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Sexual and ontogenetic morphometric variation in *Xiphopenaeus kroyeri* (Crustacea, Decapoda, Penaeidae): a new approach with linear and angular morphometric data

S. A. S. N. Moraes[a], C. E. R. D. Alencar[a,d], A. Fransozo[b], R. C. Costa[c], A. L. Castilho[b] and F. A. M. Freire[a]

[a]Grupo de Estudos em Ecologia e Fisiologia de Animais Aquáticos, Universidade Federal do Rio Grande do Norte, Natal, Brasil; [b]Núcleo de Estudos em Biologia, Ecologia e Cultura de Crustáceos, Universidade Estadual Paulista, Bauru, Brasil; [c]Laboratório de Biologia de Camarões Marinhos e de Água Doce, Universidade Estadual Paulista, Bauru, Brasil; [d]Instituto Nacional de Ciência e Tecnologia, Instituto de Geociências, Universidade Federal da Bahia, Salvador, Brasil

ABSTRACT

The present study evaluates the ontogenetic/sexual morphometric variation in *Xiphopenaeus kroyeri*. Sampling was from July 2001 to June 2003 at Ubatuba, São Paulo, Brazil. Animals were sexed and measured (cephalothorax length-CC, partial of the rostral spine-CPR, rostral spine-CR and rostral spine angulation-AR). Data analysis included linear morphometric analysis: equation $\ln y = \ln a + \ln b$ (sex/ontogeny fitting), k-means method (ontogenetic classification), analysis of covariance (morphological maturity), removal of the allometric effect, verification of parametricity and collinearity, principal component (PCA) and linear discriminant analysis (visualization of tendencies), permutational multivariate analysis of variance (hypothesis test). In addition, circular analysis was undertaken: circular normal distribution and concentration parameter, circular analysis of variance (hypothesis test), PCA (observe tendencies) and linear-circular regression (ontogenetic trajectory, RA-dependent variable, CL-independent variable). Morphological changes in the cephalothorax, in the adult stage, may be related to the increase in size of the gonads during sexual maturation and to the development of gills during the transition from arthrobranch (juvenile) to dendrobranch (adult). The rostral spine, in the adult stage, tends to become more elongated and more sharply angled. This feature may be related to predation pressure on larger specimens (adults), knowing that throughout its ontogeny the rostral spine of this species assumes phenotypic traits that make swallowing more difficult for predators.

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Multivariate morphometry; Atlantic seabob; von Mises distribution; rostral spine angulation

Introduction

Ontogeny in crustaceans is marked by morphological changes caused by differentiated growth of certain tagmata, resulting in the appearance of secondary characters with the passage from the juvenile to adult stage (Hartnoll 1978). Some secondary sexual characters are evident owing to the differentiated ontogeny for the sexes, such as the presence of a thelycum (found ventrally at the base between the fourth and fifth pair of pereiopods of female shrimps) and petasma (copulatory appendage attached to the first pair of pleopods in male shrimps), in the suborder Dendrobranchiata Spence Bate, 1888 (Pérez-Farfante 1969; Dall et al. 1990). Moreover, these shrimps have marked size sexual dimorphism, with males tending to be smaller than females (Gulland and Rothschild 1981).

Other characters, can be subtle, requiring quantitative analyses. One way to analyse quantitatively is relative growth, the correlation between body dimensions, comparing ontogenetic stages, genders or species, and their eco-evolutionary implications (Hartnoll 1978). Another way is to study variation of shape, as well as their covariance with other variables (e. g. population cohort, sex, ontogenetic stages and environmental characteristics), called morphometry (Oxnard 1978; Bookstein 1991; Konan et al. 2010).

The rostral spine, for example, is a morphological structure that is changeable in length (Jayachandran et al. 1996; Kapiris and Thessalou-Legaki 2001; Kapiris 2005; May-Kú et al. 2006), shape, and angulation during ontogenetic development and the spine is also sexually dimorphic (Dall et al. 1990; Lins Oliveira 1991). Personal observations (S. Moreas) in studies of *Xiphopenaeus kroyeri* (Heller, 1862) suggest that this structure is fairly variable in both juveniles and adults of both sexes.

The Atlantic seabob, *X. kroyeri*, is a species of penaeid shrimp very common on sand and mud in shallow tropical

CONTACT S. A. S. N. Moraes savioarcanjo@hotmail.com

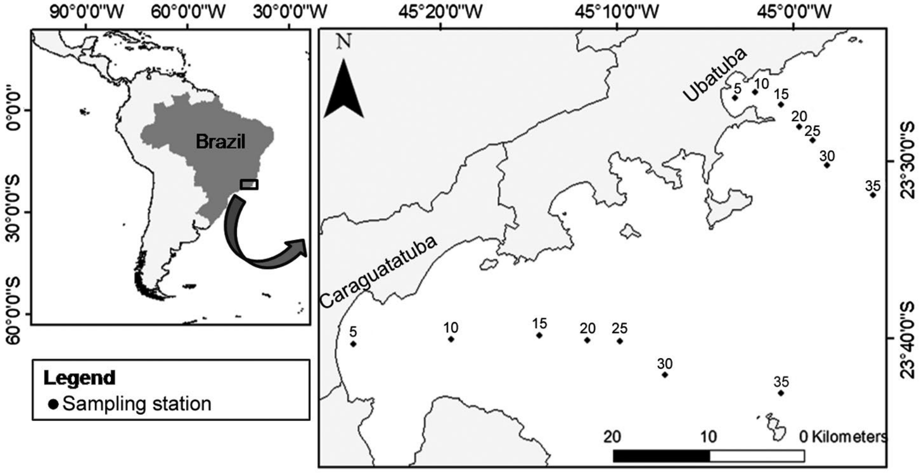

Figure 1. Sampling location in the Southeastern coast of Brazil. Ubatuba and Caraguatatuba. Sampling occurred at depths of 5, 10, 15, 20, 25, 30 and 35 m. (Source: Paulo Victor do Nascimento Araújo).

and subtropical Atlantic coastal regions. It has a wide distributional range, from Rio Grande do Sul – Brazil (32° 39′S and 52° 20′W) to Virginia – USA (36° 54′N and 75° 43′W) (D'Incao 1999; Costa et al. 2003), and is the third most important fishing resource of the coast of the state of São Paulo, Brazil. It is considered an important resource in artisanal fishing along the Brazilian coast (Branco 2005; Costa et al. 2007; Dias-Neto 2011; Thomé-Souza et al. 2014). Morphological differences that determine cohorts, ontogenetic stages and sexual dimorphism in a population may be relevant information to support future studies on a taxon (Swain and Foote 1999; Turan et al. 2006; Konan et al. 2008, 2010). For example, morphometric studies on prawns and shrimps have revealed populational variations (García-Dávila et al. 2005; Konan et al. 2008, 2010), morphotypes (Rojas et al. 2012), growth information (Jayachandran et al. 1996; Kapiris 2005; Campos et al. 2011; Reis et al. 2017; Da Silva et al. 2018), taxonomic differentiation (May-Kú et al. 2006), allometric differences between fishery stocks, (Paramo and Saint-Paul 2010; Barbosa-Saldaña et al. 2012), ontogenetic variations (Chow and Sandifer 1991), sexual dimorphism (Kapiris and Thessalou-Legaki 2001; Accioly et al. 2013), and shape variations between fishery stocks (Bissaro and Gomes-Jr 2012) and populations (Gusmão et al. 2013).

The objective of this study is to evaluate ontogenetic morphological variations of *X. kroyeri* from the south-eastern Brazilian coast through multivariate statistical techniques, making use of traditional morphometry including procedures of relative growth referring to the cephalothorax region including the rostral spine. Second, the objective is to verify a potential morphometric signature of sexual dimorphism for the species, representing the first effort in studies on Dendrobranchiata using circular statistical analysis to check more accurately the variation in the angulation of the rostral spine in the ontogenetic variation of a species.

Materials and methods

Study area and data sampling

Xiphopenaeus kroyeri were collected in the region of Ubatuba, northern coast of Brazilian state of São Paulo (23° and 25° South latitude and 45° and 48° West longitude – Figure 1), in depths varying between 5 and 35 m. Sampling was undertaken between July 2001 and June 2003 using a commercial fishing boat equipped with double rig trawling nets (Bertini et al. 2004; Castro et al. 2005). A total of 487 specimens were obtained, 247 males (71 juveniles and 176 adults) and 240 females (107 juveniles and 133 adults) (Table 1). All specimens were considered for analyses, except injured ones that were discarded.

The specimens were bagged, labelled, frozen and transported to the laboratory. They were then thawed and fixed in 10% formalin and then kept in 70% alcohol for identification (sexing) and measurement. Then, the shrimps were identified and sexed, by noticing, in males, the presence of petasma (male sexual structure present on the first pair of pleopods) and in females, the presence of a thelycum (female sexual structure), according to Pérez-Farfante and Kensley (1997).

To evaluate the ontogenetic and sexual morphometric variations, a multivariate set was made (Figure 2) from the following measurements: cephalothorax length (CL – distance between the orbital angle and posterior edge of the carapace), rostral spine length (RL – limited by the first rostral tooth to the edge of the rostrum), partial length of the rostral spine (PRL – limited between the fifth rostral tooth to the edge of the rostral spine) and angulation

Table 1. *Xiphopenaeus kroyeri*. Descriptive statistics on morphometric data for males and females (juveniles and adults).

		Males		Females	
Variables		Juveniles	Adults	Juveniles	Adults
CL (mm)	Max	11.01	25.30	15.80	26.20
	Min	1.32	8.10	1.51	7.77
	Mean	8.13	17.32	8.41	17.84
	Median	8.47	17.70	8.40	17.30
	SD	1.72	3.24	2.17	3.17
	SE	0.21	0.24	0.21	0.28
	b	–	–	–	–
RL (mm)	Max	12.09	32.80	17.10	37.70
	Min	2.62	10.55	2.95	13.80
	Mean	7.94	23.30	8.22	24.23
	Median	7.97	23.80	7.76	23.20
	SD	2.88	4.73	3.75	5.50
	SE	0.34	0.36	0.36	0.48
	b	1.51	1.51	1.50	1.50
PRL (mm)	Max	7.32	20.00	10.90	26.80
	Min	0.67	7.3	0.74	2.51
	Mean	3.92	14.13	4.22	14.41
	Median	3.90	14.80	3.70	14.20
	SD	1.91	2.91	2.60	3.01
	SE	0.23	0.22	0.25	0.26
	b	0.96	0.96	0.99	0.99
RA (degree)	Max	179.74	173.82	179.66	172.00
	Min	163.96	150.00	163.27	147.00
	Mean	173.33	160.75	172.39	159.88
	Median	174.47	161.00	172.33	161.00
	SD	4.88	5.38	4.47	5.16
	SE	0.58	0.41	0.43	0.45

Notes: Max: maximum, Min: minimum. SD: standard deviation, SE: standard error, b: allometric coefficient between measurements and CL, CL (mm): cephalothorax length, RL (mm): rostrum length, PRL (mm): partial rostrum length, RA (degree): rostrum angle.

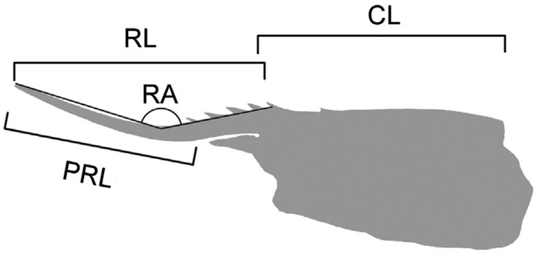

Figure 2. Morphometric measurements used in this study. Cephalothorax length (CL), rostrum length (RL), partial rostrum length (PRL) and rostrum angle (RA).

of the rostral spine (RA – angle located between the first and fifth rostral teeth and between the fifth rostral tooth to the edge of the rostral spine). For shrimps with a CL smaller than 12 mm, morphometric measurements were performed with an optical stereomicroscope Axioskop 2 Zeiss with a camera lucida, while for shrimps with a CL bigger than 12 mm a caliper rule (0.1 mm) was used. In both size groups, the standard size used was the millimetre. To estimate RA, pictures were taken of the specimens' cephalothoraxes in a lateral position. Posteriorly, the measurements of RA (in degrees) were obtained with the program Corel Draw 12.0. All pictures followed a rigorous standardization of capture, with position and focal length set by the same researcher in both the stereomicroscope pictures and in the ones captured without the equipment. The specimens were standardized always in the central portion of the pictures, at a suitable distance from the margins of the field of view to avoid marginal distortions caused by the lens of the camera and of the stereomicroscope.

Relative growth

Initially, the morphometric data were inspected for the occurrence of outliers, by visualization of Cleveland scatterplots (Cleveland 1993) for each morphometric variable, separately. After the removal of outliers, the relative growth was analysed by the allometric equation ($y = ax^b$), in its logarithmic form ($\ln y = \ln a + b \ln x$), with CL being considered the independent variable, while the other morphometric variables (RL and PRL) were considered dependents. The type of allometric growth was established from the value of the slope ('b') of the regression, which can be isometric ($b = 1$), positive allometric ($b > 1$) or negative allometric ($b < 1$). All the theoretical and mathematical foundations and application of relative growth to crustaceans mentioned previously followed those discussed by Huxley and Teissier (1936) and Hartnoll (1978).

Relative growth was analysed in two classification levels: (1) differences in line fitting between sexes, and (2) line fitting of the juvenile (immature) and adult (mature) ontogenetic stages were compared. To classify males and females as juveniles and adults, morphologically, the data were log-transformed and submitted to the non-hierarchical k-means clustering method ($k = 2$, juveniles and adults) for each bivariate relationship (CL vs. RL, CL vs. PRL). The k-means method is a multivariate procedure that distributes the data into a number of groups previously informed by means of an iterative process that minimizes variance in the groups, and maximizes the variance among the groups. This procedure generated a percentage of correct classification (%CC). Then, the result was refined by means of a discriminant function analysis according to the procedures of Sampedro et al. (1999).

The line fitting was made with the OLS procedure (Ordinary Least Square, Kendall and Stuart 1973; Sokal and Rohlf 1985). The comparison of the lines between males and females and juveniles and adults of either sex was made by an analysis of covariance (ANCOVA).

For procedures regarding the processing of data and the relative growth, Excel 2013 software was used (Microsoft Windows 2013). To compare the lines between males and females and juveniles and adults, the software Statistica 8.0 was used (Starsoft Inc 2005).

Allometric treatment and multivariate morphometry

From the results for juveniles and adults, a new set of data was created, including categorical variables 'sex' and 'morphological maturity stage' and their morphometric measurements. The maturity rating was chosen by observing the bivariate relationship that showed greater discrimination between the groups through the results of cross-validation matrix (obtained in the procedure of relative growth). Then, for multivariate analysis, each morphometric variable obtained was treated to reduce the allometric effect of data, following the proposal of Konan et al. (2010). Given that there are specimens in several classes of size and sex, therefore with the presence of an ontogenetic and sexual allometric effect (as extensively reported in the literature (Cock 1966; Klingenberg 1996) and also observed in the analyses of relative growth in this study), it became necessary to reduce the overall dimensionality effect for each morphometric variable. For this, the following equation was used:

$$Y_1 = Y_i[X_0/X_1]^b$$

in which Y_1 is the standardized measurement, Y_i is the measurement (to be standardized; dependent) of each collected specimen, X_0 is the standard measure average for every sample and X_1 is the standard measure for each specimen (Lleonart et al. 2000). In this standardization, the standard measure (independent) was also the cephalothorax length (CL) (Fransozo et al. 2000; Freire 2005). The value of 'b' (allometric coefficient) was estimated for each morphometric variable measured by the equation of allometric growth proposed by Huxley (1932) and by Hartnoll (1978). The standard measure (CL) was kept in posterior analyses to add to the multivariate morphometric set the information of size and, thereby, ontogeny. The allometric treatment of data was performed for all morphometric variables, except the variable of rostral angulation (RA).

Prior to the multivariate statistical analysis, data were tested for their parametricity, i.e. their multivariate normality (omnibus test; Doornik and Hansen 1994) and their equivalence of covariance matrices (Box's M; Seber 1984). Since normality and homogeneity were not obtained, non-parametric tests were applied to the data and results were presented with median (measures of central tendency) and standard error (dispersion). After the allometric treatment, principal component analysis (PCA) and an analysis of multivariate permutation variance (PERMANOVA) were made. First, a PCA (PCA-I) was carried out for investigation, interpretation, and reduction of multivariate variables, observing the data variation trends to highlight the most representative measures by means of the contribution of principal components and the value of the load variable (loadings) of each specimen of this study. For evaluation of the results, the main components that totalled more than 80% of the data variation were considered (Zuur et al. 2010). Additionally, bootstrapping type permutations ($n = 9999$) were used to generate confidence intervals for each principal component and test its main significance in the results. A PERMANOVA analysis was performed to test the hypothesis of morphological difference between each group of interest, observing the values of p and F with permutations ($n = 9999$) and using the Mahalanobis index as a difference distance measurement. For the differences between the factors, sequential Bonferroni correction was used.

Circular analysis

For rostral angulation data, circular statistical analyses were used. Initially, the circularity of the data was tested to verify the homogeneity of the concentration parameters for multiple directional data samples. This test verifies if all groups of interest comply with the circular normal distribution (von Mises distribution), observing the possibility of accepting the null hypothesis that all groups of interest are in the same concentration parameter, kappa (Zar 2010). For better description and visualization of circular data, polar type histograms were plotted, in which information is given in columns of values in degrees (0° a 360°). This type of chart was used to show guidelines of morphological characteristics related to rostral angulation. Thereafter, a Circular Analysis of Variance (Circular ANOVA) was applied, similar to the linear analysis of variance, with the purpose to identify, statistically, if there is a difference between the ontogenetic groups (juveniles and adults of males and females), using the rostral spine angulations.

A new Principal Component Analysis (PCA-II) for circular data was made to observe the RA data variation trends for each demographic group, considering that the Circular ANOVA does not have a *post hoc* evaluation about the maturity groups. The criteria for selection of components and evaluation of loadings used for the PCA were also applied to PCA-II. The bootstrap type permutations ($n = 9999$) were also calculated to generate the confidence intervals for each principal component based on circular data. For this purpose, a data matrix was constructed, in which the columns were maturity groups (juveniles males, adult males, juveniles females and adult females) and the lines were the values of rostral angle in each group.

Lastly, a linear-circular regression was performed to verify the shrimps' ontogenetic trajectory, in a relation to which the dependent variable was the angulation of the rostral spine (RA) and the independent variable was the cephalothorax length (CL). The multivariate statistical analyses on linear data and polar type histograms were carried

Table 2. *Xiphopenaeus kroyeri*. Results of regression analysis and ANCOVA.

Biometric relationship	Groups	R^2	Isotest	AL	*F*	*p* (F)
CL vs. PRL	JM	0.62	>0.01	+	19.51	<0.01
	AM	0.91	>0.01	+		
	JF	0.90	>0.01	+	33.50	<0.01
	AF	0.75	>0.01	+		
	M	0.83	>0.01	+	3.40	0.06
	F	0.86	>0.01	+		
CL vs. RL	JM	0.89	>0.01	+	39.04	<0.01
	AM	0.65	>0.01	+		
	JF	0.89	>0.01	+	42.73	<0.01
	AF	0.81	>0.01	+		
	M	0.88	>0.01	+	2.07	0.15
	F	0.77	>0.01	+		

Notes: CL: cephalothorax length, RL: rostrum length, PRL: partial rostrum length, R^2: coefficient of determination, AL: allometric level, *F*: variance, *p* (F): significance.

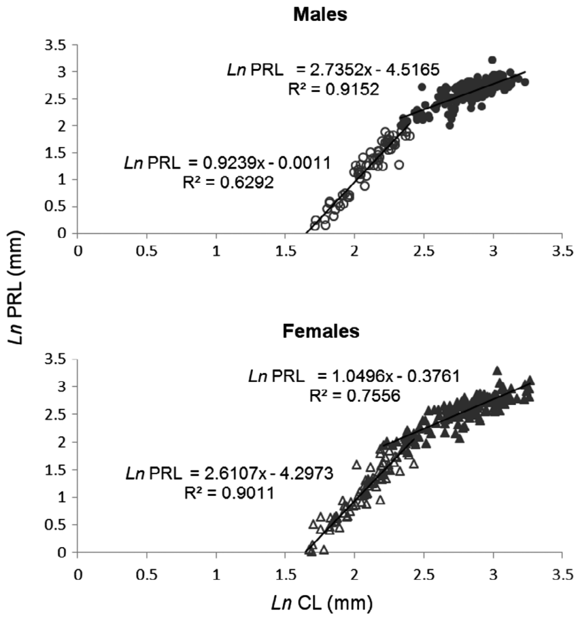

Figure 3. Relative growth between cephalothorax length and partial rostrum length in males and females, adults (filled symbols) and juveniles (blank symbols).

out with the software PAST v.2.15 (Hammer et al. 2001). For statistical analyses related to circular data, the software R v. 2.15 (R Development Core Team 2009) was used, with the 'circular' package (Agostinelli and Lund 2011).

Results

Relative growth

The procedure adopted for the study on relative growth did not show trends of sexual dimorphism (Table 2). However, differences in the angulation of allometric trajectories between ontogenetic groups were observed in both males and females (Figures 3 and 4). The %CC in each bivariate relationship was: CL vs. RL 54.12% for both sexes, CL vs. PRL 55.24% for both sexes, CL vs. RL 100.00% for juveniles and adults of both sexes, CL vs. PRL 98.77% in males (juveniles and adults) and, in same relationship, 100.00% for females (juveniles and adults). Therefore, the biometric relationship CL vs. RL was the more reliable for hierarchical ontogenetic groups.

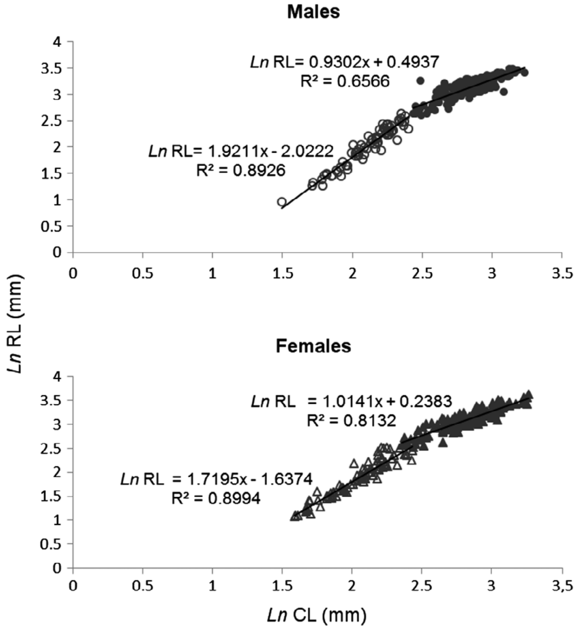

Figure 4. Relative growth between measurements cephalothorax length and rostrum length in males and females, adults (filled symbols) and juveniles (open symbols).

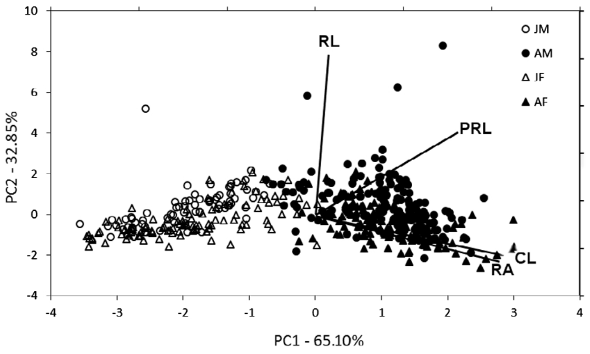

Figure 5. Principal components biplot for multivariate data on *Xiphopenaeus kroyeri*.

Notes: PC: principal component, RL: rostrum length, RA: rostrum angle, CL: cephalothorax length, PRL: partial rostrum length, JM: juveniles males, AM: adults males, JF: juveniles females, AF: adults females.

Multivariate morphometry

The measured morphometric data did not meet the assumptions of parametricity (normality: E*p* = 274.24,

$p > 0.05$; homoscedasticity, Box's $M = 612.93$, Monte Carlo $p = 0.015$).

The principal component analysis (PCA-I) explained 97.95% of data variation (65.099% for PC1 and 32.852% for PC2) (Figure 5). The principal component 1 (PC1) accounted, mainly, the rostral spine angulation – RA (variable loading: 0.5928), cephalothorax length – CL (0.5979) and part of the rostral spine – PRL (0.5367). Meanwhile, principal component 2 was defined, basically, by rostrum length – RL (0.8611). A grouping tendency was also observed among ontogenetic stages, regardless of the sexes (Figure 5).

The PERMANOVA showed significant differences between sexual maturity groups (juvenile males (JM), adult males (AM), juvenile females (JF) and adult females (AF)) ($p > 0.01$; $F = 83.69$). The greatest morphological dissimilarities were observed in comparisons between groups of adults in relation to groups of juveniles. Male adults showed the higher morphological dissimilarity in relation to the other analysed groups (JM: $p > 0.01$, $D^2 = 20.183$; JF: $p > 0.01$, $D^2 = 16.384$; AF: $p > 0.01$, $D^2 = 8.4903$). After them, the group with the highest morphological dissimilarity was AF (JM: $p > 0.01$, $D^2 = 19.051$; JF: $p > 0.01$, $D^2 = 13.479$). Among the groups of juveniles (JM and JF) the lower value of Mahalanobis distance was observed ($p > 0.01$; $D^2 = 1.3969$), indicating that little morphological variation is attributed to the comparison of these groups (Table 3).

Table 3. PERMANOVA (Permutational Multivariate Analysis of Variance) results for comparison between ontogenetic groups of *Xiphopenaeus kroyeri*.

	JM	JF	AM	AF
JM	–	>0.01	>0.01	>0.01
JF	1.40	–	>0.01	>0.01
AM	20.18	16.38	–	>0.01
AF	19.05	13.48	8.49	–

Notes: JM: juveniles males, AM: adults males, JF: juveniles females, AF: adults females. Above diagonal, significance values (p) for each combination, and below, D^2: Mahalanobis distance.

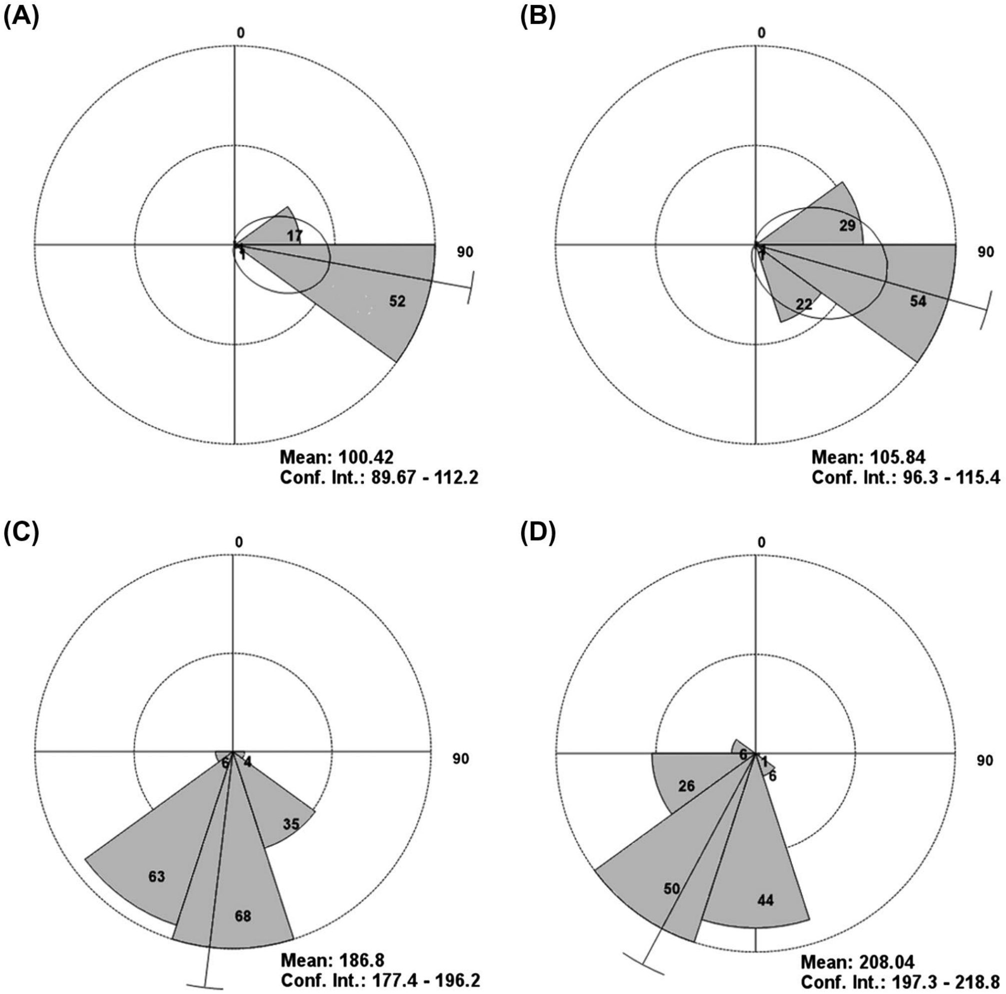

Figure 6. Polar histogram for descriptive circular representation of the rostrum angle of *Xiphopenaeus kroyeri*. (A): Juvenile males. (B): Juvenile females. (C): Adult males. (D): Adult females. Conf. Int.: Confidence interval.

Table 4. Analysis of variance for circular data results on rostrum angle of ontogenetic groups of *Xiphopenaeus kroyeri*.

	df	SS	MS	*F*	*p*
Between	3	127.21	42.4045	460.2	<0.05
Within	483	54.81	0.1135	NA	NA
Total	486	182.02	0.3745	NA	NA

Notes: df: degree of freedom, SS: sum-square, MS: mean-square, *F*: F statistic, *p*: significant value, NA: not available.

Circular analysis

The rostral spine angulation data were homogeneous with respect to circularity, showing a circular normal distribution. The frequency distribution by circular data showed similar averages for male and female juveniles (100.42° for males and 105.84° for females); whereas, for adults, it was noted that males possessed lower values of angulation when compared to females (186.8° for males and 208.04° for females) (Figure 6). In the Circular Analysis of Variance (Circular ANOVA), a statistical difference was noted, showing that rostral angulation is capable of explaining the difference between the maturity groups (Table 4).

PCA-II explained 90.68% of data variation in the two first components (71.59% to PC1 and 19.08% to PC2) (Figure 7). Thus, the two first PCs were considered in the inspection. PC1 and PC2 showed a strong tendency for differentiation between juveniles and adults, regardless of sex, showing adults next to the positive values of the principal component I axis, i.e. greater averages of rostral angulation (Figure 7).

The circular-linear regression showed a significant linear relationship between the change in cephalothorax length (CL) (Table 5). The variation of the rostral spine angulation (RA), reporting increase in the rostral angulation owing to the increase in cephalothorax length for each maturity group (Figure 8).

Discussion

The morphological variation in *X. kroyeri* was markedly toward the ontogeny, especially the angulation of the rostral spine. In all morphometric approaches used, morphological variations related to sexual dimorphism were not observed. Among the body structures of crustaceans, different growth patterns act together to make them more effective in certain functions (Hartnoll 1974). Therefore, the use of morphometry to assist in the perception of subtle morphological variations in studies of sexual dimorphism and ontogeny has proven effective (Oxnard 1978), especially with crustaceans (Chow and Sandifer 1991; Pinheiro and Terceiro 2000; Kapiris and Thessalou-Legaki 2001; Giri and Collins 2004; Ledesma et al. 2010; Accioly et al. 2013; Alencar et al. 2014).

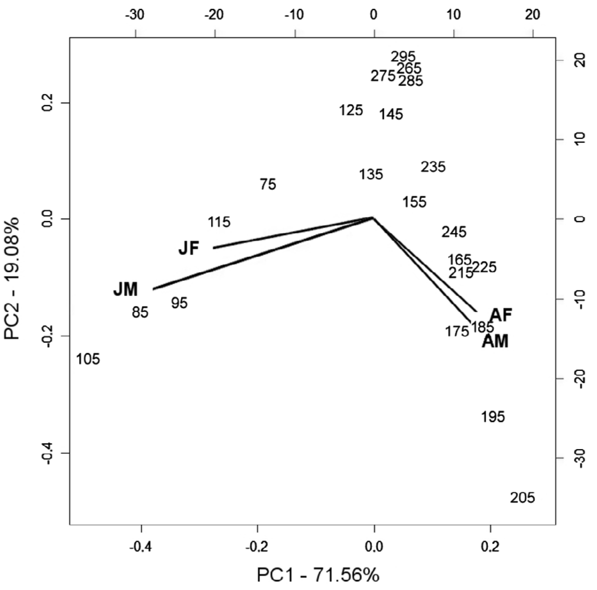

Figure 7. Principal Components Analysis biplot for association circular data (angles values, inside of biplot) on ontogenetic groups of *Xiphopenaeus kroyeri*.

Notes: JM: juvenile males, AM: adult males, JF: juvenile females, AF: adult females. The numbers inside of the biplot represent angles of rostral spine of each individual. PC: principal component.

Table 5. Statistic summary of circular-linear regression for ontogenetic groups of *Xiphopenaeus kroyeri*.

Groups	*mu*	*Kappa*	Log-like	coef	SE	*t*
JM	0.59	22.68	203.80	0.14	0.00	94.71*
AM	1.39	10.16	273.10	0.06	0.00	40.38*
JF	1.09	3.63	219.80	0.12	0.00	51.37*
AF	2.03	0.76	175.10	0.06	0.00	27.98*

Notes: *mu*: Maximum likelihood estimate of the mean direction, *kappa*: concentration parameter for each group, Log-like: logarithm of the likelihood, coef: coefficient model, SE: standard error, t: student statistical, JM: juveniles males, AM: adults males, JF: juveniles females, AF: adult females.
*$p < 0.05$ – statistical significance difference.

Ontogeny in penaeids is characterized by morphological changes caused by differentiated growth of certain tagmata, which characterize the transition from juvenile to adult, showing variation mainly on the length of the cephalothorax (Gulland and Rothschild 1981). Based on the analysis of relative growth it was possible to classify individuals into two groups (juveniles and adults) and verify a significant difference in the ontogenetic trajectory of the species. However, there was no evidence for sexual dimorphism for *X. kroyeri*, despite Boschi (1989) having observed this pattern in Penaeoidea. In Penaeoidea there may be factors that influenced the growth pattern of this taxon. Segura and Delgado (2012) reported different patterns of growth for males and females of *Pleoticus muelleri* Spence Bate, 1888 throughout its distribution, owing to the influence of local environmental conditions. In the aforementioned study, it was observed that the values

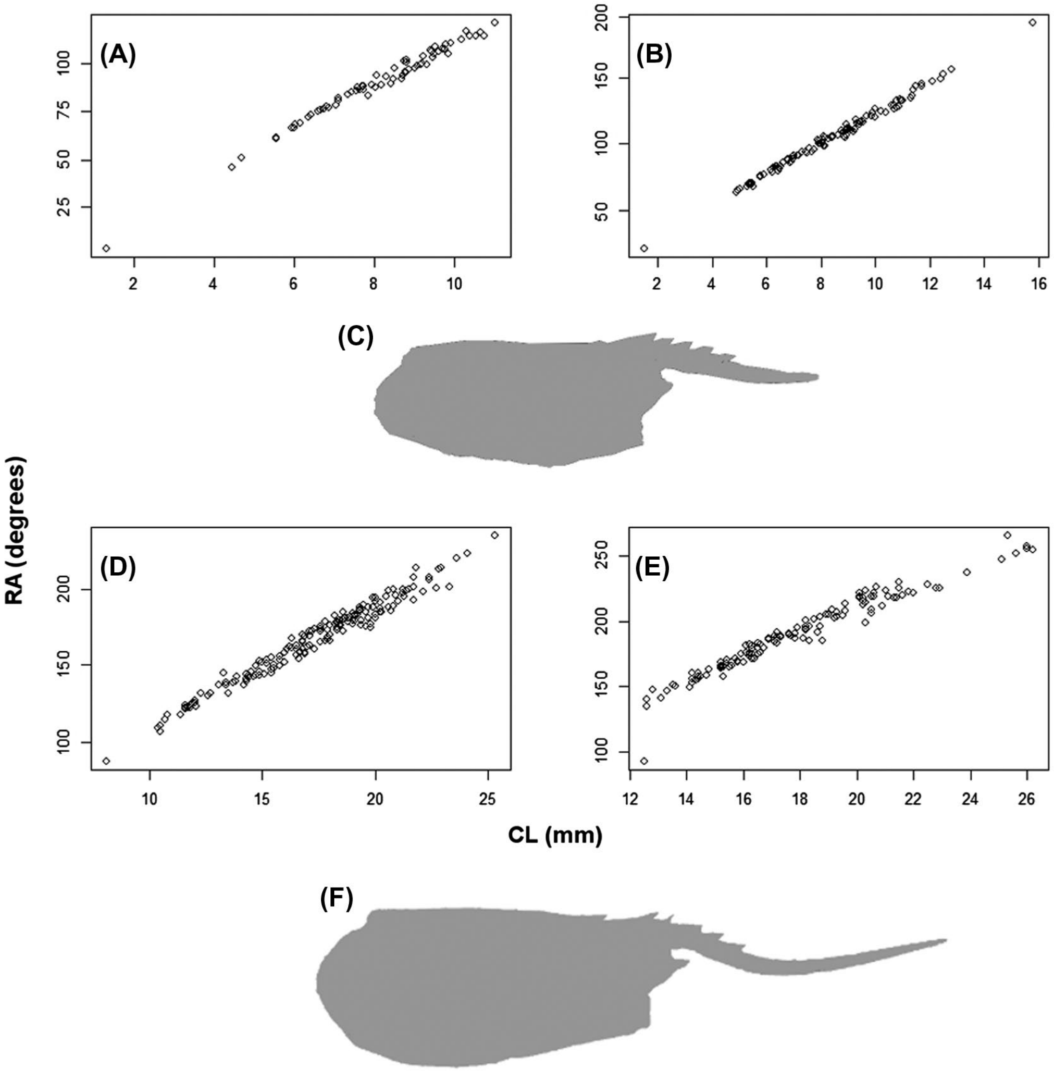

Figure 8. Circular-linear regression between CL (cephalothorax length) and RA (rostrum angle) on ontogenetic groups of *Xiphopenaeus kroyeri*. (A): Juvenile males. (B): Female juveniles. (C): Representation of juvenile specimens. (D): Adult males. (E): Adult females. (F): Representation of adult specimens.

of the angulation coefficients (allometric level), cephalothorax length and wet weight ratio, of males and females became similar in specimens collected at the highest latitudes. Also according to Segura and Delgado (2012), this is possibly owing to both phenotypic plasticity and life history aspects.

For *X. kroyeri*, variation is found in cephalothorax length with respect to sexual dimorphism and ontogeny, possibly associated with gonadal development, especially in females, owing to production of oocytes, which reflects on reproductive aspects and fertility (Gab-Alla et al. 1990; Fernandes et al. 2011; Bissaro and Gomes-Jr 2012). In histological studies, this is ratified in *X. kroyeri*, for which there was the finding of increased diameter of oocytes, from 72.03 μm to 171.30 μm, during the maturation process (Campos et al. 2009). As for the variation in cephalothorax region, the development and increase in size of the gills deserves mention. According to Schram (1986), in the juvenile stages, the arthrobranch has less volume and functional area than in its more developed stage (dendrobranch).

In the sizes related to the rostral spine (RL, PRL and RA), it was possible to highlight an ontogenetic change, indicating that the rostral spine has an increase in both length and angulation. This morphological change may be a result of selective predation pressure on larger individuals. According to Dall et al. (1990), the Penaeidae have various ways to prevent predation, including sheltering in algae, burrowing in the substratum, inhabiting turbid water, restricting their outings to times of low foraging by predators, form large groups and/or have a well-developed flight response. In addition, other authors showed factors such as palatability, size, accessibility, activity and density of the prey and of the predator as factors that could influence the predation process (Nakagaki 1999). Nakagaki (1999), in experimental study about predation in *X. kroyeri*, suggested that in addition to behavioural mechanisms, the pronounced rostral spine (more angled and long) could help in avoiding selection by potential predators. Moreover, the study concluded that specimens with more prominent rostral spines are less preyed upon. This is also strengthened by Werner and Peacor (2003) and Preisser et al. (2005), who claim that the predation rate depends on some prey characteristics such as size, trophic apparatus, speed, cripticity and external morphology. The predator-prey interaction provides the prey with responses to level of development, life history, behaviour, physiology and morphology.

It is plausible that the thorn, bigger and angulated, evidenced by this study, may be an evolutionary response of the prey–predator interaction at the morphological level: in this case the elongated and inclined rostral spine would serve as protection against being swallowed by a predator. This fact has been observed in *Daphnia* (Cladocera), which develops defensive spines from its carapace during its life cycle, providing protection against predation by fish (Barry 1994). Literature reports already showed a tendency to this variation in shrimps (Williams 1984; Dall et al. 1990; Lins Oliveira 1991), however, until this study, there was no record and knowledge of more appropriate quantitative analysis to support this phenomenon.

As the development of *X. kroyeri* juveniles to adulthood occurs, its spine increases in length and angulation, which can make the identification more accurate between juveniles and adults in the field or even in the fishing industry, both for research and for fishing activities. Of the variables analysed in this study, rostral angulation seems to be the most promising morphometric measure for practical application in the identification of juveniles and adults. However, the measurements of the cephalothorax can also be used to identify adult sex.

Body parts that show angulation are historically not analysed because of the difficulty of working with circular measures and their statistical characteristics. Either that, or they are commonly analysed using angulation data by linear statistics, which can generate biased results as angular data follow a different error distribution (von Mises distribution). Our study raises the need to conduct further assessment with angular data for *X. kroyeri* and other species of penaeid towards a better understanding of ontogenetic and sexual morphological differences. Newer study techniques such as geometric morphometry (Accioly et al. 2013), may also contribute effectively in this understanding. Experimental analyses of predation of the species focusing on the variation of size and angulation of the rostral spine are recommended to support the morphological observations of this study.

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ORCID

S. A. S. N. Moraes http://orcid.org/0000-0003-4045-9011
R. C. Costa http://orcid.org/0000-0002-1342-7340

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