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ARTICLE

Age validation and growth analysis of *Megapitaria squalida* (Bivalvia: Veneridae) in a coastal lagoon of the Gulf of California

Validación de la edad y análisis del crecimiento de *Megapitaria squalida* (Bivalvia: Veneridae) en una laguna costera del Golfo de California

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Resumen.- Este estudio contribuye al conocimiento de la dinámica poblacional de la almeja *Megapitaria squalida*, una especie para la cual la información sobre crecimiento y estructura de edades aún es limitada. Para describir su crecimiento, se recolectaron 1.116 ejemplares intermareales entre noviembre de 2012 y noviembre de 2013 en la bahía de Navachiste, una laguna costera ubicada en el golfo de California. La edad se estimó mediante el conteo de anillos de crecimiento en la superficie de la concha. La periodicidad de los anillos se validó mediante análisis del borde, considerando la alternancia anual de bandas opacas y hialinas. El crecimiento individual se evaluó mediante un enfoque multimodelo que incluyó seis versiones del modelo de crecimiento de Schnute, parametrizadas bajo distribuciones de error normal, log-normal y logística. La selección de modelos se realizó mediante el criterio de información bayesiano (BIC). Los resultados indicaron una deposición anual de los anillos de crecimiento. El borde hialino se observó entre junio y octubre, alcanzando una frecuencia del 100% en los ejemplares recolectados durante octubre. Se identificaron seis clases de edad, siendo las clases 1 y 2 las más abundantes. La curva de crecimiento sigmoidea correspondiente a la versión 1 del modelo de Schnute presentó el mejor ajuste a los datos. Los modelos parametrizados con una distribución de error logística presentaron los valores de BIC más bajos en comparación con las distribuciones normal y log-normal, lo que indica un mejor desempeño relativo entre los modelos evaluados. Los anillos externos fueron fácilmente distinguibles y pueden constituir un método práctico y de bajo costo para la estimación de la edad. Este estudio representa la primera validación de la periodicidad de los anillos de crecimiento mediante análisis del borde en *M. squalida* y demuestra el potencial de la función de densidad de probabilidad logística para parametrizar modelos de crecimiento individual.

Palabras clave: Anillos de crecimiento, estimación de edad, inferencia multimodelo, Criterio de Información Bayesiano (BIC), modelo de Schnute

Abstract.- This study contributes to the understanding of the population dynamics of the clam *Megapitaria squalida*, a species for which information on growth and age structure remains limited. To describe its growth, 1,116 intertidal clams were collected between November 2012 and November 2013 from Navachiste Bay, a coastal lagoon located in the Gulf of California. Age was estimated by counting growth rings on the shell surface. Ring periodicity was validated through edge analysis, considering the annual alternation of opaque and hyaline bands. Individual growth was evaluated using a multimodel approach that included six versions of the Schnute growth model, parameterized assuming normal, log-normal, and logistic error distributions. Model selection was based on the Bayesian Information Criterion (BIC). The results indicated annual deposition of growth rings. The hyaline edge was observed from June to October, reaching a frequency of 100% in clams collected in October. Six age classes were identified, with age classes 1 and 2 being the most abundant. A sigmoidal growth curve corresponding to Schnute model version 1 provided the best fit to the data. Models parameterized with a logistic error distribution yielded the lowest BIC values compared with those assuming normal and log-normal error distributions, indicating better relative performance among the models evaluated. External rings were readily distinguishable and may provide a practical and cost-effective method for age estimation. This study represents the first validation of growth-ring periodicity through edge analysis in *M. squalida* and provides evidence of the potential usefulness of the logistic probability density function for parameterizing individual growth models.

Key words: Growth rings, age estimation, multimodel inference, Bayesian Information Criterion (BIC), Schnute model

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INTRODUCTION

The squalid callista clam *Megapitaria squalida* (G. B. Sowerby I, 1835), inhabits shallow coastal waters and supports commercial, artisanal, and recreational fisheries throughout northwestern Mexico. In the coastal lagoon system of Navachiste Bay, located in the eastern Gulf of California, *M. squalida* is harvested by local fishers from

November to May. During this period, clams are collected by hand from exposed intertidal sandy flats during spring low tides (Castro-Ortiz *et al.* 1992). Fishers depend on the extraction of this species for personal consumption as well as a source of supplementary income when other species with high commercial value are not available or are scarce (Arellano-Martínez *et al.* 2006). The status of the fishery and important facts have been presented in different studies (López-Rocha *et al.* 2010, Aragón-Noriega 2016). There are no specific management procedures in Sinaloa and no studies identifying the potential levels of fishing effort to support sustainability of this species. For this reason, growth studies are essential to establish management guidelines.

Growth analysis of bivalves such as squalid callista includes correct interpretation and reading of growth rings and accuracy in verification. Ageing performed according to ring periodicity is crucial. Annual growth-ring formation has been documented in several clam species inhabiting shallow waters, including *Mercenaria mercenaria* (Jones *et al.* 1990, Arnold *et al.* 1991) and *Macoma balthica* (Beukema *et al.* 1985). The annual nature of growth rings in many hard-clam species has been validated using marginal ring color analysis, a method based on the seasonal alternation of opaque and hyaline shell deposits. (Beukema *et al.* 1985, Jones *et al.* 1990, Sephton & Bryan 1990, Arnold *et al.* 1998, Kilada *et al.* 2007a, Adjei-Boateng & Wilson-Gow 2013, Chute *et al.* 2016). This method is known as edge analysis and is performed by examining the alternating opaque and hyaline rings formed over the year. A pair of rings (one hyaline and one opaque), also known as an annulus, represents one year. Validating age determination with this method is important. Kilada *et al.* (2007b) argued that because populations are exposed to different environmental factors every year at the same site or at different sites in the same year, validation should encompass several populations of a species. Chute *et al.* (2012) further highlighted the importance of age validation because they discovered two sea scallop individuals with 2 annuli in 1 year, inconsistent with the generally accepted hypothesis that one annulus is formed per year. Only one study has validated age in *Megapitaria squalida*: Tripp-Quezada (2008) marked living clams and performed a 35-month study, with a focus on winter, because the hyaline ring was formed in that season, concluding that annuli are produced annually. Tripp-Quezada (2008) also reported the growth parameters of this species from the subtidal zone. Other studies on growth in subtidal zones were conducted by Castro-Ortiz *et al.* (1992), Baqueiro-Cárdenas (1998), Arellano-Martínez *et al.* (2006) and Aragón-Noriega (2016, 2017). The only study that assessed the growth of *M. squalida* in intertidal environments was conducted by Schweers *et al.* (2006). These studies will be discussed later.

The multimodel approach (MMA) is a practice commonly used to describe growth patterns in bivalves. However, growth parameters have been estimated by simply fitting the von Bertalanffy growth model (VBGM) in many clam species worldwide (Jones *et al.* 1990, Cranfield & Michael 2001, Henry & Nixon 2008, Silina 2012, Gerasimova *et al.* 2016). The MMA has been applied in other species (Kennish & Loveland 1980, Schäffer & Zettler 2007, Nanbu *et al.* 2008). The VBGM is the model most implemented in the MMA, but other models such as the Gompertz and logistic growth models have also been used. Since Katsanevakis (2006) published his study on the MMA, most subsequent studies have focused on model selection rather than on the biological interpretation of the resulting growth pattern (*e.g.*, the VBGM projects an inverted exponential curve, while the Gompertz and logistic models project a sigmoidal curve). Growth patterns depend not only on the species but also on its life stage (larval, juvenile, or adult). Consequently, the expected growth trajectory may be asymptotic, such as an inverted exponential or sigmoidal curve, or non-asymptotic, such as linear, exponential, or power functions. The Schnute model is a highly flexible growth model capable of representing all these growth patterns under specific parameter combinations and biological conditions (Schnute 1981). This model is a general four-parameter growth model that can take several mathematical forms depending on the values of its coefficients. It is most important to determine the curve that fits the set of parameters obtained for the species under study. The use of the Schnute model is also considered an MMA because it contrasts the growth patterns through different mathematical equations.

In *M. squalida* the high variability of length-at-age was a concern studied by Aragón-Noriega (2016) who hypothesized that logistic distribution might be adequate to describe their growth. The present study aimed to determine the growth pattern of the *M. squalida* population inhabiting a coastal lagoon in the eastern Gulf of California and to evaluate whether a logistic error distribution provides an appropriate fit for estimating growth parameters. It was hypothesized that a logistic distribution would provide a more appropriate representation of the residual variation in length-at-age data than normal or log-normal distributions. The use of external growth rings for age determination in bivalve species is a rapid and cost-effective method. The main contribution of this study is to demonstrate the potential advantages of the logistic distribution for modeling the high variability commonly observed in length-at-age data in growth studies.

Materials and methods

Sampling

Navachiste Bay is located in the northern part of the Mexican state of Sinaloa (25°26′19.38′′N and 108°48′43.9′′W), on the eastern coast of the Gulf of California (Fig. 1). It is a coastal lagoon system connected to the Gulf of California through two inlets, Ajoro and Vasiquilla, which allow water exchange between the lagoon and the adjacent marine environments. The lagoon

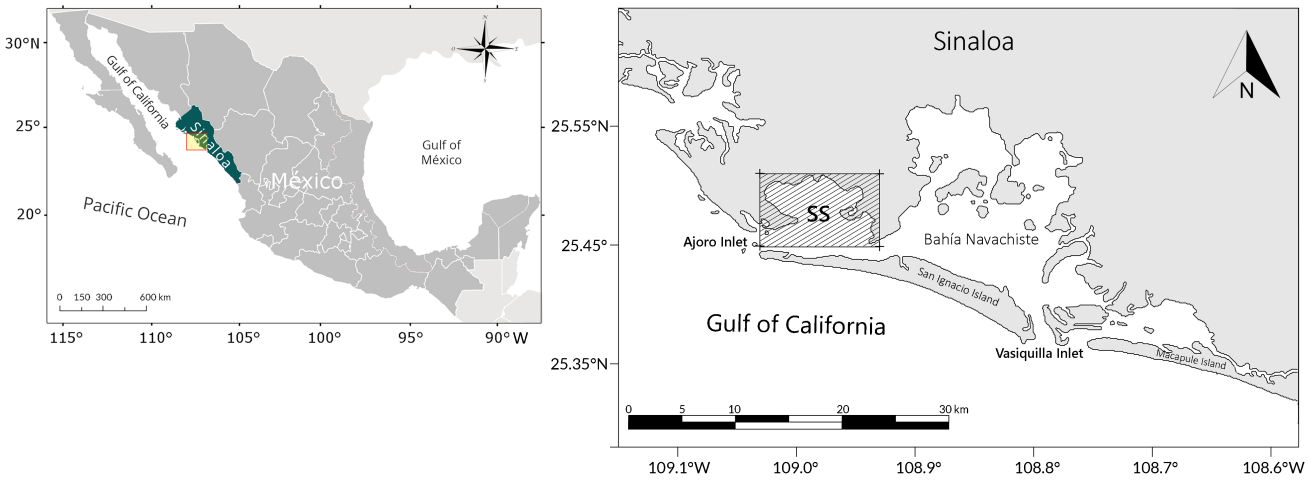

Figure 1. Study area and sampling site (SS) for *Megapitaria squalida* in the Navachiste Bay, coastal lagoon system, Gulf of California, Mexico / Área de estudio y sitio de muestreo (SS) de *Megapitaria squalida* en el sistema lagunar de Bahía Navachiste, Golfo de California, México

is generally shallow, with depths ranging from 0.5 to 5 m, except for a natural channel where depths exceed 15 m. A total of 1,116 clams were collected monthly from November 2012 to November 2013 in the intertidal zone during periods of lowest tide. Specimens were hand-collected directly from the substrate and transported to the laboratory immediately after extraction from the sediment for further processing and analysis. The collected specimens were tagged and weighed alive, with the shells closed, using a Torrey L-EQ series scale with a precision of 0.1 g. After opening, each individual valve length was measured to the nearest 0.1 mm using calipers in a straight-line distance between the anterior and posterior margins of the valve.

Aging

To estimate age in the collected squalid callista, visible rings on the surface of the shell were counted. Shells were observed using backlighting with a stereoscope to detect hyaline and opaque rings (Fig. 2). Each pair of hyaline/opaque rings was considered an annulus, and annuli were observed from the umbo to the edge. The annuli were considered annual, based on Tripp-Quezada (2008), who established, following the growth of one marked clam for 35 months, that translucent rings were deposited in winter when the temperature is low (19 °C average in March), and growth is slower, the broadest and most opaque rings corresponding to summer and fall. Monthly length frequency analysis was used to establish a birth month. Monthly size-frequency distributions showed a general increase in mean shell length over time. However, the smallest mean sizes were recorded in July, after which shell length increased again (Fig. S1). To explain this result, the average monthly sizes of age groups 1 and 2 are shown (Fig. 3). To estimate a more accurate age (in moths) it was established, for example, if a clam with one annulus (*i.e.,* one-year-old) was captured in the month following the assigned birth month, its age would be estimated 1.083 years old (*i.e.*, one year and one twelfth of a year); similarly, one captured in the second month after birth month 1.167 y, one in the third month 1.25, and so on. The same was applied with ages 0, 2, 3, 4, and 5 (*i.e.*, numbers of annual annuli). Age estimates were then used to obtain paired age-length data to be used in modeling individual growth. Finally, to determine the period of hyaline ring deposition in our study area, edge analysis was conducted: for each sampling month, the relative abundance of specimens with a hyaline or opaque ring at the shell edge was recorded.

Growth analysis

Regardless of whether the researcher utilizes a specialized model (VBGM, Gompertz, logistic, Richards or others) or the Schnute model, all the models have unknown parameters that must be determined to obtain the equation. In the older literature, the proposed method was to linearize the equations and following some graphic techniques to determine these parameters. Nonlinear techniques with iterative methods are currently used with the help of modern computers. These iterative methods need to be used with a well-developed objective function; this function is based on residual sum of squares or maximum likelihood methods. In the case of maximum likelihood, a normal (additive error) or lognormal (multiplicative error) distribution of the residuals is commonly assumed when parametrizing the models. Balakrishnan (1992) discussed the logistic distribution as a potentially appropriate alternative for highly variable data. He also demonstrated that the logistic function and the logistic distribution have found several important applications in many different fields.

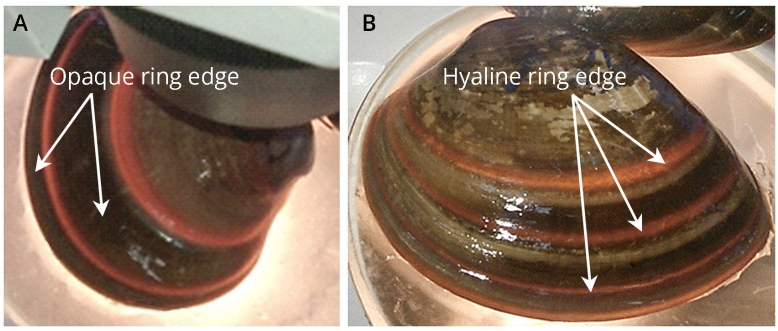

Figure 2. External growth rings observed in *Megapitaria squalida* specimens collected from the Navachiste Bay coastal lagoon system, Gulf of California, Mexico. A) Opaque ring edge. B) Hyaline ring edge. Magnification: 10× / Anillos de crecimiento externos de *Megapitaria squalida* observados en ejemplares recolectados en el sistema lagunar costero de la bahía Navachiste, Golfo de California, México. A) Margen de la concha con anillo opaco. B) Margen de la concha con anillo hialino. Aumento: 10×

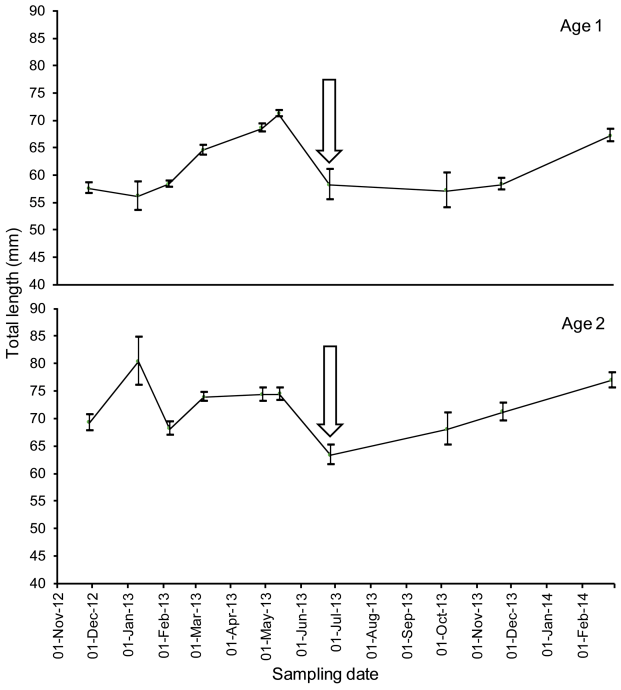

Figure 3. Scatter plot of monthly mean shell length for age-1 and age-2 *Megapitaria squalida* from the Navachiste Bay coastal lagoon system, Gulf of California, Mexico / Diagrama de dispersión de la longitud media mensual de la concha de *Megapitaria squalida* para los grupos de edad 1 y 2 en el sistema lagunar costero de la bahía Navachiste, Golfo de California, México

Once age was assigned, and paired length-age data were obtained, growth was estimated using six versions of the Schnute growth model (Schnute 1981). The versions of the model are as follows:

Version 1 ($a \neq 0$ and $b \neq 0$):

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

Version 2 ($a \neq 0$ and $b = 0$):

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

Version 3 ($a = 0$ and $b \neq 0$):

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

Version 4 ($a = 0$ and $b = 0$):

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

Version 5 ($a \neq 0$ and $b = 1$):

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

Version 6 ($a \neq 0$ and $b = -1$):

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

Where, $Y(t)$ is the predictive size at age t, Y_1 *and* Y_2 are the sizes at the references ages τ_1 and τ_2, respectively; τ_1 is the youngest and τ_2 is oldest age in the dataset; a is the parameter is the parameter controlling the relative growth rate (with units of time^{-1}) and b is the incremental parameter controlling the change in the relative growth rate and, consequently, the shape of the growth curve (dimensionless). Parameters a and b can be positive, negative or zero.

To compute asymptotic length (L_∞) for the Schnute model, the following equation was used:

When $a \neq 0$, $b \neq 0$:

$$L_\infty = \left[\frac{e^{a\tau_2} Y_2^b - e^{a\tau_1} Y_1^b}{e^{a\tau_2} - e^{a\tau_1}} \right]^{\frac{1}{b}}$$

The inflection point (t^*) of the Schnute growth model was estimated as:

When $a \neq 0$ and $b \neq 0$:

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

Where, t^* corresponds to the age at which the maximum instantaneous growth rate is attained and represents the inflection point of the sigmoidal growth curve. τ_1 and τ_2 correspond to the initial and final reference ages, respectively, selected from the dataset, whereas Y1 and Y2 represent the mean lengths or sizes estimated at these ages. The parameter a controls the rate of change in growth, whereas b is a shape parameter that determines the curvature and flexibility of the growth trajectory, influencing the position and characteristics of the inflection point.

The Schnute (1981) model might display eight shapes for growth curves depending on the values of the parameters (mainly a and b) and of course considering $\tau_2 > \tau_1$ and $Y_2 > Y_1 > 0$.

The principles used to select the appropriate curve shape are described in Schnute (1981) and included criteria such as $0 < a$ and $0 < b < 1$. Under these conditions, the curve is asymptotic with a sigmoidal shape, exhibits an inflection point, and crosses the time axis at t_0.

If the parameters satisfy $-\frac{b\,ln(Y_2/Y_1)}{(\tau_2-\tau_1)} < a$ and $b \leq 0$, then the model describes a sigmoid curve that does not extrapolate back to the time axis. Instead, the time axis acts as a lower asymptote.

Fitting model using normal distribution

Considering a normal distribution of residuals, the models were fitted using an additive error structure.

The maximum likelihood fitting algorithm was based on the equation:

$$LL(\theta \mid data) = -\frac{n}{2}\left[ln(2\pi) + 2ln(\sigma) + 1\right]$$

Where LL is the loglikelihood, θ represents the model parameters and σ represents the standard deviations of the errors, which are calculated using the following equation:

$$\sigma = \sqrt{\frac{\sum\left(L_{obs} - \hat{L}\right)^2}{n}}$$

Fitting model using log-normal distribution

Considering a log-normal distribution of residuals, the models were fitted using a multiplicative error structure. The maximum likelihood fitting algorithm was based on the equation:

$$LL = -\frac{n}{2}\left[ln(2\pi) + 2ln(\sigma) + 1\right] - \sum_{i=1}^{n} ln(L_0)$$

Where LL is the loglikelihood, L_0 represents the observed shell length and σ represents the standard deviations of the errors which are calculated using the following equation:

$$\sigma = \sqrt{\frac{\sum\left[ln(L_{obs}) - ln(\hat{L})\right]^2}{n}}$$

Fitting model using logistic distribution

Models were also fitted considering a logistic distribution (Balakrishnan 1992) of the residuals, the likelihood fitting algorithm was the following equation:

$$LL(\theta \mid data) = \sum_{i=1}^{n} ln\left[\frac{e^{-(Lt-\hat{L}t)/s}}{s\left(1+e^{-(Lt-\hat{L}t)/s}\right)^2}\right]$$

Where θ represents the model parameters to be estimated. This includes the structural growth parameters of the Schnute model plus one additional parameter for the logistic scale (s). L_t is the observed length at age t, $\hat{L}$ is the length predicted by the Schnute model, s is the logistic scale parameter.

Model selection

Model selection was performed using the Bayesian Information Criterion (BIC) to identify the growth model best supported by the data. BIC was calculated as:

$$BIC = -2LL + ln(n)\theta_i$$

Where LL is the maximum log-likelihood, n is the number of observations, and θ_i is the number of estimated parameters in the i-th model plus one. The model with the lowest BIC value was considered the best-supported model.

Differences in BIC values among candidate models were calculated as:

$$\Delta_i = BIC_i - BIC_{min}$$

Where BIC_i is the BIC value of the i-th candidate model and BIC_{min} is the lowest BIC value among all candidate models. The relative support for each candidate model (6) was assessed by calculating BIC weights (w_i) following the approach of Burnham & Anderson (2002):

$$W_i = \frac{e(-0.5\Delta_i)}{\sum_{i=1}^{6} e(-0.5\Delta_i)}$$

Where w_i is the BIC weight of the i-th model, Δ_i is the difference between the BIC of the i-th model and the minimum BIC among all candidate models. BIC weights represent the relative probability of each candidate model being the best model among those considered, given the data and the set of candidate models.

Confidence interval

The 95% confidence intervals of the growth model parameters (θ) were estimated after Venzon & Moolgavkar (1988) using the likelihood profile method. These estimates are based on a chi-square distribution with d degrees of freedom. The confidence interval was defined as all values of θ that satisfy the inequality:

$$2\left[L(Y \mid \theta) - L(Y \mid \theta_{best})\right] < \chi^2_{1,1-\alpha}$$

Where, $L(Y \mid \theta_{best})$ is the negative log-likelihood of the fitted value of θ and $\chi^2_{1,1-\alpha}$ are the values of the chi-square distribution with d= 1 (3.84).

Results

Edge analysis

A seasonal cycle of growth ring deposition was identified in the monthly observations of hyaline and opaque shell edges. Two transition points were identified in the percent of individuals showing a hyaline or opaque ring at the shell edge (Fig. 4). One transition occurred in October when 100% of the collected clams presented a hyaline edge. The other transition was in April-May when 100% of the individuals harvested had an opaque edge. The first period of change occurred from November to March, during which the percentage of individuals with a hyaline edge decreased while the percentage with an opaque edge increase. In February and March, the clams showed a high percentage of an opaque edge, 87% and 94%, respectively. The second period started in June when the percentage of clams showing opaque edge started to decline and hyaline edge started to increase (Fig. 4).

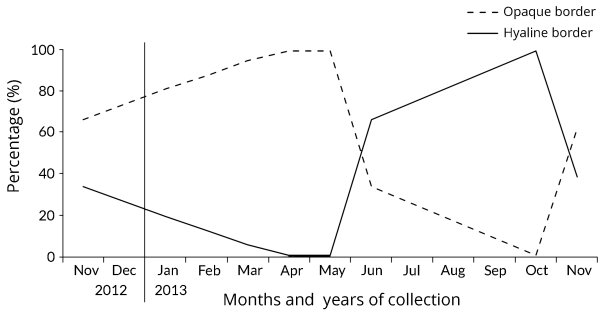

Figure 4. Annual cycle of hyaline and opaque ring formation in the *Megapitaria squalida* population (n= 1,116) from the Navachiste Bay coastal lagoon system, Gulf of California, Mexico / Ciclo anual de formación de anillos hialinos y opacos en la población de *Megapitaria squalida* (n= 1.116) en el sistema lagunar costero de la bahía Navachiste, Golfo de California, México

Age and length frequency distributions

Age-frequency distributions were strongly skewed toward younger individuals, with the 1-year age class representing 56.0% of the total sample (625 of 1,116 clams; Fig. 5). The 2-year age class comprised 305 individuals, whereas age classes 3 and 0 (individuals displaying only an opaque ring) were less abundant. Shell length (SL) varied from 28.6 to 95.7 mm. The size-frequency distribution by age class is presented in Figure 6. The smallest individuals belonged to the age-0 class, whereas the maximum SL was observed in a 3-year-old individual rather than in the oldest estimated age class (5 years). A substantial overlap in shell length among the six age classes was evident, suggesting high variability in individual growth trajectories.

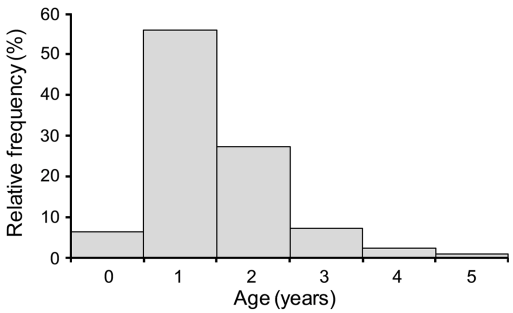

Figure 5. Age-frequency distribution of *Megapitaria squalida* from the Navachiste Bay coastal lagoon system, Gulf of California, Mexico. Data pooled from all sampling months / Distribución de frecuencias por edad de la población de *Megapitaria squalida* en el sistema lagunar costero de la bahía Navachiste, Golfo de California, México. Se presentan los datos combinados de todos los meses de muestreo

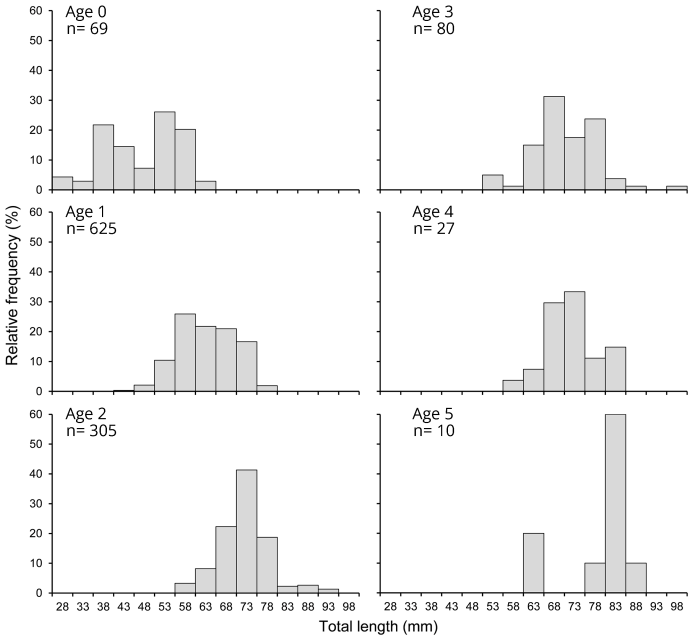

Figure 6. Frequency distribution of total shell length in *Megapitaria squalida* from the Navachiste Bay coastal lagoon system, Gulf of California, Mexico / Distribución de frecuencias de la longitud total de la concha de *Megapitaria squalida* en el sistema lagunar costero de la bahía Navachiste, Golfo de California, México

Growth patterns

The growth patterns observed for *M. squalida* were best represented by version 1 of the growth equation, with a Bayesian weighting of 100% (Table 1) showing that the other five curves had almost no support for the data. The parameters of version 1 were selected by the three criteria (normal, log-normal, and logistic distribution) and described a sigmoidal curve that did not extrapolate back to the time axis. Instead, this curve had the time axis as the lower asymptote. This curve shape was inferred because the parameters satisfied the conditions $< a$ and $b \leq 0$.

As the best-fitting model obtained 100% of the Bayesian weight, only this curve is presented in Figure 7. However, the parameter estimates for the other five models are provided in Table 1 for the three selection criteria.

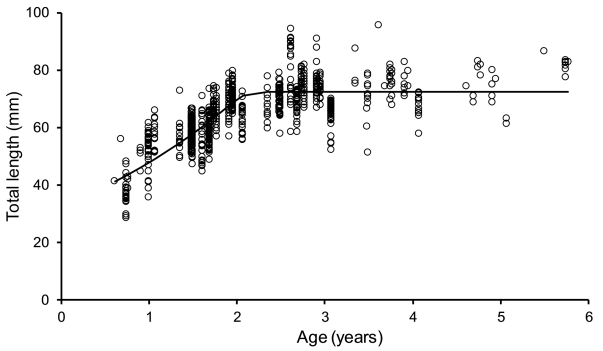

Figure 7. Estimated growth curve of *Megapitaria squalida* from the Navachiste Bay coastal lagoon system, Gulf of California, Mexico, fitted using version 1 of the Schnute model assuming a logistic probability density function for the residuals / Curva de crecimiento estimada de *Megapitaria squalida* en el sistema lagunar costero de la bahía Navachiste, Golfo de California, México, ajustada mediante la versión 1 del modelo de Schnute asumiendo una función de densidad de probabilidad logística para los residuos

Table 1. Estimated growth parameters and goodness-of-fit statistics for each growth model fitted to *Megapitaria squalida* age-length data / Parámetros de crecimiento estimados y estadísticas de bondad de ajuste para los modelos de crecimiento ajustados a los datos de edad y longitud de *Megapitaria squalida*

Distribution type	θ	BIC	Δ_i	w_i	Y_1	Y_2	a	b	s	L_∞	t^*	t_0
NORMAL												
Version 1	5	7104	0	100	41.67 (41.39, 41.97)	72.45 (71.90, 73.02)	16.60 (16.31, 16.88)	-44.73 (-43.97, -45.52)		72.45	1.87	
Version 2	4	7150	46	0	37.09	75.90	1.23	0		75.99	0.34	
Version 3	4	7231	127	0	27.75	84.08	0	5.29				
Version 4	3	7620	516	0	55.90	93.82	0	0				
Version 5	4	7156	52	0	35.74	76.36	1.01	1		76.79		-0.011
Version 6	4	7145	41	0	38.08	75.34	1.47	-1		75.38	0.60	
LOG-NORMAL												
Version 1	5	7197	0	99.99	41.22 (40.94, 41.51)	72.15 (71.50, 72.83)	17.47 (17.16, 17.77)	-46.24 (-45.44, 47.07)		72.15	1.87	
Version 2	4	7217	20	0	36.73	75.60	1.24	0		75.70	0.35	
Version 3	4	7284	87	0	30.13	85.35	0	4.85				
Version 4	3	7748	551	0	53.61	100.7						
Version 5	4	7219	22	0	35.44	76.33	1.0	1	76.57	76.57		-0.008
Version 6	4	7216	19	0.01	37.69	75.03	1.48	-1	75.06	0.61		
LOGISTIC												
Version 1	5	7081	0	100	41.28 (41.02, 41.56)	72.35 (71.80, 72.90)	17.17 (16.91, 17.44)	-45.11 (-44.41, -45.82)	3.17	72.35	1.86	
Version 2	4	7138	58	0	36.88	76.05	1.23	0	3.28	76.15	0.35	
Version 3	4	7213	133	0	25.53	84.40	0	5.24	3.38			
Version 4	3	7581	500	0	56.09	94.38	0	0	3.98			
Version 5	4	7144	63	0	35.52	76.78	1.0	1	3.29	77.02		-0.008
Version 6	4	7133	52	0	37.85	75.44	1.48	-1	3.27	75.48	0.61	

θ: numbers of parameters in each model, BIC: Bayesian Information Criterion, Δ_i: Bayesian differences, w_i: Bayesian weights, Y_1: size at age τ_1, Y_2: size at age τ_2, τ_1: minimum age in the data set, τ_2: maximum age in the data set, a: relative growth rate parameter, b: relative growth rate (incremental time constant), s: estimator of standard deviation in logistic distribution, L_∞: asymptotic length, t^*: inflection point of the sigmoid curve, t_0: is the hypothetical age at which the organism has a zero length (initial condition parameter). In parenthesis is given the confidence interval

Logistic *vs.* normal and log-normal distribution

The logistic distribution exhibited lower values of BIC than normal or log-normal distribution at each model. A chi-square goodness-of-fit test was also applied to clarify whether the residuals were better described by the logistic, log-normal, or normal distribution. Figure 8 not only displayed the residuals distribution but also demonstrated that the logistic distribution produced the lowest value of chi-square (χ^2= 28.5), as compared to those obtained with the normal and log-normal distributions of residuals (χ^2= 49.4 and χ^2= 60.5, respectively). The confidence intervals of the parameter estimates obtained under the three error distributions overlapped substantially.

Discussion

According to the percentage of individuals with opaque or hyaline edge, the annual cycle suggests that hyaline rings are formed once a year, so the age of the specimens can be determined by counting the number of hyaline rings on the external part of the shell. However, validating this approach would have required the use of clams of known age which was not possible with our study. For this reason, the age validation made by Tripp-Quezada (2008) was used as a base who tagged live clams over 35 months to follow the hyaline ring deposition and concluded that hyaline rings are deposited yearly in winter.

Extrapolating the yearly deposition of paired hyaline-opaque rings in other populations of a given species however requires caution. For example, in scallops, Chute *et al.* (2012) highlighted the importance of validating age determination in each population because they found two individuals with two annuli per year, while the rest of the scallops exhibited only one annulus per year. Additional uncertainty in estimating age by external rings is due to false-growth increments. This phenomenon occurs when the hyaline ring is not present across the entire shell surface (see Siddon *et al.* 2017 for details on false external rings in sea scallops). These features may apply to species in which the interpretation of hyaline rings is difficult, but *M. squalida* presents very distinguishable hyaline rings (Aragón-Noriega 2016, 2017; Figure 2 of present study) which are extremely easy to identify under reflected light. Despite these potential sources of uncertainty, Siddon *et al.* (2017) described the counting of external growth rings as a robust, cost-effective, and simple method for aging sea scallops. In conclusion, because our edge analysis indicated that annuli are formed annually, in agreement with the findings of Tripp-Quezada (2008), we considered the assessment of external growth increments to be a simple and reliable method for estimating age in *M. squalida*.

Tripp-Quezada (2008) reported that hyaline rings were deposited in winter, in subtidal areas in the peninsular coast of the Gulf of California (western coast of the Gulf, see Fig. 1). Conversely, we observed that hyaline rings were formed in summer and early fall, which suggests that *M. squalida* presents differentiated growth ring deposition (winter or summer-fall) according to the location it inhabits in the Gulf of California. Differences in hyaline ring formation according to latitude have been reported for *M. mercenaria* (Jones *et al.* 1990, Arnold *et al.* 1991) and *Spisula solidissima* (Chute *et al*. 2016) along the eastern coast of the U.S.A., so that while winter formation of the hyaline ring is an accepted hypothesis for most clams (Jones *et al.* 1990), latitudinal effects on hyaline ring formation must be considered when examining growth ring deposition. For example, Arnold *et al.* (1998) found that *M. mercenaria* collected on the Florida coast primarily formed annuli in summer and fall. This process occurs during summer in North Carolina (Arnold *et al.* 1991) and winter in New Jersey (Panella & MacClintock 1968). Surge *et al.* (2013) reported that *Patella vulgata* formed annual rings in winter and summer on cold-temperate and warm-temperate shells, respectively. In our study, one possible explanation for the difference in the deposition cycle between the two study areas is variation in food availability, a factor known to influence growth-ring

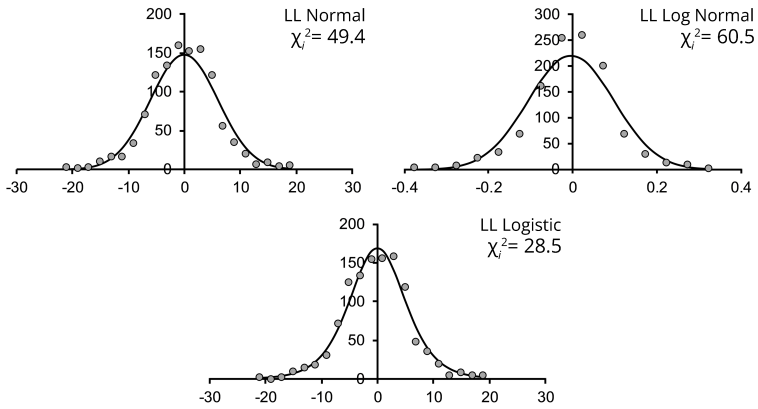

Figure 8. Error distributions and corresponding chi-square values obtained under normal, log-normal, and logistic error distributions for version 1 of the Schnute growth model fitted to *Megapitaria squalida* from Navachiste Bay coastal lagoon system, Gulf of California, Mexico / Distribuciones de error y valores de chi-cuadrado obtenidos bajo los supuestos de distribución normal, log-normal y logística para la versión 1 del modelo de Schnute aplicado a *Megapitaria squalida* en el sistema lagunar costero de la bahía Navachiste, Golfo de California, México

deposition (Arnold *et al.* 1998). According to Lluch-Cota *et al.* (2007), nutrient-rich upwellings occur in summer-autumn on the peninsular coast, and in winter-spring on the continental coast, which coincides with the periods of greatest growth (opaque ring) in each site. Another explanation may be the result of energy allocation to reproduction. When energy is allocated to reproduction, somatic growth decreases, resulting in the formation of hyaline rings, as reported for *Donax trunculus* Linnaeus, 1758 in Mediterranean waters (Ramón *et al.* 1995). Although *Megapitaria squalida* reproduces throughout the year, it exhibits two periods of peak reproductive activity in Bahía de Altata, a coastal lagoon located near the study area. The populations inhabiting Bahía de Altata and Navachiste Bay are considered part of the same stock (Álvarez-Dagnino 2013). Peak spawning activity occurs during June-July and September-October (Niebla-Rodríguez 2004), coinciding with the period of hyaline ring formation observed in the present study. Similarly, Álvarez-Dagnino *et al.* (2017) identified October as a month of maximum reproductive activity for this species.

The maximum age recorded in the present study was 5 years, consistent with the estimates reported by Schweers *et al.* (2006) and Delgado-Alvarez *et al.* (2019), both of whom studied intertidal populations inhabiting coastal lagoons. It is noteworthy that age in both studies was estimated using modal progression analysis. In contrast, Aragón-Noriega (2016, 2017) examined *M. squalida* populations from two subtidal marine areas of the Gulf of California and reported maximum ages of 8 and 10 years, respectively. Other studies investigating the age structure of this species reported ages ranging from 1 to 7 years (Castro-Ortiz *et al.* 1992, Tripp-Quezada 2008), based on counts of external growth rings. *M. squalida* occupies a wide range of habitats, from intertidal areas within coastal lagoons (Schweers *et al.* 2006, Delgado-Alvarez *et al.* 2019) to sandy bottoms at depths of up to 15 m in subtidal marine environments (Coan & Valentich-Scott 2012). In subtidal populations, age-0 individuals have not been reported, whereas in coastal lagoon populations the most abundant age class was 1 year (present study), compared with 6 years in a marine population (Aragón-Noriega 2017). These differences may reflect habitat-specific patterns in recruitment, growth, survival, or sampling selectivity. Nevertheless, given the limited number of studies and the methodological differences among them, these comparisons should be interpreted with caution, and no definitive conclusions can be drawn regarding the influence of habitat on the age structure of *M. squalida* populations.

Most studies conducted to date on the growth of *M. squalida* have selected the von Bertalanffy growth model (VBGM) to describe growth (Castro-Ortiz *et al.* 1992, López-Rocha *et al.* 2018). This model is widely used to describe growth in bivalves. However, the multimodel approach (MMA) has been applied to other bivalve species, including *Mercenaria mercenaria* from New Jersey (Kennish & Loveland 1980), *Mya arenaria* from Germany (Schäffer & Zettler 2007), and *Corbicula japonica* from Japan (Nanbu *et al*. 2008). In all three studies, a sigmoidal growth curve provided a better description of the observed growth pattern. Although the MMA has considerable advantages over a single-model approach (Katsanevakis 2006), it has been applied to *M. squalida* in only two studies (Aragón-Noriega 2016, 2017). Both studies showed that an asymptotic sigmoidal curve better described growth in *M. squalida*, consistent with the results of the present study. The VBGM produces an inverse exponential asymptotic curve, which may not adequately represent the growth pattern of *M. squalida*. One possible explanation for the predominance of the VBGM in previous studies is that, when paired length-at-age data are unavailable, modal progression analysis is commonly used, and software implementing this approach often relies on the VBGM. However, modal progression analysis may be less suitable for bivalves, particularly *M. squalida*, which exhibits a clear pattern of external growth rings on the shell that can be used to estimate age directly. In the present study, six versions of the Schnute growth model (Schnute 1981) were fitted to the length-at-age data. Version 1 provided the best fit, yielding a sigmoidal growth curve and receiving 100% of the Bayesian weight. In contrast, the inverse exponential curve characteristic of the VBGM was produced by version 5 of the Schnute model, which received no support from the data and ranked fourth in terms of Bayesian weight. Although the application of the six Schnute model versions represents a novel approach for *M. squalida*, the results are consistent with those of Aragón-Noriega (2016, 2017), who also found that a sigmoidal growth curve best described growth in subtidal *M. squalida*. The best-fitting model indicated rapid growth during the first two years of life, followed by a progressive reduction in growth rate up to five years of age.

The asymptotic length (L_∞) estimated in this study was the lowest ever reported in this species. Differences in fishing effort between the two areas may provide a possible explanation, although no direct evidence is currently available (Moura *et al.* 2013). It is recommended for further studies to explore the possible consequences of fishing efforts on growth parameters. However, this value was estimated for a population inhabiting the intertidal zone of a coastal lagoon, suggesting that comparisons between intertidal and subtidal populations should be made with caution (Schweers *et al.* 2006). Schweers *et al.* (2006), in the only other study in an intertidal zone of a coastal lagoon, estimated L_∞ = 83 mm SL with the VBGM. In the present study, the L_∞ estimated with the VBGM was 75.35 mm SL, but this model was not selected as representative of the data. The L_∞ values estimated in previous studies using the VBGM may indicate differences between subtidal populations from the eastern and western coasts of the Gulf of California. On the western coast, the asymptotic length ranged from 80.9 to 104 mm SL without a latitudinal gradient. In contrast, on the eastern coast, there is an evident decrease from north to south: 106.3 mm SL in Puerto Libertad at 29°54′N (López-Rocha *et al.* 2018), 104.6 mm SL in Guaymas at 27°58′N (Aragón-Noriega 2016) and 91.3 mm SL in Yavaros at 26°36′N (Aragón-

Noriega 2017). As the location of the present study was in the southernmost zone at 25°26′N, the lowest L_∞ was observed (75.35 mm SL), as expected. Once again, in the present study, the best curve had a sigmoidal shape. The other two studies (Aragón-Noriega 2016, 2017) which fitted sigmoidal growth curves to *M. squalida*, reported L_∞ values ranging from 85.5 to 95.0 mm SL for subtidal populations. For the logistic model, the estimated values were 90.5 mm SL at 27°58′N and 85.5 mm SL at 26°36′N, whereas for the Gompertz model they were 95.0 and 90.1 mm SL, respectively. In conclusion, this study supports the use of a multimodel approach to describe growth patterns based on either modal progression analysis or paired length-at-age data. The results also suggest that sigmoidal models may provide a better description of growth in *M. squalida* populations from both subtidal marine environments and intertidal coastal lagoons than the inverted exponential model.

The normal or log-normal distributions of residuals have been a frequent practice to parametrize the growth model. This is done by maximum likelihood approach, which means maximizing the joint probability that the residuals will be distributed according to a certain distribution. When additive error is assumed, the normal distribution of errors is assumed, when a multiplicative error is assumed, a lognormal distribution is assumed. The same can be assumed in logistic distribution to estimate the parameters. Logistic distribution of errors is a novel approach but in the present study it was the best approach as proven by the Bayesian information criteria and a chi-squared goodness of fit. For this part there is no firm conclusion, but it must be emphasized that logistic distribution has a potential use to parametrize models.

In summary, the external rings in *M. squalida* are easy to distinguish and should be used to age this species, being the most rapid and cost-effective method. The results support further consideration of the logistic distribution when parameterizing growth models and highlight the usefulness of a multimodel approach in growth studies.

Statements

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Author contributions

Y.L.V., J.F.A.G., and G.R.D. conceptualized and designed the methodology of the study. Y.L.V., J.F.A.G., and G.R.D. conducted field sampling and laboratory analyses. J.A.F.O., E.A.R., and E.A.A.N. performed the statistical analyses and prepared the figures. E.A.A.N. drafted the original manuscript, and all authors contributed to its revision and editing. Funding was obtained by G.R.D.

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Data availability

The data are available from the corresponding author upon reasonable request.

Conflict of interest

The authors declare that there are no conflicts of interest.

Ethical approval

No animal testing was performed in this study.

Use of AI tool

ChatGPT (OpenAI, GPT-5.5) was used to improve the English grammar and readability of the manuscript. The authors reviewed and edited all outputs and took full responsibility for the final content.

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Supplementary material

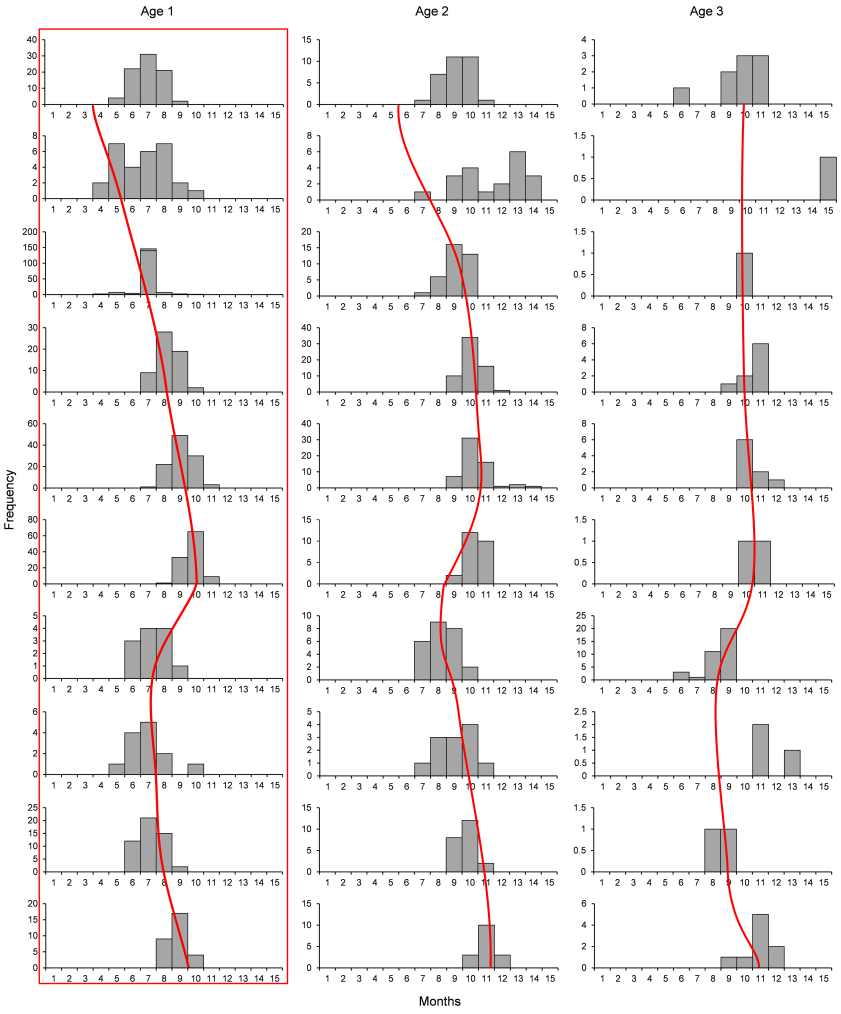

Figure S1. Monthly size-frequency distributions for age groups 1, 2, and 3 of *Megapitaria squalida*. Red lines indicate the modal size (peak) for each month and age group, illustrating the temporal progression of modal size throughout the year / Distribuciones mensuales de frecuencias de talla para los grupos de edad 1, 2 y 3 de *Megapitaria squalida*. Las líneas rojas señalan la moda mensual de cada grupo de edad, evidenciando la progresión temporal de la talla modal durante el período de estudio