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Relative growth and morphological sexual maturity of the caridean shrimp *Nematopalaemon schmitti* (Decapoda: Caridea: Palaemonidae) in an upwelling region in the Western Atlantic*

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ABSTRACT

In crustaceans, successful reproductive processes, such as the transition from juvenile to adult, exhibit important morphological changes that can be detected by analyzing relative growth. This study describes the relative growth of body structures in *Nematopalaemon schmitti* and its secondary sexual characteristics, and also estimates the morphological sexual maturity of this species in a region influenced by upwelling. The carapace length (CL), second pleuron length (PIL), cheliped carpus length (CaL), cheliped propodus length (PrL) and the length of appendix masculina (AML) of the shrimp were measured. The relationships that best demonstrated the changes in allometric coefficient between demographic categories were AML vs. CL for males, and PIL vs. CL for females. The estimated CL for morphological sexual maturity in males was 8.51 mm and 9.30 in females. Our results showed the appendix masculine and the second pleuron were secondary sexual characteristics that play roles in reaching the morphological sexual maturity necessary for reproductive success and to assure the life cycle of this species.

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Introduction

The family Palaemonidae is one of the most representative and successful members of the infraorder Caridea (Ferreira et al. 2010). Different developmental and reproductive patterns have evolved in this family, and it consequently has a wide geographical distribution; its representatives occupy diverse habitats including fresh, estuarine, and marine waters (Holthuis 1952). The palaemonid shrimp *Nematopalaemon schmitti* (Holthuis, 1950) is distributed in the marine and estuarine waters of the western Atlantic from Venezuela to Brazil (Holthuis 1980; Ferreira et al. 2010), and plays an important ecological role within the trophic web of soft-bottom environments (Fransozo et al. 2009).

Only a few studies have been conducted on *N. schmitti*, including its ecological distribution (Fransozo et al. 2009; Almeida et al. 2012; Herrera et al. 2017), population structure (Almeida et al. 2011), and fecundity and reproductive investment (Perreira et al. 2017). These studies were focused on southeastern Brazil, mainly off Ubatuba on the northern coast of São Paulo. The literature contains no studies on the size at which *N. schmitti* reaches

morphological sexual maturity, or the growth pattern of its body structures. Consequently, this present study presents work on this subject. Such studies are important, particularly for locations near upwelling, as they could reveal differences in species population dynamics, which is essential information for fishery managers.

Some phases during life are crucial to the successful reproduction of a species, such as the transition from juvenile to adult. When they reach sexual maturity, many decapod species exhibit essential and significant morphological changes, some of which can be detected by relative growth analysis (Petriella and Boschi 1997; Ahamed and Ohtomi 2014). This methodology has been used to estimate the size at morphological sexual maturity in a number of studies, such as Hartnoll (1982, 1985), Castiglioni and Negreiros-Fransozo (2003), Hirose et al. (2012), Pantaleão et al. (2012), Herrera et al. (2013), Pescinelli et al. (2014, 2015), Teodoro et al. (2014), and Davanso et al. (2016).

This study describes the relative growth of the body structures of *N. schmitti*, and explores whether secondary sexual characteristics exist that could be used to explain and estimate the morphological sexual maturity

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of this species when encountered in a region influenced by upwelling near its northern distribution limit in the Western Atlantic Ocean (Macaé, Rio de Janeiro, Brazil).

Materials and methods

Study area and sampling

The Macaé region is located off the northern coast of Rio de Janeiro state (22°33'S, 41°78'W) within the limits of the Santana Archipelago environmental protection area, near the influence of the Cabo Frio region (Figure 1). The Cabo Frio upwelling influences the Macaé region, which is characterized by temperature conditions similar to the Argentinean coast (Sancinetti et al. 2015), and promotes the transport of nutrients (N and P) from lower layers to the photic zone. As a result, upwelling regions are the most productive areas of the ocean (Coelho-Souza et al. 2012). The orientation of the Rio de Janeiro coast, particularly its coastline which changes abruptly in direction from north-south to east-west, shunts coastal water away from the coast and toward the ocean; this favors the intrusion and spread of the South Atlantic Central Water (SACW) (Herrera et al. 2017), which usually has temperatures below 20° C and high nutrient concentrations. The influence of the SACW is more intense in summer, but the Macaé coastal area is strongly influenced by this mass of water throughout the year as a result of the upwelling off Cabo Frio, resulting in low water temperatures (Valentin 1984).

Samples were collected each month in the Macaé region from July 2010 through June 2011. The collection sites were marked with GPS coordinates, and six sites were defined at depths of 5 m (sites 1–3) and 15 m (sites

4–6). The commercial fishing boat used for trawling was equipped with 10 m-long double-rig fishing nets, with a 20 mm mesh size and an 18 mm cod end. Each sampling site was trawled for 30 min at a constant speed of 2.0 knots, covering an area of approximately 18,500 m². After sampling was completed, the shrimp were bagged, stored in coolers with crushed ice, and then transported to the laboratory.

The sex of the shrimp was identified by the presence or absence of the appendix masculina on the endopodite of the second pleopod (Bauer 2004). The following structures were measured using a 0.01 mm digital slide caliper: carapace length (CL), defined as the posterior edge of the ocular orbit to the posterior edge of the carapace, and second pleuron length (PIL), defined as the distance between the median point of the anterior edge of the second abdominal segment to the median point of the posterior edge of the second abdominal segment. With the aid of a stereomicroscope fitted with an ocular micrometer (0.01 mm) the following structures were measured: cheliped carpus length (CaL), from the proximal edge to the posterior edge of the carpus (the region most proximal to the propodus), and cheliped propodus length (PrL), from the proximal edge to the tip of the fixed finger. In the males, the second pleopod was carefully removed and the length of the appendix masculina (AML), the distance between the lowest point of the insertion and the most distal tip of the appendix masculina, was measured on a glass slide using a binocular microscope (Leica, MZ12) with a calibrated ocular micrometer.

Relative growth and determination of morphological sexual maturity

Changes in the growth pattern of the body structures in relation to the independent variable (CL) were verified using relative growth analysis. The data were plotted on dispersion graphs and fitted to the allometric equation $y = ax^b$ (Hartnoll 1974, 1978, 1982), the linearized version of the model ($\log y = \log a + b \times \log x$) in which y is the dimension studied, x the carapace length, b the allometric coefficient of the structure studied, and a the intercept of the curve on the ordinate axis. The value of the allometric constant b was calculated for each biometric relationship, and the null hypothesis ($H_0: b = 1$) was tested with a Student's t -test ($\alpha = 95\%$). The values of the allometric constant correspond to isometric growth ($b = 1$), positive allometry ($b > 1$), or negative allometry ($b < 1$) (Zar 1996).

A non-hierarchical K -means clustering analysis was performed to characterize the morphometric relationships that best showed differences in the growth pattern. This method distributed the data into a previously determined number of groups (juveniles and adults) by an interactive

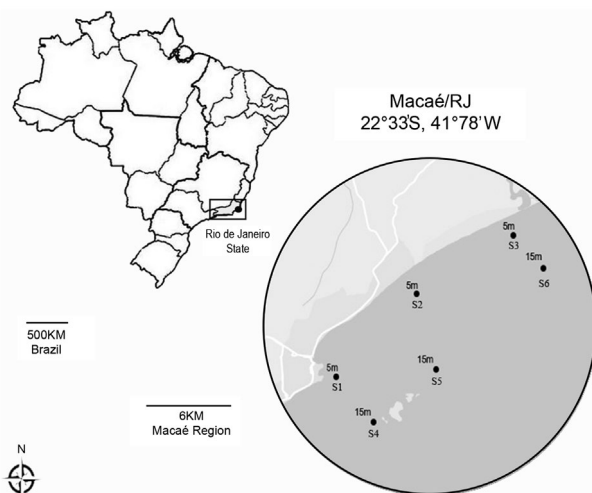


Figure 1. Location of sampling sites off Macaé, Rio de Janeiro state, Brazil.

Note: Sites 1, 2, 3 were located at depths of 5 m and sites 4, 5, 6 at depths of 15 m.

Table 1. *Nematopalaemon schmitti* (Holthuis, 1950). Regression analysis of morphometric data. CL as independent variable (log-transformed data).

Relationship	Sex	N	a	b	r ²	T (b = 1)	p	Allometry
PrL vs. CL	JM	18	-0.019	1.005	0.467	0.022	<0.001	0
	AM	82	0.639	0.332	0.066	4.778	<0.001	-
	JF	24	0.181	0.802	0.395	0.933	<0.001	0
	AF	76	0.548	0.471	0.109	3.390	<0.001	-
CaL vs. CL	JM/AM	100	-0.7013	1.0367	0.581	0.413	<0.001	0
	JF/AF	100	-0.806	1.1748	0.693	2.213	<0.001	+
PIL vs. CL	JM	128	-0.039	0.824	0.489	2.341	<0.001	-
	AM	342	0.202	0.613	0.321	8.007	<0.001	-
	JF	153	-0.296	1.101	0.644	1.522	<0.001	0
	AF	381	-0.158	0.980	0.591	0.468	<0.001	0
AML vs. CL	JM	26	-1.733	1.634	0.816	4.014	<0.001	+
	AM	77	-1.160	0.985	0.654	0.180	<0.001	0

Notes: CL = carapace length, PIL = second pleuron length, CaL = cheliped carpus length, PrL = cheliped propodus length, AML = length of appendix masculine, JM = juvenile males, AM = adult males, JF = juvenile females, AF = adult females, + = positive allometry, 0 = isometry, - = negative allometry.

process that minimizes the variance within groups and maximizes the variance between them. The result of the K-means classification was refined by applying discriminant analysis (DA) (Sampedro et al. 1999).

After the log-transformed data were divided into demographic categories, analysis of covariance (ANCOVA) was applied to test the differences between the formed groups in the angular (*b*) and linear (*a*) coefficients. This analysis allowed us to determine whether the data for each relationship should be represented by a single straight line or by different linear equations for the groups (Herrera et al. 2013). The cutoff point between the groups identified in the significant ($p < 0.05$) biometric relationships was considered as the onset of morphological sexual maturity.

When there was an overlap in growth lines (in juveniles and adults), the L_{50} method was used to identify the size at morphological sexual maturity, comprising the size at which a half of the population has morphologically matured. This procedure analyzes the distribution of individuals according to size classes based on carapace length (CL). Subsequently, the equation of the logistic curve $y = 1/(1 + e^{-r(CL-CL_m)})$ was fitted to the data by the least-squares method (Vazzoler 1996), and the size at morphological maturity was defined by the interpolation point (50%).

Results

A total of 1,004 individuals were analyzed. Of this total, 470 were male and 534 were females, 162 of which were carrying eggs. CL ranged from 5.40 to 13.80 mm (9.50 ± 1.29 mm) in males and from 5.60 to 15.70 mm (10.39 ± 1.63 mm) in females. When only the females with eggs were considered, CL ranged from 9.90 mm to 15.70 (11.64 ± 0.75 mm).

Table 2. *Nematopalaemon schmitti* (Holthuis, 1950). Results of covariance analysis (ANCOVA).

Relationship	Factor (group)	Parameters (log)	F	p
PrL vs. CL	Male J vs. A	a	-	-
		b	6.252	0.014*
	Female J vs. A	a	4.945	0.028*
		b	1.685	0.197
CaL vs. CL	Male J vs. A	a	0.849	0.358
		b	0.450	0.503
	Female J vs. A	a	3.546	0.062
		b	3.546	0.062
PIL vs. CL	Male J vs. A	a	-	-
		b	6.837	0.009*
	Female J vs. A	a	-	-
		b	4.451	0.035*
AML vs. CL	Male J vs. A	a	-	-
		b	15.253	0.000*

Notes: CL = carapace length, PrL = cheliped propodus length, CaL = cheliped carpus length, PIL = second pleuron length, AML = length of appendix masculine, J = juveniles, A = adults.

* $p < 0.05$.

A detailed description of each of the relationships analyzed can be seen in Table 1. The straight lines obtained at different stages (juvenile and adult) were best fitted to the data separately, with the exception of the CaL vs. CL relationship for males and females (ANCOVA, $p > 0.05$) (Table 2).

The PrL vs. CL relationship showed isometric growth for juveniles and negative allometry for adults, in both males and females. The PIL vs. CL relationship showed negative allometry for both male demographic categories, but isometric growth was observed for both juvenile and adult females. When the AML vs. CL relationship was calculated, positive allometric growth was observed in the juvenile males, while growth was isometric in the adults. The relationships that best showed the changes in allometric coefficient between the demographic categories were AML vs. CL for males and PIL vs. CL for females; in other words, the greatest changes were seen in the growth of

these structures between the juvenile and adult stages. The estimated value for CL at morphological sexual maturity in males was 8.51 mm (Figure 2). For females, the CL_{50} analysis of the overlap in juveniles and adults estimated size at morphological sexual maturity, resulting in a CL of 9.30 mm (Figure 3).

Discussion

Crustacean growth is a highly structured process with development divided into a series of distinct phases; within each phase, many variables conform to simple allometry (Hartnoll 1978). If a change in the growth pattern

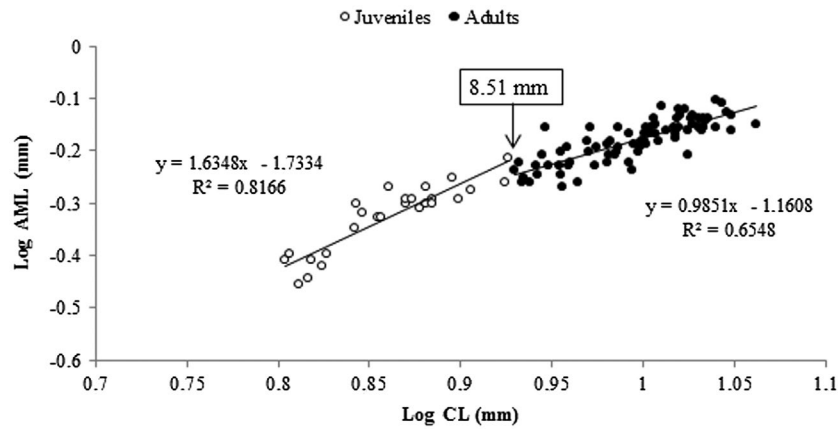


Figure 2. *Nematopalaemon schmitti* (Holthuis, 1950). Estimated size at morphological sexual maturity for males. In males the estimated sizes refer to the smallest individual after the inflection point of the equations for juveniles and adults. Notes: CL = carapace length, AML = length of appendix masculina.

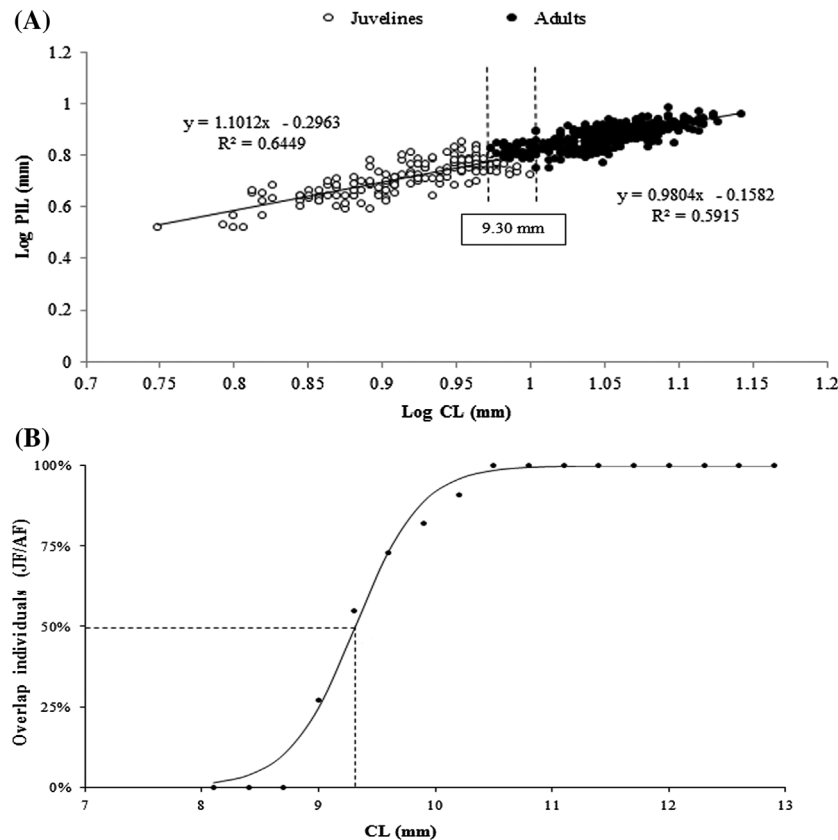


Figure 3. *Nematopalaemon schmitti* (Holthuis, 1950). (A) Estimated size at morphological sexual maturity for females. (B) In females the estimated sizes correspond to the CL of the adjusting the logistic regression of overlapping juveniles and adults, indicating the size in which females are morphologically mature.

Notes: JF = juvenile female, AF = adult female, CL = carapace length, PIL = second pleuron length.

of certain organs or body structures between the juvenile and adult stages is considered, morphologically mature individuals can be estimated, and the energy cost directed toward reproduction can consequently be estimated (Hartnoll 1982; Taylor and Gabriel 1992; Collins 2001), in turn explaining the function of structures and possible dimorphism between the sexes as well as between juveniles and adults (Hartnoll 1974). This change in growth in some relationships between two variables was observed in the present study.

The relative growth rate for cheliped propodus length in males and females of this species showed isometric growth in the juvenile stage, followed by negative allometry in the adult stage. In some caridean shrimps, the chelipeds are an important mechanism of distinguishing the sexes and their morphological maturation, for example in *Macrobrachium* Bate, 1868 (Boschi 1974) and some species of *Palaemon* Weber, 1795 (Berglund 1981; Kim 2005) such as *P. longirostris* H. Milne Edwards, 1837 (Cartaxana 2003). Nevertheless, this sexual dimorphism related to the growth of the male cheliped is not seen in *N. schmitti*. In this species, chelipeds are probably used to search for and handle food, as well as defense and grooming for both sexes; this has been observed in the caridean shrimp *P. noronhai* (Rankin, 1898) (Pralon and Negreiros-Fransozo 2006).

The allometric relationship of the second pleuron shows a different pattern of growth between sexes in this study. The isometric growth in juvenile and adult females indicates that abdominal pleura grow in the same proportion to carapace length. This is related to the different functions performed by the second pleuron in each sex (Hartnoll 1974). Nagamine and Knight (1980) state that in females, the second pleuron is elongated and expanded to form the sides of the brood chamber. This phenomenon can be observed in *N. schmitti*, which requires more area beneath its abdomen to carry and incubate the eggs until hatching (Ahamed and Ohtomi 2014).

This isometric relationship results in more space for the eggs and subsequent increased fertility, as reported by several authors (Darnell 1956; Harris et al. 1972; Katre 1977; Bond and Buckup 1982; Barros and Fontoura 1996). Additionally, according to Negreiros-Fransozo et al. (2003), Fransozo et al. (2004), and Bauer (2004), the size of the cephalothorax in caridean females can correspond to a higher production of oocytes and thus increased fecundity in the species. Meanwhile, the negative allometry found in relation to this same structure in males reflects the low importance of pleura growth for this sex, in which its function is simply structural.

In males, the relative growth rate of the appendix masculina changed from positive allometry in the juvenile stage to isometric growth in adults, which may reflect an association with morphological sexual maturity. According

to Bauer (2004), structures like the appendix masculina are associated with the correct adhesion of spermatophores to the underside of the female during copulation. The use of the appendix masculina as a secondary sexual characteristic associated with morphological sexual maturity was also proposed by Ahamed and Ohtomi (2014) for the caridean shrimp *Plesionika izumiae* Omori 1971.

Berkeley (1930) and Descouterelle (1971) suggested that the appendix masculina plays a key role in spermatophore transfer. Mating experiments with other carideans support this view, such as the studies by Bauer (1976), Berg and Sandifer (1984), and Nakashima (1995) on *Heptacarpus sitchensis* (Brandt 1851), *Palaemonetes pugio* Holthuis 1949, and *Athanas kominatoensis* (Kubo, 1942), respectively. In these experiments, males in which the endopods (and the appendices masculinae) of the second pleopods were amputated readily mated with females, but usually failed to pass on spermatophores.

The estimated size at morphological sexual maturity in females (9.30 mm CL) was reinforced by the data for functional maturity, and is close to the size of the smallest egg-bearing female sampled (9.90 mm CL), indicating that the determination of size at sexual maturity by morphometric analysis can also be used successfully in carideans, corroborating the study by Pralon and Negreiros-Fransozo (2006).

Estimated morphological sexual maturity for males (8.51 mm CL) was lower than in females, and several factors related to reproductive strategy may explain this difference; for example, greater investment in the reproductive process to produce eggs is positively correlated with female size. This reduced energy investment in male growth may reduce the risk of predation (Fonseca and D'Incao 2003), as smaller males may avoid detection by predators (Terossi et al. 2008).

The size difference between the sexes observed in *N. schmitti* can also be attributed to its mating system. In 'pure search' mating systems, the male's mating success depends primarily on its ability to find (and mate with) as many receptive females as possible, rather than on its physical defense power (Bauer and Abdalla 2001). Small and agile males are consequently more successful, because they search more efficiently for mates within the population (Correa and Thiel 2003). Males consequently do not need to grow to a large size or to develop large cheliped weapons to battle other males for females. Pure search or promiscuous mating systems are associated with non-territorial mobile species with high population densities, and low levels of precopulatory interactions or intramale agonistic behavior (Bauer 2004).

While reproductive success in females is always positively correlated with size (the larger the female, the larger the clutch size), mating systems may primarily affect the

shape of the male and thus represent an important source of variation, leading to the diversity observed in caridean sexual systems (Correa and Thiel 2003).

In this study, the analysis of the morphometric relationships in *N. schmitti* indicated morphological sexual maturity in both sexes. The growth of secondary sexual characteristics, such as the second pleuron in females and appendix masculina in males, plays a role in attaining the morphological sexual maturity necessary for reproductive success and to assure the life cycle of the species.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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