

JOINT LIKELIHOOD FUNCTION BASED ON MULTINOMIAL AND NORMAL DISTRIBUTIONS FOR ANALYZING THE PHENOTYPIC GROWTH VARIABILITY OF GEODUCK CLAM *PANOPEA GLOBOSA*

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ABSTRACT

In age and growth studies the individual variability is recognized as a source of bias, if it is not taken into account in the analyses it can lead to overestimates or subestimates of the mean length at age of a cohort. In this study, a new approach for analyzing individual shell length-at-age variability was developed for *Panopea globosa* using a joint negative log-likelihood where both shell length frequency distributions (0.105–7.04 mm) and shell length-at-age (100–187 mm) data sets were combined. Six candidate growth models were analyzed that included assumptions about the variance for each age in the population, and the best growth model was selected using a multimodel inference approach. Growth modeling including phenotypic growth variability showed that estimates of t_0 were better than those computed from conventional growth models. We found that the Johnson model was the best candidate growth model for fitting both data sets.

INTRODUCTION

A frequent assumption in stock assessment models is that individual growth in marine organisms can be described adequately through mean growth parameters. However, these parameters are usually estimated from length-at-age data, and they are highly variable (Sainsbury 1980). This means that the growth models are fit to average trajectories that ignore intrinsic biological variability about individual growth. For several marine populations is recognized that the length-at-age variability decreases with time or age (growth compensation), or the inverse pattern, where length-at-age variability increases with age (growth depensation) (Pfister and Stevens 2002). For effective fisheries management, the length structure is biologically useful; and catch-at-length analysis have been applied to Pacific cod (*Gadus*

macrocephalus), longneck croaker (*Pseudolithus typus*), and round scad (*Decapterus russellii*) (Sullivan et al. 1990); red sea urchin (*Strongylocentrotus franciscanus*) (Lai and Bradbury 1998); red king crab (*Paralithodes camtschaticus*) and tanner crab (*Chionoecetes bairdi*) (Zheng et al. 1995, 1998); jumbo squid (*Dosidicus gigas*) (Morales-Bojórquez and Nevárez-Martínez 2010); and Pacific yellowleg shrimp (*Farfantepenaeus californiensis*) (Morales-Bojórquez et al. 2013). This is associated to the facility of data collection, hence the length structure of an exploited population can be informative of biological factors useful for stock conservation (e.g. length-at-first maturity, selectivity, length-at-first capture).

Several approaches have been used to analyze the length-at-age variability based on deterministic and stochastic growth models. Sainsbury (1980) analyzed the effect of individual variability using the von Bertalanffy growth model (VB), concluding that this feature is important and can be measured from individual growth parameters; if this is not included and considered as a source of bias in the estimation of growth parameters, then the results will be overestimated, affecting the mean length at age of a cohort. Kirkwood (1983) used length increments and length-at-age data for parameterizing the VB. This study implements a proposal first suggested by Sainsbury (1980), where a joint likelihood function based on two sources of data could be more informative in comparison to simply the length-at-age data. The methodology in Kirkwood (1983) is possibly the most inclusive in following Sainsbury (1980) suggestion, however he did not analyze the individual variability in VB. Parma and Deriso (1990) also analyzed the phenotypic variability in growth assuming two hypotheses: 1) stochastic environmental effects are associated with intrinsic sources of growth variability; and 2) variability in the initial length distribution of young organisms are

caused by the individuals having intrinsically different growth potentials. This approach was applied to analyze the effects of the variability on expected yield and reproductive potential of a cohort. Specific individual variability in growth parameters for the VB were modeled based on numerical simulation, thus the phenotypic variability in growth was assessed not from empirical data but from expected parameters distribution (maximum asymptotic length and growth coefficient) (Pilling et al. 2002). Recently, Restrepo et al. (2010) analyzed length frequency and shell length-at-age data using the VB and assumed that the residuals were normally distributed with the variance increasing with the length; this approach allowed for estimating the variance for each age observed in the population.

The stochastic growth models are able to show individual-to-individual changes, their impacts on growth parameters, and provide estimates of theoretical trajectories from length-at-age data, a result which is not commonly represented by deterministic growth models. According to Troynikov et al. (1998) the mean growth rate in early stages (e.g., larvae, juveniles) increases linearly or exponentially, however when the organisms are recruits or mature the growth rate decreases, presenting a growth pattern with dual phases. The stochastic methods applied to individual variability in growth studies have been mainly based on tag-recapture data and Fabens method (von Bertalanffy growth model). Wang et al. (1995) proposed an unconditional likelihood function for analyzing the variability in growth of *Penaeus semisulcatus* from changes in asymptotic length and age-at-tagging, this procedure allows them to obtain unbiased estimation of individual growth, considering that the mean growth curve is increasing as a function of time. Troynikov and Gorfine (1998) explicitly showed a stochastic parameterization applied to Gompertz growth model assuming gamma, log normal and Weibull probability density functions for k and L_∞ parameters; an application of this approach was developed for *Heterodontus portusjacksoni* where simultaneously the length-at-age heterogeneity and random variation in growth coefficient for the von Bertalanffy growth model were analyzed, although the random variation can be included in more of its parameters (Tovar-Ávila et al. 2009). Laslett et al. (2002) proposed a modification to the von Bertalanffy growth model which included a logistic growth rate, expressing the new model with five parameters. This model was able to estimate two growth rates (juveniles and adults) representing individual changes in asymptotic length and variability in time of tagging.

Another approach to analyze phenotypic variability in growth was focused on evaluating the impact of outliers commonly observed in the length-at-age data. Thus, Francis (1988) proposed eliminating the atypical

data (outliers) using average data of age; this procedure gives the same weight to all data and a better fit to the growth curves. In addition, previous studies of growth have assumed two types of residuals commonly known as additive error and multiplicative error, which show a constant variance or homocedasticity (Wang and Liu 2006). Both approaches are based on normal and log-normal probabilistic density distributions and they have not been suitable for detecting the impact on growth parameters when atypical observations are observed in the samples. Chen et al. (2003) proposed three methods where the size of the tails of the normal distribution can be fitted with respect to the proportion of outliers in the data (known as fat tail distributions): 1) the thickness of tails is determined by the degrees of freedom using a student's t distribution, 2) the size of tails is increased by adding a fixed small value ($\lambda = 0.01$) within the normal distribution function, and 3) mixtures distributions where a new parameter is added to represent a proportion of outliers. However, these statistical procedures do not estimate length-at-age variability, assuming a constant variance. It is beyond the scope of this study to analyze the effect of outliers based on fat tail distributions. Moreover, this type of statistical procedure is only valid if the variance is constant and is influenced by the proportion of data assumed as outliers, this analyses has been documented previously for *Panopea globosa* by Morales-Bojórquez et al. (2015). In contrast, the hypothesis of this study focuses on showing a statistical procedure for estimating the variance-at-age when the variance is not constant for all ages in the population.

Given this background, studies on age and growth of geoduck populations have begun focusing on analyzing average growth trajectories of *Panopea generosa* based on VB (Hoffman et al. 2000; Bureau et al. 2002; Campbell and Ming 2003). However, a new approach was recently applied using information theory (mainly multimodel inference) whereby candidate growth models were analyzed based on different individual growth properties. However, although better trajectories were fitted to the observed shell length-at-age data, these described average growth curves (Cruz-Vázquez et al. 2012; Aragón-Noriega et al. 2015; González-Peláez et al. 2015; Hidalgo-de-la-Toba et al. 2015; Zaidman and Morsan 2015). Hence, these new efforts in age and growth modeling studies were limited since they failed to estimate the intrinsic phenotypic variability in growth of *Panopea* species. For *P. generosa* it has been reported that its lifespan may even exceed 150 years (Bureau et al. 2002); while the longevity reported for several other species is close to 50 years (Gribben and Creese 2005; Zaidman and Morsan 2015). In this study, a new approach for analyzing individual shell length-at-age variability was developed for *Panopea globosa* using a joint negative log-

likelihood combining both shell length frequency distributions and shell length-at-age data sets.

MATERIAL AND METHODS

Biological data

For illustrative purposes, two sources of data were used to estimate a combined growth curve for *P. globosa* from the southwestern Baja California Peninsula. Shell length-at-age data for individuals from 3 to 47 years were obtained from González-Peláez et al. (2015). Specific details about sample preparation (shells), reading and accuracy verification, age validation, and results of ageing error were reported by González-Peláez et al. (2015). While that shell length frequency data at early growth stages (0.105–7.04 mm, $n = 867$) were obtained under rearing experimental conditions from fertilization (in vitro) to 68th day at 19°C. The measurements of shell length (mm) of the larval and juvenile growth stages were selected assuming a simple random sampling. Thus, from the 34th day a sample of 72 organisms were sampled weekly during the following 6 weeks. We measured the shell lengths of these individuals by taking digital images and processing them with Sigma Scan Pro, ver. 5.0 (Systat Software, Richmond, CA, USA). The larvae were cultured at 1 ind/ml and the food supply given was *Isochrysis galbana*, while the juveniles were isolated individually and fed with mixture of microalgae *Isochrysis galbana* (50%) and *Chaetoceros* sp. (50%). For both developmental stages the fed ration was between 30,000 and 45,000 cells/ml (unpublished data). This study analyzed shell length-at-age and shell length frequency distribution data of the whole ontogenic cycle of the geoduck clam *Panopea globosa* (trocophora larvae, pediveliger larvae, dissoconch and juvenile stages, including adult stages) in order to describe its phenotypic growth variability. Consequently, both data sets were integrated to cover the widest shell length (SL) range possible, including ages and shell length for early stages less than 1 year, and individuals from 3 to 47 years, this age range represents a shell length from 0.105 to 187 mm SL. This approach was identified as more comprehensive since it provided a complete age range for estimating multiple parameters for each candidate growth model evaluated; this procedure inclusiveness was suitable for jointly analyzing two data sets.

Analysis of shell length-at-age data

The individual growth of *P. globosa* was analyzed using the following six candidate growth models: (1) von Bertalanffy which exhibits an initial fast growth phase, gradually decreasing to attain the asymptotic length, it has no inflexion point for $t > 0$ (Breen et al. 1991; Hoffman et al. 2000; Aragón-Noriega et al. 2015); (2) Gompertz

assumes an exponential decrease of the growth rate with size (González-Peláez et al. 2015); (3) Johnson describes a sigmoid growth with a very strong asymmetry and inflexion point very low close to 0 (Hidalgo-de-la-Toba et al. 2015); (4) Logistic considers an alternative sigmoidal curve (Cruz-Vázquez et al. 2012); (5) the generalized von Bertalanffy growth model (GVB) has a similar interpretation to the VB, however an additional parameter provide greater flexibility for fitting the curve (González-Peláez et al. 2015); and (6) the Richards model which describes several growth forms according to different values of δ_1 , the inflection point can be located in any position of the curve (Zaidman and Morosan 2015). Thus, the estimated shell length-at-age (\hat{l}) was computed from the following mathematical functions:

$$\hat{l} = L_{\infty} [1 - \exp^{-k(t - t_0)}] \quad (1)$$

$$\hat{l} = L_{\infty} \exp^{-\exp[-k(t - t_0)]} \quad (2)$$

$$\hat{l} = L_{\infty} \exp^{-\left[\frac{1}{k}(t - t_0)\right]} \quad (3)$$

$$\hat{l} = L_{\infty} [1 + \exp^{-k(t - t_0)}]^{-1} \quad (4)$$

$$\hat{l} = L_{\infty} [1 - \exp^{-k(t - t_0)}]^{\delta_1} \quad (5)$$

$$\hat{l} = L_{\infty} \left[1 + \frac{1}{\alpha} \exp^{-k(t - t_0)}\right]^{-\delta_1} \quad (6)$$

The growth parameters (θ_i) for the six candidate growth models are: L_{∞} is average maximum shell length reached by older individuals; for the von Bertalanffy growth model k represents the growth coefficient; in the generalized von Bertalanffy and Richards growth models, k has similar interpretation; for Gompertz growth model the parameter k is the rate of exponential decrease of the relative growth rate with age; in the Logistic growth model, k is the relative growth rate parameter; for the Johnson growth model k is the rate at which the asymptotic shell length is reached (Katsanevakis 2006; González-Peláez et al. 2015); t_0 parameter is the theoretical age of the fish at zero size under the assumption that the von Bertalanffy (1938) growth curve describes the growth accurately right down to zero length. Even if this unlikely assumption is true, fish will be born with some positive length, so t_0 will usually be negative. The definition changes according to candidate growth models, e.g., the Logistic, Johnson, and Gompertz models correspond to the inflection point for each curve; for generalized von Bertalanffy growth model t_0 has similar interpretation as in the von Bertalanffy assuming the equation to be valid at all ages; a similar assumption is applied to the Richards growth model (see Katsanevakis 2006; Magnifico 2007 for details). According to Cailliet

TABLE 1
Mathematical function of expected shell length ($\hat{\mu}_a$), and variance σ_a^2 for each modal group a according to shell length frequency distributions for early stages.

Model	Function $\hat{\mu}_a$	Function σ_a^2	Source	Eq.
VB	$\hat{\mu}_{aVB} = Y [1 - \exp^{-\omega(a-t_0)}]$	$\sigma_{aVB}^2 = \sigma_{YVB}^2 [1 - \exp^{-\omega(a-t_0)}]^2$	1,2	(15, 16)
GM	$\hat{\mu}_{aGM} = Y \exp^{-\exp[-\omega(a-t_0)]}$	$\sigma_{aGM}^2 = \sigma_{YGM}^2 [\exp^{-\exp[-\omega(a-t_0)]}]^2$	This study	(17, 18)
JN	$\hat{\mu}_{aJN} = Y \exp^{-[\frac{1}{\omega}(a-t_0)]}$	$\sigma_{aJN}^2 = \sigma_{YJN}^2 [\exp^{-[\frac{1}{\omega}(a-t_0)]}]^2$	This study	(19, 20)
LG	$\hat{\mu}_{aLG} = Y [1 + \exp^{-\omega(a-t_0)}]^{-1}$	$\sigma_{aLG}^2 = \sigma_{YLG}^2 [(1 + \exp^{-\omega(a-t_0)})^{-1}]^2$	This study	(21, 22)
GVB	$\hat{\mu}_{aGVB} = Y [1 - \exp^{-\omega(a-t_0)}]^{\delta_1}$	$\sigma_{aGVB}^2 = \sigma_{YGVB}^2 [(1 - \exp^{-\omega(a-t_0)})^{\delta_1}]^2$	This study	(23, 24)
RC	$\hat{\mu}_{aRC} = Y [1 + \frac{1}{\alpha} \exp^{-\omega(a-t_0)}]^{-\delta_1}$	$\sigma_{aRC}^2 = \sigma_{YRC}^2 [(1 + \frac{1}{\alpha} \exp^{-\omega(a-t_0)})^{-\delta_1}]^2$	This study	(25, 26)

The subindices are defined as: VB = von Bertalanffy, GM = Gompertz, JN = Johnson, LG = Logistic, GVB = generalized von Bertalanffy, RC = Richards. 1) von Bertalanffy (1938), 2) Restrepo et al. (2010).

et al. (2006) the t_0 parameter is largely artificial, in so far as it defines the age at which the organism would be of zero length if it grew throughout its life with the same pattern of growth as in the post-larval phase; α and δ_1 are dimensionless parameters, both providing greater flexibility for modeling the data.

According to Restrepo et al. (2010) the estimated variance for each age observed (σ_i^2) in the VB (σ_{iVB}^2) can be expressed as:

$$\sigma_{iVB}^2 = \sigma_{L\infty VB}^2 [1 - \exp^{-k(t-t_0)}]^2 \quad (7)$$

Thus, different σ_i^2 were estimated for the rest of the candidate growth models based on the following mathematical implementations (Luquin-Covarrubias et al. 2016):

Gompertz

$$\sigma_{iGM}^2 = \sigma_{L\infty GM}^2 [\exp^{-\exp(-k(t-t_0))}]^2 \quad (8)$$

Johnson

$$\sigma_{iJN}^2 = \sigma_{L\infty JN}^2 [\exp^{-\frac{1}{k}(t-t_0)}]^2 \quad (9)$$

Logistic

$$\sigma_{iLG}^2 = \sigma_{L\infty LG}^2 [(1 + \exp^{-k(t-t_0)})^{-1}]^2 \quad (10)$$

GVB

$$\sigma_{iGVB}^2 = \sigma_{L\infty GVB}^2 [(1 - \exp^{-k(t-t_0)})^{\delta_1}]^2 \quad (11)$$

Richards

$$\sigma_{iRC}^2 = \sigma_{L\infty RC}^2 [(1 + \frac{1}{\alpha} \exp^{-k(t-t_0)})^{-\delta_1}]^2 \quad (12)$$

where $\sigma_{L\infty}^2$ is the variance for older individuals, and the abbreviations associated with subindices i and $L\infty$ identify the candidate growth model. This statistical procedure

analyzes the intrinsic variability of shell length-at-age data for different candidate growth models, assuming that the residuals are normally distributed with the variance increasing as a function of the age (Restrepo et al. 2010). The negative log-likelihood function (\mathcal{L}_1) describing the best fit between observed (l_i) and estimated (\hat{l}) shell length-at-age data is expressed as follows:

$$\mathcal{L}_1 = \sum_i \left[\frac{\ln(2\pi\sigma_i^2)}{2} + \frac{(l_i - \hat{l}_i)^2}{2\pi\sigma_i^2} \right] \quad (13)$$

Analysis of shell length frequency data

Shell length data for early growth stages (0.105 to 7.04 mm) of *P. globosa* were analyzed using frequency histograms. Thus, the shell length frequency distribution for each age group (a) was estimated using a normal probabilistic density function (Zar 1999):

$$\hat{f}(L_a) = \sum_{a=1}^n \left[\int_{-\infty}^{L_{a,ai}} \frac{1}{\sqrt{2\pi\sigma_a^2}} \exp \left[-\frac{1}{2\sigma_a^2} (L_a - \hat{\mu}_a)^2 \right] dL_{a,i} \right] \lambda_{a,i} \quad (14)$$

where (L_a) is the observed shell length, ($\hat{\mu}_a$) is the average shell length for each age group a , $\lambda_{a,i}$ represents a parameter of fit for the observed frequency data within each age group a , i represents the sequential number of modal values estimated, and σ_a^2 is the variance for each age group a . The estimation of $\hat{\mu}_a$ and σ_a^2 was done for each group a following the statistical criteria as described in Table 1 (equations 15–26). The parameters associated to equations 15–26 are: Y represents the larger shell length for younger individuals; ω growth coefficient for younger individuals; σ_Y^2 is the variance for larger individuals observed in the early growth stages. The differences between the observed and expected shell length frequency distributions were fitted assuming a multinomial distribution expressed as negative log-likelihood function defined as \mathcal{L}_2 :

$$\mathcal{L}_2 = -\ln L(f|\theta_i) = \sum_{a=1}^n f(L_a | \ln) \left[\frac{\hat{f}(L_a)}{\sum \hat{f}(L_a)} \right] - \sum_{i=1}^n (f_a - \hat{f}_a)^2 \quad (27)$$

where $f(L_a)$ is the observed shell length frequency and $\hat{f}(L_a)$ is the predicted shell length frequency within the average shell length group L_a . A penalization function (eq. 27) was included in the negative log-likelihood for estimating the frequency of individuals for each age group, (f_a) is shell length frequency distribution observed in the sample, and (\hat{f}_a) represents the number of predicted observations. The age groups were identified using Akaike information criterion through: $AIC = 2\mathcal{L}_2 + 2p$, where p is the parameter number for each model fitted to shell length frequency distribution (Haddon 2001). The lowest value AIC was used for determining if the statistic fit can be improved by adding a new mode (Montgomery et al. 2010). This allows for ensuring that the age groups are close to t_0 and that an accurate estimation of all growth parameters is attained.

Parameters estimation

The candidate growth models were fitted to both data sets, minimizing a joint negative log-likelihood function (\mathcal{L}_j) through Newton algorithm contained in the Visual Basic Applications™ (Neter et al. 1996):

$$\mathcal{L}_j = \mathcal{L}_1 + \mathcal{L}_2 \quad (28)$$

To achieve a more accurate estimate of the parameters, the minimizing was done by phases, the parameters less sensitive were simultaneously estimated in the first group considering the statistical propriety of each model ($Y, \omega, \sigma_Y^2, \alpha, \delta_1, \lambda_{a1}$ and λ_{a2}), while the rest retained the values initially assigned. Once the objective function was minimized for a particular phase, the other parameters were added and evaluated gradually ($L_\infty, k, t_0, \sigma_{L_\infty}^2$), thus this was carried out in order to complete the total optimization of \mathcal{L}_j (Legault and Restrepo 1998).

Confidence intervals

The statistical χ^2 used in our study was applied as a non-parametric estimator for estimating confidence intervals ($\alpha = 0.05$). The rationale is based on the possibilities that the confidence regions can be asymmetric rather than symmetrical ellipses as assumed by asymptotic methods, and if this occurs the likelihood-profile or contour method is preferred because it is computationally more efficient than bootstrapping (Haddon 2001; Morales-Bojórquez and Nevárez-Martínez 2010). We estimated the confidence intervals (CI) for the θ_i parameters using a likelihood-profile method (Hilborn and Mangel 1997), the advantage of this approach is that it provides an estimate of the asymmetric confi-

dence intervals either individually or jointly. The estimator assumes a χ^2 distribution with $n = 1$ degrees of freedom (df), when the estimation is individual, thus all values smaller or equal to 3.84 are accepted (Morales-Bojórquez and Nevárez-Martínez 2005); this approach was solved for the following parameters: $Y, \omega, \sigma_Y^2, \alpha, \delta_1, \lambda_{a1}, \lambda_{a2}, t_0, \sigma_{L_\infty}^2$. When the estimation is joint and there is any type of correlation (covariance) between parameters, the CI become wider, in this case the likelihood-contour method is preferred (Cerdenares-Ladrón-de-Guevara et al. 2011), this was applied to L_∞ and k parameters. If there was no correlation between parameters then the confidence intervals would be unbiased (Zepeda-Benitez et al. 2014a). Thus, a χ^2 distribution with $n = 2$ degrees of freedom (df) was applied, such that values equal or less than 5.99 are accepted within CI (Zar 1999). The χ^2 estimator is described as follows by Haddon (2001):

$$CI = 2[\mathcal{L}_j - \ln L(\theta_i)] \leq \chi_{df, 1-\alpha}^2 \quad (29)$$

where \mathcal{L}_j is the joint negative log-likelihood of the most likely value of θ_i ; $-\ln L(\theta_i)$ is the negative log-likelihood based on hypotheses about the value of θ_i (profile or contour), and $\chi_{1-\alpha}^2$ is the value of χ^2 distribution with a confidence level $1-\alpha = 0.05$ and $df = 1$ (profile), or 2 (contour) (Haddon 2001).

Growth model selection

The fit of the six candidate growth models was compared using AIC_c bias corrected for small samples, this condition is defined if $n/\theta_i < 40$ (Zepeda-Benitez et al. 2014b).

$$AIC_c = 2 \times \mathcal{L}_j + 2 \times \theta_i + \frac{2 \times \theta_i (\theta_i + 1)}{n - \theta_i - 1} \quad (30)$$

where \mathcal{L}_j is the joint negative log-likelihood function (eq. 28), θ_i is the number of estimated parameters for each growth model, and n is the number of observed data (shell length-at-age and shell length frequency data). The model with the smallest AIC_c value is considered the best fit to the data (Burnham and Anderson 2002). Differences between the AIC_c for each growth model (i) were calculated as $\Delta_i = AIC_{c,i} - AIC_{c,min}$ according to Burnham and Anderson (2002). The candidate growth models with $\Delta_i > 10$ do not have statistical support and cannot be considered; with $4 < \Delta_i < 7$ have partial statistical support, and $\Delta_i < 2$ have high statistical support.

We estimated the plausibility of each candidate growth model defined as Akaike weight (w_i) (Katsanevakis 2006):

$$w_i = \frac{\exp(-0.5 \Delta_i)}{\sum_{i=1}^6 \exp(-0.5 \Delta_i)} \quad (31)$$

TABLE 2
Number of modal values selected from AIC using the shell length frequency distributions for early stages.

	Parameters	Negative log-likelihood function	AIC
Mode 1	3	3628.84	7263.69
Mode 2	6	3186.15	6384.31
Mode 3	9	3163.44	6344.89
Mode 4	12	3156.55	6337.10
Mode 5	15	3184.68	6399.37

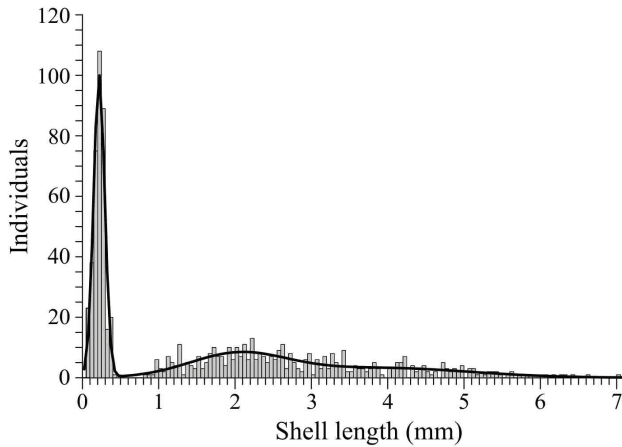


Figure 1. Shell length frequency distributions for each age group (a) estimated for early stages.

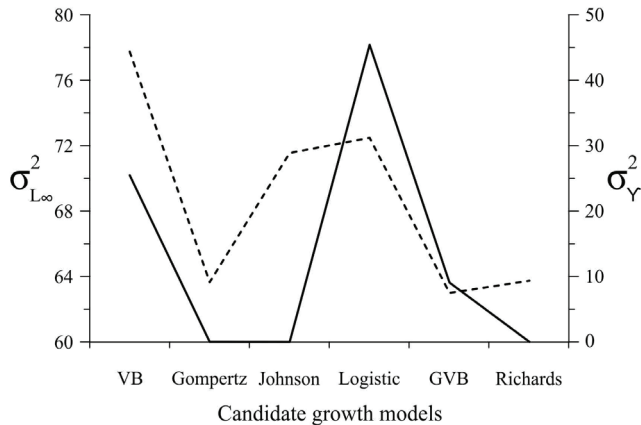


Figure 2. Comparison of the variance $\sigma_{L_\infty}^2$ for older (discontinuous line) and σ_Y^2 younger individuals (continuous line) estimated for each candidate growth model analyzed.

Following the multimodel inference approach, the model-averaged asymptotic length \bar{L}_∞ was estimated as a weighted average using all six models, with the prediction of each model weighted by w_i . Thus, the model-averaged asymptotic shell length is:

$$\bar{L}_\infty = \sum_{i=1}^6 w_i \hat{L}_\infty \quad (32)$$

The unconditional standard error of \bar{L}_∞ was estimated as (Katsanevakis 2006):

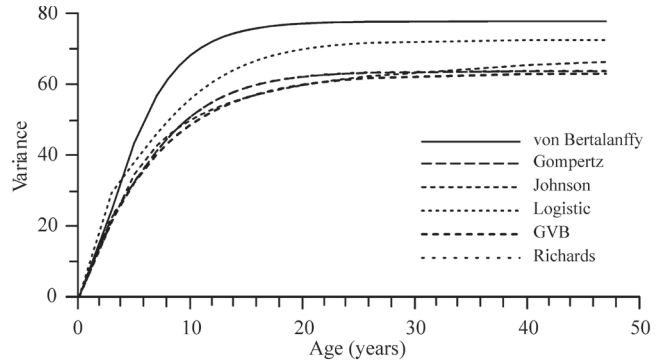


Figure 3. Trajectories of the variance for each age i according each candidate growth model analyzed.

$$SE(\bar{L}_\infty) = \sum_{i=1}^6 w_i \left[\text{var}(\hat{L}_\infty/g_i) + (\hat{L}_\infty - \bar{L}_\infty)^2 \right]^{1/2} \quad (33)$$

where $\text{var} \bar{L}_i/g_i$ is the estimate variance of observed data with respect to each candidate growth model g_i .

RESULTS

The multinomial distribution fitted to shell length frequency data for early growth stages of *P. globosa* allowed for estimating four age groups. The AIC estimated from the hypotheses of one age group until five age groups are shown in Table 2. The mean value of the age group 1 was 0.22 mm, (SD = 0.07, $\lambda_{a_1} = 18.49$), this age group was very well identified for the multinomial function; the mean value for the age group 2 was 1.15 mm, (SD = 0.14, $\lambda_{a_2} = 1.50$), while the third and fourth age groups showed mean values of 3.78 mm (SD = 1.18, $\lambda_{a_3} = 10.46$), and 2.11 mm (SD = 0.51, $\lambda_{a_4} = 9.44$). Comparatively, the fifth age group showed mean value of 4.70 mm (SD = 17.27, $\lambda_{a_5} = 2.43$), however the presence of fifth age group increased the AIC value, consequently the addition of this last age group did not improve the statistical fit of the multinomial function (fig. 1).

This preliminary estimation was useful to define the initial number of age groups to be included when shell length-at-age data were added. Thus, the parameters for both datasets were jointly optimized to each candidate growth model (table 3). The parameters estimated showed that for $\sigma_{L_\infty}^2$ and σ_Y^2 the VB (77.73 and 25.46, respectively), and Logistic model (72.47 and 45.40, respectively) had the higher values (fig. 2). The effect of $\sigma_{L_\infty}^2$ and σ_Y^2 within the VB and Logistic model were influencing the estimates, where the variance for each age i was highest. The rest of the candidate growth models showed similar trends in σ_i^2 estimates with lower values (fig. 3). The ontogenic growth trajectory from the two sources of data to geoduck clam are shown in Figure 4. Thus, the datasets were informative of the different growth parameters with respect to early or adult stages.

TABLE 3
Parameters and confidence intervals (in parenthesis) estimated from joint negative log-likelihood profile or contour ($P < 0.05$) for different growth functions. The sample size for early stages was 867 individuals, and average shell length-at-age data were 24 observations.

Parameter	von Bertalanffy	Gompertz	Johnson	Logistic	GVB	Richards
Y	12.11 (11.40–12.80)	0.36 (0.36–0.38)	0.06 (0.06–0.07)	16.18 (15.70–16.80)	7.23 (7.04–7.46)	0.29 (0.28–0.30)
L_{∞}	164.69 (159.80–170.00)	167.78 (163.50–173.50)	179.48 (175.00–182.50)	168.53 (161.80–175.80)	169.82 (164.20–176.20)	167.84 (162.55–173.60)
ω	0.27 (0.26–0.28)	30.41 (29.50–31.50)	18.66 (18.19–19.09)	32.25 (32.04–32.46)	0.02 (0.02–0.03)	87.47 (86.00–89.00)
k	0.27 (0.23–0.33)	0.21 (0.18–0.25)	0.55 (0.52–0.55)	0.20 (0.15–0.26)	0.15 (0.13–0.19)	0.21 (0.18–0.26)
t_0	0.027 (0.0263–0.0267)	0.067 (0.0671–0.0678)	0.069 (0.069–0.070)	0.23 (0.238–0.239)	0.0322 (0.0321–0.0322)	0.04 (0.0446–0.0449)
σ_Y^2	25.46 (24.46–26.46)	0.02 (0.022–0.024)	0.0008 (0.00076–0.00084)	45.40 (43.19–47.38)	9.06 (8.57–9.48)	0.014 (0.014–0.015)
$\sigma_{L_{\infty}}^2$	77.73 (48.00–144.00)	63.65 (40.00–118.00)	71.55 (48.00–132.00)	72.47 (49.00–133.00)	63.00 (38.30–111.50)	63.74 (38.60–113.00)
δ_1					0.533 (0.530–0.535)	14.31 (14.15–14.46)
α						14.11 (13.90–14.32)
λ_{a_1}	1.84 (1.83–1.84)	1.84 (1.83–1.84)	1.84 (1.83–1.84)	1.84 (1.83–1.84)	1.84 (1.83–1.84)	1.84 (1.83–1.84)
λ_{a_2}	2.17 (2.17–2.18)	2.17 (2.17–2.18)	2.17 (2.17–2.18)	2.17 (2.17–2.18)	2.17 (2.1–2.18)	2.17 (2.17–2.18)

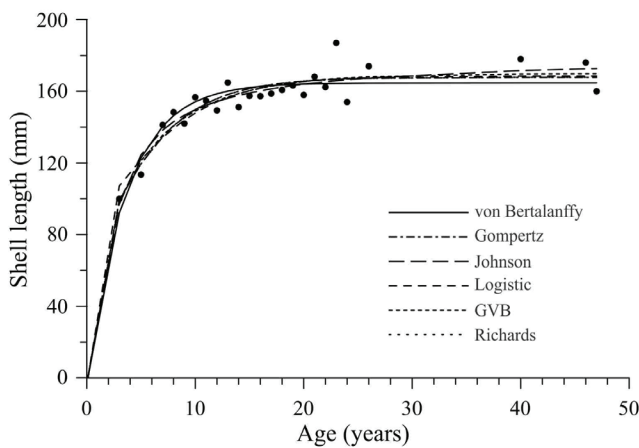


Figure 4. Candidate growth models fitted to shell length-at-age and shell length frequency data of *Panopea globosa*. Points represent shell length-at-age data observed.

The variability estimated in growth parameters showed that average maximum shell length (L_{∞}) varied from 164.69 mm (VB) to 179.48 mm (Johnson model), for the rest of the growth models this parameter was less than 169.82 mm. The k parameter changed between $k = 0.15$ and $k = 0.55$ for GVB and Johnson model,

respectively. The general pattern of variability in this parameter shows that it was commonly estimated as a value less than $k = 0.27$. The parameter associated with t_0 presented the minimum value for VB ($t_0 = 0.027$), and the maximum value for the Logistic growth model ($t_0 = 0.23$) (table 3). The variation of ω for younger individuals varied from 0.02 (GVB) to 87.47 (Richards growth model), and the larger shell length estimated for younger individuals (Y) ranged between 0.06 and 16.18 for the Johnson and the Logistic growth models, respectively (table 3).

The final parameterization including shell length frequency distributions and shell length-at-age data showed convergence in the objective function when only two age groups were assessed, the addition of the third and fourth age group caused lack in convergence. This means that the interactions between both datasets statistically discriminated the usefulness of the third and fourth age group, which were used as seed values in the joint negative log-likelihood function. Thus, new age groups in the shell length frequency distributions were reestimated to each candidate growth model, the first age group was 0.20 mm ($\sigma_a^2 = 7.6 \times 10^{-4}$), and the second was 2.91 mm

TABLE 4
Ranking of the six growth models based on the Akaike information criterion (AIC_c) according to the number of parameters for each candidate growth model (θ_i), Akaike difference (Δ_i), and the Akaike weight (w_i).

Model	θ _i	AIC _c	Δ _i	w _i
Johnson	9	6612.02	0.00	0.47
Gompertz	9	6612.44	0.41	0.38
Logistic	9	6615.35	3.32	0.08
GVB	10	6617.67	5.64	0.02
von Bertalanffy	9	6618.11	6.08	0.02
Richards	11	6625.62	13.59	0.00

(σ_d² = 0.14). Specific details on the λ_{a_i} estimates and confidence intervals are shown in Table 3.

Model selection

According to AIC_c estimates, the best fit to the shell length frequency and shell length-at-age data of *P. globosa* was described by Johnson growth model (AIC_c = 6612.02, Δ_i = 0.00, w_i = 0.47). A second function that showed statistical support was the Gompertz growth model (AIC_c = 6612.44, Δ_i = 0.41, w_i = 0.38). Despite the Logistic, GVB, and von Bertalanffy models varying within 4 < Δ_i < 7 showing partial statistical support, these functions had Akaike weight less than 0.08. Finally, the Richards growth model had no statistical support fitting both data sets (table 4). In this study, the best candidate growth models were the sigmoid functions (also known as curve S-shaped). Comparatively, the asymptotic curves crossing the t-axis (age) and without inflection point, as well as generalized growth models showed less statistical performance expressed in the AIC_c estimates. Given that five candidate growth models had Δ_i < 7, the model-averaged asymptotic length was estimated as 173.38 mm (CI = 154.71-192.05 mm P < 0.05; SE(L_∞) = 9.52 mm).

DISCUSSION

This study was based on the hypothesis of depensatory growth applied to *Panopea globosa*, previous studies ignored the effect of the individual variability commonly observed in age-at-shell length data for geoduck in the Mexican Pacific. Given that the asymptotic growth pattern in geoduck is very well known, we incorporated the individual variability in several deterministic asymptotic growth models. The new integrated shell length-at-age and shell length frequency distribution growth model has improved assumptions about geoduck clam individual growth compared to conventional growth models. In this study, individual variability in geoduck growth was explicitly included; this allows a better parameterization of the candidate growth models. Sainsbury (1980) explained that many mollusks have high variability in their individual growth parameters due to changing age

composition, and this is commonly observed in the variability of increments of length-at-age. We found that the age composition of the *Panopea globosa* is informative about L_∞ and k parameters; however, t₀ parameter estimated from average shell length-at-age growth curves may be over- or underestimated. Thus, the estimation of L_∞ and k for each candidate growth model using this joint negative log-likelihood function showed similar values to those reported by González-Peláez et al. (2015), where they found values between L_∞ = 164.6 mm SL (Richards) and L_∞ = 181.1 mm SL (Johnson), and the growth coefficient estimates varied between k = 0.14 (GVB) and k = 0.49 (Johnson). In general terms, the k parameter in the models used is a measure of the time required for specified growth increments to take place, however its comparison is not possible because the path or trajectory taken by the growth process in each model (Brisbin et al. 1987). Different studies have shown high variations for estimates of t₀; this lack in accuracy about t₀ has commonly been reported in different species of the genus *Panopea*. For *P. abbreviata* (Argentina), *P. generosa* (Canada), and *P. zelandica* (New Zealand) negative values were observed when VB was used (Breen et al. 1991; Campbell and Ming 2003; Morsan and Ciocco 2004; Gribben and Creese 2005; Morsan et al. 2010). In contrast, for *P. generosa* distributed in United States waters, estimates for t₀ parameter had positive values (Hoffman et al. 2000) (table 5).

For *Panopea* species the formation of the shell begins approximately 48 hours after fertilization, and from 1.5 mm SL they are juveniles (Goodwin and Pease 1989), therefore negative and extremely high values of t₀ do not provide useful information about this parameter in its early growth stages. Recently, the multimodel inference approach has been applied to age and growth modeling of *Panopea* spp.; however, this statistical procedure did not yield better estimates of t₀, either values highly skewed were also computed for several stocks (table 6). Our study described successfully estimates of t₀ for six growth models improved the growth curves at the origin (age 0); this was supported by the inclusion of shell length frequency distribution of early stages associated with the joint negative log-likelihood function. These new features must be adopted in growth modeling, since these allow for increasing the accuracy for t₀ estimates, thus improving its biological interpretation. For the t₀ parameter, if a lack of convergence is observed during the optimization process to estimate this parameter, then the final estimation of t₀ can vary its order of magnitude such as was reported for *P. abbreviata* (-46.96, -35.76, -31.87; 133.06, 57.76); and *P. globosa* (-2.99, -1.85, -1.31) (table 6). Pardo et al. (2013) suggested several alternatives for better estimates of t₀; the first is to modify VB using a fixed value of average length-at-age zero

TABLE 5
Estimates of the age when shell length theoretically is zero for *Panopea* spp. using the von Bertalanffy growth model.

Species	Country	Location	t_0	Source
<i>P. globosa</i>	Mexico	Bahía del Sol	-0.200	Cortez-Lucero et al. (2011)
<i>P. generosa</i>	Mexico	San Quintín	-3.190	Calderon-Aguilera et al. (2010)
		Islas Coronado	-2.040	
	United States	Hunter Point	0.719	Hoffman et al. (2000)
		Agate Passage	0.183	
		Fishermans Point	0.552	
		Dallas Bank	0.334	
	Canada	Yellow Bank	-1.420	Campbell and Ming (2003)
		Gabriola Island	-1.020	
<i>P. abbreviata</i>	Argentina	Puerto Lobos	-1.500	Morsan and Ciocco (2004)
		Puerto Lobos	-0.487	
		El Sótano	-2.397	
<i>P. zelandica</i>	New Zealand	Golden Bay	-3.800	Breen et al. (1991)
		Shelly Bay	-1.690	
		Kennedy Bay	-1.670	

defined as L_0 parameter, which is empirical or a known value of length for organisms at their early growth stages. Consequently, L_0 can be fixed, estimating only L_∞ and k parameters. However, L_0 parameter can be iteratively sampled from a normal distribution of possible values of length at an early growth stage; or it can be constrained over the range from known values of L_0 thus assessing the effect in convergence thereby fixing this range.

In this study, estimates for t_0 parameter ranged from 0.027 to 0.23, negative values for this parameter were not computed. The best candidate growth model showed $t_0 = 0.069$ (Johnson) and $t_0 = 0.067$ (Gompertz), where both estimates were very close. In previous studies of age and growth of *P. globosa*, the results estimated for t_0 were highly variable; González-Peláez et al. (2015) showed values from -1.85 (VB) to 28.91 (Schnute), and the best candidate growth model selected by AIC_c was $t_0 = 0.003$ (Gompertz). Aragón-Noriega et al. (2015) analyzed shell length-at-age data for two populations of *P. globosa* in the upper Gulf of California, they reported negative values ranging from $t_0 = -2.99$ (VB) to $t_0 = -0.005$ (Logistic) to Puerto Peñasco, Sonora, and an interval of variation from $t_0 = -1.20$ (VB) and $t_0 = 6.86$ (Gompertz) to San Felipe, Baja California. In the central Gulf of California the estimates of t_0 for *P. globosa* ranged within positive values from 0.24 (VB) to 2.26 (Logistic) (Cruz-Vázquez et al. 2012). For *P. generosa*, Hidalgo-de-la-Toba et al. (2015) analyzed five growth models, among them, three computed $t_0 = 0$ (VB, Gompertz, and Johnson), while that the Logistic growth model estimated $t_0 = 1.34$, and $t_0 = 1.78$ for the Schnute growth model. This last model was also used by Cruz-Vázquez et al. (2012) and Aragón-Noriega et al. (2015), however they did not report results associated with t_0 , assuming that $t_0 = 0$ (table 6).

We found that the combined growth curves using shell length frequency distributions and shell length-at-age data provided more information about t_0 parameter for different growth models. A similar approach was discussed by Sainsbury (1980) and Kirkwood (1983), and they concluded that a joint likelihood function applied to both data sets provided a better description of growth over the range of lengths to which VB was fitted. According to Restrepo et al. (2010), they used a penalty term for each year analyzed (1970–76), using only length frequency observations. A penalty term represents a weight governing the amount of influence of each data set (shell length-at-age and shell length frequency distribution), and this should be implemented in the joint log-likelihood function. However, according to Quinn and Deriso (1999), each penalty term is the inverse of the estimated variance of each data set, assuming that the variance is constant. In this study, we had data from early stages obtained from rearing conditions during 2013. Our analysis estimated an individual variability-at-age observed in shell length-at-age and shell length frequency distribution data, thus the variance was not constant; and consequently the inverse of the estimated variance that could represent the penalty term for each negative log-likelihood was not applicable, because we estimated variance-at-age. For any penalty term estimated, the main problem was to select the variance representing the best amount of influence of each data set, given that we estimated 26 variance-at-age values, potentially to choose arbitrarily a variance-at-age (or average value) could represent bias in the joint negative log-likelihood function affecting the optimization of parameters in the candidate growth models selected.

TABLE 6
Estimates of the age when shell length theoretically is zero for *Panopea* spp. using the multimodel inference approach.

Species	Country	Location	Model	t_0	Source	
<i>P. globosa</i>	Mexico	Bahía Magdalena	VB	-1.857	González-Peláez et al. (2015)	
			GM	0.003		
			JN	-0.301		
			GVB	0.713		
			RC	5.583		
		SC	28.911			
		Puerto Peñasco	VB	-2.990	Aragón-Noriega et al. (2015)	
			GM	-1.310		
			LG	-0.005		
			SC	-		
			SC-RC	-		
		San Felipe	VB	-1.200	Aragón-Noriega et al. (2015)	
			GM	6.860		
			LG	2.970		
			SC	-		
SC-RC	-					
Empalme	VB	0.247	Cruz-Vázquez et al. (2012)			
	GM	1.401				
	LG	2.260				
	SC-RC	-				
<i>P. generosa</i>	Mexico	Punta Canoas	VB	0.000	Hidalgo-de-la-Toba et al. (2015)	
			GM	0.000		
			JN	0.000		
			LG	1.340		
			SC	1.780		
<i>P. abbreviata</i>	Argentina	El Sótano	VB	-3.830	Zaidman and Morsan (2015)	
			GM	0.120		
			LG	-1.770		
			RC	-31.870		
			SC-RC	-		
		Punta Colorada	VB	-1.560	Zaidman and Morsan (2015)	
			GM	0.290		
			LG	0.780		
			RC	1.400		
			SC-RC	-		
		Puerto Lobos	VB	-1.750	Zaidman and Morsan (2015)	
			GM	0.230		
			LG	0.370		
			RC	-3.760		
			SC-RC	-		
La Tapera	VB	-2.670	Zaidman and Morsan (2015)			
	GM	0.200				
	LG	0.200				
<i>P. abbreviata</i>	Argentina	La Tapera	RC	-1.980	Zaidman and Morsan (2015)	
			SC-RC	-		
		Playa Fracasso	VB	-46.960		Zaidman and Morsan (2015)
			GM	0.020		
			LG	133.060		
RC	57.760					
SC-RC	-					
Punta Conos	VB	-8,720	Zaidman and Morsan (2015)			
	GM	0,070				
	LG	-1,400				
	RC	-35,760				
	SC-RC	-				

The candidate growth models used in different studies are defined as: VB = von Bertalanffy, GM = Gompertz, JN = Johnson, LG = Logistic, GVB = generalized von Bertalanffy, RC = Richards, SC = Schnute, SC-RC = Schnute-Richards.

We used a new approach based on phenotypic variability in growth observed in *P. globosa*; it allowed that the variance for each age was also computed, and this feature has not been previously modeled for *Panopea* species. Finally, our findings showed that the VB had higher variance for each age, and it was not suitable for *Panopea globosa*. We believe that if more data sources are included in this joint log-likelihood function (e.g., mark-recapture observation) then the ontogenic life cycle can be represented, and improved parameters could be used in the stock assessment models (e.g., maximum yield per recruit), which would be useful in setting management quantity guidelines for *Panopea* species in the Mexican Pacific (Aragón-Noriega et al. 2012). This analysis and methodological approach based on phenotypic variability in growth of *Panopea globosa* was found to be useful and probably its use can have wider applicability, thus allowing its use with other mollusks and marine organisms for more accurate modeling of growth.

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