

Article

Population Dynamics and Extractive Potential of the Mangrove Crab, *Ucides cordatus* (Linnaeus, 1763), in a Human-Impacted Mangrove of Northeastern Brazil

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Abstract

Ucides cordatus, a key species in Brazilian mangroves, supports both ecological processes and traditional extractive practices. Some mangrove areas in Northeastern Brazil are increasingly exposed to anthropogenic stressors. We evaluated the population density, size structure, extractive potential, and morphological maturity of this species in Acupe (state of Bahia), integrating environmental and human disturbance variables. Surveys conducted in 2018–2019 revealed a high proportion of undersized individuals (93.1% below the legal minimum catch size), with larger crabs concentrated in warmer months and near the estuarine fringe. Although solid waste and tree cutting were evident throughout the study area, no statistically significant association was detected with crab abundance or forest structure. Maturity estimates were a carapace width of 54.6 mm for males and 50.7 mm for females, suggesting early reproductive investment in females. Principal Component Analysis indicated that crab density and extraction potential correlated with rainfall, temperature, and vegetation structure, rather than local anthropogenic pressures. Despite moderate densities, the predominance of immature individuals and signs of overfishing highlight the need for improved management. We recommend that *L. racemosa*-dominated mangrove sectors, generally associated with high proportions of undersized crabs, should be considered priority areas for no-take or recovery zones.

Keywords: Decapoda; anthropogenic impact; sexual maturity; crab density; fisheries management



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1. Introduction

Mangroves are tropical and subtropical coastal ecosystems of high ecological and socioeconomic relevance, covering approximately 148,000 km² worldwide, 14.5% of which

are in South America [1]. In Brazil, mangrove forests occupy around 9900 km², predominantly concentrated in the states of Maranhão, Pará, Amapá, and Bahia, which together account for 85% of the national mangrove area [2].

Mangroves perform key ecological functions such as serving as nurseries for terrestrial and aquatic species, stabilizing shorelines, trapping sediments from rivers, and sequestering carbon [1,3–6]. These ecosystems also provide essential resources to traditional coastal communities, including food, medicinal products, fuel, and construction materials [1,7,8]. In many parts of northern and northeastern Brazil, artisanal fishing remains a critical livelihood [9–11].

Among the various crustacean species associated with mangrove systems, the mangrove crab *Ucides cordatus* (Linnaeus, 1763) (commonly known as “uçá”-crab) is particularly notable. Endemic to the western Atlantic coast, ranging from Florida (USA) to southern Brazil (state of Santa Catarina), it dominates the epibenthic biomass in Brazilian mangroves, representing up to 76% of the community [3,12].

The “uçá”-crab inhabits individual burrows up to 1.5 m deep [13] and plays a key role in bioturbation, promoting sediment oxygenation [14], drainage [15,16], energy flow, and carbon cycling [17,18]. Its herbivorous diet consists primarily of mangrove leaves and propagules, consumed mostly during nocturnal low tides [19].

Despite its ecological importance, *U. cordatus* exhibits slow growth and reaches sexual maturity (51.3 and 43.0 mm CW for males and females, respectively) only after two to three years, which increases its vulnerability to overharvesting [12,20]. Its reproductive cycle is seasonal, typically occurring from November to March [21], and is especially sensitive to fishing pressure during the mating migration known as “andada” [12,22].

An estimated 278,000 people in Brazil depend directly on mangrove-based fisheries [23], with *U. cordatus* serving as a key species for food security and income among coastal communities [7,11,24–26]. However, overfishing, deforestation, coastal development, and disease (e.g., Lethargic Crab Disease) have caused marked population declines [12,27]. Between 1994 and 2007, *U. cordatus* landings in Brazil fell by 57% [12], a trend also confirmed by ethnobiological surveys with local crab harvesters [26].

In response, management policies have been introduced, including IBAMA ordinances (#34/2003 for North/Northeast and #52/2003 for Southeast/South) and Brazilian Ministry of the Environment regulations (IN-MMA #05/2004), which officially recognized the species as overexploited. Subsequent proposals have addressed population management [9], sustainable transport [28], and population monitoring [29,30]. Nevertheless, *U. cordatus* remains listed as “Near Threatened” at the national level [31], and as “Critically Endangered” in Bahia, where it is fully protected under state law (SEMA Ordinance #37/2017, Article 4).

The Acupe district, located in “Todos os Santos” Bay, is one of the most important harvesting zones for *U. cordatus* in the state of Bahia [32,33], where signs of population decline have been reported [34,35]. Although the species has been extensively studied along the Brazilian coast, bioecological and fisheries data specific to Bahia, especially “Todos os Santos” Bay, remain scarce [36].

This study tested two central hypotheses: (1) that the *U. cordatus* population in Acupe supports commercial harvesting in terms of density and individual size and (2) that the conservation status of the mangrove forest influences the population parameters of the species. To address these questions, we evaluated the population density, size structure, extractive potential, and morphological maturity of *U. cordatus* while also analyzing environmental factors such as dominant arboreal species, tidal inundation level, solid waste density, and logging.

Given its long history of traditional crab harvesting, proximity to urban areas, and evident signs of ecological degradation, the Acupe mangrove represents a critical case study for understanding how *U. cordatus* populations respond to cumulative anthropogenic pressures. The area's predominance of *Laguncularia racemosa*, a species often associated with disturbed or regenerating mangroves, further underscores its ecological singularity. Our study provides not only a baseline assessment of the population status of this species under human-induced stress at the time of sampling but also a valuable reference for guiding region-specific management and conservation strategies in Todos os Santos Bay and in other similarly impacted estuarine systems.

2. Materials and Methods

2.1. Study Area and Sampling Design

Fieldwork was conducted monthly from December 2018 to November 2019 in a mangrove forest located in the Acupe district ($12^{\circ}39'13.94''$ S; $38^{\circ}44'44.00''$ W), Santo Amaro Municipality, within “Todos os Santos” Bay, Bahia, Brazil (Figure 1). This coastal region has a population density of 113.27 inhabitants/km² [37]. It is influenced by the Subaé River estuary, where activities such as shellfish harvesting, fishing, livestock farming, and shrimp aquaculture are prominent. The mangrove fringe features slightly elevated topography (~1 m above the tidal channel) and is located approximately 150 m from a series of aquaculture ponds and 270 m from the urban area.

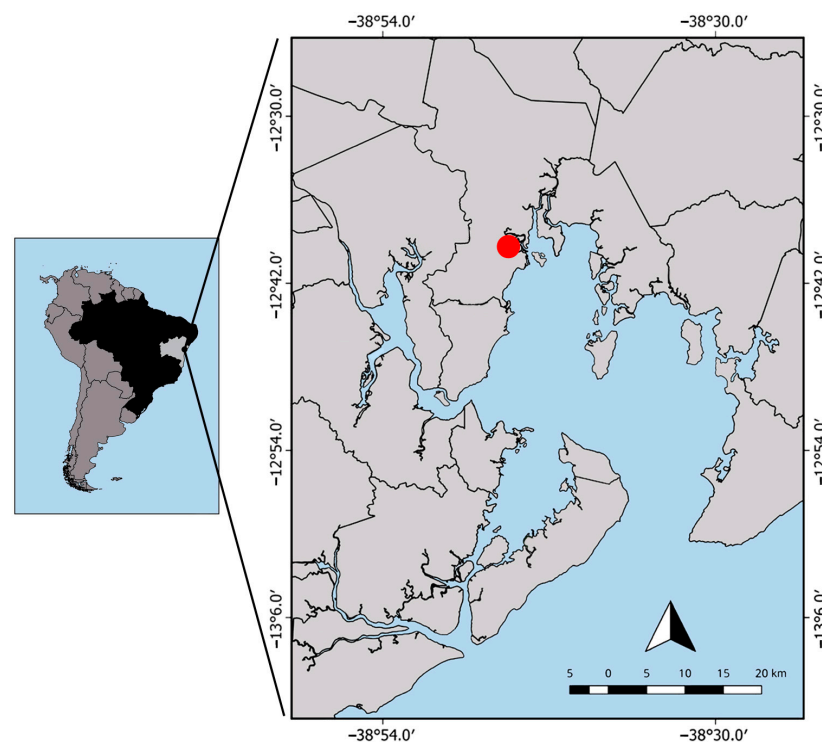


Figure 1. Map of Todos os Santos Bay, Bahia State (Brazil), showing the location of the sampling site ($12^{\circ}39'13.97''$ S, $38^{\circ}44'44.00''$ W) in the Acupe district, Santo Amaro County (red circle).

Monthly records of air temperature (TMP) and rainfall (RFL) were obtained from daily datasets [37] provided by the TRMM.4082 meteorological station, located in Saubara, 9 km from Acupe (Table 1).

Table 1. Monthly variation in climatic parameters, mangrove forest structure, anthropogenic impacts, and population data of *Ucides cordatus* in the Acupe mangrove (Bahia, Brazil) from December 2018 to November 2019.

Month/Year	Climatological Data		<i>Ucides cordatus</i> Data				Mangrove Characteristics				Mangrove Impacts	
	TMP * (°C)	RFL * (mm)	Number of Open Galleries	Number of Closed Galleries	CD (ind./m ²)	FEP (%)	DBH (cm)	TRD (ind./m ²)	SDN (ind./m ²)	TFL (cm)	CTD (ind./m ²)	SWD (g/m ²)
Dec/2018	26.5 ± 4.0	141.9	211	21	1.86 ± 0.64	87.9	na	na	na	na	na	2.9 ± 2.0
Jan/2019	27.1 ± 4.4	28.6	243	5	2.00 ± 0.64	83.4	na	na	na	na	na	0.3 ± 0.8
Feb/2019	28.5 ± 4.2	23.0	224	20	1.95 ± 0.45	92.1	4.03 ± 2.26	0.24 ± 0.10	0.06 ± 0.14	na	0.06 ± 0.09	0.4 ± 0.6
Mar/2019	28.1 ± 4.1	222.4	244	8	2.01 ± 0.58	93.4	5.19 ± 3.28	0.26 ± 0.13	0.10 ± 0.07	11.6 ± 2.0	0.10 ± 0.07	1.0 ± 0.9
Apr/2019	27.3 ± 3.7	39.8	216	7	1.78 ± 0.87	95	3.60 ± 1.08	0.28 ± 0.12	2.18 ± 2.81	na	0.34 ± 0.10	7.6 ± 4.3
May/2019	26.1 ± 3.7	63.2	136	6	1.14 ± 0.30	97.8	4.15 ± 2.60	0.22 ± 0.09	4.78 ± 4.25	na	0.10 ± 0.02	2.6 ± 2.2
Jun/2019	24.2 ± 3.8	3.6	142	5	1.20 ± 0.26	98.6	4.26 ± 2.98	0.26 ± 0.10	1.7 ± 2.10	13.7 ± 2.8	0.07 ± 0.06	2.8 ± 4.9
Jul/2019	23.4 ± 4.3	22.3	178	20	1.58 ± 0.31	91.0	3.97 ± 2.76	0.30 ± 0.07	0.20 ± 0.45	na	0.02 ± 0.05	7.9 ± 9.2
Aug/2019	23.5 ± 3.9	1.3	94	47	1.13 ± 0.40	97.9	3.45 ± 1.60	0.37 ± 0.10	0.44 ± 0.64	14.5 ± 2.8	0.14 ± 0.09	5.8 ± 7.5
Sep/2019	24.2 ± 3.8	3.6	71	56	1.01 ± 0.42	100.0	3.81 ± 1.51	0.15 ± 0.06	0	13.8 ± 2.4	0.11 ± 0.12	2.9 ± 3.0
Oct/2019	25.6 ± 4.7	0.8	182	10	1.54 ± 0.54	95.6	2.98 ± 1.38	0.35 ± 0.14	0	15.9 ± 3.6	0.18 ± 0.10	1.6 ± 1.6
Nov/2019	26.8 ± 5.1	0.0	174	2	1.41 ± 0.44	98.9	3.43 ± 1.38	0.34 ± 0.12	0	13.9 ± 3.1	0.13 ± 0.09	1.9 ± 1.5
Mean ± SD	25.9 ± 1.8	45.9 ± 68.6	176 ± 56.2	17 ± 17.4	1.55 ± 0.59	93.1	3.9 ± 0.6	0.28 ± 0.11	0.95 ± 2.18	13.8 ± 2.0	0.12 ± 0.11	3.1 ± 4.5

* Monthly data (from 1 December 2018 to 30 November 2019) from climatological station TRMM.4082; TMP, air temperature; RFL, rainfall; CD, crab density; FEP, Future Extractive Potential; DBH, diameter at breast height; TRD, Tree density; SDN, seedling density; TFL, tidal flood level; CTD, cut tree density; SWD, solid waste density; na, not available, SD, standard deviation.

2.2. Crab Sampling and Field Methods

Sampling of *Ucides cordatus* (Figure 2) was conducted using 5×5 m quadrats [29] delimited using a measuring tape and a square frame [30], totaling five units (125 m^2) per month. Quadrats were allocated along a transect perpendicular to the estuarine margin, with positions randomly selected within three predefined distance bands from the margin: 0–10 m (Q1 and Q2), 20–30 m (Q3), and 40–50 m (Q4 and Q5), representing different positions along the landward mangrove gradient and preventing quadrat overlap [29]. The unsampled intervals between distance bands were intentional and followed the standardized monitoring protocol, aiming to represent discrete sectors along the fringe–interior gradient while reducing overlap among sampling units.



Figure 2. Adult male of *Ucides cordatus* in a mangrove habitat at the Juréia-Itatins Ecological Station, São Paulo State. Photo by Marcelo Pinheiro (CRUSTA–UNESP IB/CLP).

Within each quadrat, all active burrows of *U. cordatus* were counted, following the same protocol and features established by Pinheiro et al. [30]. Open active burrows were identified by recent sediment displacement, fresh tracks, humid margins, or visible biogenic activity. Recently closed burrows were considered active when the closure was fresh and compatible with temporary sealing, especially during the molting period. Abandoned burrows were excluded when they showed collapsed entrances, dry or compacted sediment, absence of fresh excavation marks, leaf accumulation, or no evidence of recent crab activity.

The diameter of open, active burrows was measured parallel to the sediment surface using an analog caliper. To avoid overestimation due to recounting, each burrow was marked with a plastic flag. In the case of multiple-opening burrows, only the first entrance encountered was measured, and the others were sealed (following the protocol recommended by [30]) to ensure that each gallery was attributed to a single individual.

Tidal flooding level (TFL) was recorded using a measuring tape, corresponding to the maximum vertical distribution of macroalgae (“*Bostrychietum*”) on the trunks or aerial roots of five trees within each quadrat. All field protocols followed the standardized procedures outlined in the *U. cordatus* Monitoring Protocol, part of Brazil’s national “Monitora Manguezal” Program [30,38].

2.3. Mangrove Forest Characterization

Within each quadrat, arboreal vegetation was identified [38,39] and categorized into seedlings (SDN: height ≤ 15 cm) and adult trees (height ≥ 1.5 m). Adult trees had their diameter at breast height measured 1.3 m from the ground (DBH). Tree density (TRD) and cut tree density (CTD) were calculated per quadrat, with CTD as a proxy for anthropogenic disturbance (signs of cutting by axe or machete) related to wood extraction.

Solid waste (SWD) was also collected from each quadrat. Debris was washed, dried in a forced-air oven at 50 °C for 72 h, and weighed on a digital scale with 0.01 g precision, following [40]. The relative composition (%) of debris types (e.g., plastic, rubber, metal, Styrofoam, wood, fabric, and glass) was also determined.

2.4. Population Density Estimation

Population density was estimated indirectly by counting active burrows, assuming that each burrow corresponds to one individual crab [16,41]. This method has been recommended for *U. cordatus* population assessments [29] and widely applied in subsequent studies [16,36,42]. It is also incorporated in the *U. cordatus* Monitoring Protocol [30] under the national “Monitora Manguezal” Program [38].

Crab density (CD, ind. m⁻²) was calculated as the number of active burrows (i.e., open with biogenic activity or recently closed) within each quadrat divided by the quadrat area (25 m²). Abandoned burrows with no biogenic signs were excluded from the analysis [30].

2.5. Size Structure and Extractive Potential

The diameter of each open, active burrow (DG, cm) was measured using a modified analog caliper [27]. These values were converted to carapace width (CW) using the national conversion equation ($CW = 0.632DG + 24.74$, $n = 719$, $R^2 = 71.2\%$) covering the entire body size variation of *U. cordatus* in Brazil, proposed by Pinheiro et al. [43]. This equation presents a mean absolute prediction error of 4.4 mm (SD = 3.4 mm) and was specifically developed to minimize estimation variance across Brazilian mangrove populations [43]. Values of $CW \geq 96$ mm were excluded, as this is the maximum size reported for the species [20].

Extractive potential was classified as immediate (IEP) or future (FEP) based on the legal minimum catch size (60 mm CW), as defined by IBAMA regulation #034/2003-N for the North and Northeast of Brazil. IEP included crabs with $CW \geq 60$ mm, while FEP included those with $CW < 60$ mm [42].

2.6. Sex Ratio, Reproductive Period, and Morphometric Maturity

Each month, a local crab gatherer manually collected 25 individuals of *U. cordatus* across different ontogenetic stages (five individuals from within or near each sampling quadrat). The captured animals were placed in raffia bags, transported alive to the laboratory, and euthanized by freezing. Ovigerous females were recorded, measured (CW), and immediately released back into the environment.

All individuals were subjected to biometric measurements, including carapace width (CW), propodus length of the major chela (MPL) in males, and the width of the fifth abdominal segment (AB) in females. Measurements were taken with a digital caliper (precision: 0.01 mm). Sex was determined based on abdominal shape, gonopore position, and the presence (in males) or absence (in females) of gonopods [41].

Morphometric maturity (CW₅₀) was estimated separately for each sex based on biometric relationships: MPL vs. CW for males and AB vs. CW for females. These relationships have been used in prior studies to estimate the size at morphological maturity in *U. cordatus*.

tus [44–47]. The sex ratio was determined monthly and for the entire study period, while the reproductive season was inferred from the monthly occurrence of ovigerous females.

2.7. Statistical Analyses

Monthly mean crab densities were compared with each other and among estuarine distance bands (0–10, 20–30, and 40–50 m). Before analysis, data were tested for normality (Shapiro–Wilk test) and homogeneity of variances (Levene’s test), both at a 5% significance level. Assumptions were met, allowing for one-way ANOVA with Tukey’s post hoc test ($p < 0.05$).

Carapace width (CW) data, obtained via conversion from burrow diameter (DG), were used to calculate monthly mean sizes, which were compared with each other and among estuarine distance bands using one-way ANOVA (after normality and homogeneity of variances were tested). Student’s *t*-test was applied to compare CW between sexes. Monthly sex ratio deviations were tested using Yates-corrected chi-square tests ($p < 0.05$).

Associations between variables were evaluated using Spearman’s correlation coefficient (ρ), examining relationships between biotic crab parameters (density and size) and environmental variables (air temperature and rainfall), biotic forest parameters (seedling and adult tree density and diameter at breast height), and anthropogenic stress indicators (solid waste and cut tree density). Correlations were also tested between the proportions of open and closed burrows and climatological parameters (air temperature and rainfall).

A Principal Component Analysis (PCA) was performed using the Spearman correlation matrix to summarize the joint variation among environmental variables, forest structure, anthropogenic indicators, and *U. cordatus* population descriptors. Variables were standardized prior to analysis, and components with eigenvalues > 1 were retained for interpretation according to the Kaiser criterion. Variable contributions and loadings were used to identify the main gradients represented by each component.

Morphometric maturity for each sex was estimated from the MPL vs. CW and AB vs. CW relationships, with variables log-transformed prior to analysis. Successive linear regressions were performed to calculate standardized residuals. Observations with residuals $\geq |2.57|$ were considered outliers and removed iteratively. The dataset was then subjected to K-means clustering to classify individuals into two groups (presumed juveniles and adults), and the classification was validated through discriminant analysis, following [48,49]. Regression constants (intercept “a” and slope “b”) for each group were compared using Student’s *t*-tests [50] to test for significant differences between age classes.

CW₅₀ was defined as the body size (CW) at which 50% of individuals were considered morphologically mature, based on logistic regression models [51], where the response variable was the binary maturity condition (immature = 0; mature = 1).

All statistical analyses were conducted in R (version 4.3.2) [52] using the following packages:—stats [Shapiro–Wilk: `shapiro.test()`; chi-square: `chisq.test()`; ANOVA: `aov()`; Student’s *t*-test: `t.test()`; regression analysis: `lm()`; and K-means: `kmeans()`];—car [Levene’s test: `leveneTest()`];—MASS [discriminant analysis: `lda()`].

3. Results

3.1. Mangrove Forest Structure and Anthropogenic Impacts

The study site was characterized by a monodominant vegetation structure composed exclusively of *L. racemosa* (white mangrove). Tree diameter at breast height (DBH) ranged from 0.76 to 16.46 cm (mean $\pm$ standard deviation: 3.9 ± 0.6 cm). Adult tree density (TRD) varied from 0.08 to 0.56 ind. m^{−2} (0.28 ± 0.11 ind. m^{−2}), showing negative correlations with rainfall (RFL: $\rho = -0.30$, $p < 0.05$) and tree size (DBH: $\rho = -0.45$, $p < 0.01$). Seedlings (SDN) were recorded between February and August, with densities ranging from 0 to

8.8 ind. m^{-2} (0.95 ± 2.18 ind. m^{-2}), positively correlated with RFL ($\rho = 0.49$, $p < 0.001$) and DBH ($\rho = 0.37$, $p = 0.01$). Tidal flooding level (TFL) ranged from 11.2 to 18.4 cm (mean: 13.8 ± 2.0 cm) (Table 1).

Regarding anthropogenic impacts on the mangrove ecosystem (Table 1), evidence of tree cutting within the forest was recorded between February and November 2019, with cut tree density (CTD) ranging from 0 to 0.44 ind. m^{-2} (0.12 ± 0.11 ind. m^{-2}). In addition, solid waste was consistently observed throughout the sampling period, with waste densities (SWD) varying from 0 to 21.1 g m^{-2} (mean: 3.1 ± 4.5 g m^{-2}). Among the debris, plastic items were the most prevalent (85%), followed by polystyrene (6%), metal (3%), organic matter (2%), fabrics (2%), and rubber (2%).

3.2. Population Density and Burrow Types

A total of 2335 *U. cordatus* burrows were recorded and measured across the 12-month period. Open burrows were more frequent (91%) than closed ones (9%). Although closed burrows were present year-round, they exceeded 10% only in August (33%) and September (44%) 2019. Open burrow frequency was significantly positively correlated with mean monthly air temperature ($\rho = 0.77$, $p = 0.003$), with a similar but non-significant trend for rainfall ($\rho = 0.54$, $p = 0.07$). In contrast, closed burrows showed no significant correlation with air temperature ($\rho = 0.34$, $p = 0.28$) or rainfall ($\rho = 0.03$, $p = 0.93$).

The monthly density of *U. cordatus* varied from 1.01 to 2.02 ind. m^{-2} (1.55 ± 0.59 ind. m^{-2}), with a significant difference between two groups of months ($F = 2.59$; $p = 0.011$), with one of them having a higher density [37] than the other (May to November 2019) (Table 1; Figure 3A). Crab density was also positively correlated with air temperature ($\rho = 0.39$, $p < 0.01$), but not with rainfall ($\rho = 0.23$, $p > 0.05$). During warmer months (November to April; mean max temp ≥ 30 °C), mean density reached 1.84 ± 0.60 ind. m^{-2} , significantly higher than in cooler months (1.27 ± 0.41 ind. m^{-2}) ($F = 18.3$; $p < 0.001$).

Crab density also differed according to distance from the estuarine margin ($F = 7.62$; $p = 0.001$), with higher values near the waterline (0–10 m: 1.88 ± 0.64 ind. m^{-2}) than at intermediate (20–30 m: 1.32 ± 0.41 ind. m^{-2}) or more inland zones (40–50 m: 1.34 ± 0.45 ind. m^{-2}), which did not differ from each other (Figure 3B).

3.3. Size Structure and Extractive Potential

Monthly crab size ranged from 17.1 to 87.2 mm CW. The lowest and highest monthly means were 47.6 ± 5.1 mm (June 2019) and 54.5 ± 6.8 mm (January 2019), respectively. The overall mean crab size for Acupe was 50.9 ± 2.5 mm, below the legal minimum catch size (60 mm CW; IBAMA Ordinance #034/2003).

Mean size varied significantly across months ($F = 19.41$; $p = 0.001$), with January presenting the largest individuals, significantly different from those in February–May and August–November. The lowest means were in June and September, which were statistically similar only to August (Figure 4A). During the warm season (November to April), crabs reached a mean CW of 52.2 ± 2.3 mm, significantly higher than in the rest of the year (49.2 ± 3.3 mm; $F = 17.1$; $p < 0.001$). Mean monthly size was positively correlated with temperature ($\rho = 0.45$, $p < 0.01$) and rainfall ($\rho = 0.30$, $p < 0.05$).

Crab size did not significantly differ across estuarine distances ($F = 2.73$; $p = 0.07$) (Figure 4B). Individuals below the legal catch size (<60 mm CW) were observed across all sampling zones, regardless of proximity to the waterline.

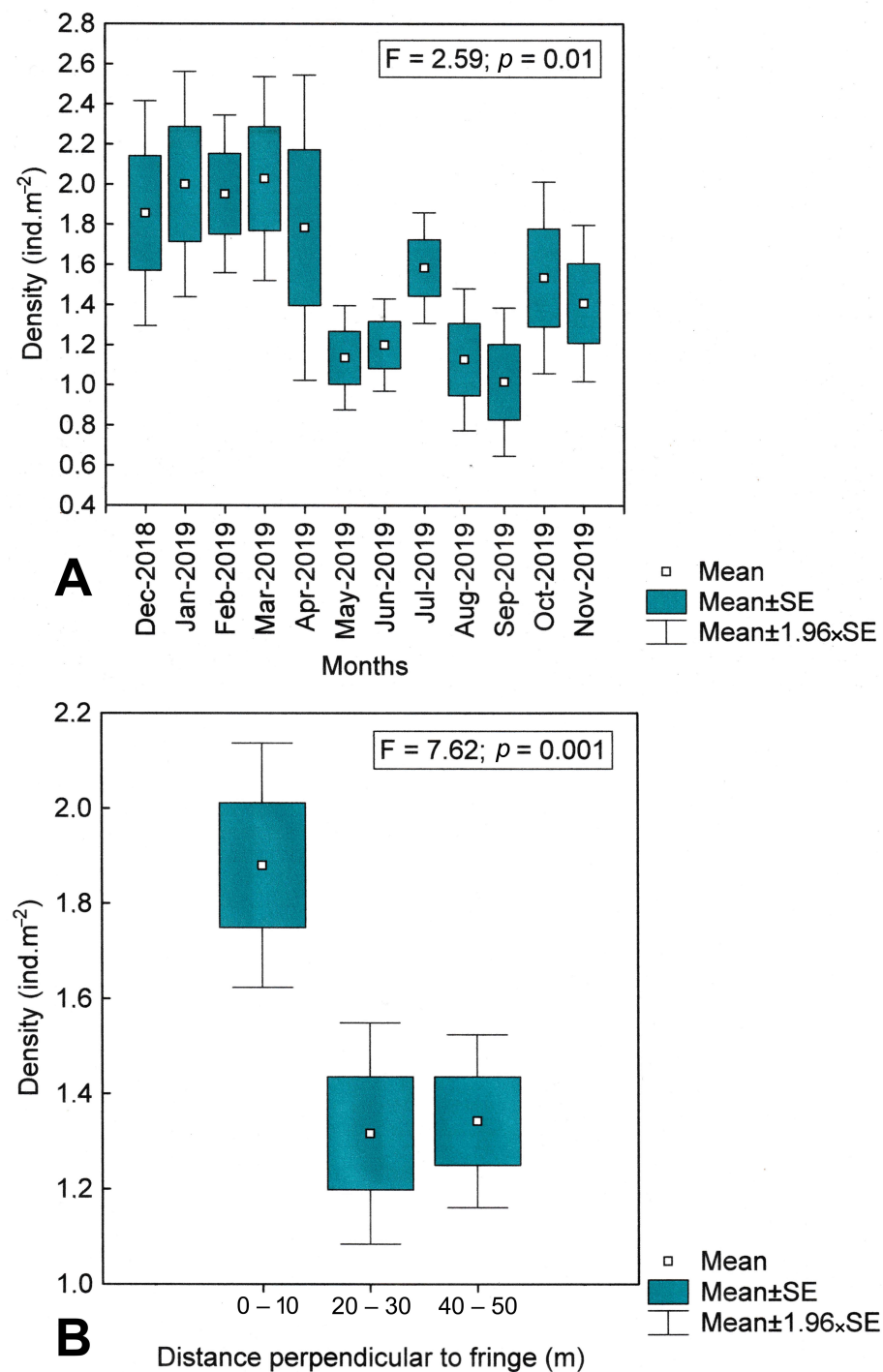


Figure 3. Density (CD, in ind. m⁻²) of *Ucides cordatus* in the Acupe mangrove from December 2018 to November 2019. (A) Monthly variation of CD over the study period. (B) CD variation across distances from the estuarine margin.

Future extractive potential (FEP) remained above 80% throughout the study period, with an overall FEP of 93.1%, indicating that most individuals were not legally harvestable (Table 1). The highest proportion of individuals (50.8%) fell into the 50–60 mm CW class, close to the threshold between immediate and future extractive potential (Figure 5). Notably, during the warmer months (≥ 30 °C; November to March), the number of individuals ≥ 60 mm CW tripled ($n = 110$) compared to cooler months ($n = 42$), although the overall extractive potential status did not change significantly.

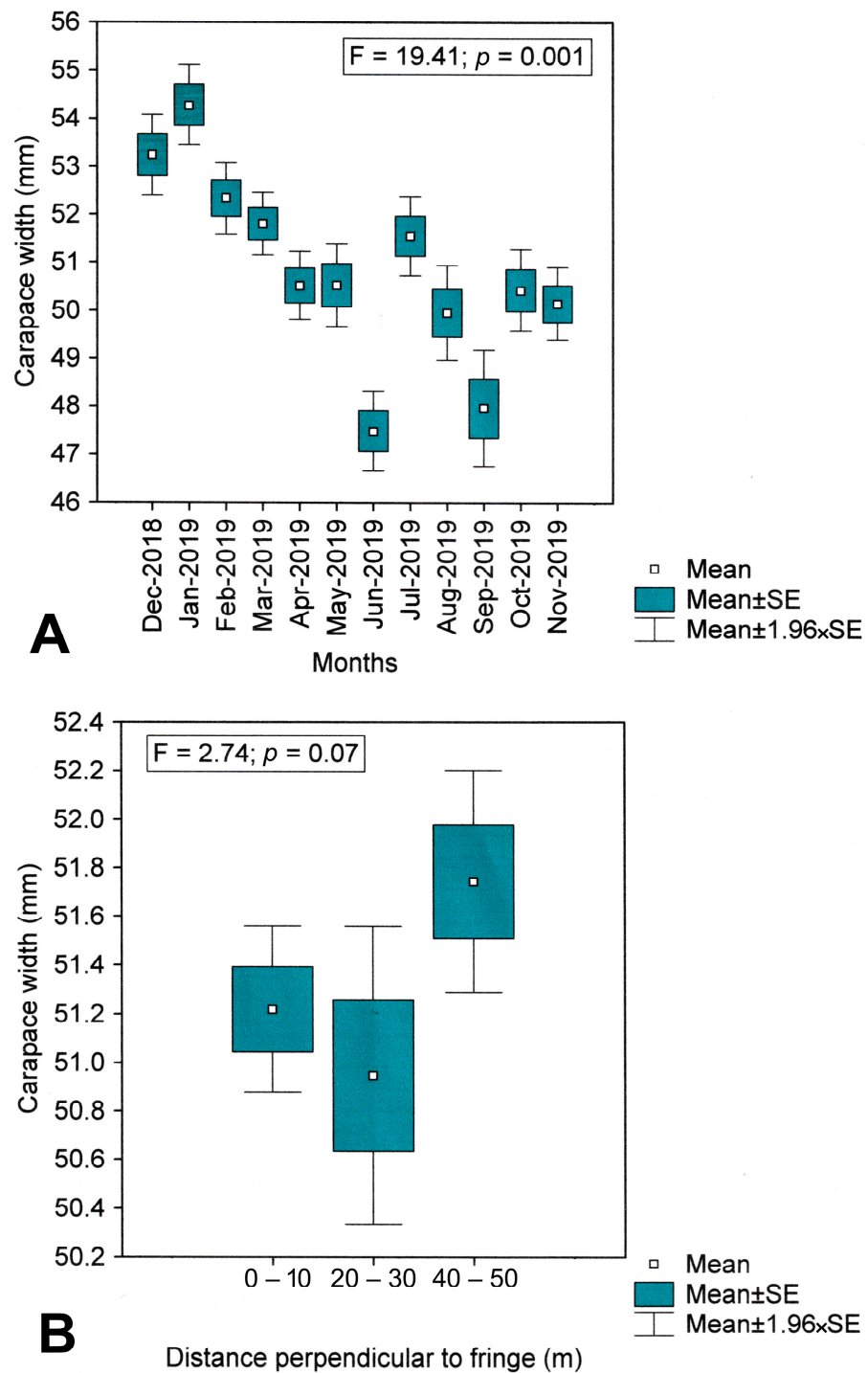


Figure 4. Carapace width (CW, in mm) of *Ucides cordatus* in the Acupe mangrove from December 2018 to November 2019. **(A)** Monthly variation of CW over the study period. **(B)** CW variation across distances from the estuarine margin.

3.4. Sex Ratio, Reproductive Period, and Maturity

A total of 298 *U. cordatus* individuals were sampled: 219 males (73.5%) and 79 females (26.5%), of which 15 (19%) were ovigerous. The sex ratio (M:F = 2.8:1) was significantly male-biased ($\chi^2 = 64.84; p < 0.001$), particularly in April, June, and from August to November. In other months, the ratio did not differ from 1:1 (Figure 6; Table S1).

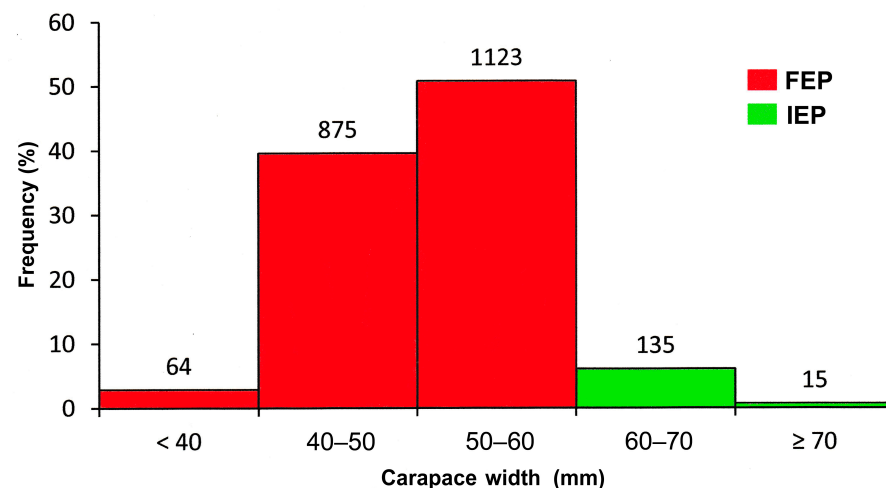


Figure 5. Size-class distribution of *Ucides cordatus* (carapace width, CW) in Acupe from December 2018 to November 2019. Red and green bars represent the relative frequencies of individuals with future extractive potential (FEP) and immediate extractive potential (IEP), respectively. Absolute frequencies showed as numbers above each column.

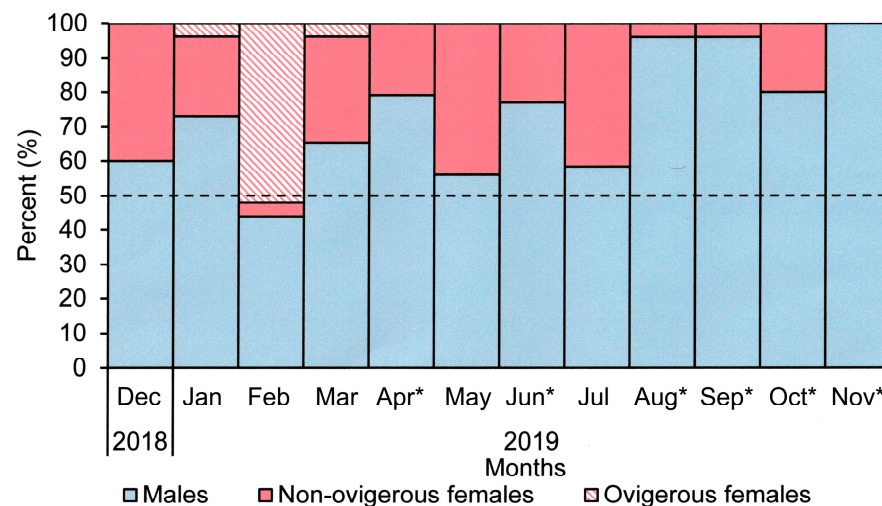


Figure 6. Percentage of males and females (ovigerous and non-ovigerous) of *Ucides cordatus* collected in the Acupe mangrove from December 2018 to November 2019. Asterisks indicate months in which the sex ratio differed significantly from 1:1 according to Yates-corrected chi-square tests ($p < 0.05$).

Male CW ranged from 26.1 to 78.7 mm (mean: 56.9 ± 7.4 mm), significantly larger ($t = 65.9$; $p < 0.001$) than females (38.5 to 61.6 mm; mean: 51.3 ± 4.4 mm). Ovigerous females ranged from 39.5 to 57.2 mm CW (mean: 50.5 ± 4.3 mm), observed between January and March, peaking in February ($n = 13$; 93%). Morphometric maturity (CW_{50}) was estimated at 54.6 mm for males and 50.7 mm for females (Figure 7).

3.5. Principal Component Analysis (PCA) and Variable Associations

Principal Component Analysis (PCA), based on Spearman's correlation matrix, was conducted to evaluate the joint variation of biotic and abiotic variables associated with mangrove forest structure and *U. cordatus* population. The first two principal components (PC1 and PC2) accounted for 45.7% of the total variance, with 27.0% and 18.7%, respectively (Figure 8A). According to the Kaiser criterion, only components with eigenvalues greater than 1.0 were retained for interpretation, namely PC1 (eigenvalue = 2.43) and PC2 (eigenvalue = 1.69).

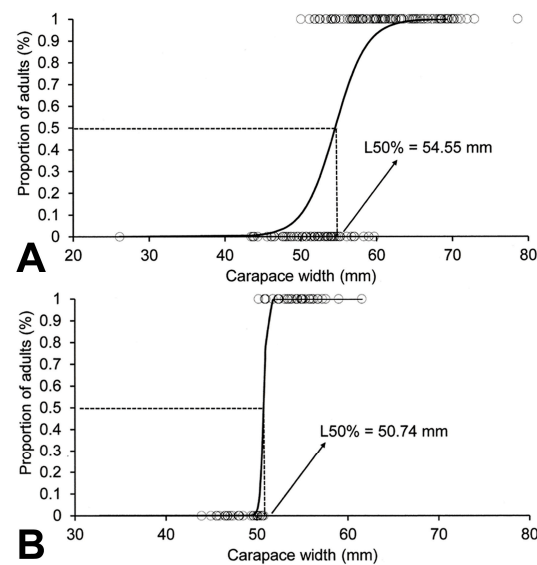


Figure 7. Size at the onset of morphological maturity of *Ucidus cordatus* in Acupe, estimated by logistic regression based on the presence or absence of external reproductive traits plotted against carapace width. (A) Males and (B) females.

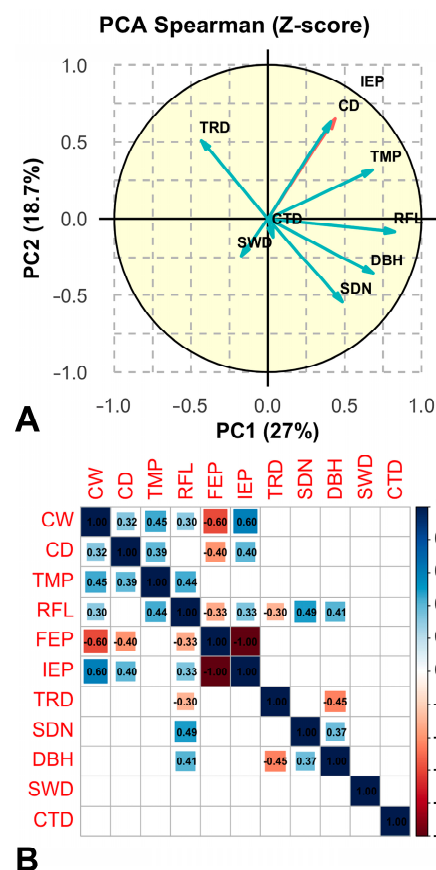


Figure 8. (A) Principal component analysis (PCA) of environmental and biological variables in the Acupe mangrove, showing the contribution of air temperature (TMP), rainfall (RFL) adult tree density (TRD), diameter at breast height (DBH), seedling density (SDN), solid waste density (SWD), cut tree density (CTD), immediate extractive potential (IEP) and crab density (CD). Independent variables (blue arrows); dependent variable (red arrow). (B) Spearman's correlation coefficients examining relationships between biotic crab parameters (CD and CW, carapace width), environmental variables (TMP and RFL), biotic forest parameters (SDN, TRD and DBH), and anthropogenic stress indicators (SWD and CTD).

Principal component 1 (PC1) was primarily influenced by rainfall (RFL; contribution = 28.0%), diameter at breast height (DBH; 19.4%), and temperature (TMP; 19.1%), all of which exhibited strong positive loadings (RFL = 0.826, DBH = 0.686, TMP = 0.682). Seedling density (SDN) and tree density (TRD) also contributed to PC1, with loadings of 0.485 and -0.433 , respectively.

Tree density (TRD) showed significant negative correlations with rainfall (RFL: $\rho = -0.68$, $p < 0.01$) and diameter at breast height (DBH: $\rho = -0.59$, $p < 0.05$) (Figure 8B). In contrast, SDN was positively correlated with both DBH ($\rho = 0.55$, $p < 0.05$) and RFL ($\rho = 0.62$, $p < 0.05$), suggesting a positive association of rain period and seedling recruitment and mangrove areas with adult trees (Figure 8B).

Principal component 2 (PC2) was mainly defined by crab density (CD; contribution = 25.2%), immediate extraction potential (IEP; 23.8%), and tree density (TRD; 15.4%), each with high positive loadings (CD = 0.439, IEP = 0.410, TRD = 0.509). These variables were positively correlated, indicating that areas with higher crab densities are associated with denser mangrove forests, as well as greater extraction potential. These associations were supported by significant correlations between CD and IEP ($\rho = 0.71$, $p < 0.01$) and between CD and TRD ($\rho = 0.66$, $p < 0.05$).

Anthropogenic impact variables, represented by solid waste density (SWD) and cut tree density (CTD), contributed minimally to both principal components (SWD: 1.2% to PC1; CTD: 0.0% to PC1) and exhibited low loadings (SWD = -0.173 and -0.240 ; CTD = 0.034 and -0.119 for PC1 and PC2, respectively). Additionally, these variables showed no significant correlations with forest structure metrics or *U. cordatus* density, suggesting a limited detectable influence of these anthropogenic stressors on the ecological parameters assessed in this mangrove system.

4. Discussion

This study presents the first comprehensive annual assessment of the population dynamics of *Ucides cordatus* in a human-impacted mangrove area in Northeastern Brazil, based on monthly sampling conducted between December 2018 and November 2019. As such, these findings provide an important baseline for future long-term monitoring of the species and habitat condition in the Acupe mangrove. Our results revealed that 93.1% of the captured individuals were below the legally established harvest size, suggesting a population structure consistent with selective removal of large reproductive individuals. The study also demonstrates seasonal variation, with higher densities and larger individuals occurring during warmer months, whereas no statistically significant associations with solid waste or cut-tree density were detected under the present sampling design. Acupe-like *L. racemosa*-dominated mangrove sectors, particularly those with high proportions of undersized crabs, should therefore be considered priority areas for no-take or population-recovery zones.

Laguncularia racemosa is a halophytic species with high ecological plasticity, capable of establishing in clayey, sandy, and muddy substrates [53]. Its monospecific dominance in the Acupe mangrove may be explained by the area's location in the innermost portion of "Todos os Santos" Bay, where tidal variation is limited and flooding levels are lower [36]. Moreover, *L. racemosa* forests are often associated with anthropogenically impacted or regenerating areas [54,55]. The higher density of seedlings recorded from April to June indicates that this is the main recruitment period for new individuals. According to [55], seedling recruitment in mangroves is strongly influenced by environmental factors, a pattern confirmed in this study, as seedling density in Acupe was positively correlated with rainfall.

According to Soares [54], in monospecific *L. racemosa* mangroves subjected to anthropogenic interference, diameter at breast height (DBH) values typically range from 3.5 to

7.7 cm. In Acupe, the predominance of low DBH values (0.8–16.5 cm; mean = 3.9 ± 0.6 cm), together with the high percentage of cut trees (30.1%), suggests that the area is undergoing environmental degradation. Furthermore, although the percentage of cut trees was high (30.1%), our analyses did not detect a direct influence of this anthropic action on the other parameters analyzed, either of the mangrove forest or of the *U. cordatus* population. However, logging can compromise the development of the forest, especially its physiological maturity [56].

Souto [32] reported that local communities use mangroves intensively for recreation, tourism, and the extraction of native species—activities that, together with increasing urbanization, exert pressure on the forest and its associated fauna. Indeed, the study site lies just 270 m from the urban perimeter of Acupe district, which is home to 7451 residents [57]. The anthropogenic influence on the mangrove is evident from both the frequency of cut trees and the high density of solid waste observed.

Mangroves function as natural physical barriers, preventing many solid waste materials from reaching estuarine waters. These materials tend to accumulate among mangrove roots, which act as structural traps and provide favorable conditions for debris retention [58]. In this context, the principal component analysis (PCA) conducted in this study indicated that solid waste density (SWD) and *U. cordatus* density (CD) exhibit opposing patterns. Although the correlation between them was not statistically significant ($p > 0.05$), further increases in solid waste pollution may negatively affect the population density of *U. cordatus* and, consequently, its harvest potential.

Ucides cordatus exhibits the behavioral adaptation of sealing its burrow entrances during the molting period as a strategy to protect itself from potential predators during this vulnerable phase of its life cycle [41,59]. According to Wunderlich et al. [42], the highest frequencies of closed burrows coincided with the molting of adult individuals between August and October along the southeastern and southern coasts of Brazil. This same pattern was reported by Souto [34] for the mangroves of Acupe (BA), although in that region, the appearance of closed burrows began as early as June—a fact also noted by Wunderlich et al. [42].

Molting itself occurs primarily between September and October, during which local crab harvesters reported increased sightings of “milky crabs”—a colloquial term for individuals in pre-molt stage with whitish hemolymph rich in calcium [34,41]. This behavior appears to be stimulated by lower winter temperatures [42,60], particularly in August and September in Acupe.

The population density of *U. cordatus* may be influenced by several natural features of mangrove ecosystems, including sediment grain size [45], salinity [60,61], tidal inundation levels, tree composition [16,36,62,63], and the availability and quality of food resources [19,64].

Several studies have reported that *U. cordatus* density varies according to the dominant tree species in mangrove stands. Forests dominated by *L. racemosa* (white mangrove) exhibited densities ranging from 0.85 ind. m^{-2} in Pernambuco [65] to 6.0 ind. m^{-2} in São Paulo [12]. In areas dominated by *Rhizophora mangle* (red mangrove), densities ranged from 0.67 ind. m^{-2} in Pernambuco [65] to 1.9 ind. m^{-2} in Pará [66] and Bahia [36]. For forests dominated by *Avicennia schaueriana* (black mangrove), values ranged from 1.3 ind. m^{-2} in Pará [66] to 2.05 ind. m^{-2} in Santa Catarina [42]. However, in mixed stands without a dominant tree species, *U. cordatus* densities also varied significantly—from 0.32 ind. m^{-2} in Bahia [36] to 3.7 ind. m^{-2} in Espírito Santo [60].

In addition to being composed exclusively of *L. racemosa*, the Acupe mangrove is characterized by a low tidal flooding level (13.8 ± 2.0 cm), a condition that favors higher *U. cordatus* densities. This contrasts with areas dominated by *R. mangle* and subjected to

deeper tidal inundation, where crab densities tend to be lower [16,45,67]. Oliveira et al. [65] reported that *U. cordatus* density in a *L. racemosa*-dominated forest (0.85 ind. m⁻²) was significantly higher than in one dominated by *R. mangle* (0.68 ind. m⁻²). Furthermore, Mota et al. [36] found that the population density of *U. cordatus* in Acupe exceeded the average value reported for “Todos os Santos” Bay (1.3 ind. m⁻²), based on assessments of nine areas with differing mangrove physiognomies.

When compared to other *L. racemosa*-dominated mangroves, the density of *U. cordatus* in Acupe was higher than that recorded for Canavieiras (1.27 ind. m⁻²) and Caravelas (1.13 ind. m⁻²) [67], and similar to that observed in Paranaguá Bay, Paraná (1.6 ind. m⁻²) [68]. On the other hand, *U. cordatus* density in Acupe was much lower than the value reported by Pinheiro [45] for Iguape on the southern coast of São Paulo State (10.3 ind. m⁻²).

Although there is a well-known association between *L. racemosa*-dominated forests and higher *U. cordatus* densities (as seen in Acupe), this relationship should not be interpreted as resulting exclusively from vegetation composition. Mangrove tree composition is strongly influenced by local environmental conditions, particularly tidal inundation, drainage, and substrate characteristics, which also influence the distribution and abundance of *U. cordatus*, as mentioned above.

In addition to vegetation type, other factors may negatively affect *U. cordatus* density, including mangrove forest degradation [40,69], fishing pressure [16,40,41], the effects of Lethargic Crab Disease [15,67], and predation by mammals such as crab-eating raccoons (*Procyon cancrivorus*) [16]. According to Pinheiro [45], populations with high densities of smaller individuals are typically found in sandier areas, suggesting that sediment granulometry also plays a role in shaping local population structures.

Pinheiro et al. [16] reported high densities (6.0 ± 2.0 ind. m⁻²) of *U. cordatus* in mangroves dominated (>80%) by *L. racemosa*, attributing these values to low fishing pressure at the time of sampling (1990s). In contrast, the population density in Acupe may be negatively affected by overharvesting, given the significant extractive activity targeting this species in the region [32,34].

Finally, it is important to note that variation in *U. cordatus* density estimates may also result from methodological differences among sampling protocols used by different researchers [see 35 for a review]. This concern prompted Pinheiro and Almeida [29] to propose a standardized sampling method, which was subsequently optimized by Pinheiro [30] in collaboration with the Federal Government’s “Monitora Manguezal” Program [38].

In the Acupe mangrove, a higher density of *U. cordatus* burrows was observed within the first 10 m from the estuarine margin. Similarly, Branco [70] recorded higher densities in the lower mesolittoral zone, corresponding to the mangrove area closest to the estuarine channel, a pattern also reported by Alves and Nishida [59] in a mangrove in Paraíba. Góes et al. [60] reported that *U. cordatus* density increases from the fringe toward the hypersaline flat, along a 0–200 m transect, which Pinheiro et al. [16] attributed to a significant negative correlation with tidal flooding levels ($r = -0.94$; $p = 0.0003$).

In the present study, no significant effect of tidal flooding level was detected during sampling. This may be due to the sampling design within a single mangrove area characterized by a narrow and relatively homogeneous slope. This condition resulted in limited variation in tidal flooding levels across the 50 m transect perpendicular to the fringe (14.5%).

Analysis of carapace width (CW) revealed that the *U. cordatus* population in Acupe follows the sexual dimorphism pattern observed in most previously studied populations, with males being larger than females [42,59,65,66,71,72]. This pattern is generally attributed to the slower growth rate in females, who divert more energy toward gonadal development and egg incubation, thereby prolonging their intermolt period [73,74]. Males, on the other

hand, invest more energy in somatic growth to increase their success in competitive and courtship behavior [41,75].

The estimation of CW based on the relationship between CW and burrow diameter (DG) validated the effectiveness of this indirect method for assessing *U. cordatus* populations. Monthly variations in crab density and size were primarily associated with seasonal temperature fluctuations between the region's two main climatic periods (warm and cool seasons). During the reproductive season (warmer months), both density and mean CW were higher, corresponding to the post-molt phase when crabs tend to be more active and aggregated. In contrast, during cooler months, lower densities and higher frequencies of closed burrows were observed.

Body sizes of *U. cordatus* have been recorded in various mangrove regions with differing forest physiognomies [36,42,45,59,66,67]. Several authors [12,16,36,45,67] have consistently shown that smaller individuals and higher population densities are typically associated with *L. racemosa*-dominated mangrove forests, regardless of local forest structure.

The association between crab size/density and *L. racemosa*-dominated stands should be interpreted as part of a broader habitat gradient, including tidal flooding, sediment characteristics, drainage, and forest structure. *Laguncularia racemosa* has a lower nutritional value when compared to *A. schaueriana* and *R. mangle* [19]. According to these authors, crabs inhabiting *L. racemosa*-dominated mangroves consume larger amounts of leaf litter but exhibit lower weight gain compared to individuals from areas dominated by *A. schaueriana* and *R. mangle*. Additionally, the roots and pneumatophores of *L. racemosa* may hinder the excavation of burrows by larger crabs [16].

An alternative explanation for the high proportion of smaller individuals is size-selective harvesting [71,76,77]. Since Brazilian fisheries regulations prohibit the capture of crabs smaller than 60.0 mm CW, undersized individuals experience lower fishing mortality than legal-sized ones [71]. Additionally, size reduction in populations subjected to long-term exploitation is documented for Decapoda populations [78,79].

Extractive potential is directly related to the average body size of *U. cordatus* in a given area. In Acupe, the low nutritional condition of the crabs due to the monospecific *L. racemosa* forest contributes to the low Immediate Extractive Potential (IEP = 6.9%). In addition, previous studies conducted in the region have reported intense harvesting pressure [32–34], which may also contribute to maintaining average body sizes below the legal minimum capture size (CW = 60.0 mm), as reported by Alves and Nishida [59] in Paraíba. Although harvesting intensity was not directly quantified in the present study, the observed population structure is consistent with these previous findings. This interpretation is further supported by the restocking of *U. cordatus* megalopae carried out in Acupe in 2016 following reports of overfishing and population decline [35]. Future studies integrating ecological monitoring with quantitative measures of harvesting effort, collector visitation, catch frequency, and CPUE would provide a more direct assessment of the relationship between exploitation and population dynamics.

Immediate and Future Extractive Potential were estimated using the national conversion equation proposed by Pinheiro et al. [43], following the standardized protocol adopted by the "Monitora Manguezal" Program. As with any predictive model, some uncertainty is associated with CW estimates, particularly for individuals close to the legal harvest threshold (60.0 mm CW). However, the national equation was specifically developed to minimize estimation variance across the Brazilian latitudinal gradient and presents a mean absolute prediction error of only 4.4 mm (SD = 3.4 mm) [43]. Consequently, although some individuals close to the legal threshold may be misclassified, this level of uncertainty is unlikely to substantially alter the overall interpretation of extractive potential in the Acupe population. Therefore, the standardized application of this method provides consistent esti-

mates of extractive potential while facilitating direct comparisons among studies adopting the same monitoring protocol.

Based on crab density and size data, Pinheiro et al. [12] and Mota et al. [36] recommended that *L. racemosa* forests be designated as conservation areas (non-extractive zones), while areas dominated by *R. mangle* and *A. schaueriana* are more appropriate for controlled harvesting of *U. cordatus*.

The male-biased sex ratio observed in Acupe aligns with findings from studies conducted in the North [66,71,72], Northeast [47,59,65], and South of Brazil [42,80]. In contrast, other studies have reported female-biased ratios [60,61,81] or balanced sex ratios [13]. These discrepancies may be influenced by forest heterogeneity [9] and selective fishing pressure [60]. In this context, Conti and Nalesso [61] attributed the predominance of females in some mangroves—particularly those near rural communities—to intensive harvesting of males, which are the preferred targets. Sampling bias may also occur, as local gatherers often capture larger males from wider burrows [80,82].

Ucides cordatus reproduces seasonally, typically from November to May, with synchronous emergence of males and females from their burrows in an event known as the “andada” [9,21,44,47,61,80,82]. Although this behavior was not directly observed in the present study, ovigerous females were recorded between January and March, confirming the seasonal reproductive pattern described in the literature [21]. Environmental factors such as temperature, photoperiod, and lunar phase influence reproduction, and higher temperatures favor larval development while reducing predation risk [83].

In Brazil, Federal and State fishing regulations prohibit the capture, processing, transportation, and commercialization of *U. cordatus* during its reproductive period (e.g., SAP/MAPA Ordinance No. 325/2020). Nevertheless, harvesting during the “andadas” remains common across many Brazilian coastal regions and involves not only professional crab collectors but also women, children, tourists, unemployed individuals, and part-time gatherers [7,22,24,25,84–86].

Souto [34] documented such practices in Acupe, attributing them to changes in crab behavior, as the animals become more accessible and less aggressive upon leaving their burrows. Capturing individuals during this critical reproductive window directly compromises the species’ reproductive potential, with negative consequences for fishery stocks and extractive sustainability. As a result, some regions in Brazil have already implemented specific regulations for a closed season also aligned with the reproductive migration periods (“andada”), as established by Ordinance SAP/MAPA No. 325/2020, which considers the occurrence of this reproductive phenomenon to be associated with new and full moon phases [21].

In the present study, females reached sexual maturity at slightly smaller sizes than males (males: 54.5 mm; females: 50.7 mm). This pattern is consistent with findings for *U. cordatus* across several regions of Brazil [41,44,46]. A comprehensive review by Pinheiro et al. [12] reported mean sizes at maturity of 51.7 mm for males and 46.7 mm for females, reinforcing the general trend of earlier female maturation.

Ucides cordatus is a slow-growing brachyuran crab, with similar growth rates (k) in both sexes (males: $k = 0.28$; females: $k = 0.26$), reaching sexual maturity at approximately 3 years in males and 2.8 years in females [20]. Earlier maturation in females is advantageous as it extends their reproductive lifespan, allowing mating across a broader size range [41]. Conversely, delayed maturation in males favors larger body sizes, consistent with the reproductive strategy of many brachyurans, in which male–male competition, mate guarding, and reproductive disputes are common [87,88]. According to Linhares and Silva [89], male competition for access to females is a typical reproductive behavior in *U. cordatus*.

In Acupe, the estimated size at first maturity for *U. cordatus* is below the minimum legal capture size (60.0 mm CW) established by current regulations for the Brazilian Northeast (IBAMA Ordinance No. 34/2003). This suggests that existing legislation has been effective in allowing reproduction prior to harvest. Nevertheless, harvesting may still negatively affect the population, particularly due to collection during reproductive migrations (“andadas”) [34] or through overfishing, which can lead to a reduction in average body size. The observed mean sizes of captured males (56.9 mm) and females (51.3 mm) are close to the estimated maturity thresholds. Additionally, the mean carapace width estimated indirectly from burrow diameter (50.9 mm) is very close to the female maturity size, indicating that many individuals in Acupe may not reproduce even once before being harvested.

The multifactorial analysis provided valuable insights to understand the complex relationship between environmental variables and the population dynamics of *U. cordatus* in Acupe. Crab density, the main biotic variable analyzed, was positively influenced by air temperature and immediate extraction potential. In turn, the recruitment of *L. racemosa*, estimated by seedling density, was positively associated with mean diameter at breast height and rainfall. Cardoso et al. [90] observed that, in southeastern Brazil, *L. racemosa* produces more propagules in the summer months, when precipitation rates are higher, revealing a pattern compatible with the data obtained in this study.

Population variables such as density and harvesting potential may be influenced by factors related to anthropogenic disturbance in the mangrove ecosystem. Although direct indicators of anthropogenic impact (solid waste density and cut tree density) did not show statistically significant correlations with the biotic variables of the forest or the crab population, the PCA revealed an antagonistic relationship between *U. cordatus* density and solid waste accumulation. These results are consistent with the findings of ICMBio [38], who reported up to a 50% reduction in *U. cordatus* density in impacted areas compared to pristine mangroves. Thus, it is plausible to assume that if waste loads exceed a certain threshold, a significant decline in both density and the immediate harvesting potential of the species may occur.

In times of increasing pressure on coastal ecosystems, ensuring the sustainability of *U. cordatus* is more than a scientific challenge: it is an ethical commitment to the future of mangroves and the human communities that depend on them to subsist and live in harmony with the environment.

5. Conclusions

The body size of *Ucides cordatus* individuals in Acupe falls below the minimum legal size established by current fisheries regulations for the species in northern and northeastern Brazil. As a result, non-commercial-sized individuals were more abundant than those above the legal threshold.

The mangrove forests in Acupe, predominantly composed of white mangrove (*L. racemosa*), exhibit high future extractive potential and should be designated as protected areas, where crab harvesting is prohibited.

Given the species’ vulnerability to overfishing, special attention must be directed toward enforcing the closed season and minimum size regulations. In this context, socio-educational initiatives are urgently needed to raise awareness among local communities about the importance of complying with legal capture sizes, protecting the reproductive period, and mitigating the effects of unsustainable harvesting. In parallel, strict enforcement is essential to prevent the capture of individuals below 60.0 mm CW and to ensure compliance during the reproductive closure period.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d18080485/s1>, Table S1: Monthly sex ratio of *Ucides cordatus* sampled in Acupe, Bahia (Brazil).

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Abbreviations

The following abbreviations are used in this manuscript:

TMP	Monthly records of air temperature
RFL	Rainfall
TFL	Tidal flooding level
SDN	Seedlings
DBH	diameter at breast height
TRD	Tree density
CTD	cut tree density
SWD	Solid waste density
CD	Crab density
DG	diameter of open, active burrow
CW	carapace width
IEP	immediate Extractive potential
FEP	Future Extractive potential
MPL	propodus length of the major chela
AB	width of the fifth abdominal segment
CW ₅₀	Morphometric maturity

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