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RELATIVE GROWTH OF THE SPECKLED SWIMMING CRAB *ARENAEUS CRIBRARIUS* (LAMARCK, 1818) (BRACHYURA, PORTUNIDAE), NEAR UBATUBA, STATE OF SÃO PAULO, BRAZIL

BY

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ABSTRACT

Arenaeus cribrarius is a mainly tropical crab that occurs in the Western Atlantic Ocean, Brazil being its type-locality. The species ranges from Vineyard Sound, Massachusetts, USA to La Paloma, Uruguay. Information about this species is scarce. The relative growth of *A. cribrarius* was analyzed, based on some morphometric relations, where the carapace width, excluding lateral spines (CW), was used as an independent variable. A total of 403 specimens (189 males and 214 females), was collected in Ubatuba, State of São Paulo, Brazil, with otter-trawls. The animals were sexed and sorted to maturation phase (juvenile or adult). Some measurements were made: carapace (length and width excluding lateral spines), abdomen (greatest width of the fifth somite in females and the sixth in males) and major chela (greatest length, width and height, dactylus length). This study was made by the application of the power function ($y=a.x^b$) which was fitted to the data and the pattern of growth established for each parameter by the "b"-value (constant of allometry), as positive allometry ($b>1$), negative allometry ($b<1$) or isometry ($b=1$). The morphometric relations of the carapace showed a tendency to isometry. In females, the abdominal width grew in positive allometry, higher in juveniles ($b=1.33$) than in adults ($b=1.18$). In this case, an overlap and discontinuity was noticed between the phases over a carapace width range of 55 to 70 mm, where the puberty molt occurs. The majority of relationships showed that the major chela of the males grew in positive allometry, however, the greatest allometric difference between the phases was observed towards the propodus length with 1.09 as juvenile and 1.26 as adult "b"-values. In the males, this variable showed an inflection between the CW range of 45 to 55 mm, where the transition to the maturation phase occurs. The relative growth of this species is similar to those of previously studied species. This indicates, that the propodus length and the abdominal width are the morphometric variables most appropriate to estimate the size at the beginning of the sexual maturity for males and females of this species, respectively.

RÉSUMÉ

Arenaeus cribrarius est un crabe tropical et subtropical présent dans l'océan atlantique occidental, sa localité type étant le Brésil. Sa distribution s'étend de Vineyard Sound, Massachusetts, USA, à La Paloma, Uruguay. La croissance relative de l'*A. cribrarius* a été analysée d'après des relations morphométriques, la largeur de la carapace (CW), épines latérales exclues, étant utilisée comme variable indépendante. Quatre-cent-trois spécimens au total (189 mâles et 214 femelles) ont été collectés à Ubatuba, Etat de São Paulo, Brésil, avec des filets otter-trawl. Les animaux ont été séparés par sexe et en fonction de la phase de maturité (juvénile ou adulte). Des mesures ont été faites à des emplacements déterminés au préalable sur la carapace (longueur et largeur, épines excluses), abdomen (plus grande largeur du cinquième somite chez la femelle et du sixième chez le mâle), et grande pince (plus grande longueur, largeur, hauteur, et longueur du dactyle). Cette étude a été faite par application de la fonction de puissance ($y=a.x^b$) ajustée aux données et au modèle de croissance établi pour chaque paramètre selon la valeur de "b" (constant d'allométrie). Les relations morphométriques de la carapace ont montré une tendance à l'isométrie. Chez les femelles, la largeur de l'abdomen présentait une allométrie positive, avec un grade plus élevé chez les juvéniles (b=1,33) que chez les adultes (b=1,18). Dans ce cas, une chevauchement et une discontinuité ont été observés entre les phases (55 < CW < 70 mm) où se produit la mue de puberté. La majorité des relations ont montré que le grand chélipède croissant suivant une allométrie positive. La plus grande différence allométrique entre les phases a cependant été observée pour la longueur du propode, avec des valeurs de "b" égale respectivement à 1,09 chez les juvéniles et à 1,26 chez les adultes. Chez les mâles, cette variable a montré une inflexion dans la tendance des points entre des largeurs de carapace comprises entre 45 et 55 mm, lorsque se produirait la transition vers la phase de maturation. La croissance relative d'*Arenaeus cribrarius* est semblable à celles d'espèces précédemment étudiées. Ceci indique que la longueur du propode et la largeur de l'abdomen sont des variables morphométriques les plus appropriées pour estimer la taille au début de la maturité sexuelle, aussi bien chez les mâles que chez les femelles.

INTRODUCTION

The relative growth in Crustacea and Insecta has been intensively studied by numerous autors, mainly because the rigid exoskeleton of these animals allows accurate measurements (Huxley & Richards, 1931; Weymouth & Mackay, 1936).

In brachyuran crabs, the morphological modifications of the chelipeds, abdomen, and pleopods are in most cases evident between sexes or phases, and thus characterize growth stages. Based on this observation, Hartnoll (1982) divided postlarval brachyuran growth into three phases (undifferentiated, juvenile, and adult), based on the differentiation of the secondary sexual characters, which may occur gradually (after various molts) or abruptly (after the puberty molt).

The regression model which has been generally used in analyses of relative growth is represented by the function $y=a.x^b$, known as the equation of allometric growth (Huxley & Teissier, 1936; Teissier, 1960; Hartnoll, 1974, 1978, 1982).

One of the first studies that dealt with the relative growth of a portunid crab is that by Huxley & Richards (1931), pertaining to *Carcinus maenas* (L., 1758). Later, other papers have been published concerning the swimming crabs, *Callinectes sapidus* Rathbun, 1896 by Gray & Newcombe (1938) and Newcombe (1948); *Portunus pelagicus* (L., 1758) by Prasad & Tampi (1954); *Bathynectes maravigna* (Prestandrea, 1834) (as *B. superbus* (Costa, 1853)) by Lewis (1977); *Ovalipes stephensoni* Williams, 1976 by Haefner (1985); *Liocarcinus depurator* (L., 1758) by Mori & Zunino (1987); *Ovalipes catharus* (White, 1843) by Davidson & Marsden (1987); *Liocarcinus puber* (L., 1767) and *L. holsatus* (F., 1798) by Choy (1988) and *Callinectes ornatus* Ordway, 1863 by Haefner (1990).

Arenaeus cribrarius (Lamarck, 1818), is found along the western coast of the Atlantic Ocean from Vineyard Sound, Massachusetts, USA to La Paloma, Uruguay (Juanicó, 1978; Williams, 1984). However, Brazil is its type-locality.

There are only a few publications that refer to the biological and ecological aspects of this species. Quite recently, Pinheiro (1991) studied its distributional patterns and population biology in Fortaleza Bay, Ubatuba, SP, Brazil.

The objective of the present study is to describe the relative growth of *A. cribrarius*, based on the analysis of some morphometric relations. So, the best fit equations have been determined for the relationship between selected variables. The results are compared with those obtained from previous studies of other species.

MATERIAL AND METHODS

Specimens were captured on Ubatuba coast, State of São Paulo, Brazil, from November, 1988 to October, 1989, using a shrimp fishery boat provided with two otter-trawls with 10 mm mesh nets.

The animals were separated, packed in plastic bags, and transported to the laboratory, where they were kept in a freezer (−10°C). Afterwards, specimens were sexed and sorted to maturation phase (juvenile or adult), according to the method commonly used for species of the genus *Callinectes* (cf. Van Engel, 1958; Tagatz, 1968a, b; Taissoun, 1970; Williams, 1974; and Pita et al., 1985).

Each individual had its carapace, abdomen, and the dactylus and propodus of its greater cheliped measured with a 0.01 mm accuracy pair of precision calipers. Those specimens with exoskeletal damage were discarded.

The dimensions used in the analysis are illustrated in fig. 1: carapace length (CL), from the basal region between the frontal teeth to the posterio-median edge; short carapace width (CW), between the bases of the lateral spines; total carapace width (TCW), between the tips of the lateral spines; abdomen width (AW), greatest width of the sixth abdominal somite for the males and of the fifth for the females; telson length (TL), from the insertion with the sixth abdominal somite to the distal tip; chelar propodus length (PL), from the tip of the fixed finger to the tip of the medial articulation tooth with the carpus; chelar propodus depth (PD), greatest depth measured from the tip of the single spine in the dorsal region of the propodus to its opposite edge; chelar propodus width (PW), greatest width between the medial and lateral faces of the propodus; chelar dactylus length (DL), from the insertion with the propodus to the distal tip.

The carapace width excluding lateral spines (CW) was considered the independent variable, and the best fit regression was calculated for each sex and maturation phase, using the least squares method (Teissier, 1960; Hartnoll, 1982; Rodrigues, 1985).

Analysis of the allometric growth constant (b), gives information about the increase of one biometric dimension in relation to another, characterizing isometric growth when $b=1$, negative allometric growth with $b<1$ and positive allometry with $b>1$. To detect the "b"-difference from unity, an interval for

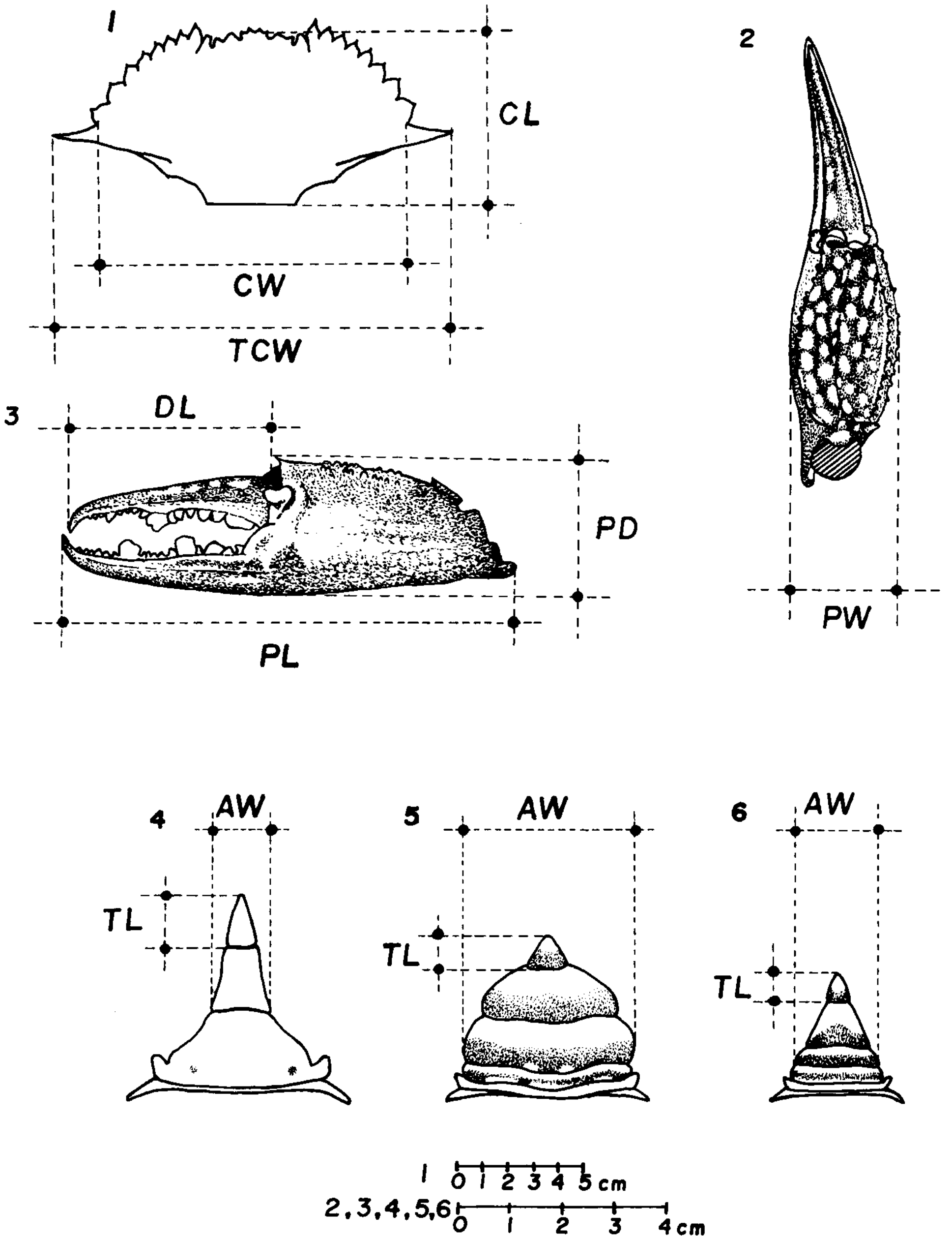

Fig. 1. *Arenaeus cribrarius* (Lamarck, 1818). Position of the morphometric variables measured in the carapace (1), chela (2 and 3) and abdomen (4, 5 and 6) of the specimens. CL=carapace length; CW=carapace width; TCW=total carapace width; PL=chelar propodus length; PW=chelar propodus width; PD=chelar propodus depth; DL=chelar dactylus length; AW=abdomen width; TL=telson length.

"b" included between 0.90 and 1.10 was used, as has been done by Kurata (1962), Kuris & Carlton (1977), and Kuris et al. (1987). When the "b"-value was equal to unity, it was omitted from the equations.

In each case, accuracy of fit of the empirical data to the power function was determined by the coefficient of determination (r^2) obtained for the log-transformed equation. The equations obtained for the maturation phases were graphically compared between each other, observing possible modifications during growth.

RESULTS

In table I the relative growth equations of carapace and abdomen for males and females of *A. cribrarius* are shown.

Analyzing the dispersion of the points of the CL×CW relation (fig. 2), one can observe that these points are well aligned and adjusted by the power function (tab. I) indicating isometric growth. Similar results were obtained when each sex and its respective maturation phases were analyzed separately.

Similarly, the TCW×CW relation showed growth near isometry for both sexes, also to be represented by a single equation comprising the total number of specimens.

It can be seen from the empirical values for the AW×CW relationship (fig. 3), that the males can be represented satisfactorily by a single equation indicating isometric growth. The females, however, showed an overlap between the phases (55<CW<70 mm), characterizing positive allometric growth for both, which was more marked in juveniles (b=1.33) than in adults (b=1.18).

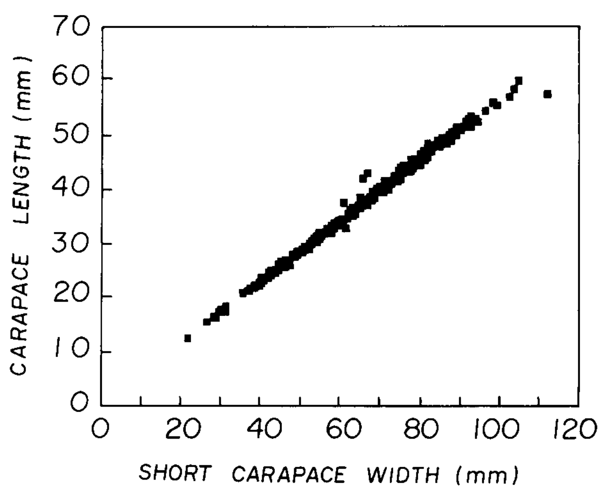

Fig. 2. *Arenaeus cribrarius* (Lamarck, 1818). Morphometric relation between carapace length (CL) and carapace width (CW) (N=403).

TABLE I

Arenaeus cribrarius (Lamarck, 1818). Regression analyses of the carapace and abdomen morphometric relations, based on carapace width without lateral spines (CW) as the independent variable. In all cases the correlation was significant ($p<0.001$) (CL=carapace length; TCW=carapace width with lateral spines; CW=carapace width without lateral spines; AW=abdominal width of the 5th segment of the females and 6th segment of the males; TL=telson length)

Variable	Sex/Stage	N	Power Function	r^2 (%)	Allometric Level
CL	JM	45	$CL=0.528CW^{1.02}$	99.64	0
	AM	144	$CL=0.613CW^{0.981}$	99.14	0
	MTOT	189	$CL=0.577CW$	99.72	0
	JF	95	$CL=0.578CW^{0.994}$	99.59	0
	AF	119	$CL=0.622CW^{0.981}$	97.43	0
	FTOT	214	$CL=0.532CW^{1.02}$	99.64	0
	TOTAL	403	$CL=0.560CW$	99.96*	0
TCW	MTOT	21	$TCW=1.55CW^{0.954}$	99.86	0
	FTOT	35	$TCW=0.84CW^{0.912}$	99.54	0
	TOTAL	56	$TCW=1.69CW^{0.932}$	99.84*	0
AW	JM	43	$AW=0.0983CW^{1.05}$	90.90	0
	AM	143	$AW=0.131CW^{0.977}$	96.57	0
	MTOT	186	$AW=0.121CW^{0.993}$	97.97*	0
	JF	93	$AW=0.0728CW^{1.33}$	96.05*	+
	AF	115	$AW=0.177CW^{1.18}$	90.01*	+
TL	JM	33	$TL=0.0287CW^{1.33}$	95.16*	+
	AM	124	$TL=0.0721CW^{1.09}$	96.21*	0
	MTOT	157	$TL=0.0561CW^{1.15}$	98.00	+
	JF	74	$TL=0.0916CW$	94.67	0
	AF	112	$TL=0.106CW^{0.953}$	79.11	0
	FTOT	186	$TL=0.137CW^{0.900}$	98.38*	0

JM=juvenile male; AM=adult male; MTOT=male total; JF=juvenile female; AF=adult female; FTOT=female total; N=number of individuals; *=The best equations to represent the relative growth; 0=isometry; +=positive allometry.

The telson length (TL) for juvenile males showed faster growth when related to the carapace width (positive allometry) in comparison to the adult phase (isometry). For the females this relation indicated isometry for both phases with the best fit obtained for the total specimens of this sex (see table I).

In table II, the relative growth equations of the propodus for both sexes of *A. cribrarius* are shown. The PL×CW relation shows that with the transition between the phases, the propodus increased more emphatically in males, remaining unchanged in females (fig. 4). Females presented isometric growth,

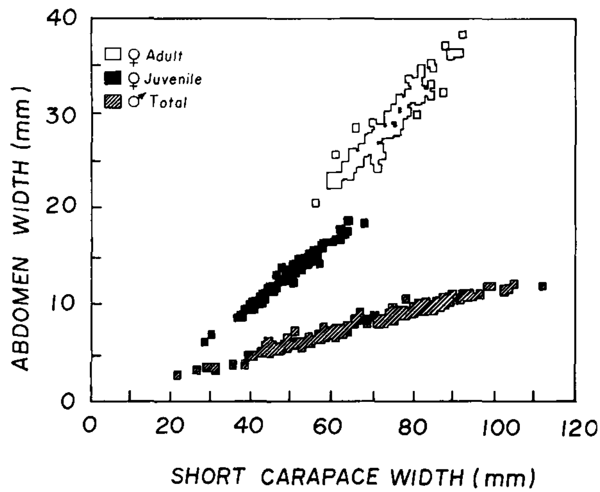

Fig. 3. *Arenaeus cribrarius* (Lamarck, 1818). Morphometric relation between abdominal width (AW) and carapace width (CW) juvenile females (N=93); adult females (N=115); total males (N=186).

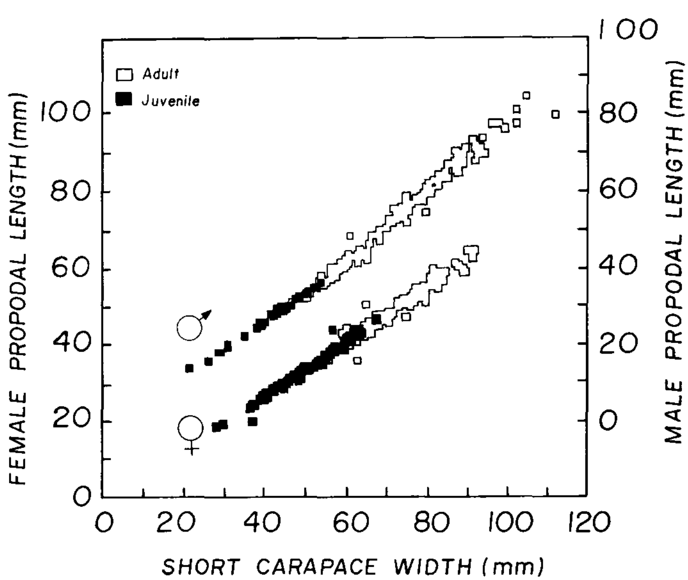

Fig. 4. *Arenaeus cribrarius* (Lamarck, 1818). Morphometric relation between propodus length (PL) and carapace width (CW) juvenile males (N=43); adult males (N=141); total females (N=205).

TABLE II

Arenaeus cribrarius (Lamarck, 1818). Regression analyses of greater cheliped morphometric relations, based on carapace width without lateral spines (CW) as the independent variable. In all cases the correlation was significant ($p<0.001$) (PL=propodus length; PW=propodus width; PD=propodus depth; DL=dactylus length)

Variable	Sex/Stage	N	Power Function	r^2 (%)	Allometric Level
PL	JM	43	$PL=0.455CW^{1.09}$	99.39*	0
	AM	141	$PL=0.237CW^{1.26}$	96.40*	+
	FTOT	184	$PL=0.307CW^{1.20}$	98.62	+
	JF	89	$PL=0.435CW^{1.10}$	97.48	0
	AF	116	$PL=0.463CW^{1.09}$	88.83	0
	FTOT	205	$PL=0.465CW^{1.08}$	98.10*	0
PW	JM	33	$PW=0.0781CW^{1.16}$	95.96*	+
	AM	114	$PW=0.0446CW^{1.30}$	95.32*	+
	MTOT	147	$PW=0.0534CW^{1.26}$	98.11	+
	JF	69	$PW=0.0602CW^{1.22}$	93.29	+
	AF	107	$PW=0.0659CW^{1.19}$	86.05	+
	FTOT	176	$PW=0.0620CW^{1.21}$	96.44*	+
PD	JM	33	$PD=0.111CW^{1.14}$	98.34*	+
	AM	116	$PD=0.0714CW^{1.24}$	96.44*	+
	MTOT	149	$PD=0.0935CW^{1.18}$	98.61	+
	JF	70	$PD=0.0993CW^{1.16}$	94.83	+
	AF	109	$PD=0.0880CW^{1.19}$	88.77	+
	FTOT	179	$PD=0.0907CW^{1.18}$	97.23*	+
DL	JM	33	$DL=0.185CW^{1.13}$	97.98*	+
	AM	116	$DL=0.103CW^{1.27}$	97.08*	+
	MTOT	149	$DL=0.147CW^{1.19}$	98.73	+
	JF	70	$DL=0.181CW^{1.13}$	94.94	+
	AF	110	$DL=0.162CW^{1.16}$	87.91	+
	FTOT	180	$DL=0.165CW^{1.15}$	97.12*	+

JM=juvenile male; AM=adult male; MTOT=male total; JF=juvenile female; AF=adult female; FTOT=female total; N=number of individuals; *=The best equations to represent the relative growth; 0=isometry; +=positive allometry.

with a better adjustment when the two phases were clustered. The males showed growth next to isometry for the juveniles (b=1.09), changing later to positive allometry in the adults (b=1.26). Changes in the degree of positive allometry were also evident for the males in transition between the phases, considering the other dimensions of the chela. The same thing seemed to happen with the females, in spite of their failure to show distinct differences when the "b"-values of the maturation phases were compared.

The values of the carapace width (CW) observed for juvenile males ranged from 22.1 to 54.7 mm, and from 46.0 to 112.0 mm for the adults. For juvenile females these ranged from 28.4 to 68.3 mm, and from 56.1 to 92.3 mm for adults. These overlaps must be taken into account when the equations are used to determine relationships between variables.

DISCUSSION

Observing the equations of relative growth for *A. cribrarius*, it is possible to ascertain the existence of a similarity with the pattern described for other portunids studied previously (tab. III), as well as for the majority of the brachyurans, according to comparison with the review by Hartnoll (1974).

TABLE III

Allometric growth constant values ("b") for some portunid species, where the carapace width (CW) was considered the independent variable

Species	Author	Males			Females		
		J	A	T	J	A	T
Carapace length (CL)							
Callinectes sapidus (1)	Newcombe et al. (1949)	–	–	0.92	–	–	0.91
Bathynectes maravigna (2)	Lewis (1977) (as *B. superbus*)	–	–	0.94	–	–	0.94
Ovalipes stephensoni (2)	Haefner (1985)	–	–	0.96	–	–	0.96
Ovalipes catharus (1)	Davidson & Marsden (1987)	–	–	0.94	–	–	0.94
Arenaeus cribrarius (2)	(present study)	0.99	0.98	1.00	1.02	0.98	1.00
Propodus length (PL)							
Carcinus maenas	Veillet (1945)	1.20	1.20	–	1.20	1.20	–
Portunus pelagicus	Prasad & Tampi (1954)	1.16	1.59	–	1.06	1.03	–
Bathynectes maravigna	Lewis (1977) (as *B. superbus*)	–	–	1.11	–	–	0.99
Ovalipes stephensoni	Haefner (1985)	(1.00-1.04)	1.40	1.15	-	–	1.02
Ovalipes catharus	Davidson & Marsden (1987)	–	–	0.94	–	–	0.98
Liocarcinus depurator	Mori & Zunino (1987)	1.08	1.03	–	1.14	1.02	–
Arenaeus cribrarius	(present study)	1.09	1.26	1.20	1.10	1.09	1.08
Abdominal width (AW)							
Portunus pelagicus (3)	Prasad & Tampi (1954)	0.99	0.99	–	1.21	1.52	–
Carcinus maenas (3)	Démeusy (1958)	–	–	–	1.25	1.21	–
Bathynectes maravigna (5)	Lewis (1977) (as *B. superbus*)	–	–	0.99	1.33	1.42	1.44
Ovalipes stephensoni (6)	Haefner (1985)	–	–	1.04	(1.29-1.52)	1.45	1.48
Ovalipes catharus (7)	Davidson & Marsden (1987)	–	–	0.99	1.00	1.55	1.35
Liocarcinus depurator (4)	Mori & Zunino (1987)	–	-	–	1.46	1.34	–
Liocarcinus puber (5)	Choy (1988)	–	–	1.07	1.45	1.41	–
Liocarcinus holsatus (5)	Choy (1988)	–	–	1.09	1.19	1.40	–
Arenaeus cribrarius (4)	(present study)	1.05	0.98	0.99	1.33	1.18	1.74

J=juvenile; A=adult; T=total; (1)=carapace width including lateral spines; (2)=carapace width excluding lateral spines; (3)=without information about the number of the abdominal somite; (4)=males (width of the sixth abdominal somite) and female (width of the fifth abdominal somite); (5)=width of the sixth abdominal somite; (6)=width of the fourth abdominal somite; (7)=width of the fifth abdominal somite.

Generally, when two carapace measurements of a brachyuran are related, e.g., CL×CW, it is not possible to notice changes during the ontogeny with a tendency to isometry. *A. cribrarius* belongs to this pattern (tab. III). This fact was also observed for the TCW×CW relation, indicating that lateral spines grow proportionally to the carapace. In spite of this, some species can present longer lateral spines in the juveniles than in adults, as has already been found by Lewis (1977) in *Bathynectes maravigna* (= *B. superbus*). It is possibly associated with an abrasion or an easier break, possibly due to fragility, after the terminal molt, a common phenomenon in decapod crustaceans.

In the literature, there are frequent citations about the importance of morphometry and growth of chelar dimensions (generally chelar propodus length or depth) to characterize a possible sexual dimorphism and maturation in crabs (Hartnoll, 1974; Vannini & Gherardi, 1988). These studies are especially relevant for males, because chela size is more important when chelae participate in intra- or interspecific combat, giving the individual crabs a disproportionately larger size. Another adaptative advantage would exist during reproduction, when the males compete with other males for females which, after having been selected, are held and manipulated by the chelipeds during copulation (Hartnoll, 1968, 1972; Warner, 1970).

The PL×CW relation showed a clear increase in propodus length of *A. cribrarius* males soon after the puberty molt, which may occur when the carapace width (CW) is between 45 and 55 mm (fig. 4) due to an increase in the level of allometric growth.

A great similarity was observed between the equation for total females ($PL=0.47CW^{1.08}$) and that calculated for juvenile males ($PL=0.46CW^{1.09}$), showing that the propodus length grew isometrically in relation to the carapace in the juvenile phase independently of sex. Modifications occurred only for males after the puberty molt, when their growth was positively allometric in this respect.

In table III, one can observe that *Ovalipes stephensoni* is the only species of swimming crab that is similar to *A. cribrarius*, as for the relative growth of the propodus length. These two species differ from the pattern described by Hartnoll (1982) for brachyuran males whose growth is isometric in the undifferentiated phase, positively allometric in the juvenile phase, and only increasing in degree after the puberty molt in the adult phase. In spite of this, the females of *A. cribrarius* followed the same pattern described by Hartnoll (1982), showing isometry in all phases.

The other chelar dimensions also showed a higher growth rate than those of the carapace, although the difference in allometric degree between the phases was more evident for the propodus length. Therefore, this variable was considered the most indicative for studies on the appraisal of the size of onset of sexual maturity in males.

The growth of the abdominal width (AW) generally characterizes a well-defined sexual dimorphism in representatives of the infraorder Brachyura. The pattern observed for *A. cribrarius* for the AW×CW relation follows that for the majority of crab species in general, as well as that for the portunids, as can be seen from table III.

From the regression AW×CW (fig. 3), it is concluded, that the puberty molt of the females ranges from CW of 55 to 70 mm, which corresponds with the size range over which females were found to have reached sexual maturity. Therefore, this relation can be used with success only in diagnosing the size at which the females of *A. cribrarius* begin their sexual maturation; for the males this does not apply.

It is important to point out that the calculation of regression by the least squares method (Model II) has been intensively used. For this reason, it has been considered as a pattern methodology. However, its use has been criticized when compared to the reduced major axis method (Model I), considered more appropriate when the two involved variables present natural variability (Lovett & Felder, 1989).

According to Finney & Abele (1981) the two methodologies are equivalent when the coefficient of correlation (r) of the regression analyzed exceeds 0.95. In such cases the "r" influence in the calculation of the slope (B) by Model II is very small (B=b/r, where "b" represents the slope obtained by Model I).

A review of the literature on relative growth in crustaceans has revealed, that there is a need to standardize the methodology because some authors still fit a simple linear regression to their data, rather than using log-transformed data to determine the constant of growth (b), which makes their results difficult to compare with those discussed in other papers as, e.g., the work by Du Preez & Mclachlan (1984) on *Ovalipes punctatus* (De Haan, 1833).

The relative growth of the swimming crab *Callinectes ornatus* was described by Haefner (1990), and in spite of his results being reliable and very similar to those obtained for *A. cribrarius*, they were excluded from table III because in this case, the variable considered as independent was the carapace length and not its width.

In the future, this work may be of help to estimate the beginning of (morphological) sexual maturity in *A. cribrarius*, by using the propodus length for males and the abdominal width for females, respectively.

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