

MODELING GROWTH OF THE PACIFIC SARDINE *SARDINOPS CAERULEUS* IN THE GULF OF CALIFORNIA, MEXICO, USING THE MULTIMODEL INFERENCE APPROACH

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ABSTRACT

To evaluate growth of the Pacific sardine in the Gulf of California, fish samples were collected from the commercial fleet during the 2010–11, 2011–12 and 2012–13 fishing seasons. Sardine samples were measured in standard length (SL) and age was determined based on counting opaque and hyaline growth increments in the otoliths. Four growth models were fitted to the age and length data: von Bertalanffy Growth Model (VBGM), Gompertz, Logistic, and Schnute, using a maximum likelihood algorithm. Confidence intervals of each parameter were calculated through likelihood profiles. The model that best explained the species growth kinetics was selected by Akaike information criteria and Akaike's weight (w_i), while growth parameter covariance was obtained by the likelihood contour method. The sardines obtained from catches ranged in age from 0.5–6 years; sizes varied from 98–218 mm (SL). The growth model that obtained the greatest weight was VBGM ($w_i = 73.11\%$) whose estimated parameters and confidence intervals (CI) for the Pacific sardine were $L_\infty = 201.28$ (200.70–201.80) mm SL, $K = 0.581$ (SD: 0.577–0.586) and $t_0 = -0.839$ (SD: $-0.855 - -0.824$), showing a more accelerated growth rate of the species in the Gulf of California compared to the same species inhabiting the coasts of Baja California and California.

INTRODUCTION

Small pelagic fish are part of one of the main fishery resources in Mexico because of their great catch volume (Cisneros-Mata et al. 1990; Nevárez-Martínez et al. 2014). The sardine fishery has contributed up to

30% annual landing weight mainly in the Gulf of California (GC), representing around 10% of national fishing economic value (Nevárez-Martínez et al. 2001; Nevárez-Martínez et al. 2014; DOF 2018). The main fishery target is the Pacific sardine (*Sardinops caeruleus* Girard 1856), which in some seasons has contributed up to 80% of the total small pelagic catches in the GC (Nevárez-Martínez et al. 2014; DOF 2018). Their distribution and abundance have been linked to environmental factors such as wind patterns (upwelling) and sea surface temperature (SST) (Nevárez-Martínez et al. 2001; Lanz-Sánchez et al. 2008; Dorval et al. 2015). Between Mexico and Canada, three stocks of Pacific sardine have been well identified with different approaches, including morphometrics, meristic, tagging, blood antigen, differentiated spawning areas and catch-sea temperature data (Clark and Jensen 1945; Clark 1947; Vrooman 1964; Mais 1972; Radovich 1982; Parrish et al. 1989; Félix-Uraga et al. 2004, 2005; Smith 2005; García-Rodríguez et al. 2011; Demer and Zwolinski 2014). The first one is the cold stock located off the northern coast of Baja California, México, to Canada; the second one is the temperate stock found in waters from southern California, U.S.A., to Bahía Magdalena, Baja California Sur, México; and the third stock and objective of this study is the one that inhabits the Gulf of California (Vrooman 1964; Smith 2005; Demer and Zwolinski 2014).

Biomass fluctuations and stock availability, within and out of the GC, depend on climate and environmental factors, which influence strongly high population variability in parameters such as cohort growth through time (Félix-Uraga et al. 2005; Dorval et al. 2015; Checkley Jr.

et al. 2017). Growth of the sardine *S. caeruleus* within the GC differed from that found in the Pacific, which may be due to the ecosystem dynamics of the GC compared to the Pacific (De Anda-Montañez et al. 1999).

Growth rate is one of the most important life history parameters of fish populations, particularly in commercially exploited species (Mercier et al. 2011; Lorenzen 2016). Growth estimation helps us to understand biological traits of the population that could be affected by overfishing (Ali et al. 2003) and determine long-term impacts deriving from fishing or environmental effects (Botsford 1981; Dorval et al. 2015). Furthermore, growth parameter values such as asymptotic length (L_{∞}) and growth rate coefficient (K) are used as seed values in multiple stock assessment models (Beddington and Kirkwood 2005; Haddon 2011).

In the Pacific sardine, most growth estimations performed until now have been based on using the von Bertalanffy (VBGM) model (Cisneros-Mata et al. 1990; Gallardo-Cabello et al. 1991; De Anda-Montañez et al. 1999; Martínez-Zavala et al. 2006) and Gompertz model for length-age data of juveniles in the GC (Quiñonez-Velázquez et al. 2000). The VBGM has been historically used in fisheries to assess fish growth (Katsanevakis and Maravelias 2008; Mercier et al. 2011; Lorenzen 2016); nonetheless, appropriate models should be selected on the indication of biological reality, statistical fit, and when the models applied are complex, also the parsimony (Burnham and Anderson 2002; Cailliet et al. 2006; Katsanevakis 2006). Thus, it was necessary to assess growth with more than one model and compare the fits among models to select the one that best described growth kinetics of the species through statistical information criteria (Burnham and Anderson 2002; Katsanevakis and Maravelias 2008; Beninger et al. 2012). Therefore, the objective of this study was to assess growth of the Pacific sardine *S. caeruleus* in the Gulf of California through the multimodel approach, including as candidate models VBGM, Gompertz, Logistics and Schnute for the sake of robustness in growth parameters estimation for this species.

MATERIALS AND METHODS

Sampling

The information analyzed for the Pacific sardine, *Sardinops caeruleus* Girard 1856, came from samples obtained from the commercial sardine fishery during the 2010–11, 2011–12 and 2012–13 seasons in the Gulf of California, Mexico (fig. 1); the fishing season starts in October and ends in July or August of the following year. Catch of this species was performed with purse seine nets, which consisted of large net walls that close and secure the bottom and then drag below sardine

schools (Lewison et al. 2004). Dimensions of this fishing gear depend on boat capacity (regularly greater than 100 tons); thus, purse seine net were between 366 and 640 m long and 40 to 100 m high with the same 25.1 mm mesh size for the entire net (DOF 2018).

Length structure and age determination

For the period that comprised the fishing seasons from 2010–11 to 2012–13, samples of the Pacific sardine *S. caeruleus* caught in the Gulf of California and landed at the ports of Guaymas and Yavaros (Sonora) were analyzed. Sampling was done in port where fishing landings were made; a sample of approximately 10 kg (from 80 to 120 sardines, depending on individual weight) was taken at random. All the sardines in the sample were measured in standard length (SL, precision of ± 1 mm), grouped into five-millimeter length intervals. Five sardines were selected from each length interval or if there were less than five, those that were in that interval were selected. This subsample of fish was measured for biological characteristics such as standard length (SL), total weight (TW, accuracy of ± 1 g), sex, and otoliths (*sagitta*) were extracted. The otoliths were rinsed with clean water to remove any remaining tissue, and then stored to dry in labeled gelatin capsules.

The age of the Pacific sardines was determined based on counting opaque and hyaline growth increments in the otoliths. For this purpose, otoliths were immersed in distilled water and observed under a stereoscopic microscope (16X and 40X), using reflected light on a dark background, which allowed observing the opaque increments in whitish color and the hyaline increments in dark color (Williams and Bedford 1974; Holden and Raitt 1974; Nevárez-Martínez et al. 1996; Yaremko 1996). The reading of growth increments in the otoliths was made by two independent readers that counted them at two different times; the results were compared and when discrepancies were reported, they were verified through a third reading. At the time of the readings, the readers did not have the information either of the size or sex. By means of a graphical analysis of the relative monthly frequency of otoliths with opaque and hyaline edges (Méndez-Da-Silveira 1987; Jiménez-Rodríguez 1991; Nevárez-Martínez et al. 1996), the periodicity of the formation of an opaque and a hyaline increment was defined. No assumption of birthdate was made. As such, the most distal of the opaque or translucent edges were counted as growth increments. Since the growth increment counts were not adjusted for the birthdate, the counted growth increments were equal to the age of the fish. For example, if the otoliths of a specific sardine were counted as three growth increments, one opaque, one hyaline, and the edge was undoubtedly opaque, this sardine was assigned an age of 1.5 years.

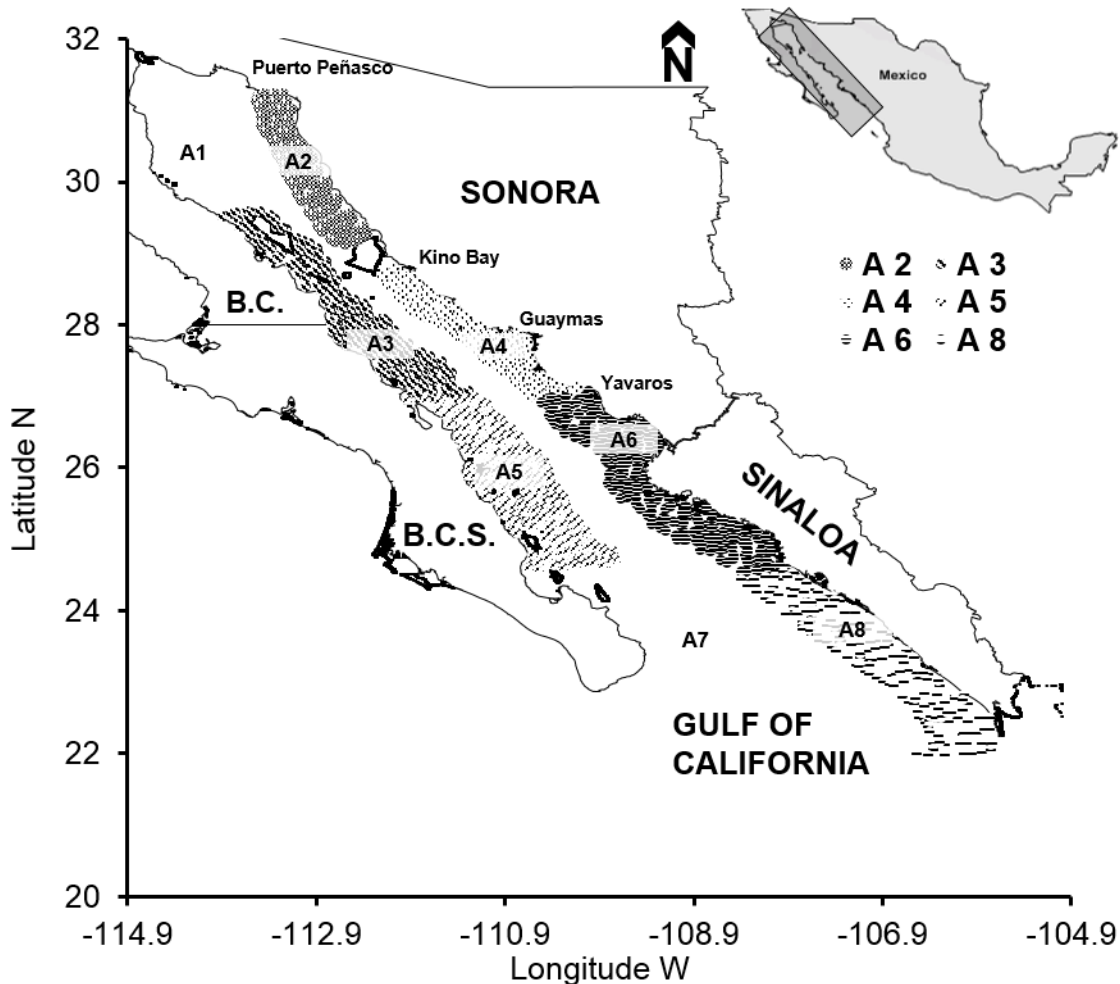


Figure 1. Total study area and regular fishing grounds or capture areas (A2 = Area 2; A3 = Area 3; A4 = Area 4; A5 = Area 5; A6 = Area 6 and A8 = Area 8) of the Pacific sardine *Sardinops caeruleus* in the Gulf of California during the seasons 2010-11 to 2012-13. Capture areas are among the states of Baja California (B.C.), Baja California Sur (B.C.S.), Sonora and Sinaloa, México.

Based on the assigned age and the standard length measured for each of the Pacific sardines sampled, a length-age key was constructed for growth modeling. Moreover, variability in length to age was estimated using that age-length key.

Growth modeling

Age in years and standard length data of the Pacific sardine were used for modeling individual growth by means of a multimodel inference approach (Katsanevakis 2006; Katsanevakis and Maravelias 2008). For this purpose, four growth models were used (table 1); von Bertalanffy (1938), Gompertz (1825), Logistic (Ricker 1975), and Schnute (1981). The Schnute model was used assuming that the parameters $a \neq 0$ and $b \neq 0$, as the required condition to denote asymptotic growth (Schnute 1981).

For parameter estimation, it was assumed that the residuals had a log-normal distribution around the

growth models. Growth parameters (θ) for all four candidate growth models were fitted using a maximum log likelihood approach, according to the next objective function (Neter et al. 1996; Haddon 2001):

$$LL_{(\theta | data)} = -\left(\frac{n}{2}\right) [\ln(2\pi) + 2 * \ln(\sigma) + 1], \quad (1)$$

Where $LL_{(\theta | data)}$ is the maximum log likelihood value; n is the number of observations; and σ is the standard deviation (SD), which was obtained by the following analytical equation (Haddon 2001):

$$\sigma = \sqrt{\frac{1}{n} \sum_{i=1}^n [\ln(SL_{obs(t)}) - \ln(SL_{est(t)})]^2}, \quad (2)$$

where $SL_{obs(t)}$ is the standard length observed (in mm) at age t (in years), and $SL_{est(t)}$ is the estimated standard length at age t . It was assumed that $L_{(t)}$ had a log-nor-

TABLE 1
 Candidate growth models for the Pacific sardine *Sardinops caeruleus* age-length data in the Gulf of California.

Model	Equation	Description
von Bertalanffy growth model (VBGM)	$L_{(t)} = L_{\infty} (1 - e^{-K(t-t_0)})$	$L_{(t)}$ is length at age t . L_{∞} is asymptotic length. K determines the rate of approach to L_{∞} (the curvature parameter).
Gompertz	$L_{(t)} = L_{\infty} e^{-e^{-K(t-t_0)}}$	t_0 in VBGM and Schnute models is the hypothetical age at which the sardines showed zero length (initial condition parameter). t_0 in Gompertz and Logistic models corresponds to an inflection point on the growth curve. t is age at size $L_{(t)}$.
Logistic	$L_{(t)} = \frac{L_{\infty}}{(1 + e^{-K(t-t_0)})}$	a is a relative growth rate (time constant). b is an incremental relative growth rate (incremental time constant).
Schnute (Solution case 1; $a \neq 0, b \neq 0$)	$L_{(t)} = \left[y_1^b + (y_2^b - y_1^b) \frac{1 - e^{-a(t-T_1)}}{1 - e^{-a(T_2-T_1)}} \right]^{\frac{1}{b}}$	T_1 is the lowest age in the data set.
To estimate τ_0 (t_0):	$\tau_0 = T_1 + T_2 - \frac{1}{a} \ln \left[\frac{e^{aT_2} y_2^b - e^{aT_1} y_1^b}{y_2^b - y_1^b} \right]$	T_2 is the highest age in the data set.
To estimate L_{∞} :	$L_{\infty} = \left[\frac{e^{aT_2} y_2^b - e^{aT_1} y_1^b}{e^{aT_2} - e^{aT_1}} \right]^{\frac{1}{b}}$	y_1 is the size at age T_1 . y_2 is the size at age T_2 .

mal distribution around the candidate growth models. The objective function was solved using Solver in Excel®.

Confidence intervals

The Pacific sardine growth parameters and their fitting values (LL) obtained by each growth model were used to calculate confidence intervals (CI) by means of profile likelihood construction, which is a robust way for construction of confidence regions (Venzon and Moolgavkar 1988; Hilborn and Mangel 1997). A likelihood interval by itself is not very informative and thus insufficient to indicate change in plausibility of the values of θ within the range. A likelihood interval must always be accompanied by the value of θ to give some idea of the symmetry of the likelihood function with respect to probable alternative values of θ , and in this sense show how plausibility changes within the interval. This estimation was made for all growth parameters and based on Chi-squared distribution (χ^2) with m degrees of freedom (Zar 1999) where confidence intervals were defined as all values θ that satisfied inequality:

$$2[LL_{(\theta|data)} - LL_{(\theta|best)}] < \chi^2_{1,1-\alpha}, \tag{3}$$

where $LL_{(\theta|best)}$ is the log likelihood of the most probable value of θ and $\chi^2_{1,1-\alpha}$ are the distribution values of χ^2 with one-degree freedom at a confidence level of $1 - \alpha$; thus, the confidence interval at 95% covered all values of

θ that were twice the difference between the log likelihood in the likelihood profile and the best estimate of θ . Those values less than 3.84 were included into confidence intervals (Haddon 2001; Pawitan 2001).

When considering more than one growth parameter, confidence intervals became wider, which only occurred if any correlation existed between parameters in growth models. The von Bertalanffy growth model had the asymptotic length and growth coefficient parameters correlated; therefore, in this case the solution was to compute the likelihood based confidence region estimated from contours of constant log-likelihood over the target surface. This procedure was applied to the L_{∞} and K parameters jointly to cope the problem of parameter correlation in describing individual growth of the Pacific sardine. In this case the equation above must satisfy the inequality associated with the χ^2 distribution with two degrees of freedom where the reference value was less than 5.99 for two parameters (Haddon 2001; Pawitan 2001).

Growth model selection

The Akaike information criterion (AIC) (Burnham and Anderson 2002; Katsanevakis 2006; Katsanevakis and Maravelias 2008) was used to select the best growth model for the Pacific sardine age and length data, according to the following equation:

$$AIC = (-2 * LL_{(\theta|data)}) + (2 * k), \tag{4}$$

TABLE 2
 Age-length key for the Pacific sardine *Sardinops caeruleus* obtained from commercial purse seine fishery
 in the Gulf of California during the seasons 2010–11 to 2012–13.

SL (mm) /	Age (years)												Total
	0.5	1	1.5	2	2.5	3	3.5	4	4.5	5	5.5	6	
98	19	0	0	0	0	0	0	0	0	0	0	0	19
103	19	0	0	0	0	0	0	0	0	0	0	0	19
108	4	0	0	0	0	0	0	0	0	0	0	0	4
113	0	1	0	0	0	0	0	0	0	0	0	0	1
118	0	5	0	0	0	0	0	0	0	0	0	0	5
123	0	8	0	0	0	0	0	0	0	0	0	0	8
128	0	11	2	0	0	0	0	0	0	0	0	0	13
133	0	24	4	0	0	0	0	0	0	0	0	0	28
138	0	41	7	3	0	0	0	0	0	0	0	0	51
143	0	34	15	14	0	0	0	0	0	0	0	0	63
148	0	28	23	22	0	0	0	0	0	0	0	0	73
153	0	12	16	46	4	0	0	0	0	0	0	0	78
158	0	0	16	51	8	2	0	0	0	0	0	0	77
163	0	0	5	52	24	3	0	0	0	0	0	0	84
168	0	0	0	39	34	11	1	0	0	0	0	0	85
173	0	0	0	20	45	21	5	0	0	0	0	0	91
178	0	0	0	9	35	32	14	5	0	0	0	0	95
183	0	0	0	1	18	37	30	13	4	0	0	0	103
188	0	0	0	0	6	26	21	29	11	3	0	0	96
193	0	0	0	0	0	4	14	22	20	13	7	3	83
198	0	0	0	0	0	0	4	8	18	21	15	10	76
203	0	0	0	0	0	0	0	1	4	6	12	15	38
208	0	0	0	0	0	0	0	0	1	1	1	2	5
	42	164	88	257	174	136	89	78	58	44	35	30	1195

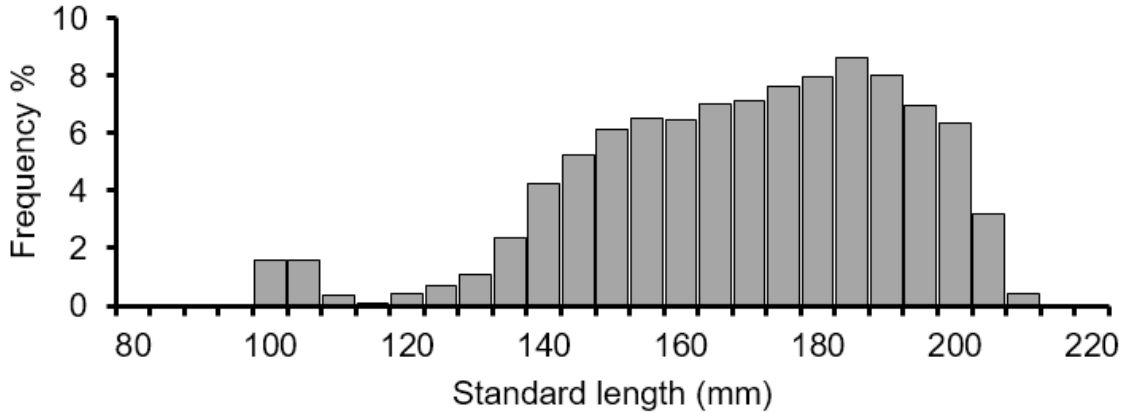


Figure 2. Standard length (mm) frequency distribution of the Pacific sardine in the Gulf of California during the study period (2010-11 to 2012-13).

where k is the number of parameters in each model, including σ (Burnham and Anderson 2002). The AIC differences (Δ_i) for each model were given by the following function:

$$\Delta_i = AIC_i - AIC_{min}, \tag{5}$$

where AIC_{min} represents the AIC for the best candidate growth model, and AIC_i is the AIC estimated for each growth model. Plausibility was estimated for candidate growth models (i) by means of the Akaike weight (w_i) given by (Burnham and Anderson 2002):

$$w_i = \frac{e^{(-0.5 * \Delta_i)}}{\sum_{i=1}^4 e^{(-0.5 * \Delta_i)}} \tag{6}$$

In accordance to the multimodel inference approach, an averaged was calculated for asymptotic length (\bar{L}_∞) taking into account predicted values for this parameter ($\hat{L}_{\infty,i}$) and w_i of all four models by the following equation (Burnham and Anderson 2002):

$$\bar{L}_\infty = \sum_{i=1}^4 w_i \hat{L}_{\infty,i} \tag{7}$$

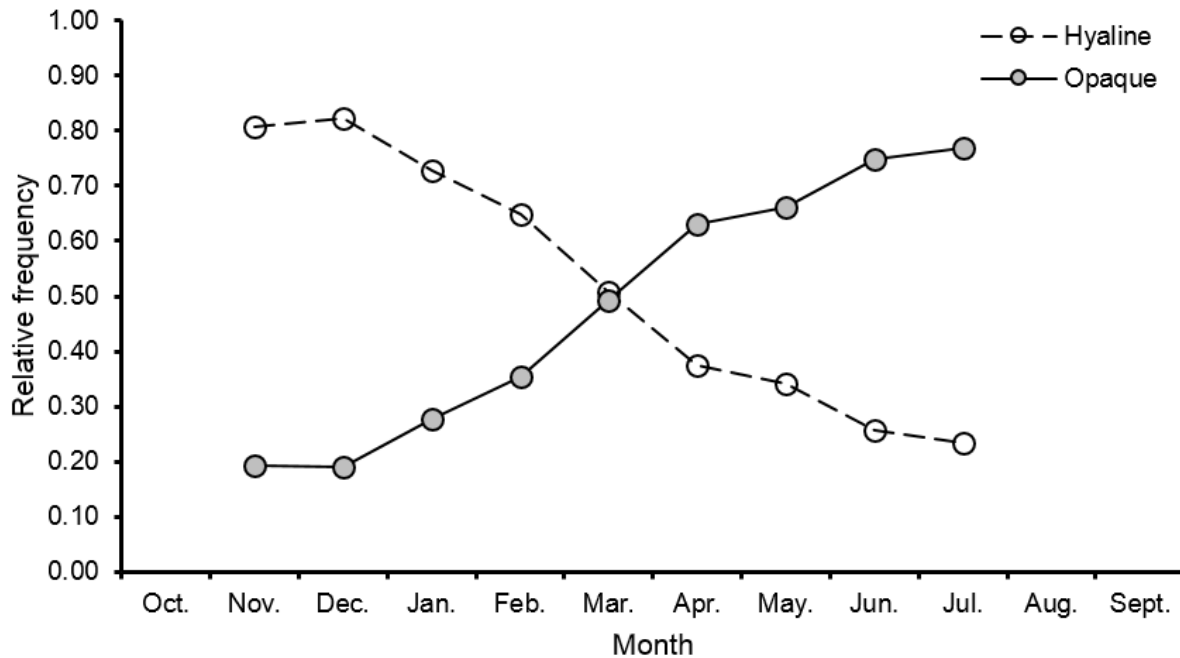


Figure 3. Monthly relative frequencies of otoliths with opaque edge (gray circle) and hyaline (white circle or empty circle) in the Pacific sardine of the Gulf of California. Period 2010–11 to 2012–13.

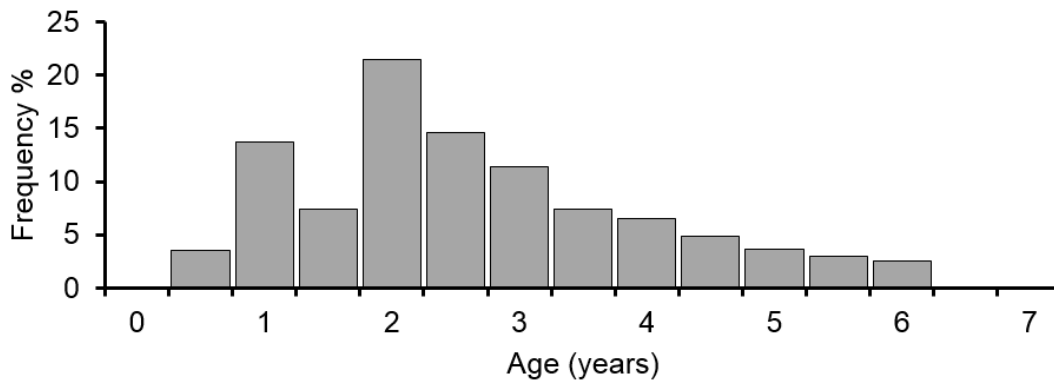


Figure 4. Age (years) frequency distribution of the Pacific sardine in the Gulf of California during the study period (2010–11 to 2012–13).

For all models, 95% confidence intervals for \hat{L}_∞ were estimated by means of t Student test with df degrees of freedom, using the following equation:

$$\hat{L}_\infty \pm t_{df,0.975}se(\hat{L}_\infty), \quad (8)$$

Here, $se(\hat{L}_\infty)$ is the asymptotic standard error.

The unconditional standard error of \bar{L}_∞ [$use(\bar{L}_\infty)$] was estimated as (Burnham and Anderson 2002):

$$use(\bar{L}_\infty) = \sum_{i=1}^4 w_i * [var(\hat{L}_{\infty,i} | g_i) + (\hat{L}_{\infty,i} - \bar{L}_\infty)^2]^{1/2}, \quad (9)$$

where $var(\hat{L}_{\infty,i} | g_i)$ is the variance of the estimated asymptotic length according to model g_i , conditional on the model.

RESULTS

A total of 1,195 Pacific sardine (*Sardinops caeruleus*) were measured and aged from the 2010–11 to the 2012–13 fishing seasons in the Gulf of California (table 2). SL frequency distribution (fig. 2) for the three seasons combined (2010–11, 2011–12 and 2012–13) showed a length range from 98 to 208 mm of SL, with average of 167.0 mm SL; and standard deviation was 23.56 mm.

The monthly relative frequency of otoliths with opaque and hyaline edges is shown in Figure 3. The percentage of opaque edges was low during autumn–winter and maximum in spring–summer while the translucent edges showed their maximum during autumn and winter and their lower values in spring–summer. This result indicates that in the course of one year an annuli (an

TABLE 3
Mean standard length (mm) and standard deviation
by age of the Pacific sardine *Sardinops caeruleus*
obtained during the study period (2010–11 to 2012–13)
in the Gulf of California. The value *n* indicates the
number of individuals observed for each age.

<i>n</i>	Age (years)	Mean standard length (mm)	Standard deviation
42	0.5	101.2	3.2
164	1.0	138.9	8.7
88	1.5	148.8	8.1
257	2.0	159.7	9.0
174	2.5	172.1	7.8
136	3.0	179.5	7.3
89	3.5	184.9	6.3
78	4.0	189.2	5.4
58	4.5	193.9	5.4
44	5.0	196.8	4.3
35	5.5	199.0	3.9
30	6.0	200.7	3.8

opaque edge plus a hyaline edge) is formed; in average growth increments (opaque or hyaline) occur in approximately half a year.

Ages of the Pacific sardine were integrated by fish from 0.5 years (one opaque edge) to 6.0 years (six opaque edges plus six translucent edges) of age (table 2); fish of age 0.5 years were in the range of 98–108 mm SL and those of age 6.0 years in the range of 193–208 mm SL. Age frequency distributions are shown in Figure 4; the highest frequency was observed at the age of two years. The average age was 2.64 years and standard deviation was 1.34 years. Table 3 shows the average standard length and standard deviation by age of the Pacific sardine.

The estimated growth parameter values, 95% confidence intervals and Chi-square probability for the

four candidate growth models are shown in Table 4. The highest asymptotic length ($L_{\infty} = 201.287$ mm SL) was estimated with VBGM, followed by Schnute model ($L_{\infty} = 199.480$ mm SL). A variation in K , the rate of approach to L_{∞} , among the candidate growth models was observed with minimum $K = 0.581$ (VBGM and Schnute model) and maximum $K = 0.822$ (Logistic model). The four growth models tested revealed a phase of rapid growth during the first two years of age (reached ~80% L_{∞} value), with the growth rate decreasing and reaching 95% L_{∞} value at age of four years (fig. 5).

The Akaike differences (Δ_i) showed that only the VBGM and Schnute models had a substantial support ($\Delta_i \leq 2$; table 5). According to the model selection criteria, the estimated AIC was the lowest for the VBGM ($AIC = -3610.87$) with Akaike weight, $w_i = 73.11\%$, followed by Schnute model with $AIC = -3608.87$ and $w_i = 26.89\%$ (table 5). According to the multi-model inference approach, it was calculated a $\bar{L}_{\infty} = 200.8$ mm (95% CI was 199.0–202.6 mm) (table 5).

The 95% confidence intervals for the best fitted model (VBGM), as well as likelihood profiles for L_{∞} , K and t_0 , are shown in Figure 6. The likelihood profiles for parameters of the Schnute growth model (the second best) are shown in Figure 7. The covariance of parameters L_{∞} and K of the VBGM and the highest likelihood values are shown by likelihood contours in Figure 8.

DISCUSSION

The periodicity validation of growth increment formation is a critical step for the use of hard parts for age and growth studies in aquatic animals (Beamish and McFarlane 1983). The analysis of the otolith edges used in this study indicated that the time a sardine requires

TABLE 4
Growth parameter values, 95% confidence intervals (95% CI) and Chi-squared probability (χ^2) for the
Pacific sardine in the Gulf of California. L_{∞} is asymptotic standard length; K is the growth coefficient, t_0 is the
hypothetical age at which the sardines showed zero length; a is relative growth rate; b is incremental relative
growth rate; Y_1 is the size at age T_1 and Y_2 is the size at age T_2 . Period 2010–11 to 2012–13.

Model	Parameter	Value	Lower 95% CI	Upper 95% CI	χ^2
VBGM	L_{∞} (mm)	201.287	200.700	201.800	0.032
	K_{annual}	0.581	0.577	0.586	0.090
	t_0 (years ⁻¹)	-0.839	-0.855	-0.824	0.016
Gompertz	L_{∞} (mm)	199.213	198.600	199.800	0.032
	K_{annual}	0.702	0.694	0.710	0.095
	t_0 (years ⁻¹)	-0.261	-0.277	-0.244	0.107
Logistic	L_{∞} (mm)	197.798	197.200	198.400	0.004
	K_{annual}	0.822	0.811	0.833	0.059
	t_0 (years ⁻¹)	0.161	0.142	0.178	0.050
Schnute	a	0.581	0.568	0.595	0.136
	b	1.002	1.001	1.003	0.292
	Y_1 (mm)	107.910	105.768	108.840	0.160
	Y_2 (mm)	195.737	195.050	196.400	0.128

For Schnute; $L_{\infty} = 199.480$ and $t_0 = -0.837$

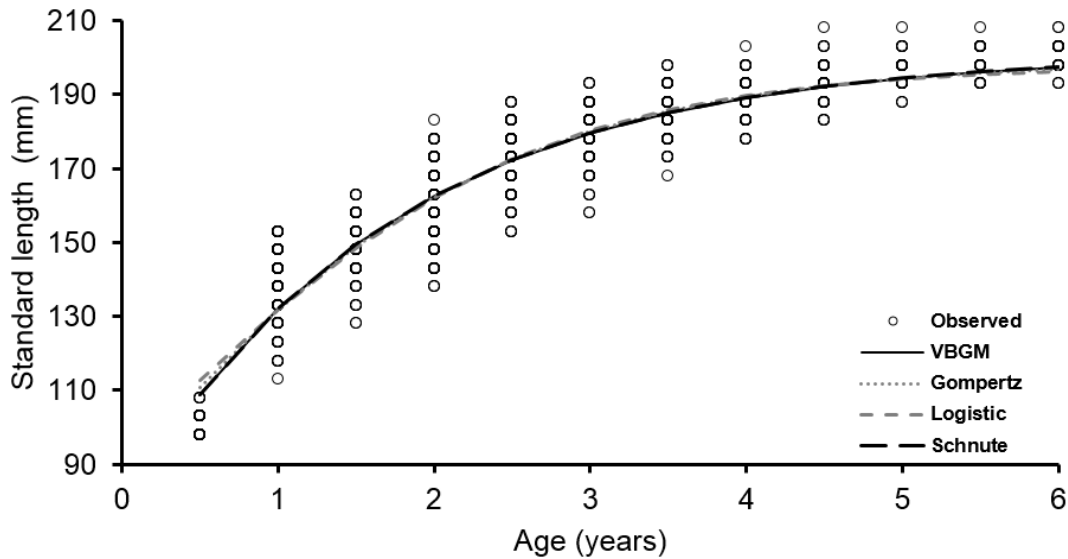


Figure 5. Growth models fitted to age-at-length data of Pacific sardine from Gulf of California ($n=1,195$). Period 2010–11 to 2012–13.

TABLE 5
Growth model selection for the Pacific sardine in the Gulf of California, where k is the number of parameters; LL is the maximum likelihood; AIC is the Akaike's information criterion; Δ_i is Akaike's differences, w_i is Akaike's weight for each model; and S.E. is the standard error.

Models	k	LL	AIC	Δ_i	$w_i\%$	L_∞ (mm)	S.E.
VBGM	4	1808.43	-3610.87	0.00	73.11	201.29	0.05
Gompertz	4	1781.74	-3557.49	53.38	0.00	199.21	0.05
Logistic	4	1758.31	-3510.63	100.24	0.00	197.80	0.06
Schnute	5	1808.43	-3608.87	2.00	26.89	199.48	0.05
Averaged multi-model						200.80	0.71

to form an opaque or a hyaline zone, on average, is approximately half a year, and showed that over a year, one opaque band plus one hyaline band were formed. Our results coincide with what was found in previous studies on the age of the Pacific sardine (Barnes and Foreman 1994; Nevárez-Martínez et al. 1996; Quiñonez-Velázquez et al. 2002).

The results of this study have demonstrated that the Pacific sardine of the GC was found in a relatively wide range of sizes (98–208 mm of SL) that corresponded to specimens from 0.5–6.0 years of age. Ages that contributed mainly to the catch were 1.0 to 3.0 years, which jointly meant almost 69% of the analyzed individuals.

The results showed that, except at a younger age, a greater variability of length at age was observed and as age increased, variability with respect to length decreased. The standard deviation was 8.19–9.03 mm in ages 1.0 to 2.0, decreasing gradually until the oldest sardine reached 3.88 mm (age 6.0). According to Parma and Deriso (1990) and Vincenzi et al. (2016), growth variability in populations results both from environmental disturbances and intrinsic differences in the maximum lengths observed in the analyzed specimens. In this case,

as the greatest variability occurred in young adults, it was probable that the environmental effects operated strongly in defining growth velocity in these age groups while older adults reached almost the same asymptotic size.

Among the growth models tested in the Pacific sardine, VBGM was the one that showed the highest asymptotic SL value ($L_\infty = 201.287$ mm) while the Logistic model was the one that obtained the lowest one ($L_\infty = 197.79$ mm). The value of K obtained both by VBGM and by Schnute (a) model were the lowest (0.581) within the candidate models while Gompertz (0.72) and Logistic (0.82) were higher. These differences in values estimated by each of the models confronted could be explained by their ability to represent growth of the Pacific sardine reliably, given the observed data. According to the AIC and w_i values obtained by the VBGM and Schnute models, they could represent better the growth kinetics of the Pacific sardine, especially the VBGM that showed a value $w_i = 73.11\%$; however, the Gompertz and Logistic models have a null Akaike weight ($w_i = 0.00\%$), that is, given the data used, apparently they have none supported to explain the growth of this species in the Gulf of California. If w_i represents the probability

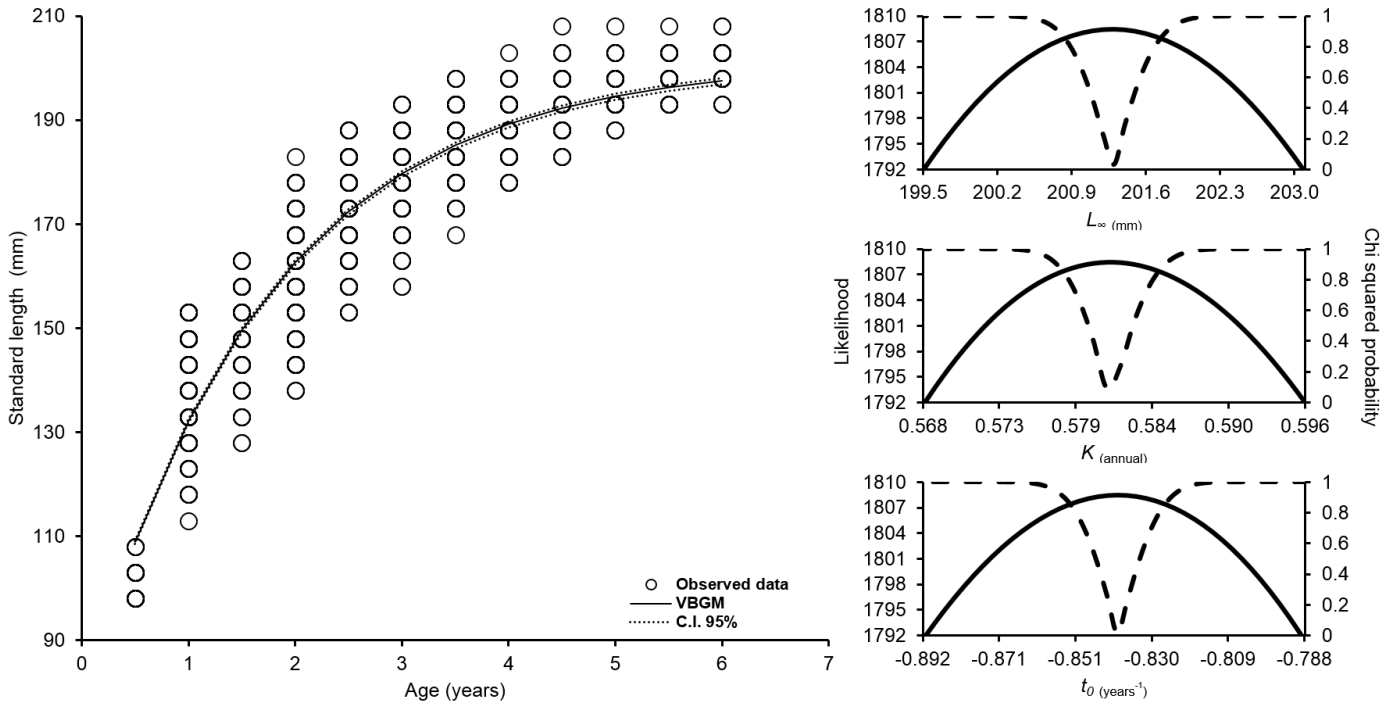


Figure 6. Average growth curve and likelihood profiles for parameters L_{∞} , K and t_0 estimated by the von Bertalanffy growth model for the Pacific sardine in the Gulf of California, during the seasons 2010–11 to 2012–13.

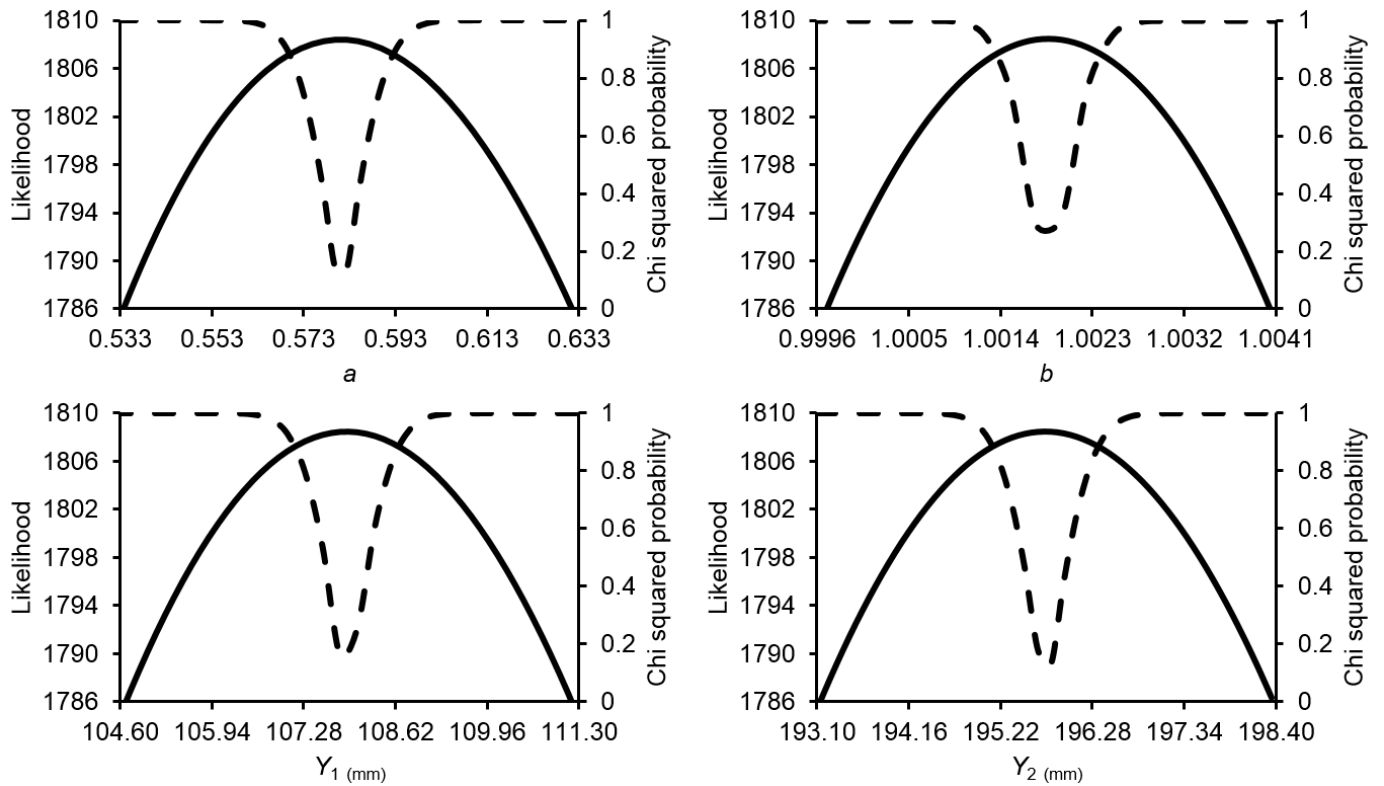


Figure 7. Likelihood profiles of parameters estimated with Schnute growth model, the second best candidate growth model for the Pacific sardine in the Gulf of California.

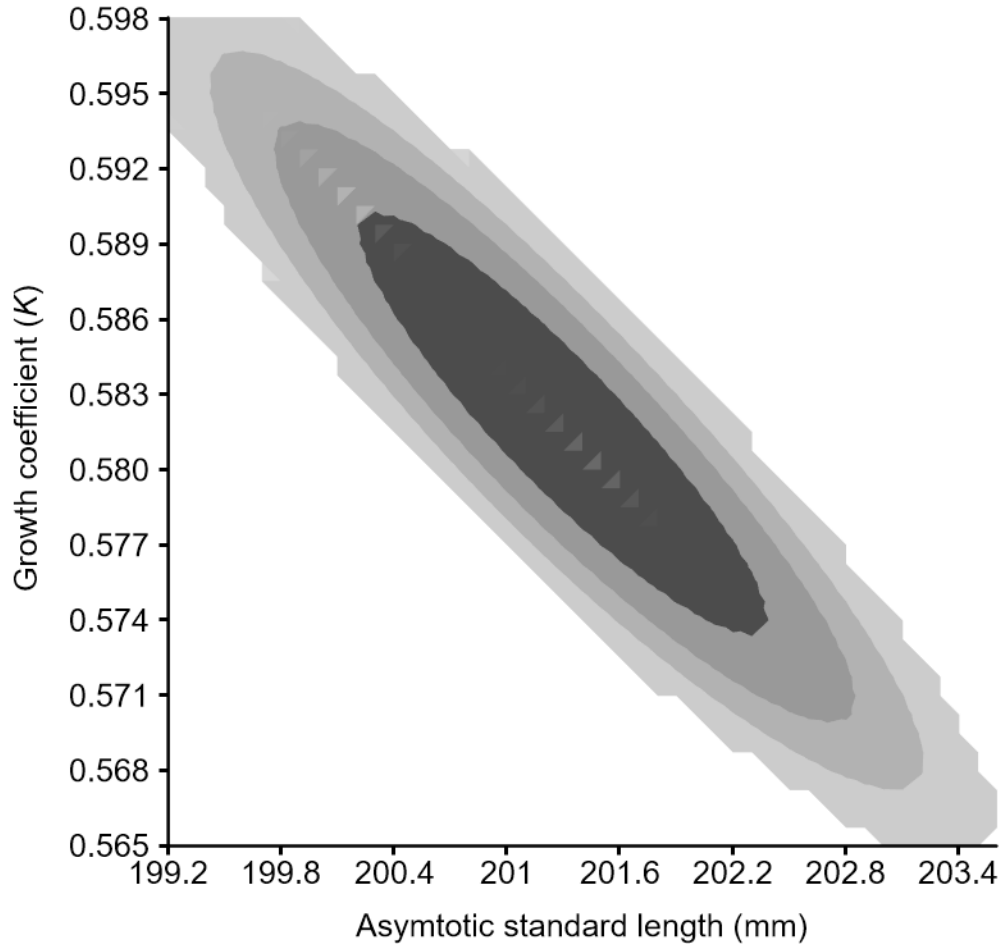


Figure 8. Likelihood contour for parameters L_{∞} and K estimated by von Bertalanffy growth model for the Pacific sardine *Sardinops caeruleus* in the Gulf of California. The area in dark gray denotes joint confidence intervals (χ^2 test, $p < 0.05$).

of choosing the correct model from the set of candidate models, given the data used (Burnham and Anderson 2002; Burnham and Anderson 2004; Burnham et al. 2011), and if we take in account that the model with the highest probability was the VBGM, we could accordingly consider it the best model. Growth parameters L_{∞} and K in the von Bertalanffy model showed the covariance characteristic; therefore, obtaining a likelihood contour for these parameters obtained in the Pacific sardine was a good way to show those regions in which the most probable parameter values are jointly found. In this study, growth parameters showed a strongly inverse correlation, so that, when one of the parameters increased its value, the other one decreased it and vice versa (fig. 8).

In previous growth studies for this species in the GC, based on age readings in otoliths and using the VBGM, Jiménez-Rodríguez (1991) and Nevárez-Martínez et al. (1996) estimated growth parameters in *S. caeruleus*, whose values compared with those obtained in our study were higher for L_{∞} (202.90 – 224.17 mm

SL) but lower for K (0.457 – 0.55). These differences in growth can reflect interannual variations in Pacific sardine growth, which could be due to density-dependent or climate factors (Checkley Jr. et al. 2017; Dorval et al. 2015; Piner et al. 2018). Quinn and Deriso (1999) support that the species uses the energy obtained by food to grow, reproduce and emigrate; thus the reason why these processes could be affected or modified in the species according to food availability, environmental conditions and density-dependent pressure, generating variation in growth.

On the other hand, Quiñonez-Velázquez et al. (2002) estimated that $L_{\infty} = 221.00$ mm SL and $K = 0.41$ when they analyzed information for the Pacific sardine in Isla de Cedros, Baja California, whereas Dorval et al. (2015) estimated the values of $L_{\infty} = 300.75$ mm SL and $K = 0.172$ in their analysis for the sardine of the coasts of California; that is, in both cases those authors found much larger values for L_{∞} and much smaller for K , based on the adjustment of

the VBGM model. In addition, Dorval et al. (2015) also made estimations with other models, but even when those models gave different results compared to the standard model of VBGM, their estimates, compared with ours, were still much higher for L_{∞} and much lower for K . This could imply that a cline exists in species growth from north to south with a more accelerated growth rate in the GC stock compared to those of Baja California or California stocks; the sardine in the coasts of California reaches around 67% at two years of age, in Isla de Cedros about 75% and in the GC about 81%.

Moreover, sardine growth studies have been performed based on the analysis of length structures in commercial catches, in which the VBGM model has been directly adjusted (Cisneros-Mata et al. 1990; De Anda-Montañez et al. 1999; Martínez-Zavala et al. 2006). In these studies, the values estimated were very different from those obtained by the VBGM and Schnute models, that is, they estimated higher values for L_{∞} and smaller values for K . Although apparently the results of this type of analysis cannot be compared directly with those obtained in this study (different methods), we want to note that if the methods based on lengths are used to analyze growth in commercial species, such as the Pacific sardine where only commercial sizes are available, and adjusted directly to the VBGM, the growth of juveniles will be poorly represented (Gamito 1998; Charnov 2008; Mercier et al. 2011). Therefore, these methods would tend to overestimate L_{∞} while underestimating K , and thus they are not suitable for use in assessment and management of fishery resources (Katsanevakis 2006).

According to the results of the inference multimodel, and strictly speaking, no clear “winning model” could be declared (that is, one with $w_i \geq 90\%$ values) within the candidates (Akaike 1998; Burnham and Anderson 2002), but two models, VBGM ($w_i = 73.11\%$) and Schnute ($w_i = 26.89\%$), were the ones that represented reliable age-length data of the Pacific sardine in the GC. In these cases, it was necessary to calculate an averaged model that weighted the asymptotic growth value of the species and performed inference on parameter L_{∞} (Burnham and Anderson 2002). The calculus of the averaged model was supported by the weighted values and weights of all the models (4) tested, following Katsanevakis and Maravelias (2008). Thus, the averaged model value had a number close to the calculus provided by a greater w_i in the analysis. If the biological point reference has been given by parameter L_{∞} , it is recommended to infer over the calculated value with the averaged model since it decreases uncertainty in the best model within those tested for a determined set of data (Burnham and Anderson 2002; Katsanevakis and Maravelias 2008). Nonetheless, if model parameters are required jointly, as well as the growth

curve form and projection, it is better to infer in von Bertalanffy, which was the one that showed the highest Akaike weight ($w_i = 73.11\%$). Recently, Mendivil-Mendoza et al. (2017) showed it was possible to obtain a true averaged model utilizing special solution cases of the Schnute (1981) model since it is versatile, capable of describing any type of growth curve according to the age-length data at hand and with interpretation bases of equivalent parameters to those obtained with VBGM. This methodology should be explored in future growth studies on the Pacific sardine.

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