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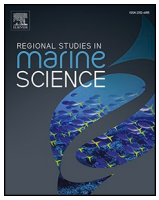

Anomalous walking events of the mangrove crab *Ucides cordatus* on the beaches of the central coast of São Paulo State, Brazil: A 20-year analysis

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ABSTRACT

During the reproductive period, the crab *Ucides cordatus* (Linnaeus, 1763) exhibits a migratory behavior known as "andada". In these events, individuals roam mangroves and sometimes aggregate in large numbers on beaches, a phenomenon referred to here as *Anomalous Walking Events* (*AWEs*). This study documents *AWEs* of the species on beaches within the Marine Protected Area of the Central Coast (APA–MLC), with data on population and reproductive biology from an event on Guaratuba Beach (Bertioga, SP, Brazil). *AWEs* were recorded through a 20-year bibliometric survey (2000–2020) and media reports. A case study in the Guaratuba Estuarine System was conducted on February 17–18, 2018, during one of the events, and estimated the population density of *U. cordatus* in mangrove and beach environments. Carapace width (*CW*) and gonadal maturation were also analyzed. Six *AWEs* were identified and distributed across two beaches: Itaguaré (66.6 %) and Guaratuba (33.4 %). These events occurred between December and February, predominantly during quarter moons (waning or waxing), with no link to significant rainfall increases. Crab density in mangroves was significantly higher than on the beach (0.82 ± 0.30 ind./m^2 *vs.* 0.32 ± 0.38 ind./m^2; $t = 8.09$; $p < 0.001$). Furthermore, individuals from the mangrove exhibited larger body sizes (*CW*) compared to those from the beach (73.2 ± 13.4 mm *vs.* 45.3 ± 7.2 mm; $W = 92.73$; $p < 0.001$). Although rare and anomalous, *AWEs* are directly associated with the reproduction of the species. Several hypotheses are proposed to explain the recorded events, but the reasons for their occurrence being restricted to only a few beaches remains unknown.

1. Introduction

Many decapod crustaceans exhibit a significant increase in locomotor activity during their reproductive season, with some undertaking extensive migrations to mate and ensure the perpetuation of the species (Wunderlich et al., 2008; Sant'Anna et al., 2014). During these episodic migratory events, population densification in specific locations facilitates copulation, promotion of the encounter and possession of females by males (Wunderlich et al., 2008). Notable examples include the seasonal migrations of up to 500 km by spiny lobsters of the genus *Palinurus* Weber, 1795, and by gecarcinid crabs such as *Gecarcoidea natalis* (Pocock, 1889). On Christmas Island, for instance, these crabs migrate from the tropical forest to the sea during the rainy season (Adamczewska and Morris, 2001 and references therein). These migratory behaviors are generally synchronized with abiotic factors such as lunar cycles, precipitation, and relative humidity (Adamczewska and Morris, 1998; Sant'Anna et al., 2014).

Among the mangrove crabs of the family Ocypodidae Rafinesque,

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1815, reproductive events are well-defined and often linked to environmental rhythms. For instance, *Leptuca pugilator* (Boschi, 1801) releases its larvae at night during periods of high tidal amplitude (Bergin, 1981). Meanwhile, *Ucides cordatus* (Linnaeus, 1763), a semiterrestrial crab endemic to mangroves, exhibits a characteristic migratory behavior, increasing locomotor activity and leaving its burrows for active movements across the sediment (Nascimento, 1993). This phenomenon, popularly known as "andada", "andança", "carnaval", "crab run", or "suatá", is well-documented (Diele and Koch, 2010; Schmidt et al., 2012). According to traditional accounts, andada occurs during the austral summer, particularly on new or full moon days (Schmidt et al., 2012).

During the andada, crabs travel long distances, with males actively seeking mates and walking for extended periods outside their burrows (Diele and Koch, 2010). This continuous exposure contrasts with their behaviour outside the reproductive period when individuals remain mostly within their burrows (Nordhaus et al., 2009) and rarely venture far from them (Piou et al., 2007). The increased exposure during andada facilitates their capture for human consumption, which is why harvesting this species is prohibited in Brazil during periods of peak activity (IBAMA, 2003).

Ucides cordatus holds high economic value and is one of the main artisanal resources in Brazilian estuarine environments (Fausto-Filho, 1969; Dias-Neto, 2011; Pinheiro et al., 2023). It is essential for traditional estuarine communities, serving as both a food source and a commercial product (Alves and Nishida, 2003; Dias-Neto, 2011; Fogaça et al., 2018). Due to ongoing exploitation and its impact on natural stocks, research on population density, structure, and reproduction has increased in various regions of Brazil (Moraes et al., 2015; Mota et al., 2023; Pinheiro et al., 2018, 2023; João and Pinheiro, 2019; Soares et al., 2024).

Beyond the characteristic andadas in mangroves, high-density crab aggregations have been reported on beaches in São Paulo, Santa Catarina and Sergipe. These phenomena, referred to here as Anomalous

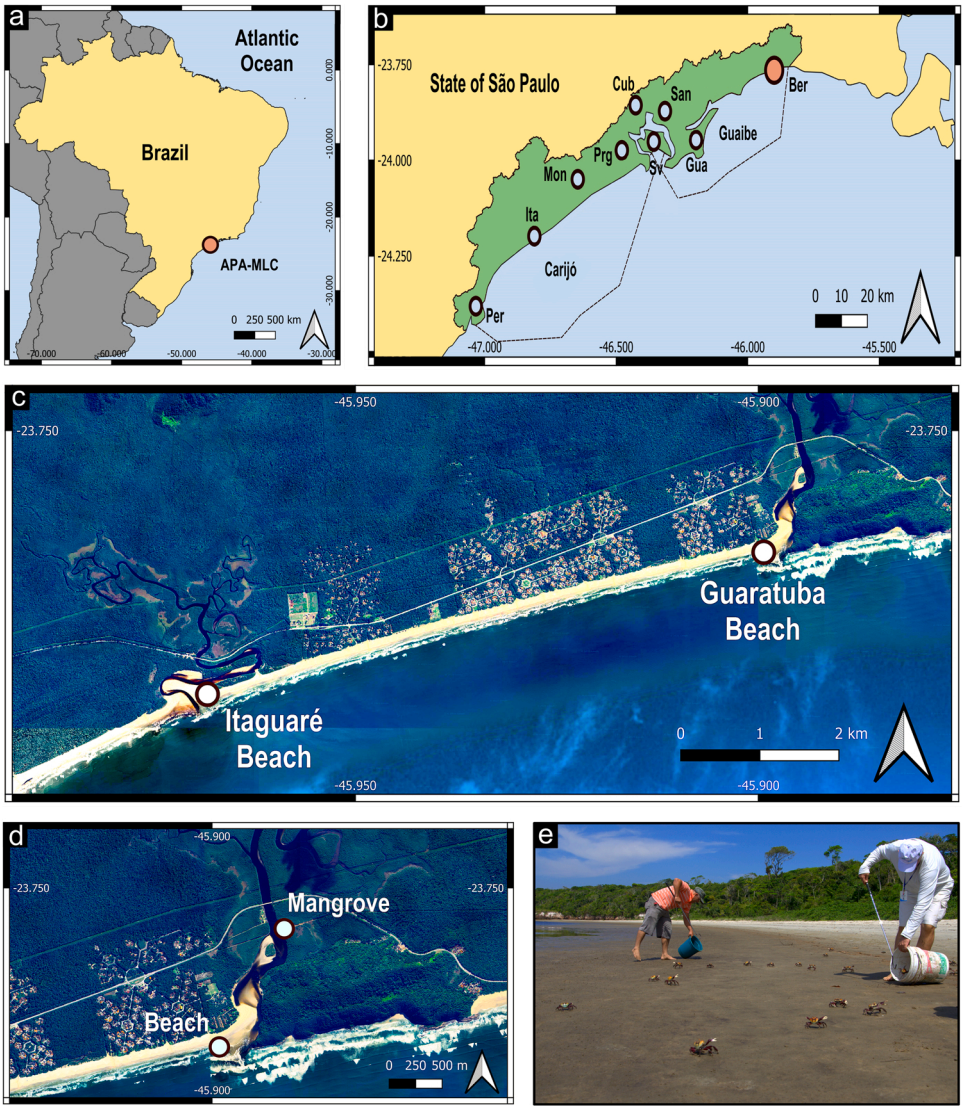

Fig. 1. Map of the study area with Anomalous Walking Events (*AWEs*); (A) Location of the Marine Protected Area of the Central Coast of São Paulo (APA-MLC), Brazil; (B) Location map of the APA-MLC, highlighting its division into sectors (Carijó and Guaibe) and the municipalities that comprise it, focusing on the municipality of Bertioga; (C) Satellite photograph highlighting the two beaches in the municipality of Bertioga where the *AWE* occurred: Itaguaré and Guaratuba; (D) Satellite photograph showing sampling sites in the Guaratuba Estuary; (E) Photograph showing the aggregation of *Ucides cordatus* (Linnaeus, 1763) at Guaratuba Beach during the *AWE*, with environmental police staff removing the animals. Photo provided by Environmental Secretary of the Municipality of Bertioga. Acronyms of municipalities: Ber, Bertioga; Cub, Cubatão; Gua, Guarujá; Ita, Itanhaém, Mon, Mongaguá; Per, Peruíbe; Prg, Praia Grande; San, Santos and Sv, São Vicente. Satellite photographs made in QGIS environment version 3.34.3.

Walking Events (*AWEs*), remain poorly studied, either due to the limited number of records or the lack of understanding of their rarity and specificity to certain beaches. This study aimed to document occurrences of *U. cordatus AWEs* in the Marine Protected Area of the Central Coast of São Paulo (APA-MLC). Additionally, it analyzed a specific event in 2018 on Guaratuba Beach, Bertioga (SP), assessing size, density population structure and gonadal maturity of specimens, comparing these data with results from the adjacent mangrove. Our main hypothesis is that crab movement has a reproductive bias, with individuals found on the beach predominantly in their first sexual maturation.

2. Materials and methods

2.1. Survey of occurrences

The survey of *U. cordatus AWEs* occurrences conducted using records collected by members of the Crustacean Biology Research Group (CRUSTA) at UNESP IB/CLP and associated researchers. Additionally, direct reports from the Environmental Secretariats (SMAS) of municipalities within the Metropolitan Region of Baixada Santista (RMBS) were considered, along with indirect observations from journalistic articles, official documents, radio and television reports and social media sources. A bibliometric survey was also conducted in the SCOPUS database using the search string *{caranguejo AND andada AND invad** AND praia AND São Paulo}. The search was restricted to the period from January 1, 2000, to December 31, 2020, using the database's date filter, within the Marine Protected Area of the Central Coast of São Paulo (APA-MLC).

The data was organized to highlight the locations where the events occurred, considering the beaches of all municipalities of the APA-MLC (Fig. 1A e B), the occurrence records and possible recurrences in subsequent years. For each recorded *AWE*, specific environmental parameters were analyzed using the NASA Prediction of Worldwide Energy Resources (POWER) – Data Access Viewer (DAV) Version 2.4.7 (NASA, 2025): 1) rainfall (mm), represented by the average for the two weeks preceding the event, considering the last day as the recorded *AWE* date; and (2) lunar phase, including the event day and the previous phase, due to the significant influence of this synodic cycle on the biology of these crabs (see Schmidt et al., 2012).

2.2. Case study

2.2.1. Study area and sampling

The study was conducted in the Guaratuba River Estuary, in the municipality of Bertioga (SP), analyzing a mangrove area (23º75'5,25''S, 45º89'3,13''W), located at 980 m from Guaratuba Beach (23º76'4,26''S, 45º89'8,35''W) (Fig. 1D) where *an AWE of U. cordatus* was recorded (Fig. 1C). The event, which occurred between February 17 and 21, 2018, was reported by the Municipal Secretariat for the Environment of Bertioga (SP), Brazil.

In the mangrove, two sampling subareas were established, corresponding to distinct zones (1) the fringe, located 0–50 m from the estuarine margin, characterized by higher tidal inundation levels and frequency; and (2) the internal, located 50–100 m from the margin, with lower tidal influence. In each subarea, 10 quadrats of 5 × 5 m (25 m^2) were placed to obtain population data.

The population structure of *U. cordatus* in the mangrove was determined using indirect methods described by Wunderlich et al. (2008) and Pinheiro and Almeida (2015), also adopted by the Monitora – Mangroves Program / ICMBio (Pinheiro, *in press*). This protocol assumes that each burrow is occupied by a single specimen (Pinheiro and Fiscarelli, 2001), with burrows having multiple openings counted as a single unit (Pinheiro, *in press*). Only Active burrows (showing biogenic activity) were included in the analysis to avoid overestimations of species density, which can reach up to 8 % (Pinheiro, *in press*).

The open burrows had their diameters measured using a modified, and values were converted to crab size (*CW*, carapace width) using the equation provided by Pinheiro et al. (2023). Population density was calculated by dividing the total number of active burrows by the sampling area (ind./m^2). The population structure was represented by the distribution of individuals in 10 mm size classes (*CW*).

On the beach, two subareas at different distances from the estuary were evaluated: one closer (360 m) and one farther away (700 m). In each subarea, data were recorded in 10 circular plots with a 5 m radius (= 79 m^2), randomly distributed with a minimum distance of 10 m between them.

Individuals of *U. cordatus* were counted and captured for carapace width (*CW*), measurement and sexed based on abdominal dimorphism (subtriangular in males and rounded in females), following Pinheiro and Fiscarelli (2001). The number of ovigerous females was also recorded. Population density and structure followed the same procedures described for the mangrove.

2.2.2. Gonadal stages

A total of 27 individuals were collected in the mangrove (20 males and 7 females) and 30 on the beach (16 males and 14 females) for inspection and classification of gonadal development stages. These specimens were provided under concession – considering the closed season for the species – by the Environmental Police of the municipality of Bertioga, and additional collections are not possible. The gonads were exposed by carefully removing the dorsal carapace and evaluated based on coloration and proportion relative to the hepatopancreas, following the classification of Pinheiro and Fiscarelli (2001). The six gonadal sub-stages were grouped into three categories: immature (IM: sub-stages 1 and 2), maturing (MT: sub-stages 3 and 4), and mature (MA: sub-stages 5 and 6).

2.2.3. Statistical analyses

Normality (Shapiro-Wilk, SW) and homoscedasticity (Levene, L) tests were applied to the two analyzed variables: body size (*CW*, mm) and population density (ind./ m^2) of the crabs. When data followed a parametric distribution, means from the two study areas were compared using Student's *t*-test (t). In cases of non-normality, medians were compared using the Wilcoxon-Mann-Whitney test (W), following the recommendations of Sokal and Rohlf (2003).

For the mangrove subareas (fringe and internal) and beaches subareas (near and far from estuary), comparative tests were conducted on central tendency measures. If no significant differences were detected between subareas, data were pooled to represent the respective ecosystems (mangrove and beach).

Population structure was assessed for each sampling area (mangrove and beach) using frequency distributions of individuals in 10 mm size classes (*CW*, mm) for histogram construction. Additionally, the skewness coefficient (*sk*) of population structure was calculated, following the methodology of Pinheiro et al. (2022) and the classification proposed by Wegner (2010). The distribution was classified as: symmetrical ($-0.5 \leq sk \leq 0.5$), indicating a balance between juveniles and adults; positively asymmetrical ($sk > 0.5$), indicating a predominance of juveniles; or negatively asymmetrical ($sk < -0.5$), indicating a predominance of adults. The intensity of skewness was also assessed and classified as moderate (positive: $0.5 < sk < 1$; negative: $-1 < sk < -0.5$) or strong (positive: $sk \geq 1$; negative: $sk \leq -1$).

For crabs collected on the beach, the male-to-female ratio was also evaluated. The analysis tested whether the observed sex ratio differed from the expected 1:1 (males: females) using a chi-square test (χ^2). This analysis was not performed for mangrove crabs, as the indirect sampling method does not allow sex-based population structure characterization (Pinheiro, *in press*).

The analysis of gonadal stages involved grouping the percentage of males and females from each area, applying a chi-square test (χ^2) when statistical assumptions were met (Sokal and Rohlf, 2003). The animals of each sex were classified by gonadal stage (IM, MT and MA), with

juveniles presenting immature gonads (IM) and adults represented by maturing (MT) or mature (MA) gonads. The percentage of each gonadal stage was compared between areas (mangrove and beach) to determine whether individuals were already reproductively active.

3. Results

3.1. Survey of occurrences

The bibliographic and media survey conducted over 20 year (2000–2020) resulted in a total of 1676 related to the topic. The anomalous walking events (AWEs) were recorded on only two beaches within the APA-MLC of São Paulo over a 20-year period (2000–2020). Among the 67 sandy beaches that make up this environmental protection area, only 51.7 % (n = 8) are directly associated with estuarine systems containing mangroves (Table 1), where AWEs could potentially occur. Thus, the two beaches (Itaguaré and Guaratuba) represent 25 % of the beaches with the potential for AWE occurrence. Six AWEs (Anomalous Walking Events) of *U. cordatus* were confirmed for these two beaches (Itaguaré: 66.6 %; Guaratuba: 33.4 % – Table 2 and Fig. 1C), both located in the municipality of Bertioga (SP), Brazil. These events were recorded between December and February, with a monthly occurrence frequency of 33.3 %.

Anomalous Walking Events were observed during different lunar phases: waning quarter (50 %), waxing quarter (33.3 %) and new moon (16.7 %). These events exhibited a temporal variation interval ranging from 7 to 13 days (mean ± standard deviation: 10 ± 3 days) relative to the peaks of the preceding lunar phase, which included the new, full and waning quarter, respectively, with the same frequencies previously mentioned. The analysis of the average accumulated rainfall in the 15 days preceding the events showed consistently low values, not exceeding an average of 10 mm across all records (Table 2), but with significant variation among events (coefficient of variation = 56 %). Specifically, the rainfall ranged from 1.7 ± 1.7 mm (Itaguaré: December 2017) to 8.1 ± 12.7 mm (Guaratuba: February 2018).

3.2. Case Study

3.2.1. Mangrove and beach

During the first recorded *AWE* at Guaratuba Beach, between February 17 and 18, 2018 (new moon), the size and population density of *U. cordatus* showed no significant differences between the fringe and internal subareas in the mangrove (*CW*: W = 19221, $p = 0.07$; density: $t = -14372$, $p = 0.11$). On the beach, no significant differences were observed, regarding proximity to the estuary, either in specimen size (W = 6935.5, $p = 0.70$) or in density ($t = -0.0561$, $p = 0.96$). Thus, the data were grouped for comparative analysis between the two ecosystems (mangrove and beach).

In total, 630 specimens of *U. cordatus* were evaluated, with 59.5 % (n = 375) from the mangrove and 40.5 % (n = 255) from the beach. The population structure exhibited positive asymmetry in both ecosystems, being moderate in the mangrove ($sk = 0.72$) and high on the beach ($sk = 2.01$) (Fig. 2). The specimens form the mangrove exhibited a larger average size (73.2 ± 13.4 mm *CW*) compared to those from the beach (45.3 ± 7.2 mm *CW*), with a statistically significant difference (W = 92734, $p < 0.001$) (Fig. 3A). The sizes (*CW*) ranged from 37.2 to 94.8 mm in the mangrove and from 25 to 65 mm on the beach, with a higher frequency of individuals in the 70–80 mm and 40–50 mm size classes, respectively (Fig. 2). The sex ratio on the beach was 1:1.2, not differing significantly from 1:1 ($\chi^2 = 2.42$, $p > 0.10$). Only one ovigerous female was recorded and sampled on the beach.

The population density in the mangrove was significantly higher than on the beach, ranging from 0.44 to 1.60 ind./m² (0.82 ± 0.30 ind./m²) in the mangrove and from 0.11 to 1.35 ind./m² (0.32 ± 0.38 ind./m²) on the beach ($t = 8.09$, $p \leq 0.001$) (Fig. 3B). These data are summarized in Table 3, which presents the size and density values for the

Table 1
Summary of beaches with direct connection to estuarine rivers* that have mangrove forests, within the Marine Protected Area of the Central Coast of São Paulo state (APA-MLC). According to SMAIF-SP (2025).

Municipality	Beach	River	Coordinates
Peruíbe	Una	Una do Prelado	24°26'40.00"S - 47° 4'41.00"W
	Guaraú	Guaraú	24°22'48.00"S - 47° 1'10.00"W
	Costão	Black	24°19'60.00"S - 47° 0'5.00"W
Itanhaém	Saudade	Itanhaém	24°11'16.00"S - 46°47'27.00"W
Guarujá	Perequê	Perequê	23°56'33.00"S - 46°10'25.00"W
Bertioga	Enseada	Itapanhaú	23°51'18.00"S - 46° 8'2.00"W
	Itaguaré	Itaguaré	23°46'54.00"S - 45°58'15.00"W
	Guaratuba	Guaratuba	23°45'46.00"S - 45°53'49.00"W

* The Santos-São Vicente Estuarine System was not considered, as it has a junction of rivers that do not flow directly into a beach.

Table 2
Summary of Anomalous Walking Events (AWEs) for the mangrove crab *Ucides cordatus* (Linnaeus, 1763) in the Marine Protected Area of the Central Coast of São Paulo state (APA-MLC). Where: Date, day of the AWE and its corresponding lunar phase (F, full moon; N, new moon; WNM, waning quarter moon; WXM, waxing quarter moon); ID, the interval of days between the peak of the previous lunar phase and the AWE; LP, the prior lunar phase, highlighting the peak day; R, mean b± standard deviation of the accumulated rainfall during the 15 days preceding the AWE, including the event day.

Local	LP	Date	ID	R (mm)	Author (Year)
Itaguaré Beach (Bertioga, SP)	F 28-Dec–2012	WNM 05-Jan–2013	8	5.0 ± 4.2	PM-BERTIOGA (2013)
	N 01-Jan–2014	WXM 08-Jan–2014	7	2.6 ± 5.1	G1 Santos (2014)
	F 03-Dec–2017	WNM 16-Dez–2017	13	1.7 ± 1.7	Globo (2017)
	N 14-Dec–2020	QC 27-Dez–2020	13	4.4 ± 4.1	Costa Norte (2020)
Guaratuba Beach (Bertioga, SP)	N 07-Fev–2018	WNM 17-Fev–2018	10	8.1 ± 12.7	**Present study**
	WXM 27-Jan–2019	N 06-Fev–2019	10	2.7 ± 6.2	Pinheiro, M.A.A. (personal communication)

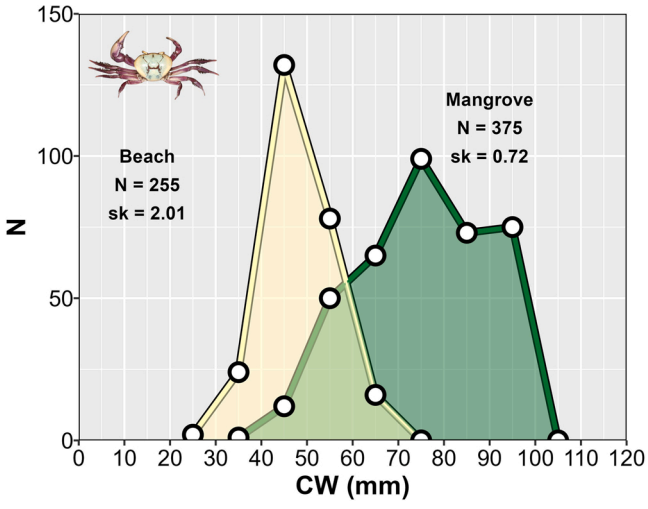

Fig. 2. Variation in the number of specimens of *Ucides cordatus* (Linnaeus, 1763) across size classes (carapace width, *CW*) at different locations in Bertioga (SP), Brazil. *Where:* sk, coefficient of asymmetry; N, number of individuals.

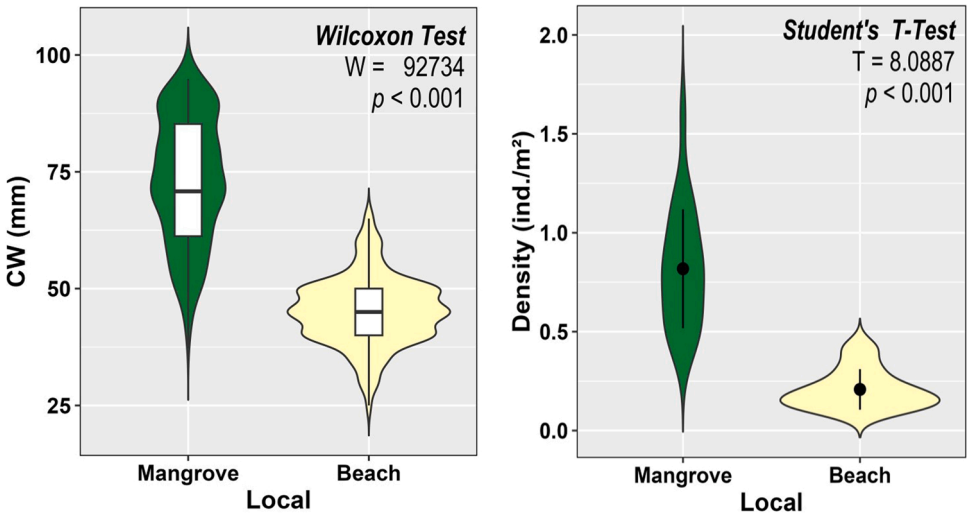

Fig. 3. Size variation (*A*: carapace width, *CW*, in mm) and density (*B*: individuals per m^2) of *Ucides cordatus* (Linnaeus, 1763) recorded in Bertioga (SP), Brazil, during an Anomalous Walking Event (*AWE*) on the beach, compared to the population in the nearby mangrove swamp. Where: box plot (median represented by the horizontal line, interquartile range [IQR] by the box, and whiskers extending up to 1.5 times the IQR); black dot and error bar (mean and standard deviation); and violin plot (kernel probability density).

Table 3
Statistical summary of body size (CW, carapace width) and density (ind./m^2) for *Ucides cordatus* (Linnaeus, 1763) during the Anomalous Walking Event (AWE) observed from February 17–18, 2018, in the mangrove forest and beach of Guaratuba (Bertioga, SP), Brazil. Where: *n*, number of crabs; $\bar{x}$, arithmetic mean, and *s*, standard deviation.

Area	*n*	*CW* (mm)			Density (ind./ m^2)		
		Min	Max	x ± s	Min	Max	x ± s
Mangrove	375	37.2	94.8	73.2 ± 13.4	0.44	1.60	0.82 ± 0.30
Beach	255	25	65	45.3 ± 7.2	0.11	1.35	0.32 ± 0.38
Total	**630**	**25**	**94.8**	**61.9 ± 17.8**	**0.11**	**1.60**	**0.60 ± 0.38**

two studied areas.

3.2.2. Gonadal stages

For the analysis of gonadal stages, 57 specimens were used (mangrove: n = 26; beach: n = 31). In the mangrove, the crabs showed no significant differences between the stages of gonadal maturation (χ^2= 2.46, $p > 0.10$), while on the beach, there was a predominance of individuals with gonads in maturation or mature ($\chi^2 = 3.90$, $p < 0.05$) (Fig. 4).

Fig. 4. The proportion of gonadal development stages (immature, maturing, and mature) for males and females of *Ucides cordatus* (Linnaeus, 1763) in two ecosystems (mangrove and beach) in Bertioga (SP), Brazil. Where: Yellow indicates immature, Orange indicates maturing, and Red indicates mature individuals.

4. Discussion

This study analyzed the Anomalous Walking Events (*AWEs*) of *Ucides cordatus* recorded in the APA-MLC, with an emphasis on the population biology of one of these events, which occurred at Guaratuba Beach, Bertioga (SP), in 2018. Although these events are poor, their occurrence raises concerns due to their peculiar nature and the abundant presence of the species on beaches, an atypical environment for the mangrove crab. This situation attracts the attention of the community, the media, and environmental institutions. The hypothesis that *AWEs* would be responses to stressors in mangroves, such as pollution or abiotic changes, as considered. However, the results obtained did not conclusively confirm this relationship.

On an annual scale, *U. cordatus* walking events are associated with the species seasonal reproductive cycle, occurring the austral summer, on full and/ or new moons, when the highest tidal amplitudes favor mating and larval release (Wunderlich et al., 2008; Diele and Koch, 2010; Schmidt et al., 2012; Sant'Anna et al., 2014). Although the periods and months of normal andada events show some similarity along the Brazilian coast, there are regional variations, with an extended duration in some locations (see Nordi, 1994; Wunderlich et al., 2008; Diele and Koch, 2010; Schmidt et al., 2012; Sant'Anna et al., 2014). However, the *AWEs* analyzed in this study predominantly occurred during the waning and waxing moon phases. During normal walking events, the search for mates begins between one and two days after the full moon or up to four days after the new moon (Sant'Anna et al., 2014), with subsequent reproductive behaviors synchronized with the highest amplitude high tides in the following months (Diele and Koch, 2010). According to Schmidt et al. (2012), normal andada events in Northeastern Brazil can occur up to seven days after the full or new moons. Comparing these data with the average of the 10 ± 3 days between the peak of the previous lunar phase and the onset of *AWEs*, it is inferred that the crabs began their movement of the mangrove under the influence of previous lunar phases. However, this does not explain the mass

movement toward the beach, which suggests the involvement of other factors.

Various abiotic factors influence the seasonal cycles of semi-terrestrial and terrestrial decapod crustaceans, as well as their reproductive fitness. Precipitation has a greater impact than temperature or photoperiod, especially in reducing desiccation during rainy seasons. (Hartnoll et al., 2010; Schmidt et al., 2012). The reduction in salinity caused by heavy rainfall may serve as trigger for movements toward areas with higher salinity (Nascimento, 1993). However, the *AWEs* recorded in Bertioga occurred during periods of low accumulated rainfall (see Table 1), making it unlikely that significant changes caused the mass displacement. Despite this, the reproduction of *U. cordatus* often coincides with the onset of the rainy season (Wunderlich et al., 2008; Sant'Anna et al., 2014), a typical pattern of terrestrial and semi-terrestrial crabs with a higher degree of terrestriality (Wolcott, 1988).

Another hypothesis would be the presence of negative stimuli in mangroves, including contamination by pollutants (see Pinheiro et al., 2012, 2022, 2023). Studies conducted by Duarte et al. (2017) detected high concentrations of metals in the mangroves of Bertioga, exceeding the limits established by current legislation (Brazil, 2005; Environment Canada, 1999). However, *U. cordatus* has already been recorded in more contaminated mangroves, demonstrating high resilience to heavy metal pollution (Pinheiro et al., 2012; Duarte et al., 2017, 2019, 2020), making it unlikely that this is the cause of the *AWEs*.

Population analysis reinforces this conclusion. According to the records of Duarte et al. (2016), the mangroves of Bertioga had an average density of 0.77 ± 0.82 ind./m^2, about 2.5 times lower than the mangroves of Juréia-Itatins Ecological Station (Peruíbe, SP), which had 1.92 ± 1.03 ind./m^2. The density of *U. cordatus* also varies regionally, as in the North Region (1.96 ± 0.31 ind./m^2 – Schories et al., 2003), Northeast (1.32 ± 0.9 ind./m^2 – Mota et al., 2023), Southeast (1.4 ± 0,7 ind./m^2 – Pinheiro et al., 2022) and South (2.1 ± 1,0 ind./m^2 – Wunderlich et al., 2008). All these densities exceeded the average recorded for the Guaratuba mangrove (0.82 ± 0.30 ind./m^2), which, in turn, was higher than that of the adjacent beach (0.32 ± 0.38 ind./m^2). Furthermore, the absence of variation in the density of *U. cordatus* as a function of the distance from the estuary indicates the nonexistence of negative stimuli originating from the mangrove.

The crabs on the beach had a smaller average size (45.3 ± 7.2 mm *CW*) compared to those in the mangrove (73.2 ± 13.4 mm *CW*), being even smaller than the functional maturity size (males: 51.3 mm; females: 39.1 mm, according to Pinheiro and Fiscarelli, 2001). However, the predominance of males with maturing or mature gonads on the beach suggest that these individuals were undergoing their first sexual maturation and were capable of reproduction (Castiglioni and Coelho, 2011). On the other hand, 56.3 % of the females had immature gonads, but they could still be copulated by males, with sperm stored in their seminal receptacles until gonads maturation, allowing fertilization of the oocytes approximately two months later (Hartnoll, 1969; Sant'Anna et al., 2007; Pinheiro and Fiscarelli, 2001). In this sense, the analysis of the gonadal stages reinforces the reproductive bias of the crabs found on the beach, even if it presents a reduced number of specimens used, considering that the crabs were provided through a concession, as mentioned previously. Furthermore, the sex-ratio for beach was 1:1, and this patterns is characteristic during the mating season for *U. cordatus* (Wunderlich and Pinheiro, 2013), where the encounter of males and females is facilitated, indicating reproductive sites (see João et al., 2024). This aspect is another indication that *AWEs* area a more intense reproductive phenomenon, with migration extending out of the mangrove towards the beaches, but only in a few locations.

Part of the normal andada events, as well as the anomalous ones (*AWEs*), occur from December onward, a month that falls within the closed season for *U. cordatus* (IBAMA, (2003)) and is associated with the species reproductive cycle. The anomalous nature of these *AWEs* remains unexplained, as they do not occur homogeneously on all beaches, which requires monitoring of beaches such as Guaratuba and Itaguaré, in the municipality of Bertioga (SP). However, *AWEs* have already been recorded with significant scope along the Brazilian coast, from the northeast (*e.g.*, Sergipe River, in Aracaju, SE – G1 SE, 2022) to the south (*e.g.*, Perequê River, in Porto Belo, SC – Diário Costa Esmeralda, 2019). Continuous monitoring is essential to better understand these events and predict their occurrences, helping to prevent the capture of crabs during these movements. The adoption of specific ordinances, similar to those existing for normal walking events in the North-Northeast of Brazil (MPA/MMA, 2024), Could serve as a basis for regulating protection periods during both normal and anomalous walking events in Bertioga. This would establish more effective management, which could be complemented by environmental education programs aimed at tourist, especially when *AWEs* occur.

CRediT authorship contribution statement

Harry Boos: Writing – review & editing, Visualization, Methodology, Validation. **Lanza Maria de Carvalho Tereza:** Writing – review & editing, Visualization, Supervision, Validation. **Pinheiro Marcelo Antonio Amaro:** Supervision, Investigation, Writing – review & editing, Resources, Formal analysis, Validation, Methodology, Conceptualization, Writing – original draft, Project administration, Data curation. **Mosna Esli Emanoel Domingues:** Writing – review & editing, Formal analysis, Software, Investigation, Methodology.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests. Marcelo Antonio Amaro Pinheiro reports financial support was provided by State of Sao Paulo Research Foundation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data is available in the repository: https://github.com/esli-mosna/Anomalous-Walking—Ucides-cordatus.git

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