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Original Article

Allometry and sexual dimorphism of the Neotropical freshwater anomuran *Aegla marginata* Bond-Buckup & Buckup, 1994 (Crustacea, Anomura, Aeglidae)

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Abstract

This study analyzes ontogenetic allometry in *Aegla marginata* Bond-Buckup & Buckup, 1994, a freshwater crustacean, in order to evaluate the growth pattern and the presence of sexual dimorphism, using a multivariate approach. The specimens were sampled from streams in Intervales State Park, São Paulo State, Brazil. For each specimen, we measured the following structures: carapace length and width, chelae height and length, and abdomen length. Allometry was evaluated using Jolicoeur's multivariate allometric coefficient. Our results showed that for females, ABL (abdomen length) and LCH (left chelae heigh) presented positive allometry; LCL (left chelae length) and RCH (right chelae heigh) isometry; and CL (carapace length), CW (carapace width), and RCL (right chelae length) negative allometry. For males, RCH, LCH, and LCL presented positive allometry; RCL (right chelae length) isometry; and CL, CW, and ABL negative allometry. In addition, sexual dimorphism was amplified with body size.

Key words

Multivariate allometric coefficient, relative growth, energy investment, sexual selection.

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Introduction

Sexual dimorphism of body size and shape is recurrent among animals and can be the result of different selective pressures on males and females (Eberhard, 2008). The different reproductive roles and investments of males and females directly lead to morphological differentiation in traits associated with reproduction. As males and females may use different strategies to achieve high fitness levels, particularly body traits involved in courtship rituals, fighting among males, mate pairing, sperm transfer, and fecundity should be subject to differential selection between the sexes (Clutton-Brock, 2007; Eberhard, 2008). In this context, allometric studies can help understand how and which traits are under differential pressures.

Allometry describes scaling relationships between traits or processes (Shingleton, 2010), and can be divided into three types: ontogenetic allometry (when the relative size of a trait changes with the size of individuals of different age groups); static allometry (when the relative size of a trait changes with the size of individuals of the same species in the same developmental stage); and phylogenetic or evolutionary allometry (when the relative size of a trait changes with the size of individuals of different species in the same developmental stage) (Shingleton, 2010). These three types of allometry may explain part of the morphological variability observed in individuals of different species, ages, and sexes.

It is expected that a structure that provides a reproductive advantage in males or females would be sexual selected, and, as a result, it may be disproportionally sized in larger individuals, leading to sexual dimorphism (Green, 2000; Kodric-Brown *et al.*, 2006). Part of this sexual dimorphism can arise during growth; therefore, identifying the main traits with ontogenetic allometric growth in males and females can provide relevant information for understanding which traits are being selected to give advantages for reproduction. On the other hand, despite the common positive allometry of secondary sexual characteristics (Kondric-Brown *et al.*, 2006), it is important to note that this may not be a universal pattern and could also be the result of a bias caused by the special interest of researchers for exaggerated traits (see discussion in Bonduriansky, 2007). Certainly, it is necessary to increase the number of theoretical and empirical studies to gain a better understanding of this issue.

Crustaceans can be good models for allometric studies due their high variability, such as the presence of morphotypes (Bueno and Shimizu, 2009; Thiel *et al.*, 2010; Lezcano *et al.*, 2016) and/or sexual dimorphism (Trevisan and Santos, 2012; Davanso *et al.*, 2016). The genus *Aegla* Leach, 1820 corresponds to a taxon of decapods represented by 83 species and is exclusively a freshwater inhabitant living in creeks, rivers, lakes, and caves (Santos *et al.*, 2014; Santos *et al.*, 2015; Moraes *et al.*, 2016) in the southern part of South America (Bond-Buckup and Buckup, 1994).

In *Aegla*, males and females have different life history, investment and behavioral strategies. Males may invest energy in claws for feeding and as weapons: post-copula, the males defend the females to ensure paternity (Almerão *et al.*, 2010), thus a larger male could have more success during this process. As for females, during the reproductive period, ovigerous females present cryptic behavior and stay in sheltered areas (Cohen *et al.*, 2011; da Silva *et al.*, 2016). In addition, as a key feature that allowed aeglids to conquer the freshwater environment, females invest energy to produce eggs with more yolk, allowing the offspring to hatch in the juvenile form (Vogt, 2013). Moreover, females can be overly aggressive during the reproductive period, as seen in other freshwater decapods (Figler *et al.*, 1995). Thus, as described above, these differences could lead to a sexual dimorphism in which larger males will be selected (sexual selection), and females who invest energy towards reproduction, as well as to claws for survivorship will be selected (natural selection).

Aegla marginata Bond-Buckup and Buckup, 1994 is a Brazilian aeglid species distributed from the south of the State of São Paulo (approx. 24°12′S 48°03′W) to the northeast region of the State of Santa Catarina (approx. 26°18′S 48°50′W) (Bond-Buckup and Buckup, 1994). Given that morphological and functional changes occur during growth, understanding the principles of ontogenetic variation can help explain the final form of the adult. In this context, our study aims to identify the particular structures that are subject to different selective pressures. In contrast with previous work by Trevisan *et al.* (2012), who found sexual dimorphism in adults (static allometry), our work focuses on ontogenetic allometry of *A. marginata* and how this allometry leads to sexual dimorphism.

Material and Methods

Sampling and identification

Individuals of *A. marginata* were sampled monthly from May 1999 to September 2000 in four streams of the same basin in Intervales State Park (ISP). Additionally, we conducted sporadic sampling in 2006 in the same four streams within ISP: 1) Roda d´Água stream (24º16'18"S 48º25'29"W), 2) Mirante stream (24º16'39"S 48º24'50"W), 3) Bocaina stream (24º16'14"S 48º27'23"W), and 4) Água Comprida stream (24º17'38"S 48º25'04"W). In each stream, the specimens were collected in the rocky substrate using a Surber sampler (0.25 mm mesh size).

The individuals were fixed and conserved in 80% ethanol and sexed according to Bond-Buckup and Buckup (1994): males were identified by the absence of pleopods and the presence of the gonopore on the coxa of the fifth pair of pereiopods (Martin and Abele, 1988; Bueno and Shimizu, 2008); females were identified by the presence of pleopods during development in the juvenile forms, which are well developed in the adults, and also by the position of the gonopore on the coxa of the third pair of pereiopods.

Measurements

A total of 78 females (carapace length 3.7–16.6 mm) and 146 males (carapace length 3.8–18.9 mm) were measured. The specimens were measured using a 0.01 mm precision digital caliper, and small individuals were measured with a ZEISS Stemi V6 stereomicroscope. We measured the following morphological structures: carapace length (CL) and carapace width (CW), length of the right (RCL) and left chelae (LCL), height of the right (RCH) and left chelae (LCH), and abdomen length (ABL) (length of the somites 5 and 6, including the telson) (Fig. 1) (Colpo *et al.*, 2005; Teodósio and Masunari, 2009; Trevisan and Santos, 2012).

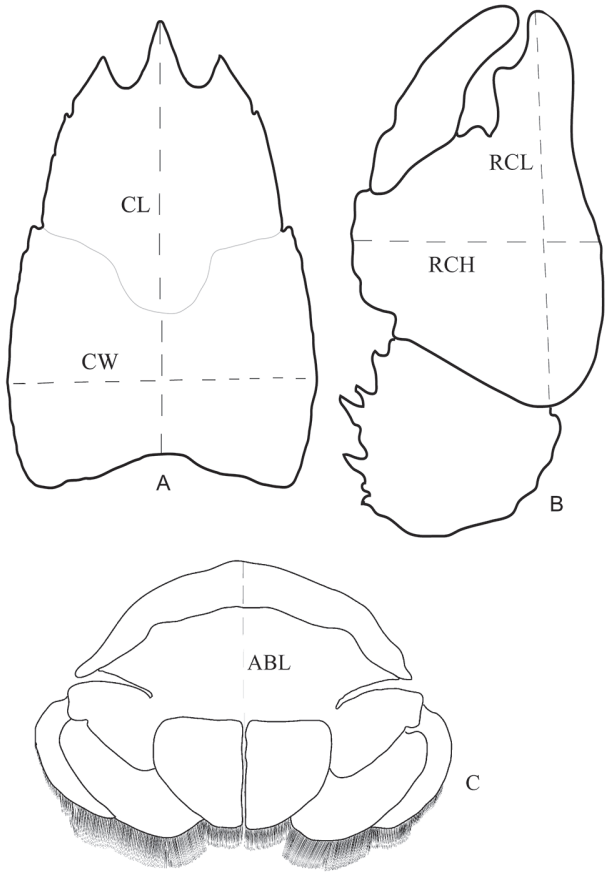

Figure 1. A: Carapace of *Aegla marginata* showing its measures. CL stands for Carapace Length; and CW stands for Carapace Width. B: Right cheliped of *A. marginata* showing the measures of chelipeds. RCL stands for Right Cheliped Length; and RCH stands for Right Cheliped Height. For the left chelae we used the same measures. C: Abdomen of *A. marginata* showing its measures. ABL stands for Abdomen Length.

Allometry and sexual dimorphism

Prior to analysis, morphometric variables were log-transformed and both sexes were evaluated separately. Allometry was evaluated using Jolicoeur's multivariate allometric coefficient (Jolicoeur, 1963; Peres-Neto, 1995). In this method, a principal components analysis (PCA) was performed for log-transformed variables based on variance-covariance criteria (Manly, 1994; Legendre and Legendre, 1998). The first axis of the PCA contains most of the variability, and as all coefficients (loadings) of the morphometric variables for this axis were positive, it can be interpreted as a generalized body size (Peres-Neto, 1995; Monteiro and Soares, 1997). Jolicoeur's multivariate allometric coefficient is the coefficient (loading) of each morphometric variable for first axis of PCA divided by $1/(\sqrt{N})$, where N is the number of variables.

According to Jolicoeur's method, 1) when the allometric coefficient is larger than one, the structure is growing at a higher rate than the generalized body size (positive allometry); 2) when the allometric coefficient is equal to one, the structure is growing at the same rate as the generalized body size (isometry); and 3) when the allometric coefficient is smaller than one, the structure is growing at a lower rate than the

generalized body size (negative allometry) (Peres-Neto, 1995). The confidence intervals of the multivariate allometric coefficient estimates were obtained using the bootstrap method (Klingenberg, 1996; Paciencia et al., 2012). The procedure was performed using Past Software (Hammer *et al.*, 2001).

Sexual dimorphism was tested using the Hotelling test (Manly, 1994). In order to test whether dimorphism increases with body size, a canonical discriminant analysis was performed to obtain the scores of individuals of the two sexes in a discriminant axis. Afterwards, an ANCOVA based on these scores was used to test the differences between sexes and the interaction with the generalized body size (first PCA axis).

Results

The first PCA axis, which represented the generalized size, explained 96.29% of the variability. Adult males and females were morphometrically different, as demonstrated by Hotelling's test (T2 = 93.742; F = 13.03; $p < 0.05$). Results of the ANCOVA showed an interaction between the morphometric differentiation of the sexes (first axis of discriminant function) and the generalized body size (first PCA axis). This result showed that the morphometric differences between the sexes increased with increasing body size (Tab. 1, Fig. 2).

Females showed the following growth pattern: positive allometry for ABL and LCH, isometry for LCL and RCH, and negative allometry for the measurements of CL, CW, and RCL (Fig. 3). The males presented positive allometry for RCH, LCH, and LCL, isometry for RCL, and negative allometry for CL, CW, and ABL (Fig. 3).

Table 1. *Aegla marginata*. ANCOVA of the scores for males and females individuals (sex), using the generalized body size (first axis of the principal component analysis, PC1) as a covariate. The scores were obtained using canonical discriminant analysis. SS: Sum of Squares; DF: Degrees of Freedom; MS: Mean Squares.

Effect	SS	DF	MS	F	p
Sex	115.23	1	115.23	74.88	<0.05
PC1	64.24	1	64.24	41.75	<0.05
Sex*PC1	42.03	1	42.03	27.31	<0.05

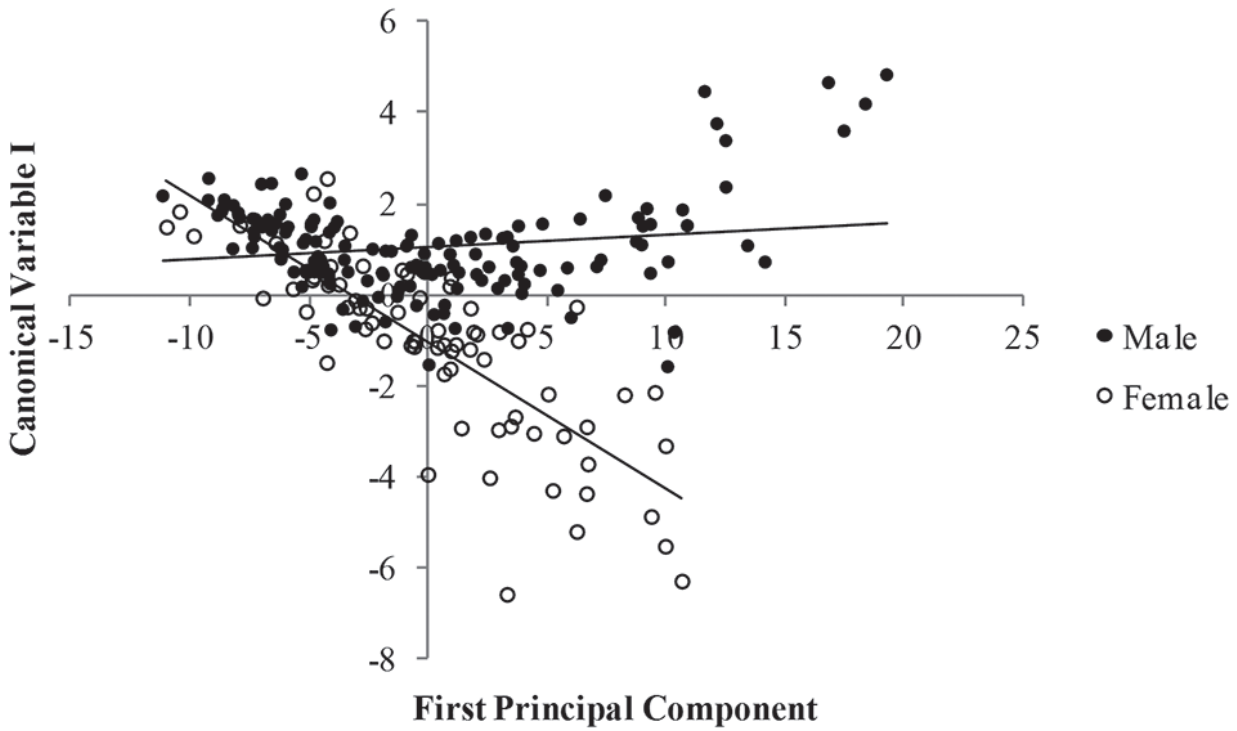

Figure 2. Relationship between the scores and the generalized size (first principal component) in individuals of both sexes of *Aegla marginata*. The scores were obtained using canonical discriminant analysis.

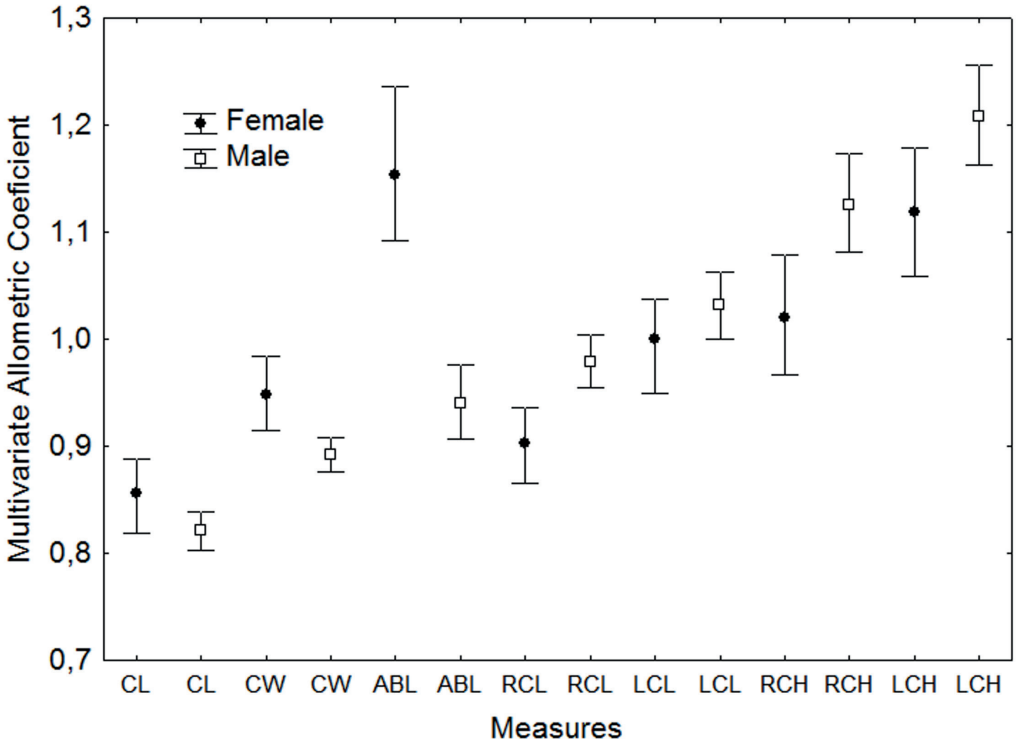

Figure 3. Multivariate allometric coefficient calculated for females and males of the *Aegla marginata*. Carapace Length (CL), Carapace Width (CW), Abdomen Length (ABL), Length of the Right (RCL) or Left (LCL), Cheliped, Height of the Right (RCH) or the Left (LCH) Cheliped.

Discussion

Our results showed that sexual dimorphism of *A. marginata* increases with body size. In the early stages of development, males and females were more similar than in the late stages. Our results suggest that during growth, the animals shift the allocation of energy to structures related to reproduction (Anderson *et al.*, 2013) and, since males and females have different reproductive roles (Fairbairn, 1997), this leads to sexual dimorphism of adults as seen in *A. marginata*. Thus, in adult stages, the individuals of the two sexes are morphometrically different, with males being larger than females.

The males particularly invest in increasing the size of the chelipeds, which provides advantages during fights with other males, and possibly during courtship and mating. For example, Palaoro *et al.* (2014) found that the size of the cheliped (claw height), when combined with body size, was a good predictor of contest outcome between males. For males of *A. marginata,* the cheliped is a pronounced secondary sexual characteristic, which presents high positive allometry for left chelae measurements. This result, combined with behavior data (Palaoro *et al.*, 2013; 2014), allows us to propose that the chelae is undergoing positive selection and that its size gives advantages for inter-male fighting. In other words, larger individuals with disproportionally larger chelipeds may have advantages during fights.

In addition to contests, in *Aegla,* males can use the chelipeds in a variety of other ways. For example, in *Aegla platensis* Schmitt, 1942, the cheliped is used in agonistic displays towards the female in the pre-copulatory phase (Almerão *et al.*, 2010). Also during mating, the male uses the cheliped to hold and raise the female in a supine position, then rotate her approximately 90° and place himself under her for mating (Almerão *et al.*, 2010). During the post-copulatory phase, the male guards the female, which means that a male with a pronounced cheliped can also monopolize and ensure paternity more easily (Almerão *et al.*, 2010). Therefore, both investment in pre- and post-copula could have led to the positive allometry found for the cheliped measures of *A. marginata* males, which provide advantages over other males in reproductive aspects.

Besides reproduction, heterochely can be linked to feeding behavior (Abby-Kalio and Warner, 1989;

Tsuchida and Fujikura, 2000). Although the allometric coefficient was higher for male chelipeds, it is important to note that females also showed positive allometry for the length of the left cheliped. Considering that the male cheliped is being sexually selected, female heterochely could be linked to feeding behavior, since other decapods have larger chelae to crush and/or cut different types of food (Abby-Kalio and Warner, 1989; Tsuchida and Fujikura 2000), thus this heterochely (which is not as pronounced as males) in females could have been naturally selected, i.e. females with heterochely could obtain better food and present higher survivorship.

The positive allometry of female abdomen length could be related to the expected direct relationship between abdomen size and fecundity (number of eggs) (Gonçalves *et al.*, 2006; Bueno and Shimizu, 2008). In addition, abdomen size may be related to the size of the incubatory chamber that protects the developing embryos and the newly hatched juveniles that stay in the female abdomen for three to four days (López-Greco *et al.*, 2004). This pattern has been observed for *A. marginata* under laboratory conditions (unpublished data). Therefore, females invest energy in increasing the size of the abdomen, which can improve their reproductive efficiency (Hartnoll, 1969; 2001).

In *A. marginata*, the important traits for reproduction, courtship, and agonistic interactions present ontogenetic positive allometry. Behavioral studies in *Aegla* and the ontogenetic positive allometry of sexual traits found in *A. marginata* suggest that these traits can be subject to sexual selection. The results suggest that most of the shape changes during ontogeny of *Aegla* lead to improved reproductive efficiency at sexual maturity, resulting in sexual dimorphism of the adults.

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