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Relative growth of *Menippe frontalis* (Crustacea: Brachyura) in the Gulf of Guayaquil, Ecuador, by multi-model approach

René Zambrano Dorcid.org/0000-0002-0603-7475

John Ramos (orcid.org/0000-0002-9325-7256

Departamento de Ciencias del Mar, Carrera de Biología, Facultad de Ciencias Naturales, Universidad de Guayaquil. Av. Raul Gómez Lince S/N y Av. Juan Tanca Marengo, Guayaquil, Guayas 090601, Ecuador. RN E-mail: eddie_zam89@hotmail.com JR E-mail: lex_ramos92@outlook.es

ZOOBANK: http://zoobank.org/urn:lsid:zoobank.org:pub:6ED24F4B-851C-4951-80DB-B074ABBA9F75

ABSTRACT

Relative growth can help to identify dimorphism between individuals, and it is also used to determine changes in ontogeny related to sexual maturity. The morphometric variables recorded were width, length and height in carapace and chelae. The abdomen width was taken only in females. Data analysis was made separating males and females. Exploratory analysis used maximum, minimum and mean values and compared these values between sexes using MANOVA, ANOVA and LSD-Fisher methods. A weight-size relationship was also determined. Relative growth was estimated using a multi-model approach. Six models were applied, and the best was selected using Akaike and Bayesian information criteria. Residual versus predicted graphics were also produced based on the selected models. The mean sizes were similar between sexes, but the maximum values were observed in males. The weight-size relationships showed a negative allometry. The best model varied by morphometric variables and sex, but the type of relative growth was principally isometric and negative allometry. Biometric characteristics in Menippe frontalis A. Milne-Edwards, 1879 did not show abrupt changes in the relative growth. The threshold was not assumed as an indicator of morphometric sexual maturity however, they may be used for establishing legal minimum size in *M. frontalis*.

Keywords

Morphometry, multi-model approach, Pangora, relative growth, stone crab

CORRESPONDING AUTHOR René Zambrano eddie_zam89@hotmail.com

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INTRODUCTION

The stone crab *Menippe frontalis* A. Milne-Edwards, 1879 is distributed from México to Peru, and it inhabits the rocks between the edges of protected beaches and the boulders or cliffs that form the promontory adjacent to the beach (Crane, 1947; Hendrickx, 1992; 1995). *Menippe frontalis* have been reported from the continental coast of Ecuador, and it is considered an analogous species with *M. mercenaria* (Say, 1818), which inhabits the Atlantic Ocean (Mayer and Giesbrecht, 1883; Faxon, 1895; Garth, 1946).

No formal fisheries of *M. frontalis* exist, and therefore they are captured as fauna associated with lobster fisheries (genus *Panulirus* White, 1847) in the Gulf of California (Mexico) and Peru (Hendrickx, 1995; Carbajal and Santamaría, 2017). In Ecuador, *M. frontalis* is known as "pangora" and supports an unregulated commercial fishery.

Ayón-Parente and Hendrickx (2002) noted that the publications about *M. frontalis* are principally systematic studies as well as checklists and field guides (Milne-Edwards, 1879; Mayer and Giesbrecht, 1883; Faxon, 1895; Rathbun, 1930; Garth, 1946; Crane, 1947; Holthuis, 1954; Hendrickx, 1992; 1993; 1995). Three studies exist (as grey literature) on *M. frontalis* in Ecuador. One suggests that it is a species of commercial importance (Correa, 1993), while another characterizes the fishery in Posorja. We found only one work related to relative growth in *M. frontalis*, which is only briefly descriptive due to the low number of specimens analyzed (54 individuals) (Ayón-Parente and Hendrickx, 2002).

Relative growth analyzes the body shape and identifies differences through morphometric relationships (Toro-Ibacache *et al.*, 2010). It is used as a tool in determining changes in body proportions associated with sexual dimorphism, differences between development phases (*i.e.*, juveniles and adults), and differences between sexes or within each sex (Dalabona *et al.*, 2005; Hartnoll, 2012). These latter differences are important for estimating morphometric sexual maturity, which is a relevant population parameter for commercial species, like *M. frontalis*, due to its application in fishery management (Bertini *et al.*, 2007).

Analyses of relative growth apply common logarithmic transformations and linear models, and is

based principally on Huxley's work (1932). Geometric morphometrics is another way used in crustaceans (Silva and Paula, 2008; Alencar *et al.*, 2014; Kalate *et al.*, 2018) using specialized software. Rodríguez-Domínguez *et al.* (2018) studied the relative growth in *Callinectes bellicosus* Stimpson, 1859 based on a multimodel approach. They showed that it is incorrect to define *a priori* the linear or power model as the best for representing the data. Clayton (1990) mentioned that relative growth does not always show developmental phases (*i.e.*, juveniles and adults) that allow estimates of morphometric sexual maturity.

Weight-size relationships are not of great interest to current fisheries science (Hilborn and Walters, 1992; Froese, 2006) however, they are useful for ecological studies like estimating fish weight for underwater visual censuses, or for estimating input data in stock assessment models (Kulbicki *et al.*, 2005; King, 2007). For *M. frontalis*, there is no previous record documenting a weight-size relationship, which is necessary for stock assessments and management, considering that data recorded are usually sizes, and the information necessary for establishing catches and estimation of biomass is weight (Froese, 2006; Froese *et al.*, 2014).

Due to the divergence in the criteria, the aim of this paper is to determine the best model for analyzing relative growth in *M. frontalis* by a multi-model approach, as well as to identify some morphometric relationships useful for estimating sexual maturity.

MATERIAL AND METHODS

The crabs (n = 280) were collected in May, July and October 2018 from commercial catches in Posorja port, Gulf of Guayaquil, Ecuador. The recorded variables included width, length and height for the carapace (CW, CL, CH), right chelae (RCW, RCL, RCH) and left chelae (LCW, LCL, LCH) by sex (Fig. 1). The individual weight (W) was measured for males and females and the abdomen width (AW) was recorded only for females. The measures were recorded by a digital Vernier caliper and a digital balance, with an accuracy level of 0.01 mm and 0.01 g, respectively (Overton and Macintosh, 2002; Maccormack and DeMont, 2003; Josileen, 2011). The database was uploaded to Mendeley Data (Zambrano and Ramos, 2019).



Figure 1. A: Sampling site in Posorja, Gulf of Guayaquil, Ecuador. B: Morphometric variables recorded for *Menippe frontalis*. CL, carapace length; CW, carapace width; CH, carapace height; RCW, right chela width; RCH, right chela height; RCL, right chela length.

The data analysis was made separating males and females. An exploratory analysis used minimum and maximum sizes, mean (\bar{x}) and standard deviation (SD) values. Also, the carapace variables (CW, CL, CH) were compared between sexes by a multivariate analysis of variance (MANOVA), including the Hotelling test for multiple comparisons with Bonferroni's correction using InfoStat software (Di Rienzo *et al.*, 2016; Kalate *et al.*, 2018). The differences between carapace variables were established by an analysis of variance (ANOVA) and the least difference test of Fisher, assuming normality in the data by the central limit theorem (Dytham, 2011).

The weight-size relationship was made fitting the power function ($y = a + x^b$) to the raw data using the least-squares method (Dalabona *et al.*, 2005; Josileen, 2011). The W × CW and CL relationships

were complemented with the data collected by Vélez-Cedeño (2017); those data (in cm) were transformed to millimeters and decimal numbers were added as random numbers with a uniform distribution (Sanvicente-Añorve *et al.*, 2003). That process was completed in Stata 15.1 software using the following code sequence: *gen dec= uniform()* \rightarrow *gen decimals= dec-0.5* \rightarrow *gen var2=var1+decimals; var1* is the variable entered (*i.e.*, size, weight), and *var2* is the same variable with decimals.

The pattern of allometry for weight-size relationships was established as follows: negative, b < 3; positive, b > 3; isometry, b = 3 (Widigdo *et al.*, 2017). The relative growth was analyzed by log-transforming all measurements. The carapace dimensions were used as the independent variable, and the chelae were the dependent variables (Silva *et al.*, 2014).

The CL × CW and CH × CW relationships, as well as AW × CW, CL, and CH, were analyzed too. Six candidate models were fitted to the transformed data (Hall *et al.*, 2006; Prototapas *et al.*, 2007; Rodríguez-Domínguez *et al.*, 2018) for selecting the best model (Chart 1):

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Models	Abb.	Equations
Linear	LM	$Ln(y) = Ln(a_1) + b_1 Ln(x)$
Quadratic	QM	$Ln(y) = Ln(a_1) + b_1Ln(x) + b_2Ln(x)^2$
Cubic	СМ	$Ln(y) = Ln(a_1) + b_1 Ln(x) + b_2 Ln(x)^2 + b_3 Ln(x)^3$
Broken stick	BSM	$Ln(y) = Ln(a_1) + b_1Ln(x) \text{ if } x \le B_1$ $Ln(y) = Ln(a_1) + (b_1 - b_2) Ln(B_1) + b_2Ln(x) \text{ if } x > B_1$
Two segments	TwSM	$Ln(y) = Ln(a_1) + b_1Ln(x) \text{ if } x \le B_1$ $Ln(y) = Ln(a_2) + b_2Ln(x) \text{ if } x > B_1$
Three segments	ThSM	$ \begin{aligned} Ln(y) &= Ln(a_{1}) + b_{1}Ln(x) \text{ if } x \leq B_{1} \\ Ln(y) &= Ln(a_{2}) + b_{2}Ln(x) \text{ if } B_{1} < x < B_{2} \\ Ln(y) &= Ln(a_{2}) + b_{3}Ln(x) \text{ if } x > B_{2} \end{aligned} $

Where, a = intercept; b = slope; x = independent morphometric variable; y = depending morphometric variable; and $B_1 =$ threshold.

The initial values for *a* (intercept), *b* (slope) and B_1 (threshold) were established *a priori*. The parameters were optimized using the maximum log-likelihood $LL = -\frac{n}{2}[Ln(2\pi) + 2Ln(\hat{\sigma} + 1]]$, where

$$\hat{\sigma} = \sqrt{\sum_{i=1}^{n} \frac{\left(Ln(x_i) - Ln(\hat{x}_i)\right)^2}{n}} \quad \text{(Haddon, 2011). } B_2 \text{ and}$$

 B_3 were estimated by a threshold regression model included in Stata 15.1 software.

The code used was threshold y x, nthresholds(2) threshvar(x) where y and x are the names of the dependent (e.g., chelae) and independent (i.e., carapace) morphometric variables, respectively. Graphics of residual versus predicted values were generated for analyzing the data distribution in relation to all the models (Salgado-Ugarte, 2013).

The best model was selected using "the weight of evidence" in favor of model $i(W_i)$, estimated for the Akaike and Bayesian information criteria (*AIC* and *BIC*) (Akaike, 1973; Schwarz, 1978). For *AIC*, the bias corrected version (*AIC*) was used due to n/K < 0

40 for the model with the largest value of *K* (Hurvich and Tsai, 1989; Burnham and Anderson, 2004). The procedure is discussed in detail in Burnham and Anderson (2002; 2004).

The best models were selected using three criteria: *i*) the best model showed the highest $W_i AIC_c$ -BIC values; *ii*) the best model presented W_i value > 0.6 and the highest W_i values were different between criteria, but these models did not include the two-segment model; *iii*) the best model showed the highest W_i value. In this case, one of the models that was selected was a two-segment model, and therefore the Draper and Smith (1966) test was used.

The Draper and Smith (1966) test performed validation by statistically fitting two lines to the data (Somerton, 1980) if $F_{tab} < F_{cal}$. That procedure was used in scenario *i* as well, when the best model consisted of two segments, and it was compared with a linear model (Corgos and Freire, 2006; Koga *et al.*, 2010). The allometry level for the morphometric relationships was established using the following slope values: negative, b < 1; positive, b > 1; isometry, b = 1 (Huxley, 1932; Hartnoll, 1974; 1983; 2012; McLay, 2015).

RESULTS

The total sample consisted of 155 females and 125 males. The minimum and average values of CW, CL and CH were similar between sexes, while, maximum values where higher in males (Tab. 1). The CH was different by sex (p < 0.05), but the CW and CL did not show significant differences between males and females (Tab. 1).

The weight-size relationship showed slope values (b) that were higher in males, with differences of 15%, 16% and 33% for CW, CL and CH, respectively (Fig. 2). All cases presented negative allometric growth (b < 3). The residual × predicted showed unbiased and heteroscedastic data (Fig. 2). The morphometric relationship presented differences on the best model selected (Figs. 3, 4).

Table 1. Minimum, maximum, mean and standard deviation (SD) size values recorded by sex in *Menippe frontalis* in the Gulf of Guayaquil. Probability values (p) from the ANOVA to test for differences in size between sexes, and least significative differences of Fisher (LSD).

		Males			Females			
	Min	Max	Mean ± SD	Min	Max	Mean ± SD	р	LSD Fisher
CW	50.65	144.80	92.84 ± 15.42	50.65	120.90	93.41 ± 16.63	0.7699	3.81
CL	37.60	117.17	67.87 ± 13.84	33.35	102.54	68.64 ± 15.26	0.6624	3.47
СН	17.29	49.28	32.78 ± 5.79	17.00	48.41	34.41 ± 6.65	0.0321	1.49



Figure 2. Weight-Size relationships of *Menippe frontalis* in Posorja, Gulf of Guayaquil, Ecuador, and residuals vs predicted values obtained from the power model. CW, carapace width; CL, Carapace length; CH, carapace height.



Figure 3. Raw data and the best models fitted to each morphometric relationship established for *Menippe frontalis* in the Gulf of Guayaquil, Ecuador. CW, carapace width; CL, carapace length; CH, carapace height; LCL, left chelae length; LCH, left chelae height; LCW, left chelae width; RCL, right chelae length; RCH, right chelae height; RCW, right chelae width.

The linear model was the best principally for chelae dimensions \times CW and CH in males. For chelae variables \times CL, the two-segments model was the best in both sexes. For females, the best models were the quadratic model for chelae \times CW and the cubic model for chelae \times CH (Tab. 2).

In the carapace relationships and abdomen, the best models were linear for $CH \times CW$ (both sexes) and $CL \times CW$ (females), quadratic for $CL \times CW$

(males) and AW × CW (females), cubic for AW × CH (females), two-segments for CH × CL (both sexes) and AW × CL (females). The types of relative growth based on the best models were principally isometric and negative allometric (Tab. 2). The threshold values were between 50 to 70 mm CL and 85 to 95 mm CW (Figs. 3, 4). The residual × predicted values showed unbiased and heteroscedastic data (Figs. 5, 6).



Figure 4. Raw data and the best models fitted to the morphometric relationships of *Menippe frontalis* in the Gulf of Guayaquil, Ecuador. CW, carapace width; CL, Carapace length; CH, carapace height; AW, abdomen width.

Table 2. Parameters of the best models (BM) selected based on the criteria i (*), ii (**) and iii (***) for the morphometric relationships of *Menippe frontalis* in the Gulf of Guayaquil, Ecuador. LCL, left chelae length; LCH, left chelae height; LCW, left chelae width; RCL, right chelae length; RCH, right chelae height; RCW, right chelae width; CW, carapace width; CL, Carapace length; CH, carapace height; AW, abdomen width. LM, linear model; QM, quadratic model; CM, cubic model; TwSM, two segment model.

	Males							Females						
Carapace width <i>vs</i>														
	BM	a_1	b_1	a_2	b_{2}	B_1	BM	a_1	b_1	a_2	b_2	b_{3}	B_{1}	
LCL	TwSM (*)	0.79	0.76	-0.04	0.98	4.47	QM (*)	2.04	0.35		0.07			
LCH	LM (***)	-1.28	1.07				QM (*)	9.58	-3.85		0.55			
LCW	LM (***)	-1.62	1.07				QM (*)	7.25	-2.93		0.44			
RCL	LM (*)	-0.39	1.06				CM (*)	59.64	-50.80		15.15	-1.47		
RCH	LM (**)	0.09	1.03				CM (**)	45.35	-39.34		11.95	-1.18		
RCW	LM (*)	-1.54	1.07				LM (***)	-1.17	0.96					
CL	QM (*)	6.31	-2.06		0.35		LM (**)	-0.83	1.11					
СН	LM (*)	-1.04	1.00				LM (***)	-1.12	1.03					
AW							QM (*)	3.34	-0.92		0.21			
Carapace leng	th vs													
LCL	QM (***)	-6.82	4.45		-0.43		QM (***)	-3.63	3.03		-0.28			
LCH	TwSM (*)	-1.54	1.24	-0.03	0.85	4.24	LM (**)	0.26	0.75					
LCW	TwSM (*)	-1.11	1.03	0.54	0.65	3.97	TwSM (***)	-0.78	0.93	-0.28	0.79		4.25	
RCL	TwSM (*)	0.49	0.92	1.59	0.67	3.97	TwSM (*)	0.03	1.02	1.01	0.77		4.25	
RCH	LM (***)	0.11	0.85				TwSM (*)	-0.59	1.00	0.73	0.67		4.25	
RCW	TwSM (*)	-1.67	1.2	0.55	0.66	3.97	TwSM (*)	-0.96	1.00	0.66	0.6		4.25	
CH	TwSM (*)	-0.99	1.08	0.23	0.77	4.24	TwSM (*)	-0.64	1.00	0.16	0.79		4.25	
AW							TwSM (*)	-0.43	0.96	0.67	0.68		4.25	
Carapace heig	ht vs													
LCL	LM (***)	0.56	1.09				LM (**)	1.19	0.85					
LCH	LM (**)	0.02	1.02				CM (*)	62.49	-53.62		15.85	-1.53		
LCW	LM (***)	-0.3	1.02				CM (*)	45.65	-39.73		11.97	-1.17		
RCL	LM (***)	0.88	1.01				CM (*)	28.33	-23.1		7.07	-0.69		
RCH	LM (*)	0.09	1.03				LM (***)	0.44	0.89					
RCW	LM (***)	-0.27	1.03				LM (**)	0.04	0.89					
AW							CM (*)	28.83	-24.78		7.70	-0.77		



Figure 5. Residual values from the best models fitted to the morphometric data of *Menippe frontalis* in the Gulf of Guayaquil, Ecuador. CW, carapace width; CL, Carapace length; CH, carapace height; LCL, left chelae length; LCH, left chelae height; LCW, left chelae width; RCL, right chelae length; RCH, right chelae height; RCW, right chelae width.



Figure 6. Residual values from the best models fitted to the morphometric data of *Menippe frontalis* in the Gulf of Guayaquil, Ecuador. CW, carapace width; CL, Carapace length; CH, carapace height; AW, abdomen width.

DISCUSSION

The relative growth differed according to morphometric relationship and sex in *M. frontalis,* and consequently the parameter and allometry must be specifically analyzed. In addition, we did not find an abrupt change in the relative growth which could be related to morphometric sexual maturity. Our results show that the linear model is not always the best option for estimating the relative growth. Similarly, for *Pachygrapsus marmoratus* (Fabricius, 1787) and *Callinectes bellicosus* Stimpson, 1859 the best models included cubic, broken stick, and twosegments model depending on the morphometric variable used (Prototapas *et al.*, 2007; Rodríguez-Domínguez *et al.*, 2018).

In relative growth studies of crustaceans, the most common is to use a linear model with logtransformation (Huxley, 1932; Hartnoll, 2012; Kalate et al., 2018). Based on this, many works have been developed in different species, such as Leptuca thayeri Rathbun, 1900, Aratus pisonii (H. Milne Edwards, 1837), Armases rubripes (Rathbun, 1897), Halicarcinus cookii (Filhol, 1885), Portunus sanguinolentus (Herbst, 1783), P. pelagicus (Linnaeus, 1758), and Eriocheir japonica (De Haan, 1835) (McLay and Van den Brink, 2009; Sukumaran and Neelakantan, 2010; Araújo et al., 2012; Zhang et al., 2017; Marochi et al., 2018). For relative growth studies it is best to not use the linear model a priori, but instead to test several models, selecting the most appropriate one according to the biology of the species.

Our morphometric relationship presented isometry and negative allometry for the best models, while Ayón-Parente and Hendrickx (2002) found positive allometry between CL × CW in *Menippe frontalis*. This difference probably can be related to sample size, since Ayón-Parente and Hendrickx (2002) only collected 54 specimens and in this study, there were 280 individuals. The negative allometry found in *M. frontalis* means that the weight increases slower than the size. This type of allometry has been observed for crab species such as *Scylla serrata* (Forskål, 1775), *Pachygrapsus marmoratus* (Fabricius, 1787), *Carcinus aestuarii* Nardo, 1847, *Liocarcinus depurator* (Linnaeus, 1758), *L. navigator* (Herbst, 1794) and Eriphia verrucosa (Forskål, 1775) (Widigdo et al., 2017; Aydın, 2018).

We recorded CW sizes greater than those reported by other authors for males and females (*e.g.*, 115.9– 128 mm CW and 98.4–100 mm CW, respectively) (Hendrickx, 1995; Ayón-Parente and Hendrickx, 2002). *Menippe frontalis* also shows sizes generally larger than *M. mercenaria*, which has maximum sizes reported as 89.5 mm CW in Mexico, and 127.4 mm CW in males and 114.6 mm CW in females for the Florida coast, USA (Cervantes-Martínez and Ramírez-González, 2001; Crowley *et al.*, 2018).

The observed differences in the relative growth and sizes of *M. frontalis* and *M. mercenaria* could be related to geographical distribution and environmental variables, which may be explained by variations in the genetic structure of populations, phenotypic plasticity related to environmental heterogeneity, or a combination of both (Maszczyk and Brzeziński, 2018). Additionally, the difference in maximum sizes between the sexes could be due to female crustaceans commonly preferring dominant males, which are often larger (Subramoniam, 2017).

The weight-size relationship showed that the males of *M. frontalis* were bigger and heavier than the females. This has also been evidenced in other crabs such as *Ucides cordatus* (Linnaeus, 1763) (Pinheiro and Fiscarelli, 2009). In this sense, it is necessary to separate the data by sex for stock assessment when the models are using the allometry value of weight. Our results suggest that changes in the relative growth of *M. frontalis* are explained by different models, including but not limiting to, the linear model.

The threshold values (B_1) could be assumed to be indicators of morphometric sexual maturity in M. *frontalis*. We assume 70 mm CW as the size at onset of morphometric sexual maturity due to it being the most repetitive threshold value in the best models in both sexes. For M. *mercenaria*, M. *adina* Williams and Felder, 1986 and their hybrids, the morphometric sexual maturity reported was 71 mm CW in males and 59.6 mm CW in females (Gerhart and Bert, 2008). On the other hand, for M. *mercenaria* sexual maturity at 63.1 mm CW in males and 66.3 mm CW in females have been recorded (Crowley *et al.*, 2018). Differences in sexual maturity between congeners could be because *M. frontalis* reaches greater sizes, as was mentioned previously. All other species used CW as an independent variable, but in *M. frontalis* the produced threshold values are so high that we do not consider them as references of sexual maturity. Additionally, this species does not show an abrupt change in their relative growth. Therefore, the results and comparisons should be treated with some caution considering that the data, the analysis and the statistic interpretations could be misleading as biological interpretations (Clayton, 1990).

The linear model was the only one where a morphometric variable useful for determining sexual maturity in *M. frontalis* was not found. A similar case has been observed for males of *Homarus americanus* H. Milne Edwards, 1837, where sexual morphometric maturity was not detected in their chela (Conan *et al.*, 2001). It is therefore necessary to include more than one model for estimating relative growth in crustaceans, as well as the chelae and other morphometric variables (*e.g.*, carapace dimensions) for estimating sexual maturity. Based on previous guidelines (FAO, 1995), we propose to use our threshold values as the minimum legal size for commercially harvesting *M. frontalis*.

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