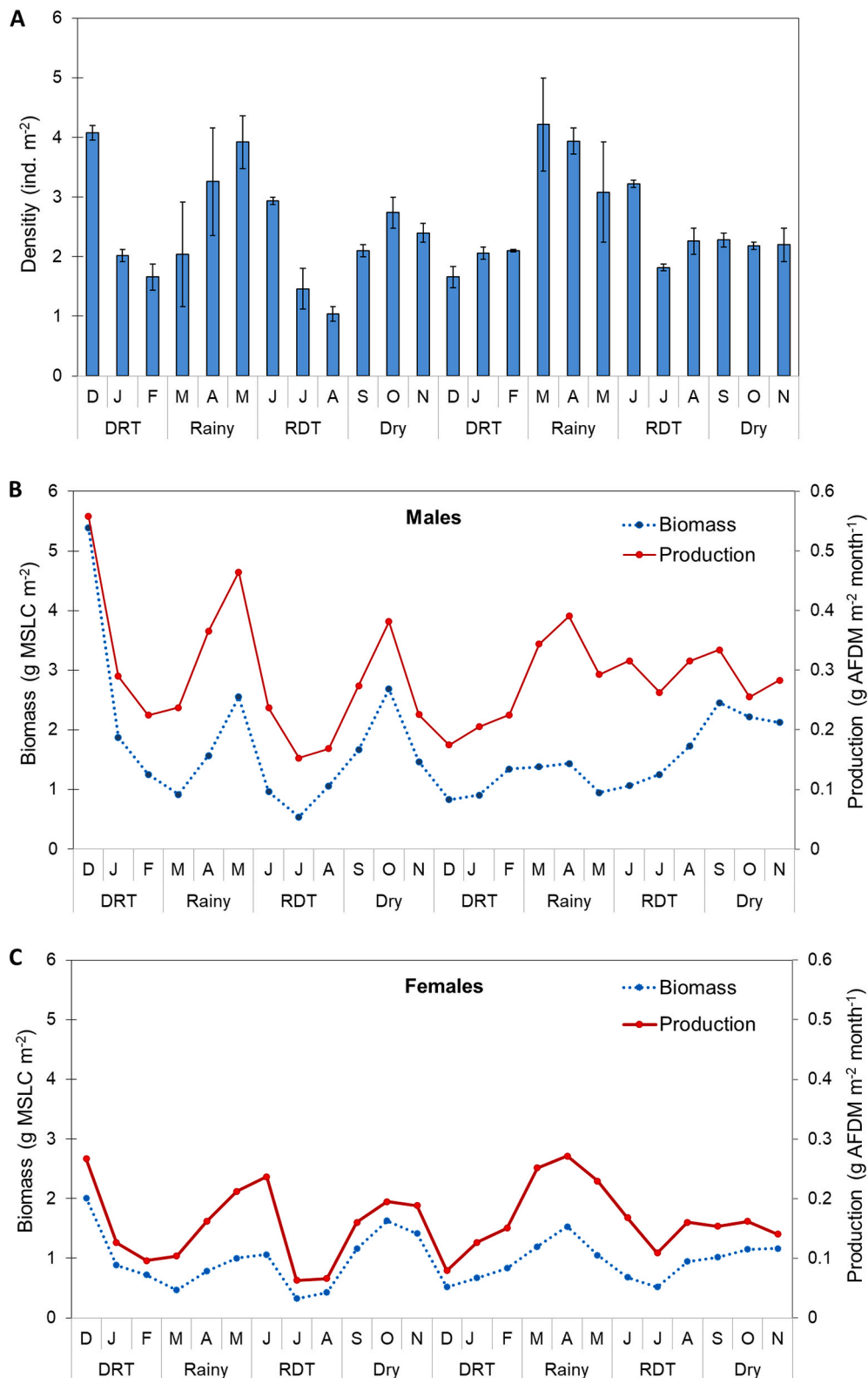


Fig. 8. Monthly density (mean ± SE) of crabs (A), biomass, and production of *Uca maracoani* males (B) and females (C). Seasonal periods: Dry-Rainy Transition (DRT); Rainy; Rainy-Dry Transition (RDT); Dry.

the significant variance between biomass and, subsequently, production across populations (Table 6). The P/B at Japerica was lower than the estimates at Caeté, which varied from 4.53 (*Minuca rapax* (Smith, 1870)) to 9.99 yr.⁻¹ (*Leptuca cumulanta* (Crane, 1943)) on the Amazonian coast. However, in comparison to non-Amazonian fiddler crab populations, the

P/B ratio of *U. maracoani* is either higher or comparable (Table 6). Referring to data about global benthic invertebrate production patterns (Cusson and Bourget, 2005), fiddler crabs typically demonstrate a high turnover rate and production. Thus, it supports the significance of fiddler crabs as they provide a critical connection to upper trophic levels

Table 4
Population aspects of *Uca maracoani* from different localities on the Brazilian coast.

Locality	Carapace width				Sex ratio	Salinity range (‰)	Air Temperature range (°C)	Font
	Mean	Maximum Male	Maximum Female	Minimum Ovigerous Female				
Japerica Bay Estuary (0°S)	21.3	36.2	32.7	15.2	0.9:1	0–39	27–32	1
Caeté Estuary (0°S)	–	32.0**	–	–	1:1	15–39	24–32	2
Baixa Grande Estuary (4°S)	25.3	38.0	36.7	24.2	3.5:1*	2–42	25–32	3
Formoso River (8°S)	21.6	36.1	32.1	14.6	1.7:1*	21–28	28–32	4
Jabaquara Estuary (23°S)	30.4	45.0	40.2	22.5	1:0.8*	25–27	18–31	5
	26.7	43.7	38.7	–	0.8:1*	–	–	6
Portinho, Praia Grande (23°S)	20.0	33.6	31.8	21.4	0.9:1	7–34	18–25	7
Baixio Mirim, Rio de Janeiro (25°S)	24.4	35.8	31.8	19.9	1:1	8–25	17–29	8
	20.3	34.2	29.2	–	3.2:1*	–	–	9

(1) Study present; (2) Koch et al. (2005); (3) Silva et al. (2016); (4) Azevedo et al. (2017); (5) Hirose and Fransozo (2008); (6) Hirose and Fransozo (2007); (7) Machado et al. (2021); (8) di Benedetto and Masunari (2009); (9) Masunari et al. (2005). * Indicate significant deviation from a ratio of 1:1. ** Maximum value assigned to the population.

Table 5
Comparison of growth and secondary production parameters between populations of *Uca maracoani* from the Amazon coast.

Parameters	Japerica Bay (0°S) ¹		Caeté Estuary (0°S) ^{2,3}	
	Male	Female	Male	Female
L _∞ (CW mm)	38.35	34.2	35.2	31
Life Span (yr.)	1.77	1.55	1.47	1.23
K	1.48	1.3	2.03	2.44
Growth index (φ')	3.33	3.18	3.2	3.0
Max age (yr.)	1.77	1.55	1.47	1.23
Mortality rate (Z yr ⁻¹)	2.91	3.51	4.9	6.0
P/B	2.08	–	4.96	–

(1) Study present; (2) Koch and Wolff (2002); (3) Koch et al. (2005).

Table 6
Growth parameters, mortality, production, and P/B ratios of different species of fiddler crabs.

Species	Sex	L _∞ (CW mm)	Max age (yr.)	Mortality rate (Z yr ⁻¹)	P/B	The study area (latitude)	Font
<i>Uca maracoani</i>	Male	38.35	1.77	2.91	2.08	Japerica Bay (0°S), Brazil	1
	Female	34.20	1.55	3.51	–	–	–
<i>Leptuca cumulanta</i>	Male	13.1	0.71	10.1	9.99	Caeté Estuary (0°S), Brazil	2,3
	Female	11.1	0.70	9.1	–	–	–
<i>Minuca vocator</i>	Male	21.6	1.10	5.7	6.48	Caeté Estuary (0°S), Brazil	2,3
	Female	20.6	1.01	7.6	–	–	–
<i>Minuca rapax</i>	Male	20.5	1.44	4.6	4.53	Caeté Estuary (0°S), Brazil	2,3
	Female	20.0	1.40	5.5	–	–	–
<i>Minuca rapax</i>	Male	31.50	1.75	5.85	1.44	Camboatá Channel (22°S), Brazil	4
	Female	27.30	1.93	4.40	–	–	–
<i>Minuca rapax</i>	Male	32.55	3.79	0.87	2.29	Itaipu Lagoon (22°S), Brazil	4
	Female	25.20	2.23	3.28	–	–	–
<i>Minuca rapax</i>	Male	32.55	2.45	1.77	2.87	Caceribu River (22°S), Brazil	4
	Female	25.20	1.63	2.43	–	–	–
<i>Minuca rapax</i>	Male	23.9	4.43	–	–	Itamambuca (23°S), Brazil	5
	Female	23.8	5.00	–	–	–	–
<i>Austruca lactea</i>	Male	11.9	2.00	1.26	0.08	Sirik Estuary (26°N), Iran	6
	Female	10.7	1.80	1.16	–	–	–

(1) Study present; (2) Koch and Wolff (2002); (3) Koch et al. (2005); (4) Costa and Soares-Gomes (2015); (5) Silva-Castiglioni et al. (2004); (6) Mokhtari et al. (2008)

development (Johnson, 2003; Hartnoll, 2006), whereas males invest in energetically expensive courtship and exert energy in agonistic interactions with other males (Hyatt and Salmon, 1978; Heatwole et al., 2018). Even though recruitment events can initially lead to an increase in density, successive reductions in the number of organisms primarily serve as a mechanism of natural population control related to density-dependent processes such as competition for limited food or space (Bertness, 1989; Olafsson et al., 1995).

5. Conclusions

Our results showed that *Uca maracoani* has a well-established population in the mangroves of Japerica Bay Estuary, Amazon coast of northern Brazil. This population demonstrates continuous reproduction and recruitment, along with significant seasonal changes in density, biomass, and production throughout the year. The species benefits from the vast muddy intertidal areas and the copious organic matter delivered by estuaries despite salinity fluctuations. We recommend further studies on a broader spatial scale to validate the observed patterns. Even with evident seasonal shifts, different population responses may occur in other parts of the estuary, near the river mouth, where environmental variations could differ, especially regarding salinity. Moreover, it is crucial to better understand survival mechanisms in the face of low salinity, including behavioral and physiological responses, as well as their impacts on growth and secondary production.

CRedit authorship contribution statement

Daiane Aviz: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization. **Marcelo Petracco:** Writing – review & editing, Writing – original draft, Formal analysis. **Priscila Amorim Carmona:** Writing – original draft, Methodology. **Cleerson Rannieri Meira dos Santos:** Writing – review & editing, Resources, Methodology, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2024.106603>.

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