PANAMJAS
Pan-American Journal of Aquatic Sciences

Relative growth and determination of morphological sexual maturity of the fiddler crab *Uca thayeri* Rathbun (Crustacea, Ocypodidae) in two mangrove areas from Brazilian tropical coast

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Abstract. The aim of this paper was to study the relative growth and the morphological sexual maturity of *Uca thayeri* from two mangrove areas of the State of Pernambuco, Northeast Brazil. The crabs were manually collected monthly at the Ariquindá and Mamucabas Rivers, during spring low tide, from April 2008 to March 2009. Crabs were measured at the following dimensions: carapace width (CW); carapace length (CL); cheliped propodus length (CPL); abdomen width (AW) and gonopod length (GL). The growth was described by the equation $y = a\ x^b$. The sexual maturity was estimated through a logistic equation. A total of 2,711 individuals of *U. thayeri* were collected. Females presented larger CW than males, an adaptation to increase the production of eggs. In the relationship CPL vs. CW, males showed positive allometric and females, negative allometric growth. On the other hand, in the relationship AW vs. CW, males showed negative allometric and females, positive allometric growth. This pattern is a reflex of the growth of the cheliped in males and of the abdomen in females, due to their sexual functions. Males reached maturity at larger sizes than females in both mangroves areas, probably due to their greater investment in somatic growth, while females spend their energy in the reproductive process.

Keywords: allometric growth, biometric relationships, morphometry, sexual maturity

Resumo. Crescimento relativo e determinação da maturidade sexual morfológica do caranguejo violinista *Uca thayeri* Rathbun (Crustacea, Ocypodidae) em duas áreas de manguezais da costa tropical brasileira. O objetivo deste trabalho foi estudar o crescimento relativo e a maturidade sexual morfológica de *Uca thayeri* em duas áreas de mangue do Estado de Pernambuco, Nordeste do Brasil. Os caranguejos foram coletados manualmente nos Rios Ariquindá e Mamucabas, durante a maré baixa de sizígia, mensalmente de abril/2008 a março/2009. Os caranguejos foram medidos nas seguintes dimensões: largura da carapaça (LC); comprimento da carapaça (CC); comprimento do própodo do quelípodo (CPQ); largura do abdome (LA) e comprimento do gonópodo (CG). O crescimento foi descrito pela equação $y = a\ x^b$. A maturidade sexual foi estimada através de uma equação logística. Um total de 2.711 indivíduos de *U. thayeri* foi coletado. As fêmeas apresentaram maior LC que os machos, uma adaptação para aumentar a produção de ovos. Na relação CPQ vs. LC, os machos apresentaram crescimento alométrico positivo e as fêmeas, crescimento alométrico negativo. Por outro lado, na relação LA vs. LC, os machos apresentaram crescimento alométrico negativo e fêmeas, crescimento alométrico positivo. Este padrão é um reflexo do crescimento do quelípodo nos machos e do abdômen nas fêmeas, devido às suas funções sexuais. Os machos atingem a maturidade em tamanhos maiores do que as fêmeas em ambas as áreas de manguezais, provavelmente devido ao seu maior investimento no crescimento somático, enquanto as fêmeas gastam sua energia no processo reprodutivo.

Palavras chave: crescimento alométrico, maturidade sexual, morfometria, relações biométricas

Introduction

Among the macroinvertebrates found in mangroves, the decapod crabs (mainly Brachyura) are one of the most important taxa due to their high density and biomass (Litulo 2005 a,b). Among the Infraorder Brachyura, the fiddler crabs of the genus *Uca* Leach, 1814 (Ocypodidae) stand out for their cosmopolitan character, being found in mangroves and estuarine beaches on temperate, subtropical and tropical zones (Crane 1975).

This genus is relatively well studied, especially on the Brazilian coast, with papers dealing on many aspects of its biology, standing out those on their relative growth, for example: Masunari & Swiech-Ayoub (2003) for *U. leptodactyla* Rathbun, 1898, Negreiros-Fransozo *et al*. (2003) for *U. thayeri* Rathbun, 1900, Benetti & Negreiros-Fransozo (2004) for *U. burgersi* Holthuis, 1967, Castiglioni & Negreiros-Fransozo (2004) and Costa & Soares-Gomes (2008) for *U. rapax* (Smith, 1870), Masunari & Dissenha (2005) for *U. mordax* (Smith, 1870), Masunari *et al.* (2005) and Hirose & Negreiros-Fransozo (2007) for *U. maracoani* (Latreille, 1802) and Pralon & Negreiros-Fransozo (2008) for *U. cumulanta* Crane, 1943.

Nearly 100 species of the genus *Uca* are known worldwide (Rosenberg 2001, Beinlich & von Hagen 2006, Shih *et al.* 2010) and for the Brazilian coast, Melo (1996) registered ten species of this genus, which nine of them have been recorded for the littoral of the State of Pernambuco: *Uca leptodactyla*, *U. maracoani*, *U. mordax*, *U. rapax*, *U. burgersi*, *U. cumulanta*, *U. vocator* (Herbst, 1804), *U. victoriana* von Hagen, 1987 and *U. thayeri* (see Coelho 1994, Castiglioni *et al.* 2011a).

The species *U. thayeri* occurs in muddy regions of the mangrove periphery, under shaded areas, through the West coast of the Atlantic Ocean, in Florida, Gulf of Mexico, Antilles, Guatemala, Panama, Venezuela and Brazil (from the State of Maranhão to Santa Catarina) (Melo 1996). Negreiros-Fransozo *et al.* (2003) have accomplished the only study on the relative growth and sexual maturity of *U. thayeri*, in a population at Ubatuba, State of São Paulo, Southeast Brazil. However, time, place and environmental factors may influence the growth rates of Brachyura (Baptista-Metri *et al.* 2005), and intraspecific variations in the size of sexual maturity occur at different spatial scales (Díaz & Conde 1989, Hines 1982). Such facts highlight the importance of performing more studies on growth and maturity, even if a given species has been studied in other regions.

The studies on relative growth are based on the association between two biometric variables, being one of them the independent (x), relative to the size of the animal, and the other dependent, represented by a certain segment or tagma (y). The power function, or the equation of allometric growth, has been the most used in such studies (Hartnoll 1978, 1982, Araújo *et al*. 2012).

The development of the crustaceans is characterized by morphological changes related to sex and puberty (Hartnoll 1982), which includes the differential growth of some tagmata. The chelipeds in males and the abdomen in females are some of the tagmata that are under this phenomenon, especially in the transition of the last immature instar to the first mature, i.e., the puberty molt (Hartnoll 1974). This transition can be detected by the inflection or discontinuity in a series of linear or curvilinear relationships of bivariate analysis (Haefner 1990) and it is called morphological maturity. Thus, studies on relative growth dealing with these two cited variables are the most used to detect the beginning of the morphological maturity (Negreiros-Fransozo *et al*. 2003).

The aim of this study was to characterize the relative growth and to determine the morphological sexual maturity of males and females of *U. thayeri* from two mangrove areas located in Brazilian Northeast.

Materials and methods

Description of the sampling area

The State of Pernambuco is located in Northeast Brazil (07º32’00” and 08º55’30” S; 34º48’35” and 41º19’54” W). The coastal zone of Pernambuco is 187 km long, being one of the most important human population agglomerate of Northeast Brazil. The region has a climate within the As' type of Köeppen system, i.e., hot and humid with rainy autumn and winter. Both areas chosen for the development of this work are located at the Southern littoral of Pernambuco: estuaries of Ariquindá (8º 41’ 26” S, 35º 06’ 07” W) and Mamucabas (8º 46' 42” S, 35º 06’ 25” W) Rivers, Municipality of Tamandaré (Figure 1). The sampling areas at each estuary were 9.69 km distant from each other. At Tamandaré, the mean air temperature varies from 25 to 30 ºC, the mean rainfall is around 2,000 mm (Duarte 1993, Moura & Passavante 1995), the wind speed varies from 3.1 to 4.7 $m.s^{-1}$ (CPRH 2003), and the mean relative air humidity during the sampling period was 74.93 %, according to the database of the National System of Environmental Data (SINDA).

The Ariquindá River is inserted at the Guadalupe Environmental Preservation Area. Together with its affluent União, it becomes an important component of Formoso River basin (CPRH 1999). It is considered one of the last non-polluted rivers of Pernambuco. The mangrove area chosen for the crabs' samplings is located near the confluence of Ariquindá and Formoso Rivers, at Carneiros Beach, and its vegetation is mainly composed of *Rhizophora mangle* L., *Laguncularia racemosa* (L.) Gaertn. f. and, less frequently, *Avicennia schaueriana* Stapf and Leechman ex Moldenke. The substratum was visually characterized as muddy sand.

The Mamucabas River is located, almost entirely, in the Municipality of Tamandaré. It rises at West of the Saltinho Biological Reserve. By entering in the Reserve, it suffers the first environmental impact, being dammed to form the reservoir that supplies Tamandaré. It meets the Ilhetas River and together they discharge into a spit (CPRH 2003). Besides the damming, it is considered an impacted river due to the great deposition of solid waste and deforestation, as well as the housing occupation in the surrounding areas (Santos *et al*. 2001). The vegetation was mainly composed by *L. racemosa*, *R. mangle* and few trees of *A. schaueriana.* The substratum was also visually classified as muddy sand.

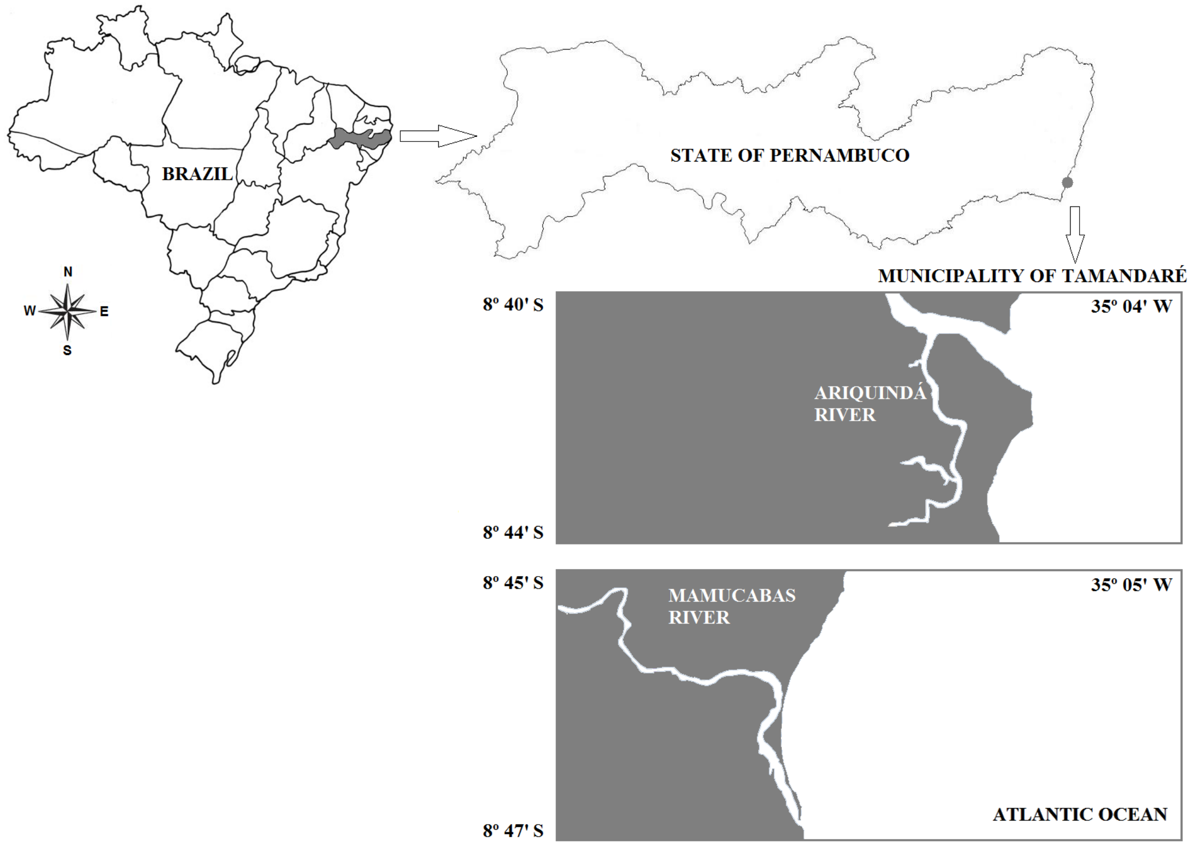

Figure 1. Map of the study area, at Ariquindá and Mamucabas Rivers, Pernambuco.

Field procedures

In each estuary, two sampling stations were chosen. The samplings of *Uca thayeri* were monthly accomplished from April 2008 to March 2009, through manual collections during 30 minutes at each estuary (15 minutes at each station), at low tide. The crabs were captured above the substratum, as well as extracted from the burrows with a gardening shovel. The sampling area had nearly 100 m². The crabs were kept in plastic bags and preserved in ice, and in the laboratory, they were preserved in alcohol 70%. Some specimens were integrated into the scientific collection of the Centro Acadêmico de Vitória, Vitória de Santo Antão Campus, Universidade Federal de Pernambuco, State of Pernambuco (CAV-UFPE). Others were discarded after study.

Laboratory procedures

The species *U. thayeri* was identified based on Melo (1996). For the sexual differentiation, observations of the secondary sexual characters of the abdomen were made.

The following variables of each individual were taken with a digital caliper (0.01 mm): CW – carapace width, CL – carapace length, CPL – major cheliped propodus length of males and right cheliped of females, AW – abdomen width, GL – gonopod length, in males.

Data analyses

The minimum, mean (± standard deviation) and maximum values of each variable were estimated. The Student *t* test was applied to compare the biometric values between sexes and estuaries ($\alpha = 0.05$) (Zar 1996).

For the determination of the age groups (juveniles and adults), the statistic methodology was based in the paper of Sampedro *et al.* (1999). For that, the biometric data were log-transformed, and an analysis of K-means clustering, followed by a bivariate discriminant analysis, was performed. After that, the growth of *Uca thayeri* for each phase was described by the allometric equation $y = a\ x^b$ (Huxley 1950). The carapace width (CW) was considered the independent variable (x) and related to the other body dimensions (dependent variables, y). The type of growth for each phase (juvenile male, adult male, juvenile female and adult female) was established by the value of the constant 'b' of the potency function, which can be isometric (b = 1), allometrically positive (b > 1) or allometrically negative (b < 1). The statistical significance of the constant 'b' in relation to the unity was calculated with a *t* test ($\alpha = 0.05$). To verify the possibility of grouping juveniles and adults under the same equation, the intercepts (a) and the regression coefficients (b) were tested by an analysis of covariance (ANCOVA) ($\alpha = 0.05$) (Zar 1996).

The morphological sexual maturity was estimated to all allometric relationships, but the relationships CPL vs. CW for males and AW vs. CW for females were chosen to represent the size at which 50% of males and females were already in the adult phase ($CW_{50\%}$), taking into account the importance of propodus and abdomen in the reproductive processes of males and females, respectively (Araújo *et al.* 2012). After the separation of groups, each age category was divided in size classes (1.5 mm of CW) and the proportion of juveniles and adults in each class was calculated, with the proportion of adults being adjusted to the logistic distribution [($y = a/(1+be^{-cx})$)], a commonly used normalized form of the logistic equation of Verhulst. After this, an interpolation was performed to determine the $CW_{50\%}$.

Results

Ariquindá River

A total of 1,411 individuals of *Uca thayeri* were sampled at the estuary of Ariquindá River, being 627 males and 784 females.

The minimum, mean, standard deviation and maximum values of each evaluated variable are shown in Table I. The *t* test showed that the sizes differed between sexes, with females showing larger CW (t = -4.18), CL (t = -4.10) and AW (t = -28.46), and the males, larger CPL (t = 19.90) ($p < 0.05$).

Table I. *Uca thayeri*. Minimum, mean, standard deviation and maximum values of the measured morphological variables for males and females at Ariquindá River, Pernambuco.

Sex		CW	CL	CPL	AW	GL
Males	Min	4.05	3.41	2.60	1.45	1.93
	Mean	12.50	8.71	12.83	3.49	5.26
	Sd	3.06	2.22	6.12	1.44	1.16
	Max	26.58	22.38	32.18	11.13	9.33
Females	Min	4.65	1.31	1.90	1.36	(-)
	Mean	13.16	9.20	5.00	7.31	(-)
	Sd	2.76	2.00	1.39	2.50	(-)
	Max	23.01	19.47	15.64	14.14	(-)

Min, minimum; Sd, standard deviation; Max, maximum; CW, carapace width; CL, carapace length; CPL, cheliped propodus length; AW, abdomen width; GL, gonopod length; (-), data not available.

The dispersion of points in the graphic of the relation CL vs. CW was allometrically negative for both juvenile (b = 0.91, t = 6.75, $p < 0.05$) and adult males (b = 0.94, t = 3.14, $p < 0.05$) (Figure 2a). In females, the growth for this relationship was also allometrically negative in both developmental phases (juveniles: b = 0.94, t = 3.92, $p < 0.05$, adults: b = 0.97, t = 2.60, $p < 0.05$) (Figure 3a) (Table II).

In the relationship CPL vs. CW, males showed a positive allometric growth in both juvenile and adult phases, with higher growth rate in adults (b = 1.71, t = 17.43 and b = 1.82, t = 17.08, respectively) ($p < 0.05$) (Figure 2b), and the growth of females was isometric in both juvenile and adult phases (b = 0.97, t = 0.65 and b = 0.92, t = 1.93, respectively) ($p > 0.05$) (Figure 3b) (Table II).

In the relationship AW vs. CW, males showed negative allometric growth in juveniles (b = 0.78, t = 6.73, $p < 0.05$), and adults (b = 0.82, t = 2.96, $p < 0.05$) (Figure 2c). However, the females showed an allometric positive growth, both for juveniles (b = 1.39, t = -8.72, $p < 0.05$) and for adults (b = 1.19, t = -8.62, $p < 0.05$), with higher growth rates in the juvenile phase (Figure 3c) (Table II).

In the dispersion of points of the relationship GL vs. CW for males, the growth was isometric in the juvenile phase (b = 0.99, t = 1.53, $p > 0.05$) and allometrically negative in the adult phase (b = 0.83, t = 4.36, $p < 0.05$), i.e., the growth rates were higher in the juvenile phase (Figure 2d) (Table II).

The analysis of covariance showed significant differences in the intercepts and/or in the regression coefficients between juveniles and adults of all analyzed relationships ($p < 0.05$) (Table II), which justifies the elaboration of graphics and equations separately for juveniles and adults from Ariquindá River.

Table II. *Uca thayeri*. Linear equation, coefficient of determination (r^2), results of the analysis of covariance (ANCOVA) and t test, and allometry (Al) for males and females at Ariquindá River, Pernambuco.

Relation	Phase	n	Linear equation Log y = log a + b log x	r^2	ANCOVA a	ANCOVA b	*t* test b	Al	$CW_{50\%}$
CL vs. CW	JM	253	LogCL = -0.07+0.91LogCW	0.94	20.52*	0.00	6.75*	-	12.6
	AM	290	LogCL = -0.10+0.94LogCW	0.91			3.14*	-	
	JF	260	LogCL = -0.10+0.94LogCW	0.94	120.7*	120.81*	3.92*	-	12.4
	AF	464	LogCL = -0.12+0.97LogCW	0.93			2.60*	-	
CPL vs. CW	JM	109	LogCPL = -0.83+1.71LogCW	0.92	655.46*	630.04*	17.43*	+	11.8
	AM	121	LogCPL = -0.89+1.82LogCW	0.88			17.08*	+	
	JF	119	LogCPL = -0.40+0.97LogCW	0.86	182.70*	168.28*	0.65	0	12.5
	AF	188	LogCPL = -0.34+0.92LogCW	0.76			1.93	0	
AW vs. CW	JM	120	LogAW = -0.38+0.78LogCW	0.83	12.12*	9.68*	6.73*	-	19.0
	AM	150	LogAW = -0.31+0.82LogCW	0.68			2.96	-	
	JF	141	LogAW = -0.82+1.39LogCW	0.89	769.40*	815.81*	8.72*	+	11.2
	AF	437	LogAW = -0.45+1.19LogCW	0.87			-8.62*	+	
GL vs. CW	JM	101	LogGL = -0.37+0.99LogCW	0.90	138.84*	100.24*	1.53	0	12.6
	AM	143	LogGL = -0.19+0.83LogCW	0.76			4.36*	-	

CW, carapace width; CL, carapace length; CPL, cheliped propodus length; AW, abdomen width, GL, gonopod length; JM, juvenile male; AM, adult male; JF, juvenile female; AF, adult female; *, significant result ($\alpha = 0.05$); +, positive allometric growth; -, negative allometric growth; 0, isometric growth.

Mamucabas River

A total of 1,300 individuals of *Uca thayeri* were sampled at the estuary of Mamucabas River, being 565 males and 735 females.

The minimum, mean, standard deviation and maximum values of each evaluated variable are presented in Table III. The t test showed that the sizes differed between sexes, with females presenting larger CW (t = -4,85), CL (t = -6,10) and AW (t = -31,02), and the males, larger CPL (t =

19,78) ($p < 0.05$).

The dispersion of points in the graphic of the relationship CL vs. CW was allometrically negative for juvenile (b = 0.95, t = 6.04, $p < 0.05$), and adult males (b = 0.93, t = 8.00, $p < 0.05$) (Figure 4a), like at Ariquindá River. Both juvenile and adult females also showed negative allometric growth (b = 0.97, t = 6.09 and b = 0.99, t = 3.17, $p < 0.05$) (Figure 5a) (Table IV), like at Ariquindá River.

In the relationship CPL vs. CW, males showed positive allometric growth in both juvenile and adult phases, and changes in the degree of the cheliped allometry were more evident than at Ariquindá River (juveniles: b = 1.43, t = 9.94, adults: b = 1.88, t = 15.65, $p < 0.05$) (Figure 4b). On the other hand, females showed negative allometric growth in the juvenile phase (b = 0.89, t = 3.89, $p < 0.05$) and isometric in the adult phase (b = 0.98, t = 0.70, $p < 0.05$) (Figure 5b) (Table IV), a result a little different from the observed at Ariquindá River.

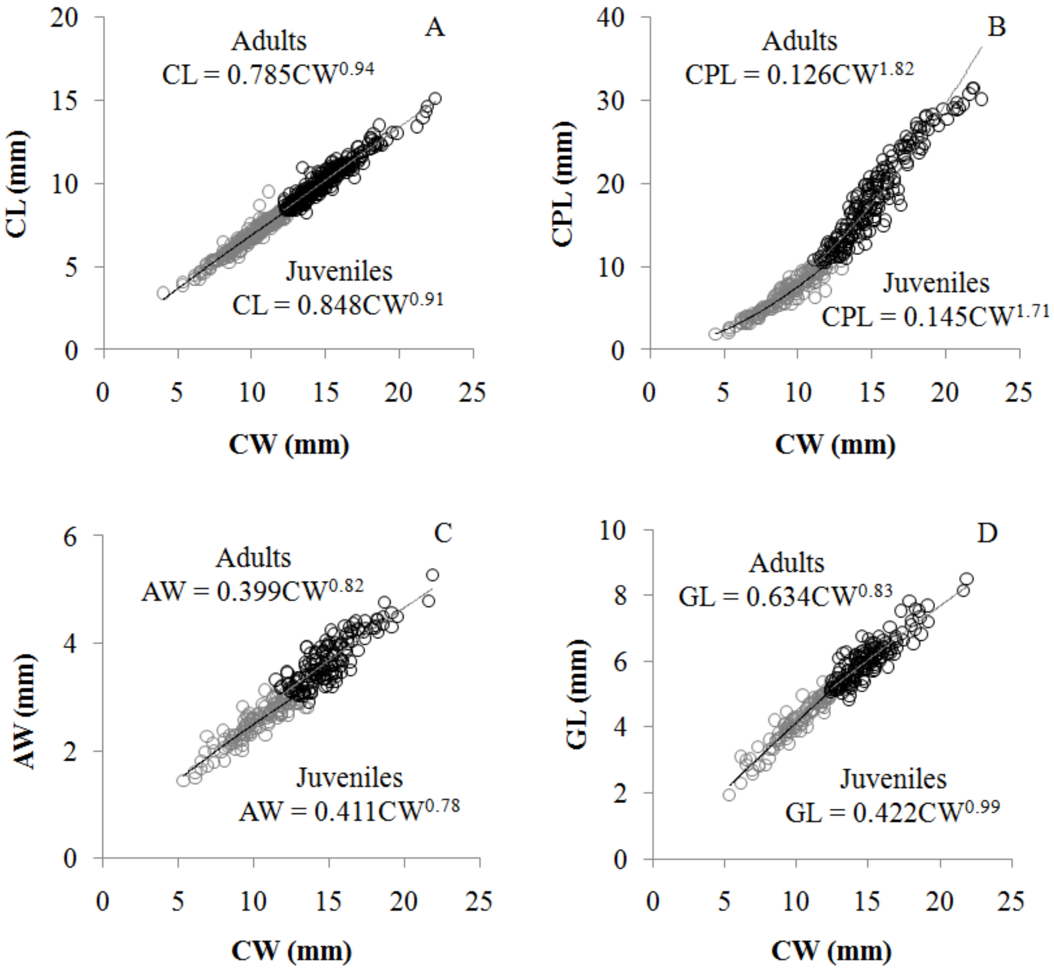

Figure 2. *Uca thayeri*. Dispersion of points and growth equations of the relationships between the carapace width (CW) and the dependent variables [A - carapace length (CL), B – cheliped propodus length (CPL), C - abdomen width (AW), D - gonopod length (GL)] for juveniles and adults of males at Ariquindá River, Pernambuco. Juveniles = gray points; adults = black points.

In the relationship AW vs. CW, males exhibited negative allometric growth, both in the juvenile (b = 0.88, t = 2.54, $p < 0.05$) and adult phase (b = 0.86, t = 4.43, $p < 0.05$) (Figure 4c). However, juvenile and adult females showed positive allometric growth, with a higher growth rate during the juvenile phase (juveniles: b = 1.51, t = -13.58, $p < 0.05$, adults: b = 1.27, t = 9.55, $p < 0.05$) (Figure 5c) (Table IV), like at Ariquindá River.

In the relationship GL vs. CW, males showed isometric growth in the juvenile phase (b = 1.05, t = 1.43, $p < 0.05$) and negative allometric in the adult phase (b = 0.80, t = 8.82, $p < 0.05$) (Figure 4d) (Table IV), as also observed at Ariquindá River.

The analysis of covariance showed significant differences in the intercepts and/or in the regression coefficients between juveniles and adults of all analyzed relationships ($p < 0.05$) (Table IV), which justifies the elaboration of graphics and equations separately for juveniles and adults of *U. thayeri* from Mamucabas River.

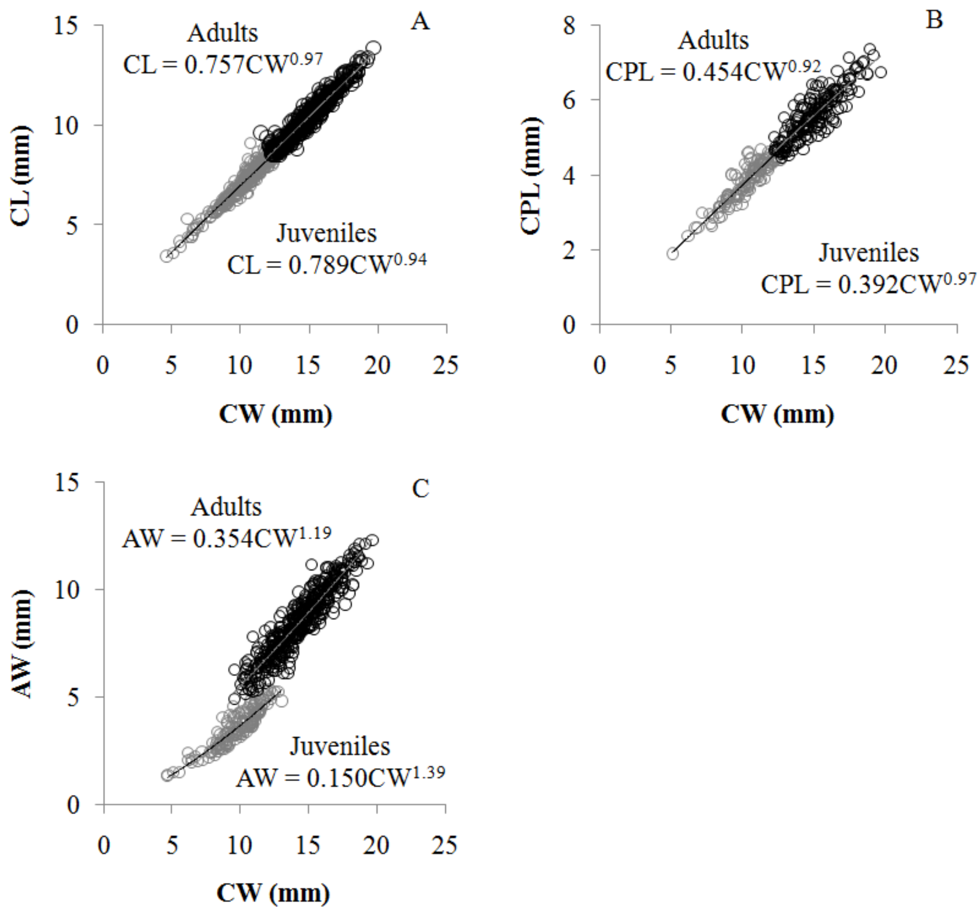

Figure 3. *Uca thayeri.* Dispersion of points and growth equations of the relationships between the carapace width (CW) and the dependent variables [A - carapace length (CL), B – cheliped propodus length (CPL), C - abdomen width (AW)] for juveniles and adults of females at Ariquindá River, Pernambuco. Juveniles = gray points; adults = black points.

Sexual Maturity

The size at morphological sexual maturity was obtained for all biometric relationships for Ariquindá (Table II) and Mamucabas Rivers (Table IV). However, the most adequate relationships to determine the beginning of the reproductive activity are the CPL vs. CW in males and AW vs. CW in females. At the Ariquindá River, the size at which males of *U. thayeri* were considered morphologically mature was 11.80 mm (largest immature male CW = 12.98 mm, smallest mature male CW = 11.10 mm). Females reached the morphological maturity at 11.20 mm (largest immature female CW = 12.76 mm, smallest mature female CW = 9.56 mm). At the Mamucabas River, these values were, respectively, 12.10 mm for males (largest immature male CW = 13.75 mm, smallest mature male CW = 11.31 mm), and 11.90 mm for females (largest immature female CW = 13.62 mm, smallest mature female CW = 10.45 mm).

Comparison of size between estuaries

Comparing the size, it was possible to observe that males showed larger CL and AW at Ariquindá River ($p < 0.05$), while the other morphological variables did not differ between estuaries ($p > 0.05$). The only variable to differ between estuaries for females was AW ($p < 0.05$), being larger at Ariquindá River. Due to these differences, the regressions were made for each estuary separately.

Discussion

The study of relative growth and the determination of the size at sexual maturity are important attributes in crustaceans for a better comprehension of population and reproductive biology (Castiglioni *et al.* 2011b). Crustacean growth is discontinuous, and some body parts show differential growth throughout the ontogenetic phases (Hartnoll 1978, 1982). Among the Brachyura, the body parts that exhibit these changes with more evidence are the cheliped, abdomen and pleopods of both sexes, during the transition from juvenile to adult phases (Hartnoll 1974, 1978). Thus, patterns of growth can indicate at which size an organism reaches the size of sexual maturity (González-Gurriáran & Freire 1994).

Table III. *Uca thayeri.* Minimum, mean, standard deviation and maximum values of the measured morphological variables for males and females at Mamucabas River, Pernambuco.

Sex		CW	CL	CPL	AW	GL
Males	Min	4.30	3.24	2.42	1.40	1.58
	Mean	12.26	8.35	12.16	3.19	5.15
	Sd	3.00	1.95	6.29	0.92	1.25
	Max	22.38	14.62	35.20	10.15	8.50
Females	Min	5.12	3.49	2.05	1.44	(-)
	Mean	13.06	9.03	4.94	6.85	(-)
	Sd	2.88	2.00	1.11	2.69	(-)
	Max	22.10	15.64	7.84	14.62	(-)

Min, minimum; Sd, standard deviation; Max, maximum; CW, carapace width; CL, carapace length; CPL, cheliped propodus length; AW, abdomen width; GL, gonopod length; (-), data not available.

Table IV. *Uca thayeri.* Linear equation, coefficient of determination (r^2), results of the analysis of covariance (ANCOVA) and *t* test, and allometry (Al) for males and females at Mamucabas River, Pernambuco.

Relation	Phase	n	Linear equation Log y = log a + b log x	r^2	ANCOVA a	ANCOVA b	*t* test b	Al	$CW_{50\%}$
CL vs CW	JM	235	LogCL = -0.12+0.95LogCW	0.94	10.73*	0.34	6.04*	-	11.4
	AM	322	LogCL = -0.08+0.93LogCW	0.94			8.00*	-	
	JF	267	LogCL = -0.13+0.97LogCW	0.96	31.43*	1.51	6.09*	-	12.4
	AF	462	LogCL = -0.15+0.99LogCW	0.94			3.17*	-	
CPL vs CW	JM	131	LogCPL = -0.55+1.43LogCW	0.87	316.28*	391.67*	9.94*	+	12.1
	AM	171	LogCPL = -0.99+1.88LogCW	0.85			-15.65*	+	
	JF	161	LogCPL = -0.32+0.89LogCW	0.86	157.37*	94.88*	3.89*	-	12.5
	AF	265	LogCPL = -0.41+0.98LogCW	0.82			0.70	0	
AW vs CW	JM	139	LogAW = -0.48+0.88LogCW	0.74	298.09*	297.49*	2.54*	-	11.4
	AM	215	LogAW = -0.46+0.86LogCW	0.80			4.43*	-	
	JF	211	LogAW = -0.95+1.51LogCW	0.88	543.13*	42.24*	-13.58*	+	11.9
	AF	417	LogAW = -0.55+1.27LogCW	0.84			9.55*	+	
GL vs CW	JM	121	LogGL = -0.43+1.05LogCW	0.85	162.51*	189.49*	1.43	0	11.3
	AM	217	LogGL = -0.16+0.80LogCW	0.86			8.82*	-	

CW, carapace width; CL, carapace length; CPL, cheliped propodus length; AW, abdomen width, GL, gonopod length; JM, juvenile male; AM, adult male; JF, juvenile female; AF, adult female; *, significant result (α = 0.05); +, positive allometric growth; -, negative allometric growth; 0, isometric growth.

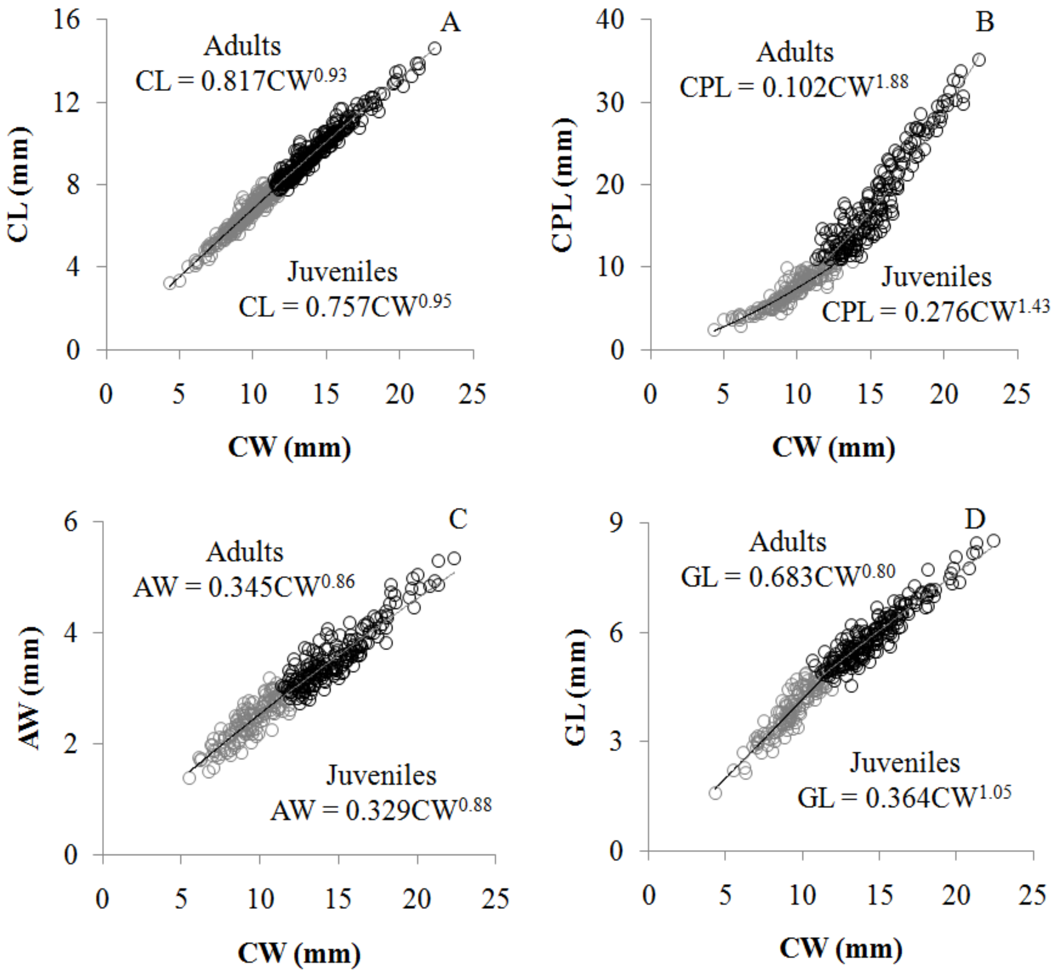

Figure 4. *Uca thayeri.* Dispersion of points and growth equations of the relationships between the carapace width (CW) and the dependent variables [A - carapace length (CL), B – cheliped propodus length (CPL), C - abdomen width (AW), D - gonopod length (GL)] for juveniles and adults of males at Mamucabas River, Pernambuco. Juveniles = gray points; adults = black points.

In the present study, in both estuaries, females were larger than males, an unusual result among species of crab. Sexual dimorphism, with males larger than females, was observed in several populations of *Uca* (Johnson 2003, Litulo 2005a,b, Benedetto & Masunari 2009). Bedê *et al.* (2008), studying eight species of the genus *Uca*, observed that males were larger than females in *U. cumulanta*, *U. mordax* and *U. rapax*, females were larger than males in *U. thayeri* and *U. victoriana*, and males and females of *U. leptodactyla*, *U. uruguayensis* and *U. vocator* had similar sizes. Studies with *U. thayeri* from São Paulo State coast also showed females larger than males (Costa & Negreiros-Fransozo 2003, Negreiros-Fransozo *et al.* 2003). However, Bezerra & Matthews-Cascon (2007) did not observe sexual dimorphism in size for *Uca thayeri* coming from another locality of northeastern Brazil. Despite of being larger than males, females reached sexual maturity at a smaller size, as it will be discussed later, indicating that other factors besides growth, such as selective predation (Du Preez & Mclachlan 1984) may influence the size in which females attain maturity. Besides, this dimorphism may be an adaptation to increase the production of eggs (Costa & Fransozo 2004, Castilho *et al*. 2008). Different mortality rates, migration, higher tolerance of one sex to environmental adversities, differences in foraging efficiency, acquisition or assimilation of food and behavioral patterns between sexes may be cited as other factors that may influence these size differences (Crane 1975, Wolf *et al*. 1975, Johnson 2003).

In the present study, while females of *U. thayeri* showed larger AW, males showed larger CPL. These secondary sexual characters are related with the roles played by each sex during reproduction (Tsuchida & Fujikura 2000, Castiglioni

& Negreiros-Fransozo 2004). The crabs of the genus *Uca* are characterized by the presence of the enormous chelae in one of the males' cheliped, being the other of small size (Crane 1975). The giant chelae increase the apparent size of the crab and play an important role in agonistic encounters, defense, food capture, territory demarcation and copula (Christy & Salmon 1984, Masunari & Swiech-Ayoub 2003, Costa & Soares-Gomes 2008). In females, a large abdomen is important in the perpetuation of the species, since the egg incubation takes place inside it (Hartnoll 1982, Araújo *et al.* 2012).

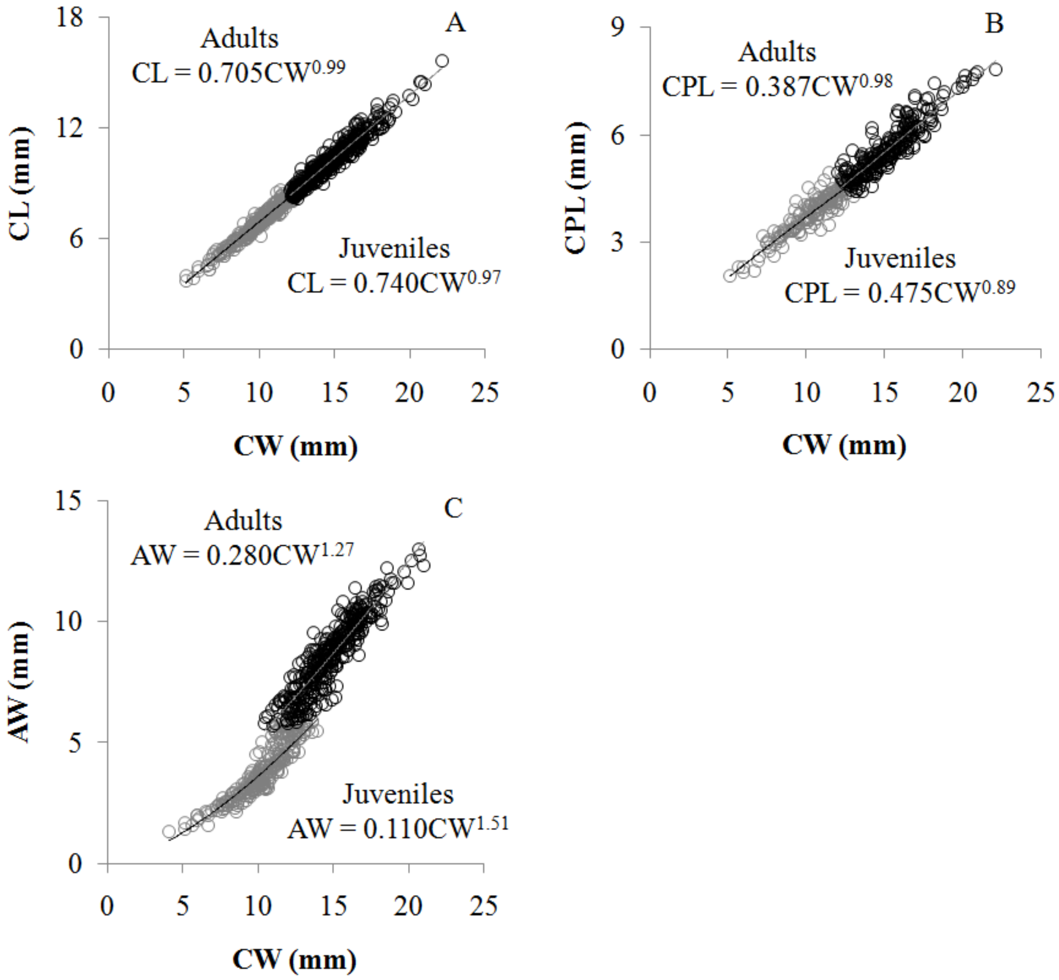

Figure 5. *Uca thayeri*. Dispersion of points and growth equations of the relationships between the carapace width (CW) and the dependent variables [A - carapace length (CL), B – cheliped propodus length (CPL), C - abdomen width (AW)] for juveniles and adults of females at Mamucabas River, Pernambuco. Juveniles = gray points; adults = black points.

The CW has been generally considered the independent variable in morphometric studies of Brachyura because it exhibits few morphological changes throughout the crab's life (Castiglioni & Negreiros-Fransozo 2004, Araújo *et al.* 2012, Castiglioni & Coelho 2011). In the relationship CL vs. CW, males and females of both estuaries showed negative allometric growth, indicating a higher growth of the CW in relation to the CL. This result is very similar to that obtained by Negreiros-Fransozo *et al.* (2003) for the same species and by Castiglioni & Negreiros-Fransozo (2004) for *U. rapax*, except for adult females, which showed isometric growth for this relationship in both studies. However, this relationship is not the most appropriate to express biological changes with reproductive meaning that occur in the life of crabs (Santos *et al*. 1995). Other body parts, as the abdomen, cheliped and gonopod shows changes in the degree of allometry with puberty (Castiglioni & Negreiros-Fransozo 2004, Castiglioni & Coelho 2011) and are the most adequate for studies of relative growth and determination of morphological maturity.

In both estuaries, in the relation CPL vs. CW, males showed positive allometric and females, negative allometric growth. On the other hand, in the relationship AW vs. CW, males showed negative allometric and females positive allometric growth. This observed pattern is a reflex of the growth of the cheliped in males and of the abdomen in females, due to their sexual functions, as discussed before. In some studies with *Uca,* the growth of the abdomen was only analyzed for females and the growth of the cheliped, only for males (Masunari & Swiech-Ayoub 2003, Masunari & Dissenha 2005, Masunari *et al.* 2005, Costa & Soares-Gomes 2008). However, according to Negreiros-Fransozo *et al.* (2003), the abdomen and the cheliped are the dimensions that better distinguish the growth of males and females. This was observed in the present study, which reveals the importance of analyzing these structures for both sexes, as in the studies made by Castiglioni & Negreiros-Fransozo (2004), Hirose & Negreiros-Fransozo (2007) and Pralon & Negreiros-Fransozo (2008).

The growth pattern determined by Hartnoll (1974) shows a considerable positive allometry in the growth of the largest cheliped in males, both in the juvenile and adult phases, as observed in several species of Brachyura, as *Ucides cordatus* (Linnaeus, 1763) (Ucididae) (Castiglioni *et al.* 2011b) and in species of the genus *Uca,* as in *U. thayeri* (Negreiros-Fransozo *et al.* 2003), *U. burgersi* (Benetti & Negreiros-Fransozo 2004), *U. mordax* (Masunari & Dissenha 2005) and in the present study. This high level of the cheliped allometry is responsible for its larger size in males of *Uca,* resulting in crabs that can exhibit chelae larger than their carapaces (Crane 1975, Masunari *et al.* 2005). Even though at some phase of their development, females may show a positive allometric growth of their chelipeds, as in *U. maracoani* (Hirose & Negreiros-Fransozo 2007), the values of *b* are always smaller than the observed in males (Negreiros-Fransozo *et al.* 2003, Hirose & Negreiros-Fransozo 2007).

In many male Brachyura, the growth of the chelipeds after the maturity becomes greater than in the juvenile phase, as a secondary sexual character (Hartnoll 1982), as observed in *U. thayeri* (Negreiros-Fransozo *et al.* 2003), *U. burgersi* (Benetti & Negreiros-Fransozo 2004), *U. maracoani* (Hirose & Negreiros-Fransozo 2007), *U. cumulanta* (Pralon & Negreiros-Fransozo 2008) and in the present study, a fact evidenced by the increase of *b* in the adult phase. However, as cited by Negreiros-Fransozo *et al.* (2003), the differences in the size and shape of the chelae between sexes are noticeable even when the crabs are still small. This high allometry of males is very important because the courtship behavior on this genus is mainly visual, through the waving with the giant chela during the reproductive period (Crane 1975). The genus *Uca* presents, among the brachyuran, males with the highest values of *b* for the growth of the cheliped (Masunari & Dissenha 2005). In other species of the superfamily Ocypodoidea, as in *Ucides cordatus,* the values of *b* do not exceed 1.50 (Pinheiro & Hattori 2006, Castiglioni *et al.* 2011b), while in *Uca, b* usually exceeds this value (Benetti & Negreiros-Fransozo 2004, Castiglioni & Negreiros-Fransozo 2004, Masunari & Dissenha 2005), which stands out again the importance of the giant chela on the ecology of these animals.

In the *U. thayeri* females studied herein, the relation AW vs. CW follows a pattern distinct from what is found in other brachyuran crabs, showing positive allometry in both juvenile and adult phases. However, this fact corroborates previous studies on *U. thayeri* (Negreiros-Fransozo *et al.* 2003), *U. burgersi* (Benetti & Negreiros-Fransozo 2004), *U. mordax* (Masunari & Dissenha 2005) and *U. rapax* (Castiglioni & Negreiros-Fransozo 2004). Thus, this seems to be a pattern for the genus *Uca*. Castiglioni & Negreiros-Fransozo (2004) described that juvenile females of *U. rapax* present a higher rate of abdomen growth than adult ones, which was also found by Masunari & Swiech-Ayoub (2003) for *U. leptodactyla* and by Negreiros-Fransozo *et al.* (2003) for *U. thayeri,* as well as in the present study. Probably the juvenile females invest in the abdomen growth and, by reaching the sexual maturity, they will be ready to incubate the eggs. As the abdomen is not an independent appendage as chelipeds, and it must work associated to the sternum, any disproportional growth after the puberty molt would difficult the movement of the pereopods (Masunari & Dissenha 2005).

In the relation AW vs. CW, males exhibited negative allometric growth in both phases and estuaries, as observed by Negreiros-Fransozo *et al.* (2003) for the same species. The abdomen of male Brachyura stores two pairs of gonopods, responsible for the transference of spermatophores during copula (Hartnoll 1982). Due to this simple function, especially when compared to the functionality of the female's abdomen, the growth of male's abdomen is allometrically negative or isometric in all ontogenetic phases (Benetti & Negreiros-Fransozo 2004, Castiglioni & Negreiros-Fransozo 2004, Pralon & Negreiros-Fransozo 2008).

In the relation GL vs. CW, juvenile males presented higher growth rates than adult males, as observed by Negreiros-Fransozo *et al.* (2003) for the same species, Castiglioni & Negreiros-Fransozo (2004) for *U. rapax* and Pralon & Negreiros-Fransozo (2008) for *U. cumulanta*. Juvenile males may invest in the growth of the gonopods and, by reaching sexual maturity, they will be ready to fertilize females. The lower growth rates of gonopods in adults may be explained by the fact that they have to be accommodated inside the abdomen, which in turn exhibited negative allometric growth, which restricts the length of the gonopods.

The regression coefficients and/or the intercepts of all relations differed between juveniles and adults in both sexes of *U. thayeri*, indicating contrasting growth patterns, also observed by Negreiros-Fransozo *et al.* (2003). This points out the need to analyze the relative growth separately for juveniles and adults, which was observed in other studies with species from the genus *Uca* (Negreiros-Fransozo *et al.* 2003 for *U. thayeri*; Masunari & Swiech-Ayoub 2003 for *U. leptodactyla*; Masunari & Dissenha 2005 for *U. mordax*; Masunari *et al.* 2005 for *U. maracoani*). These differences also demonstrate the changes in body parts throughout the ontogeny (Hartnoll 1974, 1978, Negreiros-Fransozo *et al.* 2003).

Through statistical analyses, it was possible to observe that males presented larger CL and AW at Ariquindá River, and the females, larger AW at Ariquindá River. Regarding the dispersion of points, the relationships presented similar growth patterns between estuaries, except for the relation CPL vs. CW for females. Baptista-Metri *et al.* (2005) and Araújo *et al.* (2012) listed the locality, time and abiotic variables as factors that may determine variations in the growth rate of organisms, which may explain the differences observed between the estuaries here studied.

It is well known that in Brachyura the most appropriate dimensions to determine the onset of morphological sexual maturity are the cheliped and abdomen for males and females, respectively (Masunari & Swiech-Ayoub 2003, Araújo *et al.* 2012). Thus, the CPL and AW were the variables chosen in the present study to better illustrate the maturity in *U. thayeri*. In both studied estuaries, males reached maturity at larger CW than females. This phenomenon was already observed in other species from the genus *Uca: U. burgersi* by Benetti & Negreiros-Fransozo (2004), *U. rapax* by Castiglioni & Negreiros-Fransozo (2004, 2006) and *U. cumulanta* by Pralon & Negreiros-Fransozo (2008). Males mature with larger sizes than females probably due to their greater investment in somatic growth, while females spend their energy in the reproductive process, saving energy for the production of eggs (Hartnoll 2006, Castiglioni & Negreiros-Fransozo 2006, Araújo *et al.* 2012). According to Crane (1975), small males avoid combating with large and dominant males. Thus, it is more advantageous to invest more energy in growth than in reproduction.

Despite of impact signs observed in Mamucabas River mangrove, males and females of this area reached maturity at sizes larger than those observed at Ariquindá River. Among the environmental factors that regulate the size at sexual maturity, stands out the availability of food (Hines 1989). It is probable that the population of *U. thayeri* of Mamucabas River is taking advantage from the greater availability of organic matter from pollution, as observed for *U. burgersi* by Benetti & Negreiros-Fransozo (2004).

Variations in the size at sexual maturity for a same species may occur in different spatial scales (Díaz & Conde 1989, Hines 1982, Araújo *et al*. 2012), even at near localities, as the Ariquindá and Mamucabas Rivers. Such fact also justifies the differences between the sizes at morphological sexual maturity in the present study and those observed by Negreiros-Fransozo *et al.* (2003) ($CW_{50\%♂}$ = 13.80 mm; $CW_{50\%♀}$ = between 10.70 and 16.80 mm).

The present study is the first contribution on the relative growth and morphological sexual maturity of *U. thayeri* in tropical areas, where despite of the abundance of this species, no study had been carried out on such aspects. As it could be observed, this species presented growth patterns similar to those found for other species of *Uca* and also with a population of *U. thayeri* from subtropical areas, São Paulo State (Negreiros-Fransozo *et al.* 2003). However, the size at morphological sexual maturity differed from the observed by these authors, showing latitudinal intraspecific differences in these values. Meanwhile, more studies are needed to better comprehend the ecology of this species in the tropical region.

Acknowledgements

The authors are thankful to: Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco (FACEPE), for financial support (APQ: 0108-2.04/07); to CNPq and CAPES for the fellowships; to the anonymous reviewers, for the special attention on our manuscript; to Adriano Martins for his help during fieldwork; to Dr. Tereza Cristina dos Santos Calado (UFAL), Dr. Jesser

Fidelis de Souza Filho (UFPE) and Dr. Sigrid Neumann Leitão (UFPE) for the important suggestions on this doctorate qualification; and especially to Dr. Petrônio Alves Coelho *in memoriam*, for being a great supervisor and friend. All sampling in this study was conducted in compliance with current applicable state and federal laws (ICMBio 14340-1).

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Received June 2012
Accepted October 2012
Published online November 2012