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Research Article

Estimation of growth parameters of male blue crabs *Callinectes arcuatus* (Brachyura: Portunidae) from the Gulf of California using the Schnute model

Gilberto G. Ortega-Lizárraga[1], Guillermo Rodríguez-Domínguez[1], Raúl Pérez-González[1] Nicolás Castañeda-Lomas[1] & E. Alberto Aragón-Noriega[2]
[1]Facultad de Ciencias del Mar, Universidad Autónoma de Sinaloa, 82000 Mazatlán, Sinaloa, México
[2]Unidad Sonora del Centro de Investigaciones Biológicas del Noroeste
Estero de Bacochibampo, Guaymas, Sonora 85454, México
Corresponding author: E. Alberto Aragón-Noriega (aaragon04@cibnor.mx)

ABSTRACT. This study describes the growth parameters of males of the blue crab *Callinectes arcuatus* based on samples from a coastal lagoon in the southern Gulf of California and from individuals raised under controlled conditions. The models assessed were the four variants of the Schnute growth model and a special case of the von Bertalanffy model (VBGM). The Akaike information criterion was used to select the best model. The models with the best fit were Case 3 of the Schnute model for the separated wild and captive-reared data sets, but the combined data set fit better to the VBGM function, indicating linear growth, and Case 5 suggesting asymptotic growth of the *C. arcuatus*. Our results depend on the assumption that reared and fished individuals were covering the entire benthic growth period. It is concluded that 1) modeling growth by treating cohorts as individuals yields accurate estimations of *k* and the L_∞ equivalent that can be used directly in stock assessment models, and (2) the ranges of validity of the best growth models for *C. arcuatus* growing in wild and cultured environments overlapped in the size range of 62 to 85 mm of carapace/width, but they have a continuity that represents blue crab growth throughout their benthic life.

Keywords: *Callinectes arcuatus*, growth, multi-model, wild population, controlled conditions, Gulf of California.

Estimación de los parámetros de crecimiento de los machos de la jaiba azul *Callinectes arcuatus* (Brachyura: Portunidae) del Golfo de California, utilizando el modelo de Schnute

RESUMEN. Se describen los parámetros de crecimiento de machos de la jaiba azul *Callinectes arcuatus*, de una laguna costera del sureste del Golfo de California y de ejemplares mantenidos en condiciones controladas. Los modelos evaluados fueron las cuatro variantes de Schnute y el de von Bertalanffy (VBGM). El criterio utilizado para seleccionar el mejor modelo fue el de Akaike. Los modelos que presentaron un mejor ajuste fueron el Caso 3 de Schnute para datos separados, del medio natural o en condiciones controladas, indicando una relación lineal; y el Caso 5 de VBGM para los datos combinados, lo que sugiere un crecimiento asintótico para *C. arcuatus*. Estos resultados corresponden al análisis de los datos conjuntos de los organismos obtenidos del medio natural y de los estanques en condiciones controladas. Se concluye que 1) el modelo de crecimiento obtenido a través del análisis de las cohortes individuales presenta estimaciones adecuadas de *k* y L_∞, que se puede considerar equivalente al utilizado en modelos evaluación de stocks, y 2) los rangos de validez de los mejores modelos de crecimiento para la jaiba azul *C. arcuatus* en el medio natural y en condiciones de cultivo coinciden en el rango de tamaño de 62 a 85 mm de ancho de cefalotórax, teniendo una continuidad que ajusta adecuadamente su crecimiento durante su etapa de vida bentónica.

Palabras clave: *Callinectes arcuatus*, crecimiento, multi-modelo, individuos salvajes, condiciones controladas, Golfo de California.

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INTRODUCTION

The most important groups in commercial fisheries are fishes, mollusks and crustaceans. For all three, knowledge of growth is necessary if sustainable management is the target. However, growth rate estimations in fishes or mollusks are easier to obtain when compared to crustaceans, which have no retained hard parts upon which to base age determinations. Age determination studies on these invertebrates have to concentrate on techniques that do not use hard parts, including tag-recapture studies, modal analysis of length distribution data, raising animals under laboratory conditions, and quantifying lipofuscin accumulation in nerve tissue (Shinozaki-Mendes *et al.*, 2012).

The swimming crabs (*Callinectes* spp.) (Williams, 1974) have been fished at increasing intensity for the last three decades in the Gulf of California (Rodríguez-Domínguez *et al*., 2012). Catches were officially recorded in 1982 with 401 ton; in 1990, total catches reached 3,251 ton, and for 2000 and 2012, catches were 10,351 and 11,809 ton, respectively. In 2008, catches reached a maximum of 16,992 ton (SAGARPA-CONAPESCA, 2014). The coastal lagoons of Sinaloa State produce more than 65% of this volume of crab catches. Three main species are caught: 1) *Callinectes arcuatus* Ordway, 1863, a euryhaline species with a salinity tolerance from 1 to 65, 2) *C. bellicosus* Stimpson, 1859, a stenohaline species (30-38), and 3) *C. toxotes* Ordway, 1863, a euryhaline species (0-55; Paul, 1982). However, studies on the tropical species of *Callinectes* in the Eastern Tropical Pacific are scarce, and our knowledge on the rates of growth and development of these species is limited. We found mostly “gray literature” and six published articles dealing with *C. arcuatus*; four of them were carried out in estuarine lagoons along the Pacific coast (Paul, 1982; Fischer & Wolff, 2006; Hernández & Arreola-Lizárraga, 2007; Ramos-Cruz, 2008) and two with laboratory-reared animals (Dittel & Epifanio, 1984; Vega-Villasante *et al.*, 2007).

Undoubtedly, individual growth parameters are very useful as a tool for fisheries management and are used to assess the population response to exploitation pressure (Sparre & Venema, 1998; Haddon, 2001). The body growth rate is also used for ecological studies because it provides insights about population dynamics of species, such as mortality rates and other parameters that are commonly used in life-history studies (Sparre & Venema, 1998; Haddon, 2001). There exist many mathematical equations that describe the individual growth parameters for populations, but in fisheries, the most used is the von Bertalanffy growth model (VBGM) (Von Bertalanffy, 1938). This model is designed for fish populations; however, it is useful to evaluate other fisheries using such models as yield per recruit (Zhu *et al.*, 2009). Other commonly used alternatives are the Gompertz growth model (Gompertz, 1825), the logistic model (Ricker, 1975), and the Schnute model (Schnute, 1981). The Schnute model consists of a differential equation forming eight families of curves depending on the parameter values. The Schnute model is a general four-parameter growth model whose alternative solutions contain the preceding models as special cases. Rather than modeling the instantaneous rate of change, the Schnute model concentrates on the relative rate of change. Montgomery *et al.* (2010) used length-distribution data for the school prawn, *Metapenaeus macleayi* (Haswell, 1879) to demonstrate how the Schnute growth model can be used to model invertebrate growth and select between alternative growth curves when no direct information about length-at-age is available.

The aim of the present investigation was to determine the individual growth parameters of the blue crab *C. arcuatus* from a coastal lagoon of Sinaloa State in the Gulf of California, Mexico, using the five variants of Schnute's growth model. The growth curve was validated by rearing crabs in the laboratory.

MATERIALS AND METHODS

Study area

The Santa María de la Reforma lagoon-estuarine system is located on the continental shelf of the central Mexican Pacific (25°3’50.54”N, 108°8’25.93”W) and represents a type IIIA, inner-shelf coastal lagoon (Lankford, 1977) with mangrove vegetation. The salinity ranged from 25.1 to 38.6 during our study period. The maximum depth of the lagoon is 24 m, and the mean depth is 7 m. The lagoon connects with the Pacific Ocean through two 5 km wide channels with depths of 12-17 m (Fig. 1).

Biological field sampling

Monthly crab samples were collected between January 2011 and July 2012 with ring nets using small commercial fishing vessels at different locations in the Bahía Santa María de la Reforma (Fig. 1). A technician was always present in these small vessels to ensure that the data were collected. The carapace width (CW) was measured in the field as the distance between the tips of the longest lateral spines.

Rearing procedure

Megalopae of *Callinectes arcuatus* for laboratory rearing were collected in the delta of the Presidio River (23°5’34.24”N, 106°17’26.86”W) and fed in the

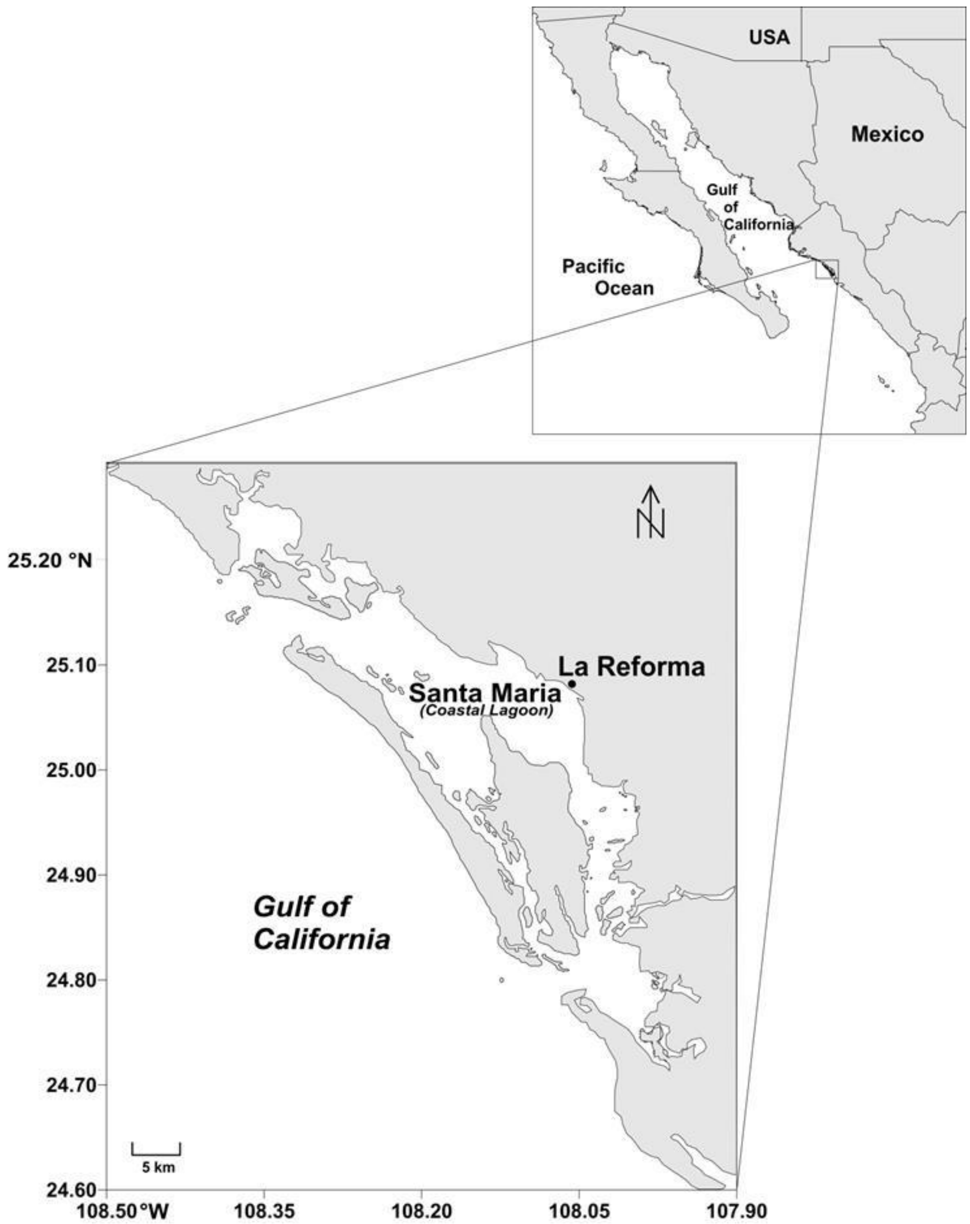

Figure 1. Study area in Santa María, La Reforma Bay, Sinaloa, México.

laboratory, and juvenile blue crabs were separated after 15 days from the other portunid crabs. Juveniles of 21 mm CW were assigned a relative age of 0.041 years (15/365 days), and based on this initial age; the crabs were sampled every 15 days during the 5.5 months of the culture period. The culture tanks were maintained with 35.5 to 38.5 salinity and 18-29ºC temperature, with an aeration device and filter operating. Crabs were reared for 165 days and were fed for the first 15 days with *Artemia* nauplii, for the subsequent 15 days with a mix of *Artemia* nauplii and fishmeal, and after one month with fishmeal only. Biometry was performed as for wild crabs.

Data analysis

Wild cohort

The crabs were sexed and grouped in 5-mm CW intervals prior to frequency analysis. A multinomial model was used to identify age groups and the average CW and standard deviation of each group according to the equation:

$$F_i = \sum_{a=1}^{n} \left[\frac{1}{\sigma_a \sqrt{2\pi}} e^{\frac{(x_i - \mu_a)^2}{2{\sigma_a}^2}} \right] * P_a$$

where x_i is the group mean point for size group i, μ_a is the mean size of cohort a, σ_a is the standard deviation of size in cohort a, P_a is the weight factor of cohort a, and F_i is the total frequency of size group i in the entire sample cohort.

This model was fitted by maximizing the following likelihood function:

$$LL\{X|\mu_a, \sigma_a, P_a\} = -\sum_{i=1}^{n} f_i Ln\left(\frac{F_i}{\sum F_i}\right) * \left[\sum f_i - \sum F_i\right]^2$$

where $\{X|\mu_a, \sigma_a, P_a\}$ is the data log likelihood for the parameters μ_a, σ_a, P_a; f_i is the total observed frequency of size group i; and F_i is the total expected frequency of size group *i* according to the multinomial model.

Age groups were defined according to the following criteria:

a) Mean separation index greater than two (Sparre & Venema, 1998):

$$I.S. = 2 * \frac{(\mu_2 - \mu_1)}{(\sigma_1 + \sigma_2)}$$

b) In cases where it was unclear whether the number of modes had been selected appropriately, the criterion used to select the best model was the Akaike information criterion (AIC) (Burnhan & Anderson, 2002). The smallest AIC_c value was used to determine whether the statistical fit was improved by adding a new mode:

$$AIC_c = 2(k - LL) + \left(2k(k+1)/(n-k-1)\right)$$

where *k* is the total number of estimated parameters in each growth model and *n* is the number of observations.

Growth curves for wild crabs

After identifying all cohorts, the length distributions showing the separated cohort components were plotted in time-ordered sequence. This permitted a visual comparison through time; it was possible to generate alternative hypotheses concerning the exact modal progression. Given a particular modal progression, the mean length and standard deviation parameters from each mode relating to a particular date were identified and used as the data for fitting a standard growth curve. The growth model of Schnute (1981) allows comparisons of growth functions for both asymptotic and non-asymptotic growth. Data were fitted to the Baker *et al.* (1991) derivatives of the growth model of Schnute, using all four cases of the model and the special case for the VBGM equivalent for circumstances where no direct information about length-at-age were available (Baker *et al.*, 1991) as follow:

Case 1, where $k \neq 0$ and $\gamma \neq 0$

$$Y_{2j} = [Y_{1j}^{\gamma} e^{-k\Delta t_j} + \varepsilon^{\gamma}\left(1 - e^{-k\Delta t_j}\right)]^{1/\gamma}$$

Case 2, where $k \neq 0$ and $\gamma = 0$

$$Y_{2j} = exp\left[ln\left(Y_{1j}\right)e^{-k\Delta t_j} + \ln(\varepsilon)\left(1 - e^{-k\Delta t_j}\right)\right]$$

Case 3, where $k = 0$ and $\gamma \neq 0$

$$Y_{2j} = (Y_{1j}^{\gamma} + \varepsilon^{\gamma}\Delta t_j)^{1/\gamma}$$

Case 4, where $k = 0$ and $\gamma = 0$

$$Y_{2j} = Y_{1j}\varepsilon^{\Delta t_j}$$

Case 5, where $k \neq 0$ and $\gamma \neq 1$

$$Y_{2j} = \left[Y_{ij} e^{-k\Delta t_j} + \varepsilon\left(1 - e^{-k\Delta t_j}\right)\right]$$

where Y_1 and Y_2 are average size of the cohort t_j and t_{j+1}, k is the growth parameter with day^{-1} units, γ is related to the inflection point 'S' in growth curve shape, Δt is time passed between t_j y t_{j-1}, and ε for cases 1, 2 and 5 is the asymptotic length, similar to the L_∞ in VBGM.

The models were fitted by maximum likelihood. Both additive and multiplicative error structures were considered. The maximum likelihood fitting algorithm was based on the equation:

$$LL(\Phi|datos) = -\left(\frac{n}{2}\right)(ln(2\pi) + 2 * ln(\sigma) + 1)$$

where Φ represents the parameters of the models, and σ represents the standard deviations of the errors calculated by the following equations:

$$\sigma = \sqrt{\sum \frac{(lnLt_{observed} - lnLt_{computed})^2}{n}}$$ for multiplicative error

$$\sigma = \sqrt{\sum \frac{(lt_{observed} - lt_{computed})^2}{n}}$$ for additive error

Growth curves for reared crabs

Because the age was known for reared crabs, the Schnute model was applied directly without the derivations:

Case 1, $a \neq 0$ and $b \neq 0$

$$Y(t) = \left[Y_1^{\ b} + \left(Y_2^{\ b} - Y_1^{\ b}\right)\frac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}}\right]^{\frac{1}{b}}$$

Case 2, $a \neq 0$ and $b = 0$

$$Y(t) = Y_1 exp\left[\log\left(\frac{Y_2}{Y_1}\right)\frac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}}\right]$$

Case 3 $a = 0$ and $b \neq 0$

$$Y(t) = \left[Y_1^{\ b} + \left(Y_2^{\ b} - Y_1^{\ b}\right)\frac{t - \tau_1}{\tau_2 - \tau_1}\right]^{\frac{1}{b}}$$

Case 4 $a = 0$ and $b = 0$

$$Y(t) = Y_1 exp\left[\log\left(\frac{Y_2}{Y_1}\right)\frac{t - \tau_1}{\tau_2 - \tau_1}\right]$$

Case 5 $a = 0$ and $b = 1$

$$Y(t) = \left[Y_1 + (Y_2 - Y_1) \frac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}} \right]$$

Model selection was made using the sample size-corrected form (AIC_c) of the Akaike information criterion (AIC) (Hurvich & Tsai, 1989; Shono, 2000; Burnhan & Anderson, 2002; Katsanevakis, 2006; Katsanevakis & Maravelias, 2008). The model with the lowest AIC_c value was selected as the best model. The value of AIC_c was calculated with the equations:

$$AIC_c = AIC + (2k(k+1)/(n-k-1) \text{ and}$$

$$AIC = -2LL + 2k$$

where: *LL* is the maximum log likelihood, *n* is the number of observations, *k* is the number of parameters in each model.

In the analyses using multiplicative errors for model fitting, σ and *LL* were recalculated on an additive error scale to obtain consistent scales and comparable AIC_c values.

For all of the fitted models, the differences between AIC values were calculated as:

$$\Delta_i = AIC_i - AIC_{\min}$$

For each model *i*, the plausibility was estimated with the Akaike weight w_i, given by

$$w_i = \frac{\exp(-0.5\Delta_i)}{\sum_{k=1}^{4} \exp(-0.5\Delta_k)}$$

For each of the four models, the expectation $\widehat{CW}_\infty$, the asymptotic standard error SE ($\widehat{CW}_\infty$), and the 95% confidence interval (CI) of the asymptotic CW length were estimated. The asymptotic 95% CI was estimated as:

$$\widehat{CW}_\infty \pm t \text{ d.f., } 0.975 \text{ SE } (\widehat{CW}_\infty)$$

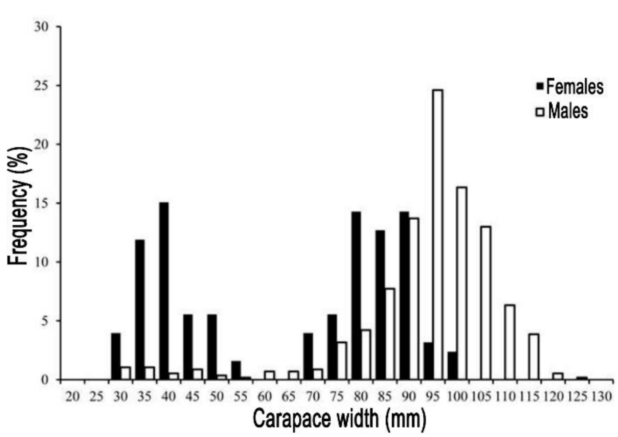

Figure 2. Size frequencies of *Callinectes arcuatus* caught in Santa Maria La Reforma Bay (n = 749).

Growth analysis of combined data

The lowest average CW used in the growth model adjusted to the commercial catch data was assigned an absolute age using the model that best fitted the data for reared crabs. Monthly increases in size were subsequently estimated with the best model obtained from the crabs of the commercial catch. Subsequently, size and age data of the crabs with the best models of the cultivated crabs and crabs of commercial catches were pooled to estimate a single growth model using the same procedure as for the cultivated crabs.

RESULTS

Wild crabs

The CWs of 126 females and 623 males of *C. arcuatus* were measured during the sampling period in the Santa Maria La Reforma coastal lagoon. The CW frequency distribution of these 749 individuals is shown in Figure 2. The CWs of females and males ranged from 35 to 105 mm and from 35 to 130 mm, respectively. Only the data of the males were subsequently used to assess the individual growth parameters for wild and reared crabs because they were more abundant in the commercial catches.

The size structures for males collected from commercial catches allowed us to identify four size groups, but one was much more frequent than the others (97.5 mm) (Fig. 3). Even so, six cohorts were identified successfully with modal progression analysis (Fig. 4). Multiplicative and additive error structures were used to select the best-fitted model (Table 1). In each of the five models tested, the additive error structure resulted in smaller AIC values for the male data. Case 3 of the Schnute model was the best model for wild male crabs; Case 5 and Case 2 were also supported to some extent by the data, whereas the other two cases (1 and 4) were not supported by the data. Parameters for all these models are shown in Table 2, which also indicates the AIC and W_i values.

Reared crabs

We started the rearing with juveniles of 21 mm CW and finished after 165 days at an average size of 85 mm CW, with a maximum size of 94.5 mm (Fig. 5). The additive error structure resulted in smaller AIC values of reared males (Table 1). Case 3 of the Schnute model was also found to be the best model for the reared male crabs; cases 5, 1 and 2 (in order of decreasing importance) were supported to some extent by the data, whereas the other case (4) was not supported by the data. The parameters for all these models are shown in Table 3, as well as the AIC and W_i values.

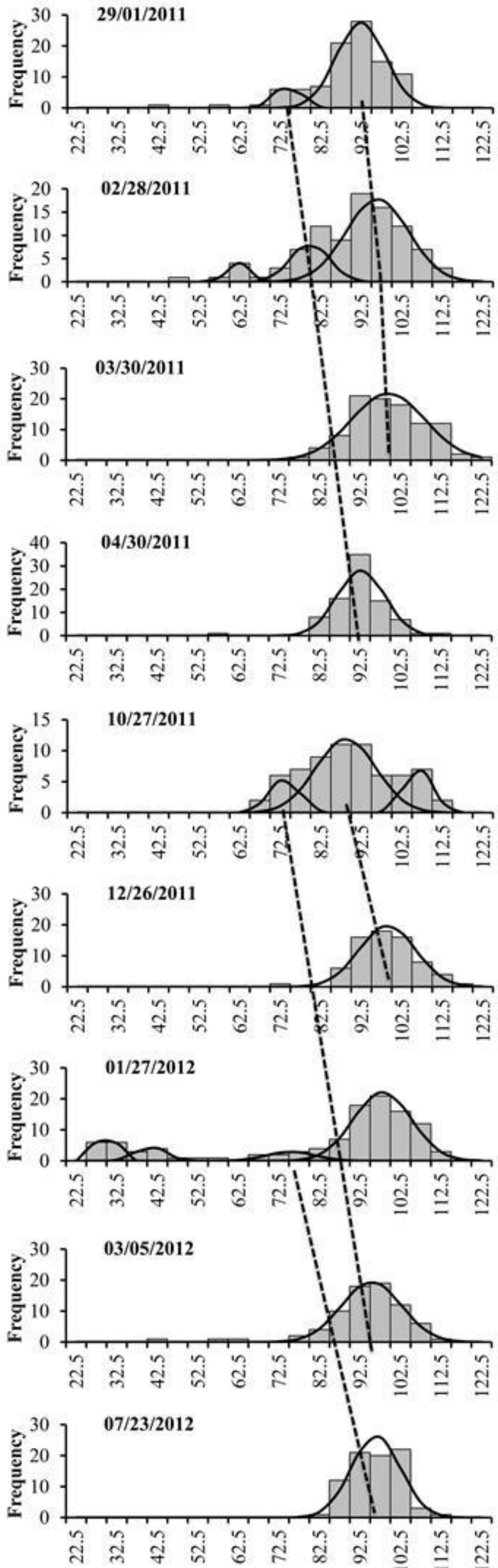

Figure 3. Size structure of male *Callinectes arcuatus* caught in Santa Maria La Reforma Bay. Dotted lines denote different cohorts.

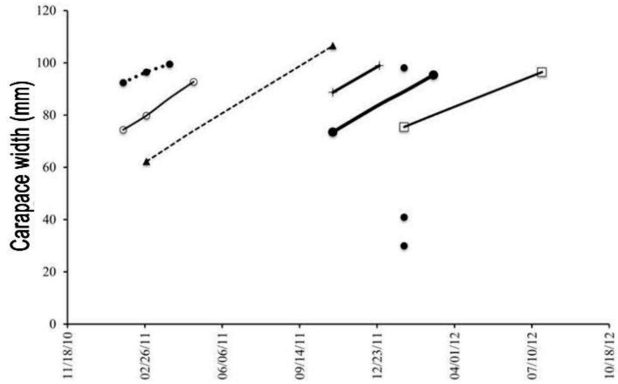

Figure 4. Modal progression of male *Callinectes arcuatus* caught in Santa Maria La Reforma Bay.

Pooled data

The best growth model for the combined data from both sources (wild + reared crabs) was Case 5 of the Schnute model with a W_i of 77.5% (Table 3). The ranges of validity of the best growth models for *C. arcuatus* growing in wild and rearing environments overlapped in the range between 62 and 85 mm CW (Fig. 6), but they showed a continuity that represented blue crab growth throughout their benthic life.

DISCUSSION

Growth of *Callinectes arcuatus* has been described by Paul (1982), Fischer & Wolff (2006) and Hernández & Arreola-Lizárraga (2007). In addition, Dittel & Epifanio (1984) and Vega-Villasante *et al.* (2007) provided information on laboratory-reared animals. In wild populations, Fischer & Wolff (2006) reported an asymptotic CW of 142 mm for males. Hernández & Arreola-Lizárraga (2007) mentioned an asymptotic CW of 140 mm for both sexes combined; these authors attributed the growth differences to the different sampling methods, whereas in the present study growth models were the basis for growth estimations. All the previous studies used the von Bertalanffy growth model. In the present study, the Schnute model for the VBGM yielded an asymptotic CW of 112 mm for males, which is lower when compared to the above-mentioned values. We propose two possible explanations for this difference: 1) Fischer & Wolff (2006) and Hernández & Arreola-Lizárraga (2207) used only juvenile or adult blue crabs, while in this study the analysis was realized with individuals covering the entire benthic life cycle; 2) the smaller asymptotic CW found in the present study could be symptomatic for a fishing-down effect in asymptotic CW. It is important to recall that previous asymptotic CW reports were obtained from data collected a decade

Table 1. Values of Akaike information criterion (AIC) of the models fitted using additive and multiplicative error structures. Numbers in bold are the best models.

	Error	Case 1	Case 2	Case 3	Case 4	Case 5
Wild males	Additive	49.03	44.21	**43.41**	50.03	44.04
	Multiplicative	49.14	44.22	43.44	50.05	44.05
Reared males	Additive	68.18	68.28	**65.40**	70.57	66.28
	Multiplicative	70.58	70.63	65.52	74.28	67.30

Table 2. Asymptotic carapace width (ε) and standard errors for wild males of *Callinectes arcuatus* from each growth model. The models were fitted using the minimum value of AIC. The error structure used was additive. Numbers in bold are the best models.

Case	K	γ	ε	AIC	Wi
1	0.058 (0.049 - 0.069)	4.72 (4.45 - 4.982)	203.58 (196.3 - 210.78)	49.03	2.42
2	3.12 (2.556 - 3.83)		110.35 (106.18 - 114.56)	44.21	26.85
3		4.8 (2.55 -4.982)	110.97 (106.95 - 114.85)	**43.41**	**39.99**
4			2.02 (2.445 - 4.195)	50.03	1.46
5	2.41 (1.99 - 2.93)		113.15 (108.88 - 117.43)	44.04	29.28

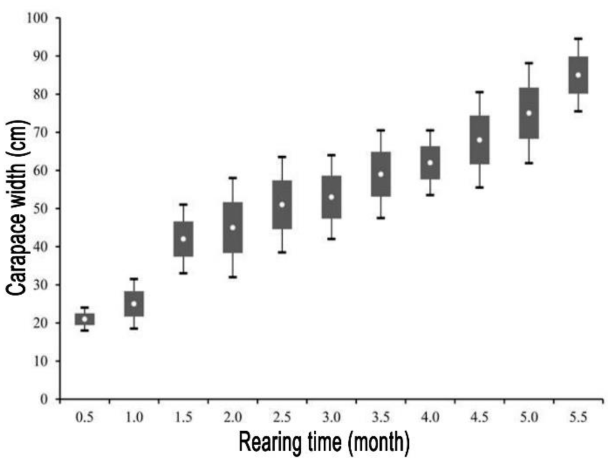

Figure 5. Relationship of size to age for *Callinectes arcuatus* males under controlled conditions. Error bar represents 95% confidence interval around the mean. The boxes denote mean ± SE (standard error).

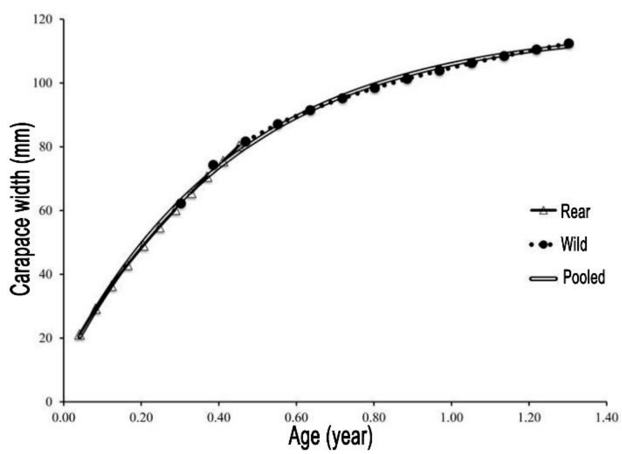

Figure 6. Growth curves for *Callinectes arcuatus* males fitted with Case 5 of the Schnute model.

ago, and the data reported in our study are from 2011 and 2012, when fishing efforts have been very high over the last decade. Therefore, the smaller asymptotic CW in the present study may reflect increased mortality rates at larger size of *C. arcuatus*.

Here we followed a new approach described by Montgomery *et al*. (2010) to modal analyses and how these data can be used with the Schnute model to describe growth. As far as we know no previous study has used the Schnute (1981) growth model to describe growth in any *Callinectes* species, despite its wide acceptance in the literature on fish growth (*e.g.*, Katsanevakis, 2006). All other studies of *C. arcuatus* have directly fitted the VBGM (Fischer & Wolff, 2006; Hernández & Arreola-Lizárraga, 2007; Ramos-Cruz, 2008) rather than also examining alternative growth functions. This is especially relevant when much of the

Table 3. Growth parameter values from each growth model of reared males and pooled data of *Callinectes arcuatus*. The models were fitted using the minimum value of AIC. The error structure used was additive. Numbers in bold represent the best models.

	Case	y_1	y_2	a	b	AIC	W_i
Reared males							
	1	20.19	82.20	-6.219	3.534	68.18	10.33
	2	23.91	80.50	3.523	0.000	68.28	9.80
	3	21.16	80.31	0.000	1.469	**65.40**	**41.45**
	4	29.77	85.80	0.000	0.000	70.57	3.13
	5	22.40	80.68	0.966	1.000	66.28	26.75
Pooled data							
	1	20.74	112.37	2.313	0.928	81.91	22.46
	2	24.56	110.25	3.602	0.000	105.79	0.00015
	3	17.79	70.69	0.000	2.560	141.25	2.92E-12
	4	51.53	129.90	0.000	0.000	201.03	3.04E-25
	5	20.42	112.56	2.214	1.000	**79.43**	**77.54**

early life history incorporates linear growth, which is not consistent with the VBGM. Therefore, we suggest to use several growth models and to select between alternative growth curves.

Montgomery *et al.* (2010) proposed a novel approach to model growth by treating cohorts as individuals. Mean length-at-time data for individual cohorts were fitted in our analyses to the functions of the Schnute model derived by Baker *et al.* (1991) for data with known lengths L_1 and L_2 of an individual at two different times, t_1 and t_2, respectively. This approach allowed us to fit the data to both asymptotic and non-asymptotic growth functions, which is especially important when studying the growth of short-lived species where growth may be linear for much of the species' life cycle.

In this study, we assessed the feasibility of combining data from laboratory-reared and wild individuals of *C. arcuatus*. We were able to develop a growth model for each type of data and to suggest realistic growth parameters. The most important result was that we detected an overlap in the range of 62 to 85 mm CW, suggesting ongoing growth. We proposed a blue crab growth curve covering their entire benthic lifespan, which opened an opportunity to obtain a better assessment of growth parameters than it is available from either wild data or culture environment data alone. As separate data sets (wild and reared), Case 3 of the Schnute model provided the best fit to the data set, which means the dataset fitted best to a power function, indicating linear growth of *C. arcuatus* in the study area. However, the combined data set fitted better to the quadratic function (Case 5) suggesting asymptotic growth of *C. arcuatus*. Our results, however, depend upon the assumption that the entire period of growth was covered by these reared and fished individuals.

It is concluded that (1) modeling growth by treating cohorts as individuals yields adequate estimates for *k* and the $L\infty$ equivalent that can be used directly in stock assessment models, and (2) the ranges of validity of the best growth models for blue crabs *C. arcuatus* growing in the wild and reared in the laboratory overlapped in the range of 62 to 85 mm CW, but they have a continuity that recreated the blue crab growth throughout their benthic life.

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