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Relative growth, morphological sexual maturity, heterochely, and handedness in *Panopeus occidentalis* (Brachyura, Panopeidae)

Fernanda Monchelato Santos[a], Régis Augusto Pescinelli[a], João Alberto Farinelli Pantaleão[a,b] and Rogério Caetano Costa[a]

[a]Laboratory of Biology of Marine and Freshwater Shrimp (LABCAM), Faculty of Sciences, Department of Biological Sciences, São Paulo State University (UNESP), São Paulo, Brazil; [b]Department of Environmental Engineering, Federal University of Triângulo Mineiro (UFTM), Uberaba, Brazil

ABSTRACT
Studies on relative growth and sexual maturity are important to understand the reproductive biology of a species. The aims of this study were to determine the relative growth and to estimate the size of *Panopeus occidentalis* at morphological sexual maturity, as well as to confirm whether this species demonstrates heterochely or handedness. Individuals were collected every two months from March 2013 to July 2014 in the intertidal estuarine zone of Cananeia, São Paulo, Brazil. The following measurements were taken: carapace width (CW), carapace length (CL), right and left cheliped propodus length (CPL), right and left cheliped propodus height (CPH), right and left cheliped propodus width (CPW), abdomen width (AW), and first pleopod length (FPL). The morphometric relationship used to estimate the size at morphological sexual maturity were CW *vs*. AW for females and CW *vs*. FPL for males; these comparisons yielded estimated CW values of 15.60 mm and 16.67 mm, respectively. Heterochely was observed but handedness was not present. The species has a major cheliped on one side, but the side is not constant. This study provides the first insights on the relative growth, sexual maturity, heterochely, and handedness on a population of *P. occidentalis* in a conserved area.

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Crustacea; allometry; development; heterochely; reproduction

Introduction

Studies of relative growth in crustaceans are of great interest because growth in this group is marked by ontogenetic differentiation during the development of body structures (Hartnoll 1978; Vaninni and Gherardi 1988; Dalabona et al. 2005). The body structures of brachyuran crabs grow in different proportions during ontogenetic development, producing morphological differences between juvenile and adult stages (Hartnoll 1978; Vaninni and Gherardi 1988; Dalabona et al. 2005). This phenomenon is called relative growth (Hartnoll 1978) and can be an effective tool for determining morphological sexual maturity and describing different growth proportions in males and females, which in turn provides important information for population biology (Fernández-Vergaz et al. 2000; McLay and Brink 2009).

Heterochely, the difference between the size and morphology of the right and left chelipeds, is common in the Pleocyemata (Góes and Fransozo 1998; Scalici et al. 2008), and may result in handedness (major cheliped always occurring on the same side). The presence of handedness should be evaluated prior to relative growth analysis, and involves the dimensions of the cheliped in species that exhibit heterochely (Davanso et al. 2016). Differences in cheliped development and functionality in crustaceans generate great interest among researchers because these differences may be related to the diverse functions that the two chelipeds exert in food acquisition, courtship display, or territorial defense (Schafer 1954; Vermeij 1977; Lee 1995; Palmer 1996; Mariappan et al. 2000). According to Lee (1995), foraging behavior, agonistic interactions, and sexual selection may explain cheliped dimorphism.

Crabs in the family Panopeidae Ortmann, 1893 are commonly found in intertidal regions and may also inhabit hypersaline lagoons and freshwater ecosystems (Schubart et al. 2000). Panopeid crabs play an important role in the food chain as consumers of oysters, barnacles, and sponges (Guida 1976). *Panopeus occidentalis* Saussure, 1857 is distributed in the western Atlantic, the east coast of the United States, Central America, the Antilles, northern

CONTACT Rogério Caetano Costa rccosta@fc.unesp.br

South America, and Brazil (from the states of Pernambuco to Rio Grande do Sul) (Melo 1996). This specie is found in areas ranging from estuarine intertidal regions among algae and mangrove roots, burrows in sand, under rocks and gravel, at depths down to 20 meters (Calado and Sousa 2003).

Little information is available on the biology, ecology, and morphology of *P. occidentalis*, especially with respect to body growth patterns and the size at which this species reaches morphological sexual maturity. The only research on this species addressed its biology (Oliveira 1940); in other cases, this species was only cited in studies on biodiversity, faunal composition of certain regions, phylogeny, distribution, and morphological comparisons with other species (Martin et al. 1984; Martin and Abele 1986; Martin 1988; Schubart et al. 2000; Bertini et al. 2004; Braga et al. 2005; Araújo et al. 2014; Thoma et al. 2014).

Considering the importance of body structure development in the reproductive biology of Brachyura (for example, in estimating the size of morphological sexual maturity or investigating behaviors such as defense against predators or territorial disputes), the aim of this study is to determine patterns of relative growth and estimate size at morphological sexual maturity in *P. occidentalis* and to confirm whether this species demonstrates heterochely and handedness.

Materials and methods

Study area

The Cananeia estuarine complex (25°S, 48°W) off the southeastern coast of Brazil is known for its conservation and is considered one of the most productive estuaries in the world (Diegues 1987; Cunha-Lignon et al. 2011). The intertidal sampling area (600 m^2) in this study (25,804′11.2′′S 48,803′08.9′′W, Figure 1) comprised of sediment containing a mixture of sand, mud, and rocks which are randomly dispersed throughout the site.

Sampling and data analysis

Crabs were collected every two months from March 2013 to July 2014 at low tide along with collections of a project on the biodiversity of Crustacea in the region. The crabs were sampled every two months to obtain organisms from all seasons of the year without impacting the population. The sampling area was divided into three smaller areas perpendicular to the water line, and these smaller areas were further divided into three 1 m^2 units set equidistant 10 m from each other, totaling nine sample units (methodology adapted from Pescinelli et al. 2017). The specimens were collected manually by two researchers with a catch effort of 2 h per person. Upon collection, the crabs were

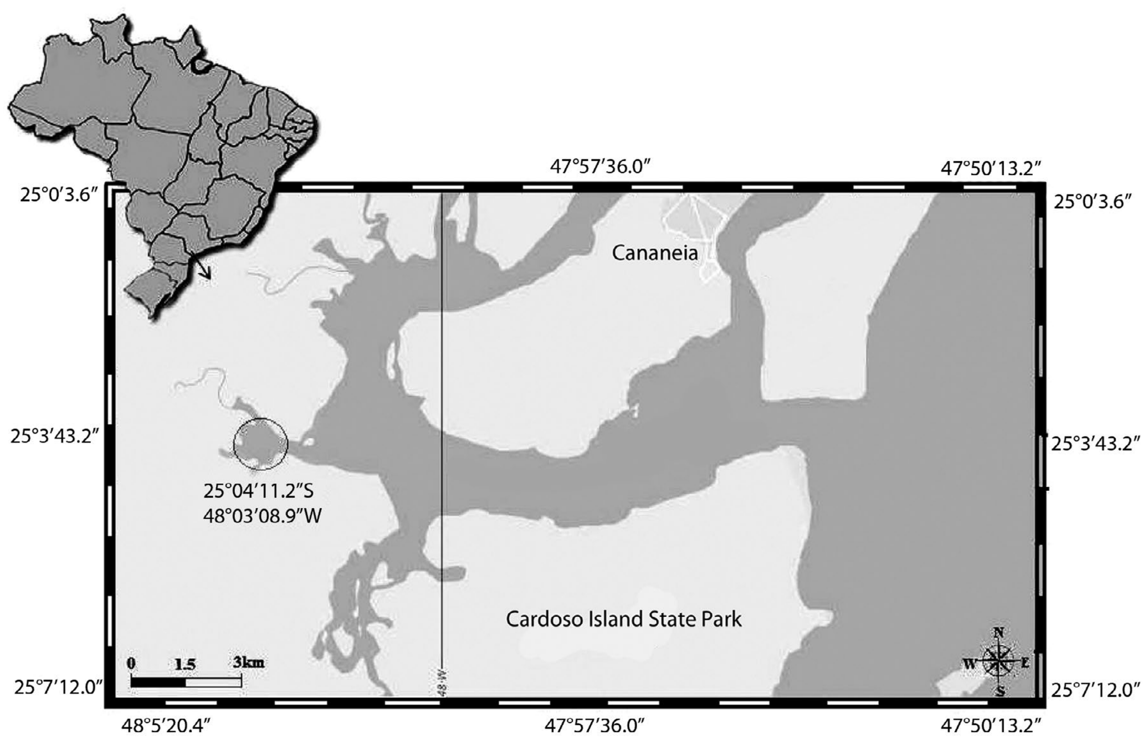

Figure 1. Location of the study area, water represented by dark gray in the map of intertidal estuarine zone of Cananéia, São Paulo, southeastern Brazil.
Note: Adapted from Pescinelli et al. 2017.

maintained in coolers with crushed ice before transport to the laboratory, where measurements were recorded.

All individuals were identified to species according to Melo (1996); each crab was sexed according to abdominal morphology and the presence of paired gonopods in males (Pinheiro and Taddei 2005). The following measurements were taken using a 0.01 mm caliper: carapace width (CW), carapace length (CL), right and left cheliped propodus length (CPL), right and left cheliped propodus height (CPH), right and left cheliped propodus width (CPW), abdomen width (AW), and first pleopod length (FPL).

Tests for homoscedasticity (Levene test) and normality (Shapiro-Wilk test) were performed using software SIGMAPLOT 12.0. A Mann-Whitney test was used to analyze the differences in mean CW between males and females ($\alpha = 0.05$).

Relative growth of the crabs was analyzed using morphometric data, using the allometric equation $y = ax^b$ in the linearized version ($\log y = \log a + b \log x$), where y is the dependent variable or the dimension studied, x is the independent variable, b is the allometric coefficient of the studied structure, and a is the point at which the straight line intersects the ordinate axis (Hartnoll 1982).

A non-hierarchical K-means clustering analysis was performed to separate individuals into the groups of interest (juveniles and adults). This method distributes data into a previously determined number of groups defined by an iterative process that minimizes the variance within groups and maximizes the variance among them. The result of the classification (k-means) was refined by applying a discriminant analysis using software PAST 3.16 (Paleontological Statistics 3.16). This statistical methodology was based on the work of Sampedro et al. (1999).

The allometric condition b for each structure was analyzed ($b = 1$: isometry; $b < 1$: negative allometry; $b > 1$: positive allometry) using a Student's t-test (Ho: $b = 1$, $\alpha = 5\%$) (Zar 1996). After the size categories were determined, the log-transformed data for each category were submitted to a covariance analysis (ANCOVA) to test the angular and linear coefficients between juveniles and adults for each relationship, and to verify whether the groups found could be represented by different linear equations using STATISTICA 7.0 (StatSoft, 2004) (Zar 1996).

Table 1. *Panopeus occidentalis* Saussure, 1857. Descriptive statistics for each sex (CW = carapace width, SD = standard deviation).

Sex	*N*	CW mm (min–max)	Mean ± SD
Female	120	5.1–33.04	17.16 ± 6.69
Female with embryos	5	15.6–24.95	21.48 ± 3.50
Male	141	6.62–40.78	17.69 ± 7.21
Total	266	5.1–40.78	17.37 ± 6.97

Heterochely and the difference between the length of the right and left chelipeds (CPLr and CPLl) were tested using t-tests ($p < 0.05$). We also used the allometry index (AI) proposed by Van Valen (1962) for all measured dimensions, represented by the equation ($AI = -L/R + L$), where R and L indicate the measure of the dimensions of the right and left cheliped respectively. The results of this AI analysis for length, height, and width were plotted on dispersion graphs. The existence of handedness was analyzed according to the graphs and the morphology of the right and left chelipeds. The methodology used to test for heterochely and handedness was based on the studies by Sanvicente-Añorve and Hermoso-Salazar (2011) and Davanso et al. (2016).

Results

During the study period, 269 crabs were captured, including 120 females, 5 females with embryos, 141 males, and 3 undifferentiated juveniles (which were excluded from the statistical analyses). The size ranges recorded for each demographic class are shown in Table 1. The carapace width of females and males ranged from 5.10 to 33.04 (mean 17.16 ± 6.69) and 6.62 to 40.78 mm (mean 17.69 ± 7.21), respectively. There was no statistically significant difference in mean CW between females and males (Mann-Whitney test, $p > 0.73$).

The relationship between carapace width and abdomen width (CW *vs.* AW) showed positive allometric growth for both juvenile females and adults (Table 2). The same type of growth was observed in the relationship between CW *vs*. FPL in juvenile males; comparison of CW *vs*. AW resulted in isometry, while in adults negative allometric growth was seen (Table 2).

The relationships of cheliped length, height, and width (CPL, CPH, and CPW) were isometric in the juvenile phase and positive allometric in the adult phase in both sexes (Table 2). According to ANCOVA, the following relationships showed a significant difference ($p < 0.05$): CW *vs.* FPL in males, CW *vs.* AW in females, CW *vs.* CPL, CW *vs.* CPH, and CW *vs*. CPW in both sexes (Table 3).

The relationships that best showed changes in the allometric coefficient between the demographic categories (juveniles and adults) were CW *vs*. AW for females and CW *vs*. FPL for males (ANCOVA, $p < 0.05$). The estimated values of morphological sexual maturity for females and males were 15.60 mm and 16.67 mm CW, respectively (Figure 2).

The difference between the sizes of the right and left cheliped was not significant in either sex ($p < 0.05$; $t = 11{,}480.5$ and $p = 0.361$ for females, $t = 11{,}265.0$ and $p = 0.671$ for males). However, the plotted graph resulting

Table 2. *Panopeus occidentalis* Saussure, 1857. Regression analyses of morphometric data.

Relationship	Sex/Phase	N	A	b	r^2	t (b = 1)	p	Allometry
CW *vs.* AW	JF	60	0.851	1.172	0.782	2.117	<0.001	+
	AF	65	1.042	1.359	0.909	6.639	<0.001	+
	JM	69	0.839	0.995	0.840	0.094	>0.001	0
	AM	71	0.729	0.903	0.848	2.112	<0.001	–
CW *vs.* CPL	JF	56	0.210	1.000	0.956	0.000	>0.001	0
	AF	53	0.368	1.140	0.971	5.109	<0.001	+
	JM	60	0.239	1.032	0.965	1.253	>0.001	0
	AM	63	0.461	1.214	0.971	7.972	<0.001	+
CW *vs.* CPH	JF	49	0.552	1.043	0.898	0.839	>0.001	0
	AF	60	0.967	1.245	0.967	8.220	<0.001	+
	JM	62	0.538	1.037	0.926	0.977	>0.001	0
	AM	59	0.741	1.225	0.928	4.997	<0.001	+
CW *vs.* CPW	JF	52	0.690	0.979	0.858	0.374	>0.001	0
	AF	57	0.921	1.192	0.955	5.543	<0.001	+
	JM	61	0.713	1.019	0.912	0.462	>0.001	0
	AM	61	0.972	1.238	0.931	5.429	<0.001	+
CW *vs.* FPL	JM	67	1.418	1.716	0.813	7.026	<0.001	+
	AM	71	0.636	1.092	0.936	2.675	<0.001	+

Notes: CL = carapace length; CW = carapace width; CPH = cheliped propodus height; CPL = cheliped propodus length; CPW = cheliped propodus width; AW = abdomen width; FPL = first pleopod length; JM = juvenile males, AM = adult males, JF = juvenile females, AF = adult females, + = positive allometry, 0 = isometry, – = negative allometry.

Table 3. *Panopeus occidentalis* Saussure, 1857. Results of the covariance analysis (ANCOVA).

Relationship	Group	Par. (Log)	F	p
CW *vs.* AW	JF *vs.* AF	*a*	5.022	<0.05
		b	2.916	>0.05
	JM *vs.* AM	*a*	0.034	>0.05
		b	1.685	>0.05
CW *vs.* CPL	JF *vs.*AF	*a*	–	–
		b	9.279	<0.05
	JM *vs.* AM	*a*	–	–
		b	23.800	<0.05
LC *vs.* CPH	JF *vs.* AF	*a*	–	–
		b	10.927	<0.05
	JM *vs.* AM	*a*	–	–
		b	0.002	<0.05
LC *vs.* CPW	JF *vs.* AF	*a*	–	–
		b	8.503	<0.05
	JM *vs.* AM	*a*	–	–
		b	12.836	<0.05
LC *vs.* FPL	JM *vs.* AM	*a*	–	–
		b	33.249	< 0.05

Notes: CL = carapace length;CW = carapace width; CPH = cheliped propodus height; CPL = cheliped propodus length; CPW = cheliped propodus width; AW = abdomen width; FPL = first pleopod length; JM = juvenile males, AM = adult males, JF = juvenile females, AF = adult females, + = positive allometry, 0 = isometry, – = negative allometry.

from the asymmetry index of each analyzed dimension verified the presence of heterochely for females and males without the occurrence of handedness; this species exhibits one major cheliped in relation to the other, without constancy in relation to side (Figure 3). In females, 69.72% of the individuals had the major cheliped on the right side, which was similar to the results for the males, with 63.93% of individuals also having the major cheliped on the right.

Discussion

The significant differences recorded for the relative growth of the abdomen and chelipeds for females and males, respectively, as well as for the first pleopod between juvenile and adult males are consistent with the general relative growth pattern proposed for brachyuran crabs (Hartnoll 1974; Castiglioni and Negreiros-Fransozo 2004). The results for the abdomen width (AW), length of the first pleopod (FPL), length, height and width of the major cheliped (CPL, CPH, and CPW) showed important structures to identify the relative growth patterns of *P. occidentalis* and to determine the size at which it reaches morphological sexual maturity. Differences were observed in the relative growth of body structures during development of both sexes, indicating differences in energy investment between the sexes during ontogenetic development.

The positive allometric growth observed between carapace width (CW) and abdomen width (AW) in both juvenile and adult phases in females indicates a high investment in abdominal growth during development. The abdomen in brachyuran females is related to reproduction, since it is used for egg incubation (Hartnoll 1974; Castiglioni and Negreiros-Fransozo 2004; Pescinelli et al. 2014; Carvalho-Batista et al. 2015). A larger abdomen increases reproductive efficiency (Castiglioni and Negreiros-Fransozo 2004; Cobo and Alves 2009; Pescinelli et al. 2014; Carvalho-Batista et al. 2015), because it provides a wider area for egg protection, improving incubation conditions (Mantelatto and Fransozo 1994).

For males, a greater investment in the growth of the first pleopod was demonstrated by the positive allometry in juveniles and adults for the relationship between this structure and the width of the carapace (CW *vs.* FPL).

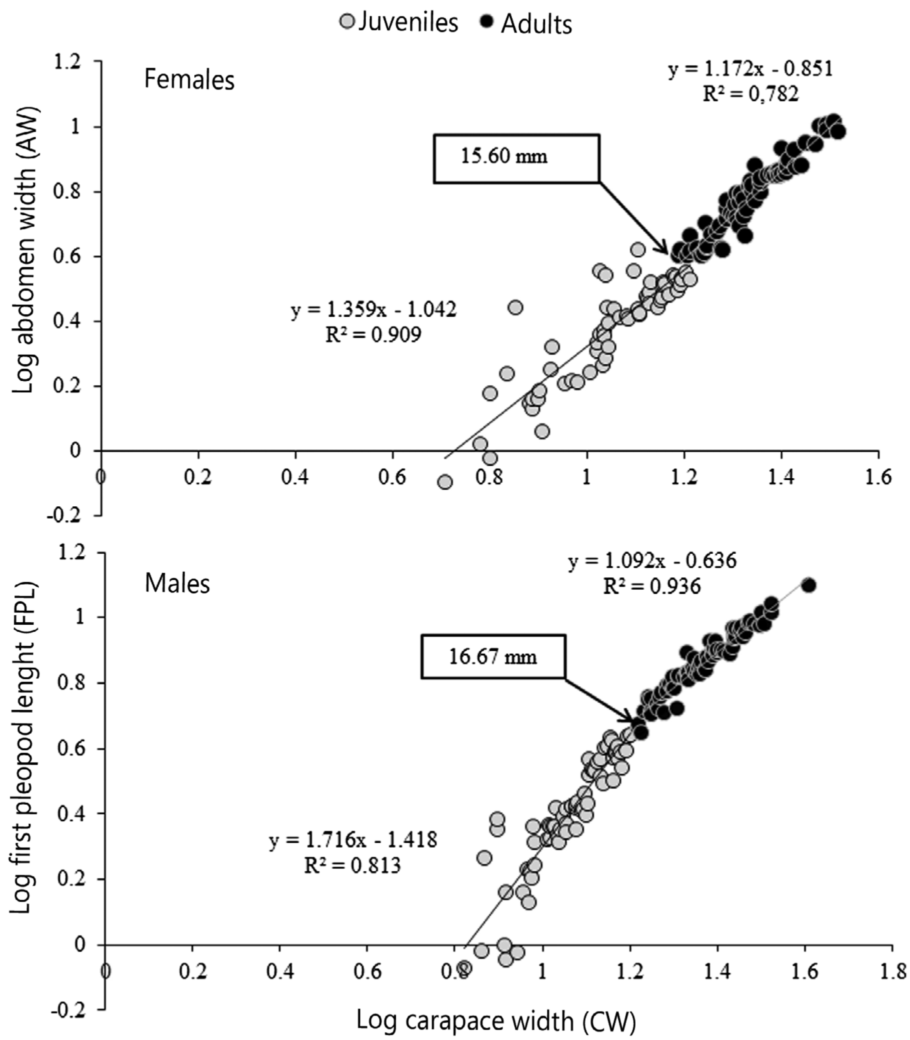

Figure 2. *Panopeus occidentalis* Saussure, 1857. Estimated size at morphological sexual maturity for males and females.
Notes: The estimated size refers to the smallest individual after the inflection point of the equations for juveniles and adults.

In male brachyurans the junction of the first and second pleopods constitute the gonopodium, an organ used to transfer spermatophores to the female during reproduction (Hartnoll 1978). Carvalho-Batista et al. (2015) found a significant difference in relation to gonopodium length (or FPL) and carapace width in *Panopeus americanus* Saussure, 1857, as we found in *P. occidentalis*. Consequently, the gonopodium is an external morphological structure that may indicate the size at which the males of the species reach morphological sexual maturity.

The size of the cheliped in crabs is related to agonistic behavior (disputes over females and territory, for example), defense against predators, and the construction of burrows (Hartnoll 1974; Dalabona et al. 2005). The results we found for cheliped height in the males showed the passage of isometric growth in juveniles to positive allometry in adults. As a result, the change in the allometric coefficient may reveal changes in the type of growth of this structure after the puberty molt (Tsuchida and Fujikura 2000). Similar results were found for the females of *P. occidentalis* for cheliped size, which also changed from isometric to positive allometric growth after morphological sexual maturity. The cheliped in females is related to protection of the eggs and early juveniles stored in the incubation chamber against predators (Daniels 2001). This structure is consequently very important during the reproductive period.

A comparison between CW and AW showed a similar type of relative growth as that found for *Acantholobulus schmitti* Rathbun, 1930 (Silva et al. 2014), and also followed the pattern found for *Panopeus austrobesus* Williams, 1983 (Negreiros-Fransozo and Fransozo 2003), which belong to the same family and genus, respectively. According to Hartnoll (1982), the allometric coefficient of abdomen width increases after the puberty molt because of the increased energy investment in the growth of this

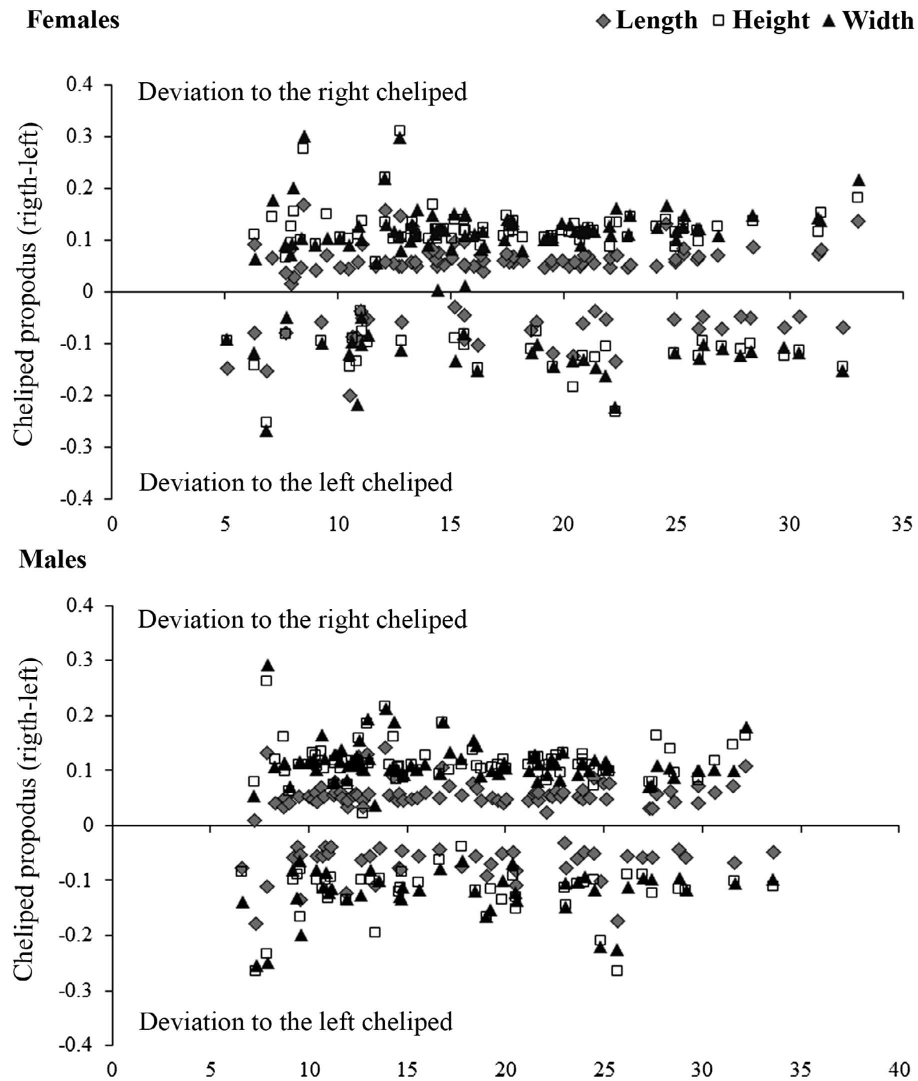

Figure 3. *Panopeus occidentalis* Saussure, 1857. Heterochely and handedness observed from the asymmetry index (AI) between of right and left cheliped propodus dimensions (length, height and width).
Notes: The X axis corresponds to carapace width (CW) of each specimen.

structure. This was observed in the present study, and in other studies on *Trichodactylus fluviatilis* Latreille, 1828 (Lima et al. 2013), *A. schmitti* (Frigotto et al. 2013), and *P. americanus* (Carvalho-Batista et al. 2015).

Panopeus occidentalis males were larger than females when they reached morphological sexual maturity (16.67 mm and 15.60 mm, respectively). This fact may be related to the reproductive strategy of the species. In some cases, males protect females during and after copulation, so larger males may be able to perform this function more efficiently (Guimarães and Negreiros-Fransozo 2002). According to Haefner and Spaargaren (1993), female crabs may exhibit slower growth than males, especially after sexual maturity because the energy is directed to reproduction such as in the development of gonads and egg production.

Heterochely was observed for *P. occidentalis*, although the *t*-test showed no significant difference between cheliped size ($p < 0.05$). One possible explanation for this result is the lack of handedness; since both sides may be larger, the average of the larger cheliped was similar and influenced the test result.

In crabs of the genus *Cancer*, when one cheliped is injured, the other grows to a greater proportion to make up for the lost one; this promotes heterochely, but handedness is not present (Smith and Palmer 1994). It is possible that this same process of loss and regeneration of one of the chelipeds occurs in *P. occidentalis*. In Brachyura the smaller cheliped is generally used to cut and manipulate food (Govind and Blundon 1985; Pynn 1998), while the larger one is used during territorial fights and display behavior (Levington et al. 1995). As a result, injury to or loss of the major cheliped is common, and is followed by compensatory growth of the uninjured cheliped. However, the proportion of right-handed and left-handed individuals predicted and observed under normal conditions in populations with this type of cheliped development is usually 1:1 (Smith and Palmer 1994).

The results obtained in the present study are extremely important to better understand the relative growth patterns of *P. occidentalis*, since no studies have examined these patterns with regards to the reproductive biology of the species. In addition, our results provide morphological information on a population in a conserved area (Cananeia, São Paulo, Brazil), and will be useful for comparisons with subsequent research conducted in locations with greater human interference.

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Disclosure statement

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ORCID

Régis Augusto Pescinelli http://orcid.org/0000-0003-4109-3859
João Alberto Farinelli Pantaleão http://orcid.org/0000-0003-0067-5465
Rogério Caetano Costa http://orcid.org/0000-0002-1342-7340

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