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GROWTH PHASES AND DIFFERENTIAL GROWTH BETWEEN SEXES OF *UCA MARACOANI* LATREILLE, 1802–1803 (CRUSTACEA, BRACHYURA, OCYPODIDAE)

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ABSTRACT Among crustacean decapods, fiddler crabs of the genus *Uca* are the most characteristic of the intertidal zones of tropical and subtropical estuaries. The present study determined the growth phases and the beginning of differential growth between the sexes, based on analyses of relative growth of *Uca maracoani*. Collections were made in the Jabaquara mangrove, located in Paraty, Rio de Janeiro, Brazil. Specimens were collected manually during low tide periods. In the laboratory, crabs were sexed and measured. We measured carapace width (CW), carapace length (CL), propodus length (PL; the right one for females and the major one for males), propodus height (PH), abdomen width (AW), and gonopod length (GL; for males). The beginning of differential growth between the sexes could be identified by the allometric technique. Males and females showed 3 distinct growth phases. Differential growth between sexes began when males reached 7 mm and females 9.2 mm CW. The growth pattern among different phases and the beginning of differential growth seemed to maintain a strict relationship with the ontogenetic changes, mainly those related to behavioral and reproductive aspects. This information is important for general biological knowledge of this species, mainly concerning aspects of its growth.

INTRODUCTION

Fiddler crabs of the genus *Uca* Leach, 1814 show a distinct sexual dimorphism. The chelipeds of females are symmetrical and small; both are adapted for catching and passing substrate particles to the mouth appendages. In males, one cheliped is more developed than the other, and is used for interaction with other males and defense of territory; only the smaller cheliped is utilized to scoop a small amount of material from the substrate and transport it to the mouth for feeding (Yamaguchi 1977, Christy and Salmon 1984, Rosenberg 2002), like those of the female.

The study of growth in crabs is facilitated by the hard tegument and the periodic change in the exoskeleton at molting. This makes possible exact measurements and observations of ontogenetic subdivisions in the body size at the beginning of morphological sexual maturity (Huxley and Teissier 1936).

Several aspects of the minor and major chelipeds of fiddler crabs have been studied. These studies have treated the morphological structures (Crane 1975, Yamaguchi 2001), variations in shape (Rosenberg 1997, 2002), sexual differences (Yamaguchi, 2005), handedness (Jones et al. 1982, Williams et al. 1981, Yamaguchi et al. 2001), and growth (Hartnoll 1974, 1978, 1982). The differential growth of the large chelipeds of males, as well as other body parts such as male gonopods and the abdomen of females (Hartnoll 1974, 1978), reveal the transition from juvenile to adult phases (Negreiros-Fransozo et al., 2003). Allometric growth has been studied in several species of

ocypodid crabs, including *Uca tangeri* (see Von Hagen 1987, Colpo et al. 2003), *Uca thayeri* (see Negreiros-Fransozo et al. 2003), *Uca burgersi* (see Benetti and Negreiros-Fransozo 2003), *Uca rapax* (see Castiglioni and Negreiros-Fransozo 2004), *Uca mordax* (see Masunari et al. 2005), and *Uca maracoani* (see Masunari et al. 2005).

We investigated a population of *U. maracoani* Latreille, 1802–1803 from the mud beach of the Jabaquara mangrove at Paraty, Rio de Janeiro, Brazil focusing on the determination of growth phases and the beginnings of differential growth between the sexes, based on relative growth.

MATERIAL AND METHODS

Uca maracoani occurs along coastlines in the Western Atlantic, including the Antilles, Venezuela, and the Guyanas. It is found along nearly the entire coast of Brazil, from the state of Maranhão south to Paraná (Melo 1996).

Sampling was carried out monthly on the mud beach of the Jabaquara mangrove (23°12'10.0"S, 44°43'14.1"W) from January to July 2003. The crabs were removed from their burrows manually during low tide. Each month, a capture effort of 60 min by 2 collectors was employed. The crabs were packed in plastic bags and frozen for about 2 h.

In order to ensure that the smallest classes were also collected, additional sampling was carried out by 2 people for 20 min, utilizing a small spoon. These small crabs were isolated in small containers, labeled, and transported to the laboratory.

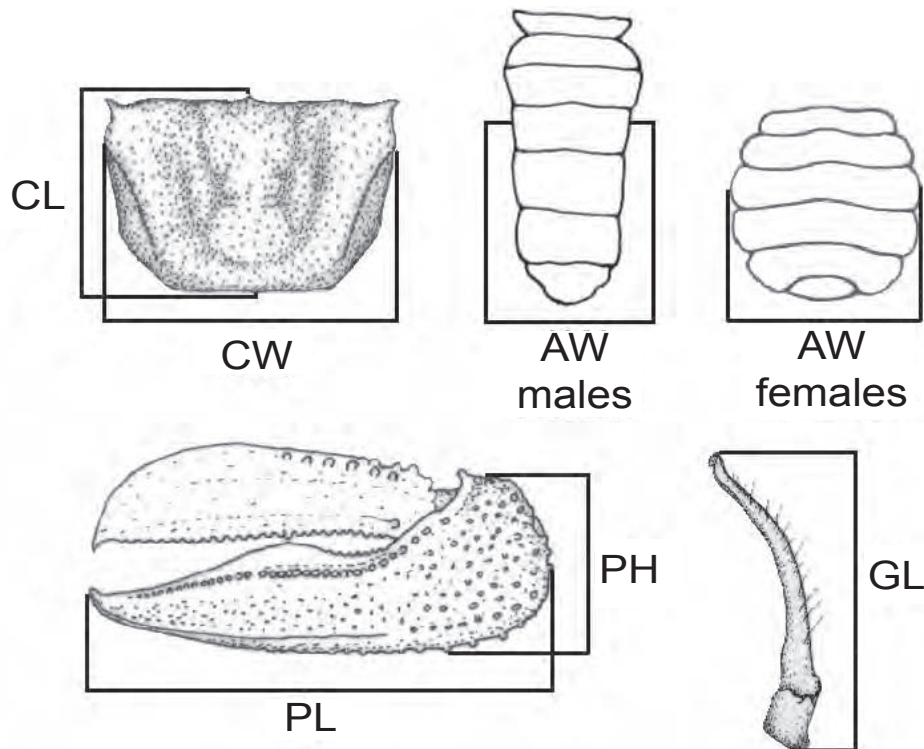


Figure 1. The body parts of *Uca maracoani* measured in this study. (CW = Carapace Width; CL = Carapace Length; AW = Abdomen Width; GL = Gonopod Length; PH = Cheliped Propodus Height; PL = Cheliped Propodus Length.)

In the laboratory, crabs in the intermolt stage were sexed and measured with a digital caliper (0.01 mm), for the following dimensions: carapace width (CW), carapace length (CL), propodus length of the cheliped (PL; right in females and major in males), propodus height of the cheliped (PH), abdomen width (AW) and gonopod length (GL; in males). The measured dimensions are illustrated in Figure 1. Crabs with an imperfect carapace or with body parts in regeneration were not used for analysis.

The smallest individuals, obtained in the additional samplings, were maintained alive in plastic containers with about 20 ml of sea water and fed daily with nauplii of *Artemia* sp. They were monitored daily for the presence of molts until they reached the juvenile stage when they could be identified to species.

The exuvia from each of the first 3 molts only (to minimize the effect of laboratory conditions) were sexed by counting the number of pleopods. Each exuvia was measured under a stereomicroscope for the same body dimensions described above for the adult crabs, except for gonopod length.

Statistical analyses

Relative growth was analyzed based on the allometric technique, for observation of changes in growth of certain body parts in relation to others (Huxley 1950). The data

were plotted in dispersion graphics. Next, the equation of function type $Y = aX^b$ was adjusted to the empirical points and linearized to the form $\log Y = a + b \log X$, where X = the independent variable, using the carapace width (CW); Y = dependent variables, utilizing the other body dimensions; b = allometric constant that expresses the allometric coefficient of body parts in the study. Growth could thus be characterized as positive allometry, when $b > 1$; negative allometry, when $b < 1$; or isometric, when $b = 1$ (Huxley 1950). The “ b ” value found was tested by Student’s t test with significance level $\alpha = 0.05$. To test the similarity of slopes and the intercepts of lines for each phase of development and between sexes, we used a covariance analyses (ANCOVA) ($\alpha = 0.05$) (Zar, 1996).

The programs Mature I and II (Somerton 1980a, b) were used to estimate the size at which males and females changed growth phase, based on the regression analysis of relative growth.

To determine the size at which the differentiation between sexes began, a series of successive covariance analyses was carried out, using intervals of 0.1 mm CW. This proceeded until the point where the lines of growth diverged, or the point at which the males and females attained growth represented by distinct lines ($\alpha = 0.05$).

RESULTS

A total of 563 crabs was collected (253 males and 310 females). Their sizes ranged from 4.9 to 43.7 mm CW (28.5 ± 10.1 mm) for males and from 5.1 to 38.7 mm CW (24.9 ± 7.9) for females. We obtained 92 exuvia from the small individuals raised. The sizes of exuvia ranged from 1.2 to 5.1 mm CW (2.8 ± 0.93); of these, only 7 specimens could be identified as males and 12 as females. The sizes of males ranged from 3.7 to 5.1 mm CW (4.4 ± 0.48) and of females from 3.5 to 5.0 mm CW (4.0 ± 0.51).

The change in growth phases and the beginning of differentiation in growth between the sexes could be expressed by PL vs. CW for males and AW vs. CW for females. The inflexion points of the growth lines related to the change of phases were estimated by means of the Mature I and II programs. Males (< 9.4 ; $9.4 \leq \text{CW} < 21.2$; ≥ 21.2 mm) and females (< 10.3 ; $10.3 \leq \text{CW} < 19.4$; ≥ 19.4 mm) showed 3 distinct growth phases. For females, Mature I indicated the CW50 (19.4 mm) equivalent to the interval of superposition of lines ($16.5 \geq X < 20.9$ mm CW) for juvenile and adult. The regression equations obtained for the growth phases and between sexes were submitted to ANCOVA, which verified that the pattern of growth differed ($P < 0.05$) between sexes and among phases. Thus, we can assume that the lines for different phases (undifferentiated, juvenile, and adult phase) and for sexes (males and females) could be better adjusted to isolated data than in a single line. Exceptions were obtained only for some phases in the relationships CL vs. CW and PH vs. CW. (Table 1)

Males and females showed different growth patterns of the carapace. For the relationship CL vs. CW, males showed negative allometry for all phases, whereas the females showed negative allometry only for the juveniles ($b = 0.819$), passing to discrete positive allometric growth in subsequent phases. A slight difference in the shape of the adult male carapace compared with females explained this.

The cheliped relationships PH vs. CW and PL vs. CW showed similar growth patterns. The males, for all age groups, showed positive allometry beginning in the undifferentiated phase ($b = 1.195$; $b = 1.147$ for PL vs. CW and PH vs. CW, respectively), passing to a more positive slope in the later phases ($b = 2.047$ and $b = 1.329$). The females showed less positive allometry compared with the males ($b = 1.056$ for the relationship PL vs. CW), passing to isometry or negative allometry in the case of the juvenile phase and adult females in the relationship PH vs. CW ($b = 0.831$).

For the relation AW vs. CW, sexual dimorphism in growth was very evident. However, in this case, the females showed positive allometry in all age group categories, increasing the slope in the juvenile-phase females ($b = 1.887$). The males showed isometric growth (undifferentiated $b = 0.958$), passing to a positive allometric (juvenile phase $b = 1.174$) and later to a negative allometric growth (adult $b = 0.944$).

Males (smaller than 4 mm CW) were not included in the analyses of the relationship GL vs. CW. The crabs were distributed in 2 age group categories, with different growth patterns ($b = 1.646$ and $b = 0.909$ juvenile phase and adults, respectively).

The onset of differential growth between sexes was at 7 mm CW for males and 9.2 mm CW for females (Figure 2D). Below these points, there was a single line of growth for both sexes ($\alpha = 0.05$).

The patterns of growth found for relationships performed with the data on sex differentiation determined by ANCOVA were the same among the ontogenetic phases, showing positive allometry for the 2 relationships analyzed in both sexes for the undifferentiated and juvenile phases. (Table 2)

DISCUSSION

Morphometric data are widely utilized in papers on crustaceans for the study of relative growth (Hartnoll 1974, 1982), especially for detection of changes in the level of allometry, which can be related to certain biological features of the species. Most of the studies on morphological structures in brachyuran crabs have used the dimensions of the carapace, abdomen, and chelipeds as a reference and found distinctive changes in such structures between sexes or growth phases.

In the population studied, *U. maracoani* showed 3 phases of growth. Similar patterns have been reported for other species of the genus: *U. tangeri* studied by von Hagen (1987), and *U. thayeri* studied by Negreiros-Fransozo et al. (2003). Other brachyuran crabs, mainly in the superfamily Majoidea, show similar patterns, although the growth phases are known by different names (Sainte-Marie et al. 1995, Alunno-Bruscia and Sainte-Marie 1998, Sampedro et al. 1999).

The first phase of growth found for *U. maracoani* is represented by morphologically undifferentiated crabs, which only show visible secondary sexual characters in the largest classes. They may not have initiated gonad development; this phase can be called the undifferentiated period.

The first point of the transition is from undifferentiated to a second phase of growth that, probably, is the

TABLE 1

Regression analyses of morphometric data of *Uca maracoani*. Carapace width (CW) was used as the independent variable. CW = Carapace Width; CL = Carapace Length; AW = Abdomen Width; PL = Cheliped Propodus Length; PH = Cheliped Propodus Height; and GL = Gonopod Length. UMF = undifferentiated males and females; UJF = undifferentiated and juvenile female; JAM = juvenile and adult males; JAF = juvenile and adult female UF = undifferentiated females; JF = juvenile females; AF = adult females; UM = undifferentiated males; JM = juvenile males; AM = adult males; + and - = allometry; 0 = isometry.)

Relationship	Sex	N	Intercept		r^2	T ($b=1$)	P	Allometry	Results of	
			(log)	Slope					Mature I and II	Change of phases
			a	b					F value	
CL vs. CW	UMF	196	0.240	0.819	0.981	22.60	0.00	-		
	JAM	255	-0.108	0.967	0.997	29.73	0.00	-		
	JF	56	-0.216	1.060	0.978	2.82	0.00	+		
	AF	136	-0.198	1.043	0.992	5.66	0.00	+		
AW vs. CW	UM	91	-0.626	0.958	0.854	0.97	0.00	0		
	JM	64	-0.818	1.174	0.936	4.47	0.00	+		
	AM	189	-0.495	0.924	0.944	5.00	0.00	-		
	UF	109	-0.680	1.105	0.937	3.74	0.00	+	16.94	10.30 mm
	JF	65	-1.481	1.887	0.927	13.43	0.00	+	72.94	19.30 mm
	AF	221	-0.808	1.377	0.968	22.35	0.00	+		
PL vs. CW	UM	86	-0.500	1.195	0.916	5.00	0.00	+	20.62	9.40 mm
	JM	61	-0.819	1.576	0.969	16.00	0.00	+	140.13	21.20 mm
	AM	180	-1.454	2.047	0.982	50.00	0.00	+		
	UJF	157	-0.453	1.056	0.986	6.60	0.00	+		
	AF	134	-0.377	1.003	0.969	0.00	1.00	0		
PH vs. CW	UM	75	-0.927	1.147	0.855	2.67	0.00	+		
	JM	75	-0.851	1.329	0.967	11.38	0.00	+		
	AM	179	-1.239	1.613	0.976	32.10	0.00	+		
	UF	99	-0.858	0.948	0.923	1.88	0.00	0		
	JAF	190	-0.768	0.831	0.945	12.14	0.00	-		
GL vs. CW	JM	71	-1.177	1.646	0.872	8.53	0.00	+		
	AM	189	-0.269	0.909	0.955	6.43	0.00	-		

beginning of gonad maturation (juvenile phase). In a study on *U. tangeri*, von Hagen (1987) considered the interval between the points of inflexion as a phase of transition or maturation, which extends to the second inflexion point that identifies the transition of individuals to the adult phase.

Adult fiddler crabs can successfully copulate (functional maturity) only when their gonads are mature, i.e., producing gametes, and when they can display specific behaviors, such as the male “waving” display to attract females. Sexual maturation is an extended process that involves gradual ontogenetic changes, rather than a precise moment, such as after the puberty molt (Luppi et al. 2004).

Uca maracoani showed positive allometric growth in the change of phases for sexes and age group categories. The chelipeds of males showed a gradual increase

in allometry among phases, reaching the highest level in adult males. Females showed low, positive allometry in the juvenile phase, considerable positive allometry after the first inflexion point, and then a subsequent decrease after they reached morphological maturity. This growth pattern may reflect the higher energetic investment of females in reproduction during the adult phase. According to Hartnoll (2006), the major energetic needs are for ripening of gonads and formation of associated reproductive products.

Slower growth can also reflect reduced energy intake because of restrictions on feeding. In females, a more general phenomenon is a restriction on feeding during incubation. A further limitation on growth in reproducing females is that they cannot molt while incubating eggs (Hartnoll 2006).

The increase in allometry of chelipeds, in the case of fiddler crab males, just after they reach sexual maturity,

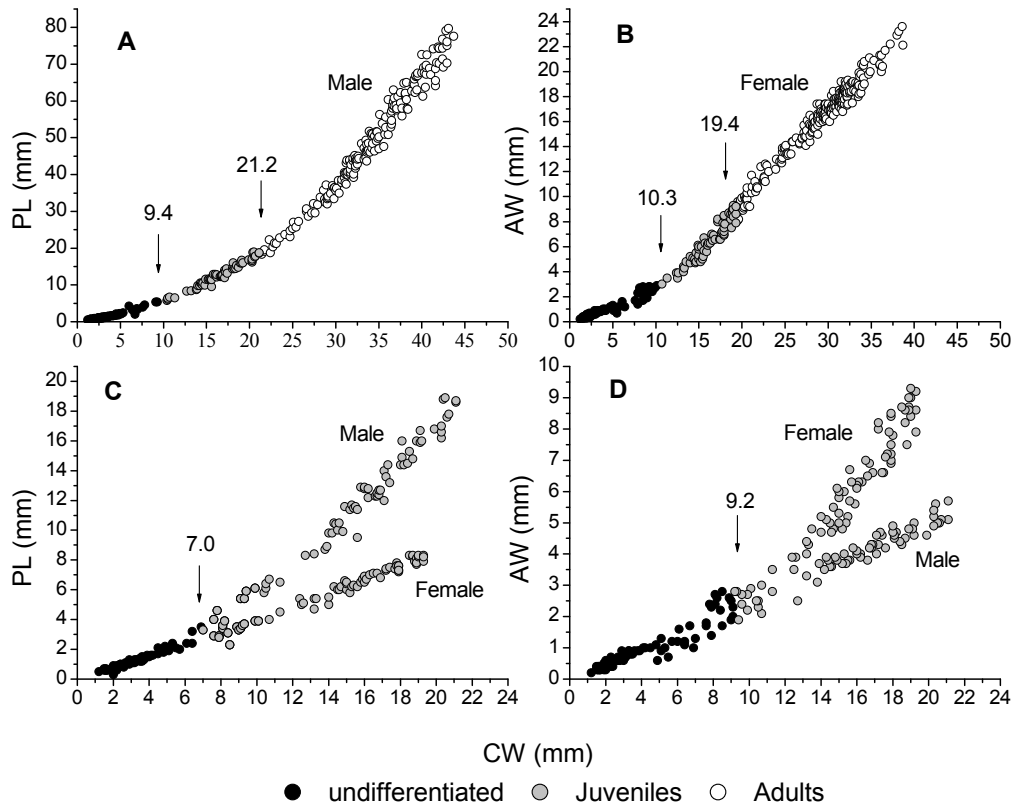


Figure 2. *Uca maracoani*. Dispersion points of relations between the carapace width and the dependent variables. PL = Cheliped Propodus Length; AW = Abdomen Width. A and B are dispersion points related to the changes of growth phases. C and D are dispersion points related to the onset of differential growth between the sexes.

can be very important, because the behavior of cohorts in this genus is predominantly visual. An experimental study with *U. tangeri* by Oliveira and Custódio (1998) found that females spend more time near males with larger claws, in binary choice tests. Large chelipeds are possibly more easily seen by females, increasing the chances that a male's burrow will be visited and he will be chosen for reproduction (Crane 1975, Yamaguchi 1971, Latruffe et al. 1999). In some species, *U. vocans vocans* studied by Salmon (1984) and *U. bebei* studied by Christy (1987), for instance, there is no apparent preference of females for males with larger chelipeds. In such cases, the advantage may be related to the results of fights among males (Crane 1975).

Contests consist of a series of behavioral elements in which the major claw of males plays the principal role (Crane 1975, Salmon and Hyatt 1983, Pratt et al. 2003). In fiddler crabs, the contest duration is expected to reflect the endurance of the weaker of 2 contestants, typically the smaller individual (Hyatt and Salmon 1978, Jennions and Backwell 1996, Pratt et al. 2003). Fighting ability is correlated with carapace width and size of the claw (Hyatt and Salmon 1978), and represents an important feature. Although some contest elements appear dangerous, death or serious injury seldom result (Pratt et al. 2003).

In females, the abdomen widens during growth. This may be related to protection of the gonopores and the mass of eggs during incubation (Hartnoll 1982). The female carapace also widens in relation to that of males, which increases the capacity of the incubatory chamber where the eggs will be carried.

The sexes differed in size at maturity. The larger size of males may reflect strong competition among them, considering that larger males can exert strong influence over smaller males. According to Crane (1975), *U. maracoani* shows a hierarchical behavior, where smaller males avoid combat with the larger, dominant males, leaving the interaction area. In this context, it could be more advantageous for young males to initially invest in growth rather than in reproduction.

Comparing the Paraty population of *U. maracoani* (present study) with the population from Guaratuba studied by Masunari et al. (2005), it is easily realized that there exist significant population differences in relation to growth and morphological sexual maturity. (Table 3) For both sexes, the size at sexual maturity found for the *U. maracoani* population at Jabaquara was greater than for the population at Guaratuba studied by Masunari et al. (2005). This was also seen when the size at differentiation of cheliped (males)

TABLE 2

Regression analyses of morphometric data, based on the growth differentiation between the sexes of *Uca maracoani*. CW = Carapace width; AW = Abdomen Width; PL = Cheliped Propodus Length. UT = undifferentiated males and females; JM = juvenile males; JF = juvenile females; + positive allometry.

Relationship	Sex	N	Intercept		r^2	T (b=1)	P	Allometry	Size at differentiation	Results of ANCOVA (P value)
			(log) a	Slope b						
AW vs. CW	UT	191	-0.663	1.055	0.89	2.20	0.00	+	9.2 mm	0.06
	JM	65	-0.950	1.281	0.90	13.56	0.00	+		
	JF	70	-1.343	1.773	0.94	15.77	0.00	+		
PL vs. CW	UT	167	-0.458	1.079	0.88	2.63	0.00	+	7.0 mm	0.06
	JM	65	-0.737	1.509	0.97	18.17	0.00	+		
	JF	72	-0.542	1.133	0.95	4.92	0.00	+		

is analyzed. Probably, the large difference between the populations may be responsible for these differences in size at sexual maturity and cheliped differentiation. According to Masunari et al. (2005), the size at differentiation of the cheliped in fiddler crabs apparently is correlated with the maximum size that the species can reach.

The population of *U. maracoani* studied by Masunari et al. (2005) represents, according to Melo (1996), the southern limit of distribution for this species on the Brazilian coast. Consequently, the environmental conditions such as temperature, salinity, food, and size of sediment particles, to which these crabs are exposed, are different from for the population at Jabaquara. This may reflect the differential growth, development, and size of those individuals.

Size variations are common and may reflect the phenotypic plasticity of the organisms or the influence of

environmental factors such as photoperiod, temperature, and food availability (Campbell and Eagles 1983). Such factors can explain the larger CW of specimens of *U. maracoani* from Jabaquara compared with the population at Guaratuba. For a precise determination of which factor or factors are more important for the size difference between these populations, a further, more detailed study would be necessary.

The growth patterns during the different phases, as well as the beginning of differential growth, and morphological sexual maturity seem to maintain a strict relationship with ontogenetic changes, mainly related to behavioral or reproductive aspects and/or environmental factors. This information is important for general biological knowledge of the species, mainly for understanding its growth processes.

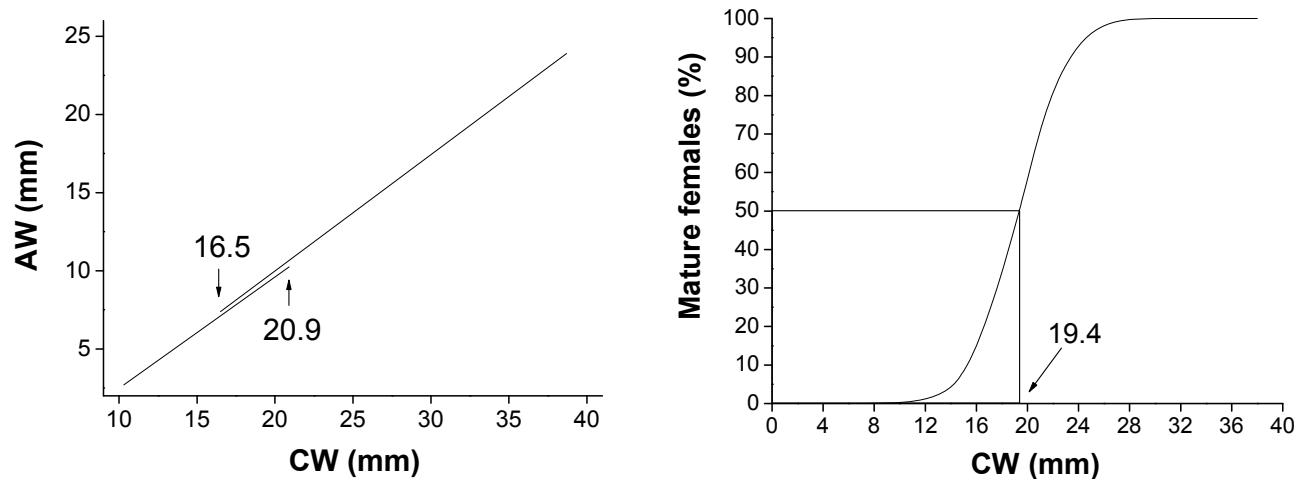


Figure 3. *Uca maracoani*. A – Lines representing the relationships between carapace width (CW) and abdomen width for females. The arrow shows the size at which the puberty molt occurs. B – The logistic equation indicating the size in which 50 % of females are mature.

TABLE 3

Growth features in 2 populations of *Uca maracoani*. Dimensions are in mm. *s* = standard deviation.

Population (reference)	Sex	Maximum size	Mean size $\pm s$	Growth phase	Size at differentiation	Sexual maturity
Paraty, RJ (present study)	male	43.7	28.50 \pm 10.1	3	7.0	21.20
	female	38.7	24.90 \pm 7.9	3	9.2	19.30
Guaratuba, PR (Masunari et al. 2005)	male	34.12	21.53	2	3.27	17.85
	female	29.20	19.13	2	–	11.75

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