Fisheries Research 265 (2023) 106733

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Density and extractive potential of "uçá"-crab, *Ucides cordatus* (Linnaeus, 1763), in mangroves of the "Todos os Santos" Bay, Bahia, Brazil

Thaís Arrais Mota [a], Marcelo Antonio Amaro Pinheiro [b], Norma Suely Evangelista-Barreto [a], Sérgio Schwarz da Rocha [c,*]

[a] *Programa de Pós-Graduação em Ciência Animal, UFRB - Centro de Ciências Agrárias, Ambientais e Biológicas, Brazil*
[b] *Universidade Estadual Paulista (UNESP), Instituto de Biociências (IB), Campus do Litoral Paulista (CLP), Laboratório de Biologia da Conservação de Crustáceos (LBC), Grupo de Pesquisa em Biologia de Crustáceos (CRUSTA), Praça Infante Dom Henrique, s/n, Parque Bitaru, 11330–900 São Vicente, SP, Brazil*
[c] *Universidade Federal do Recôncavo da Bahia (UFRB) - Centro de Ciências Agrárias, Ambientais e Biológicas, Laboratório de Macroinvertebrados Bentônicos, Rua Rui Barbosa, 710, Centro, 44.380–000, Cruz das Almas, BA, Brazil*

A R T I C L E I N F O

Handled by Jason M Cope

Keywords:
Crustacean
Decapoda
Fishery
Management
Population

A B S T R A C T

Ucides cordatus is one of the main fishery resources of the "Todos os Santos" Bay (BTS), State of Bahia, Brazil. Population parameters (structure, density, and fishery potential) of this crab species were analyzed in the dry and rainy seasons in nine mangrove areas of BTS. Five sample quadrats (5 × 5 m) were used to record the number and diameter of active open burrows (with biogenic activity) and closed burrows of *U. cordatus*, tree variables (composition, density, and diameter), and flood level. Crab density (ind.m^{-2}) was indirectly estimated by counting galleries. The diameter of open galleries was converted into carapace width (CW) using a regression model to later characterize the *U. cordatus* population structure. There were more galleries in the dry season than in the rainy season. Crab density ranged from 0.32 to 2.63 ind.m^{-2} (1.32 ± 0.90 ind.m^{-2}), and the mean density was higher during the dry period ($t = 0.02$; $p < 0.05$). Crab density differed among sampling areas regardless of seasonal period. Crab size (CW) in BTS was 52.4 ± 16.7 mm, with specimens significantly larger during the dry period ($t = 0.01$; $p < 0.05$), and there was a significant difference ($F = 4.57$; $p = 000.1$) among mangrove areas. Non-commercial size animals (CW < 60.0 mm) were more abundant (65.2%) than those with commercial size (34.8%) in BTS. Crab density and flood level showed significant negative correlation ($\rho = -0.51$; $p < 0.05$), while there was a positive correlation between CW and flooding level ($\rho = 0.40$; $p < 0.05$). *U. cordatus* population parameters differed significantly among BTS sampling sites due to their heterogeneity. This study is the first assessment of "uçá"-crab populations in BTS mangroves and reveals a need for a sustainable management in the area. Furthermore, this study could be a model for monitoring other large brachyuran species inhabiting estuarine systems, which are economically and biologically relevant.

1. Introduction

Ucides cordatus (Linnaeus, 1763) is a semi-terrestrial crab, popularly known as "uçá"-crab. This species is endemic to mangrove areas. It digs galleries in the sediment (Pinheiro and Fiscarelli, 2001; Pinheiro et al., 2018). It occurs in the Western coast of the Atlantic Ocean, from the State of Florida (USA) to the city of Laguna (Santa Catarina State, Southern Brazil) (Melo, 1996; Pinheiro et al., 2016). This species is one of the main constituents of mangrove-associated fauna and is considered a key species in this ecosystem (Wolff et al., 2000; Santos et al., 2016). In this context, bioturbation during the construction of galleries revolves sediment, favoring oxygenation (Pülmanns et al., 2014), drainage (Koch and Wolff, 2002; Santos et al., 2016; Pinheiro et al., 2018), nutrient cycling (Wolff et al., 2000), and carbon retention (Andreetta et al., 2014). Together, these factors are responsible for the high productivity these environments show (Pinheiro et al., 2015).

In addition to its ecological importance, the species is also economically relevant, as the extraction of *U. cordatus* in Brazilian mangroves is one of the oldest fishing activities practiced in Brazil (Lima et al., 2018). It is also one of the main fishery resources of estuarine systems in Brazil, serving as food and source of income for traditional communities living on the coast (Jankovski et al., 2006; Côrtes et al., 2014), especially in the

* Corresponding author.
E-mail address: ssrocha@ufrb.edu.br (S.S. da Rocha).

https://doi.org/10.1016/j.fishres.2023.106733
Received 13 October 2022; Received in revised form 17 April 2023; Accepted 21 April 2023

North (Freitas et al., 2015; Maia et al., 2016) and the Northeast regions of Brazil (Souto, 2007; Soares et al., 2009; Fogaça et al., 2018; Lima et al., 2018).

In the early 2000s, "uçá"-crab appeared in the "National List of Aquatic Invertebrates and Fish Species Overexploited or Threatened with Overexploitation" – Normative Instruction no. 5/2004. It was classified as an overexploited species. From then onwards, species protection policies were elaborated (IBAMA Ordinances # 34/2003 and # 52/2003), as well as a proposal of a National Management Plan (Dias-Neto, 2011). Finally, the last official assessment of the risk of extinction of Brazilian crustaceans (Pinheiro et al., 2016) classified *U. cordatus* as a "Near Threatened" (NT) species, as its population size in Brazilian territories decreased by 28%. Therefore, given the importance of *U. cordatus* for mangroves, environmental agencies and researchers are permanently concerned with the conservation of this species in Brazil (Pinheiro and Rodrigues, 2011; Pinheiro et al., 2016).

However, the small-scale traditional fishing of the "uçá"-crab makes it difficult to monitor its removal from Brazilian mangroves (Fogaça et al., 2018). This requires evaluating the effectiveness of the proposed protection policies for this species. In this context, the Environmental Brazilian Institution (ICMBio) has recently started the MONITORA Program – Mangrove Component (Ribeiro, 2018), which has used an indirect protocol (i.e. counting the number of galleries per square meter) similar as that previously developed by Pinheiro and Almeida (2015) and adopted in the present study.

Although *U. cordatus* on the Brazilian coast has been widely studied, there are still few biology studies on the bioecology and fisheries in the State of Bahia, mainly in southern and northern parts of this state's coast (see Schmidt et al., 2008, 2009, 2013; Moraes et al., 2015). In respect to "Todos os Santos" Bay (BTS), although *U. cordatus* has already been identified as one of the main fishery resources (Souto, 2007; Soares et al., 2009), there is only one study focusing on ethnobiology aspects (see Souto, 2007).

Population parameters, such as density (individuals per square meter – ind.m^{-2}), crab size, and extraction potential (Pinheiro et al., 2018), as well as reproductive period (Wunderlich et al., 2008), are extremely important data for assessing stocks and fishing potential in a given area (Moraes et al., 2015; Pinheiro et al., 2018). In fact, this information contributes to the management of this species, assisting Brazilian government agencies (e.g., ICMBio and IBAMA) in the development of fishery protection and management policies (Dias-Neto, 2011; Costa et al., 2014; Pinheiro et al., 2016). This paper is also a study case that could be a model for monitoring other large brachyuran species inhabiting estuarine systems that are economically and biologically relevant. Among them we may mention another *Ucides* congeneric species – *Ucides occidentalis* (Ortmann, 1897) from eastern Pacific; two *Cardisoma* species – *C. crassum* Smith, 1870, from eastern Pacific (see Vega et al., 2018; Zambrano and Meiners, 2018; Zambrano and Solano, 2018) and *C. guanhumi* (Latreille, 1828) from western Atlantic (see Rodríguez-Fourquet and Sabat, 2009; Carmona-Suárez and Guerra-Castro, 2011; Santos et al., 2022); and four *Scylla* species – *S. serrata* (Forsskål, 1775), *S. olivacea* (Herbst, 1796), *S. tranquebarica* (Fabricius, 1798), and *S. paramamosain* Estampador, 1949, from different areas of the world (Fondo et al., 2010; Mirera et al., 2013; Rahman et al., 2020; Leoville et al., 2021).

The central hypotheses of this study are: 1) Are populations of *U. cordatus* in "Todos os Santos" Bay (State of Bahia, Brazil) suitable for commercial exploitation in terms of size and density of individuals?, and 2) Which characteristics of mangroves affect the population parameters of the species the most? The aim of this study is to evaluate some population parameters of *U. cordatus* (structure and population density, mean body size, and extractive potential) under a possible seasonal effect (dry and rainy seasons) in "Todos os Santos" Bay, Bahia State, Brazil. These parameters are also associated with the peculiar characteristics of selected mangroves that provide fundamental data on the "uçá"-crab.

2. Material and methods

The "Todos os Santos" Bay (BTS) is located in the State of Bahia, Brazil. It comprises an area of 1223 km^2, making it the second largest bay in Brazil (Andrade et al., 2017). In total, it has approximately 160 km^2 of mangroves, which are located mainly in the estuarine portion of the Paraguaçu, Jaguaripe and Subaé Rivers, the Aratu Bay, and the coast of the Itaparica Island (Barros et al., 2012; Costa et al., 2015).

The present study was carried out in nine mangrove areas (Fig. 1) in "Todos os Santos" Bay (BTS). Table 1 and Fig. 2 show their geographic coordinates and characteristics. Data collection was carried out seasonally in the dry season (January to March 2019) and in the rainy season (July to September 2019) in order to cover the reproductive and non-reproductive periods of the "uçá"-crab (Pinheiro and Almeida, 2015), respectively.

Random sampling quadrats measuring 5×5 m (25 m^2) were demarcated with fiberglass measuring tape and setsquare and they were used to record data for the population study (Pinheiro and Almeida, 2015). In each area, five quadrats' replicates were established, representing a total area of 125 m^2. The quadrats were placed in ranges of 0–10 m ($n = 2$), 25–30 m ($n = 1$), and 45–50 m ($n = 2$) from the riverbank towards the inside of the mangrove, established by fifty-meter fiberglass measuring tape. According to the method described by Pinheiro and Almeida (2015), some variables were recorded in each sampling unit: 1) number and diameter of galleries (active opened and closed) of *Ucides cordatus*, 2) identification of tree species and their density (ind.m^{-2}), 3) diameter of trees at breast height (cm), and 4) flooding height (cm).

The estimate of the number of individuals per mangrove area was carried out using the indirect method (Wunderlich et al., 2008; Pinheiro and Almeida, 2015). The number of galleries was counted considering the occurrence of one *U. cordatus* specimen per gallery (Pinheiro and Fiscarelli, 2001; Pinheiro et al., 2018). For this purpose, only galleries with animals inside them were considered and represented by two categories, namely: 1) open galleries with biogenic activity, confirmed by the presence of animal tracks or recent movement of sediments, and 2) closed galleries, without a visible opening, requiring confirmation by excavation (Wunderlich et al., 2008; Pinheiro and Almeida, 2015). To reduce sampling error, galleries without biogenic activity (abandoned) were not counted. When galleries with more than one opening (burrow) were found, only one of them was counted (Pinheiro and Almeida, 2015). Crab density was calculated by dividing the total active galleries by sampling area (25 m^2). The result was represented as individuals per square meter (ind.m^{-2}).

To characterize population structure, the diameter of each gallery was measured with an analog caliper (0.05 mm) with stainless steel rods (Schmidt et al., 2008; Pinheiro and Almeida, 2015). Each gallery measured was marked to prevent it from being counted again. The diameter of open galleries (DG) was converted into carapace width (CW) according to the equation of Schmidt et al. (2008) for southern Bahia. Finally, the mean size of *U. cordatus* in each of the nine mangrove areas was calculated, excluding those with CW $\geq$ 96 mm (largest specimen ever obtained, according to reviews by Pinheiro et al., 2005, and Dias-Neto, 2011).

The extraction potential (IEP, immediate; and FEP, future) was calculated according to Wunderlich et al. (2008). IEP and FEP are obtained by the percentage of animals with CW $\geq$ 60 mm and CW $<$ 60 mm, respectively. This reference size was established in accordance with current fishing defense ordinance for the "uçá"-crab in the Northern and Northeastern regions of Brazil (IBAMA no. 034/03-N, 2003).

In each sampling quadrat, adult tree specimens (height $\geq$ 1.5 m) were identified to represent the arboreal composition (AC, in %), density of trees (DT, as ind.m^{-2}), and diameter at breast height (DBH), measured at 1.30 m from the sediment. In addition, flooding height by tides (FH, in cm) in each area was estimated based on macroalgae height

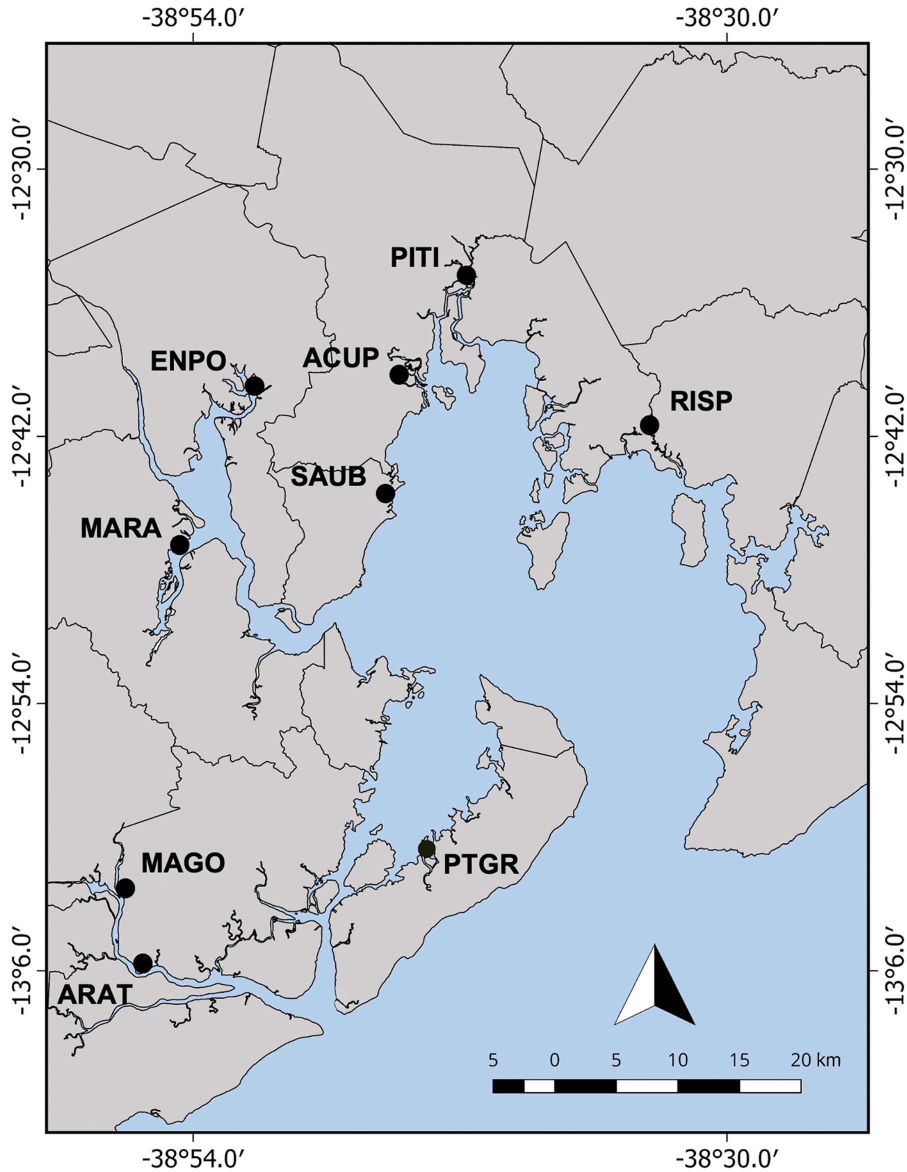

Fig. 1. Map of the "Todos os Santos" Bay, Bahia, Brazil, with nine mangrove areas under study (black circles). ACUP, Acupe; ARAT, Aratuípe; ENPO, Engenho da Ponte; MAGO, Maragogipinho; MARA, Maragogipe; PTGR, Ponta Grossa; RISP, Rio São Paulo; and SAUB, Saubara.

("Bostrychietum") adhered to the base of mangrove trunks ($n = 25$/area) using a measuring tape (in cm) (Pinheiro et al., 2018).

2.1. Statistical analysis

All statistical analyses were performed using the *RStudio* version 1.2.1335 (R Core Team, 2021), following the statistical indications of Sokal and Rohlf (2003). To compare the density and mean size of animals among mangrove areas within a same period (dry or rainy), one-way ANOVA was performed followed by Tukey test ($p < 0.05$) using the five squares as replicates. To compare climatic seasons, the t test was used ($p < 0.05$). Finally, it is worth mentioning that data normality was previously tested (Shapiro-Wilk test), resulting in normal distributions. The homoscedasticity of variances was also evaluated (Levene test) according to Sokal and Rohlf (2003).

To analyze the extractive potential in each area, the Chi-square test, corrected by Yates (Zar, 1996), was performed to compare extractive potential frequencies (IEP vs. FEP) for each evaluated mangrove area and for the BTS as a whole. Animal size at each sampling point was distributed into animal size class frequency histograms. The skewness coefficient (sk) of the frequency distribution was also evaluated considering the following categories mentioned by Pinheiro et al. (2022): 1) symmetric ($-0.5 \leq sk \leq 0.5$), expressing a balance between juveniles and adults; 2) positive asymmetric ($sk > 0.5$), indicating predominance of juveniles; and 3) negative asymmetric ($sk < -0.5$), when there is a predominance of adults.

Variables related to arboreal vegetation (FH, flood height by tides; DT, density of trees; and DBH, diameter at breast height), related to crustacean population (DC, density of crabs; and CW, carapace width), and the names of the nine mangrove areas (categorical variable) were organized in a 45×6 matrix (45 sampling unities vs. six variables). Previously, the association among variables was evaluated according to Spearman's correlation coefficient (ρ) using the *corrplot* package (Wei et al., 2021). Dataset was also submitted to multifactorial analysis and evaluated by principal component analysis (PCA) using the *FactoMineR* package (Le et al., 2008; Husson et al., 2018) and cluster analysis using the *factoextra* package (Kassambara and Mundt, 2016). In this latter, it was based on correlation as a similarity index to establish the distances.

Table 1
Geographic coordinates and characterization of mangrove areas evaluated at "Todos os Santos" Bay (BA, Brazil). Where: DBH, diameter at breast height; FH, flooding height by tides; DT, density of trees; RM, *Rhizophora mangle;* LR, *Laguncularia racemosa*; AS, *Avicennia schaueriana* (AS).

Mangrove Area	Identification (coordinates)	Characteristics	Demographic Density[a] (inhabit./Km^2)	DBH (cm)	DT (ind. m^{-2})	Arboreal species (Predominance)	FH (cm)
ENPO	**Engenho da Ponte** 12º 39′ 46.70″ S 38º 51′ 15.00″ W	Quilombola community. Inside of the Extractive Reserve (RESEX) 'Baía do Iguape' (Cachoeira municipality). The mangrove studied is 460 m from the community of Engenho da Ponte.	81.03	5.2 ± 3.4	0.14 ± 0.08	2 (LR=AS)	29.8 ± 1.6
MARA	**Maragogipe** 12º 46′ 46.60″ S 38º 54′ 38.90″ W	Inside of the Extractive Reserve (RESEX) 'Baía do Iguape' (Maragogipe municipality). The mangrove studied is 200 m away from the urban area.	97.27	5.0 ± 2.9	0.18 ± 0.10	2 (LR>RM)	38.0 ± 13.7
SAUB	**Saubara** 12º 44′ 35.11″ S 38º 45′ 00.03″ W	Mouth of the Paraguaçu river - Northwestern BTS (Saubara municipality). The mangrove studied is located 360 m from the urban area of the municipality of Saubara.	68.51	8.1 ± 4.1	0.18 ± 0.13	2 (AS>RM)	33.5 ± 11.0
ACUP	**Acupe** 12º 39′ 13.97″ S 38º 44′ 44.00″ W	Subaé river. Acupe district - Northern BTS (Santo Amaro municipality). The studied mangrove is 150 m from shrimp farms and 270 m from the urban area of the district of Acupe.	117.26	3.9 ± 2.7	0.30 ± 0.06	1 (LR)	13.8 ± 2.0
PITI	**Pitinga** 12º 34′ 46.00″ S 38º 41′ 45.00″ W	Pitinga river (Santo Amaro municipality). The mangrove studied is 1.23 km from the city of Santo Amaro.	117.26	6.5 ± 4.3	0.16 ± 0.02	3 (LR>RM>AS)	33.2 ± 3.6
MAGO	**Maragogipinho** 13º 00′ 48.30″ S 38º 57′ 13.40″ W	Jaguaripe river tributary. Maragogipinho district - Southern BTS (Aratuípe municipality). The mangrove studied is 4.55 km from the district of Maragogipinho.	47.47	10.6 ± 6.3	0.07 ± 0.03	1 (LR)	18.7 ± 3.1
ARAT	**Aratuípe** 13º 05′ 32.50″ S 38º 57′ 17.90″ W	Jaguaripe river. Southern BTS (Aratuípe municipality). The mangrove studied is 3.84 km from the district of Maragogipinho.	47.47	5.0 ± 2.4	0.42 ± 0.05	1 (LR)	35.7 ± 3.3
PTGR	**Ponta Grossa** 13º 00′ 32.00'' S 38º 43′ 30.00″ W	Itaparica island (Vera Cruz municipality). The mangrove studied is located 100 m from the urban area of the Ponta Grossa community.	125.33	2.3 ± 1.5	0.18 ± 0.07	2 (RM>LR)	12.3 ± 2.6
RISP	**São Paulo River** 12º 42′ 17.30″ S 38º 33′ 15.40″ W	São Paulo river at Metropolitan Region of Salvador (Candeias municipality). The mangrove studied is 400 m from the limits of the Landulpho Alves Refinery.	321.87	12.8 ± 5.8	0.14 ± 0.06	1 (AS)	21.0 ± 4.0

[a] IBGE (2010)

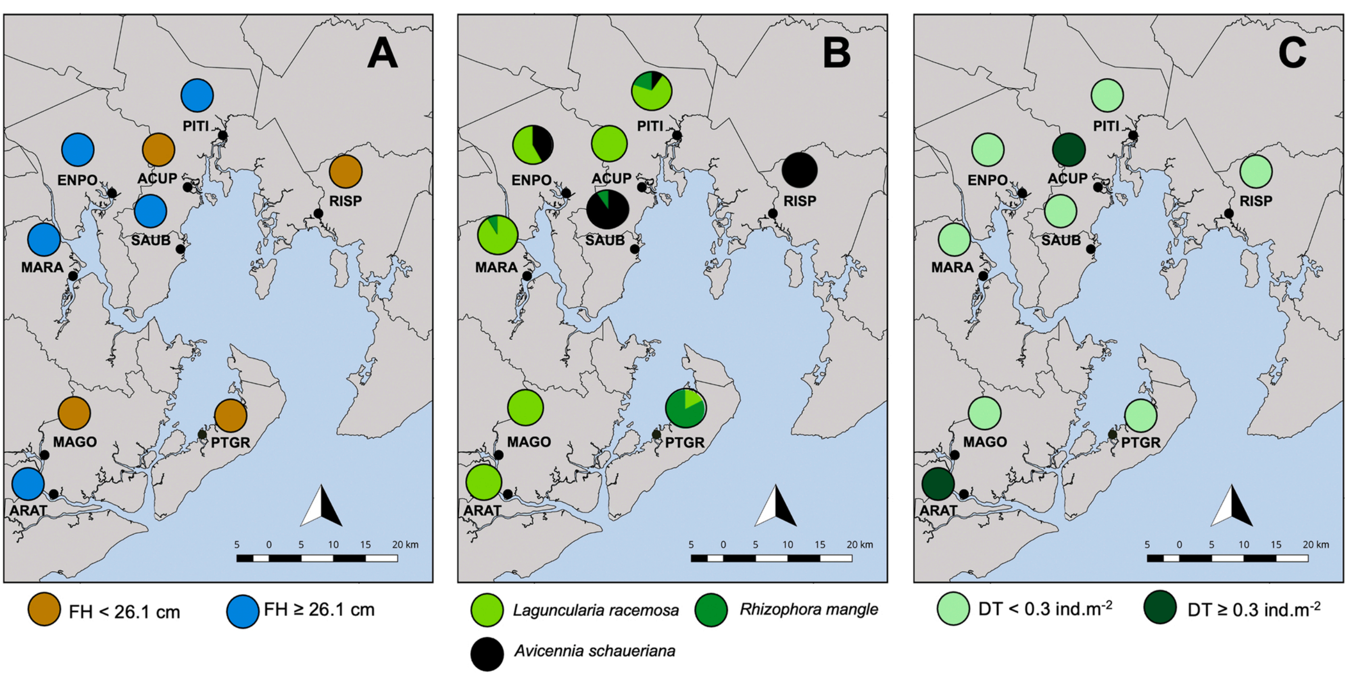

Fig. 2. Spatial distribution of environmental characteristics in nine mangrove areas of the "Todos os Santos" Bay (BTS), Brazil, in relation to (A) flooding height by tides, (B) arboreal species, (C) density of trees. Where: ACUP, Acupe; ARAT, Aratuípe; ENPO, Engenho da Ponte; MAGO, Maragogipinho; MARA, Maragogipe; PTGR, Ponta Grossa; RISP, Rio São Paulo; and SAUB, Saubara.

3. Results

A total of 2963 *U. cordatus* open galleries were recorded and measured during the study in the nine sampling areas. There was a higher absolute abundance (and percentage) in the dry season (n = 1729; 58.4%) compared to rainy season (n = 1234; 41.6%) (χ^2 = 82.69; $p < 0.01$). In relation to the percentage of closed galleries, there was an inverse pattern, with the frequency during the dry season (6.8%) lower than that in the rainy season (32.3%) (χ^2 = 150.85; $p < 0.01$).

In general, crab density was normally distributed (W = 0.954;

$p = 0.49$), with values ranging from 0.32 to 2.63 ind.m^{-2} (mean ± standard deviation: 1.32 ± 0.9 ind.m^{-2}; $CI_{95\%}$, 95% confidence interval: 1.13–1.51 ind.m^{-2}). The mean density in each climatic season differed significantly. The dry season (1.54 ± 0.81 ind.m^{-2}) was 41.3% higher than the rainy season (1.09 ± 0.49 ind.m^{-2}) ($t = 0.02$; $p < 0.05$). Comparing mean crab density among sampling areas (Fig. 3A), there was a significant difference regardless of seasonal period (dry season: $F = 7.60$; $p = 0.001$; rainy season: $F = 4.00$; $p = 0.003$). Fig. 8A shows the spatial distribution of the crab density (DC) in the BTS.

The mean size (CW) of *U. cordatus* per mangrove area ranged from 34.4 to 69.3 mm in the dry season and from 31.9 to 60.4 mm in the rainy season, with the former presenting a 20.7% greater range of variation. Considering all sampling points in the BTS, the mean size of the "uçá"-crab was 52.4 ± 16.7 mm CW ($CI_{95\%}$: 48.9–55.9 mm), with a larger size in the dry season (55.1 ± 10.7 mm) compared to rainy season (49.7 ± 9.5 mm) ($t = 0.01$; $p < 0.05$). In general, disregarding the seasonal effect, crab size (CW) also differed significantly among areas ($F = 4.57$; $p = 000.1$) (Fig. 3B). Usually, smaller crabs were recorded at MARA, SAUB, ACUP, MAGO, and PTGR ($n = 50$; 45.0 ± 18.1 mm CW) in relation to larger ones found at ENPO, PITI, ARAT, and RISP ($n = 40$; 61.1 ± 8.4 mm) ($t = 5.19$; $p < 0.001$). Finally, it is noteworthy that MARA and SAUB showed absence of galleries in some of the sampling quadrats, generating high coefficients of variation (MARA: 50.1%; and SAUB: 84.3%) (Fig. 3B). Fig. 8B shows the spatial distribution of crab size (CW) in BTS.

The analysis of the population structure of the "uçá"-crab in each mangrove area showed two mangrove areas (22.2%) with asymmetric distribution (ARAT and PTGR), while the other seven areas (77.8%) have a symmetric distribution (MARA, ENPO, SAUB, ACUP, PITI, RISP and MAGO) (Fig. 4). The extractive potential of "uçá"-crab had an IEP > FEP only in RISP ($\chi^2 = 47.78$; $p < 0.05$), with an opposite situation (IEP < FEP) observed in MARA, ACUP, MAGO, ARAT, and PTGR ($\chi^2 \geq 5.32$; $p < 0.05$). Only three areas (PITI, SAUB and ENPO) showed no significant difference between extractive potential categories (IEP = FEP) ($\chi^2 \leq 3.44$; $p > 0.05$). Figs. 8C and 8D show the spatial distribution of the symmetry of distribution by size (sk) and predominant category (juvenile or adult) in the mangrove areas in BTS, respectively.

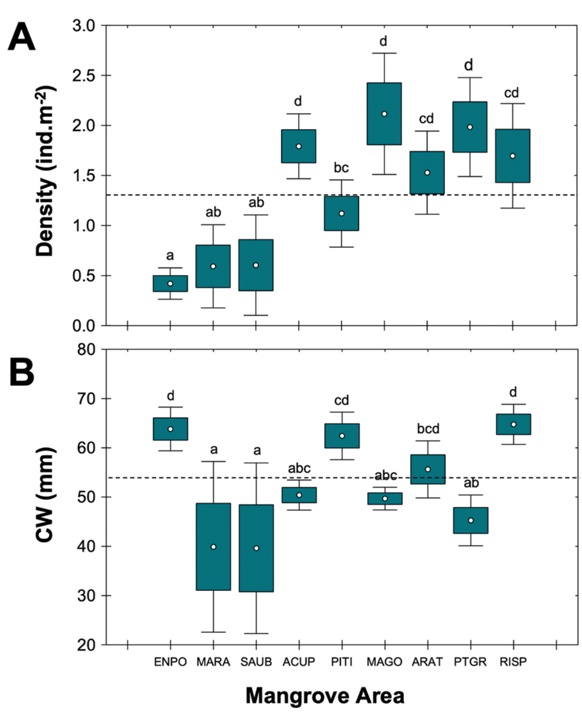

Fig. 3. Populational variables of the mangrove crab *Ucides cordatus* in nine mangrove areas of the "Todos os Santos" Bay, Bahia, Brazil, from January to August 2019. **(A)** Density (DC, in ind.m^{-2}), **(B)** carapace width (CW, in millimeters). Means followed by different letters indicate significant difference ($p < 0.05$). Where: ACUP, Acupe; ARAT, Aratuípe; ENPO, Engenho da Ponte; MAGO, Maragogipinho; MARA, Maragogipe; PTGR, Ponta Grossa; RISP, Rio São Paulo; and SAUB, Saubara.

Considering all samples collected in BTS, crab size distribution followed a normal distribution ($W = 0.991$; $p = 2.14$). Thus, there was a higher percentage of animals in the 50–60 mm CW range (24.5%), which corresponds to the limit between future and immediate extraction potential (Fig. 5A). Considering only IEP, the size class of 60–70 mm had the highest number of individuals (17.8%). Therefore, non-commercial size animals (CW < 60.0 mm) were more abundant (65.2%) than those with a commercial size (34.8%) ($\chi^2 = 227.6$; $p < 0.001$) (Fig. 5B).

Flooding height by tides (FH) differed significantly among sampling areas ($F = 6131$; $p = 0.0001$), with means ranging from 12.3 to 38.0 cm. PTGR and MARA mangroves showed extremes of flood levels, corresponding to the lowest and the highest records, respectively (Table 1). In general, FH recorded in BTS was 26.1 ± 11.2 cm ($CI_{95\%}$: 22.7–29.4 cm). Therefore, mangrove areas were divided into two groups characterized by high (PITI, ENPO, SAUB, MARA, and ARAT) and low (ACUP, RISP, MAGO, and PTGR) tidal inundation height (see Fig. 2A).

There was an absolute presence of *Laguncularia racemosa* (white mangrove) in ACUP, ARAT and MAGO mangroves, while *Avicennia schaueriana* (black mangrove) was monospecific in the RISP mangrove. Finally, the other sampling areas had more than one arboreal species with a peculiar composition. In general, *L. racemosa* was the most frequent arboreal species in mangroves (Table 1; Fig. 2B).

The highest mean density of trees (DT) was in ARAT (0.42 ind.m^{-2}) and the lowest in MAGO (0.07 ind.m^{-2}). Considering all sampling points in the BTS, the mean DT was 0.18 ± 0.13 ind.m^{-2} ($CI_{95\%:}$ 0.14–0.21 ind. m^{-2}). Therefore, BTS mangroves were divided into two groups characterized by high (ARAT and ACUP) and low (PITI, RISP, ENPO, SAUB, MARA, PTGR and MAGO) density of trees (Fig. 2C). Finally, the mean values of DBH ranged from 2.3 to 12.8 cm. PTGR and RISP were the areas with the lowest and highest values, respectively (Table 1).

Cluster analysis based on *U. cordatus* parameters (DC, density of the crabs; and CW, carapace width) and mangrove characteristics related with flooding by tides (FH) and arboreal parameters (DT, density of trees; and DBH, diameter at breast height) reveals two groups of mangrove areas (Fig. 6 A), properly spatialized at BTS (Fig. 6B). Two variables (DC and FH) were more powerful in this hierarchical clustering, presenting two groups. Group 1 (G1: blue cluster – Fig. 6) was represented by four areas (RISP, ACUP, PTGR and MAGO), properly characterized by the highest means of crab densities (DC general mean: 1.82 ± 0.77 ind.m^{-2}), with lowest flooding height by tides (FH general mean: 16.40 ± 4.41 cm). On the other hand, Group 2 (G2: red cluster – Fig. 6) was represented by five areas (ARAT, PITI, ENPO, SAUB and MARA), with an inverse pattern (DC general mean: 0.63 ± 0.58 ind. m^{-2}; and FH general mean: 33.84 ± 8.58 cm). Therefore, these groups differed significantly in relation to density of crabs (G1 = 3 *G2; $t = 7.90$; $p < 0.001$) and flooding by tides (G1 = 0.5 *G2; $t = 8.25$; $p < 0.001$).

Considering all mangroves and parameters previously described, the sum of the two dimensions (Dim1 and Dim2) of the PCA explained 71% of data variability (Fig. 7). PCA analysis indicated that flood height (FH) and crab density (DC) were antagonistic variables, with a significant negative correlation confirmed by Spearman's correlation analysis ($\rho = -0.58$; $p = 7.93 \cdot 10^{-5}$). The same negative correlation occurred between DBH and tree density (DT) ($\rho = -0.53$; $p = 44.2 \cdot 10^{-5}$). On the other hand, there was a significant positive correlation for FH vs. CW ($\rho = 0.41$; $p = 0.008$).

4. Discussion

Ucides cordatus density is directly affected by the natural characteristics of mangrove areas, such as composition of the arboreal vegetation

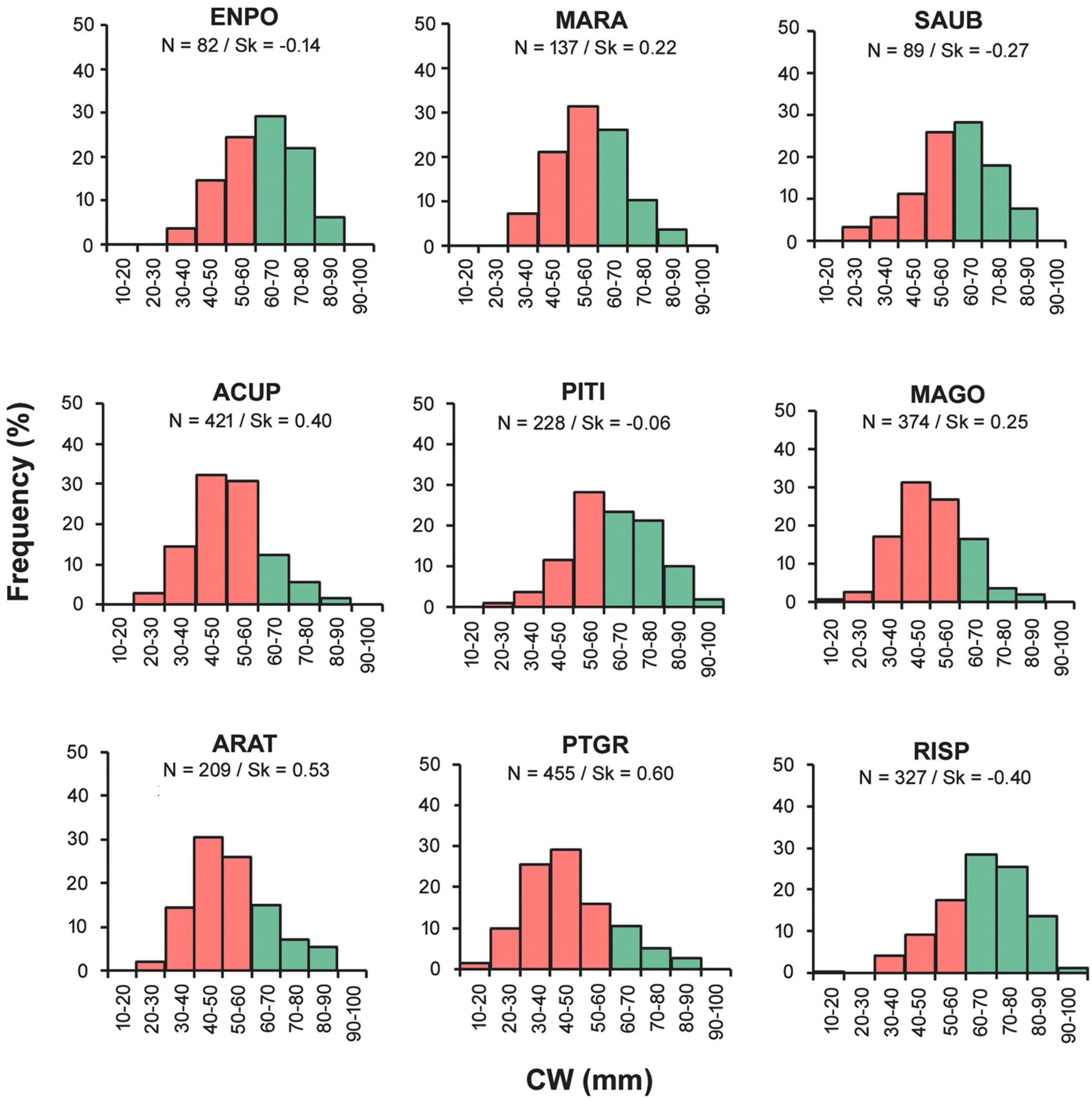

Fig. 4. Populational structure of *Ucides cordatus*. Size class distribution (CW, carapace width in millimeters) of nine mangroves in the "Todos os Santos" Bay, Bahia, Brazil, from January to August 2019. Where: Juveniles (salmon bars: CW<60 mm), adults (CW≥60 mm). N, number of individuals; sk = asymmetry coefficient; ACUP, Acupe; ARAT, Aratuípe; ENPO, Engenho da Ponte; MAGO, Maragogipinho; MARA, Maragogipe; PTGR, Ponta Grossa; RISP, Rio São Paulo; and SAUB, Saubara.

(Schmidt et al., 2013; Wunderlich and Pinheiro, 2013), food availability and type (Northaus and Wolff, 2007; Christofoletti et al., 2013), tidal flooding level (Wunderlich and Pinheiro, 2013; Pinheiro et al., 2018), and salinity (Conti and Nalesso, 2010; Góes et al., 2010). Other factors related to human interference, such as degree of mangrove degradation (Pinheiro et al., 2013; Duarte et al., 2016) and fishing incidence (Pinheiro and Fiscarelli, 2001), should also be considered. This considerable variation among mangrove areas characterizes each one as a particular "population signal" to be monitored in a long-term study using the results to plan and direct conservation actions if necessary. In BTS mangroves, the investigated areas have quite distinct characteristics, for example in terms of phytophysiognomy and height of mangrove trees. Thus, the "uçá"-crab density varies considerably among the nine areas under study and among Brazilian mangrove areas. Finally, for the same reasons, the literature review (Table 2) did not confirm a pattern of variation in population density related to latitude among Brazilian mangrove areas.

The literature review (Table 2) also reveals that the variation in density estimates for *U. cordatus* may be related to the absence of a single sampling protocol that minimizes the effects of indirect method errors. In this context, the density of this species can be influenced by some variables, such as 1) size of the ideal sample quadrat, 2) sampling mangrove zone (fringe, basin or transition/apicum), 3) type of burrow quantified (active: opened and closed, with exclusion of abandoned), and 4) correct identification of the burrow's morphology of *U. cordatus* and the contrast to those buried by other crab species. For these reasons, species density estimates differ broadly among studies carried out along the Brazilian coast (see Table 2).

Considering variable 1 (size of the ideal sample quadrat), sometimes density values may not correspond to reality since the size of the sample unit depends on the spatial distribution of the "uçá"-crab. There are three patterns of spatial distribution (uniform, random, and aggregate) that occur as a function of the species' preference for environmental factors or its interaction with other organisms (Pinheiro and Almeida, 2015; Pinheiro et al., 2018). In this context, Pinheiro and Almeida (2015) and results from the MONITORA Program support a 5 × 5 m (25 m^2) quadrat to minimize the effects of such spatialization. For variable 2 (sampling mangrove zone), literature data show that density

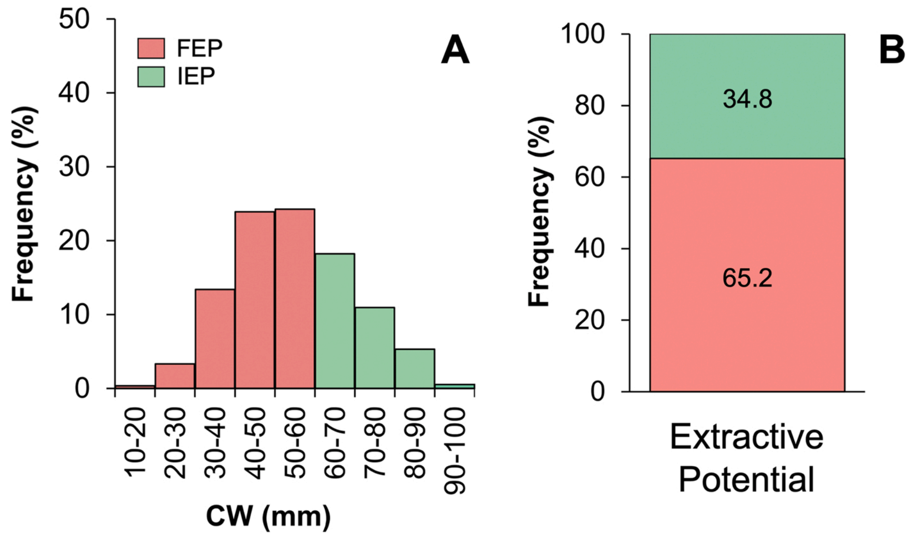

Fig. 5. Populational structure of *Ucides cordatus* at "Todos os Santos" Bay, Brazil, from January to August 2019. **(A)** General distribution in size classes (CW, carapace width), **(B)** Frequency of extractive potential (IEP, immediate; and FEP, future).

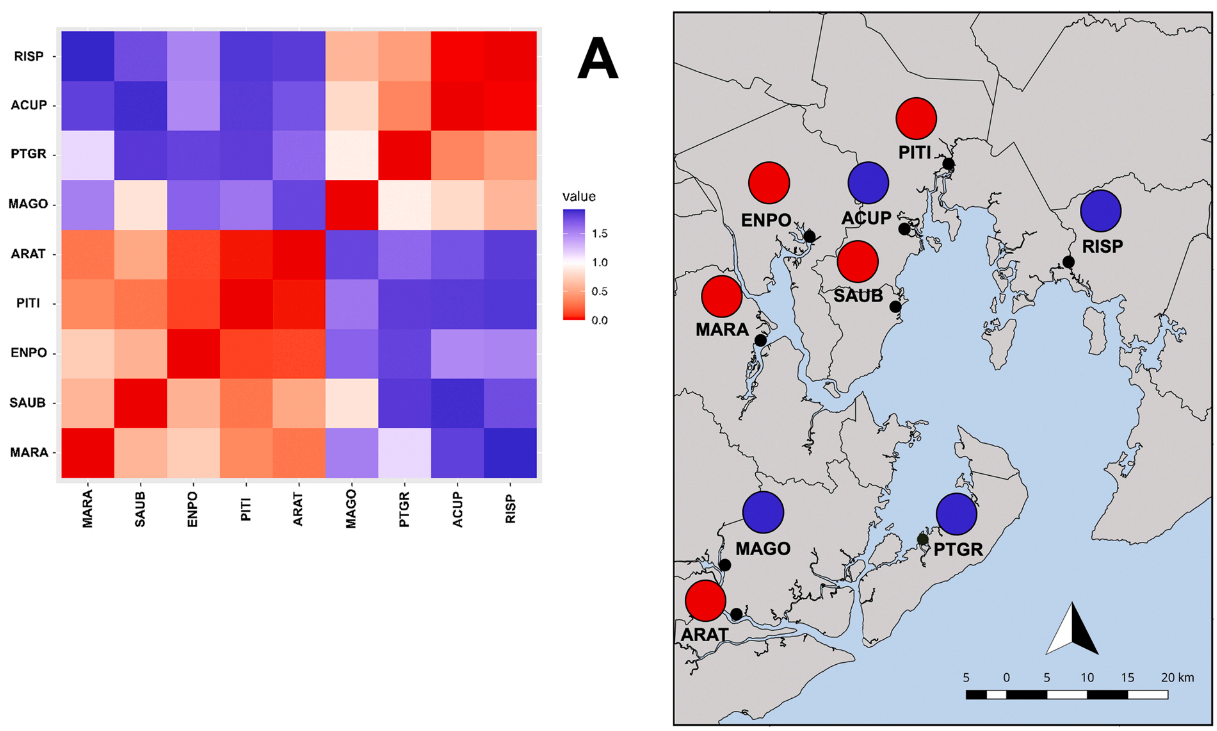

Fig. 6. Hierarchical clustering matrix **(A)** using correlation as similarity index (pure red, higher similarity; and pure blue, higher dissimilarity) among mangrove areas in "Todos os Santos" Bay and their spatial representation **(B)** based on *Ucides cordatus* parameters (DC, density of crabs; CW, carapace width of crabs) and mangrove's characteristics (FH, flooding height by tides; DBH, diameter at breast height; DT, density of trees). ACUP, Acupe; ARAT, Aratuípe; ENPO, Engenho da Ponte; MAGO, Maragogipinho; MARA, Maragogipe; PTGR, Ponta Grossa; RISP, Rio São Paulo; and SAUB, Saubara.

varies due to vegetation composition and flood tide level of mangroves (Piou, 2009; Conti and Nalesso, 2010, Sandrini-Neto & Lana, 2012; Pinheiro et al., 2018; present study). Thus, for consistent sampling, it is necessary to randomize the sampling units as much as possible in different mangrove zones. Finally, variables 3 and 4 (type and correct identification of burrows) are directly related to the researcher's familiarity with the characteristics of *U. cordatus*. Hiring an experienced fisherman is essential and minimizes such errors.

It is highly recommended, therefore, that all these variables be verified when adapting the "uçá"-crab sampling protocol to other mangrove brachyuran species of commercial interest in order to generate data in different locations that can be compared.

In BTS, there was an increase in the frequency of closed galleries during the rainy season (winter in the southern hemisphere). This condition also appeared in previous studies carried out in other Brazilian regions (Northeastern: Souto, 2007; Southeastern: Conti and Nalesso, 2010; Góes et al., 2010; and Southern: Wunderlich et al., 2008). According to Pinheiro and Fiscarelli (2001), the highest frequency of closed galleries coincides with the molting period of "uçá"-crabs, when individuals close the opening of their galleries and go down to greater

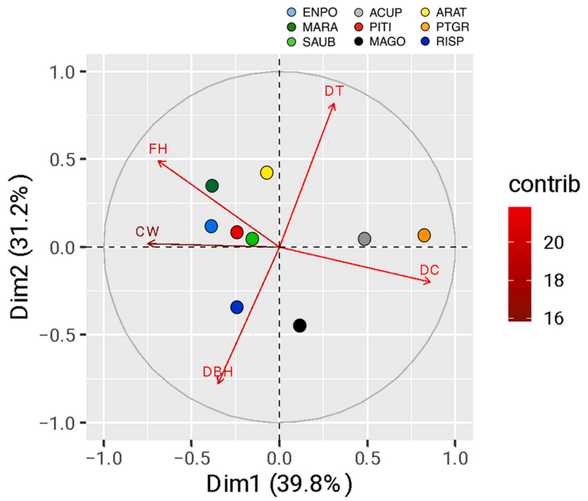

Fig. 7. Multivariate analysis of nine mangrove areas of the "Todos os Santos" Bay, Brazil, represented by principal component analysis (PCA) using a biplot function. The percentual contribution of each variable is associated with mangrove flooding (FH, flooding height by tides), arboreal vegetation (DT, density of trees; DBH, diameter at breast height), and mangrove crab *Ucides cordatus* (CW, carapace width; DC, density of crabs).

depths to molt. According to Wunderlich et al. (2008) and Góes et al. (2010), this behavior of *U. cordatus* of closing galleries is stimulated by lower temperatures during winter. Thus, the occurrence of a greater number of closed galleries between the months of June and August could be related to the molting period of this species in BTS.

Population density of the "uçá"-crab is dependent on the flood level resulting from tides and the predominant arboreal species in a given mangrove area. In this context, *L. racemosa* forests, which are generally associated with lower levels of flooding, show a higher crab density, while areas with predominance of *R. mangle* (generally associated with higher levels of flooding) have a lower crab density (Pinheiro, 2006). In BTS, with the exception of PTGR, mangrove areas with specimens of *R. mangle* areas had a lower crab density, while areas with predominance of *L. racemosa* ($> 70\%$) generally presented a higher crab density. In PTGR, although there is predominance of *R. mangle* (82.6%), flood level was lower, thus justifying the high population density in that area.

In addition to the natural characteristics of mangroves, it is important to note that the crab population parameters can also be negatively affected by mangrove forest degradation and/or fishing pressure (see Duarte et al., 2016; Pinheiro et al., 2018), or even diseases such as lethargic crab disease (LCD), as Schmidt et al. (2009) reported.

In BTS, most mangroves under study ($n = 5$; 55.6%) had a predominance of *L. racemosa* ($\geq 70\%$), with a crab density ranging from 0.59 to 2.12 $ind.m^{-2}$ (1.4 ± 0.6 $ind.m^{-2}$). Such values are below those Pinheiro et al. (2018) observed for *L. racemosa* in mangroves of the Southeastern Brazil, where *U. cordatus* density ranged from 3.0 to 8.0 $ind.m^{-2}$. These authors concluded that the absence of fishing activity in mangrove areas with *L. racemosa* and the highly sandy sediment is responsible for the high crab densities. According to Souza and Pinheiro (2021), crab collectors prefer to explore mangrove areas with muddy sediment, generally with prevalence of *R. mangle* and larger sizes of this species, due to the ease of collecting animals in these areas, as informed by 67% of these traditional fishermen in the Itanhaém Estuary (SP, Brazil). On the other hand, during field activities, it was possible to observe that crab-gatherers explore areas of *L. racemosa* in the BTS (authors' personal observation). Therefore, it is possible that "uçá"-crab populations from BTS areas with predominance of *L. racemosa* are being affected by anthropogenic factors such as overfishing.

The highest crab densities clustered in only one group, totaling 44.4% of sampling points (i.e., PTGR, ACUP, MAGO, ARAT and RISP) often associated with the lowest animal size means. These mangrove areas broadly contrasted to arboreal composition: there was no pattern of a prevalent species (monospecific forest). In general, higher crab densities were observed in mangrove areas where *L. racemosa* was the predominant vegetation, a fact previously verified by Pinheiro (2006), Schmidt et al. (2009) and Pinheiro et al. (2018). Nevertheless, Santos et al. (2016) reported differences in animal size in relation to arboreal composition in mangrove areas in the State of Sergipe (Northeastern Brazil) and mentioned a high frequency of small crabs associated with the predominance of *L. racemosa*. Similarly, Pinheiro (2006) observed in Southeastern Brazil high crab densities (10.3 ± 5.3 $ind.m^{-2}$) of *U. cordatus* associated with mangrove forests in which *L. racemosa* predominated compared to *R. mangle* (1.8 ± 0.9 $ind.m^{-2}$) and *A. schaueriana* (1.5 ± 0.9 $ind.m^{-2}$). The latter author concluded that mangroves with a denser population of "uçá"-crab are composed by small animals, with a dependence of texture and granulometry of the sediment, generally sandier in these places.

This small individual size of *U. cordatus* in *L. racemosa* forests is also dependent on the supply of nutrients provided by leaves and propagules to crabs. In this context, Christofoletti et al. (2013) observed that crabs living in mangroves with predominance of *L. racemosa* (LR) ingested more leaves but showed a lower degree of fattening compared to animals from areas with a predominance of *A. schaueriana* (AS) and *R. mangle* (RM). These authors also concluded that the leaves of these three different mangrove species had a different nutritional value and followed a hierarchical order: $AS > RM > LR$. However, these authors considered that leaf litter (leaves and propagules) available as food to crabs in monospecific forests sometimes is not composed exclusively of the predominant arboreal species. Thus, *U. cordatus* can grow more in mangrove forests with a higher diversity of leaf litter, particularly if most of it is *A. schaueriana* and *R. mangle*. In the present study, the largest animals were found in the RISP mangrove, the only area with an exclusive predominance of *A. schaueriana* (100%), although this species have occurred in SAUB (90.9%) and ENPO (41.7%) without showing the same effect. In addition, there was no fishing activity in RISP (maybe due to the proximity to petrochemical industries), allowing the population to grow and individuals to reach larger sizes without being captured.

Because of this better nutritional status and absence of crab collectors, RISP also showed the highest IEP (69.1%) among the nine areas under study. ENPO, SAUB and PITI, which have a mixed mangrove forest (*R. mangle*, *A. schaueriana* and *L. racemosa*), showed IEP ranging from 53.9% to 57.3%. On the other hand, in ACUP, MAGO and ARAT mangroves, where vegetation was almost exclusively composed of *L. racemosa*, IEP values were below 30%.

The results obtained in this study corroborate those of Pinheiro (2006), who found higher IEP percentages in mixed forest areas with predominance of *R. mangle* (55.1%) and lower percentages in *L. racemosa* areas (maximum of 27.4%). Similarly, Santos et al. (2016) observed a higher frequency of commercial-sized animals (IEP) in mangroves of the São Francisco River estuary (Sergipe/Alagoas, Brazil), which is mainly composed of red mangrove (*R. mangle*). Recently, Pinheiro et al. (2018) reported a higher frequency of non-commercial-sized animals ($CW < 60$ mm) in mangroves in Southeastern Brazil in forests with a predominance of *L. racemosa*. Thus, considering that, in the present study, most mangrove areas evaluated showed predominance of *L. racemosa*, FEP percentages in BTS were, in general, higher than those of IEP.

The principal component analysis (PCA) indicated that flood level was a relevant variable, explaining the relationships with arboreal vegetation and crab population. In this context, flood height (FH) and DBH was positively correlated with crab size (CW), while crab density (DC) was not correlated to these variables. Thus, areas with higher flooding by tides and more developed trees (higher DBH) had lower density of larger crabs, while areas with lower flooding had a higher density of smaller crabs.

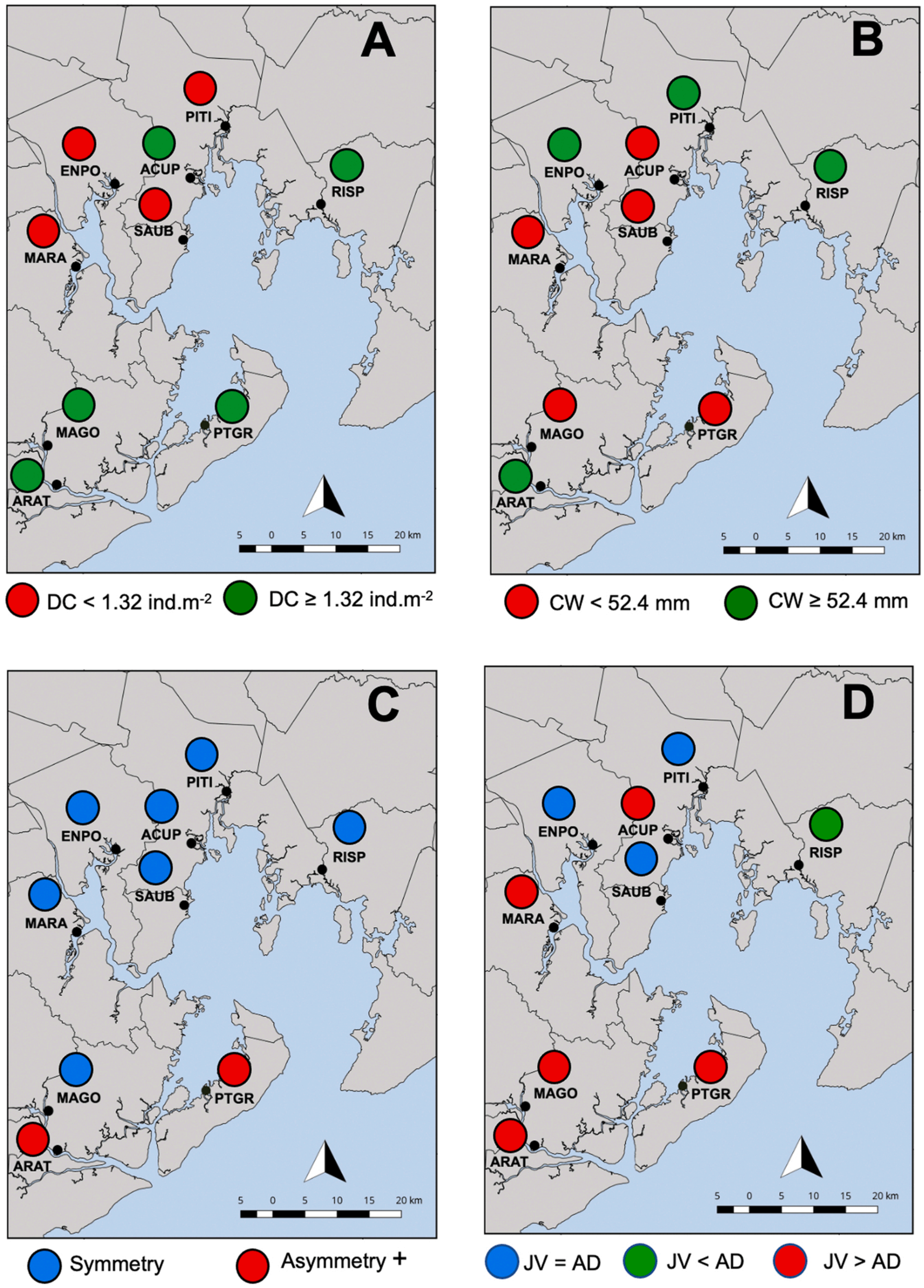

Fig. 8. Spatial distribution of *Ucides cordatus* in nine mangrove areas of the "Todos os Santos" Bay (BTS), Brazil, in relation to **(A)** density of crabs, **(B)** size of crabs, **(C)** population structure, and **(D)** category of the ontogenetic phase (JV, juvenile; and AD, adult). ACUP, Acupe; ARAT, Aratuípe; ENPO, Engenho da Ponte; MAGO, Maragogipinho; MARA, Maragogipe; PTGR, Ponta Grossa; RISP, Rio São Paulo; and SAUB, Saubara.

Pinheiro et al. (2018) also observed a strong negative correlation ($r = -0.94$; $p < 0.05$) between crab density and flood level. Schmidt et al. (2009) also reported a relationship between these two variables, although they have not tested their correlation. Pinheiro (2006) suggested that flooding caused by high tides in mangroves affects food availability (nutrients and leaf litter), resulting in lower crab densities in higher flooding areas.

The positive association observed between crab size (CW) and flood height (FH) also occurred when CW was related to variables that represent the development of trees (such as height and DBH) because all of them are covariates. In this context, the presence of *R. mangle* is associated with high-flooding mangroves, with the presence of larger crabs. On the other hand, *L. racemosa* is an arboreal species that generally occurs in a higher topography and less flooded mangroves, in which smaller crabs occur (Schmidt et al., 2009; Pinheiro et al., 2018).

The second group, represented by 55.6% of the mangrove areas sampled (i.e., MARA, SAUB, ENPO, PITI and ARAT), was characterized by a higher flooding by tides (FH), and most of them associated with a higher structural development of the mangrove forest and with a lower density of trees (DT) of greater diameter (DBH) (see Cunha-Lignon et al., 2011). These areas are often relevant for crab extraction, mainly mangroves composed by two or more arboreal species, a fact not verified in some areas (e.g., ARAT) due to prevalence of *L. racemosa* even if associated with high flood levels.

In this study, most mangroves were composed of *L. racemosa*. In accordance with the suggested management for the sustainable use of

Table 2
Mean density of crabs (DC, ind.m^{-2}) and crab size (CW, carapace width in millimeter) of *Ucides cordatus*, sampling protocol and arboreal predominance in mangrove areas along the Brazilian coast. Where: RM, *Rhizophora mangle*; LR, *Laguncularia racemosa* (LR); AG, *Avicennia germinans*; AS, *Avicennia schaueriana*; CE, *Conocarpus erectus*; AP, Apicum; n, number of quadrats; M, male; F, female; na, not available.

Region	State	Latitude	DC (ind. m^{-2})	CW (mm)	n	Quadrat Size	Arboreal predominance	Reference
North	Amapá	01°48'29.06" N	5.7	na	30	5 × 5 m	1 Site RM 1 Site AG 2 Sites RM/AG	Fernandes and Carvalho (2007)
	Amapá	02°35'35.50" N	1.1	69.1 M 59.6 F	54	5 × 5 m^2 Density calculated using the number of inhabited burrows, empty burrows and capped burrows.	AG	Amaral et al. (2014)
	Pará	0°52'30.23" S	6.1	na	6	Five areas (1 ×3 m) and one area (3 ×5 m) plotted from pictures Density calculated using only occupied galleries	Site 1 RM Site 2 LR	Piou et al. (2009)
	Pará	0°50'19.69" S	1.7	60.8 M 54.6 F	18–24	5 × 5 m Density calculated by correcting the crab catch with the capture efficiency	RM	Diele et al. (2005)
	Pará	0°57'19.15" S	1.8	55.0 M 51.0 F	45	5 × 5 m Density calculated using only active galleries	5 sites LR 2 sites RM 2 sites AG	Aviz et al. (2020)
	Pará	0°50'53.77" S (*)	2.1	71.4	12	5 × 5 m Density calculated using only active galleries	N/A	Maia et al. (2016)
Northeast	Ceará	3°42'29.48" S (*)	4.8	60.3 M 56.9 F	54	1 × 1 m Density calculated using the number of inhabited burrows, empty burrows and capped burrows.	N/A	Alcântara-Filho (1978)
	Paraíba	6°46'34.50" S (*)	1.7	56.0 M 50.0 F	16	10 × 10 m Density calculated using only active galleries	RM, AG, AS, LR, CE	Alves and Nishida (2004)
	Pernambuco	08°44'6.59" S (*)	0.8	46.2 M 40.1 F	6	5 × 5 m Density calculated using open or sealed galleries	LR	Oliveira et al. (2013)
	Sergipe	10°30′27′ S	1.2	na	36	5 × 5 m Density calculated using only active galleries	RM	Santos et al. (2016)
	Bahia	12°50'8.87" S (*)	1.3	52.4	45	5 × 5 m Density calculated using only active galleries	2 Site AS 6 Sites LR 1 Site RM	Present Study
	Bahia	16°36'1.28" S (*)	1.3	37.5 LR 43.0 RM 26.0 AP	24	5 × 5 m Density calculated using the number of inhabited burrows, empty burrows and capped burrows.	Zone 1 LR Zone 2 RM Zone 3 AP	Schmidt et al. (2009)
Southeast	Espírito Santo	19°54′0.0″ S	2.5	47.7 M 49.8 F	90	1 × 1 m Density calculated using open or sealed galleries	2 Sites RM 1 Site LR	Conti and Nalesso (2010)
	Espírito Santo	20°14′20″ S	3.7	54.6	4	bands along four transects-200 m in length Density calculated using open or sealed galleries	RM, LR, AS, AG	Góes et al. (2010)
	São Paulo		10.3 LR 1.8 RM 1.5 AS	56.1 LR 67.9 RM 66.3 AS	40	2 × 2 m Density calculated using only active galleries	3 Sites LR 3 Sites RM 3 Sites AS	Pinheiro (2006)
	São Paulo	24°42'5.32" S	6.0	49.6	60	2 × 2 m Density calculated using only active galleries	LR	Pinheiro et al. (2018)
	Paraná	25°30′0.0″ S	0.9–1.4	na	45	2 × 2 m Density calculated using only active galleries	1 Site RM/LR/AS 1 Site RM/AS 1 Site LR	Sandrini-Neto and Lana (2011)
South	Santa Catarina	26°11′12″ S	2.1	68.0 M 58.7 F	10	2 × 2 m Density calculated using only active galleries	1 Site LR 1 Site AS	Wunderlich et al. (2008)
	Santa Catarina	27°34′48″ S	1.1	na	10	1 × 1 m Density calculated using open or sealed galleries	N/A	Branco (1993)

(*) approximate coordinates.

"uçá"-crab (see Dias-Neto, 2011), these should be considered as fishing-free areas as they have a higher density of juvenile crabs (> FEP), which should be preserved to guarantee the sustainability of the fishing resource. On the other hand, the most suitable areas for *U. cordatus* fishing are mangroves with predominance of *R. mangle* and *A. schaueriana,* in which the density of crabs (DC) is lower but the specimens are larger, resulting in a greater immediate extractive potential (Dias-Neto, 2011). This was extensively discussed in Pinheiro (2006) and later confirmed by Santos et al. (2016) and Pinheiro et al. (2018). This management strategy is simple and fundamental for the conservation and exploitation of *U. cordatus* as a fishing resource and should be established in all estuarine systems to be effective.

The greater fishing potential (IEP ~ 70%) occurred in RISP indicating that the "uçá"-crab population in this mangrove area was suitable for commercial exploitation. In addition, it is necessary to carry out constant monitoring regarding the extractive activity with *U. cordatus* populations in BTS mangroves. This practice, combined with environmental education studies and an effective government management, may allow the implementation of public policies that ensure the protection of populations of this species in the region.

Ucides cordatus population parameters differed significantly among BTS mangroves due to peculiar characteristics among the mangrove areas under study. RISP mangrove showed the best fishing potential due to the high density of large adult animals. On the other hand, ACUP, MAGO, ARAT and PTGR mangroves have a low fishing potential due to the high density of small animals.

This study represents the first assessment of *U. cordatus* populations in BTS mangroves (Brazil). The results presented here could be used for the management of the "uçá"-crab in the "Todos os Santos" Bay, especially using the strategies suggested in a management plan for sustainability of the "uçá"-crab as proposed by Dias-Neto (2011).

5. Conclusions

The population parameters of *U. cordatus* differ significantly between BTS mangroves due to peculiar characteristics between the mangrove areas under study. In general, BTS mangrove forests with a predominance of *L. racemosa* have a higher density of smaller crabs. However, the density of *U. cordatus* in these areas are below the values reported in the literature, which suggests overfishing in these locations. Therefore, our recommendation is to avoid an extractive activity of *U. cordatus* in these areas. In this way, *L. racemosa* mangroves in BTS should be considered as fishing-free areas. On the other hand, our data show that BTS crab gatherers could benefit from exploring some mangrove forests with a predominance of *A. schaueriana* since in these areas the IEP is higher (e.g. RISP).

During the dry season, BTS crab gatherers benefit from a higher population density and size of *U. cordatus*. However, considering the nine areas investigated, crab size in the "Todos os Santos" Bay is below the current fishing defense ordinance for the "uçá"-crab in the Northern and Northeastern regions of Brazil (CW $\geq$ 60.0 mm). Therefore, noncommercial animals are more abundant than those with a commercial size. This reinforces the need for monitoring fishing activity in the region and the size of the crab sold by gatherers. In this context, the standardization of a single sampling protocol is necessary to allow a better comparison of density and size estimates of *U. cordatus* along its geographic distribution.

Funding

This work was supported by the National Council of Scientific and Technological Research – CNPq (Grant no. 441389/2017–1) and the Coordination for the Improvement of Higher Education Personnel – CAPES (TAM, Grant no. 88882.424479/2019–01).

CRediT authorship contribution statement

Thaís Arrais Mota: Investigation, Validation, Formal analysis, Data curation, Writing – original draft, Writing – review & editing. **Marcelo Antônio Amaro Pinheiro:** Methodology, Formal analysis, Validation, Visualization, Conceptualization, Writing – original draft, Writing – review & editing, Resources. **Norma Suely Evangelista-Barreto:** Project administration, Visualization, Writing – original draft. **Sérgio Schwarz da Rocha**: Supervision, Project administration, Funding acquisition, Visualization, Data curation, Resources, Writing – original draft, Writing – review & editing, Investigation, Formal analysis, Conceptualization, Methodology.

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

Data will be made available on request.

Acknowledgments

The authors express their sincere gratitude to the Programa de Pós-Graduação em Ciência Animal (PPGCA) and the Centro de Ciências Agrárias, Ambientais e Biológicas – Universidade Federal do Recôncavo da Bahia for providing all laboratory facilities; to MSc. Monica Arlinda Vasconcelos Ramos, Robert Wagner dos Santos Cardim and local crab catchers for their help during field activities. MAAP is grateful to the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the research fellowship awarded (Grant no. 305957/2019–8).

References

Alcântara-Filho, P., 1978. Contribuição ao estudo da biologia e ecologia do caranguejo-uçá, *Ucides cordatus* (Linnaeus, 1763) (Crustacea, Decapoda, Brachyura) no Manguezal do Rio Ceará (Brasil). Arq. Ciên. Mar. 18, 1–41.

Alves, R.R.N., Nishida, A.K., 2004. Population structure of the mangrove crab *Ucides cordatus* (Crustacea: Decapoda: Brachyura) in the Estuary of the Mamanguape River. Northeast Braz. Trop. Oceano 32, 23–37. https://doi.org/10.5914/tropocean.v32i1.5031.

Amaral, K.D.S., Vieira, I.M., Osório, F.M., Rocha, J.D.M., Lima, J.F., 2014. Bioecology of the crab *Ucides cordatus* (Crustacea, Decapoda) in mangroves influenced by the Amazon River, Brazil. Acta Amaz 44, 213–222. https://doi.org/10.1590/S0044-59672014000200007.

Andrade, R.L.B., Hatje, V., Masqué, P., Zurbrick, C.M., Boyle, E.A., Santos, W.P.C., 2017. Chronology of anthropogenic impacts reconstructed from sediment records of trace metals and Pb isotopes in Todos os Santos Bay (NE Brazil). Mar. Pollut. Bull. 125, 459–471. https://doi.org/10.1016/j.marpolbul.2017.07.053.

Andreetta, A., Fusi, M., Cameldi, I., Cimo, F., Carnicelli, S., 2014. Mangrove carbon sink. Do burrowing crabs contribute to sediment carbon storage? Evidence from a Kenyan mangrove system. J. Sea. Res 85, 524–533. https://doi.org/10.1016/j.seares.2013.08.010.

Aviz, B.P., Simith, D.J.B., Fernandes, M.E.B., 2020. Natural recovery of the crab *Ucides cordatus* (Ocypodidae) in replanted mangroves on the Brazilian Amazon Coast. Wetlands 40, 2367–2379. https://doi.org/10.1007/s13157-019-01206-2.

Barros, F., Costa, P.C., Cruz, L., Mariano, D.L.S., Miranda, R.J., 2012. Habitats bentônicos na Baía de Todos os Santos. Rev. Virtual Quim. 4, 551–565. https://doi.org/10.5935/1984-6835.20120043.

Branco, J.O., 1993. Aspectos ecológicos do caranguejo *Ucides cordatus* (Linnaeus, 1763) (Crustacea, Decapoda) do manguezal do Itacorubi, Santa Catarina, Brasil. Arq. Biol. Tecnol.. 36, 133–148.

Carmona-Suárez, C.A., Guerra-Castro, E., 2011. Comparison of three quick methods to estimate crab size in the land crabs *Cardisoma guanhumi* Latreille, 1825 and *Ucides cordatus* (Crustacea: Brachyura: Gecarcinidae and Ucididae). Rev. Biol. Trop. 60, 139–149.

Christofoletti, R.A., Hattori, G.Y., Pinheiro, M.A.A., 2013. Food selection by a mangrove crab: temporal changes in fasted animals. Hydrobiologia 702, 63–72. https://doi.org/10.1007/s10750-012-1307-6.

Conti, R.C., Nalesso, R.C., 2010. Status of the population structure of the mangrove crab *Ucides cordatus* (Decapoda: Ocypodidae) on the Piraquê-Açu river estuary. Espírito St., Braz. Braz. J. Oceano 58, 81–92.

R. Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Côrtes, L.H.O., Zappes, C.A., Di Beneditto, A.P.M., 2014. Extração e cadeia produtiva do caranguejo-uçá no Norte do Rio de Janeiro. Bol. Inst. Pesca 40, 639–656.

Costa, P., Dórea, A., Neto, E.M., Barros, F., 2015. Are there general spatial patterns of mangrove structure and composition along estuarine salinity gradients in Todos os Santos Bay? Estuar. Coast. Shelf. Sci.. 166, 83–91. https://doi.org/10.1016/j.ecss.2015.08.014.

Costa, T.M., Pitombo, F.B., Soares-Gomes, A., 2014. The population biology of the exploited crab *Ucides cordatus* (Linnaeus, 1763) in a southeastern Atlantic Coast mangrove area, Brazil. Invertebr. Reprod. Dev. 58, 259–268. https://doi.org/10.1080/07924259.2014.917126.

Cunha-Lignon, M., Coelho, C., Almeida, R., Menghini, R.P., Schaeffer-Novelli, Y., Cintrón, G., Dahdouh-Guebas, F., 2011. Characterisation of mangrove forest types in view of conservation and management: a review of mangals at the Cananéia region, São Paulo State, Brazil. J. Coast. Res SI-64, 349–353.

Dias-Neto, J., 2011. Proposta de Plano Nacional de Gestão para o Uso Sustentável do Caranguejo-Uçá, do Guaiamum e do Siri-Azul, first ed. Brasília, IBAMA.

Diele, K., Koch, V., Saint-Paul, U., 2005. Population structure, catch composition and CPUE of the artisanally harvested mangrove crab *Ucides cordatus* (Ocypodidae) in the Caeté estuary. In: Aquat. Living Resour, 18. indications for overfishing, North Brazil, pp. 169–178. https://doi.org/10.1051/alr:2005018.

Duarte, L.F.A., Souza, C.A., Nobre, C.R., Pereira, C.D., Pinheiro, M.A.A., 2016. Multi-level biological responses in *Ucides cordatus* (Linnaeus, 1763) (Brachyura, Ucididae), as indicators of conservation status in mangrove areas from the Western Atlantic. Ecotoxicol. Environ. Saf. 133, 176–187. https://doi.org/10.1016/j.ecoenv.2016.07.018.

Fernandes, M.E.B., Carvalho, M.L., 2007. Bioecologia de *Ucides cordatus* Linnaeus, 1763 (Decapoda: Brachyura) na costa do Estado do Amapá. Bol. Lab. Hidrobiol. 20, 15–22.

Fogaça, F.H.S., Fernandes-Góes, L.C., Souza, L.O., Silva, K.P., Góes, J.M., Pereira, A.M.L., Mai, M.G., Magalhães, J.A., 2018. Monitoring mangrove crab *Ucides cordatus* Linnaeus, 1763 (Crustacea: Ucididae) landing in the Parnaíba River Delta: fishing characteristics, social and economic aspects. Nauplius 26, 327–345. https://doi.org/10.1590/2358-2936e2018020.

Fondo, E.N., Kimani, E.N., Odongo, D.O., 2010. The status of mangrove mud crab fishery in Kenya. East Afr. Int. J. Fish. Aquac. 2, 79–86. https://doi.org/10.5897/IJFA.9000037.

Freitas, A.C., Furtado-Junior, I., Tavares, M.C.S., Borcem, E.R., 2015. Análise socioeconômica e esforço de pesca na captura do caranguejo-uçá- *Ucides cordatus* (Crustacea: Ucididae) - na Reserva Extrativista Maracanã-costa amazônica do Brasil. Bol. Mus. Para. Emílio Goeldi. Cienc. Hum. 10, 711–723. https://doi.org/10.1590/1981-81222015000300012.

Góes, P., Branco, J.O., Pinheiro, M.A.A., Barbieri, E., Costa, D., Fernandes, L.L., 2010. Bioecology of the Uçá-crab, *Ucides cordatus* (Linnaeus, 1763), in Vitória Bay, Espírito Santo state, Brazil. Braz. J. Oceanogr.. 58, 153–163.

Husson, F., Josse, J., Le, S.; Mazet, J., 2018. FactoMineR: Multivariate Exploratory Data Analysis and Data Mining. R package (version 1.41). http://CRAN.Rproject.org/package=FactoMineR.

Jankovski, M., Pires, J.S.R., Nordi, N., 2006. Contribuição ao manejo participativo do caranguejo-uçá, *Ucides cordatus* (Linnaeus, 1763), em Cananéia – SP. B. Inst. Pesca 32, 221–228.

Kassambara, A., Mundt, F., 2016. Package 'factoextra': Extract and Visualize the Results of Multivariate Data Analysis. R package (version 1.0.3). http://www.sthda.com/english/rpkgs/factoextra.

Koch, V., Wolff, M., 2002. Energy budget and ecological role of mangrove epibenthos in the Caeté estuary, North Brazil. Mar. Ecol. Progr 228, 119–130. https://doi.org/10.3354/meps228119.

Le, S., Josse, J., Husson, F., 2008. FactoMineR: an R package for multivariate analysis. J. Stat. Softw. 25, 1–18. https://doi.org/10.18637/jss.v025.i01.

Leoville, A., Lagarde, R., Grondin, H., Faivre, L., Rasoanirina, E., Teichert, N., 2021. Influence of environmental conditions on the distribution of burrows of the mud crab, *Scylla serrata*, in a fringing mangrove ecosystem. Reg. Stud. Mar. Sci. 43, 101684 https://doi.org/10.1016/j.rsma.2021.101684.

Lima, C.D.M., Silva, H.R.C., Bernard, E., 2018. Efetividade do defeso do caranguejo-uçá (*Ucides cordatus*): Análise de percepção de consumidores e vendedores. Ambient. Soc. 21, 1–22. https://doi.org/10.1590/1809-4422asoc0046r3vu18l1ao.

Maia, C., Lima, M.C.P., Silva, M.M.T., Paiva, R.S., 2016. Densidade e estrutura populacional do caranguejo-uçá, *Ucides cordatus* (Linnaeus, 1763) na Reserva Extrativista Marinha de Tracuateua, Pará, Brasil. Biota Amaz. 6, 86–92. https://doi.org/10.18561/2179-5746/biotaamazonia.v6n2p86-92.

Melo, G.A.S., 1996. Manual de Identificação dos Brachyura (Caranguejos e Siris) do Litoral Brasileiro, first ed. São Paulo, Editora Plêiade.

Mirera, D.O., Ochiewo, J., Munyi, F., Muriuki, T., 2013. Heredity or traditional knowledge: Fishing tactics and dynamics of artisanal mangrove crab (*Scylla serrata*) fishery. Ocean. Coast. Manag 84, 119–129. https://doi.org/10.1016/j.ocecoaman.2013.08.002.

Moraes, E.E.B., Nunes-Maia, B.J.B., Pinheiro, M.A.A., 2015. Population biology of the "uçá"-crab, *Ucides cordatus* (Linnaeus, 1763) (Brachyura: Ucididae), in mangroves of the Joanes River. Bahia State, Braz. Naupl. 23, 59–71. https://doi.org/10.1590/S0104-64972015002309.

Northaus, I., Wolff, M., 2007. Feeding ecology of the mangrove crab *Ucides cordatus* (Ocypodidae): food choice, food quality and assimilation efficiency. Mar. Biol. 151, 1665–1681. https://doi.org/10.1007/s00227-006-0597-5.

Oliveira, P.J.A., Coelho, P.A., Castiglioni, D.S., 2013. Population biology of *Ucides cordatus* (Linnaeus, 1763) (Crustacea, Brachyura, Ucididae) from two tropical mangroves sites in northeast coast of Brazil. Pan-Am. J. Aquat. 8, 89–103.

Pinheiro, M.A.A., 2006. Biologia e manejo do caranguejo-uçá, Ucides cordatus (Linnaeus, 1763) (Crustacea, Decapoda, Brachyura). Final Scientific Report FAPESP no 2002/05614–2. São Vicente: UNESP Campus do Litoral Paulista.

Pinheiro, M.A.A., Almeida, R., 2015. Monitoramento de populações do caranguejo-uçá, *Ucides cordatus* (Brachyura, Ucididae). In: Turra, A., Denadai, M.R. (Eds.), Protocolos para o Monitoramento de Habitats Bentônicos Costeiros. Instituto Oceanográfico da Universidade de São Paulo, São Paulo, pp. 122–133.

Pinheiro, M.A.A., Fiscarelli, A.G., 2001. Manual de Apoio à Fiscalização do Caranguejo-Uçá (Ucides cordatus), first ed. São Paulo, IBAMA/CEPSUL.

Pinheiro, M.A.A., Rodrigues, A.M.T., 2011. Crustáceos sobre-explotados e o Plano Nacional de Gestão dos caranguejos Uçá (*Ucides cordatus*), Guaiamú (*Cardisoma guanhumi*) e do Siri-Azul (*Callinectes sapidus*): uma estratégia para evitar que passem ao "status" de ameaçados de extinção. Rev. CEPSUL – Biodivers. e Conserv. Mar. 2, 50–57. https://doi.org/10.37002/revistacepsul.vol2.30550-57.

Pinheiro, M.A.A., Fiscarelli, A.G., Hattori, G.Y., 2005. Growth of the mangrove crab *Ucides cordatus* (Brachyura, Ocypodidae). J. Crustac. Biol. 25, 293–301.

Pinheiro, M.A.A., Duarte, L.F.A., Adam, M.L., Torres, R.A., 2013. Habitat monitoring and genotoxicity in *Ucides cordatus* (Crustacea: Ucididae), as tools to manage a mangrove reserve in southeastern Brazil. Environ. Monit. Assess. 185, 8273–8285. https://doi.org/10.1007/s10661-013-3172-9.

Pinheiro, M.A.A., Souza, C.A., Borba, H., 2015. Meat yield of the mangrove crab, *Ucides cordatus* (Linnaeus, 1763) (Crustacea, Brachyura, Ucididae). Bol. Inst. Pesca 41, 43–56.

Pinheiro, M.A.A., Santos, L.C.M., Souza, C.A., João, M.C.A., Neto, J.D., Ivo, C.T.C., 2016. Avaliação do caranguejo-uçá (Ucides cordatus) (Linnaeus, 1763) (Decapoda: Ucididae), in: Pinheiro, M.A.A., Boos, H. (Eds.) Livro vermelho dos crustáceos do Brasil. Avaliação 2010–2014. Sociedade Brasileira de Carcinologia, Porto Alegre, pp. 441–456.

Pinheiro, M.A.A., Souza, M.R., Santos, L.C.M., Fontes, R.F.C., 2018. Density, abundance and extractive potential of the mangrove crab, *Ucides cordatus* (Linnaeus, 1763) (Brachyura, Ocypodidae): subsidies for fishery management. . Acad. Bras. Ciên. 90, 1381–1395. https://doi.org/10.1590/0001-3765201820170090.

Pinheiro, M.A.A., Souza, F.V.B., Boos, H., Duarte, L.F.A., 2022. Cytotoxicity, genotoxicity, and impact on populations of the mangrove sentinel species, *Ucides cordatus* (Linnaeus, 1763) (Brachyura, Ocypodidae) after an environmental disaster at Cubatão, São Paulo, Brazil. e2022025 Nauplius 30. https://doi.org/10.1590/2358-2936e2022025.

Piou, C., Berger, U., Feller, I.C., 2009. Spatial structure of a leaf-removing crab population in a mangrove of a North-Brazil. Wetl. Ecol. Manag. 17, 93–106. https://doi.org/10.1007/s11273-008-9089-3.

Pülmanns, N., Diele, K., Mehlig, U., Nordhaus, I., 2014. Burrows of the semi- terrestrial crab *Ucides cordatus* enhance CO_2 release in a north Brazilian mangrove forest. PloS One 9, 1–13. https://doi.org/10.1371/journal.pone.0109532.

Rahman, M.M., Haque, S.M., Galib, S.M., Islam, M.A., Parvez Md, T., Hoque, Md.N., Wahab, M.A., Egna, H., Brown, C., 2020. Mud crab fishery in climate vulnerable coastal Bangladesh: an analysis towards sustainable development. Aquacult. Int. 28, 1243–1268. https://doi.org/10.1007/s10499-020-00523-2.

Ribeiro, K.T., 2018. Estratégia do Programa Nacional de Monitoramento da Biodiversidade – Programa Monitora: estrutura, articulações, perspectivas. ICMBio, Brasília.

Rodríguez-Fourquet, C., Sabat, A.M., 2009. Effect of harvesting, vegetation structure and composition on the abundance and demography of the land crab *Cardisoma guanhumi* in Puerto Rico. Wetl. Ecol. Manag. 17, 627–640. https://doi.org/10.1007/s11273-009-9139-5.

Sandrini-Neto, L., Lana, P.C., 2011. Distribuition patterns of the crab *Ucides cordatus* (Brachyura, Ucydidade) at different spatial scales in subtropical mangroves of Paranaguá Bay (Southern Brazil). Helgol. Mar. Res. 66, 167–174. https://doi.org/10.1007/s10152-011-0258-z.

Santos, L.C.M., Rollo Júnior, M.M., Costa, T.M., Pinheiro, M.A.A., Guebas, F.D., Bitencourt, M.D., 2016. Spatial analyses of a coastal area for conservation and fishery of mangrove edible crab (*Ucides cordatus*). J. Coast. Res. 75, 685–689. https://doi.org/10.2112/SI75-137.1.

Santos, L.C.M., Boos, H., Sano, E.E., Freitas, D.M., Pinheiro, M.A.A., 2022. Management and conservation of the land crab *Cardisoma guanhumi* (Crustacea: Gecarcinidae) based on environmental and fishery factors: a case study in Brazil. Wetl. Ecol. Manag. 30, 389–403. https://doi.org/10.1007/s11273-022-09868-2.

Schmidt, A.J., Oliveira, M.A., Souza, E.P., May, M., Araújo, S.M.B., 2008. Relação entre abertura de galeria e comprimento de cefalotórax do caranguejo-uçá, *Ucides cordatus* (Linnaeus, 1763) (Crustacea, Decapoda-Brachyura). Bol. Téc. Cient. CEPENE 16, 51–58.

Schmidt, A.J., Oliveira, M.A., Souza, E.D., May, M., Araújo, S.M.B., 2009. Estudo comparativo da dinâmica populacional de caranguejo-uçá, *Ucides cordatus* (Linnaeus, 1763) (Crustacea-Decapoda-Brachyura), em áreas afetadas e não afetadas por uma mortalidade em massa no Sul da Bahia, Brasil. Bol. Téc. Cient. CEPENE 17, 41–64.

Schmidt, A.J., Bemvenuti, C.E., Diele, K., 2013. Sobre a definição da zona de apicum e sua importância ecológica para populações de caranguejo-uçá *Ucides cordatus* (Linnaeus, 1763). Bol. Téc. Cient. Cepene. 19, 9–25.

Soares, L.S.H., Salles, A.C.R., Lopez, J.P., Muto, E.Y., Giannini, R., 2009. Pesca e Produção Pesqueira, in: Hatje, V., Andrade, J.B. (Eds.), Baía de Todos os Santos: Aspectos Oceanográficos. Editora da Universidade Federal da Bahia, Salvador, pp. 157–206.

Sokal, R.R., Rohlf, F.J., 2003. Biometry: The Principles and Practice of Statistics in Biological Research, third ed. W.H. Freeman, New York.

Souto, F.J.B., 2007. Uma abordagem etoecológica da pesca do caranguejo, *Ucides cordatus*, Linnaeus, 1763 (Decapoda: Brachyura), no manguezal do distrito de Acupe (Santo Amaro-BA). Biotemas 20, 69–80. https://doi.org/10.5007/%25x.

Souza, F.V.B., Pinheiro, M.A.A., 2021. Local Ecological Knowledge (LEK) on the mangrove crab *Ucides cordatus* (Linnaeus, 1763): Fishery profile of mangrove areas in Itanhaém (Southeast Brazil). Ethnocientia 3, 15–42. https://doi.org/10.18542/ethnoscientia.v6i3.10515.

Vega, Á.J., Mena, C., Robles, Y., 2018. Pesca artesanal de *Cardisoma crassum* (Cangrejo) y *Ucides occidentalis* (Mangote) en el sector nororiental del Golfo de Montijo. Pac. De. Panamá. Tecnociencia 20, 5–22.

Wei, T., Simko, V., Levy, M., Xie, Y., Jin, Y., Zemla, J., Freidank, M., Cai, J., Protivinsky, T., 2021. Corrplot: Visualization of a Correlation Matrix. R package (version 0.90). https://CRAN.R-project.org/package=corrplot.

Wolff, M., Koch, V., Victoria, I., 2000. A trophic flow model of the Caeté mangrove estuary (North Brazil) with considerations for the sustainable use of its resources. Estuar. Coast. Shelf. Sci. 50, 789–803. https://doi.org/10.1006/ecss.2000.0611.

Wunderlich, A.C., Pinheiro, M.A.A., 2013. Mangrove habitat partitioning by *Ucides cordatus* (Ucididae): effects of the degree of tidal flooding and three-species composition during its life cycle. Helgol. Mar. Res. 67, 279–289. https://doi.org/10.1007/s10152-012-0322-3.

Wunderlich, A.C., Pinheiro, M.A.A., Rodrigues, A.M.T., 2008. Biologia do caranguejo-uçá, *Ucides cordatus* (Crustacea: Decapoda: Brachyura), na Baia da Babitonga, Santa

Catarina, Brasil. Rev. Bras. Zool. 25, 188–198. https://doi.org/10.1590/S0101-81752008000200005.

Zambrano, R., Meiners, C., 2018. Notas sobre taxonomía, biología y pesquería de *Ucides occidentalis* (Brachyura: Ocypodidae) con énfasis en el Golfo de Guayaquil, Ecuador. Rev. Peru. De. Biol. 25, 55–66. https://doi.org/10.15381/rpb.v25i1.13821.

Zambrano, R., Solano, F., 2018. Análisis de las capturas de cangrejo rojo de manglar (*Ucides occidentalis*) en el Golfo de Guayaquil-Ecuador durante el 2013. Rev. Biol. Mar. Oceanogr. 18, 72–82.

Zar, J.H., 1996. Biostatistical Analysis, third ed. London, Prentice-Hall.