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Crustaceana 97 (5-9) 1095-1114

CRUSTACEANA



Christoph D. Schubart Memorial Issue

PROGRESSIVE CHELAR POLYMORPHISM IN THE MANGROVE CRAB,
UCIDES CORDATUS (LINNAEUS, 1763) (DECAPODA, BRACHYURA,
OCYPODIDAE) FROM THE SOUTH-WESTERN ATLANTIC

BY

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ABSTRACT

Morphological variation of body size and appendages is defined as polymorphism and may be associated with important structures linked to the sexual selection process. Some studies have suggested an expressive heterochely (i.e., dissimilar chelipeds) in the male adult phase of the semi-terrestrial crab *Ucides cordatus*, an important decapod species of mangrove systems from the western Atlantic. Here, the morphology, size, and growth pattern of male chelipeds in *U. cordatus* from the Brazilian coast were examined to test for polymorphism, considering that adult males usually develop one ornamented and hypertrophied cheliped. Two cheliped morphs were detected in *U. cordatus* males: chelipeds can be either homochelous or heterochelous and both morphotypes occur from the juvenile to adult phase. The higher frequencies of heterochelous males in larger size classes (71%: ≥ 51 mm CW) and homochelous males in smaller ones (56%: < 51 mm CW) confirmed that the prevalence of each morph is also associated with the ontogeny in males. The ornamentation of both morphs mainly differed in the dentition of cutting edges, but it was similar in the presence and position of tubercles. Adult crabs with homochelous and heterochelous chelipeds reached a similar body size, but their major chelipeds were significantly different in size and growth pattern. The presence of both cheliped morphs suggests the existence of distinct functions in this species, associated with feeding habits and behavioral displays (sexual / agonistic interactions). Our results indicate that more than one morph can participate in the reproductive process in species with mating systems (e.g., explosive breeding) allowing for this, as in the subfamily Ucidinae.

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Key words. — Chela, chelar functionality, mating system, polymorphism, reproduction

ZUSAMMENFASSUNG

Morphologische Variationen der Körpergröße und der Gliedmaßen werden als Polymorphismus definiert und können mit wichtigen Strukturen im Zusammenhang mit dem sexuellen Selektionsprozess verbunden sein. Einige Studien deuten auf eine ausgeprägte Heterochelie (d. h. unterschiedliche Chelipedien) in der Erwachsenenphase der Männchen der semiterrestrischen Krabbe *Ucides cordatus* hin, einer wichtigen Dekapodenart der Mangrovensysteme im Westatlantik. Hier wurden die Morphologie, Größe und das Wachstumsmuster männlicher Chelipedien in *U. cordatus* von der brasilianischen Küste untersucht, um den Polymorphismus zu testen, wobei berücksichtigt wurde, daß erwachsene Männchen normalerweise einen verzierten und hypertrophierten Cheliped entwickeln. Bei *U. cordatus* Männchen wurden zwei Cheliped-Morphotypen nachgewiesen. Bei dieser Art können männliche Chelipedien entweder homochele oder heterochele sein, und beide Morphotypen kommen von der Jugend- bis zur Erwachsenenphase von *U. cordatus* vor. Die höhere Häufigkeit heterocheler Männchen in größeren Größenklassen (71%: ≥ 51 mm CW) und homocheler Männchen in kleineren (56%: < 51 mm CW) bestätigte, daß die Prävalenz jedes Morphs auch mit der Ontogenese bei Männchen zusammenhängt. Die Verzierung beider Morphen unterschied sich hauptsächlich in der Bezahnung der Schneidkanten, ähnelte sich jedoch in der Anwesenheit und Position von Tuberkeln. Erwachsene Krabben mit homochelen und heterochelen Chelipedien erreichten eine ähnliche Körpergröße, und heterochele Chelipedien unterschieden sich deutlich in Größe und Wachstumsmuster voneinander. Das Vorhandensein beider Cheliped-Morphotypen deutet auf die Existenz unterschiedlicher Funktionen bei dieser Art hin, die mit Ernährungsgewohnheiten und Verhaltensweisen (sexuelle/agonistische Interaktionen) verbunden sind. Unsere Ergebnisse deuten darauf hin, daß bei Arten, deren Paarungssysteme dies zulassen (z. B. explosive Paarung), wie in der Unterfamilie Ucidinae, mehr als ein Morph am Fortpflanzungsprozess beteiligt sein kann.

Schlüsselwörter. — Chela, Chelar-Funktionalität, Paarungssystem, Polymorphismus, Reproduktion

INTRODUCTION

Individuals of the same species often differ in behavioral, functional, and/or morphological traits (Van Maurik & Wortham, 2012). When intraspecific variation is phenotypic (i.e., color, ornamentation, size of body, and structures), a group of individuals with similar characteristics is a morph. Populations with a single morph are monomorphic; those with two or more morphs are polymorphic (Kuris et al., 1987). Phenotypic polymorphism of secondary sexual traits arises when sexual selection or intersexual conflict, often in conjunction with natural selection, favors two or more discrete heritable characteristics (Svensson et al., 2009).

In crustaceans, chelar polymorphisms are common, well studied, and often linked to male dominance and success in competition for access to scarce resources (e.g., receptive females) (Kuris et al., 1987; Correa et al., 2003; Thiel & Correa, 2004). Hartnoll (2012) argued that a chelar polymorphism occurs when two or more chelar morphs are observed in individuals of the same growth phase, without

any link with sex or maturity. This is observed in adult males of many decapod crustaceans that use their chelipeds to fight for receptive females or to defend their territory against invasion from male or female conspecifics (Emlen & Oring, 1977; Shuster & Wade, 2003; Baeza & Asorey, 2012). In species where more than one chelar morph occurs, a relation with functional maturity is usually postulated (Bueno & Shimizu, 2009) or differential sexual strategies used for each morph (Shuster, 2008; Svensson et al., 2009). For example, depending on the availability of receptive females, all male morphotypes can use the same strategy (e.g. female guard tactic and extended dominance) (Garner & Neff, 2020). In another context, when more than one morph competes, a less dominant morph adopts a quick behavior, without courtship and guarding of mates (Correa et al., 2000; Dennenmoser & Thiel, 2008; Sal Moyano et al., 2016). Differences in the investment of energy or nutrients in the growth of the chelipeds may result in subequal or extremely dissimilar male chelipeds, generating homochelic or heterochelic individuals, respectively (Rio et al., 2019).

Hartnoll (2012) recognized three types of chelar polymorphism in decapods: (1) cyclical polymorphism, where individuals change between different morphs on a seasonal basis, (2) definitive polymorphism, where specimens are fixed in each morph once they reach maturity, and (3) progressive polymorphism, where males progress through an ontogenetic sequence of morphs. Although chelar polymorphism is poorly studied in most decapods, research on this topic in the palaemonid prawn *Macrobrachium* genus stands out (Karplus & Barki, 2019). The strategies and morphotypes are described also for the commercial prawn *M. rosenbergii* (De Haan 1849) (Kuris et al., 1987; Pinheiro & Hebling, 1998; Van Maurik & Wortham, 2012) and for non-commercial species *M. brasiliense* (Heller, 1862) and *M. amazonicum* (Heller, 1862) (Nogueira et al., 2020, 2022). These studies revealed considerable variation in chelar forms in both sexes and during the development of one sex. Other contributions regarding the anomuran crab *Aegla franca* Schmitt, 1942 and the deep-sea lobster *Thaumastocheles japonicus* Calman, 1913, indicated, respectively, the formation of two sequential morphotype groups of adult males after the sexual maturity of *A. franca* (see Bueno & Shimizu, 2009) and the existence of male polymorphism in the major chela of *T. japonicus* (see Chang & Chan, 2018). Chelar polymorphism in males with the presence of homochelous and heterochelous adult individuals have been described in the burrowing shrimps *Callichirus seilacheri* (Bott, 1955) and *C. corruptus* Hernández, Miranda, Rio & Pinheiro, 2022, as well as in the terrestrial brachyuran crabs *Johngarthia lagostoma* (H. Milne Edwards, 1837), *Epigrapsus notatus* (Heller, 1865), and *E. politus* Heller, 1862 (Hartnoll et al., 2017; Hernández & João, 2018; Doi et al., 2019; Rio et al., 2019; João et al., 2024).

We examined the chelar polymorphism of the semi-terrestrial mangrove crab *Ucides cordatus* (Linnaeus, 1763). This species, known as ‘uçá-crab’ by local harvesters in Brazilian communities, is one of the most common and commercially harvested brachyuran crabs in Brazilian mangrove systems (Pinheiro et al., 2018). It occurs along the western tropical Atlantic coast (Melo, 1996), where it is an important ecosystem engineer (Pinheiro et al., 2003; Nordhaus et al., 2009; Christofolletti et al., 2013). In general, the individuals eat mainly senescent leaves of mangrove trees (Nordhaus et al., 2009; Christofolletti et al., 2013), which does not indicate any pressure to select for strong chelipeds because of feeding behavior.

A study of the breeding cycle of *U. cordatus* confirmed seasonal reproduction of a population from the southeast region of Brazil, with ovigerous females appearing from November to February (Sant’Anna et al., 2014) while a second study verified a slower pattern of growth with only one molt per year after sexual maturity (Pinheiro et al., 2005). Some authors suggest that *U. cordatus* adult crabs of both sexes are heterochelous (i.e., different-sized chelipeds), with the heterochely of the adult males more developed than in females (Dalabona et al., 2005; Pinheiro & Hattori, 2006). During mating, males of *U. cordatus* display the chelipeds to attract females (Linhares & Silva, 2012). Cheliped size and the difference in size between the two chelae (i.e., heterochely) are important for sexual recognition and for male success in competition for receptive females (Alencar et al., 2014).

In this study, we were particularly interested in examining the occurrence of chelar polymorphism in *U. cordatus* males with attention to differences in frequency of homochelous and heterochelous males during ontogeny and comparing cheliped shape (i.e., ornamentation, referred to as the presence of tubercles and teeth), size, and growth pattern between both morphotypes. We expected to find a progressive chelar polymorphism, with the male heterochelous morph being more predominant than the homochelous morph in the adult phase, due to the use of chelae to compete for and attract females. This type of chelar polymorphism is the most common in other species of brachyuran crabs (Hartnoll et al., 2017; Doi et al., 2019).

MATERIAL AND METHODS

Study area and crab sampling

Specimens of *Ucides cordatus* were collected during three expeditions (August 2016, August 2017, and March 2018) in the mangrove area of the Juréia-Itatins Ecologic Station (fig. 1). This ecological station is located in Peruíbe municipality, southeastern region of Brazil (fig. 1A), and is part of the Environmental Protected Area of Cananéia-Iguape-Peruíbe. This area is included in a biological reserve

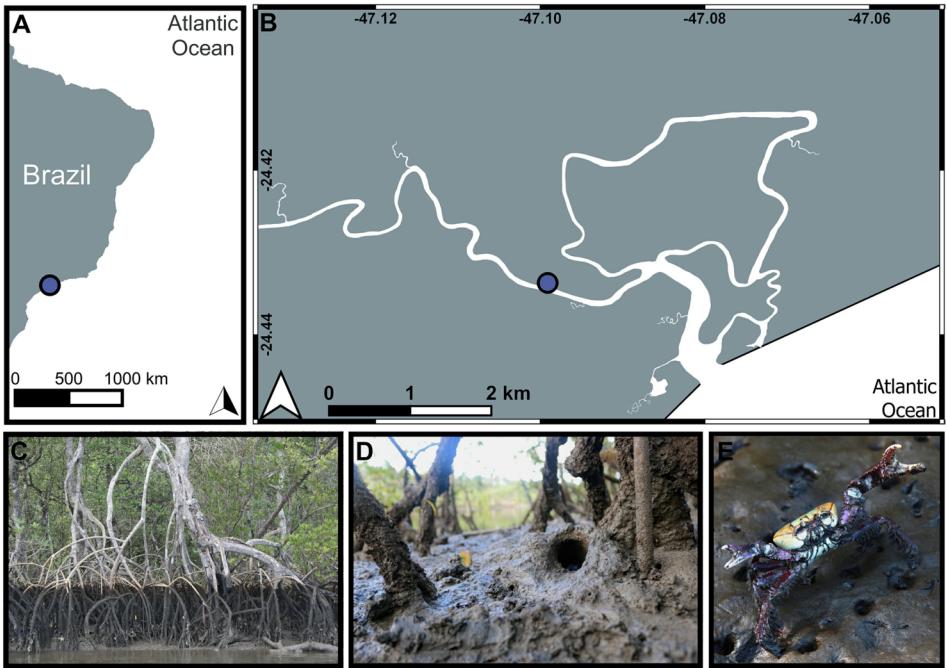


Fig. 1. A, General view of the South America and southeast Brazilian coast; B, geographic position of the study area; C, mangrove area of Juréia-Itatins Ecologic Station; D, characteristic burrow opening of *Ucides cordatus* (Linnaeus, 1763) in the mangrove sediment associated with *Rhizophora mangle* Linnaeus roots; E, frontal view of heterochelous adult male of *U. cordatus* in the mangrove mud. [Photo credits: C, Marcelo Pinheiro; D, Klaus Krieger (CRUSTA — UNESP, IB/CLP); E, Delson Gomes CRUSTA — UNESP, IB/CLP.]

that comprises the estuary of the Una River (fig. 1BC). Samples were taken from two mangrove zones, fringe and tidal flat (called ‘apicum’), with the fringe dominated by the red-mangrove (*Rhizophora mangle* L.) and apicum by the white-mangrove (*Laguncularia racemosa* (L.) C.F. Gaertn) and grass species (Wunderlich & Pinheiro, 2013). In each zone, *U. cordatus* individuals (fig. 1E) were captured manually in their active galleries (fig. 1D, open and closed burrows) by two harvesters, with a total effort of two hours per sampling day. After capture, male crabs were carefully washed with estuarine water, placed in an individual plastic bag, and transported to the laboratory where they were frozen until further examination in the laboratory.

In the laboratory, the species identity of each crab was confirmed using the diagnostic characters proposed by Melo (1996), and the sex of each crab was determined according to the morphology of the pleon and the number of pleopods in males (thin and narrow pleon, with two pairs of pleopods) and females (large and wide pleon, with four pairs of pleopods), following Pinheiro & Fiscarelli (2001). The following measurements were taken from all collected crabs using

a vernier caliper (nearest 0.05 mm): carapace width (CW, the widest measure between the lateral margins of carapace), and chelipeds (PL, propodus length of the left and right chelipeds, between the tip of manus finger until the teeth in the articulation with carpus). Additionally, the morphology of the chela (i.e., ornamentation referred to as the presence of tubercles and teeth) for the first pair of pereopods was examined.

Chelar polymorphism

We explored chelar polymorphism based on the presence/absence of extremely asymmetric chelipeds. For this purpose, we used the heterochely ratio to identify if the specimen was homochelous or heterochelous (following Hartnoll et al., 2017), with the ratio between major and minor chelar propodus length: Heterochely Ratio (HR) = $PL_{\text{major}}/PL_{\text{minor}}$. Crabs were classified as homochelous (HO) when $HR = 1$, and as heterochelous (HE) when $HR > 1$. To minimize misclassification individuals were classified as being homochelous when $1.0 < HR \leq 1.1$ and heterochelous when $HR > 1.1$. Posteriorly, we reobserved each individual classified as HO and HE checking their chelae robustness (e.g. propodus height and thickness) and morphology (e.g. number and size of teeth and tubercules) to avoid misclassification. The proportion of homo- and heterochelous specimens in the sample was contrasted by using a Chi-square goodness of fit test of the null hypothesis of equal proportions of HO and HE (Sokal & Rohlf, 2012).

The allometric growth of chelipeds in both male types (HO and HE) was evaluated by relative growth using the relationship $PL \times CW$. The empiric points of this biometric relationship were submitted to regression analysis and fitted to power function model ($Y = aX^b$, following Hartnoll, 1974 and 1978), both for HO and HE males, in this last case using the major PL value between right and left cheliped. The slope value (b constant) of all log-log transformed linear regressions calculated for HO and HE represents a positive ($b > 1$) or negative ($b < 1$) allometric growth of the chela (PL) about the crab's body size (CW). We used separate t -tests to examine whether the b -value of each log-regression line deviated from the expected isometry ($b = 1$). Finally, we conducted an analysis of covariance (ANCOVA) to test whether the relationship between the dependent variable (PL) and the covariate (CW) is influenced by cheliped morphotypes (HO and HE) (Sokal & Rohlf, 2012). When the interaction between the covariate and the factor is significant, the slopes (b) of the fitted regression lines differ between the levels of the respective factor. Crabs with broken or missed chelipeds were excluded from the relative growth and ANCOVA analysis. All these analyses were conducted in the software R (R Core Team, 2020), based on a minimum statistical significance of 5%.

Functional polymorphism

After the separation of HO and HE male types, we examined the differences in CW and PL sizes, and in the frequency of occurrence between these two morphotypes. First, we separated juveniles and adults using the size at onset of sexual maturity (=51.6 mm CW) estimated by Pinheiro & Hattori (2006) for males of *U. cordatus* in the Environmental Protected Area of Cananéia-Iguape-Peruíbe. For both juvenile and adult phases of males, we tested if HO and HE groups exhibited differences in body size and chelipeds by comparing the average of CW and major PL by a *t*-test. We then compared the proportions of HO and HE males in the total collection using a Chi-square test to test for significant differences between the frequencies (Sokal & Rohlf, 2012). We determined whether the proportion of male types varied with the ontogeny of *U. cordatus* as a signal of progressive polymorphism. The proportions were calculated in size classes (10 mm CW) and compared by a Chi-square test. In each size class, we considered a minimum of 15 crabs as an adequate sample size for the statistical comparison of these two groups. Progressive polymorphism is confirmed if the proportion of HE increases after reaching the size of sexual maturity. Additionally, we used multiple proportion tests (Zar, 2010) to assess whether the frequency of individuals of both chelar morphotypes differed between juvenile and adult crabs, to determine whether there was an association between the ontogenetic phases and the chelar polymorphism.

RESULTS

Chelar polymorphism

A total of 797 males of *Ucides cordatus* were collected during this study, of which 540 were heterochelous (67.8%) and 257 homochelous (32.2%), based on visual differences in the cheliped shape in crabs with similar sizes (fig. 2A–B). Chelipeds in heterochelous and homochelous males showed several characteristic differences (fig. 3A–H). Major chelipeds in heterochelous males (fig. 3A and C) were heavy and strongly calcified; length of the manus was about 1.1 times its width; outer and inner faces of manus with well-spaced tubercles obliquely positioned and ridges of tubercles from the articulation with carpus to pollex, superior and inferior margins denticulate; predactylus ridge present; pollex arcuate, slightly shorter than dactylus, cutting edge with large blunt teeth; dactylus broad, small tubercles on the outer face and large tubercles on the inner face, cutting edge with a large subsquare tooth at the proximal third (see also fig. 2B), the remainder of cutting edge with sparse acute teeth. Minor cheliped in heterochelous males (fig.



Fig. 2. Individuals of the mangrove crab *Ucides cordatus* (Linnaeus, 1763), both with similar sizes (60–65 mm of carapace width). A, Frontal view of homochealous morphotype; B, frontal view of heterochealous morphotype. Scale bars: 10 mm.

3B and D) appeared less heavily calcified than major cheliped; minor chelipeds were different from major chelipeds as follows: length of manus about 1.3 times its width; pollex almost equal in length with dactylus, tip slightly upward; cutting edge of the fixed finger and dactylus not arcuate, both armed with large subtriangular teeth. Chelipeds in homochealous males (fig. 3E–H) were similar in shape compared to minor chelipeds in heterochealous males but smaller; both left and right chelipeds similar in ornamentation to each other; length of manus about 1.2 times its width; pollex almost equal in length with dactylus, not arcuate, cutting edge of fixed finger with large subtriangular teeth; dactylus more arcuate than minor cheliped dactylus.

The frequency of homochealous crabs differed significantly from heterochealous in the sampled male individuals (HE : HO = 2.1 : 1.0; $\chi^2_{(1)} = 100.5$, $P < 0.001$). In heterochealous males, 48.8 and 51.2% had the larger chela on the right and left side, respectively, without any evidence of laterality ($\chi^2_{(1)} = 0.07$, $P = 0.79$). Overall, homochealous males measured from 17.0 to 88.7 mm CW (mean \pm SD: 62.6 ± 15.7 mm CW), whereas heterochealous males ranged from 26.6 to 90.1 mm CW (66.7 ± 10.7 mm CW). Heterochealous males were significantly larger than homochealous males (CW body size: heterochealous > homochealous; $t_{(374)} = 3.78$, $P = 0.0002$).

HO and HE male types showed a positive relationship of PL \times CW during ontogeny (table I). We detected positive allometric growth of the propodus relative

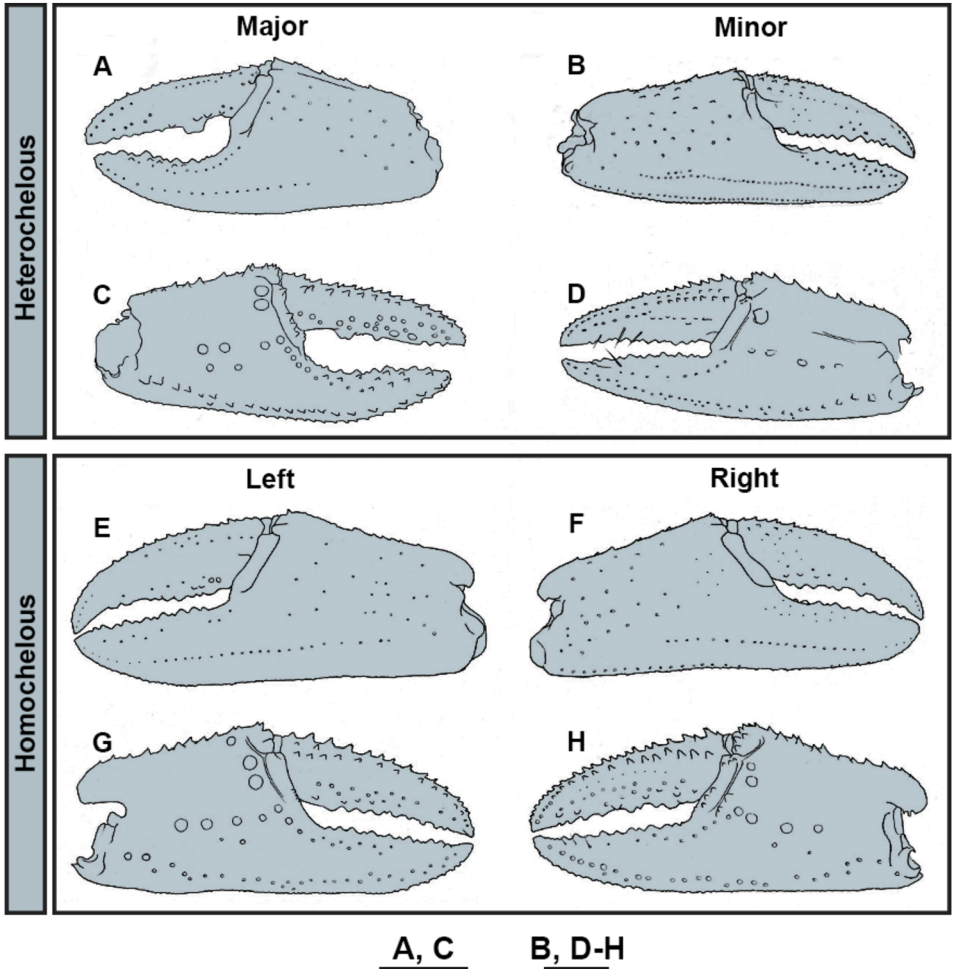


Fig. 3. Chelar polymorphism in the mangrove crab *Ucides cordatus* (Linnaeus, 1763). A-D, Heterochelous morphotype (HE: CW = 77.7 mm), major and minor chelipeds; A, Lateral view of heterochelous major cheliped; B, lateral view of heterochelous minor cheliped; C, mesial view of heterochelous major cheliped; D, mesial view of heterochelous minor cheliped; E-F, homochelous morphotypes (HO: CW = 76.2 mm) left and right chelipeds; E, lateral view of homochelous right cheliped; F, lateral view of homochelous left cheliped; G, mesial view of homochelous right cheliped; H, mesial view of homochelous left cheliped. Scale bars: A, C = 2 cm; B, D-H = 1 cm.

to body size in both morphotypes (fig. 4), but this relationship exhibited a growth curve with a slightly deeper slope in heterochelous males than homochelous males (1.39 versus 1.21, respectively; table I). The ANCOVA analysis demonstrated a significant effect of CW, morphotypes, and the interaction of both variables on cheliped size (table II).

TABLE I

Relative growth of the mangrove crab *Ucides cordatus* (Linnaeus, 1763) from ESEC Juréia-Itatins, Peruíbe (SP), southeast region of Brazil. A, the relationship between the cheliped propodus length (PL) and carapace width (CW) of males HO (homochelous) and HE (heterochelous)

Male type	Propodus Length × Carapace Width				
	Equation	r^2	SE _t	P	Allometry
HO	PL = 0.61CW ^{1.21}	0.92	0.019	< 0.001*	+*
HE	PL = 0.48CW ^{1.39}	0.94	0.014	< 0.001*	+*

The regression equations, correlation coefficients (r^2), standard errors of the slopes (SE), correspondent p -values are shown, and allometry of each regression with negative (-) or positive (+) confirmed by the t -test.

Functional polymorphism

Regardless of morphotype, most sampled males (85.4%) were sexually mature and there was an association between the ontogenetic phase and the cheliped morphotypes ($\chi^2_{(1)} = 31.35, P < 0.001$) (table III). The mean CW and PL of heterochelous juveniles was greater than that of homochelous juveniles (CW:

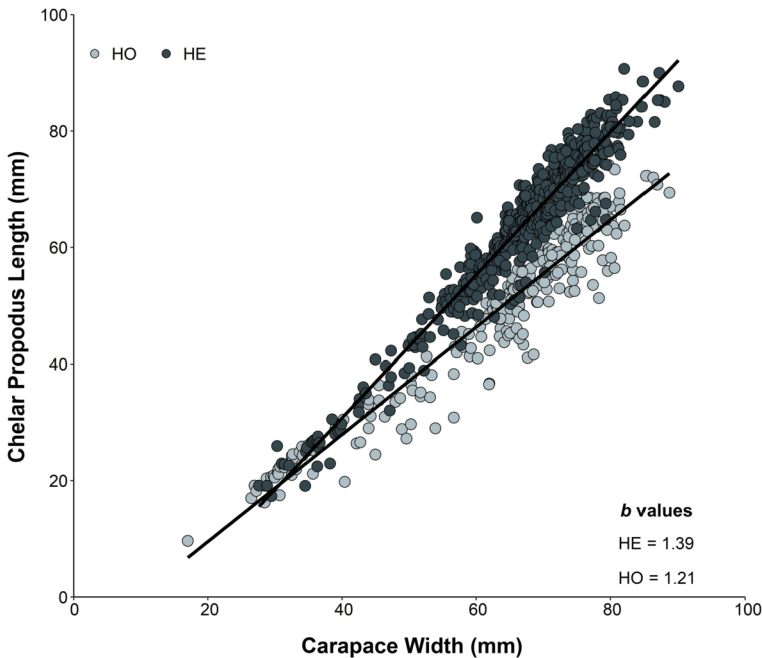


Fig. 4. Relationship between carapace width (CW, mm) and chelar propodus length (PL, mm) in both morphotypes of males (HO, homochelous; and HE, heterochelous) of *Ucides cordatus* (Linnaeus, 1763). The slopes (b) of the separate regression lines of both morphotypes (HO and HE) are shown in the corner of the graph.

TABLE II

Relative growth of the mangrove crab *Ucides cordatus* (Linnaeus, 1763) from ESEC Juréia-Itatins, Peruíbe (SP), southeast region of Brazil: Summary results of the Analysis of Covariance (ANCOVA) testing the effects of male type and CW on the PL of *U. cordatus* individuals. Data were \log_{10} -transformed to attend ANCOVA assumptions

Source of variation	ANCOVA Propodus Length			
	df	SS	F	P
Carapace width (CW)	1	15.42	16 115	<0.001*
Male type	1	1.07	1121.7	<0.001*
CW × Male type	1	0.068	71.4	<0.001*
Residuals	793	0.76		

Data were \log_{10} -transformed to attend ANCOVA assumptions. Significant *P* values ($P < 0.001$) are marked by asterisks.

$t_{(99)} = 2.22$, $P = 0.03$; PL: $t_{(84)} = 3.67$, $P = 0.0004$). By contrast, the CW mean did not differ between morphotypes during the adult phase ($t_{(361)} = 1.53$, $P = 0.13$), but the PL of heterochelous males was significantly larger than of homochelous males ($t_{(391)} = 14.47$, $P < 0.0001$).

HE males predominated but the proportion of both morphotypes varied during ontogeny. Males with CW in the interval $10 \leq CW \leq 50$ mm were mainly homochelous or in equal proportion to heterochelous males (fig. 5A). Heterochelous males predominated after they attained sexual maturity (≥ 51.6 mm CW). The results of the multiple proportion test indicated that the frequency of homochelous and heterochelous males differed statistically between the ontogenetical phases ($\chi^2_{(3)} = 31.35$, $P < 0.001$), with juvenile crabs being mainly homochelous (55.2%) and adult crabs mainly heterochelous (71.7%) (fig. 5B).

TABLE III

General overview of occurrence, carapace width (CW) and major cheliped propodus length (PL) of each chelar morphotype (HO, homochelous; HE, heterochelous) of juvenile and adult males (OP, ontogenetical phase) of the mangrove crab *Ucides cordatus* (Linnaeus, 1763) of ESEC Juréia-Itatins, Peruíbe (SP), the southeastern region of Brazil

Male type	OP	N (%)	Carapace Width (mm)		Propodus Length (mm)	
			Min–Max	Mean ± SD	Min–Max	Mean ± SD
HO	Juvenile	58 (56.3%)	17.0–50.5	37.2 ± 8.1	9.7–43.5	25.8 ± 6.6
	Adult	199 (43.7%)	51.7–88.7	70.0 ± 7.3	29.0–74.2	55.4 ± 8.9
HE	Juvenile	45 (28.7%)	27.6–51.6	40.5 ± 7.1	17.4–44.6	31.3 ± 8.1
	Adult	495 (71.3%)	51.8–90.1	69.1 ± 7.2	38.9–90.7	66.4 ± 9.6

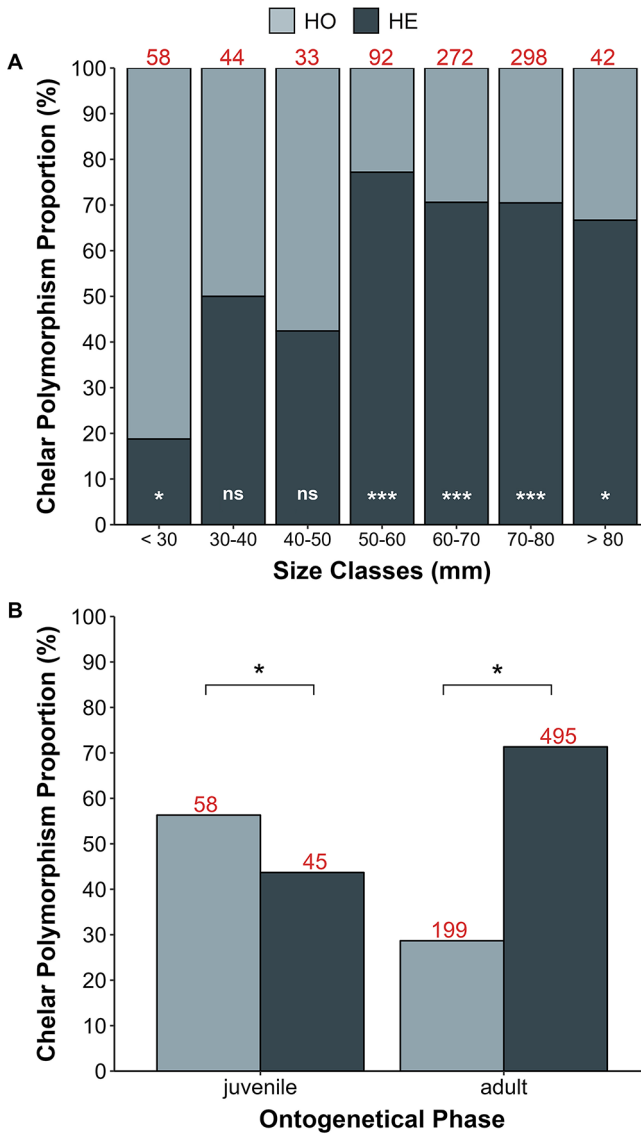


Fig. 5. Proportion of both morphotype males (HO, homochelous; and HE, heterochelous) of *Ucides cordatus* (Linnaeus, 1763). A, Proportions of both morphotypes along the ontogeny, considering 10 mm size classes (CW, carapace width); B, proportions of both morphotypes between both ontogenetic phases (juvenile and adult). Light and dark gray bars correspond to homochelous and heterochelous individuals, respectively; numbers above the bar represent the total number of individuals per size class and ontogenetic phase; * indicates significant differences between proportions (* $P < 0.05$; *** $P < 0.001$) and ns indicates no significant differences.

DISCUSSION

Morphological variations of one sex often are expressed after sexual maturity (Andersson, 1994). In males, changes in body shape and size, including some appendages (e.g., chelipeds), are associated with the development of secondary sexual characters that mediate the sexual behavior of adults. Here we show that *Ucides cordatus* males have homochelic and/or heterochelic chelipeds and that these claw forms begin in the juvenile phase leading to a claw form dimorphism in adults. The heterochelic form is the predominant morphotype in adult male *U. cordatus*. Morphologically, heterochelous crabs have thicker and larger chelipeds than do homochelous crabs, suggesting a greater investment in this more robust claw form. The frequency of each type, however, varied with ontogeny with HO being more common among juveniles and HE among adult males. Thus, *U. cordatus* chelipeds have a progressive polymorphism, consistent with the function of HE in reproductive activities of adults.

The two chelar morphotypes in the adults of *U. cordatus* differ in size independent of differences in carapace width. While the left and right chelipeds in homochelous males had a similar morphology (i.e., ornamentation and size), the claws of heterochelous males differed substantially, suggesting that they have different functions. A substantial body of literature indicates that the major (referred to as crusher) and minor chela (referred to as cutter) of many decapods are associated with courtship/fight and feeding, respectively (Schenk & Wainright, 2001; Spani et al., 2020). The two chelipeds also have distinct functions in reproduction: the male major chela is used in mate choice, manipulation of females, and fights with other males for sexual access to females, whereas the male minor cheliped exclusively serves for the manipulation of females (Crane, 1975; Baeza & Asorey, 2012; Sant'Anna et al., 2014). The presence of tubercles and teeth of the major chela has an important function as a weapon during male-male combats, generating injuries, especially in those most competitive males (Rypien & Palmer, 2007; Rojas et al., 2012).

We suggest that the major cheliped in HE males' functions primarily for reproduction, and especially in the mating context. During the reproductive period, both sexes emerge from their burrows where they recognize potential mates, and males use their major chelae to fight other males for and manipulate receptive females (Pinheiro & Fiscarelli, 2001; Alencar et al., 2014). *Ucides cordatus* feeds on easily macerated plant tissue (e.g., senescent leaves and propagules) from mangrove trees (Nordhaus et al., 2006; Christofoletti et al., 2013) and do not use their major cheliped to crush their food. Positive allometry of the major cheliped of *U. cordatus* has been found in other studies consistent with the use of this claw in competition for mates (Leite et al., 2006; Pinheiro & Hattori, 2006; Castiglioni et al., 2013).

If the major chela functions are important in reproduction, why do some adult male *U. cordatus* have equal size chelipeds? We expect that HE males have an advantage in combat against HO males, and these fights generally occur between them (Alencar et al., 2014; Sant'Anna et al., 2014). Given the usual “andada” behavior, which consists of many *U. cordatus* individuals aggregating to mate over a short period (i.e. full/new moon of rainy seasons — Pinheiro & Fiscarelli, 2001; Diele et al., 2005) and an unbiased sex ratio in reproductive areas (Wunderlich & Pinheiro, 2013), males may not always need to fight for access to receptive females. This possibility was described previously for other species (Christy, 1987) and could be related to the species' mating system. The pattern observed here for *U. cordatus* is related to the explosive breeding mating system, which generally presents reproductive aggregations of many receptive individuals, making the monopolization of mates difficult and leaving undefended and accessible females available to less dominant males (Emlen & Oring, 1977). This mating system was described previously for other brachyuran crabs (e.g. *Cancer magister*; see Orensanz & Gallucci, 1988) and, if it is true, both HO and HE individuals can access receptive females. Despite this, future studies need to clarify if distinct reproductive tactics were used for both morphotypes (Shuster & Wade, 2003), like the observed for male types of the mangrove crab *Neohelice granulata* (see Sal Moyano et al., 2016).

Homochelous and heterochelous morphotypes also occur in the congener *U. occidentalis* (Ortmann, 1897) (see Zambrano & Aragón-Noriega, 2016). This cheliped dimorphism apparently is a specific characteristic only in the monogeneric subfamily Ucidinae. In the fiddler crabs, subfamilies Gelasiminae and Ocypodinae, all males exhibit extreme heterochely, with a hypertrophied major chela that can reach a third of the body mass (Rosenberg, 2001), and where this claw is used exclusively to court females and fight other males, with only a minor function in defense (Crane, 1966, 1975). In ghost crabs from the genus *Ocypode* all adult males develop unequal chelipeds (Shih et al., 2016), as for example in *O. quadrata* (Fabricius, 1787) (see Schenk & Wainwright, 2001). These observations emphasize the differences in claw morphotypes occurrence indistinctly in three subfamilies of Ocypodidae, confirming that only Ucidinae species exhibit a chelar polymorphism.

Our study provides evidence supporting the progressive polymorphism hypothesis by Hartnoll (2012). Hartnoll (2012) proposed two other models of chelar polymorphism in decapods, namely cyclical polymorphism, and definitive polymorphism. Cyclical polymorphism does not match our observations because the two *U. cordatus* morphs were sampled during the mating and non-mating seasons. We also reject the definitive polymorphism hypothesis, since in that growth model,

the predominant morphotype is similar between juvenile and adult phases (Hartnoll, 2012), which is the opposite of what we observed in *U. cordatus*. Since the proportion of HE males progressively increases after males reach maturity, progressive polymorphism is the most probable model, as found in other decapods (Bueno & Shimizu, 2009; Hartnoll et al., 2017; Doi et al., 2019).

On the Brazilian coast, *U. cordatus* is one of the most important fisheries resources in mangrove areas, both for social and economic value, principally as a source of food for artisanal communities (Pinheiro & Fiscarelli, 2001; Duarte et al., 2014; Machado et al., 2018; Pinheiro et al., 2018). Brazilian law establishes a minimum capture size of 60 mm (CW) and a fishery closure from October to December each year, with a prohibition to selling entire individuals or crab parts, like chelipeds (IBAMA, 2003). The larger males are the principal focus of harvesters (Machado, 2007; Cavalcante et al., 2011) because of the larger chelipeds (which corresponds to 40% of their weight) and the economic yield of these specimens in local markets and restaurants (Pinheiro et al., 2015). Therefore, the catch is focused mainly on HE males.

The sampling site studied here is not used by the traditional fishery of *U. cordatus*. This fact reinforces the need for new studies in areas where this species is harvested to confirm how fisheries extraction affects the proportions of HE : HO in local populations. If progressive chelar polymorphism is a constant trait for the species, a more intense catch of HE crabs could reduce this morphotype, possibly allowing reproductive success for HO individuals. However, it is still unclear whether fishing pressure on *U. cordatus* individuals promotes remarkable changes in the species' population, especially considering its reduced management along the Brazilian coast (Dias-Neto, 2011). Therefore, future fishery studies could clarify if harvesting especially HE crabs affects the proportion of these two morphotypes (HO and HE) during the reproductive process.

ACKNOWLEDGEMENTS

Thanks to Mr. Otto Hartung, Manager of the Juréia-Itatins Ecologic Station (JIES) from Forest Foundation (FF), for all the support offered during field expeditions, mainly for the use of accommodation in the Perequê Base and the aid of the environmental monitor Sr. Ílson Prado. We are also extremely grateful to Sr. Andre Rodrigues for the crab capture during the 'Uçá'-Project, as well as for CRUSTA members' help in the field and laboratory activities. The authors thank FAPESP for the fellowships (MCAJ: No. 2017/22770-3; NK No. 2017/13510-8; PH: No. 2015/09020-0) and for FAPESP-FGB that funded the 'Uçá'-Project (No. 2014/50438-5), coordinated by MAAP. We thank the 'Instituto Chico Mendes

de Conservação da Biodiversidade' (ICMBio) and the 'Sistema de Autorização e Informação da Biodiversidade' (SISBIO) that conceived all sample permissions (No. SISBIO 50925-1). Finally, we are extremely grateful to Dr. John Christy, one anonymous reviewer, and Dr. Martin Thiel for their constructive suggestions and criticism of our manuscript.

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