

ALLOMETRIC GROWTH AND MORPHOLOGICAL SEXUAL MATURITY OF THE ATLANTIC GHOST CRAB *OCYPODE QUADRATA* (FABRICIUS, 1887) (CRUSTACEA: DECAPODA: OCYPODIDAE) FROM THREE DIFFERENT GEOGRAPHIC REGIONS

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ABSTRACT: We provide a comparative analysis of the relative growth and morphological sexual maturity in populations of the widespread ghost crab *Ocypode quadrata* from three different regions of the western Atlantic coast. The populations of *O. quadrata* selected for this study were located at Punta Arenas Beach, Margarita Island, Macanao Peninsula in Venezuela; at Vermelha do Norte Beach, Ubatuba, State of São Paulo, Brazil; and Atalaia Beach, Aracaju, State of Sergipe, Brazil. We used the allometric technique to determine the size at onset of the morphological sexual maturity of *O. quadrata* in all samples. The analyzed variables were major cheliped length and height, abdomen width for males and females and gonopod length for males. The values estimated to the size at onset of sexual maturity of each population, expressed in carapace width, were: Vermelha do Norte = 15.46 mm (males) and 19.4 mm (females); Atalaia = 15.77 mm (males) and 17.77 mm (females); and Arenas = 14.46 mm (males) and 20.34 mm (females). The absolute size at onset of sexual maturity varied little among the populations. When the proportional size at onset of sexual maturity (size at onset of sexual maturity/maximum size) was considered, influence of the body growth pattern became evident in Atalaia. The size at onset of sexual maturity and body size and growth in each population seemed to reflect local environmental stimuli rather than those related to latitude.

Key words: latitudinal variation, crab size, allometry, Brazil, Venezuela.

INTRODUCTION

The ghost crab *Ocypode quadrata* (FABRICIUS, 1787) is a conspicuous and widespread (QUIJÓN *et al.* 2001; BLANKENSTEYN 2006) species of the sandy beach macrofauna closely related to the beach features (QUIJÓN *et al.* 2001; BLANKENSTEYN 2006; YOUNG & LIM 2009), with records from New Jersey, USA (MILNE & MILNE 1946) to Rio Grande do Sul, Brazil (MELO 1996; ALBERTO & FONTOURA 1999). There is an extensive literature concerning biological and ecological aspects of ghost

crab species, including *O. quadrata* (HALEY 1969, 1972; WOLCOTT 1978; STEINER & LEATHERMAN 1981; LEBER 1981; WOLCOTT & WOLCOTT 1984; ALBERTO & FONTOURA 1999; BARROS 2001; QUIJÓN *et al.* 2001; FRANZOZO *et al.* 2002; NEGREIROS-FRANZOZO *et al.* 2002; TURRA *et al.* 2005; NEVES & BEMVENUTI 2006; VALERO-PACHECO *et al.* 2007; ROSA & BORZONE 2008; LÓPEZ-GRECO *et al.* 2009). In particular, data on abundance/density are numerous, due to studies that propose *Ocypode* species as potential indicators of sandy beaches quality based on this variable (e.g., BARROS

2001; TURRA *et al.* 2005; ROSA & BORZONE 2008; YONG & LIM 2009; POMBO & TURRA 2013; BORZONE *et al.* 2015; SCHLACHER *et al.* 2016).

Conversely, information on the relative growth and morphological sexual maturity in ghost crab species is scarce in the literature. For *O. quadrata*, studies on only two populations are available (HALEY 1969; FRANSOZO *et al.* 2002). These investigations allow identification of ontogenetic phases and estimation of body sizes at the onset of sexual maturity in these crustaceans (HUXLEY & TEISSIER 1936). This is achieved by assessing quantitative change in morphology of body structures that are directly involved in reproductive activities in the juvenile-adult transition. In Ocypodoidea, these structures are chelipeds and gonopods of males, abdomen and pleopods in females (HALEY 1969; VON HAGEN 1987; COLPO *et al.* 2003; NEGREIROS-FRANSOZO *et al.* 2003; BENETTI & NEGREIROS-FRANSOZO 2004; HIROSE & NEGREIROS-FRANSOZO 2007). Chelipeds are used by adult males during courtship and agonistic interactions (CRANE 1975; FRANSOZO *et al.* 2002). Adult females incubate eggs in the abdomen, where they remain adhered to the pleopods, during embryonic development (HARTNOLL 1982).

In populations of a species with such a wide geographical range as *O. quadrata*, variations in reproductive patterns can occur. Detection and interpretation of these variations are required for adequate understanding of the adaptations of the species to different environmental conditions (SASTRY 1970). Information on relative growth and sexual maturation complements to the general knowledge of reproductive pattern and other aspects of the biology of a species, and serve as a tool to evaluate variations in life history and population dynamics at different geographical scales, as well as for the development of management programs for natural species conservation (COBB & PHILLIPS 1980; HINES 1989).

This paper described the relative growth and the size at onset of morphological sexual maturity of *O. quadrata* from three populations located in different geographical regions along the Western Atlantic coast (Venezuela and Brazil). We compared the results of these populations and those available in the literature in order to assess the influence of latitudinal and local factors on the relative growth pattern, the size at onset of morphological sexual maturity, and the maximum size attained by individuals.

MATERIAL AND METHODS

The studied populations of the ghost crab *O. quadrata* were obtained from Punta Arenas Beach (11°3'59.5"N;

64°15'11.12"W), Margarita Island, Venezuela; Atalaia Beach (10°58'46"S; 37°2'11"), Aracaju, Sergipe, Brazil; and Vermelha do Norte Beach (23°24'48"S; 44°02'18"W), Ubatuba, São Paulo, Brazil. All localities are steeply sloping sandy beaches facing the open sea. Punta Arenas and Vermelha do Norte beaches have coarse sediment, while Atalaia beach have finer sediment.

We sampled ghost crabs from January through December 2002 at Vermelha do Norte (Brazil), from February 2007 through January 2008 at Punta Arenas Beach (Venezuela), and from February through July 2016 at Atalaia (Brazil). We captured the crabs, manually, along the entire length of the beaches. Two collectors sampled each beach for 30 min each, during nocturnal low tide. In the laboratory, we assessed the sex of each specimen; and measured, with a digital caliper (0.01 mm), the following body dimensions: carapace width (CW), propod length of the major cheliped (PL), propod height of the major cheliped (PH), abdomen width (AW), and gonopod length (GL). The measurement for each dimension followed that described by FRANSOZO *et al.* (2002) for the same species.

Allometric growth analysis

The analysis of relative growth of the crabs was based on the allometric equation: $y = aCW^b$, in which y = dimension studied, CW = carapace width (reference variable), b = relative growth rate of the body structure (slope), and a = line intercept on the y axis. The parameters of the equations were estimated by a linear regression on log-transformed morphometric data, which provided the linearized version of equation ($\log y = \log a + b \cdot \log CW$). The allometric level of each body structure ($b > 1$ – positive allometry; $b < 1$ – negative allometry; $b = 1$ – isometry) was assessed by testing the null hypothesis H_0 : $b = 1$ with the t test for linear regression coefficient ($\alpha = 0.05$), described in ZAR (2010).

Separation of data points (CW , y) into development stage categories (juveniles and adults) was performed with the K -means clustering method. It distributes the data in groups of numbers previously established by iteration, which minimize the within groups variance and maximize the among group variance. The result of this classification was refined using the discriminant analysis. We used the same statistical procedure suggested by SAMPEDRO *et al.* (1999) and CORGOS & FREIRE (2006).

Comparisons of the obtained linear functions were performed with analysis of covariance (ANCOVA) according to two approaches:

- between adult and juvenile specimens of each population to assess differences during the course of development; in cases in which non-significant results were obtained for both allometric coefficient (b) and intercept (a), a single linear function was obtained for the entire corresponding dataset;

- each development stage category between localities to assess regional differences.

Size at Onset of Morphological Maturity

The maturation size was determined as the carapace width at which 50% of the specimens showed morphometric relationships that characterize the adult condition (carapace width 50%). This value was obtained by logistic function interpolation ($PA = a/(1+be^{-cx})$), adjusted to the data for adult proportion (PA) vs. size classes (1.5 mm) plots.

For comparisons of size at onset of sexual maturity (SOM) among populations of different individual sizes, the proportional size at onset of morphological maturity (PSOM) was calculated by dividing the SOM by the maximum size based on the proposed by TAKANO *et al.* (2016).

RESULTS

At Vermelha do Norte beach we obtained 423 ghost crabs, including 203 males (carapace width range = from 9.6 mm to 37.8 mm) and 221 females (from 9.8 mm to 36.7 mm). At Atalaia beach, we obtained 375 crabs, including 234 males (from 7.39 mm to 38.74 mm) of carapace width and 141 females (from 8.82 mm to 38.50 mm). At Punta Arenas beach, we obtained 366 specimens, including 192 males (7.4 mm to 42.94 mm) and 174 females (5.8 mm to 50.82 mm).

Level of allometry and change in the allometric growth pattern with development stages

All analyzed body structures of both males and females showed positive allometry, except AW of males from Punta Arenas (Venezuela), which showed negative allometry in juveniles and isometry in adults (TABLES 1, 2). In males, relative growth patterns differed between juveniles and adults in all analyzed variables, except AW in the Vermelha do Norte and Atalaia populations. In the Vermelha do Norte population, comparison of slopes provided a marginally significant result for PH of females. Most of the detected differences occurred in the relative growth rate (slope). In the case of the Punta Arenas population, the obtained functions differed in terms of the

intercept (TABLE 1). In females, the relative growth rate varied among development stages in AW (Punta Arenas), PL (Atalaia), and PH (Punta Arenas and Atalaia). All other significant results were obtained in intercept comparisons.

The most evident change in allometric growth pattern between juveniles and adults occurred in GL and AW for males and females, respectively. Thus, we employed these variables to estimate the size at onset of maturity of each sex of the studied populations.

Variation of allometric growth pattern among populations

The allometric growth of almost all development stage categories of males differed between populations. The only exceptions were related to juvenile males: no significant difference occurred in the PH vs. CW relationship between Punta Arenas population and the other two populations; and the GL vs. CW relationship did not differ between Punta Arenas and Vermelha do Norte populations. In the case of females, we did not find difference in the AW vs. CW relationship of juveniles between Vermelha do Norte and Atalaia populations, neither for the PH vs. CW relationship of adults between Punta Arenas and Atalaia populations (TABLE 3, 4).

Size at Onset of the sexual Maturity (SOM)

The SOM values estimated with the GL vs. CW relationship for males were 15.46 mm for the Vermelha do Norte population, 14.46 mm for the Punta Arenas population and 15.77 mm for the Atalaia population. The carapace width of the smallest adult males was 14.9 mm for Vermelha do Norte, 14.40 mm for Punta Arenas and 12.57 mm for Atalaia (Fig. 1).

The SOM values for females estimated with the AW vs. CW relationship were 19.42 mm for Vermelha do Norte; 20.34 mm for Punta Arenas; and 17.77 mm for Atalaia. The CW values of the smallest mature female were 19.4 mm, 18.59 mm, and 21.34 mm of carapace width, for the Vermelha do Norte, Punta Arenas and Atalaia populations, respectively (Fig. 2).

DISCUSSION

All populations studied showed the same relative growth pattern, with positive allometric growth for all relationships analyzed, except carapace width vs. abdomen width, for males from Venezuela. The increase in allometry found in males' chelipeds after they reach sexual maturity can be considered relevant to reproduction, since the chelipeds in ghost crabs can be used to maximize

TABLE 1 - *Ocypode quadrata* (FABRICIUS, 1887). Results of linear regression and state allometry of body parts of males and results of juveniles vs. adults comparison.

Relationship	Population	n	Intercept	Slope	r ²	t (b=1)	p	Allometry	ANCOVA	
									a	b
AW vs. CW	VNT	192	-0.764	1.067	0.96	6.70	0.00	+	0.15	0.50
	ATT	203	-0.818	1.146	0.97	89.31	0.00	+	0.57	0.72
	ARJ	106	-0.501	0.841	0.89	3.80	0.00	-	---	0.01
	ARA	65	-0.679	1.00	0.89	23.10	0.00	=	---	0.01
	VNJ	50	-0.212	1.050	0.97	2.29	0.00	+	0.18	0.00
PL vs. CW	VNA	130	-0.550	1.322	0.97	18.94	0.00	+	0.18	0.00
	ATJ	72	-0.316	1.123	0.98	62.94	0.00	+	---	0.00
	ATA	145	-0.666	1.401	0.96	68.11	0.00	+	---	0.00
	ARJ	138	-0.256	1.080	0.96	4.68	0.00	+	0.00	0.11
	ARA	38	-0.641	1.362	0.94	6.70	0.00	+	---	0.00
PH vs. CW	VNJ	50	-0.599	1.111	0.95	3.36	0.00	+	---	0.00
	VNA	130	-0.929	1.387	0.96	16.12	0.00	+	---	0.00
	ATJ	73	-0.694	1.180	0.98	60.32	0.00	+	---	0.00
	ATA	146	-1.012	1.439	0.94	48.81	0.00	+	---	0.00
	ARJ	106	-0.649	1.147	0.92	4.74	0.00	+	---	0.00
GL vs. CW	ARA	68	-0.996	1.412	0.95	11.13	0.00	+	---	0.00
	VNJ	37	-1.960	2.220	0.73	5.47	0.00	+	---	0.00
	VNA	148	-0.587	1.157	0.96	8.92	0.00	+	---	0.00
	ATJ	32	-1.938	2.130	0.78	10.69	0.00	+	---	0.00
	ATA	186	-0.794	1.295	0.97	79.79	0.00	+	---	0.00
	ARJ	60	-1.960	2.265	0.56	4.75	0.00	+	---	0.00
	ARA	106	-0.711	1.229	0.93	7.15	0.00	+	---	0.00

CW = Carapace Width; AW = Abdomen Width; PL = Cheliped Propodus Length; PH = Cheliped Propodus Height; and GL = Gonopod Length; VNT= (Vermelha do Norte) Juvenile + Adult; VNJ = (Vermelha do Norte) Juvenile; VNA = (Vermelha do Norte) Adult; ATT = (Atalaia) Juvenile + Adults; ATJ = (Atalaia) Juvenile; ATA = (Atalaia) Adult; ARJ (Punta Arenas) juveniles; ARA (Punta Arenas) Adult; “+” = positive allometry; “-” = Negative allometry, and “0” = isometry.

mating (NEGREIROS-FRANZOZO *et al.* 2002) or in agonistic interaction with other males. Females also showed positive allometric growth of the chelipeds, but without marked changes during their ontogeny. This is probably associated with the predatory habit of this species that uses the chelipeds often to capture prey (TROTT & ROBERTSON 1984).

The gonopod length showed an inverse pattern with allometry level decreasing from juveniles to adults. In this case, we presume that this is due to the morphology of the female gonopore, because a large gonopod could constrain mating, making copulation involving large males small- or medium-sized mature females difficult or impossible. A decrease in the growth rate of the gonopod,

after attained the sexual maturity, would thus allow large males to mate with females of a wider size range. Further comparative morphological studies of the gonopod and gonopore are required to clarify this aspect. The increase in relative size observed in the abdomen of females in the transition from juveniles to adults has been attributed to gonopores protection and enhancement of egg-bearing capacity during the incubation period (HARTNOLL 1982).

Although differences in relative growth relationships were detected among the studied populations, no clear trend or pattern related to environment gradients (sediment type, conservation state or geographical position). This indicates that environmental factors have influenced relative size of body parts locally.

TABLE 2 – *Ocypode quadrata* (FABRICIUS, 1887). Results of linear regression and state allometry of females body parts and results of juveniles vs. adults comparison.

Relationship	Population	n	Intercept	Slope	r ²	t (b=1)	p	Allometry	ANCOVA		
									a	p	b
AW vs. CW	VNJ	69	-1.291	1.604	0.93	11.76	0.00	+	0.00	0.46	
	VNA	145	-1.141	1.566	0.95	20.21	0.00	+			
	ATJ	68	-1.082	1.435	0.79	16.24	0.00	+	0.00	0.52	
	ATA	67	-0.798	1.355	0.86	20.30	0.00	+			
	ARJ	112	-0.867	1.211	0.88	4.98	0.00	+	---	0.00	
	ARA	57	-1.475	1.741	0.95	18.52	0.00	+			
PL vs. CW	VNT	200	-0.293	1.114	0.99	19.00	0.00	+	0.81	0.12	
	ATJ	63	-0.336	1.132	0.96	38.47	0.00	+	---	0.00	
	ATA	63	-0.645	1.354	0.94	33.91	0.00	+			
	ART	167	-0.244	1.069	0.96	7.37	0.00	+	0.08	0.04	
PH vs. CW	VNT	195	-0.729	1.216	0.98	22.97	0.00	+	0.21	0.05	
	ATJ	63	-0.693	1.166	0.94	32.60	0.00	+	---	0.00	
	ATA	63	-1.151	1.500	0.91	26.03	0.00	+			
	ARJ	109	-0.583	1.06	0.95	3.0	0.00	+	---	0.00	
	ARA	56	-0.789	1.24	0.98	10.0	0.00	+			

CW = Carapace Width; AW = Abdomen Width; PL = Cheliped Propodus Length; PH = Cheliped Propodus Height; VNT= (Vermelha do Norte) Juvenile + Adult; VNJ = (Vermelha do Norte) Juvenile; VNA = (Vermelha do Norte) Adult; ATT = (Atalaia) Juvenile + Adults; ATJ = (Atalaia) Juvenile; ATA = (Atalaia) Adult; ARJ (Punta Arenas) juveniles; ARA (Arenas) Adult; “+” = positive allometry; “-” = Negative allometry, and “0” = isometry.

The size at onset of maturity did not differ markedly among most of the *O. quadrata* populations analyzed in this study. Comparisons to results obtained in other studies (TABLE 5) reveal a considerable higher value of the size at onset of sexual maturity that was estimated for males of the Vermelha do Sul beach (FRANSOZO *et al.* 2002) is considerably higher than those of the other South American populations. Since Vermelha do Norte and Vermelha do Sul beaches are located in the same geographic region and their respective populations show individuals with similar size range, factors concerning beach features or conservation state should be considered due the differences found between them (NAKAGAKI & PINHEIRO 1999; ROCHA 2008). The relatively high values obtained for the Texas population (HALEY 1969) should be considered with caution, as the criterion adopted by the author to evaluate the morphological sexual maturity (histological evidences) was not the same as the one used in other studied populations. These results differs from the finding for the grapsid crab *Helice crassa*, studied by JONES & SIMONS (1983); for some brachyuran species (HINES 1989); for the caridean shrimp *Betaeus truncatus* studied by LARDIES (1995); and for the pinnotherid crab *Pinnaxodes chilensis* studied by LARDIES & CASTILLA (2001). These

authors assumed that the size at onset of sexual maturity and also asymptotic size (see below) increases with the latitudinal gradient, due the environmental variation found in those different regions. Apart from latitude, differences of the size at onset of sexual maturity among populations have been attributed to influences of local conditions such as temperature, food availability, population density, and subtle changes on substrate on the life history of species which can also diminish individuals' growth (HINES 1989; BENETTI & NEGREIROS-FRANSOZO 2004; SILVA *et al.* 2014). In the case of the considered *O. quadrata* population these local environmental peculiarities seem to affect the size at onset of sexual maturity more strongly than factors related to latitudinal gradient.

In relation to sex, all compared populations showed higher values of size at onset of sexual maturity from females in comparison to males (Fig. 3 A). This result shows that males can increase their opportunities to mate, when they reach sexual maturity at relatively small sizes (POWELL *et al.* 1974; JIVOFF 2003; ALMEIDA *et al.* 2013).

When the proportional size at onset of maturity is considered, the variability becomes narrower as expected

TABLE 4 - *Ocypode quadrata* (FABRICIUS, 1887). Comparisons of allometric relationships of females from the three studied populations.

Relationship	Factor (Group)	VN		AR		F	p
		Par. (log)	Value	Par.(log)	Value		
AW vs. CW	Juvenile	a	-1.291	a	-0.867	---	---
		b	1.604	b	1.211	25.11	0.00*
	Adult	a	-1.141	a	-1.475	---	---
		b	1.566	b	1.741	11.91	0.00*
PL vs. CW	Total	a	-0.293	a	-0.244	---	---
		b	1.114	b	1.069	16.40	0.00*
PH vs. CW	Total vs. Adult	a	-0.729	a	-0.789	14.08	0.00*
		b	1.22	b	1.24	1.20	0.27
		VN		AT			
		Par. (log)	Value	Par.(log)	Value		
AW vs. CW	Juvenile	a	-1.291	a	-1.082	1.85	0.17
		b	1.604	b	1.435	2.85	0.09
	Adult	a	-1.141	a	-0.798	---	---
		b	1.566	b	1.355	10.84	0.00*
PL vs. CW	Total vs. Adult	a	-0.293	a	-0.645	70.38	0.00*
		b	1.114	b	1.354	0.54	0.46
PH vs. CW	Total vs. Adult	a	-0.729	a	-1.151	53.05	0.00*
		b	1.22	b	1.500	1.95	0.16
		AR		AT			
		Par. (log)	Value	Par.(log)	Value		
AW vs. CW	Juvenile	a	-0.867	a	-1.082	---	---
		b	1.211	b	1.435	5.48	0.02*
	Adult	a	-1.475	a	-0.798	---	---
		b	1.741	b	1.355	18.26	0.00*
PL vs. CW	Total vs. Adult	a	-0.244	a	-0.645	23.08	0.00*
		b	1.069	b	1.354	3.26	0.07
PH vs. CW	Juvenile	a	-0.583	a	-0.693	---	---
		b	1.06	b	1.166	31.43	0.00*
	Adult	a	-0.789	a	-1.151	3.75	0.05
		b	1.24	b	1.500	3.62	0.05

CW = Carapace Width; AW = Abdomen Width; PL = Cheliped Propodus Length; PH = Cheliped Propodus Height; VN = Vermelha do Norte beach; AR = Ponta Arenas beach; AT = Atalaia beach. * = significant statistical difference (ANCOVA, $\alpha = 0.05$); Par = Parameter.

(Fig. 3 B). The low values from Punta Arenas beach population reflect either higher growth rate or longer lifespan of individuals which is a matter that deserve further investigations. It is also noteworthy that in terms of proportional SOM data from the Mustang Island population is closer to those of the Brazilian populations analyzed in this study, the SOM obtained with a different method from the former population did not provide a markedly overestimated result. Conversely, maturation size of the Vermelha beach population remained high

even removing the size effect, suggesting that it was conditioned independently of body growth pattern.

The available values of maximum size did not show a latitudinal gradient as predicted by the Bergmann's rule, in which specimens' body size increases with latitude (BLACKBURN *et al.* 1999). Instead, values seem to be higher in populations from the northern hemisphere (Fig. 3 C). Although additional data of other populations in the analyzed geographic range are required to confirm or refute

TABLE 5 – *Ocypode quadrata* (FABRICIUS, 1887). Size at the onset of maturity, maximum (Asymptotic) size, and proportional (relative) size at the onset of maturity of three populations located at different geographic localities. Sizes are expressed in carapace width.

Sampling site	Latitude	Sex (n)	Procedure	SOM (mm)	Maximum CW (Asymptotic CW) (mm)	Proportional SOM (RSOM)	Author
New Jersey Beach, New Jersey, USA	39° N	---	---	---	48 (50.5)		MILNE & MILNE (1946)
Mustang Island, Texas, USA	27° N	Male (124)	Spermatozoa in sperm ducts	24.9	53.5 (56.3)	0.47 (0.44)	HALEY (1969)
		Female (375)	Spermatozoa in seminal receptacles	25.7	52 (54.7)	0.34 (0.32)	
Punta Arenas, Margarita Island, Venezuela	11° N	Male (192)	Relative growth (GL vs.CW)	14.46	42.9 (45.2)	0.41 (0.39)	Present study
		Female (174)	Relative growth (AW vs.CW)	18.59	50.82 (53.5)	0.49 (0.46)	
Atalaia Beach, Aracaju, Sergipe, Brazil	11° S	Male (234)	Relative growth (GL vs.CW)	15.77	38.74 (40.77)	0.41 (0.39)	Present study
		Female (141)	Relative growth (AW vs.CW)		38.5 (40.52)	0.47 (0.44)	
Vermelha do Sul Beach, Ubatuba, São Paulo, Brazil	23° S	Male (278)	Relative growth (AW vs. CW)	18.3	37.5 (39.5)	0.34 (0.32)	FRANSOZO <i>et al.</i> (2002)
		Female (209)	Relative growth (GL vs. CW)	19.2	39.2 (41.3)	0.41 (0.39)	
Vermelha do Norte Beach, Ubatuba, São Paulo, Brazil	23° S	Male (203)	Relative growth (GL vs.CW)	15.46	37.8 (39.8)	0.49 (0.46)	Present study
		Female (221)	Relative growth (AW vs.CW)	19.4	36.7 (38.6)	0.41 (0.39)	
Pinhal Beach, Balneário Pinhal, Rio Grande do Sul, Brazil	30° S	Male (?)	---	---	Not mentioned		ALBERTO & FONTOURA (1999)
		Female (?)	---	---	34.4 (36.2)		

--- Not mentioned.

this preliminary trend, the currently available data suggests that maximum size too is more strongly affected by local conditions than by factors related to latitudinal gradients.

Variation in body size among populations inhabiting sandy beach has been related to morphodynamics (DEFEO *et al.* 2001; TURRA *et al.* 2005) and conservation condition

Sexual maturity of the Atlantic *Ocypode quadrata* from different regions

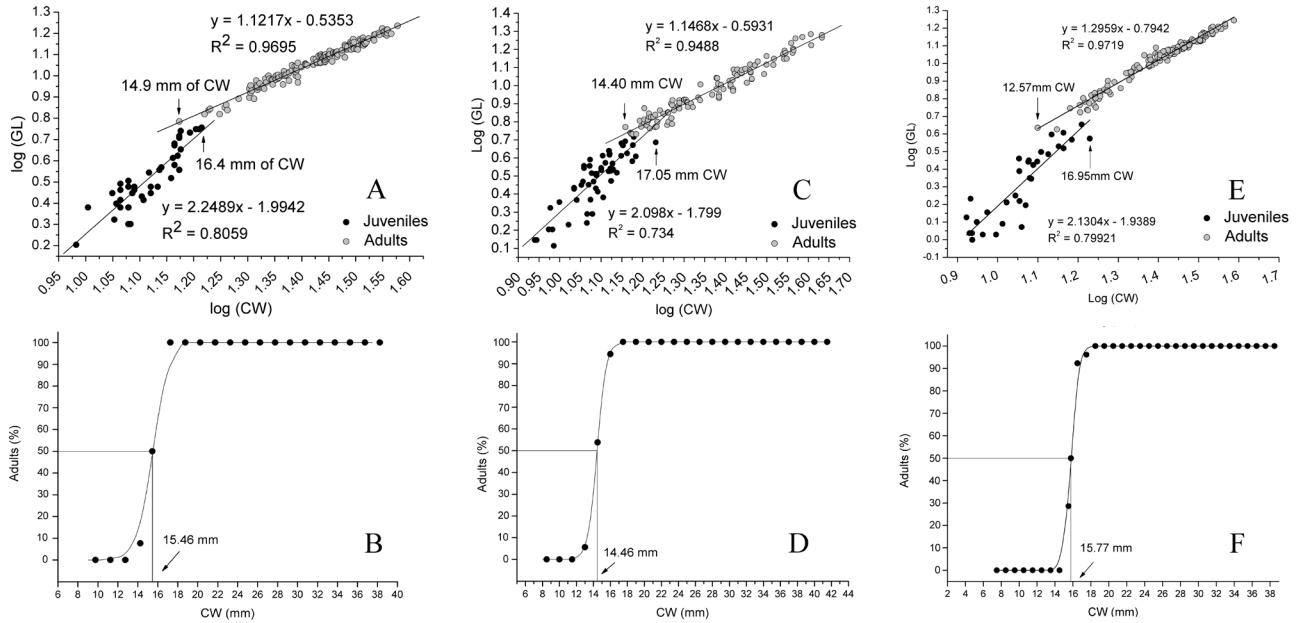


Fig. 1 – *Ocypode quadrata* (FABRICIUS, 1887). Males. Regression lines of the log gonopod length (GL) vs. log carapace width (CW) for juveniles and adults (A, Vermelha do Norte Beach; C, Punta Arenas Beach; E, Atalaia Beach) and Proportions of adult individuals in size classes of carapace width (B, Vermelha do Norte Beach; D, Punta Arenas Beach; F, Atalaia Beach). Arrows indicate the size at which 50% of the individuals are adult.

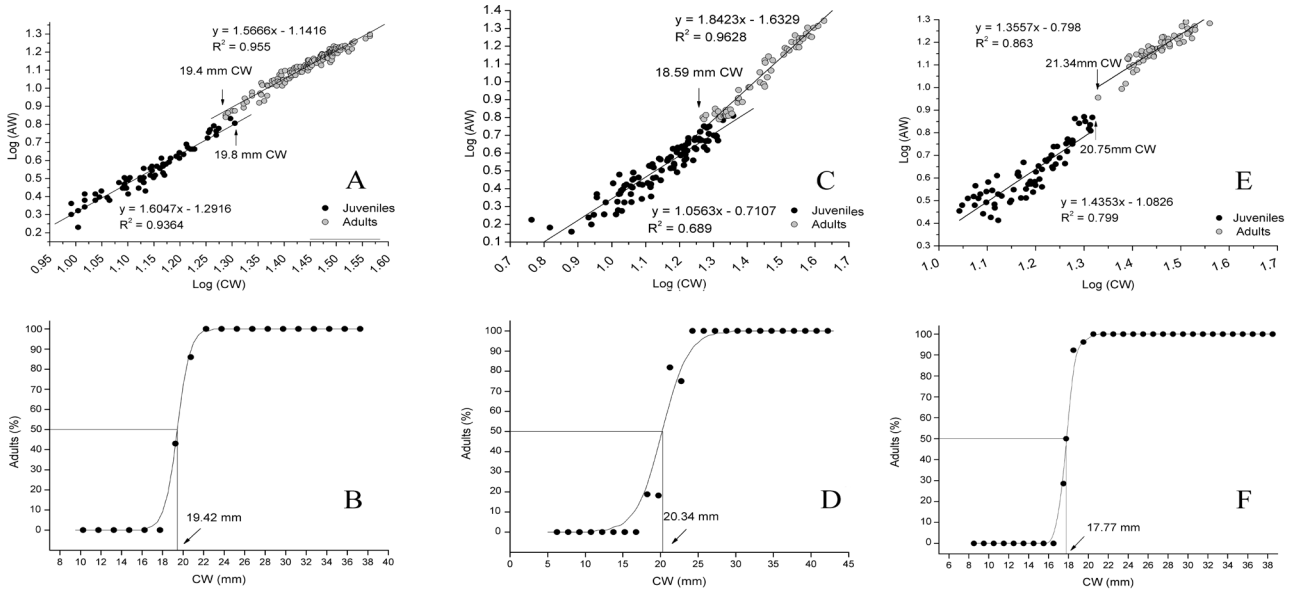


Fig. 2 – *Ocypode quadrata* (FABRICIUS, 1887). Females. Regression lines of the log abdomen width (GL) vs. log carapace width (CW) for juveniles and adults (A, Vermelha do Norte Beach; C, Punta Arenas Beach; E, Atalaia Beach) and Proportions of adult individuals in size classes of carapace width (B, Vermelha do Norte Beach; D, Punta Arenas Beach; F, Atalaia Beach). Arrows indicate the size at which 50% of the individuals are adult.

(OCAÑA *et al.* 2016) of beaches, population density (DEFEO & CARDOSO 2004) and food availability, (HINES 1989; CASTIGLIONI & NEGREIROS-FRANZOZO 2004).

Size and abundance of ghost crabs can also be influenced by anthropic disturbance (TURRA *et al.* 2005). According to BLANKENSTEYN (2006), in sandy beaches

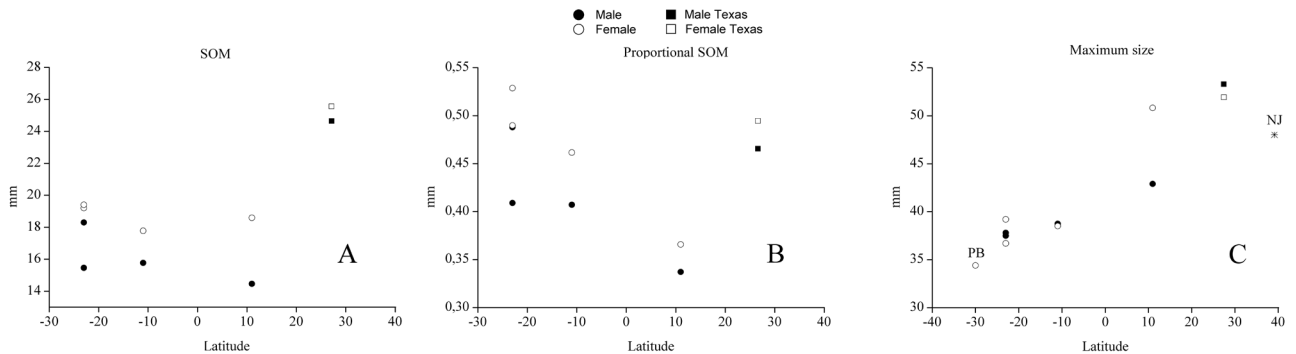


Fig. 3 – *Ocypode quadrata* (FABRICIUS, 1887). Geographic comparison of populations distributed along the Western Atlantic in terms of size at onset of the sexual maturity (A); proportional size at onset of the sexual maturity (B); and maximum size (C).

with intense human use, the density of crabs is lower in comparison to not impacted ones. Although, the anthropic impact level noticed in the studied beaches refute the suggested by BLANKENSTEYN (2006), then supplementary data acquired through new studies about the relationship size-abundance-anthropic impact in *O. quadrata* are necessary to better evaluate this effect.

In spite of the limited number of populations investigated, the results obtained together with those provided by other studies indicates that geographical variations of the relative growth, the size at onset of the sexual maturity, body growth and maximum size of *O. quadrata* are primarily influenced by local conditions than by the latitudinal gradients. This is an important aspect to be considered in future studies involving comparisons among populations, especially those aimed to assess conservation conditions of sandy beaches.

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