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ORIGINAL ARTICLE

Use of pleopod morphology to determine sexual dimorphism and maturity in hermit crabs: *Isocheles sawayai* as a model

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Abstract In the Anomura, studies on growth patterns are infrequent, possibly because the heterogeneity of the group, especially in terms of morphology, makes it difficult to construct generalized growth models. Particularly hermit crabs are an interesting group to evaluate aspects of growth, because of their unique body. *Isocheles sawayai,* a hermit crab found only in the western Atlantic Ocean, poorly known with respect to its sexual dimorphism and maturity, was investigated here based on morphometry. Monthly collections (July 2001 through June 2003) were made from a shrimp fishing boat in the Caraguatatuba region on the northern coast of the state of São Paulo, Brazil. The specimens were measured and weighed, and had their sex checked. Throughout the sampling period, 374 specimens of *I. sawayai* were collected (11.23% nonovigerous females, 6.69% ovigerous females, 79.41% males and 2.67% intersexes). The size at which morphological sexual maturity was reached by both sexes ranged from 4.0 to 4.3 mm shield length, according to the relative growth and the size of the smallest ovigerous female. Sexual dimorphism was shown by males, which were significantly larger than females, and by differences in growth pattern between the sexes, especially for relationships that involved the pleopods, which is related to their different functions in males and females. The present study is one of the first to use pleopod morphometry to determine sexual maturity and dimorphism in hermit crabs, especially for species with intersexuality such as *I. sawayai*.

Keywords Anomura · Diogenidae · Relative growth

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Introduction

In spite of the undisputed importance and prominence of the Anomura in the evolutionary context (Cunningham et al. 1992) and the large number of described species, relatively little research has been done on hermit crabs, particularly with respect to sexual maturity and dimorphism; this may be attributed to their lack of commercial value. Studies on the growth patterns of anomurans are even less frequent, possibly because of the heterogeneity of the group, which makes it difficult to construct generalized growth models (Hartnoll 1985). However, studies undertaken during the last two decades have revealed important features of growth in different families and/or genera (Biagi and Mantelatto 2006), signaling and encouraging the continuity of such investigations. Studies of relative growth provide important information on the establishment of morphological sexual maturity and sexual dimorphism, and also supply useful information for systematics (Wenner et al. 1974; Mantelatto and Martinelli 2001).

Some investigators have used the size of the smallest ovigerous female to determine the size at which the population reaches morphological sexual maturity (Bertini and

Fransozo 1999, 2000; Fransozo et al. 2003). However, environmental changes and genetic factors can cause great variability in a population, and bring about changes in metabolism, growth, reproduction and behavior (Sastry 1983). Considering this potential variability, if possible other features should be used to help establish the size interval at which the puberty molt occurs.

In many species, there are significant differences in behavior and metabolism between males and females, or in the size, shape and growth of individuals or organs, which is termed sexual dimorphism. These between-sex differences can be related to behavior patterns, and are greater when the sexes do not play equal ecological roles (Hartnoll 1974). Such differences are potentially important, both in determining the nature of population regulation within a species, and in determining the nature of interactions between species (Abrams 1988). Sexual dimorphism has been extensively reported for many hermit crabs; almost all studies have focused on the propodus chelipeds and/or these appendages in relation to resource use (Fotheringham 1976; Bertness 1980; Abrams 1988; Manjón-Cabeza and García Raso 1996; Gherardi and Nardone 1997; Fransozo and Mantelatto 1998; Mantelatto and Sousa 2000; Garcia and Mantelatto 2001; Branco et al. 2002; Martinelli et al. 2002; Litulo 2005; Mantelatto et al. 2005). Recently, we demonstrated that the pleopods may be an important aspect to be considered in such studies (Biagi and Mantelatto 2006).

Isocheles sawayai Forest and Saint-Laurent 1968, endemic to the western Atlantic, is the only species of the five members of the genus that is widely distributed along the Brazilian coast, and was also recently reported from Venezuela (Nucci and Melo 2000; Galindo et al. 2008). Recent efforts to improve knowledge of the hermit crabs of Brazilian waters have revealed important and relevant aspects of *I. sawayai* in terms of biogeography, systematics (Mantelatto et al. 2006), biology and reproduction (Fantucci et al. 2007, 2008; Mantelatto et al. 2009), such as intersexuality. We used this species as a model to evaluate morphological parameters as instruments to establish the size at which sexual maturity occurs, and to evaluate the presence of sexual dimorphism.

Methods

The hermit crabs were collected monthly from July 2001 through June 2003, in the Caraguatatuba region (23°36′08″–23°47′07″S; 45°20′03″–45°08′30″W), southern coast of São Paulo, Brazil, from a fishing boat equipped with two double-rig trawl nets (20-mm mesh size in the net body and 15 mm in the cod end). The region is sheltered against the direct action of ocean waves by São Sebastião Island (Ilhabela), and is influenced by the São Sebastião Channel, resulting in moderate hydrodynamics and homogeneous morphology of the bottom (Barros et al. 1997). The region is influenced by three different water masses, the South Atlantic Central Water (SACW) with low temperature and salinity, Tropical Water (TW) with high temperature and salinity, and Coastal Water (CW) with high temperature and low salinity, in different periods of the year (Castro-Filho et al. 1987). Each trawl was made parallel to the coast, at 5-m depth (Fantucci et al., in preparation), and lasted approximately 30 min, at a mean speed of two knots.

After collection, the specimens were sorted, frozen, and transported to the laboratory. There, they were removed from their shells, counted, and weighed (wet weight, WW) (0.01 g), and the sex was checked according to the gonopore position and pleopod morphology. For the evaluation of sexual dimorphism, intersexes were grouped with males because the analysis of external primary (gonopores) and secondary (pleopods) sexual characters revealed a greater similarity between males and intersexes, than between intersexes and females, suggesting that intersex individuals are functional males (Fantucci et al. 2007).

Individuals were measured for cephalothoracic shield length and width (SL and SW) and left cheliped propodus length and width (CPL and CPW), using a caliper (0.01 mm). As described by Biagi and Mantelatto (2006), the second pleopod protopod, endopod and exopod length (PPL, EPL and XPL) were measured by means of a stereomicroscope equipped with a camera lucida. Hermit crabs with damaged or absent appendages were excluded from analyses of relationships that involved the dimensions of these appendages.

Sizes of males and females were compared by Student's t test for parametric values and by Mann–Whitney for non-parametric ones, to check sexual dimorphism. The relationships between size and weight were analyzed by regression and dispersion diagrams of the empirical points, using the power function $y = ax^b$ (Zar 1996), and linear equation ($\ln y = \ln a + b \ln x$) (y SW, CPL, CPW, WW, PPL, EPL, XPL; $\times$ SL; a intercept; b slope). Departures from isometry (H_0, $b = 1$; H_1, $b \neq 1$ for size dimensions, and H_0, $b = 3$; H_1, $b \neq 3$ for weight) (Huxley and Teissier 1936; Hartnoll 1982; Biagi and Mantelatto 2006) were tested using the Student's t test on the slope values obtained (Zar 1996).

Data were analyzed statistically at the level of significance $P < 0.05$ (Zar 1996), and by the program Sigma Stat for Windows, Version 2.03. Voucher specimens were deposited in the Crustacean Collection of the Department of Biology, Faculty of Philosophy, Science and Letters of Ribeirão Preto (FFCLRP), University of São Paulo (USP), Brazil (CCDB/FFCLRP/USP, accession numbers 1687–1691).

Results

During the sampling period, 374 specimens of *I. sawayai* were collected: 297 males (79.41%), 42 nonovigerous females (11.23%), 25 ovigerous females (6.69%) and 10 intersexes (2.67%). The smallest and the largest individuals were both males, and measured 3.4 and 9.8 mm SL. The smallest ovigerous female measured 4.3 mm SL (Table 1).

A clear break in the growth pattern of CPL and XPL occurred, for both sexes, between 4.0 and 4.3 mm SL (Fig. 1). Thus, morphological sexual maturity was estimated for the interval from 4.0 to 4.3 mm SL. Few recruits or juveniles (smaller than this estimated size interval) were collected (four males and two females only).

This population of *I. sawayai* showed pronounced sexual dimorphism. Males were significantly larger than females ($P < 0.05$), except for the pleopods (Table 1). Sexes

Table 1 *Isocheles sawayai*: dimensions for each group of interest

Dimensions	*N*	Sex	Minimum	Maximum	x ± SD	*T*	*P*
SL	307	M	3.4	9.8	7.0 ± 1.2	5,752.0	≤0.001
	67	F	3.8	8.0	5.6 ± 0.9		
SW	307	M	3.4	10.5	7.4 ± 1.2	−9.218*	≤0.001
	67	F	4.1	8.4	6.0 ± 0.9		
CPL	306	M	4.3	12.3	8.8 ± 1.5	4,223.0	≤0.001
	66	F	5.1	9.0	6.5 ± 0.8		
CPW	306	M	2.9	8.4	5.9 ± 1.0	5,434.0	≤0.001
	66	F	3.3	6.4	4.7 ± 0.7		
WW	307	M	0.30	10.53	3.55 ± 1.84	4,624.0	≤0.001
	67	F	0.39	4.19	1.42 ± 0.67		
PPL	305	M	0.5	3.3	1.6 ± 0.4	14,952.0	0.002
	66	F	0.7	3.7	1.9 ± 0.6		
EPL	305	M	2.1	9.6	5.4 ± 1.3	10,738.5	0.028
	66	F	2.4	8.2	4.9 ± 1.4		
XPL	266	M	0.3	2.7	0.8 ± 0.3	19,869.0	≤0.001
	66	F	1.1	5.5	2.9 ± 0.9		

M males, *F* females, *SL* cephalothoracic shield length (mm), *SW* cephalothoracic shield width (mm), *CPL* left cheliped propodus length (mm), *CPW* left cheliped propodus width (mm), *WW* hermit crab wet weight (g), *PPL* second pleopod protopod length (mm), *EPL* second pleopod endopod length (mm), *XPL* second pleopod exopod length (mm), *N* number of individuals, *x* mean, *SD* standard deviation, *T* Mann–Whitney value

* *t* test value

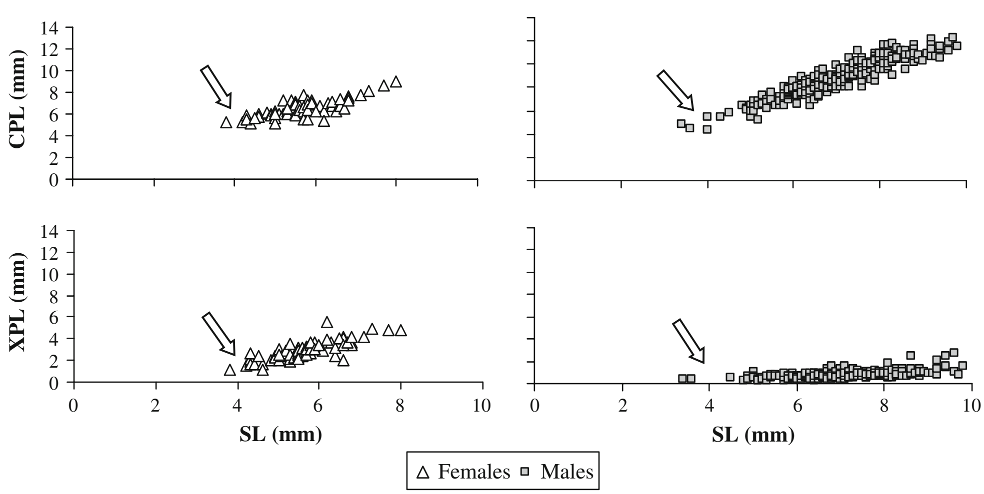

Fig. 1 *Isocheles sawayai*. Relative growth of left cheliped propodus length (CPL) and second pleopod exopod length (XPL) in relation to cephalothoracic shield length (SL). *Arrows* indicate the interval at which the discontinuity of points suggests the size at which sexual maturity occurs

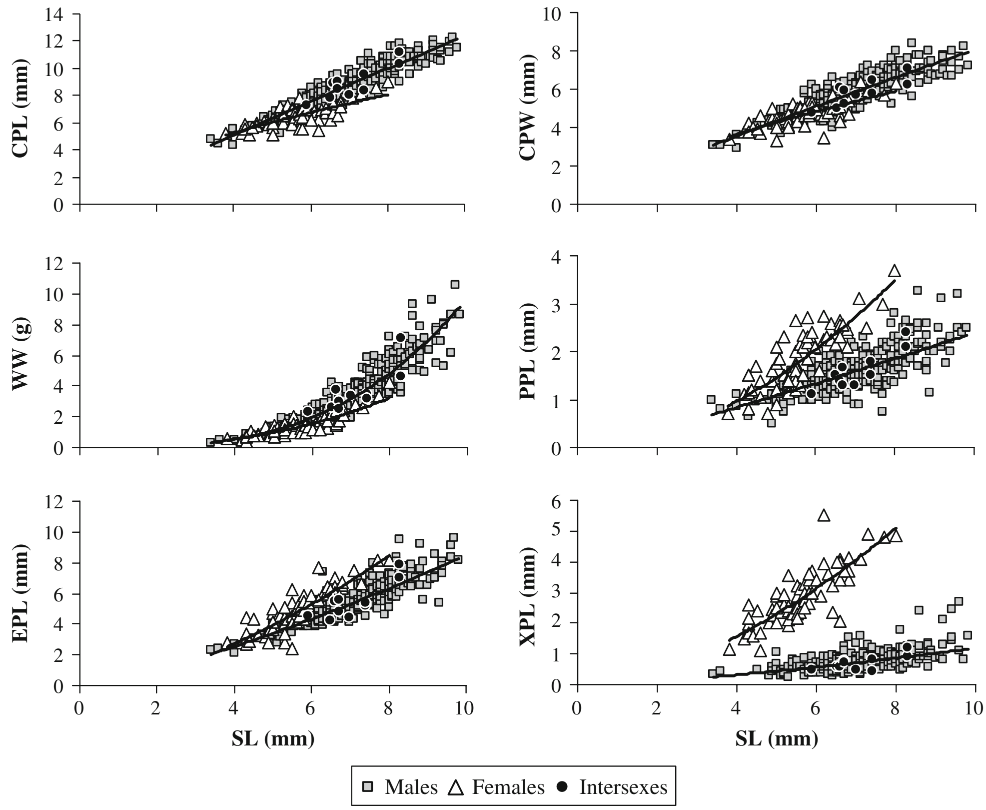

Fig. 2 *Isocheles sawayai*. Diagrams of dispersion of empirical points for relationships that showed sexual dimorphism: *SL* cephalothoracic shield length, *CPL* left cheliped propodus length, *CPW* left cheliped propodus width, *WW* hermit crab weight, *PPL* second pleopod protopod length, *EPL* second pleopod endopod length, *XPL* second pleopod exopod length

differed in growth patterns, which was best evidenced by relationships that involved the left cheliped propodus length (CPL), weight (WW) and the second pleopod (PPL, EPL and XPL) (Fig. 2; Table 2).

Regarding the intersex individuals, the relationships of pleopod morphometry corroborated the decision to group them with the males (Fig. 2).

Discussion

Sexual dimorphism was evidenced by differences in growth pattern between sexes, especially for relationships that involved the pleopods, which is related to the different function of these appendages between the sexes. The present study is one of the first to use pleopod morphometry to determine sexual maturity and dimorphism in hermit crabs, especially for species with intersexuality such as *I. sawayai*.

When morphometric parameters are utilized to describe growth in crustaceans, it is important to analyze these parameters in individuals of different sizes in order to distinguish adults and juveniles (Hartnoll 1982). However, studies on hermit crabs have demonstrated that juveniles may not be common in samples, as reported for *Paguristes tortugae* Schmitt, 1933, *Pagurus brevidactylus* (Stimpson, 1859), *Dardanus deformis* (H. Milne-Edwards, 1836) and *Pagurus exilis* (Benedict, 1892) (Mantelatto and Sousa 2000; Mantelatto et al. 2005; Litulo 2005; Mantelatto et al. 2007, respectively), even in studies conducted for several months, as the present study. Collection of small numbers of juveniles could be a consequence of sampling failure, or could reflect the existence of different spatial distributions in juveniles and adults. Different distributions may be related to juvenile migration, because hermit crabs migrate looking for better food supplies, shells of adequate size, and protection against predators (Fotheringham 1975).

Although the absence or the low number of juveniles in collections may not allow the adults and juveniles' growth patterns and their differences to be estimated, other indicators can be used to characterize the transition between the juvenile and adult phases. According to Hartnoll (1982), the morphological and physiological maturity may not be in synchrony. However, in the population studied here, the estimated size for morphological maturity in the relative growth (dispersion of empirical points) was corroborated by the size of the smallest ovigerous female found.

Isocheles sawayai showed sexual dimorphism in size, as do the majority of hermit crab species that have been

Table 2 *Isocheles sawayai*: regression equations for each sex

Relationship	*N*	Sex	Power function $y = ax^b$	Linear equation $\ln y = \ln a + b \ln x$	*r*	A	$b \neq 1$
SL × SW	307	M	$SW = 1.220SL^{0.924}$	$\ln SW = 0.199 + 0.924 \ln SL$	0.951	–	4.42*
	67	F	$SW = 1.2587SL^{0.900}$	$\ln SW = 0.230 + 0.900 \ln SL$	0.928	–	2.23*
SL × CPL	306	M	$CPL = 1.286SL^{0.985}$	$\ln CPL = 0.252 + 0.985 \ln SL$	0.935	=	0.701
	66	F	$CPL = 2.234SL^{0.617}$	$\ln CPL = 0.804 + 0.617 \ln SL$	0.760	–	5.08*
SL × CPW	306	M	$CPW = 1.022SL^{0.898}$	$\ln CPW = 0.0219 + 0.898 \ln SL$	0.881	–	3.70*
	66	F	$CPW = 1.414SL^{0.687}$	$\ln CPW = 0.347 + 0.687 \ln SL$	0.749	–	4.12*
SL × WW	307	M	$WW = 0.007SL^{3.148}$	$\ln WW = -4.971 + 3.148 \ln SL$	0.946	+	2.39[a]
	67	F	$WW = 0.016SL^{2.547}$	$\ln WW = -4.123 + 2.547 \ln SL$	0.864	–	2.46[a]
SL × PPL	305	M	$PPL = 0.165SL^{1.163}$	$\ln PPL = -1.801 + 1.163 \ln SL$	0.731	+	2.62*
	66	F	$PPL = 0.072SL^{1.863}$	$\ln PPL = -2.626 + 1.863 \ln SL$	0.801	+	4.96*
SL × EPL	305	M	$EPL = 0.410SL^{1.314}$	$\ln EPL = -0.891 + 1.314 \ln SL$	0.903	+	8.72*
	66	F	$EPL = 0.289SL^{1.623}$	$\ln EPL = -1.242 + 1.623 \ln SL$	0.845	+	4.83*
SL × XPL	266	M	$XPL = 0.0456SL^{1.412}$	$\ln XPL = -3.139 + 1.438 \ln SL$	0.623	+	3.95*
	66	F	$XPL = 0.151SL^{1.693}$	$\ln XPL = -1.891 + 1.693 \ln SL$	0.807	+	4.47*

M males, *F* females, *SL* cephalothoracic shield length (mm), *SW* cephalothoracic shield width (mm), *CPL* left cheliped propodus length (mm), *CPW* left cheliped propodus width (mm), *WW* hermit crab wet weight (g), *PPL* second pleopod protopod length (mm), *EPL* second pleopod endopod length (mm), *XPL* second pleopod exopod length (mm), *N* number of individuals, *r* correlation coefficient, *A* allometry

* Significant correlation, $P < 0.05$

[a] $b \neq 3$

studied. The larger size attained by males has been attributed to differential energy consumption, because as males do not produce eggs they can channel their energy into somatic growth. Being larger may also be advantageous because it influences sexual selection, with larger males being more successful in fights for mating pairs, causes a differential shell occupation pattern between sexes, reducing competition for adequate shells, and causes different food-supply use and risk of death, in case of differential habitat occupation between sexes (Abrams 1988).

This population of *I. sawayai* was also sexually dimorphic in relative growth. The chelar propodi of males and females grew at different rates. This may be attributed to the males using this appendage in territorial defense, intra- and inter-specific fights, the shell selection process, and also in mating behavior (Hazlett 1966), explaining the adaptive significance of the larger chelae in males. Males not only grew more, but also showed different rates of weight gain than did females (positive allometry vs. negative allometry, respectively). This can be explained by the females diverting energy from somatic growth, and channeling it into egg production and care (Bertness 1981; Abrams 1988; Mantelatto and Martinelli 2001; Fransozo et al. 2003).

The pleopods of hermit crabs were shown to be important features that must be investigated in relative growth studies, because of their known changes throughout development and functionality in reproduction (Biagi and Mantelatto 2006). However, this aspect has been little studied in hermit crabs.

Members of the genus *Isocheles* have unpaired biramous pleopods on the second to fifth abdominal somites (Forest and Saint-Laurent 1968). These pleopods have different morphologies and functions in each sex. Therefore, the growth pattern of these structures is very useful for determining sexual dimorphism. The pleopods of female decapod crustaceans are robust and setose, which allows the eggs to adhere to them (Ingle 1993). As shown for *Paguristes erythrops* Holthuis, 1959 (Biagi and Mantelatto 2006), the female pleopods of *I. sawayai* grew more (positive allometry for all relationships) than those of the males; this can be explained by their reproductive function in mature females, because in males, these structures function only to move the water inside the shell, contributing to cleaning and aeration.

In addition to demonstrating the importance of using other morphometric parameters to determine sexual dimorphism and sexual maturity, the present study corroborated the use of pleopods as an important tool to identify the sex, especially in species of hermit crabs with intersex individuals, such as *I. sawayai*. Furthermore, although relative growth is considered a trustworthy tool to determine size at sexual maturity, mainly for hermit crab species with clear cheliped dimorphism, such as the diogenids (Fransozo et al. 2003), the present study showed that there are other features, such as the pleopods, that allow this kind of analysis.

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