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Research Article

Morphometric analysis of the mud crab *Hexapanopeus paulensis* Rathbun, 1930 (Decapoda, Xanthoidea) from the southeastern coast of Brazil

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ABSTRACT. In this study, we estimated the size at onset of maturity (carapace width, CW_{50}) and analyzed the relative growth of some body parts and the heterochely of the mud crab *Hexapanopeus paulensis*. A total of 800 crabs were collected, from January 1998 to December 1999, on the southeastern coast of Brazil. Each specimen was sexed and measured. CW_{50} was estimated to be 6.7 mm in males and 6.3 mm in females. Carapace length growth was negatively allometric in both sexes. Cheliped length and height was positively allometric for both males and females. Gonopod growth was isometric (b = 1) and negatively allometric (b < 1) in both juvenile and adult males, respectively. Abdomen relative growth was positively allometric (b > 1) for both juvenile and adult females. In males and females, the right cheliped was larger and higher than the left cheliped. Such heterochely may be related to the feeding habits of *H. paulensis*. Most xanthoid crabs, including the studied species, feed upon mollusks with dextral shells, which require complicated handling. In this sense, the heterochely in *H. paulensis* might facilitate the food manipulation.

Keywords: *Hexapanopeus paulensis***,** Panopeidae, sexual maturity, sexual secondary characters, bycatch, Ubatuba, southeastern, Brazil.

Análisis morfométrico del cangrejo de fango *Hexapanopeus paulensis* Rathbun, 1930 (Decapoda, Xanthoidea) del litoral sureste de Brasil

RESUMEN. En esto estudio se investigó la talla de primera madurez sexual (ancho del caparazón CW_{50}), crecimiento relativo de varias estructuras corporales y la ocurrencia de heteroquelia en machos y hembras de *Hexapanopeus paulensis*. Se recolectó un total de 800 ejemplares, de enero 1998 diciembre 1999 en la región de Ubatuba, costa sureste de Brasil. Cada cangrejo recolectado fue sexado y medido. El CW_{50} ocurre a los 6,7 mm en machos y 6,3 mm en hembras. En machos juveniles y adultos, el crecimiento relativo (basado en el CW) del gonopodio fue isométrico (b = 1) y alométrico negativo (b < 1), respectivamente. El crecimiento relativo del abdomen fue alométrico positivo (b > 1) en hembras juveniles y adultas. El crecimiento relativo del ancho del caparazón fue alométrico negativo en los dos sexos. El alto y largo del quelípedo presentaron alometria positiva. El quelípedo derecho (largo y alto) fue más grande que el quelípedo izquierdo tanto en los machos como hembras. Consecuentemente, *H. paulensis* exhibe heteroquelia, lo que sugiere especialización de los quelípedos en relación a su hábito alimentario. Tanto *H. paulensis* como otros cangrejos xantoideos se alimentan de moluscos con conchas dextrógiras, y la destrucción de dichas conchas requiere de un manejo complejo de sus quelípedos. De este modo, los quelípedos heteroquélicos pueden facilitar la manipulación del alimento en el cangrejo *H. paulensis*.

Palabras clave: *Hexapanopeus paulensis*, Panopeidae, madurez sexual, caracteres sexuales secundarios, fauna acompañante, Ubatuba, sureste de Brasil.

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INTRODUCTION

Throughout the ontogeny of decapod crustaceans, the occurrence of differential growth rates between distinct parts or organs of the body is expected. Such phenomenon is referred to as relative growth (Hartnoll, 1974). The hard integument of these crustaceans, the molting frequency, and the subdivisions during the ontogeny favor accurate measurements resulting in different growth rates between the sexes and between the phases of development (Hartnoll, 1978). Consequently, several studies dealing with relative growth of decapod crustaceans have been published in recent years, with most of them being focused on investigations concerning the morphological sexual maturity of these organisms (Bertini *et al.*, 2007; Fumis *et al.*, 2007; Miranda & Mantelatto, 2010).

Size estimates at the onset of sexual maturity are among the most important information of a population (Pinheiro & Fransozo, 1998), providing the backbone for development of conservation strategies and management. The morphological sexual maturity results in changes in the allometric patterns of somebody structures such as sexual appendices, abdomen, and chelipeds, suggesting the size at which the animal becomes morphologically mature (González-Gurriarán & Freire, 1994). Among these body structures, classified as secondary sexual characters, the size and form of the chelipeds are very important for the crabs since they are used during many agonistic interactions, reproduction, and feeding (Bloch & Rebach, 1998).

Due to the importance of this body structure, some studies have examined the occurrence of heterochely in decapod crustaceans. According to Hartnoll (1982), heterochely is generally recorded in both males and females, with few cases where it is restricted to only one sex, as observed for males of the genus *Uca* Leach, 1814 (Negreiros-Fransozo *et al.*, 2003; Castiglioni & Negreiros-Fransozo, 2004; Hirose & Negreiros-Fransozo, 2007; Pralon & Negreiros-Fransozo, 2008). Heterochely is widespread among Brachyurans and has been reported for species such as *Callinectes ornatus* Ordway, 1563 studied by Haefner (1990), *Carcinus maenas* (Linnaeus, 1758) by Kaiser *et al.* (1990), *Eriphia gonagra* (Fabricius, 1781) by Góes & Fransozo (1998), *Ocypode quadrata* (Fabricius, 1787) by Fransozo *et al.* (2002), and *Acantholobulus schmitti* (Rathbun, 1930) by Fumis *et al.* (2007). Among the few studies carried out on the genus *Hexapanopeus* Rathbun, 1898 considering xanthid crabs, nothing is known about their morphological sexual maturity and heterochely.

Along the non-consolidated substrate of the Ubatuba region, the Xanthoidea crabs are well represented; Mantelatto & Fransozo (2000) found eight species, from 1995 to 1996, while Bertini *et al.* (2010a) recorded seven species in the same region, between the years of 1998 and 1999. Their abundance, in association with the predatory habits of some species, might play an important ecological role within the marine ecosystems where they can occupy different trophic levels, such as predator and prey.

Among the species of this superfamily, the crab *Hexapanopeus paulensis* Rathbun, 1930 is part of the accompanied carcinofauna (bycatch) of trawl fishing, targeting commercial-interest shrimp species on the southeastern coast of Brazil, such as *Farfantepenaeus paulensis* (Perez-Farfante, 1967), *F. brasiliensis* (Latreille, 1817), *Litopenaeus schmitti* (Burkenroad, 1936), and *Xiphopenaeus kroyeri* (Heller, 1862) (Bertini *et al.*, 2010a). Such activity is considered predatory and destabilizing for benthic communities (Ruffino & Castello, 1992; Branco & Fracasso, 2004). The lack of information about the population biology and reproduction of the species of the genus *Hexapanopeus* encourages investigations on these subjects, especially in regions such as Ubatuba, which is constantly affected by anthropogenic effects of fishing and tourism.

Thus, in order to obtain information about the population biology of *H. paulensis*, the present study aimed to: 1) determine the sizes in which males and females reach their morphological sexual maturity, 2) characterize the relative growth of the species based on allometric changes of carapace length, width, and height of the cheliped propodus, gonopod length, and abdomen width in relation to the carapace width, and 3) verify the occurrence of heterochely in both sexes. Importantly, this is the first study focusing on population biology of *H. paulensis* that will contribute to further studies on many biological subjects of the species.

MATERIALS AND METHODS

Data collection and laboratory procedures

Crabs were collected monthly, from January 1998 to December 1999 in Ubatumirim, Ubatuba, and Mar Virado bays on the northern coast of São Paulo State, Brazil (23º32'S, 44º44'W). Six sampling sites were established in each bay, three in protected areas from wave action (with depths of 5, 7.5, and 10 m) and three in exposed areas (10, 15, and 20 m).

Sampling was carried out using a shrimp fishing boat equipped with double-rig nets consisting of a main net body with 20 mm mesh and a terminal cod with 15 mm mesh. Trawling was carried out for 30 min each, sampling a total area of approximately 18,000 m^2.

Captured specimens were identified according to Melo (1996). After, the crabs were sexed and the following measurements were taken under a stereomicroscope: maximum carapace width (CW) and carapace length (CL); length and height of the right and left cheliped propodus (CPL, CPH); gonopod length of males (GL), and abdomen width of females (AW) from the greatest width of 5th segment.

Data analysis

All data sets were Ln-transformed prior to analysis of morphological sexual maturity and relative growth. The results are expressed as non-transformed values.

Maturation stages (juvenile and adult) were distinguished by the size at which differential growth of the secondary sexual characters (males = gonopodium length; females = abdomen width) in relation to the independent variable (CW). For this purpose, a K-means non-hierarchical clustering procedure was applied to Ln(GL) *vs* Ln(CW) (males) and Ln(AW) *vs* Ln(CW) (females) data points. This clustering analysis distributes the data set in groups previously established; in this case two groups (juveniles and adults), by an iterative process that minimizes the variance within groups and maximizes it among them. The result of the classification (K-means) was refined using a discriminant analysis. This statistical methodology was based on Sampedro *et al.* (1999) and Hirose *et al.* (2012).

Size frequency distributions were constructed including all demographic categories (juvenile males, juvenile females, adult males, and adult females). Student's t-test (α = 0.05) was used to compare differences in the mean carapace width of males and females.

Based on results of the K-means non-hierarchical clustering procedure, the overall size at the onset of morphological sexual maturity was estimated for each sex separately. The method used to estimate sexual maturity was based on fitting logistic function: $y = 1/(1 + e^{(-r(CW-CW50))})$; where y is the proportion of mature male and female crabs, CW is the carapace width class, CW_{50} is the size at the onset of sexual maturity, and r is the coefficient for the slope of the logistic curve. The logistic curve was fitted by least squares to the proportion per size class (Vazzoler, 1996). After adjusting the model regression, the size at which y = 50% reached sexual maturity was estimated (CW_{50}).

Analyses of relative growth were performed separately for each sex based on allometric equation (Huxley, 1950), $y = ax^b$, converted to the linear form by means of natural logarithm transformation ($Ln(y) = Ln(a) + b\,Ln(x)$), where y = dependent variables (CL, CPL, CPH, GL, AW), x = independent variable (CW), a = intercept on y axis, and b = allometric growth coefficient. In the present study, the variables CPL and CPH correspond to the largest measures of the major cheliped propodus. Growth was classified as positively allometric when $b > 1$, negatively allometric when $b < 1$, or isometric when $b = 1$. Student's t-test was utilized to assess deviations from the isometric condition, with significance level $\alpha = 0.05$ (Zar, 1999). A covariance analysis (ANCOVA, $\alpha = 0.05$) was used to test differences in slopes and intercepts of lines for each phase of growth in each sex.

A covariance analysis (ANCOVA, $\alpha = 0.05$) was also used to compare length and height measures of the right and left cheliped propodus between sexes. Next, the paired Student's t-test ($\alpha = 0.05$) was used to compared the same measures for each sex.

RESULTS

A total of 800 crabs (355 males and 445 females) were analyzed in this study, with CW ranging from 3.7 to 17.4 mm (mean ± SD = 7.5 ± 2.2 mm) in males, and from 2.9 to 14 mm (mean ± SD = 7.0 ± 2.0 mm) in females (Fig. 1). The average size of males was significantly larger than females (Student's t-test = 3.062, $P = 0.002$). From the results of the K-means non-hierarchical clustering procedure, the crabs were classified into 152 juvenile males, 203 adult males, 187 juvenile females, and 258 adult females.

Morphological sexual maturity

Males attained morphological sexual maturity at 6.7 mm CW (Fig. 2a). Carapace width of the largest immature crab and the smallest mature crab were 7.3 and 6.4 mm CW, respectively. For females, the size at onset of morphological sexual maturity was 6.3 mm CW (Fig. 2b). The carapace of the largest immature crab was 7.5 mm, while that of the smallest mature crab was 5.9 mm, which corresponded to the smallest ovigerous female obtained during the investigation.

Relative growth

All equations of relative growth analysis are described in Table 1. For the relationship CL *vs* CW, distinct equations were obtained for juvenile and adult males (ANCOVA, $P < 0.05$). In both maturation stages, growth was negatively allometric. For females, the relationship was the same for juvenile and adult individuals, and the growth in length of carapace was also negatively allometric.

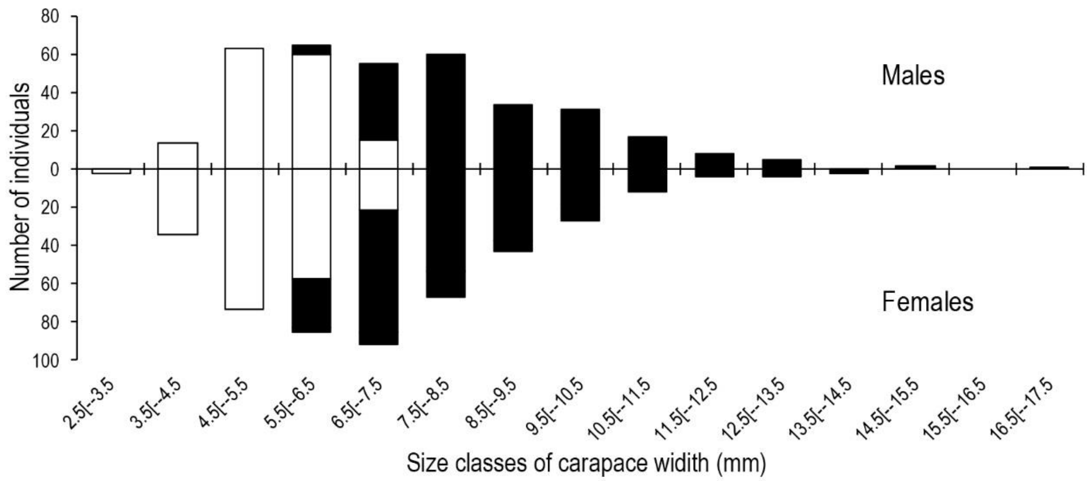

Figure 1. Size frequency distribution for males and females.

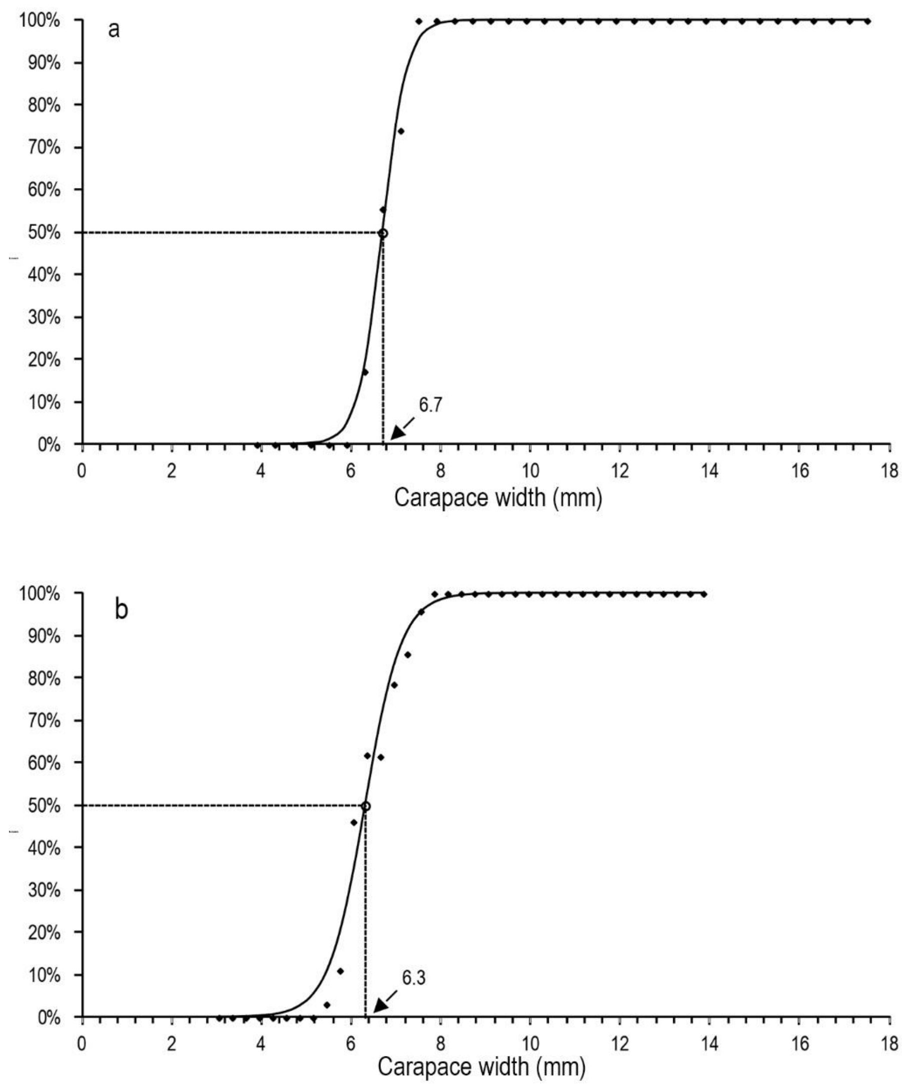

Figure 2. Size at the onset of morphological sexual maturity: a) males and b) females.

Table 1. Summary of power function regression analyses, based on the carapace width (x = CW). CW: carapace width, CL: carapace length, CPL: cheliped propodus length, CPH: cheliped propodus height, GL: gonopod length, AW: abdomen width, JM: juvenile males, AM: adult males, JF: juvenile females, AF: adult females, n: number of individuals; = isometry; + positive allometry; - negative allometry; CW_{50} = size at the onset of morphological sexual maturity.

Variable	Group	n	Power function	R^2	*t* (b=1)	Alometry level	CW_{50} (mm)
CL	JM	152	$CL = 0.878CW^{0.898}$	0.93	5.26	-	
	AM	202	$CL = 0.804CW^{0.957}$	0.97	5.47	-	
	TF	445	$CL = 0.831CW^{0.928}$	0.98	13.44	-	
CPL	TM	347	$CPL = 0.517CW^{1.124}$	0.96	9.65	+	
	TF	424	$CPL = 0.563CW^{1.054}$	0.97	6.05	+	
CPH	TM	343	$CPH = 0.226CW^{1.211}$	0.91	10.6	+	
	TF	421	$CPH = 0.256CW^{1.109}$	0.93	7.42	+	
GL	JM	152	$GL = 0.289CW^{0.943}$	0.70	1.12	=	6.7
	AM	203	$GL = 0.505CW^{0.704}$	0.73	10.73	-	
AW	JF	187	$AW = 0.16CW^{1.235}$	0.80	5.18	+	6.3
	AF	258	$AW = 0.257CW^{1.127}$	0.82	3.95	+	

Dimensions of chelipod (CPL and CPH) showed positive allometric growth for males and females, with no significant difference between juvenile and adult individuals (ANCOVA, $P > 0.05$).

The growth pattern obtained for the GL *vs* CW relationship was isometric for immature males and negatively allometric for mature males (ANCOVA, $P < 0.05$) (Fig. 3a). For females, the relationship AW *vs* CW showed a positive allometric growth for both immature and mature individuals (ANCOVA, $P < 0.05$) (Fig. 3b).

Heterochely

The size range, mean, and standard deviation of the cheliped propodus for each sex are shown in Table 2. The mean length and height of the right and left cheliped propodus differed significantly between the sexes (ANCOVA, $P < 0.05$), being larger in males. For both sexes, the right cheliped propodus was statistically larger than the left cheliped propodus, considering the length and height measures (paired Student's t-test, $P < 0.05$).

In Table 3, values of relative frequency (%) of males and females showing the major cheliped propodus are described. For all males and females analyzed, 83.8% and 79.3% had the right cheliped propodus larger than the left, respectively.

DISCUSSION

In the present study, the larger body size of adult males was considered a secondary sexual dimorphism for *H. paulensis*. This is a feature commonly observed in other species of brachyuran crabs, such as *Hepatus pudibundus* (Herbst, 1785) studied by Mantelatto *et al.* (1995), *Callinectes ornatus* Ordway, 1963 by Mantelatto & Fransozo (1999a), *Panopeus austrobesus* Williams, 1983 by Negreiros-Fransozo & Fransozo (2003), *Persephona mediterranea* (Herbst, 1794) and *P. punctata* (Linnaeus, 1758) by Bertini *et al.* (2010b) and Almeida *et al.* (2013). This result is related to the pre-mating behavior, which is displayed by males of several species, comprising agonistic behavior during competition for females, manipulation of them between their pereopods, protection, and mating (Cobo & Fransozo, 1998; Costa & Negreiros-Fransozo, 1998; Hartnoll, 2006). So, larger males can efficiently protect females. However, behavioral studies might confirm this information for *H. paulensis*.

Males of *H. paulensisis* also reached morphological sexual maturity at larger sizes compared to females, as well as other xanthid crabs-*Eurytium limosum* (Say, 1818) studied by Guimarães & Negreiros-Fransozo (2002), *P. austrobesus* by Negreiros-Fransozo & Fransozo (2003), and *Acantholobulus schmitti* by Fumis *et al.* (2007), suggesting a common pattern among them. According to Hartnoll (2006), investment in growth of males is due to many factors related to reproduction, such as visual displays, competition for females, and their protection. Conversely, Alunno-Bruscia & Saint-Marie (1998) have related such results to the extended growth period of males, usually showing high molting increments. For females, the energy is commonly directed to breeding, as the production of oocytes requires a greater amount of energy resources than sperm production (Alunno-Bruscia & Saint-Marie, 1998). In the present study, it is assumed that males of *H. paulensis* can invest more

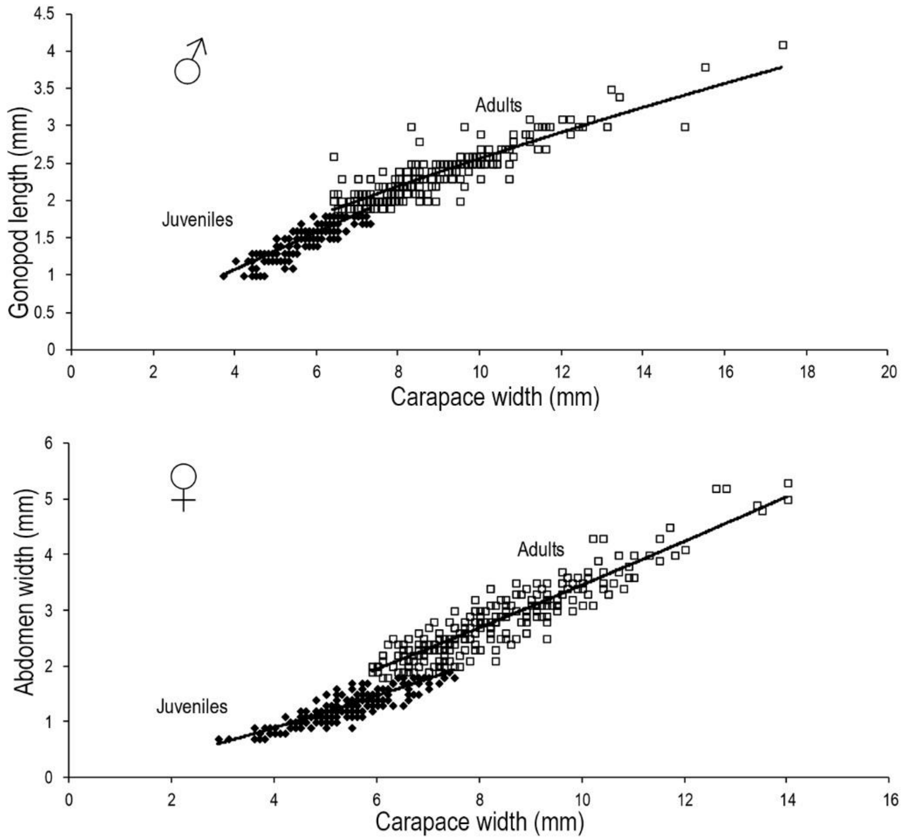

Figure 3. Linear representations of the relationships: ♂) gonopod length (GL) and carapace width (CW), ♀) the abdomen width (AW) and carapace width (CW), for males and females, respectively.

Table 2. Length and height of the cheliped propodus. M: males, F: females, SD: standard deviation. Lowercase letters (a, b): male *vs* female (ANCOVA; α = 0.05). Capital letters (A, B): right *vs* left (paired Student's t-test; α = 0.05).

Propodus	Right				Left			
	Sex	Mín	Max	Mean ± SD	Sex	Mín	Max	Mean ± SD
Length	M	1.8	14.4	4.43 ± 1.82 aA	M	1.5	12.7	4.12 ± 1.68 aB
	F	1.6	9.2	4.07 ± 1.31 bA	F	1.6	9.2	3.84 ± 1.22 bB
Height	M	0.8	8.2	2.32 ± 1.82 aA	M	0.6	6.4	1.92 ± 0.85 aB
	F	0.7	5.2	2.07 ± 1.06 bA	F	0.7	4.4	1.76 ± 0.57 bB

Table 3. Major cheliped occurrence in males and females. N: number of individuals.

Sex	Larger chela			
	Right		Left	
	n	%	n	%
Males	361	83.8	70	16.2
Females	409	79.3	107	20.7
Total	770	81.3	177	18.7

energy in growth in order to protect the females, as well as to compete for them.

In general, the CL *vs* CW relationship shows isometric growth, lacking changes during ontogeny, as recorded for different brachyuran crabs [*Eriphia gonagra* (Fabricius, 1781), Góes & Fransozo, 1997; *Goniopsis cruentata* (Latreille, 1803), Cobo & Fransozo, 1998; *Sesarma rectum* Randall, 1840, Mantelatto & Fransozo, 1999b; *Panopeus austrobesus* Willians, 1983, Negreiros-Fransozo & Fransozo, 2003 and *Menippe nodifrons* Stimpson, 1859, Bertini *et al.*, 2007]. However, such relationship showed negative allometry for both sexes in this study. A different pattern of isometry was also recorded for *A. schmitti* by Fumis *et al.* (2007), which observed a negative allome-

Table 4. Some brachyuran species (Xanthoidea) allometric coefficients along the Brazilian coast. CW: carapace width; CPL: cheliped propodus length; CPH: cheliped propodus height; GL: gonopod length; AW: abdomen width; A: allometric level; isometry; + positive allometry; - negative allometry; JM: juvenile males; AM: adult males; TM: total number of males; JF: juvenile females; AF: adult females; TF: total number of females.

Species	Group	CPL	A	CPH	A	GL	A	AW	A
Eurytium limosum (Say, 1818)	JM					1.705	+		
(cf. Guimarães & Negreiros-Fransozo, 2002)	AM					0.905	-		
	TM	1.094	+	1.148	+				
	TF	1.029	=	1.037	=			1.24	+
Panopeus austrobesus Willians, 1983	JM	1.040	=	1.09	+	2.14	+		
(cf. Negreiros-Fransozo & Fransozo, 2003)	AM	1.180	+	1.25	+	1.08	=		
	JF							1.19	+
	AF							1.36	+
	TF	1.080	+	1.14	+				
	T								
Acantholobulus schmitti (Rathbun, 1930)	JM	1.239	+	1.402	+	0.836	-		
as *Hexapanopeus schmitti*	AM	0.979	=	0.855	=	1.228	+		
(cf. Fumis *et al.*, 2007)	JF	1.009	=					1.448	+
	AF	1.177	+					1.291	+
	TF			1,09	+				
Hexapanopeus paulensis Rathbun, 1930	JM	1.056	+	1.158	+	0.943	=		
(present study)	AM	1.123	+	1.23	+	0.704	-		
	TM	1.124	+	1.211	+	0.937	-		
	JF	1.012	=	1.06	=			1.235	+
	AF	1.049	+	1.086	+			1.127	+
	TF	1.054	+	1.11	+			1.547	+

try for juvenile males and females, isometry for adult males, and positive allometry for adult females. According to the authors, changes in the shape of the carapace might be related to a better accommodation of the gonads after the individuals reached sexual maturity, which also might be related to the results obtained in the present study for the same relationship (CL *vs* CW).

Both length and height of cheliped propodus showed positive allometry for males and females of *H. paulensis* with no distinction between juvenile and adult stages. Thus, these dimensions are not adequate descriptors of the morphological sexual maturity of *H. paulensis*. Similar results were obtained for other species of the same superfamily by Fumis *et al.* (2007) for *A. schmitti*, and for the eriphid species *E. gonagra* and *M. nodifrons* investigated by Góes & Fransozo (1997) and Bertini *et al.* (2007), respectively. However, the cheliped propodus reveals great importance during the life cycle of *H. paulensis*. Comparing the current results of relative growth to those of other Xanthoidea species (Table 4), the dimensions of the cheliped propodus do not exhibit negative allometry. According to Hartnoll (1974), this body structure demonstrates reproductive functions for crabs, being used during courtship in order to maximize mating as well as during feeding, protection against predators, and territorial competition. In the present study, the GL *vs* CW relationship was the most suitable to distinguish juveniles and adults, indicating that GL is the best variable for the determination of morphological sexual maturity of *H. paulensis* males.

The isometry and the negative allometry observed during juvenile and adult phases, respectively, reveals that when males reach maturity the gonopod is developed enough to ensure reproductive success, favoring mating of males with females of different sizes (Hartnoll, 1974, 1982). So, adult males can allocate energy intake in other functions, such as the search and protection of females during mating, defense of territory, and somatic growth (Hartnoll, 1974, 2006). Similar results were also observed for the xanthid crab *E. limosum* by Guimarães & Negreiros-Fransozo (2002) and for the eriphid crab *M. nodifrons* by Bertini *et al.* (2007).

Considering the relationship of AW *vs* CW, the positive allometric growth observed for both juvenile and adult females is also significant. Most crabs belonging to the infraorder Brachyura show a distinct sexual dimorphism in the abdomen, being wider in females compared to males of the same species. According to Hartnoll (1982), the pronounced positive allometric growth of the abdomen might be an adaptive characteristic for females, showing important reproductive functions such as protecting their eggs during the incubation period. Thus, a wider abdomen provides a larger area to maintain and protect the eggs (Haefner, 1990; Mantelatto & Fransozo, 1994). Interestingly, in the present study the juvenile females showed a positive allometry for the relationship AW *vs* CW, suggesting that such body structure shows differential growth since the juvenile stage. So, when the females reach adult stage, the abdomen will present the necessary morphological characteristics for effective egg incubation. This result is consistent with those recorded for other brachyuran crabs, especially for the xanthoids studied so far (Table 4).

The predominant occurrence of right major cheliped was previously observed in the superfamily Xanthoidea (Negreiros-Fransozo & Fransozo, 2003; Fumis *et al.*, 2007). These same authors obtained a similar relative frequency (%) of individuals showing larger right cheliped propodus as the current study. The difference observed, considering both length and height of the right cheliped propodus, between males and females, being larger in males, also represents a secondary sexual dimorphism. Tsuchida & Fujikura (2000) observed that in some species of brachyuran crabs, the growth pattern of the cheliped propodus might be more related to their feeding and defense behavior than to breeding. Crabs are important predators of mollusks, and according to Negreiros-Fransozo & Fransozo (2003), the high growth rate of the right cheliped propodus might be related to feeding due to the usefulness and effectiveness of this body structure in handling and opening dextral gastropod shells, common in the studied region. This appears to be occurring in *H. paulensis*, but additional studies concerning this subject are needed for a better understanding of the cheliped propodus' functions.

This study was the first investigation on the morphological sexual maturity, relative growth, and heterochely of a *H. paulensis* population on the southeastern coast of Brazil. Future studies focusing on reproduction, population structure, and spatial and temporal distribution will contribute to a better understanding of the biology of this species.

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REFERENCES

Almeida, A.C., C.M. Hiyodo, V.J. Cobo, G. Bertini, V. Fransozo & G.M. Teixeira. 2013. Relative growth, sexual maturity, and breeding season of three species of the genus *Persephona* (Decapoda: Brachyura: Leucosiidae): a comparative study. J. Mar. Biol. Assoc. UK., 93(6): 1581-1591.

Alunno-Bruscia, M.B. & B. Saint-Marie. 1998. Abdomen allometry, ovary development, and growth of female snow crab, *Chionoecetes opilio* (Brachyura, Majidae), in the northwestern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci., 55: 459-477.

Bertini, G., A. Fransozo & M.L. Negreiros-Fransozo. 2010a. Brachyuran soft-bottom assemblage from marine shallow waters in the southeastern Brazilian littoral. Mar. Biodivers., 40: 277-291.

Bertini, G., G.M. Teixeira, V. Fransozo & A. Fransozo. 2010b. Reproductive period and size at the onset of sexual maturity of mottled purse crab, *Persephona mediterranea* (Herbst, 1794) (Brachyura, Leucosioidea) on the southeastern Brazilian coast. Invertebr. Reprod. Dev., 54(1): 7-17.

Bertini, G., A.A. Braga, A. Fransozo, M.O.D.A. Corrêa & F.A.M. Freire. 2007. Relative growth and sexual maturity of the stone crab *Menippe nodifrons* Stimpson, 1859 (Brachyura, Xanthoidea) in southeastern Brazil. Braz. Arch. Biol. Technol., 50(2): 259-267.

Bloch, J.D. & S. Rebach. 1998. Correlates of claw strength in the rock crab *Cancer irroratus* (Decapoda: Brachyura). Crustaceana, 71(4): 468-473.

Branco, J.O. & H.A.A. Fracasso. 2004. Ocorrência e abundância da carcinofauna acompanhante na pesca do camarão sete-barbas *Xiphopenaeus kroyeri* Heller (Crustacea, Decapoda), na Armação do Itapocoroy, Penha, Santa Catarina, Brasil. Rev. Bras. Zool., 21(2): 295-301.

Castiglioni, D.S. & M.L. Negreiros-Fransozo. 2004. Comparative analysis of the relative growth of *Uca rapax* (Smith) (Crustacea, Ocypodidae) from two mangroves in São Paulo, Brazil. Rev. Bras. Zol., 21(1): 137-144.

Cobo, V.J. & A. Fransozo. 1998. Relative growth of *Goniopsis cruentata* (Crustacea, Brachyura, Grapsidae) on the Ubatuba region, São Paulo, Brazil. Iheringia Ser. Zool., 84: 21-28.

Costa, T.M. & M.L. Negreiros-Fransozo. 1998. The reproductive cycle of *Callinectes danae* Smith, 1869 (Decapoda, Portunidae) in the Ubatuba region, Brazil. Crustaceana, 71(6): 615-627.

Fumis, P.B., A. Fransozo, G. Bertini & A.A. Braga. 2007. Morphometry of the crab *Hexapanopeus schmitti* (Decapoda: Xanthoidea) in the northern coast of the State of São Paulo, Brazil. Rev. Biol. Trop., 55(Suppl. 1): 163-170.

Fransozo, A., M.L. Negreiros-Fransozo & G. Bertini. 2002. Morphometric studies of the ghost crab *Ocypode quadrata* (Fabricius, 1787) (Decapoda, Ocypodidae) from Ubatuba, São Paulo, Brazil. In: E. Escobar-Briones & F. Alvarez (eds.). Modern approaches to the study of Crustacea. Kluwer Academic Publishers/ Plenun Publishers, New York, pp. 189-195.

Góes, J.M. & A. Fransozo. 1997. Relative growth of *Eriphia gonagra* (Fabricius, 1781) (Crustacea, Decapoda, Xanthidae) in Ubatuba, State of São Paulo, Brazil. Nauplius, 5(2): 85-98.

Góes, J.M. & A. Fransozo. 1998. Heterochely in *Eriphia gonagra* (Fabricius, 1781) (Crustacea, Decapoda, Xanthidae) of the rocky coast from Praia Grande, Ubatuba (SP), Brazil. Biotemas, 11(1): 71-80.

González-Gurriarán, E. & J. Freire. 1994. Sexual maturity in the velvet swimming crab *Necora puber* (Say, 1818) (Brachyura, Portunidae): morphometric and reproductive analysis. ICES J. Mar. Sci., 51(2): 133-145.

Guimarães, F.J. & M.L. Negreiros-Fransozo. 2002. Sexual maturity of *Eurytium limosum* (Say, 1818) from a subtropical mangrove in Brazil. In: E. Escobar-Briones & F. Alvarez (eds.). Modern approaches to study of Crustacea, Kluwer Academic Publishers/ Plenum Publishers, New York, pp. 157-161.

Haefner Jr., P.G. 1990. Morphometry and size at maturity of *Callinectes ornatus* (Brachyura, Portunidae) in Bermuda. B. Mar. Sci., 46(2): 274-286.

Hartnoll, R.G. 1974. Variation in growth pattern between some secondary sexual characters in crabs (Decapoda: Brachyura). Crustaceana, 27: 131-136.

Hartnoll, R.G. 1978. The determination of relative growth in Crustacea. Crustaceana, 34: 282-292.

Hartnoll, R.G. 1982. Growth. In: D.E. Bliss (ed.). The biology of Crustacea: embryology, morphology and genetics. New York Academic, New York, pp. 11-196.

Hartnoll, R.G. 2006. Reproductive investment in Brachyura. Hydrobiologia, 557(1): 31-40.

Hirose, G.L. & M.L. Negreiros-Fransozo. 2007. Growth phases and differential growth between sexes of *Uca maracoani* Latreille, 1802-1803 (Crustacea, Brachyura, Ocypodidae). Gulf Carib. Res., 19: 43-50.

Hirose, G.L., V. Fransozo, C. Tropea, L.S. López-Greco & M.L. Negreiros-Fransozo. 2012. Comparison of body size, relative growth and size at onset sexual maturity of *Uca uruguayensis* (Crustacea: Decapoda: Ocypodidae) from different latitudes in the south-western Atlantic. J. Mar. Biol. Assoc. UK., 93(3): 781-788.

Huxley, J.S. 1950. Relative growth and form transformation. Proc. R. Soc. London, 137(B): 465-469.

Kaiser, M.J., R.N. Hughes & A.G. Reid. 1990. Chelal morphometry, prey-size selection and aggressive competition in green and red forms of *Carcinus maenas* (L.). J. Exp. Mar. Biol. Ecol., 140: 121-134.

Mantelatto, F.L.M. & A. Fransozo. 1994. Crescimento relativo e dimorfismo sexual em *Hepatus pudibundus* (Herbst, 1785) (Decapoda, Brachyura) no litoral norte paulista. Papéis Avulsos Zool., 39(4): 33-48.

Mantelatto, F.L.M. & A. Fransozo. 1999a. Reproductive biology and moulting cycle of the crab *Callinectes ornatus* (Decapoda, Porunidae) from the Ubatuba region, São Paulo, Brazil. Crustaceana, 72(1): 63-76.

Mantelatto, F.L.M. & A. Fransozo. 1999b. Relative growth of the crab *Sesarma rectum* Randall, 1840 (Decapoda, Brachyura, Grapsidae) from Bertioga, São Paulo, Brazil. Pak. J. Mar. Biol., 5(1): 11-21.

Mantelatto, F.L.M. & A. Fransozo. 2000. Brachyuran community in Ubatuba Bay northern coast of São Paulo State, Brazil. J. Shellfish Res., 19(2): 701-709.

Mantelatto, F.L.M., A. Fransozo & M.L. Negreiros-Fransozo. 1995. Population structure of *Hepatus pudibundus* (Decapoda: Callapidae) in Fortaleza Bay, Brazil. Rev. Biol. Trop., 43(1-3): 265-270.

Melo, G.A.S. 1996. Manual de identificação dos Brachyura (caranguejos e siris) do litoral brasileiro. Plêiade/FAPESP, São Paulo, 604 pp.

Miranda, I. & F.L.M. Mantelatto. 2010. Sexual maturity and relative growth of the porcellanid crab *Petrolisthes armatus* (Gibbes, 1850) from a remnant mangrove area, southern Brazil. Nauplius, 18(1): 87-93.

Negreiros-Fransozo, M.L. & V. Fransozo. 2003. A morphometric study of the mud crab, *Panopeus austrobesus* Willians, 1983 (Decapoda, Brachyura) from a subtropical mangrove in South America. Crustaceana, 76(3): 281-294.

Negreiros-Fransozo, M.L., K.D. Colpo & T.M. Costa. 2003. Allometric growth in the fiddler crab *Uca thayeri* (Brachyura, Ocypodidae) from a subtropical mangrove. J. Crustacean Biol., 23(2): 273-279.

Pinheiro, M.A.A. & A. Fransozo. 1998. Sexual maturity of the speckled swimming crab *Arenaeus cribrarius*

(Lamarck, 1818) (Crustacea, Brachyura, Portunidae) in Ubatuba coast. State of São Paulo, Brazil. Crustaceana, 71(4): 434-452.

Pralon, B.G.N. & M.L. Negreiros-Fransozo. 2008. Relative growth and morphological sexual maturity of *Uca cumulanta* (Crustacea: Decapoda: Ocypodidae) from a tropical Brazilian mangrove population. J. Mar. Biol. Assoc. UK., 88(3): 569-574.

Ruffino, M.L. & J.P. Castello. 1992. Alterações na ictiofauna acompanhante da pesca do camarão-barba-ruça (*Artemesia longinaris*) nas imediações da Barra de Rio Grande, Rio Grande do Sul, Brasil. Nerítica, 7(1-2): 43-55.

Sampedro, M., E. González-Gurriarán, J. Freire & R. Muiño. 1999. Morphometry and sexual maturity in the spider crab *Maja squinado* (Decapoda: Majidae) in Galicia, Spain. J. Crustacean Biol., 19(3): 578-592.

Tsuchida, S. & K. Fujikura. 2000. Heterochely, relative growth and gonopod morphology in the bythograeid crab, *Austinograea williamsi* (Decapoda, Brachyura). J. Crustacean Biol., 20(2): 407-414.

Vazzoler, A.E.A.M. 1996. Biologia da reprodução de peixes teleósteos: teorias e prática. EDUEM, Maringá, 169 pp.

Zar, J.H. 1999. Biostatistical analysis. Prentice-Hall, New Jersey, 915 pp.

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