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### ECOSYSTEMS

# Influences of environmental variables on the weight-length relationship of the shrimp *Xiphopenaeus kroyeri*: Do variations occur along time?

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**Abstract:** This study analyzes the influences of environmental variables on the weightlength relationship of the penaeid shrimp *Xiphopenaeus kroyeri* during nine consecutive years (2005 to 2013) in northern Rio de Janeiro State. The main questions raised are: i) Does species relative growth vary along time? and ii) How are the environmental variables sea surface temperature, salinity, chlorophyll-a and/or organic matter related to the relative growth? For males, the long-term mean of the allometric coefficient stayed <3 (immature: 2.49; mature: 2.91), whereas for females they were >3 (immature: 3.08; mature: 3.10). The sine-consine models highlighted the wave T period in which the allometric coefficient values complete one cycle of increase-decrease: 4.72 years and 14.72 years for immatures female and male, respectively; and 9.08 years and 9.98 years for matures male and females, respectively. The relative growth behavior varies in a predictable time scale; however, none of the environmental variables strongly supported the variation. Changes in the relative growth behavior are probably drive by intrinsic mechanisms to maintain the population locally.

**Key words:** morphometric relationships, seabob shrimp, environmental features, fishery, Atlantic Ocean.

# INTRODUCTION

The relative growth of animals is estimated through the morphometric relationships that involves weight and body length (King 2007). From these relationships, it is possible, for instance, to compare the life history at different spatial and temporal scales, to assess the population dynamics, to estimate the production and biomass of a given population and to estimate the average weight of individuals at a given length (Santos et al. 2002, King 2007, Ferreira et al. 2008, Severino-Rodrigues et al. 2016). In the weight-length relationship, herein referred as WLR, the allometric coefficient is representative of the relative growth of the species, allowing temporal comparisons in body measurements, or on how the weight and length dimensions are influenced by the species' energy allocation (Santos et al. 2002, Andreu-Soler et al. 2006, Froese 2006).

In shrimps, the morphometric relationships can present spatial-temporal variations due to changes in the environmental conditions along the home range, such as water temperature, salinity and food availability (Pérez-Castañeda & Defeo 2002, Bissaro et al. 2013, Sousa et al. 2019). Changes in environmental conditions can affect the base of marine food chains and the availability of local resources (Lewandowska et al. 2012). This may have an immediate impact on the shrimps' growth, since they are secondary consumers (Di Beneditto et al. 2012, Willems et al. 2016). Futhermore, pressures caused by commercial fishing can influence both growth rates and maturity size of target species, leading to early gonadal maturation with smaller body size (King 2007, Fonteles Filho 2011).

The shrimps from Penaeidae family are the most important targets in commercial fisheries of crustaceans in tropical waters (FAO 2018). The Atlantic seabob shrimp, Xiphopenaeus kroyeri Heller, 1862, is a penaeid from Western Atlantic Ocean (36°N to 30°S) widely caught in marine fisheries practiced up to 30 m depth on sand or mud bottoms (FAO 2018). According to the more recent data on fisheries in southeast Brazil. X. *kroyeri* is the main target from shrimp fisheries in Rio de Janeiro State (FIPERJ 2017) and São Paulo State (Instituto de Pesca 2019). Gusmão et al. (2013) reviewed the available information on the population genetic structure of X. kroyeri in Brazil, identifying two sibling species in southeast Brazil, with overlapping stocks in certain locations. According to the authors, in the fishing area of Atafona fishing port, where this study was conducted, there is only one species whose taxonomic unit is still X. kroyeri.

Xiphopenaeus kroyeri spends its entire life cycle in marine coastal waters, and it is not an estuarine-dependent species, as most penaeids (Boos et al. 2016). The species reproduces throughout the year, with two main peaks per year, and the mean longevity is 2 years (Fernandes et al. 2011, Andriguetto-Filho et al. 2016, Davanso et al. 2017). The species longevity may impose susceptibility to changes in the environmental conditions because they have a strong influence in the development and/or survival of short-living organisms (Fonteles Filho 2011). Meanwhile, X. kroyeri is a tolerant species, living in waters from 15 °C to 30 °C and salinity from 9 to 36 (Boss et al. 2016). Furthermore, the species has feeding plasticity with a broad

spectrum of food items, such as primary sources (phytoplankton and macroalgae) and small animals from both sea bottom and water column (Branco & Moritz-Júnior 2001, Willems et al. 2016). Thus, *X. kroyeri* can quickly adapt itself to environmental changes, maintaining their populations and fisheries in a long-term (Graça-Lopes et al. 2007).

This study analyzes the influences of environmental variables on the WLR of X. kroveri caught by coastal fishery practiced by a smallscale fleet from northern Rio de Janeiro State. southeast Brazil, during nine consecutive years. The main questions raised are: i) Does species relative growth vary along time? and ii) How are the environmental variables sea surface temperature, salinity, chlorophyll-a and/or organic matter related to the relative growth? Despite analyzing past data (2005 to 2013), the results allow understanding how the relative growth of an important target species from small-scale fishery may be or not affected by eventual changes in its habitat, which is relevant to fisheries management.

### MATERIALS AND METHODS

### Sampling and environmental variables

The shrimps were obtained through fisheries practiced from Atafona fishing port (21º37'S; 41º00'W), located in northern Rio de Janeiro State, with monthly samplings from 2005 to 2013. Every year, the shrimp-fishing season in this region is closed ("defeso" period) from March 1 to May 31 to protect species recruitment (Normative Instruction nº 189/2008, available at: https://www.icmbio.gov.br/cepsul/images/ stories/legislacao/Instrucao\_normativa/2008/ in\_ibama\_189\_2008\_defesocamaroes\_revoga\_ in\_ibama\_91\_2006\_92\_2006.pdf). Since A.P.M. Di Beneditto has a Permanent License emitted by the Brazilian Government (nº 16401-4) to collected zoological samples for research purposes, the samplings were done even during the "defeso" period, contacting a local boat to simulate a fishery commonly practiced.

Xiphopenaeus kroyeri is the main target in local shrimp fishery, predominating in local landings (Fernandes et al. 2011, 2014). The fishing area extends from 21º35'S to 21º50'S and 1-3 miles from the coastline, totalling 100-200 km<sup>2</sup> in marine coastal waters (Fernandes et al. 2014) (Figure 1). Stable isotopes data from this *X. kroyeri* stock demonstrated site fidelity (A.P.M. Di Beneditto, unpublished data), and we considered that the species stock (population) is resident in the fishing area.

The local boats operate inside the above boundaries, but we did not record the exactly area of each sampling. From 1 to 2 kg of shrimps were selected randomly from the total volume caught in a given boat. The gear used for shrimp fishery is the bottom trawl net measuring 8-10 m long with a horizontal opening of 6 m and cod-end mesh size of 15 mm from knot to knot. The local boats operated with two nets simultaneously.

In the laboratory, all intact individuals were separated in male or female according the primary sexual characters, i.e. presence of male gonopore in the 5<sup>th</sup> pair of pereiopods and petasma for males, and presence of female gonopore in the 3<sup>rd</sup> pair of pereiopods and telicum for females (Hartnoll 1982). Then, each individual was macroscopically classified according to maturity stage. For males, individuals with no fused petasma were considered immature or juvenile, and those



Figure 1. Xiphopenaeus kroyeri fishing area in northern Rio de Janeiro State, SE Brazil. The dashed area represents the boundaries of the shrimp fishing area.

with a fused petasma were considered mature or adult (Pérez-Farfante 1969). For females, the chromatic scale of the ovaries was used to visually define the maturity stage, according to Campos et al. (2009): mature or adult females ready for reproduction or that already spawned had dark green and white ovaries, respectively. Females without these ovarian characteristics were considered immature or juvenile. Each individual was measured for the total length (from tip of rostrum to end of telson) and carapace length (from edge of posterior orbital to end of posterior margin of cephalothorax) with a calliper (±0.1 mm). The total wet weight was measured in a digital scale (±0.1 g).

The environmental variables were obtained for each sampling year from two official database: National Oceanic and Atmospheric Administration of the U.S. Department of Commerce - NOAA (sea surface temperature - SST, salinity and chlorophyll-a) and Agência Nacional de Águas - ANA (Paraíba do Sul River flow) (Table I). The chlorophyll-a values represent the measure of primary production in

Variable	Database and link	Data set	Search parameters	
Sea surface temperature – SST (ºC)	National Oceanic and Atmospheric Administration of the U.S. Department of Commerce - NOAA https://coastwatch.pfeg.noaa.gov/ erddap/griddap/erdHadISST.html	HadISST Average Sea Surface Temperature, 1°, Global, Monthly, 1870-present	-20.5 until -22.5 decimal degrees (latitude) and -41.5 decimal degrees (longitude)	
Salinity	National Oceanic and Atmospheric Administration of the U.S. Department of Commerce - NOAA https://coastwatch.pfeg. noaa.gov/erddap/griddap/ hawaii_9d34_0512_2367_LonPM180. html	SODA 3.3.1 Ocean State, 1/2°, Global, 1980-2015, Monthly Composite, Lon+/- 180	-21.75 until -22.75 decimal degrees (latitude) and -41.75 decimal degrees (longitude) Salinity measures in areas of 5, 15 and 25 m deep, with an annual mean value based on these data	
Chlorophyll-a (mg m <sup>-3</sup> )	National Oceanic and Atmospheric Administration of the U.S. Department of Commerce - NOAA https://coastwatch.pfeg.noaa.gov/ erddap/griddap/erdMH1chla8day. html	Chlorophyll-a, Aqua MODIS, NPP, L3SMI, Global, 4km, Science Quality, 2003-present (8 Day Composite)	-20.95 until -22.97 decimal degree (latitude) and -40.02 decimal degrees (longitude)	
Paraíba do Sul River flow (m³ s⁻¹)	Paraíba do Sul River flow (m³ s <sup>-1</sup> ) Agência Nacional de Águas - ANA http://www.snirh.gov.br/hidroweb/ serieshistoricas		Type of station: fluviometric Station code: 58974000 Basin: Atlantic West Sub-basin: Paraíba do Sul River River: Paraíba do Sul State: Rio de Janeiro City: Campos dos Goytacazes	

 Table I. Parameters to search for the environmental variables in the fishing area from 2005 to 2013.

the fishing area (Huot et al. 2007). The Paraíba do Sul River flow is the main organic matter contributor to coastal waters along the fishing area, and it is an indirect measure of organic matter availability (Marques et al. 2017). Since X. *kroyeri* is positioned at the base of local trophic chains, as a secondary consumer (Di Beneditto et al. 2012), both chlorophyll-a and organic matter were considered indirect local proxies for food availability.

In the databases, the values are available in a monthly basis (SST and river flow), twice a month (chlorophyll-a) and six times a month (salinity). From these values, we calculated the mean annual value to correlate with the shrimp's relative growth in a temporal series (2005 to 2013). The central point of the fishing area (21º40'S-21º45'S; 40º56'W, or -21.66/-21.76; -40.94 decimal degrees) was chosen to drive the search in NOAA database (Figure 1). Since the exactly coordinate is not available to search for SST, salinity and chlorophyll-a values, we select the closest points, as indicated in Table I. The coordinates in NOAA database are always present as decimal degrees. For the river flow values, ANA has a monitoring point in Campos dos Goytacazes, 30 km far from the Paraíba do Sul River mouth (Table I, Figure 1).

## Weight-length relationships

Since penaeid shrimps have sexual dimorphism in body size, with females larger and heavier than males, and immature and mature individuals have differences in the growth rate (Hartnoll 1982, King 2007), the genders and maturity stages were separated for the regressions (Table II). The WLR may be represented by the equation:

# $W = a \cdot L^{b}$

where W is weight, L is length, and *a* and *b* are parameters; or in a logarithmic form (Froese 2006):

# $\log (W) = \log (a) + b \cdot \log(L)$

This study applied a log10-transformation in both weight and length.

Parameter b, also known as allometric coefficient, is the exponent of the arithmetic form of the WLR, and the slope of the regression line in the logarithmic form (Froese 2006). If b= 3 (isometric growth), the small individuals in the sample have the same form and condition as large individuals. If b > 3 (positive-allometric growth), then large individuals have increased in weight more than in length. Conversely, if b< 3 (negative-allometric growth), large individuals have changed their body shape to become more elongated than heavier. In a meta-analysis about WLR in fishes (also applied to crustaceans, Sousa et al. 2019), Froese (2006) demonstrated that the allometric coefficient is expected to fall between 2.5 and 3.5. In the WLR, the parameter b usually does not vary significantly throughout the year, and can be considered a mean annual value, as suggested by Santos et al. (2002) and Andreu-Soler et al. (2006). Since the aim of this study is to analyze the relative growth in a yearbasis, the monthly samplings were grouped to represent each year.

First, an exploratory analysis tested how the shrimp's length dimensions (total length or carapace length) are related to each other. For this analysis, genders and maturity stages were considered as a single sample. The relationship between them was strong ( $R^2$ = 0.93; p< 0.0001), and both could be applied as representative of shrimp's length (Figure S1 – Supplementary Material). Since our interesting is to investigate the WLR, a second regression analysis was done (weight and each length dimension) to verify the  $R^2$  values: weight-total length had  $R^2$ = 0.94, and weight-carapace length had  $R^2$ = 0.91, both with *p*-values< 0.0001 (Figure S2). The allometric coefficient of the weight-total length

Year	Maturity	Gender	Total length (mm)	Carapace length (mm)	Weight (g)	Sample Size
2005		Female	84.9 ± 14.9	16.9 ± 3.3	3.6 ± 1.8	834
	Immature	Male	63.8 ± 9.6	12.3 ± 1.8	1.5 ± 0.6	133
		Female	109.2 ± 9.4	22.7 ± 2.6	7.7 ± 2.2	390
	Mature	Male	88.6 ± 10.6	17.5 ± 2.4	3.9 ± 1.5	844
	Immature	Female	81.7 ± 16.1	16.3 ± 3.7	3.2 ± 2.1	2686
		Male	66.9 ± 9.9	12.8 ± 2.1	1.7 ± 0.8	462
2006	Matura	Female	106.4 ± 11.7	22 ± 2.8	7.1 ± 2.6	497
	Mature	Male	86.8 ± 11.9	17 ± 2.5	3.8 ± 1.6	2643
		Female	79.1 ± 16.2	15.7 ± 3.7	3.1 ± 2.1	1132
2007	Immature	Male	63.4 ± 5.2	12.1 ± 1.1	1.5 ± 0.4	271
2007		Female	104.2 ± 13.2	21.4 ± 3	6.8 ± 2.6	262
	Mature	Male	83.1 ± 10.5	16.1 ± 2.2	3.5 ± 1.4	1060
		Female	94.4 ± 16.7	18.1 ± 4.1	5.1 ± 2.5	692
2000	Immature	Male	68.3 ± 9.6	12.4 ± 2	1.8 ± 0.8	95
2008		Female	114.8 ± 10.4	23.3 ± 3	8.7 ± 2.5	328
	Mature	Male	95.8 ± 10.8	18 ± 2.5	5 ± 1.7	1013
	Immature	Female	83.4 ± 16.3	15.9 ± 3.9	3.4 ± 2	2092
2009		Male	65.4 ± 8.3	12.3 ± 1.9	1.6 ± 0.6	330
	Matura	Female	108.9 ± 11.6	22.3 ± 3.3	7.4 ± 2.6	586
	Mature	Male	88.1 ± 11.7	16.8 ± 2.9	3.9 ± 1.7	2432
	la seconda de la constanción de la constancincincinción de la constanción de la constanción de la cons	Female	85.5 ± 13.9	16.7 ± 3.1	3.5 ± 1.7	864
	Immature	Male	66.4 ± 9.1	12.6 ± 2	1.7 ± 0.7	125
2010	Mature	Female	106 ± 9.9	21.4 ± 2.6	6.7 ± 2.2	313
		Male	88.5 ± 10.4	17.2 ± 2.3	3.9 ± 1.4	969
2011	Immature	Female	88.7 ± 15.2	17.6 ± 3.5	3.9 ± 2.1	885
		Male	67.4 ± 6.7	12.8 ± 1.4	1.8 ± 0.5	172
	Matura	Female	109.2 ± 10.6	22.6 ± 3	7.6 ± 2.6	439
	Mature	Male	93.1 ± 10.3	18.2 ± 2.4	4.8 ± 1.7	1194
	las as stures	Female	91.1 ± 14.7	18 ± 3.5	4.2 ± 2.2	927
2012	Immature	Male	68.4 ± 7.1	12.9 ± 1.5	1.8 ± 0.6	149
	Matura	Female	109.7 ± 10	22.6 ± 2.9	7.7 ± 2.4	459
	Mature	Male	92.3 ± 9.8	17.9 ± 2.3	4.4 ± 1.5	1181
	Immatura	Female	87.4 ± 14.7	17.5 ± 3.8	3.9 ± 2	1076
2012		Male	68.3 ± 7.5	12.8 ± 1.5	1.7 ± 0.5	137
2013	Matura	Female	105.1 ± 11.1	21.9 ± 3.2	6.8 ± 2.4	656
	Mature	Male	90.1 ± 9.2	17.8 ± 2.4	4.1 ± 1.4	1239

**Table II.** Body dimensions and sample size of *Xiphopenaeus kroyeri* from northern Rio de Janeiro State, southeast Brazil for each year, maturity stage and gender. Values are mean ± standard deviation.

equation (b= 3.0674) is within the confidence interval of the meta-analysis made by Froese (2006). This suggests that the total length is a better estimator of the allometric coefficient when compared to the weight-carapace length relationship (b= 2.5708). Thus, the weight-total length relationship was chosen for this study.

### Data analysis

All data analysis was done in R Program ( $\alpha$ = 0.05) (R Core Team 2020). To answer the first question raised in this study (Does species relative growth vary along time?) both weight and length data of each gender and maturity stage were log10transformed. Each slope (allometric coefficient) of the year-gender-maturity combination was estimated through an ANCOVA adjusted with weight as a function of length, years, genders and maturity stages (I m function, base package, R Core Team 2020). Since ANCOVA detected a significant interaction between years, genders and maturity stages (p-value = 0.004768), the slopes were extracted from the ANCOVA (emtrends function, emmeans package, Lenth 2020) and compared using Tukey's multiple comparations test (pairs function, base package, R Core Team 2020). The parameters of each equation, R<sup>2</sup> values and significant differences among slopes are in Table SI – Supplementary Material.

Since the allometric coefficients distribution along the years had a wave shape for both genders-maturity stages, we fit the data using a trigonometric model (sine-cosine model), represented by the equation:

$$Y = a \cdot \sin \frac{(\pi)}{(c \cdot X)} + b \cdot \cos \frac{(\pi)}{(c \cdot X)} + d$$

where parameters *a* and *b* control the wave range and *c* is half of the wave T period, i.e. it is the time the wave takes to travel a distance equal to its wavelength (to complete a cycle). The *c* parameter that would best fit the data was found empirically: 9901 regressions were recursively adjusted to the data using *c* values ranging from 0.1 to 10 in 0.001 increments. For each regression, the R<sup>2</sup> values were extracted (Rsquared function, Fisheries Stock Analysis package, Ogle et al. 2020). The *c* parameter associated with the highest R<sup>2</sup> value found was used in each model. Finally, the *d* parameter represents the central value at which the stationary wave described by the model oscillates around. This parameter can be understood as the long-term mean of the allometric coefficient for each fitted model.

To answer the second question (How are the environmental variables related to the relative growth?), linear regressions were used to access the relationship between the allometric coefficients and annual mean values of each environmental variable to determine how strong the relationships are ( $R^2$  values). Parameters *a* and *b* and *p*-values were reported.

### RESULTS

## Does species relative growth vary along time?

The length and weight recorded in male and female shrimps in both maturity stages are in Table II, showing the sexual dimorphism regarding body size. The males' allometric coefficients were always lower than females in the same maturity stage (Figure 2, Table SI). For males, the long-term mean of the allometric coefficient stayed <3 (immature: 2.49, mature: 2.91, Table III), whereas for females they were >3 (immature: 3.08, mature: 3.10, Table III). The sine-cosine models presented a good fit for both genders, with R<sup>2</sup>> 0.82 for females and R<sup>2</sup>> 0.73 for males (*p*< 0.05) (Table III). The wave T period in which the allometric coefficients increase-decrease are 4.72 years and 14.72 years for immatures female and male, respectively and 9.08 years and 9.98 years for mature male and females, respectively (Table III). Since all  $R^2$  values were above 0.73, these periods are predictable for X. kroyeri along this fishing area.



coefficients of males (triangles) and females (circles) of Xiphopenaeus kroveri from northern Rio de Janeiro State. SE Brazil. during the sampling years (2005 to 2013). Close and open symbols represent mature and immature stages. respectively. The allometric coefficients for each combination of year, gender and maturity are in Table SI. Sine-cosine models' statistics (equations, determination coefficients (R<sup>2</sup>) and p-values are in Table II.

Table III. Sine-cosine models' statistics (equations, determination coefficients (R<sup>2</sup>) and p-values) of allometric coefficients variation over time (see Figure 2). Equation coefficients (a, b, c and d) refers a general sine-cosine equation: , where a and b control the wave range, c is half of the wave T period and d is the the long-term mean of the allometric coefficient.

Maturity	Gender		Regression	<b>D</b> <sup>2</sup>			
		а	b	C	d	R*	<i>p</i> -value
Immature	Female	0.1742	0.1316	2.3600	3.0809	0.8274	0.0051
	Male	0.1400	-0.2677	7.3600	2.4972	0.9753	0.0000
Mature	Female	0.0861	-0.1189	4.5400	3.1032	0.7367	0.0183
	Male	0.0727	-0.1235	4.9900	2.9119	0.8650	0.0025

# How are the environmental variables related to the relative growth?

The relationship between the allometric coefficients and SST, salinity, chlorophyll-a and Paraíba do Sul River flow were weak and no significant for most combinations gendermaturity stage (Table IV). The only noteworthy relationships, despite moderate ( $R^2$ = 0.45) and marginally significant (*p*-values close to 0.05),

refer to the allometric coefficient of mature males and salinity and river flow (Table IV). Since the allometric coefficient is the weight/ length ratio in a log10-basis, individuals become longer than heavier when the salinity increases and heavier than longer when the river flow increases (Table IV).

**Table IV.** Linear regressions between allometric coefficients of males and females from different maturity stages of *Xiphopenaeus kroyeri* from northern Rio de Janeiro State, southeast Brazil, and environmental variables (sea surface temperature - SST, salinity, chlorophyll-a, Paraíba do Sul River flow (or organic matter availability). The equations, determination coefficients (R<sup>2</sup>) and *p*-values are shown. Equation coefficients (*a* and *b*) refers a general linear equation.

Variable	Maturity	Gender	Regression	coefficients	<b>D</b> <sup>2</sup>	<i>p</i> -value
			а	b	R <sup>2</sup>	
Chlorophyll-a (mg/m³)	Immature	Female	3.1320	-0.2371	0.0007	0.9454
		Male	2.8781	-1.4409	0.0342	0.6339
	Mature	Female	2.7075	2.3637	0.1310	0.3386
		Male	2.8225	0.6036	0.0109	0.7895
Salinity	Immature	Female	-30.4664	0.9281	0.3834	0.0754
		Male	12.4151	-0.2704	0.0419	0.5974
	Mature	Female	5.0583	-0.0540	0.0024	0.9008
		Male	26.6504	-0.6562	0.4466	0.0491
SST (°C)	Immature	Female	11.4778	-0.3444	0.2525	0.1680
		Male	-0.9484	0.1472	0.0594	0.5276
	Mature	Female	9.9027	-0.2792	0.3039	0.1239
		Male	6.4427	-0.1445	0.1036	0.3982
River flow (m³/s)	Immature	Female	3.3967	-0.0004	0.1266	0.3474
		Male	2.1787	0.0006	0.3677	0.0834
	Mature	Female	2.8894	0.0003	0.1151	0.3717
		Male	2.5470	0.0005	0.4515	0.0474

# DISCUSSION

The body size (length and weight) recorded in *X. kroyeri* caught during small-scale fisheries in northern Rio de Janeiro State, southeast Brazil, confirms the sexual dimorphism, as expected for a penaeid shrimp (Hartnoll 1982, King 2007) and widely recorded for the species along its home range (e.g., Fernandes et al. 2011, Andriguetto-Filho et al. 2016, Davanso et al. 2017, Reis et al. 2017). Penaeid males grow faster than females in the early stages of development, when still immatures, besides reaching smaller length, less weight and shorter longevity than females (Hartnoll 1982, King 2007). For this fishing area, the daily growth rate of males *X. kroyeri* is 1.3

times faster than females, but its asymptotic length is 8% lower (Fernandes et al. 2011).

The negative-allometric growth for males (total length increases at a higher rate than weight) and positive-allometric growth for females (weight increases at a higher rate than total length) in both maturity stages were verified here, as expected. Fernandes et al. (2011) analyzed part of the sampling considered in this study (2005 to 2010) to assess *X. kroyeri* population parameters in northern Rio de Janeiro State. The authors adjusted WLR, indicating negative and positive-allometric growth for males and females, respectively; however, they included all individuals in a single WLR. The annual analysis done in this study that considered the maturity

stages was more suitable to detect the relative growth differences over time.

The sine-cosine models highlighted variations in the relative growth behavior of the shrimps in a predictable temporal scale. During the nine consecutive years (2005 to 2013) the variation was greater for immature females. The model predictions showed ~15 years until a cycle of increase-decrease happens in immature males' allometric coefficient: whereas for immature females this time-interval was 3 times shorten (~5 years). Furthermore, a dyssynchrony between genders is noted for immature individuals, i.e. when males increase their allometric coefficients, being heavier than longer, females decrease it, being longer than heavier, and vice-versa (Figure 2). For mature individuals, the relative growth behavior was similar (9-10 years) and synchronic between genders.

The influence of the environmental variables on WLR might be one possible explanation behind the patterns highlighted by the models; however, SST, salinity, chlorophyll-a and Paraíba do Sul River flow were poor predictors for X. kroyeri relative growth. The only exceptions that deserve some consideration might be the influence of salinity and river flow (organic matter availability) on the allometric coefficient of mature males. These variables are inversely related because when the river flow increases the salinity in coastal waters decreases (Zalmon et al. 2015). However, as the relationships between the allometric coefficient and these variables were just marginally significant (p-values close to 0.05, Table IV), any explanation would be speculative.

In general, during the time interval considered by this study, the environmental variables did not interfere in how individuals for both genders and maturity stages increase in weight and length. Since shrimps' growth depends on gender, maturity stage and environmental conditions, such as food quantity and quality, water temperature and salinity (Dall et al. 1990), we can argue that in northern Rio de Janeiro State the environmental conditions were within the tolerable/optimum range (SST, salinity) and nutrition needs (chlorophyll-a and river flow as indirect indicative of food availability) to the shrimps' development locally. Since reproductive individuals and recruits occur throughout the year in this fishing area (Fernandes et al. 2011), we suppose that the environmental conditions were adequate for the maintenance of both genders and maturity stages from 2005 to 2013.

The SST and salinity values did not present remarkable variations from 2005 to 2013, remaining close to 24°C and 36. respectively (Table SII). According to Sastry (1983), temperature is a proximate factor for crustaceans' decapods, effecting mainly the reproductive season. Xiphopenaeus kroveri has a life cycle independent of estuaries, living in marine coastal waters (Boos et al. 2016). The higher concentration of salts in the water helps shrimps to harden the carapace within a short time period, which is especially important to immatures with shorter intermolt periods (Vogt 2012). In an environment whose mean salinity is 36, such as in the fishing area, the conditions for species carapace development are ideal.

Bottom water temperature and bottom salinity are environmental variables strongly related to *X. kroyeri* distribution and life cycle (Andriguetto-Filho et al. 2016). Zalmon et al. (2015) measured both variables in the fishing area during field campaigns in 2009 (21°C to 26°C and 34 to 36, respectively), and these values match with the SST and salinity in sea surface applied in this study (Table SII). Therefore, in the bathymetric range where the *X. kroyeri* fishing is carried out (less than 20 m, Figure 1), the vertical

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stratification regarding water temperature and salinity is negligible.

The chlorophyll-a, an indicator of phytoplankton abundance and biomass in coastal waters (Huot et al. 2007), ranged from 0.14 to 0.20 mg/m<sup>3</sup> in the fishing area (Table SII). This range was not large enough to represent possible variations in food availability associated with primary production with effects on shrimps' relative growth. Primary production is a late factor for crustaceans' decapods, because food availability in the larval phase is decisive to its survival (Sastry 1983).

The northern Rio de Janeiro State is strongly influenced by the Paraíba do Sul River flow (Figure 1). The river flow was an indirect measure of organic matter availability to marine coastal waters and, ultimately, of food availability to X. kroyeri. In the inner continental shelf, this river plays a fundamental role in sediment and nutrient transport, structuring coastal benthic communities (Zalmon et al. 2015). The relation between life cycle and distribution pattern of X. kroyeri with the regime of estuarine plumes is strong (Andriguetto-Filho et al. 2016). The Paraíba do Sul River plume can extend until 30 km from coastline, depending on the flow season (Souza et al. 2010). Oliveira et al. (2012) verified that due to local currents and winds regimes that predominate in most part of the year the plume disperses southwards, parallel to coastline, increasing solid material retention in coastal areas. Thus, the effects of Paraíba do Sul River flow are more intense within the fishing area of X. kroyeri.

If extrinsic factors, such as aforementioned environmental variables, were poor predictors for *X. kroyeri* relative growth behavior in the fishing area, the reasons behind variations may be supported by intrinsic factors. Penaeid shrimps' growth is a discontinuous process regulated by the moult cycle, characterized by a rapid weight gain during the immature stage followed by the achievement of asymptotic length of matures, when both number of moult cycles and growth rate decrease (Dall et al. 1990). Therefore, the relative growth behavior for mature shrimps is expected to be similar regardless of gender, such as recorded in the fitted models (Figure 2).

For immature shrimps, in turn, the relative growth behavior oscillates three times faster in females when compared to males (5 vs. 15 years), with a dyssynchronous response between genders. In northern Rio de Janeiro State, the feeding habits of X. kroyeri have never been investigating, but previous studies elsewhere showed both genders sharing the food resources, with differences between maturity stages: mature shrimps feed on larger prev (Branco & Moritz-Júnior 2001. Willems et al. 2016). Thus, the feeding overlap between genders probably happens locally. In experimental tanks with the sexually dimorphic penaeid Litopenaeus vannamei, Moss & Moss (2006) tested the effects of gender and size on feed acquisition time. Their results showed that even being smaller than females, males had a competitive advantage over females in acquiring feed. Assuming that the same feeding behaviour occurs in natural populations of X. kroyeri, the difference in the response-time predicted by the relative growth models might be an intrinsic mechanism to compensate the feeding overlap between immature individuals, for instance. Food availability is a sensitive factor for immature shrimps, but not a limiting growth factor for later stages (Franco et al. 2006); so, the male's competitive advantage over female will affect more immature than mature shrimps. The allometric coefficients of immature males oscillated slower than females over time, which support the competitive advantage hypothesis. The dyssynchronous response between genders

might be a temporal compensation so that immature individuals can meet the rapid growth demand at this life stage, maintaining the population locally.

# Correction proposal for future studies regarding WLR in *Xiphopenaeus kroyeri*

The misunderstanding in allometric coefficient (*b*) interpretation when only carapace length is applied as the shrimp's length dimension, such as demonstrated in Materials and Methods section, deserves attention. In the exploratory analysis, the *X. kroyeri* relative growth was biased when carapace length was the body dimension measurement: the allometric coefficient was 16% lower compared to when total length was used. Therefore, a mathematical formula can be applied to standardised the WLR in *X. kroyeri* when carapace length is the only available measurement:

### Total lenght<sub>Estimated</sub> $(cm) = [(4.12 \cdot Carapace lenght) + 16.76]$

Since the sample size per year was large (Table II) and the relationships between the body's dimensions were strong during nine consecutive years for both genders (R<sup>2</sup> values in Table SI), this adjustment is reliable for this species. Andriguetto-Filho et al. (2016) stated that carapace length measurement encompasses the most rigid structure of the shrimps' body, justifying its utilization as representative of shrimps' length. The carapace length is a good length estimator, but the weighttotal length relationship is a better estimator for the allometric coefficient compared to weightcarapace length relationship. The correction proposed allows a more suitable allometric coefficient that may serve as reference for reliable comparisons among different spatialtemporal scales, which is desirable since X. kroyeri has a wide spatial distribution in Western Atlantic Ocean.

In conclusion, the relative growth behavior of *X. kroyeri* caught by fisheries in northern Rio de

Janeiro State varies in a predictable time scale; however, none of the environmental variables (water temperature, salinity, chlorophyll-a and organic matter availability) strongly supported the variation, at least during nine consecutive years (2005 to 2013). During this time interval, changes in the relative growth behavior are probably drive by intrinsic mechanisms, allowing individuals to share both habitat and available resources and maintaining local fisheries.

The understanding of the relative growth of X. kroyeri measured by WLRs may contributed to the fishery management locally and elsewhere. Biometric data of target species, such as length and weight, are variables easy to obtain, generating important metrics for the fishery management. Estimations of WLRs allow fisheries scientists and stakeholders to convert growth-in-length equations to growthin-weight in stock assessment models; to compare biometric aspects among stocks from different fishing areas; to estimate biomass from length frequency distributions; and to calculate individuals' condition factor, a measure of wellbeing of the stock (King 2007, Famoofo & Abdul 2020). We recommend the regular monitoring of this fishing stock because seven years passed since the sampling analyzed in this study.

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APMDB did conceptualization, investigation, funding acquisition, writing - first draft and writing - review and editing. LPF did sampling, investigation and methodology. IAP did formal analysis and writing - review and editing.

