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, CW₅₀) 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. CW₅₀ 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 este estudio se investigó la talla de primera madurez sexual (ancho del caparazón CW₅₀), 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 CW₅₀ 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 length, 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 (23°32’S, 44°44’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 m².
Morphology and maturity of *Hexapanopeus paulensis*

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 ($\alpha = 0.05$) 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: $y = 1/(1 + e^{-(r(CW-CW_{50}))})$; 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 compare 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.
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 australis* Williams, 1983 by Negreiros-Franzo & 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, 1998; Hartnoll, 2006). So, larger males can efficiently protect females. However, behavioral studies might confirm this information for *H. paulensis*.

Males of *H. paulensis* 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-Franzo (2002), *P. australis* by Negreiros-Franzo & Fransozo (2003), and *Acantholobulus schmidtii* 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

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**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.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Group</th>
<th>n</th>
<th>Power function</th>
<th>$R^2$</th>
<th>$t$ (b=1)</th>
<th>Alometry level</th>
<th>CW_{50} (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CL</td>
<td>JM</td>
<td>152</td>
<td>$CL = 0.878CW^{0.898}$</td>
<td>0.93</td>
<td>5.26</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td>AM</td>
<td>202</td>
<td>$CL = 0.804CW^{0.957}$</td>
<td>0.97</td>
<td>5.47</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td>TF</td>
<td>445</td>
<td>$CL = 0.831CW^{0.928}$</td>
<td>0.98</td>
<td>13.44</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>CPL</td>
<td>TM</td>
<td>347</td>
<td>$CPL = 0.517CW^{1.124}$</td>
<td>0.96</td>
<td>9.65</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td></td>
<td>TF</td>
<td>424</td>
<td>$CPL = 0.563CW^{1.054}$</td>
<td>0.97</td>
<td>6.05</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>CPH</td>
<td>TM</td>
<td>343</td>
<td>$CPH = 0.226CW^{1.211}$</td>
<td>0.91</td>
<td>10.6</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td></td>
<td>TF</td>
<td>421</td>
<td>$CPH = 0.256CW^{1.109}$</td>
<td>0.93</td>
<td>7.42</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>GL</td>
<td>JM</td>
<td>152</td>
<td>$GL = 0.289CW^{0.943}$</td>
<td>0.70</td>
<td>1.12</td>
<td>=</td>
<td>6.7</td>
</tr>
<tr>
<td></td>
<td>AM</td>
<td>203</td>
<td>$GL = 0.505CW^{1.704}$</td>
<td>0.73</td>
<td>10.73</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>AW</td>
<td>JF</td>
<td>187</td>
<td>$AW = 0.16CW^{1.235}$</td>
<td>0.80</td>
<td>5.18</td>
<td>+</td>
<td>6.3</td>
</tr>
<tr>
<td></td>
<td>AF</td>
<td>258</td>
<td>$AW = 0.257CW^{1.127}$</td>
<td>0.82</td>
<td>3.95</td>
<td>+</td>
<td></td>
</tr>
</tbody>
</table>
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).

<table>
<thead>
<tr>
<th>Propodus</th>
<th>Right</th>
<th>Left</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sex</td>
<td>Mín</td>
</tr>
<tr>
<td>Length</td>
<td>M</td>
<td>1.8</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>1.6</td>
</tr>
<tr>
<td>Height</td>
<td>M</td>
<td>0.8</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0.7</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Sex</th>
<th>Larger chela</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Right</td>
<td>Left</td>
</tr>
<tr>
<td>Males</td>
<td>361</td>
<td>83.8</td>
</tr>
<tr>
<td>Females</td>
<td>409</td>
<td>79.3</td>
</tr>
<tr>
<td>Total</td>
<td>770</td>
<td>81.3</td>
</tr>
</tbody>
</table>

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 australbesus Williams, 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-

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

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

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 $AW \div CW$, 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 $AW \div CW$, 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-Franoso & 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-Franoso & 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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