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Population structure and sexual maturity of *Minuca vocator*: insights from a Brazilian mangrove ecosystem

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ABSTRACT

The population biology of the fiddler crab *Minuca vocator* was analysed in the mangroves of the Itanhaém Estuary (SP), Brazil, focusing on population structure, sex ratio, handedness, and morphological maturity. A total of 407 individuals were collected, with a male-biased sex ratio of 1:0.6 (M:F), significantly different from the expected 1:1 ratio ($\chi^2 = 26.1$; $p < 0.05$). Specimens were sexed and measured (CW: carapace width; AW: abdominal width of the 5th somite; and PL: propodus length of the major chela), using precision callipers or an image analysis system. The morphological maturity size was estimated at 9.9 mm for males and 10.9 mm for females. Relative growth analysis confirmed positive allometry for cheliped growth in males ($b = 1.29$ for juveniles and $b = 1.88$ for adults; $F = 32.87$; $p < 0.001$) and for abdomen in females ($b = 1.52$ for juveniles and $b = 1.18$ for adults; $F = 39.99$; $p < 0.001$). The population structure showed moderate negative skewness, with adults prevailing over juveniles. No significant handedness preference was observed among males, with a 1:1 ratio between right- and left-clawed individuals. A review of morphological maturity sizes in Brazilian fiddler crab species was provided to identify possible patterns for each sex. These findings highlight the importance of population studies for a better understanding of species life history traits and conservation strategies.

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Fiddler crabs; handedness; maturity; population structure; reproductive traits

Introduction

Fiddler crabs (Ocypodidae) are semi-terrestrial brachyurans characterized by distinct sexual dimorphism, particularly in the morphology of their chelipeds (Crane 1975). Males possess one hypertrophied cheliped, which is used in agonistic interactions (Crane 1966Nallos and Macusi 2023; Borges et al. 2024) and reproductive displays (Crane 1975; Callander et al. 2012; Kim et al. 2024), while the smaller cheliped is used for feeding (Valiela et al. 1974). In contrast, females have two small, similarly sized chelipeds used for food manipulation. These crabs play a crucial ecological role, either as deposit feeders consuming organic matter from sediments (Sayão-Aguiar et al. 2012) or as bioturbators, modifying sediment physicochemical properties (Chowdhury 2015, Natalio et al. 2017). Due to their impact on ecosystem structure and function, they are recognized as 'ecosystem engineers' (Kristensen 2008), creating habitats that support other species (Zeil et al. 2006).

Fiddler crabs are widely distributed worldwide, comprising 107 species (Shih and Chan 2022). In Brazil, only 10 species have been recorded (Crane 1975; Melo 1996; Thurman et al. 2013). They are particularly abundant in Brazilian mangroves (Koch et al. 2005; Freitas et al. 2021), serving as prey for various fish and bird species (Zeil et al. 2006; Krumme et al. 2007; Silva and Olmos 2015). Despite their ecological importance, population-level data for these crabs are often scarce or nonexistent, hindering precise assessments of their conservation status (Berger and Weis 2008; Pinheiro and Pardal-Souza 2016; Waiho et al. 2022).

Population structure provides valuable insights into species dynamics, while additional metrics, such as sexual maturity estimation, help assess population stability and future trends (Hirose and Negreiros-Fransozo 2008; Waiho et al. 2017; Herrera and Costa 2024). Crustaceans, with their rigid exoskeleton, allow for precise morphometric measurements (Pinheiro and Fransozo 1993), facilitating the detection of growth changes in body segments throughout ontogeny (Hartnoll 1978, 1982).

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In brachyurans, such changes occur during the pubertal moult, marking the transition from juveniles to adults and the development of secondary sexual characteristics, such as enlarged chelipeds in males and wider abdominal somites in females (Hartnoll 1969, 1974; Pinheiro and Fransozo 1998; Castiglioni and Negreiros-Fransozo 2004; Pinheiro and Hattori 2006). Analysing these ontogenetic shifts enables estimating morphological maturity size, a key parameter that may vary geographically (Hines 1989; Helfer and Cobo 2023). Other relevant population traits include sex ratio (Johnson 2003; Machado et al. 2021), cheliped handedness (Santos et al. 2020; Rozaimi et al. 2023), reproductive periodicity (Costa and Negreiros-Fransozo 2002; Colpo and Negreiros-Fransozo 2003), and juvenile recruitment (Brodie et al. 2005; Pinheiro et al. 2024).

Comparative studies of fiddler crab populations at different latitudes provide insights into interspecific and intraspecific variations (Bedê et al. 2008; Colpo et al. 2022). Such research is essential for assessing population stability in different environments and determining how mangrove habitat quality influences these species (Bedê et al. 2008; Scalco et al. 2016).

Among fiddler crab species, *Minuca vocator* is distributed along the Brazilian coast from Amapá to São Paulo (Masunari et al. 2020). This species is strongly associated with muddy mangrove sediments, particularly those dominated by silt fractions (Colpo and Negreiros-Fransozo 2003; Thurman et al. 2013) and is typically found in oligohaline to mesohaline environments (salinities from 0.9 to 15) with dense arboreal shading. Due to its specific habitat requirements, *M. vocator* is considered one of Brazil's most stenotopic fiddler crab species (Thurman et al. 2013). Approximately 10% of its population occurs in the southeastern region, while the remaining 90% is distributed across the northern and northeastern regions.

Previous studies on *M. vocator* have focused on larval migration and recruitment in northeastern Brazil (Simith et al. 2010, 2012) and population dynamics (Koch et al. 2005). In southeastern Brazil, research has primarily addressed population structure (Colpo and Negreiros-Fransozo 2003, 2004, 2016; Bedê et al. 2008) and morphological maturity (Colpo et al. 2022). Further investigations into the population biology of *M. vocator* are crucial for understanding its life history and conservation needs (Pinheiro et al. 2016), particularly in the mangrove of the Itanhaém River, an estuary near Santos, where a decline of this species has already been recorded (Thurman et al. 2013).

This study aims to assess the population biology of *M. vocator* in the Itanhaém Estuarine System (IES), located on the central-southern coast of São Paulo State, Brazil. Specifically, we estimate morphological maturity size, analyse population structure, evaluate sex ratio, and investigate cheliped handedness in males.

Methods

Study area

The Itanhaém Estuarine System (IES) is located on the central-southern coast of São Paulo State, Brazil, comprising the coastal plain of the Itanhaém River Basin, the largest exclusively coastal basin in the state (Camargo and Cancian 2016). The natural vegetation in this region consists primarily of mangrove forests covering approximately 4.92 km^2, surrounded by an expanding urban area, which exerts significant anthropogenic pressure. Specimen collection was conducted in one of the remaining mangrove areas of the IES (24°09′36″S – 46° 48′19″W) (Figure 1), previously characterized by Souza (in press) based on its vegetation physiognomy and edaphic factors. This mangrove area is dominated by red mangrove (*Rhizophora mangle*, 58%), followed by white mangrove (*Laguncularia racemosa*, 40%) and black mangrove (*Avicennia schaueriana*, 2%). Souza (in press) classified this site as a mangrove fringe zone, extending approximately 30 m from the waterline, with an average tidal flooding height of 23.7 ± 2.0 cm, muddy sediment with high silt-clay content (57%), and elevated organic matter levels (89.8%).

Crab collection, identification, and biometric measurements

Two field expeditions were conducted on 15 July 2022, and 20 January 2023. Crabs were manually collected during low tide using stainless steel spatulas without targeting specific species. Specimens were initially stored in plastic bags containing sediment and mangrove twigs to minimize interactions, aggression, and limb loss. They were subsequently placed in an insulated container and transported to the Crustacean Conservation Biology Laboratory (LBC) at UNESP IB/CLP, where they were cryoanaesthetized (−15°C for 1 h) and later preserved in 70% ethanol in labelled vials.

In the laboratory, individuals were identified using taxonomic keys (Bezerra 2012; Masunari et al. 2020) and were sorted based on abdominal morphology, with males exhibiting a subtriangular abdomen and females a semi-oval one. When abdominal dimorphism was ambiguous, sex was confirmed by counting pleopod pairs, as males possess two pairs on the 1st and 2nd abdominal somites. In contrast, females have four pairs on the 2nd to 5th somites. Biometric measurements

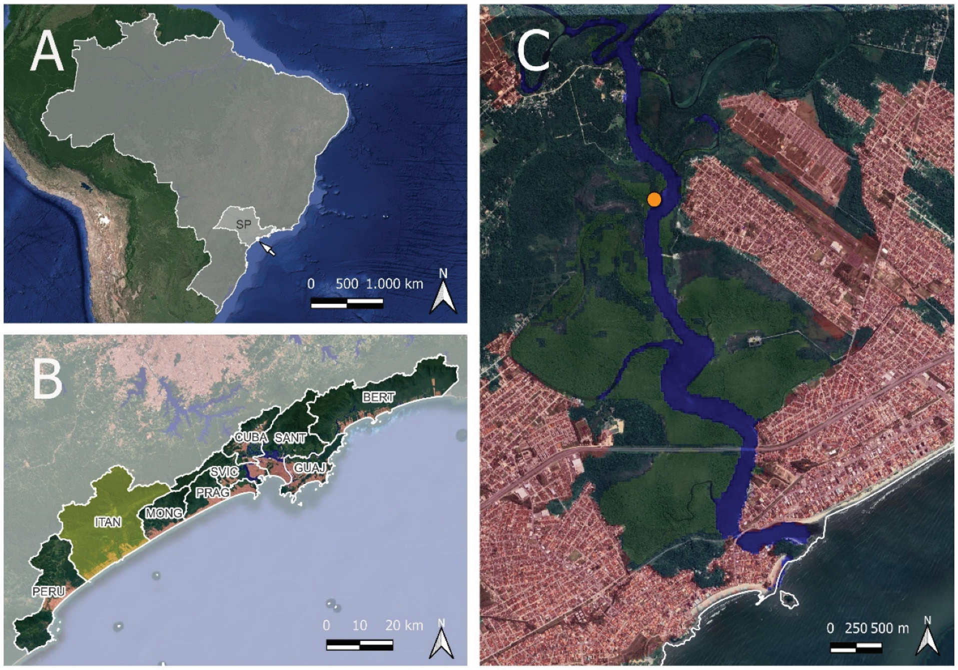

Figure 1. Mangroves of the Itanhaém River Estuary. A) The municipality of Itanhaém, São Paulo, Brazil, indicated by an arrow. B) Itanhaém municipality (ITAN) within the metropolitan region of Baixada Santista (MRBS), located on the southern coast of São Paulo state (SP), Brazil, grouping nine municipalities (PERU, Peruíbe; ITAN, Itanhaém; MONG, Mongaguá; PRAG, Praia Grande; SVIC, São Vicente; CUBA, Cubatão; SANT, Santos; GUAJ, Guarujá; and BERT, Bertioga). C) The urban region of Itanhaém (red) in the lower part of the basin shows the Itanhaém River (blue) and mangrove forests (green), with the collection site highlighted (orange dot).

included carapace width (*CW*), representative of body size, propodus length of the major cheliped (*PL*) in males, measured from the fixed fingertip to the propodal denticle, and abdominal width (*AW*) in females, measured at the 5th abdominal somite. All measurements were obtained using a computerized image analysis system (KS-300® - Zeiss®) coupled with a stereomicroscope (Axiolab® - Zeiss®), with a precision of 0.01 mm.

Sex ratio

The sex ratio was analysed across ontogeny, with individuals grouped into 2-mm *CW* size classes. The chi-square test (χ^2) assessed deviations from the expected 1:1 male-to-female ratio, considering only size classes with a minimum of five individuals per sex to meet statistical assumptions (Zar 1999). A significance level of 5% was applied to determine significant deviations.

Morphological maturity

Morphological maturity was estimated separately for each sex by analysing the relationship *PL* × *CW* in males and *AW* × *CW* in females, with *CW* as the independent variable (X-axis). Individuals with damaged or missing structures were excluded. The data were log-transformed and analysed using the segmented function in R 4.0.0 (R Development Core Team 2020) to detect potential growth pattern shifts. Following a broken-line model, this method identifies an inflection point (or *breakpoint*) between juvenile and adult growth phases (Muggeo 2008). In cases where no clear *breakpoint* (size at morphological maturity) was observed due to overlapping developmental phases lines, the proportion of adults as a function of body size was used to estimate maturity size, we adjusted a sigmoidal curve to the percentage of adults for each size class considering the point at which 50% of individuals were morphologically mature (*CW50%*) (see Pinheiro and Fransozo 1998). If distinct juvenile and adult growth phases were detected, linear regression analysis was applied, fitting empirical data to the power function $ln\,Y = ln\,a + b \cdot ln\,X$, as commonly used in relative growth studies (Hartnoll 1974, 1978). The growth coefficient (b-value) was used to classify growth patterns as isometric ($b = 1$), positively allometric ($b > 1$), or negatively allometric ($b < 1$). A t-test was performed to determine whether b-values significantly differed from 1 ($p \leq 0.05$), and an ANCOVA was conducted to compare juvenile and adult growth phases, with *PL* and *AW* as dependent variables, *CW* as the covariate, and ontogenetic phases as factors.

Population structure

Size frequency histograms were generated, and Fisher's skewness coefficient (*sk*) was calculated following Wegner (2010), a method successfully applied in brachyuran population studies (Pinheiro et al. 2022; João et al. 2023). Skewness was classified as symmetric ($-0.5 \leq sk \leq 0.5$), moderately asymmetric ($0.5 < sk < 1$ or $-1 < sk < -0.5$), or highly asymmetric ($sk \geq 1$ or $sk \leq -1$), as suggested by these authors.

The population structure of *M. vocator* was analysed for each sex, and the total sample was taken using 2-mm CW size class histograms. Modal component analysis was performed separately for each sex using the Bhattacharya method, posteriorly confirmed by *NORMSEP* in *FiSAT II* software (Gayanilo et al. 2005). This method identifies size distribution components, providing the Separation Index (*SI*), mean, standard deviation ($\bar{X} \pm s$), and number of individuals per modal component (Pinheiro and Pardal-Souza 2016), with $SI > 2$ considered as an adequate threshold for separation.

Cheliped handedness

Cheliped handedness data (*H*) were recorded for males, with χ^2 tests applied to assess deviations from a 1:1 right-handed (dextral) to left-handed (sinistral) ratio. The handedness distribution was also analysed graphically, as suggested by Rio et al. (2019), plotting $H_1 = PL_R/PL_L$ for right-handed individuals and $H_2 = PL_L/PL_R$ for left-handed individuals, where PL_R is the major right chela propodus length and PL_L is the major left chela propodus length. Linear regression analysis was conducted on H_1 x *CW* and

H_2 x *CW* biometric relationships and the resulting equations were compared using ANCOVA to determine whether right- and left-handed growth patterns significantly differed ($p < 0.05$).

Results

Sex ratio

A total of 407 individuals of *Minuca vocator* were collected, comprising 255 males and 152 females, of which 132 were non-ovigerous and 20 were ovigerous. Male carapace width (*CW*) ranged from 2.5 to 22.1 mm (mean ± standard deviation: 15.3 ± 3.5 mm *CW*) and did not differ significantly from that of females (4.3 to 21.9 mm; 15.4 ± 3.5 mm *CW*) ($W = 19.79$, $p > 0.05$). Ovigerous females measured 12.5 to 20.1 mm *CW* (16.2 ± 2.3 mm *CW*), representing 13.2% of the female population. The overall sex ratio of *M. vocator* was 1:0.6 (M:F), with a significantly higher proportion of males ($\chi^2 = 26.07$, $p \leq 0.05$). However, a significant male bias was observed in only three size classes (12–14 mm, 14–16 mm and 20–24 mm; $\chi^2 \geq 4.55$, all $p \leq 0.05$), while other size classes showed no significant differences between sexes (Figure 2).

Morphological maturity

For the *PL x CW* relationship in males, a growth phase transition was detected at 9.9 mm *CW* (Figure 3A). Both juveniles ($b = 1.29$; $t = 5.12$, $p \leq 0.001$) and adults ($b = 1.88$; $t = 17.90$, $p \leq 0.001$) exhibited positive allometric growth, with a significant difference between phases (ANCOVA: $F = 32.87$, $p < 0.001$).

For the *AW x CW* relationship in females, an overlap between juvenile and adult phases was observed, and the *CW 50%* (size at morphological maturity) was estimated at 10.9 mm *CW* (Figure 3B). The relative growth rate (b) in females also varied ontogenetically, showing positive allometric growth in both phases (juveniles: $b = 1.52$; adults: $b = 1.18$; $t \geq 5.29$, $p < 0.001$), with a significant difference between them (ANCOVA: $F = 39.99$, $p < 0.001$).

Considering the estimated *CW 50%* values, males exhibited a lower proportion of juveniles ($n = 12$; 5.2%) compared to adults ($n = 220$; 94.8%), a pattern similar to that of females, with 10.6% juveniles ($n = 16$) and 89.4% adults ($n = 135$). Among adult females, ovigerous individuals accounted for 14.8%.

Population structure

Size frequency histograms revealed a moderately negative skewed distribution, similar between sexes, with $sk = -0.79$ for males (Figure 4A) and $sk = -0.74$ for females (Figure 4B). The population was predominantly

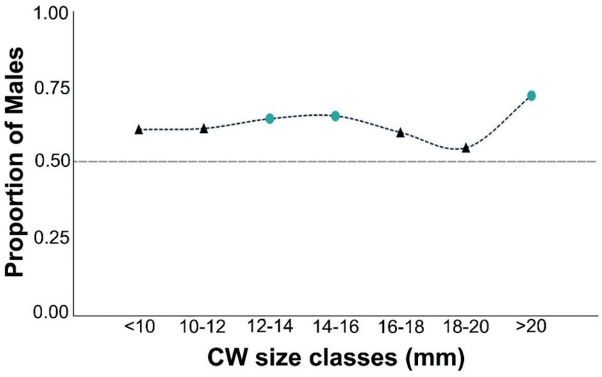

Figure 2. Sex ratio of *Minuca vocator* across ontogeny in the mangroves of Itanhaém (SP), Brazil. CW, carapace width; black triangles, sex ratio not significantly different from 1:1 ($p > 0.05$); blue circles, significantly male-biased proportion ($p \leq 0.05$).

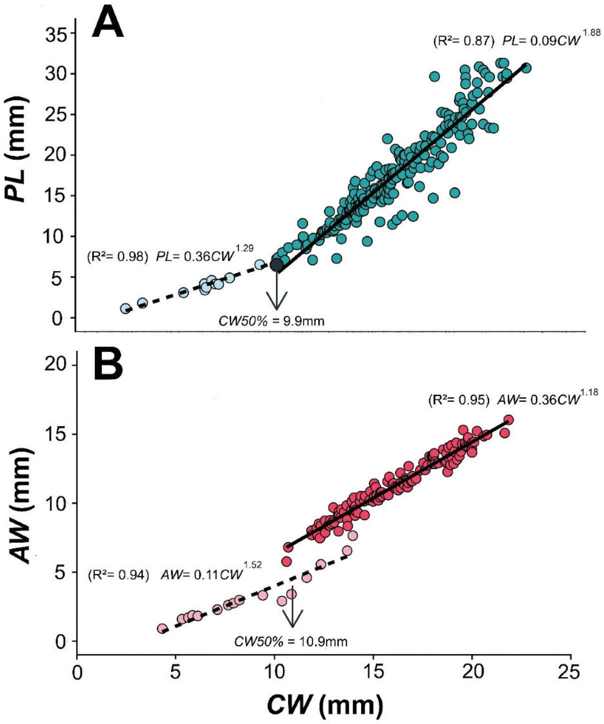

Figure 3. Relative growth and morphological maturity of *Minuca vocator*. A) *PL* x *CW* biometric relationship for males, indicating the relative growth rate for juveniles (light blue; b = 1.29) and adults (dark blue; b = 1.88). B) *AW* x *CW* biometric relationship for females, represented by juveniles (light red; b = 1.52) and adults (dark red; b = 1.18) females. The arrow indicates the morphological maturity size (*CW 50%*). *AW*, abdominal width (5th somite); *CW*, carapace width; *PL*, propodus length of major chela.

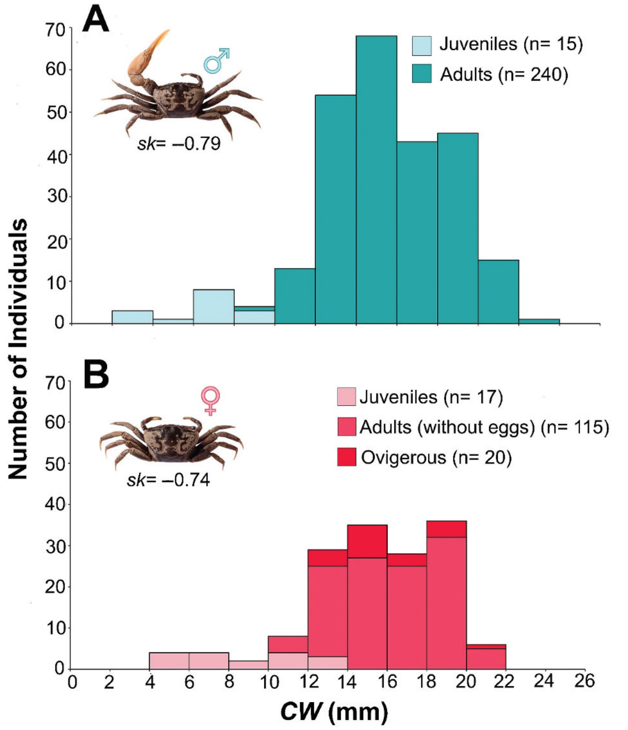

Figure 4. Population structure of *Minuca vocator* in the mangrove of Itanhaém (SP), Brazil, based on the frequency distribution of individuals in body size classes (2 mm). A) For males (n = 255), and B) for females (n = 152), categorized into their respective interest groups. *CW*, carapace width.

Table 1. Modes of the body size (*CW*, carapace width) for males and females) of *Minuca vocator*, in the Itanhaém Estuarine System (Itanhaém, SP), Brazil. Where: n, number of individuals; x ± sd, mean ± standard deviation; and *SI*, separation index.

Sex	Modes	n	*CW* (x ± sd, mm)	*SI*
Males	1	18	7.13 ± 2.48	0.00
	2	152	14.28 ± 1.69	3.43
	3	85	18.74 ± 1.53	2.76
Females	1	8	6.02 ± 1.06	0.00
	2	144	15.92 ± 2.78	5.17

composed of adults, as mentioned previously. However, the number of modal components differed between sexes, with males displaying three modes and females only two (Table 1).

In terms of cheliped handedness, 51.7% ($n = 120$) of males exhibited right-handed heterochely, which was not significantly different from the proportion of left-handed individuals (47.4%; $n = 110$; $\chi^2 = 0.43$, $p > 0.05$). The relationship between right-handed heterochely (H_1) and *CW* was described by the equation $H_1 = 0.642 + 0.144\ CW$ ($n = 120$; $R^2 = 0.70$), while the relationship for left-handed heterochely (H_2) followed the equation $H_2 = 0.267 + 0.165\ CW$ ($n = 110$; $R^2 = 0.71$). These equations did not differ significantly in their intercept ('a') or slope ('b') values (ANCOVA: $F = 2.53$, $p > 0.05$). Consequently, the data were combined into a single equation: $H = 0.459 + 0.154\ CW$ ($n = 230$; $R^2 = 0.70$) (Figure 5).

Discussion

The sex ratio of fiddler crabs varies considerably among species (Di Benedetto and Masunari 2009). However, many populations worldwide exhibit a male-biased ratio (Johnson 2003), a pattern confirmed in this study for *Minuca vocator*. The 1:0.60 (M:F) sex ratio observed in the mangrove site studied (Itanhaém, SP) was similar to that previously reported by Colpo and Negreiros-Fransozo (2004) for populations in three other locations along the Brazilian coast of São Paulo state: Bertioga (1:0.52), part of the central coast; and Ubatuba (Indaiá, 1:0.56; Itamambuca, 1:0.78), in the northern coast. Similar male-biased sex ratios have been recorded in other *Minuca* species (Benetti et al. 2007; Santos et al. 2020), in Rio de Janeiro state (Itacuruçá mangrove, RJ), including *M. rapax* (1:0.65), *M. mordax* (1:0.55), and *M. vocator* (1:0.17) (Bedê et al. 2008).

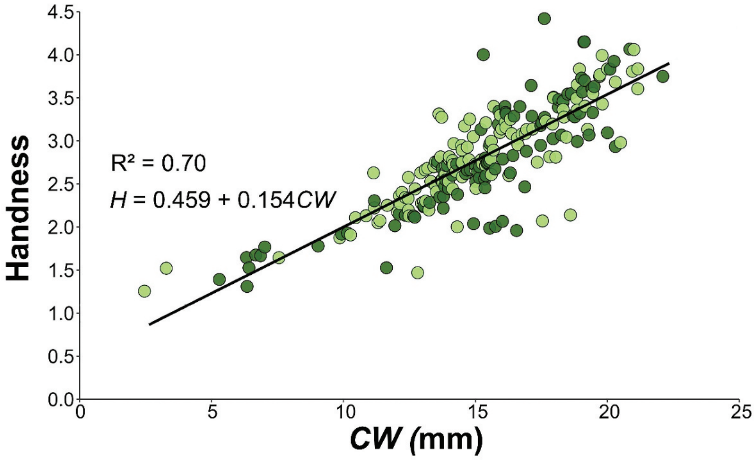

Figure 5. Handness in *Minuca vocator* males, with the dispersion of points for specimens with right heterochely (PL_R/PL_L: ligth green) and left heterochely (PL_L/PL_R: dark green) to body size (*CW*, carapace width). PL_R, propodus length of major right chelae; PL_L, propodus length of major left chelae.

In marine crustaceans, sex ratios frequently diverge from the expected 1:1 ratio, making it essential to analyse how this parameter varies with body size (Wenner 1972). In this study, the sex ratio remained close to 1:1 in smaller size classes but showed a male-biased peak in three *CW* classes (12–14 mm, 14–16 mm, and 20–24 mm), following the 'standard pattern' described by Wenner (1972). Given that the present study used an active sampling of individuals on the sediment surface, deviations from the 1:1 ratio could be interpreted in two ways based on differential mortality between sexes, as follows: (1) higher female mortality, as they may be more vulnerable to predation due to their smaller, equally sized chelipeds, which facilitate ingestion by predators, unlike males, which have one enlarged chela (Jaroensutasinee and Jaroensutasinee 2004); (2) higher male mortality, as males spend nearly twice as much time exposed on the surface, feeding on sediment-associated organic matter with only their smaller cheliped, whereas females can use both (Valiela et al. 1974); or (3) Differential sampling technique, which according to Costa and Negreiros-Fransozo (2002), may result in a skewed sex ratio (e.g. in transect sampling the ratio tends to favour males, whereas in capture per unit effort the ratio is typically 1:1). The higher male frequency in certain size classes is likely due to greater visibility in the field because of their hypertrophied cheliped, which plays a key role in courtship and combat behaviours (Milner et al. 2010; Takeshita and Nishiumi 2022).

Hartnoll (1974) described that, in Brachyura, the relative growth of the male cheliped and female abdomen generally follows positive allometry during juvenile stages but diverges after the pubertal moult. Males exhibit a higher growth rate in the dominant cheliped, whereas female abdominal growth slows. In adult male fiddler crabs, the accelerated growth of the major chela is linked to its use in male–male competition, mate selection, and territory defence (Crane 1966), a pattern observed across most brachyuran species (Pinheiro and Fransozo 1993; Pinheiro and Hattori 2006; Santos et al. 2023). In females, the reduction in abdominal allometry is related to coordinated growth between the abdomen and thoracic sternites, unlike the independent growth observed in chelipeds (Costa and Soares-Gomes 2008). The highest relative growth rate of the abdomen occurs during juvenile stages, declining after the pubertal moult, as its primary function shifts to protecting gonopores and eggs, which Pleocyemata incubate on pleopodal endopodites (Hartnoll 1969).

The *PL x CW* relationship in males showed positive allometric growth in both juvenile and adult phases, consistent with patterns previously described for Brachyura (Hartnoll 1974, 1978). Similar results were reported by Colpo et al. (2022) for *M. vocator* and other Brazilian *Minuca* species (Table 2). However, Costa and Soares-Gomes (2008) identified a different pattern in *M. rapax* from Itaipú (RJ), where juveniles exhibited positive allometry, followed by negative allometry in adults. The same positive allometric growth pattern for the major chela has been confirmed in males of other fiddler crab genera (*Leptuca* and *Uca*), except for *L. leptodactyla*, which displayed positive allometry in juveniles but isometry in adults for the *PL x CW* relationship (Masunari and Swiech-Ayoub 2003). According to Masunari et al. (2005), the high allometric growth in juveniles of *L. leptodactyla* allows the chela to reach functionally adequate sizes before adulthood, eliminating the need for further energy investment after the pubertal moult, resulting in isometric growth. In females, the *AW x CW* relationship followed the expected positive allometry for

Brachyura in both developmental phases (Hartnoll 1974, 1978), consistent with observations in *M. vocator* and other *Minuca* species (Table 2). These patterns are likely species-specific and influenced by phenotypic plasticity, which depends on food availability, habitat conditions, and anthropogenic impact levels.

The morphological maturity size of *M. vocator* in Itanhaém (SP) was similar between males (9.9 mm *CW*) and females (10.9 mm *CW*), diverging from the pattern observed in some other Brazilian Gelasiminae species (Table 2). However, the maturity size in males (9.9 mm *CW*) of the present study (Itanhaém, SP) was like those recorded in Itapanhaú (Bertioga, SP: 10.9 mm *CW*) and Indaiá (Ubatuba, SP: 11.8 mm *CW*), but smaller than in Itamambuca (Ubatuba, SP: 15.1 mm *CW*) (Colpo et al. 2022). A similar pattern was observed for females, with maturity sizes in Itanhaém (10.9 mm *CW*) comparable to those of Itapanhaú (Bertioga, SP: 10.7 mm *CW*) and Indaiá (Ubatuba, SP: 11.1 mm *CW*), but smaller than in Itamambuca (Ubatuba, SP: 14.6 mm *CW*) (Colpo et al. 2022).

Several factors, including latitude, can influence crab growth and maturity size (Hines 1989). According to this author and also Masunari and Dissenha (2005) suggested that brachyuran species from lower latitudes tend to mature at larger sizes than those from higher latitudes. Temperature and photoperiod may also contribute to these differences (Masunari et al. 2017; De Grande et al. 2021). However, Colpo et al. (2022) reported that populations of *M. vocator* from the same latitude, experiencing similar temperatures, exhibited different maturity sizes, likely due to site-specific environmental characteristics, such as mangrove structure and sediment composition (Colpo and Negreiros-Fransozo 2004; Colpo et al. 2022). Notably, organic matter concentration in mangrove sediments plays a crucial role, as deposit-feeding fiddler crabs depend on this resource (Masunari et al. 2017), and its availability varies with tidal dynamics and leaf litter biomass (Colpo and Negreiros-Fransozo 2003; Colpo et al. 2022).

Minuca vocator in Itanhaém exhibited a negatively skewed size distribution for both sexes, with adults (92.1%) outnumbering juveniles (7.9%), indicating low juvenile recruitment. Colpo and Negreiros-Fransozo (2004) found higher juvenile percentages (16.9% in Itamambuca, SP, to 37.8% in Indaiá, SP), up to five times greater than in the present study. Only two sampling events were conducted in Itanhaém: one in summer (21.4% juveniles), when juvenile proportions tend to be lower due to increased reproductive activity, and another in winter (78.6% juveniles), when recruitment

Table 2. Allometric growth levels (b-values: 0, isometry; –, negative allometry; and +, positive allometry) in different developmental phases (JU = juveniles; AD = adults) of Brazilian fiddler crab species, based on the power function for biometric relationships in males (*PL* × *CW*) and females (*AW* × *CW*). The dependent variables are *AW* (abdominal width of the 5th somite in females) and PL (propodus length of the major cheliped in males), analysed as a function of the independent variable *CW* (carapace width). Bold b-values indicate higher growth differences between developmental phases within the same biometric relationship. Where: min, minimum size; Max, maximum size; *MM*, morphological maturity size; X̄ mean; s, standard deviation; and *, total mean size.

		Males - *PL* x *CW* Relationship						Females - *AW* x *CW* Relationship					
				CW (mm)						*CW* (mm)			
Species	Sampled Estuary/ Mangrove (State, Brazil)	b-value (JU)	b-value (AD)	*MM*	Min	Max	x ± s	b-value (JU)	b-value (AD)	*MM*	Min	Max	x ± s
Leptuca leptodactyla	Itapoá (SC)[1]	**2,19 (+)**	1,24 (0)	8,4	3,9	11,5	–	**1,30 (+)**	1,07 (0)	7,4	3,1	10,6	–
Leptuca uruguayensis	Guaratuba (PR)[2]	1,72 (+)	**2,58 (+)**	4,1	2,3	8,3	–	1,02 (+)	**1,73 (+)**	3,5	1,6	7,8	–
Leptuca thayeri	Arinquindá (PE)[3]	1,71 (+)	**1,82 (+)**	11,8	4	26,6	12,5 ± 3,1	**1,39 (+)**	1,19 (+)	11,2	4,6	23,0	13,1 ± 2,8
	Mamucabas (PE)[3]	1,43 (+)	**1,88 (+)**	12,1	4,3	22,4	12,3 ± 3,0	**1,51 (+)**	1,27 (+)	11,9	5,1	22,1	13,1 ± 2,9
Uca maracoani	Guaratuba (PR)[4]	1,39 (+)	**1,95 (+)**	17,8	3,4	34,1	21,5	1,00 (0)	**1,51 (+)**	11,7	3,2	29,2	19,1
Minuca panema	Ubatumirim (SP)[5]	1,63 (+)	**2,04 (+)**	7,5	–	–	11,0*	1,40 (+)	**1,59 (+)**	6,2	–	–	11,0*
Minuca mordax	Itamambuca (SP)[6]	1,65 (+)	**2,24 (+)**	11,9	4,9	22,9	15,9 ± 2,7	**1,68 (+)**	1,42 (+)	11,5	4,3	20,8	14,6 ± 2,8
	Guaratuba (PR)[7]	1,51 (+)	**2,36 (+)**	11,7	1,9	20,0	–	1,21 (+)	**1,60 (+)**	8,8	2,5	18,8	–
Minuca rapax	Igaraçu (PI)[8]	**1,82 (+)**	1,71 (+)	12,4	6,3	25,1	17,2 ± 3,7	**1,46 (+)**	1,41 (+)	10,1	6,8	22,0	15,1 ± 3,2
	Itaipú (RJ)[9]	**1,98 (+)**	0,84 (–)	12,1	2,6	21,9	10,3 ± 2,5	**1,44 (+)**	1,31 (+)	6,8	2,2	18,2	9,3 ± 2,2
	Itamambuca (SP)[10]	**1,55 (+)**	1,52 (+)	15,2	4,3	28,3	15,2 ± 4,6	**1,67 (+)**	1,23 (+)	12,1	4,3	27,3	13,8 ± 4,6
	Ubatumirim (SP)[10]	1,43 (+)	**1,86 (+)**	13,5	4,0	24,2	13,5 ± 4,8	**1,45 (+)**	1,31 (+)	11,2	4,0	22,0	12,9 ± 4,4
Minuca vocator	Itapanhaú (SP)[11]	1,49 (+)	**1,66 (+)**	10,9	4,8	20,6	11,2 ± 3,7	**1,74 (+)**	1,30 (+)	10,7	4,9	21,1	12,4 ± 4,0
	Indaiá (SP)[11]	1,64 (+)	**1,92 (+)**	11,8	4,7	22,8	12,3 ± 4,7	**1,72 (+)**	1,19 (+)	11,1	6,4	23,0	13,8 ± 4,6
	Itamambuca (SP)[11]	1,38 (+)	**2,02 (+)**	15,1	6,0	24,8	16,7 ± 5,2	**1,47 (+)**	1,19 (+)	14,6	6,1	25,2	18,1 ± 4,2
	Itanhaém (SP)[12]	1,29 (+)	**1,88 (+)**	9,9	2,5	22,1	15,3 ± 3,5	**1,52 (+)**	1,18 (+)	10,9	4,3	21,8	15,4 ± 3,5

[1] Masunari and Swiech-Ayoub (2003); [2] Martins and Masunari (2013); [3] Araújo et al. (2012); [4] Masunari et al. (2005); [5] Benetti and Negreiros-Fransozo (2004); [6] Fransozo et al. (2009); [7] Masunari and Dissenha (2005); [8] Santos et al. (2020); [9] Costa and Soares-Gomes (2008); [10] Castiglioni and Negreiros-Fransozo (2004); [11] Colpo et al. (2022); [12] Present study.

peaks occur (Colpo and Negreiros-Fransozo 2004; Benetti et al. 2007; Santos et al. 2020).

These findings highlight the importance of population studies for understanding species' biological plasticity, conservation, and the potential vulnerability of *M. vocator* due to its stenotopic habitat preference and the ongoing environmental degradation in southern São Paulo mangroves.

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

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Author contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Ligia Modenesi and Nicholas Kriegler. The first draft of the manuscript was written by Ligia Modenesi and all authors commented on previous versions of the manuscript. Supervision was performed by Marcelo Antonio Amaro Pinheiro. All authors read and approved of the final manuscript.

Data availability statement

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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