



Article Modeling the Individual Growth of the Bonnethead Shark Sphyrna tiburo of the Western Gulf of Mexico Using the Multimodel Approach

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Abstract: To describe the growth pattern of the bonnethead shark (*Sphyrna tiburo*) in the Gulf of Mexico, a von Bertalanffy (VB) model has been automatically fit, which indicated a single–phase continuous growth without oscillations, though this would generate biases if this hypothesis is not confirmed. The objective of this research was to describe the growth pattern of *S. tiburo* under a multimodel approach based on information theory and contrasting single–phase models (VB, Gompertz, logistic models, and variants) and biphasic models (Soriano model and variants). The VB model was not supported. The Soriano model, with the variant in growth rate (k) and including length at birth (L_0), was selected with 100% supporting evidence. The hypothesis of the two–phase growth of *S. tiburo* with an increase in k, more than L_{∞} , fitted to L_0 , is confirmed, and a correspondence was identified between growth–phase change sizes and the sizes reported in the literature for change in the juvenile–adult stages in females and for onset of reproductive maturity in males and both sexes.

Keywords: multimodel inference; model selection; biphasic models; Sphyrna tiburo; maximum likelihood

1. Introduction

Along the coast of the Gulf of Mexico (GM) coexist several highly important fisheries, including of the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) [1]. In the particular case from the coast of Tamaulipas, Mexico, this fishing resource ranks 10th in value and volume among the main fisheries from the state [2]. Specifically, the bonnethead shark *Sphyrna tiburo* [3] represents 50% of the total volume contributed by the group of small coastal sharks in the southeastern United States and 15% of the volume of the annual catch in the GM [4]. Recently, it was found that the bonnethead shark, along with the Atlantic sharpnose shark, were the two most captured shark species in the southeastern GM [5].



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Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). In the coast of Tamaulipas are found the group of dogfish sharks made up of the following species: Atlantic sharpnose shark, bonnethead shark, blacknose shark (*Carcharhi-nus acronotus*) [6] and porous shark (*C. porosus*) [7], characterized by being small in size (<150 cm in total length) and recognized as a species of "high biological productivity" for having a rapid growth rate, high reproductive potential and reaching the age of first maturity during their first four years of life [8,9].

In this same coastal region, as in the rest of Mexico, there is a commercial shark fishery, managed through commercial fishing permits, which is why it represents a directed fishery, whose target species are sharks. This shark fishery in Mexico is represented by three fishery units: the coastal artisanal fishery that is carried out along the two sea coasts with vessels smaller than 10.5 m in length, which contributes to approximately 40% of national production; the medium height one, which is carried out with boats between 10 and 27 m in length in coastal waters on both coasts; and deep—sea fishing in which vessels of more than 27 m in length operate to capture sharks both in coastal waters and in oceanic waters within the Exclusive Economic Zone of the Pacific Ocean [10].

The bonnethead shark, the Atlantic sharpnose shark, the blacknose shark, and the finetooth shark *Carcharhinus isodon* [11] make up the group of small coastal sharks [12] on the east coast of the United States of America. *S. tiburo* is a very abundant small shark that is found in shallow waters such as the estuaries and bays of the coasts of the Atlantic and Pacific oceans of the Americas, including the GM [13], and whose regional migrations show spatial and temporal variations [14].

In the modelling of fish growth, it is generally chosen a priori to fit the von Bertalanffy model to the data of observed age frequencies [15,16], so it is assumed that the fish species follow an isometric growth pattern without oscillations and with continuity at all ages; sharks are no exception [17]. This a priori choice carries with it the risk of overestimating or underestimating parameters. Therefore, it is always advisable to test more than one growth model to find the one that best describes the observed data [18,19]. There is a rising trend in growth model selection, and specifically in multimodel inference, of estimating average parameters based on the specific statistical weight of each model [16].

In most vertebrate and plant growth investigations, the growth pattern is described as a single curve [20], but this approach has been criticized [21]. The most common single phase models (Von Bertalanffy, Logistic, and Gompertz) are generally easy to fit and generally apply to length-at-age data. In the case of fish, a criticism of these models is that growth throughout life comprises two or more stages that result from reproductive investment [21–23] or changes in habitat, food, or other stressors [21,24,25]. Describing these stages with a single curve can obscure important ecological and evolutionary information [21]. This is how the two state or biphasic models arise, where the growth acceleration generally changes around a transition age [26]. Such biphasic models have already been successfully applied to elasmobranch species, where such transitions are detectable only from length-at-age data [21]. It is important to estimate the growth parameters because they are inputs for the estimation methods of the instantaneous rates of total, natural and fishing mortality, directly, and they also represent inputs for the predictive models of yield per recruit of Beverton and Holt [27] and Thompson and Bell [28], directly and indirectly, respectively.

Research on the growth of *S. tiburo* is scarce. It has been studied on both sides (east and west) of the state of Florida, USA [29–32]. With the exception of Frazier et al. [32], all studies have chosen a priori to use the VB model to fit the data and model the growth pattern of the species, but biases will arise if this model is not confirmed to be right. Frazier et al. [32], in their research on the species in the Atlantic Ocean (east side of Florida), have been the only ones that have used the multimodel approach along with information theory to choose the model with the best fit for this species. They did not apply multimodel inference, and even though it was not the best model, they selected the VB model based on one biological criterion. It is presumed that in the west of the GM, *S. tiburo* has two growth phases.

The objective of the present study was to describe the growth pattern of the bonnethead shark *S. tiburo* of western GM under the multimodel approach, fitting single phase and biphasic models and making use of information theory to choose the best fitting model or applying the multimodel inference, as needed, to provide more robust estimates of its growth parameters.

2. Materials and Methods

2.1. Study Area

Samples of artisanal fishing were carried out in the Carbajal Fishing Zone, in the Municipality of San Fernando and in the towns of La Pesca and Miguel de la Madrid Hurtado (El Canal) in the Municipality of Soto La Marina, Tamaulipas, Mexico (Figure 1), from September 2016 to April 2019. The fishing gear used was mainly longlines and *cazonera* (shark) nets. The longlines were monofilaments with lengths between 600 and 1500 m on average and included snoods of 1.5 to 2.5 m in length, between 150 and 500 on average per longline, and between 350 and 750 "eagle claw" size 5–6 hooks per longline. The *cazoneras* were made of nylon and polyethylene, with lengths between 450 and 1000 m, a drop of 6 m, and a mesh opening of 12.5 cm. The sex of each captured organism was determined by the presence or absence of the (male) myxopterygium (copulatory organ). The total length (TL) in centimeters and the gutted weight in kilograms were taken with an ichthyometer (± 1 mm) 1 m in length, graduated at every millimeter, and a Torrey OLEQ5–N digital scale with a capacity of 5 kg (\pm 0.1 g), respectively.

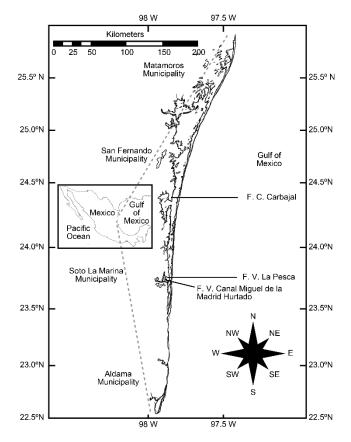


Figure 1. Sampling sites of the bonnethead shark Sphyrna tiburo in the western Gulf of Mexico.

2.2. Multinomial Analysis

The modes present in the size distribution of the annual samples of females, males, and the total catches were determined through multinomial distribution with the following density probability function [33]:

$$P\left\{x_{i} \middle| n, p_{1,}, p_{2}, \dots, p_{k}\right\} = n! \prod_{i=1}^{k} \frac{p_{i}^{x_{i}}}{x_{1}!},$$

where x_i is the number of times that an i-type event occurs in n samples, n is the sample size, and p_i is the probability of the i-type event. Haddon (2001) recommends that to estimate the parameters of the model, the equation must be converted into a likelihood expression as follows:

$$-\ln L\Big\{x_i\Big|n,p_{1,\prime}p_2,\ldots,p_k\Big\}=\sum_{i=1}^n[x_i\ln{(p_i)}].$$

The main assumption underlying the estimation of the parameters is that the size distribution for each average or modal length assumes a normal distribution, each mode corresponding to a different cohort in the population. Under this condition, the estimates of the expected relative proportions of each length category were described through the following density function:

$$P_{L_F} = \frac{1}{\sigma_n \sqrt{2\pi}} \times e^{\frac{-(L_F - \mu_F)^2}{2\sigma_n}},$$

where μ_F and σ_F are the mean and standard deviation of the total length of each cohort, respectively. The starting values of the parameters in the previous equation were assigned according to a visual inspection of the frequency distributions of the data [34]. Then, to estimate the expected frequencies and the parameters of the models, the estimated and observed values were contrasted through the negative of the logarithm function of the maximum likelihood of the multinomial distribution [33,35]:

$$-\ln L\{L|\mu_{F},\sigma_{F}\} = -\sum_{i=1}^{n} L_{i} \ln (\hat{p}_{i}) = -\sum_{i=1}^{k} L_{i} \ln (\frac{\hat{L}_{i}}{\sum \hat{L}_{i}}).$$

where the parameters μ_F and σ_F correspond to the mean and standard deviation of the total length corresponding to the n means that are present in the length distribution. The model parameters were estimated when the likelihood function (the latter expression) was minimized with Newton's direct search algorithm [36].

2.3. Age Determination

For age determination, the separation index (SI) of a mean greater than 2 was used, according to Sparre and Venema [37] and the following equation:

SI =
$$2 * \frac{(\mu_2 - \mu_1)}{(\sigma_1 - \sigma_2)}$$

where μ and σ correspond to the mean and standard deviation of the total length. In the first year of life, the bonnethead shark *S. tiburo* reaches 58.69 cm on average in females (range 50.73 to 62.38 cm), while in males the average size reached is 56.99 cm (range 41.17 to 62.32 cm), in Tampa Bay, Florida [38]. The smallest TLs observed in the modes obtained in this study (female = 56.02 cm and male = 59.43 cm) lie within these confidence intervals, so it was assumed that the TLs we found corresponded to the first year of life of *S. tiburo*.

2.4. Candidate Models

To identify the model that best described the growth of *S. tiburo*, 13 models were fit to the three data series (females, males, and both) of average TL of the modes and

their correlative ages to estimate the growth parameters of each model and of the average models (Table 1). Seven models were applied in their basic forms, as were eight variants of them. The models fit in their basic form were von Bertalanffy [39], Soriano et al. [40] (S), Gompertz [41] (G), Johnson [42] (J), and logistic [41] (L). Variations of all the models but J were tested. The variation was done by substituting the parameter t₀ by the parameter L₀, according to the algorithm of each model with its respective source. In sum, the 13 models were VB1, VB2, S1, S2, S3, S4, S5, S6, G1 [43], G2 [44], J, L1, and L2 (Table 1). S and its variants were biphasic models, and the other models and their variants were single—phase models. These models were selected because they have been used traditionally to describe growth in fishes such as sharks.

Model	Туре	Function	Parameters to Be Estimated	Reference
VB1 (3 parameters)	S	$L_{(t)}=L_\infty(1-e^{-k(t-t_0)})$	L_{∞} ; k; t ₀	von Bertalanffy [26]
VB2 (3 parameters)	S	$L_{(t)}=L_{\infty}-(L_{\infty}-L_0)(e^{-kt})$	L_{∞} ; k; L_0 ;	Fabens [32]
S1 (5 parameters)	В	$L_{(t)} = L_{\infty} (1 - \frac{h}{(t-th)^2 + 1}) (1 - e^{-k(t-t_0)})$	L_{∞} ; k; t ₀ ; th; h	Soriano et al. [27]
S2 (5 parameters)	В	$L_{(t)} = L_{\infty}(1 - e^{-k(1 - \frac{h}{(t-th)^2 + 1})(t-t_0)})$	L_{∞} ; k; t ₀ ; th; h	Soriano et al. [27]
S3 (5 parameters)	В	$ \begin{split} L_{(t)} = \\ \left\{ \begin{array}{l} L_{\infty MS1}(1-e^{-k_{MS1}(t-t_{0MS1})}) \text{; Sit} th \end{array} \right. \end{split} $	$L_{\infty}S1;$ k S1; t $_{0}S1$ $L_{th};$ $L_{\infty}S2;$ k S2; th S1	Soriano et al. [27]
S4 (5 parameters)	В	$L_{(t)} = L_{\infty} - (L_{\infty} - L_0) \left(e^{-kt\left(1 - \frac{h}{(t-th)^2 + 1}\right)} \right)$	L_{∞} ; L_0 ; k; h; th;	Soriano et al. [27]
S5 (4 parameters)	В	$L_{(t)} = L_{\infty} - (L_{\infty} - L_0) \left(e^{-kt(1-\frac{h}{(t-th)^2+1})} \right)$	L_{∞} ; L_0 VB2; k; h; th;	Soriano et al. [27]
S6 (4 parameters)	В	$L_{(t)} = L_{\infty} - (L_{\infty} - L_0) \left(e^{-kt(1 - \frac{h}{(t-th)^2 + 1})} \right)$	L_{∞} ; L_0G2 ; k; h; th;	Soriano et al. [27]
G1 (3 parameters)	S	$L_{(t)} = L_{\infty} \; e^{-e^{-k_2(t-t_1)}}$	L_{∞} ; k; t ₀	Ricker [30]
G2 (3 parameters)	S	$L_{(t)} = L_0 \; e^{ln (\frac{L_\infty}{L_0})(1-e^{-k_2 t_1})}$	L _∞ ; k; L ₀	Mollet et al. [31]
J1 (3 parameters)	S	$L_{(t)}=L_{\infty}e^{-[\frac{1}{k}(t-t_0)]}$	L_{∞} ; k; t ₀	Grosjean [29]
L1 (3 parameters)	S	$L_{(t)} = L_{\infty} (1 + e^{-k_3(t-t_2)})^{-1}$	L_{∞} ; k; t ₀	Ricker [30]
L2 (3 parameters)	S	$L_{(t)} = L_{\infty} (1 + (\tfrac{L_{\infty} - L_0}{L_{\infty}}) e^{-k_3 t_2})^{-1}$	L _∞ ; k; L ₀	Ricker [28]

Table 1. A comparison of models describing the growth pattern of the bonnethead shark (*Sphyrna tiburo*) in the western Gulf of Mexico.

 $L_{(t)}$ = length at time t, L_{∞} = theoretical maximum length, k = growth rate, t₀ = hypothetical age when L is 0, L_0 = length at birth, h = magnitude of the maximum difference between VB1 and S1, t_h = age where the transition between the two growth phases occurs, k₂ = rate of exponential decay with age of the relative growth rate (unit: year⁻¹), t₁ = $\frac{\ln \lambda}{k_2}$, λ = initial theoretical relative growth rate at age 0 (with units year⁻¹), k₃ = relative growth rate parameter, t₂ = inflection point of the sigmoidal curve, U = uniphasic, B = biphasic.

2.5. Model Fitting

The models were fit using an iterative process with the Excel solver function that used Newton's direct search algorithm [36], assuming the types of error in the residuals were additive and multiplicative and maximizing the objective likelihood function [33]:

$$\mathcal{L}(\Phi|\text{data}) = -(\frac{n}{2})(\text{Ln}(2\pi) + 2 \cdot \text{Ln}(\sigma) + 1)$$

 $\sigma = \sqrt{\frac{(TL - \hat{TL})^2}{n}}$, for the additive error, and $\sigma = \sqrt{\frac{(\ln TL - \ln T\hat{L})^2}{n}}$ for the multiplicative error, where TL = total length observed and \hat{TL} = total length estimated. When the analysis was performed using the multiplicative error for the modelling, σ and $\mathcal{L}(\hat{\theta}|y)$ were recalculated at an additive error scale to obtain consistent scales and comparable information criteria (indicated below).

2.6. Selection of Models

For the selection of models, the Akaike information criterion (AIC) was used [45] in its corrected version for small samples (AICc) [18] because n/Φ was less than 40, where n = sample size and $\Phi =$ is the number of parameters. The formula is: AICc = AIC + (2k(k + 1)/(n - k - 1), where AIC = -2 ML + 2k; k = number of parameters, n = number of data points, and LL is the log–likelihood maximum. It was assumed that the deviations were normally distributed, with constant variances. The model with the lowest AICc was selected as the one that best fit the data.

2.7. Differences and Plausibility of the Models

Once the growth parameter and AICc values were determined, the statistical support was evaluated, and the evidence of each of the models was quantified by estimating the differences (Δ_i) and the plausibility (the weight of evidence supporting model i) of each model (w_i) according to the criterion of Burnham and Anderson [18]. To estimate Δ_i , we started with the following formula:

$$\Delta_i = IC - IC_{min}$$

where IC = AICc and IC_{min} = the model with the lowest AICc. According to Burnham and Anderson [18], the scale of Δ_i is as follows: $\Delta_i > 10$ indicates a candidate model without statistical support and should not be considered further; $\Delta_i < 2$ indicates a candidate model supported by strong evidence; and $4 < \Delta_i < 7$ indicates a candidate model that can be considered, though with less statistical support than the second category. The w_i were calculated from the following probability model:

$$w_{i} = \frac{\exp\left(-\frac{1}{2}\Delta_{i}\right)}{\sum_{k=1}^{k}\exp\left(-\frac{1}{2}\Delta_{i}\right)}$$

where Δ_i = AICc difference and k = number of parameters. To choose the model with the best fit, the criterion proposed by Burnham and Anderson [18], which holds that a winning model is one with $w_i \ge 0.90$, was used; in case no model reached this value of w_i , we proceeded with multimodel inference (MMI).

2.8. Multimodel Inference

The average values of L_{∞} , k, L_0 , t_h (age at which the shark transitions between the two growth phases), h, and L_{th} , were estimated for females, males, and both by adding the products of the original value of the parameter of each candidate model to their respective w_i , according to the following equations: $\hat{\theta} = \theta * w_i$; where θ is the original value of the parameter of each candidate model, and $\hat{\theta} = \sum_{i=1}^{R} w_i \hat{\theta}_i$, where $\hat{\theta}$ = estimated average parameter of θ and R = number of models.

2.9. Uncertainty in the Average Model

Based on the criterion of Burnham and Anderson [18] and with a confidence level of 95%, the confidence intervals (CIs) of the parameters of the individual models and of the average model were estimated as follows: $L_{sup} = \hat{\theta} + (1.96) \times SE$; and $L_{inf} = \hat{\theta} - (1.96) \times SE$,

where L_{sup} is the upper limit, L_{inf} is the lower limit, $\hat{\theta}$ is the average parameter, and SE is the standard error. SE was calculated as: $SE = \sum_{i=1}^{R} w_i \sqrt{v \hat{a}r(\hat{\theta}_i | g_i) + (\hat{\theta}_i - \hat{\theta})^2}$, where $v \hat{a}r(\hat{\theta}_i | g_i)$ represents the variance of the estimate $\hat{\theta}_i$ of the given model g_i .

2.10. Statistical Tests

Based on the criterion and procedure of Zar [46], significant differences were tested (a) between the average TL of females and males through Student's t–test, (b) between the growth curves by applying the χ^2 test, and (c) between the values of ML, IC, and w_i for each type of error assumed (additive and multiplicative) in the residuals when running the Newton search algorithm [36] while fitting the selected or average models, as the case may be, by performing a single factor analysis of variance on females, males, and both. A single–factor analysis of variance on females, males, and both was also performed to identify the relationship, its magnitude, and its statistical significance between the AICc value (dependent variable) and the number of model parameters (independent variable), measured by the coefficient of determination (r²) and verifying the relationship's statistical significance by applying Student's *t* test to the slope [46] found for females, males, and both.

3. Results

3.1. Structure of Total Lengths and Gutted Weights

TL (cm) and gutted weight (kg) data were taken from 119 specimens of *S. tiburo*, 64 females and 55 males. The average TL values for females and males were 71.58 ± 2.07 and 70.59 ± 2.21 , respectively (range: females 50-98, males 51-94, overall 50-98). The mean gutted weights were 1.559 ± 0.15 and 1.302 ± 0.12 for females and males, respectively (range: female 0.62-3.55, male 0.38-2.48, overall 0.38-3.55).

3.2. Identification of Modes in the Size Frequency Distributions

In months other than February, females and males presented the same number of modes: 3 in April and 4 in May (in February, there were three in females and two in males) (Table 2 and Figure 2). Overall, three were recorded in February 2017 and two in February 2018, four were observed in April and five were estimated in May. The range of average sizes (cm) of the modes varied between females and males. In April in females, the range was from 62.41 to 98.21, and in males it was from 62.34 to 85.11; in May the range in females was from 56.02 to 86.45 and in males from 59.34 to 94.73, while overall in April a mode of 101.23 was recorded, and in May a fifth mode of 96.02 was reached.

Month/Year CI (cm) SI Ngm n Mean (cm) Females September 2016 54.40 1 1 20 3.98 February 2017 59.09 56.11, 62.07 2 5 68.00, 74.04 2.65 71.02 3 4 76.03, 82.21 79.12 September 2017 1 81.00 2 February 2018 85.50 5 May 2018 1 52.52, 59.52 3.40 56.02 2 1 65.72 63.51, 67.93 2.41 3 2 73.12 69.20, 77.04 3.53 4 6 82.81, 90.09 86.45 April 2019 1 6 62.41 58.41,66.41 6.49 2 9 84.83, 93.23 89.03 2.19 3 2 94.01, 102.41 98.21

Table 2. Modes identified in the total length frequency distributions in females, males, and combined sexes of the bonnethead shark (*Sphyrna tiburo*) in the western Gulf of Mexico.

Month/Year	Ngm	n	Mean (cm)	CI (cm)	SI
Males					
February 2017		1	57		
December 2017	1	6	86.13	85.89, 86.37	2.35
February 2018	1	14	59.43	55.2, 63.66	2.89
·	2	6	71.12	67.25, 74.99	
May 2018	1	11	59.34	54.34, 64.34	3.81
-	2	3	78.37	73.37, 83.37	2.24
	3	4	86.21	84.21, 88.21	2.84
	4	2	94.73	90.73, 98.73	
April 2019	1	6	62.34	57.34, 67.34	3.70
-	2	1	78.37	74.7,82.04	2.02
	3	1	85.11	82.11, 88.11	
Combined					
September 2016		1	54.40		
February 2017	1	20	59.09	56.11, 62.07	3.98
2	2	6	71.02	68.00, 74.04	2.65
	3	4	79.12	76.03, 82.21	
September 2017		1	81.00		
December 2017	1	6	86.13	84.67, 87.59	
February 2018	1	21	59.43	55.20, 63.66	2.89
2	2	1	71.12	67.25, 74.99	
May 2018	1	13	56.02	53.02, 59.02	3.88
	2	1	65.72	63.72, 67.72	2.50
	3	2	73.12	69.20, 77.04	4.54
	4	17	86.56	84.56, 88.56	6.31
	5	1	96.02	95.02, 97.02	
April 2019	1	7	62.34	59.84, 64.84	7.37
*	2	10	86.21	82.23, 90.19	2.42
	3	7	95.87	91.85, 99.89	2.14
	4	1	101.23	100.25, 102.21	

Table 2. Cont.

Ngm = modal group number, CI = confidence interval, SI = separation index, Combined = both sexes combined. The SI corresponds to the place that separates the value and the subsequent ascending mode.

3.3. Fit of Growth Models

The VB1 model was not supported by any evidence ($\Delta_i > 10$) in any of the three datasets (females, males, total) or according to either types of error assumed in the residuals (additive or multiplicative) (Table 3), while the model of Soriano et al. [40], with the variation in k and including L₀ instead of t₀, was the one selected for three datasets (females and total: S6; males: S4) with practically 100% of the evidence (w_i) in its favor (females = 0.971, males = 1.00, total = 0.881) (Table 3 and Figure 3). In the total sample, S6 was selected because it was the only one that met the criterion of $\Delta_i < 2$ (Table 3). This strong evidence in favor of the Soriano et al. [40] models selected with the L₀ variation, estimated by the Gompertz model (S6) and by the same model (S4), in all three datasets (Figure 3) negated the need to use MMI.

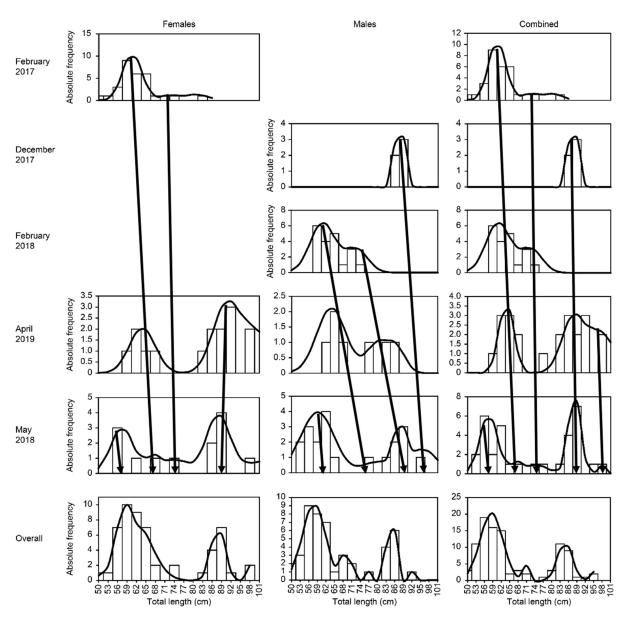


Figure 2. Size frequency distribution (bars) and modal groups (lines) estimated for the bonnethead shark (*Sphyrna tiburo*) in the western Gulf of Mexico. (The months of the year are sorted sequentially without considering the year).

Table 3. Values of the maximum likelihood, the information criterion, and the specific weight of each candidate model, contributing to the description of growth patterns in females, males, and combined sexes of the bonnethead shark (*Sphyrna tiburo*) in the western Gulf of Mexico, under additive and multiplicative errors.

Model –		Additiv	ve Error		Multiplicative Error					
would	ML	AICc	Δi	w _i	ML	AICc	Δi	w _i		
				Females						
VB1	-13.859	33.719	99.212	0.000	-14.116	34.231	101.123	0.000		
VB2	-11.726	27.453	95.742	0.000	-11.794	29.588	96.480	0.000		
S1	33.022	-56.044	8.052	0.017	33.064	-56.128	7.968	0.018		
S2	26.168	-42.336	21.759	0.000	26.168	-42.336	21.759	0.000		
S3	-20.084	54.168	111.253	0.000	-20.084	40.168	111.253	0.000		
S4	18.355	-26.711	37.385	0.000	18.420	-26.841	37.255	0.000		

Model		Additiv	e Error		Multiplica	ative Error		
Widdei	ML	AICc	Δi	wi	ML	AICc	Δi	wi
S5	32.286	-56.572	8.922	0.011	32.286	-56.572	8.922	0.011
S6	36.747	-65.494	0.000	0.971	36.747	-65.494	0.000	0.971
G1	-11.518	29.036	95.927	0.000	-11.530	29.060	95.952	0.000
G2	-11.514	27.027	95.317	0.000	-11.514	27.027	95.317	0.000
J	-20.484	46.969	113.860	0.000	-26.296	58.592	125.484	0.000
L1	-11.492	28.985	95.877	0.000	-11.536	29.072	95.964	0.000
L2	-14.292	32.583	100.873	0.000	-14.418	32.836	101.126	0.000
				Males				
VB1	-15.009	36.019	101.928	0.000	-15.009	36.019	102.099	0.000
VB2	-5.215	16.430	82.340	0.000	-5.341	14.682	82.063	0.000
S1	-9.224	28.447	91.755	0.000	-9.224	28.447	91.925	0.000
S2	-11.192	32.383	95.691	0.000	-11.192	32.383	95.861	0.000
S3	-27.127	54.254	124.067	0.000	-26.923	53.845	123.829	0.000
S4	36.654	-63.308	0.000	1.000	36.739	-63.478	0.000	1.000
S5	-3.403	14.807	79.416	0.000	-3.403	14.807	79.586	0.000
S6	-4.402	16.803	81.412	0.000	-4.391	16.782	81.561	0.000
G1	-5.615	17.230	83.140	0.000	-5.615	17.230	83.310	0.000
G2	-5.607	15.214	82.424	0.000	-5.607	15.214	82.595	0.000
J	-13.890	33.781	99.690	0.000	-13.994	33.988	100.068	0.000
L1	-5.959	17.918	83.828	0.000	-5.959	17.918	83.998	0.000
L2	-10.645	25.290	92.501	0.000	-10.817	25.633	93.015	0.000
			C	Combined sexe	es			
VB1	-11.839	29.677	77.981	0.000	-11978	29.955	79.638	0.000
VB2	-4.379	12.758	63.858	0.000	-4461	14.923	64.605	0.000
S1	23.151	-36.302	10.604	0.004	23679	-37.357	9.529	0.007
S2	26.402	-42.804	4.103	0.113	26402	-42.804	4.082	0.114
S3	-19.365	52.731	96.841	0.000	-21140	42.279	96.156	0.000
S4	-10.987	31.974	78.881	0.000	-8074	26.148	73.035	0.000
S5	21.978	-35.956	12.348	0.002	21978	-35.956	12.328	0.002
S6	28.152	-48.304	0.000	0.881	28142	-48.284	0.000	0.877
G1	-4.091	14.182	63.885	0.000	-4176	14.351	64.034	0.000
G2	-4.091	14.182	63.885	0.000	-4091	12.182	63.262	0.000
J	-49.778	105.556	155.258	0.000	-49778	105.556	155.238	0.000
L1	-3.773	13.546	63.249	0.000	-3863	13.725	63.408	0.000
L2	-11.189	26.378	77.478	0.000	-11189	26.378	77.458	0.000

Table 3. Cont.

ML = log - likelihood maximum, AICc = corrected Akaike information criterion, $\Delta i = difference of the model$, $w_i = specific weight of each model$. The specifications of the models are listed in Table 1.

Several models overestimated L_{∞} in females (VB2, G1, G2, J, and L1), in males (VB2, S5, S6, G1, and G2), and overall (VB2, S4, G1, G2, and J), and some also overestimated k in females (S1, S2, and S3), males (S1, S2, S3, and J), and overall (S1, S2, and S3) (Table 4). Several models underestimated k in females (G1, M2, and J), males (S6), and C (VB2). Based on the selected models (females and total: S6; males: S4), L_0 was smaller in females (42.63 cm) than in males (44.37 cm) and the total sample (46.45 cm) (Table 4), and t_h occurred earlier in females (1.641 ± 0.061) than in males (3.48 ± 0.025), corresponding to L_{th} values of 53.34 cm (±0.919) and 81.35 cm (±0.025), respectively, while the overall t_h was 1.45 (±0.202) which was similar to the t_h in females, corresponding to a TL of 64.31 cm (Table 4).

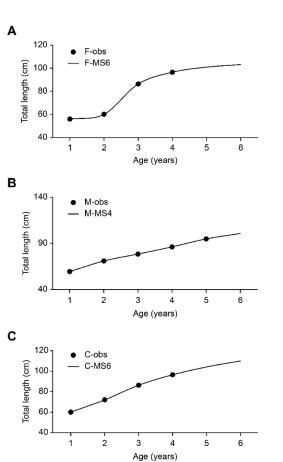


Figure 3. Growth curves of females (**A**), males (**B**), and combined sexes (**C**) of *Sphyrna tiburo* from the western Gulf of Mexico. Dark filled circles are the observed values, and the lines are the estimated values. F-obs = observed values for females; F-S6 = model selected for females; M-obs = observed values for males; M-S6 = model selected for males; C-obs = observed values for combined sexes; and C-S6 = model selected for combined sexes.

Table 4. Number of parameters (Φ) and values of the parameters estimated per model for females, males, and both sexes combined for the bonnethead shark (*Sphyrna tiburo*) in the western Gulf of Mexico.

Model	Φ	L_{∞} (Annual)	k (Annual)	t ₀ (Annual)	L ₀	t _h	h	L _{th}	Condition
				ales					
VB1	3	102.51	0.60	0.000					
VB2	3	2.153.65	0.00		37.672				
S1	5	103.76	1.38	0.000		1.699	0.416	54.806	
S2	5	98.76	1.11	0.000		2.220	0.603	61.457	
62	3	103.76	1.38	0.000					If $t < t_h$
S3	4	98.76	1.11			2.220		61.46	If $t > t_h$
S4	5	111.86	0.31		74.034	1.237	2.377	47.561	
S5	4	104.99	0.58		37.672 *	1.732	0.700	55.319	
S 6	4	105.96	0.54		42.628 **	1.641	0.791	53.342	
G1	3	1.101.29	0.07	15.994					
G2	3	1.878.97	0.06		42.628				
J	3	1.042.01	0.12	0.000					
L1	3	258.86	0.28	5.753					
L2	2	98.66	0.51						

Model	Φ	L_{∞} (Annual)	k (Annual)	t ₀ (Annual)	L ₀	t _h	h	L _{th}	Condition
				Ma	ales				
VB1	3	89.23	0.93	0.000					
VB2	3	165.02	0.10		48.837				
S1	5	95.84	1.08	0.000		2.476	0.199	71.444	
S2	5	91.84	1.19	0.000		2.641	0.527	71.061	
62	3	95.84	1.08	0.000					If $t < t_h$
S3	4	91.84	1.19			2.641		71.061	If $t > t_h$
S 4	5	122.18	0.2184		44.368	3.479	0.151	81.355	
S5	4	165.63	0.10		48.837 *	3.695	0.070	83.552	
S6	4	216.14	0.07		49.735 **	4.160	0.061	87.288	
G1	3	135.61	0.20	0.000					
G2	3	133.44	0.21		49.735				
J	3	99.89	1.74	0.000					
L1	3	121.12	0.32	1.060					
L2	2	101.90	0.43						
				Combin	ed sexes				
VB1	3	108.79	0.54	0.000					
VB2	3	263.38	0.07		45.610				
S1	5	102.90	2.42	0.546		2.120	0.283	72.11	
S2	5	98.05	1.25	0.085		2.460	0.542	72.90	
C 2	3	102.90	2.42	0.55					If $t < t_h$
S3	4	98.05	1.25			2.460		72.90	If $t > t_h$
S4	5	140.87	0.16		60.016	1.653	0.575	68.82	
S5	4	102.83	0.69		45.610 *	2.337	0.368	65.12	
S 6	4	132.63	0.23		46.457 **	1.449	0.290	64.31	
G1	3	156.65	0.23	0.844					
G2	3	156.81	0.23		46.457				
J	3	156.65	0.23	0.844					
L1	3	132.67	0.40	1.506					
L2	2	102.31	0.53						

* L_0 estimated with VB2. ** L_0 estimated with G2. Φ = Number of parameters. S3 uses the parameters L_∞ , k, and t_0 of S1 and L_∞ , k, t_h and L_{th} of S2, so no parameter was estimated for this model. L_{th} is the transformation of t_h into total length and is not a parameter included in the models. The values in bold correspond to the selected models.

In females, the AICc values were explained in a significant way (40%) by the number of parameters of the models ($r^2 = 0.399$) (t = -3.4966, df = 1 and p < 0.05), but this hypothesis was not corroborated in males ($r^2 = 0.012$; t = -0.3761, df = 1 and p > 0.05) or overall ($r^2 = 0.257$, t = -2.0424, df = 1 and p > 0.05).

3.4. Differences in Total Lengths and Growth Curves

No significant differences were found between (a) the average sizes of females and males ($t_{(1.98)} = 0.329$; df = 118; p > 0.05), (b) the values of ML, IC, and w_i of the selected models in females (females_(1, 5.317) = 3.60 × 10⁻⁷; p > 0.05), males (females_(1, 5.317) = 3.10 × 10⁻⁶; p > 0.05) and C (females_(1, 5.317) = 5.66 × 10⁻⁸; p > 0.05) (Table 3), or (c) the growth curves ($\chi^2_{(9.488)}$; df = 4; p > 0.05) of (i) the individual models selected from females (S6) and males (S4) ($\chi^2 = 3.476$), (ii) the individual selected and average models for females ($\chi^2 = 0.1564$), males ($\chi^2 = 0.0641$), and overall ($\chi^2 = 0.0647$), or (iii) the average model of females and males ($\chi^2 = 4.0768$) (Table 5). Therefore, based on a biological interpretation of the parameters, for both sexes, the S6 model, fit using the additive error in the Newton search algorithm [36], is adequate for representing the growth pattern of *S. tiburo* (Table 5).

Table 4. Cont.

Parameter	Estimates		Selected Model			Average Mode	1
i ululletel	LStimates	Females (S6)	Males (S4)	Combined	Females	Males	Combined
	Ер	105.957	122.182	132.628	106.453	122.182	128.581
L ₀	Linf	105.099	122.158	125.643	105.605	122.158	121.662
	L _{sup}	106.815	122.207	139.612	107.300	122.207	135.499
	Ep	0.541	0.218	0.226	0.537	0.218	0.275
k	Linf	0.530	0.194	0.137	0.526	0.194	0.191
	L _{sup}	0.552	0.243	0.314	0.549	0.243	0.359
t _h	Ep	1.641	3.479	1.449	1.606	3.479	1.566
	L _{inf}	1.580	3.455	1.245	1.545	3.455	1.364
	L _{sup}	1.703	3.504	1.653	1.666	3.504	1.769
h	Ep	0.791	0.151	0.290	0.930	0.151	0.318
	L _{inf}	0.551	0.126	0.234	0.694	0.126	0.264
	L _{sup}	1.032	0.176	0.345	1.166	0.176	0.373
	Ep	42.628	44.368	46.457	45.511	45.996	46.455
L ₀	Linf	37.566	42.273	46.428	40.484	44.208	46.427
~	L _{sup}	47.691	46.462	46.486	50.537	47.783	46.484
	Ep	53.342	81.355	64.314	52.853	81.355	65.322
Lt	Linf	52.497	81.330	62.574	52.019	81.330	63.599
	L _{sup}	54.186	81.379	66.053	53.687	81.379	67.044

Table 5. Point estimates and confidence intervals of the growth parameters for the selected models and average models of the bonnethead shark (*Sphyrna tiburo*) in the western Gulf of Mexico.

Ep = point estimate, L_{inf} = lower limit, L_{sup} = upper limit, k = growth rate, L_{∞} = theoretical maximum length, k = growth rate, L_0 = length at birth, h = magnitude of the maximum difference between VB1 and S1, t_h = age at which the transition between the two growth phases occurs, L_{th} = the transformation of th into total length and is not a parameter included in the models.

4. Discussion

The objective of the present investigation was to describe the growth pattern of the bonnethead shark *S. tiburo* of western GM under the multimodel approach by fitting single–phase and biphasic models. In the three datasets (females, males, and both), the VB1 model did not present any statistical evidence in its favor ($\Delta_i > 10$), and the model of Soriano et al. [40], with the second variant of the VB curve and including L₀, was selected among the three datasets (females and total: S6; males: S4). L₀ was similar in the three datasets (females = 42.63 cm, males = 44.37 cm, total = 46.45 cm). The age at which the transition between the two growth phases occurs in the selected model of Soriano et al. [40] was similar in females (1.641 ± 0.061) and total samples (1.449 ± 0.202) and lower than in males (3.48 ± 0.025). The model selected in C (S6) was sufficient to represent the growth pattern in *S. tiburo*.

To better characterize the growth of sharks, it is always recommended to use more than one growth function [19]. This study fit 13 growth models to frequency data of lengths with relative ages of *S. tiburo*. Multimodel inference was not applied because the selected models already provided enough evidence to choose them ($w_i = 0.90$ or $\Delta_i < 2$) [18]. The VB1 model did not provide enough statistical support to be selected, and the values of its parameters were not congruent with the biological reality of the species. Five studies that have described the growth pattern of *S. tiburo*: four in the GM [30,31,38,47], which were all on the western side of the state of Florida; and one for the Atlantic Ocean (east of Florida) [32]. The studies on the growth of this species in the GM have not applied the multimodel approach; only the one on the Atlantic population did. The studies carried out in the GM have only fit the VB1 model, and the study in the Atlantic used the multimodel approach to fit the classic growth models, VB, Gompertz, and logistic, finding that the best–fitting models were the Gompertz in females and VB in males.

Models with more than three parameters show better fits in large samples (n > 100) [48]. This was corroborated in this study, where the sample size was 104 specimens, and the best fitting model was Soriano et al. [40] model S6 with four parameters, while in males and females separately, the selected models were also those of Soriano et al. [40], S6 and S4

with four and five parameters, respectively. That is, they also had the greatest number of parameters. In some situations, several models (e.g., Gompertz and logistic) provide more precision than others (Von Bertalanffy and Schnute) in the estimation of the parameters in small samples ($n \le 100$) [48].

There is mounting evidence of biphasic growth in some species of sharks and rays, a group of large and a group of small organisms [17,49–51]. Braccini et al. [49] studied the growth pattern of the shark Squalus megalops in southeastern Australia by fitting five models whose base models were VB and Gompertz. In VB, the number of parameters 2 and 3 varied, and the second VB variant of the model of Soriano et al. [40] in its original version was applied (that is, without the recommendation of Cailliet et al. [19] to replace L_0 by t₀). The outcome was a choice of models and not a multimodel inference, favoring the model mentioned by Soriano et al. [40], both for females ($w_i = 0.54$) and for males ($w_i = 95$) because no model presented a value of $\Delta_i < 2$. Mejía–Falla et al. [51] fit 10 monophasic and one biphasic growth model [40], using the model's own variants and with different L₀ values, to the age and size data of the round ray *Urotrygon rogersi*, which inhabits the Pacific coast of Colombia. In females and males, the model selected was the two-phase model of Soriano et al. [40]; in females it was variant 2 with five parameters, and in males it was the same model but with 4 parameters, where L_0 was included according to Cailliet et al. [19] and its value was obtained from the literature. Biphasic growth in bony fishes has also been recently revealed. Aversa et al. [52] investigated the Argentine hake (Merluccius *hubbsi*) fishery and evaluated growth by fitting three models: VB, Gompertz, and the two-phase model, variant 2 of the Soriano et al. [40]. Like Braccini et al. [49] in their study of the Squalus megalops shark in southeastern Australia, the result was a choice of models and not a multimodel inference, thanks to the strong evidence in favor of the model of Soriano et al. [40] ($w_i = 0.99$). In short, the studies on the growth pattern of elasmobranchs that have included the Soriano et al. [40] model among their set of candidate models have found that the observed data are better represented by this model than traditional models (Von Bertalanffy, Gompertz and Logistic).

The presence of these growth phases should be recognized by the models, but the models in use (VB, Gompertz, and logistic) usually do not record such growth phases (monophasic models) and tend to hide important ecological and evolutionary information [21]. This was the main hypothesis to be tested in this investigation in *S. tiburo:* the possible presence of two growth phases. In this study, seven single phase models (VB1, VB2, G1, G2, J, L1, and L2) and six biphasic models (all variants of [40]) with and without L_0 competed. The model selected in females and overall was variant 2 of Soriano et al. [40] with the modification of L_0 added by Caillet et al. [19], which was the one estimated with the Gompertz model and offered the best fit; in males, the model chosen was the same as in females but with the exception that L_0 was estimated by the model of Soriano et al. [40] in its variant 2. The hypothesis guiding the study was corroborated: *S. tiburo* does present two growth phases. The possible causes of these growth phases are (a) energy investment in the reproductive process [22,23], (b) changes in habitat, (c) changes in diet, and (d) stressful situations [21,24,25].

The values of the growth parameters of *S. tiburo* estimated in this study are within the range of those reported in the literature [8,9,29–32,47,53–56]. In our study, the values of L_{∞} for females (106.45 cm) and males (122.18) were within the range of values reported in the literature: 80.40–139.80 cm and 70.30–125.08 cm, respectively (Table 6). The reported overall value (L_{∞} = 128.58 cm) is slightly higher than that estimated in the study based on the Castillo–Géniz [8] data for Playa Bagdad, Tamaulipas (127.10 cm). In the literature in some cases, L_{∞} was not estimated, and for comparative purposes in this study, it was calculated using the empirical method of Froese and Binohlan [57] (Table 6). Our value of k for males (0.22) was within the range of values reported in the literature (0.21–0.69 year⁻¹) (Table 6), while those corresponding to females and overall were outside the estimated published limits (females = 0.16-0.37 year⁻¹ and total = 0.17-0.24 year⁻¹) (Table 6). Some

studies have not reported k values, so we estimated it for comparative purposes using the empirical method of Munro and Pauly [58] and Moreau et al. [59] (Table 6).

The parameter t_h , according to the literature, varies by the biological event to be represented, based on the species. In teleosts, as fit by Soriano et al. [40], this parameter corresponds to a change in diet, mainly from juvenile to adult, while Araya and Cubillos [17] point out that t_h represents the age of onset of gonadal maturity. These authors found a significant linear relationship ($r^2 = 0.6797$) between L_{th} and the size at gonadic maturity in sharks. Minte–Vera et al. [60] define the model of Soriano et al. [40] as that which includes two sequential VB model–type curves, whose point where the phases intersect corresponds to the beginning of reproductive maturity. In the case of the ray *Urotrygon rogersi*, this is not the case: Mejía–Falla et al. [51] fit the model of Soriano et al. [40] with the second variant of the VB curve to age and size data of *U. rogersi*, an endemic species of the Pacific coast of Colombia, indicating that t_h does not correspond to the size at reproductive maturity, but more likely to the size at fecundity.

In this study, t_h in females (1.64 years, equivalent to $L_{th} = 53.34$ cm) and both sexes (1.45 years, equivalent to $L_{th} = 64.31$ cm) would correspond more to the change in diet between the juvenile and adult stages, while in males (3.48 years, equivalent to $L_{th} = 81.35$ cm) it would correspond more to the size at the beginning of reproductive maturity. Kroetz et al. [61] point out that in this species, growth may decelerate because the organisms undergo a dietary change when transitioning from the juvenile phase to the adult phase; and Bethea et al. [62] managed to measure this change through the relative importance index (RII). They found that in the juvenile phase (1 year old), the dietary trend is to consume plant material (RII = 62.1), while the adult diet is composed mainly of crustaceans (RII = 73.1). As for reproductive maturity, the females matured between 85 and 90 cm and 80 and 85 cm in Tampa Bay and Florida Bay in the state of Florida [14], and in the GM, its size ranged from 77 to 91.2 cm [9,31,32,59]; in males, reproductive maturity occurs between 63.6 and 83 cm [31,32,59] in the GM; and in the overall population, Lombardi–Carlson [47] identified a reproductive maturity size of 77 cm over the combined areas of the state of Florida (northeast Florida, Tampa Bay, and Florida Bay) for the combined sexes. It is likely that this sexual dimorphism in the diet-change size and the reproductive—maturity size is because females (both juveniles and mature) inhabit estuarine waters, and males (juveniles and adults) mainly occur in coastal waters [63]. In this study, t_h occurred first in females (t_h = 1.64 years; L_{th} = 53.34 cm) and then in males ($t_h = 3.48$ years; $L_{th} = 81.35$ cm). Considering the reproductive-maturity size of females reported in the literature (80-90 cm) and assuming that in males the value of t_h (3.48 years; $L_{th} = 81.35$ cm) obtained in this study represents the size at reproductive maturity, the order of size at reproductive maturity in females and males that we found coincides with Araya and Cubillos [17], who identified such a pattern in seven of 10 analyzed shark species. The same was found by Cortés [64] studying S. tiburo off the coast of Florida, where females became reproductively mature at ages (2-3 years) older than males (2 years) off the coast of Florida. The point values of L₀ estimated in this study are similar to those recorded for the Bays of Florida in the western part and greater than those indicated for the Atlantic Ocean side of Florida, and for the coastal states of the GM (Veracruz, Tabasco, Campeche, and Yucatan) (Table 6). However, the point values and the ranges of values obtained in this study (females 37.56–47.70 cm, males 42.27–46.46 cm, total 46.43–46.48 cm) lie within the range of values reported by the literature for the GM (females 37.21-55.18, males 36.02-55.54) (Table 6). The values in Table 6 for the GM were not estimated directly by Lombardi–Carlson [47] but were calculated by Frazier et al. [32] for comparative purposes between the GM and the Atlantic Ocean and were established based on the furcal length. With the same algorithms derived by Frazier et al. [32], we converted L_0 values into total lengths (Table 6). The differences in the lengths of the offspring at birth (L_0) may be due mainly to environmental factors at the localities where the organisms live [65].

Author	Year	Place	Method -		L_∞			k			L ₀	
Autor	Icai	Thee	Method =	F	М	С	F	Μ	С	F	Μ	С
This study	2021	Tamaulipas (Mexico)	sfd	105.96	122.18	132.63	0.54	0.22	0.23	42.63	44.37	46.46
Palacios–Hernández et al. [51]	2020	Tabasco and		97.48 *	123.06 *		0.24 ***	0.21 ***				31.5
	2020	Campeche (Mexico)		124.07 *	125.08 *		0.21 ***	0.21 ***				33
García–Álvarez [50]	2014	Campeche (Mexico)	nmu	115.99 *	107.91 *		0.22 ***	0.23 ***				37.8
González de Acevedo [49]	2014	Atlantic coast	iiitu									30.2
Frazier et al. [19]	2014	East Coast of Florida (Atlantic Ocean)		128.02 **	97.59 **		0.18	0.29		38.77 **	37.57 **	
Hernández–Betancourt et al. [48]	2011	Yucatan (Mexico)				112.96 *			0.22 ***			40
Lombardi–Carlson [35]	2007	West Coast of Florida GM		89.40	70.30		0.28	0.54		52.31 **	52.55 **	
		North-West Florida	hs	139.80	100.70		0.18	0.35				
Lombardi–Carlson et al. [18]	2003	Tampa Bay		127.70	86.80		0.16	0.44				23.7
		Florida Bay		93.90	85.80		0.29	0.25				21.5
		Tamaulipas (Mexico)				127.10 *			0.20 ***			
		Veracruz (Mexico)				100.32 *			0.24 ***			
Castillo–Géniz [47]	2001	Tabasco (Mexico)				124.07 *			0.21 ***			35 - 40
		Campeche (Mexico)	nmu			124.58 *			0.21 ***			
		Yucatan (Mexico)				121.04 *			0.21 ***			
	1000	Southeastern Gulf of										
Márquez–Farías et al. [46]	1998	Mexico										30-35
Carlson and Parsons [17]	1997	North-West Florida		122.6	89.7		0.28	0.69				
		Tampa Bay	hs	115	88.8		0.34	0.58				34.7
Parsons [25]	1993b	Florida Bay		103.3	81.5		0.37	0.53				27.2

Table 6. Growth parameters (L_{∞} , k, and L_0) of the bonnethead shark *Sphyrna tiburo* reported in the literature.

* These are values estimated from the conversion of maximum length (L_{max}) to L_{∞} using the following algorithm: $LogL_{\infty} = 0.044 + 0.9841 * log (<math>L_{max}$) (n = 551; $r^2 = 0.959$) [52]. ** These are values estimated from the conversion of furcal length (FL) into total length (TL) using the following algorithm: TL = 1.198 (FL) +39.1 ($r^2 = 0.994$; n = 2747) [19]. *** Values estimated from converting L_{∞} using the following algorithm: k = 5.4 (L_{∞}) -0.6811 [21,22]. Method = method of obtaining the age groups; sfd = size frequency distribution; hs = hard structures; nmu = no method used.

Our findings have important implications. The main contribution of this study is the confirmation of the hypothesis of the biphasic growth pattern of the *S. tiburo* stock located in the west GM. Now the challenge is to corroborate this hypothesis in the rest of the stock throughout the entire GM. To do this, it is advisable to fit two—phase growth models to the average age and size data reported in the literature for the coasts of Florida [30–32,38] and to include biphasic models in the sets of candidate models for future investigations on the growth pattern of this species in the southeastern GM. In this way, the hypothesis that this species follows a growth pattern that has no oscillations but rather is isometric and continuous over all ages (VB1 model) in all areas of the GM would be indirectly tested.

Choosing only the VB1 model a priori brings the risk of underestimating or overestimating parameters, ignoring the uncertainty associated with model selection and losing the advantages of fitting the data to a parsimonious model [66]. If this research had been carried out in the traditional way, where only the VB1 model is chosen a priori, biased results would have been obtained. An example is the estimation of longevity with the Fabens [67] model specific to sharks [(5(ln2))k⁻¹]. Using the values of k (0.54 year⁻¹) obtained by the VB1 model in this study would have resulted in a longevity of 6.42 years, while using the value of k (0.23 year⁻¹) estimated by the S6 model for both sexes in this work resulted in a longevity of 15.36 years, which is less biased than the values reported by the literature (12 years) [13].

Carefully estimating L_{∞} and k is essential to accurately assessing parameters and the fishing management reference points of any stock. One of the core parameters in any fisheries assessment is natural mortality, and in the literature many methods are reported to estimate it, several of which require the parameters L_{∞} and k, among others. Kenchington [68] indicated 17 methods of estimating mortality in fishes in general that require the value of the parameter k, while Zhou et al. [69] indicated nine methods that use mortality and one that uses k directly to estimate biological reference points in teleosts and chondrichthyans.

This study confirms the latitudinal variation pattern of the maximum lengths (L_{max}) observed and the values of the growth parameters (L_{∞} and k) of *S. tiburo*, proposed by Lombardi–Carlson et al. [31]. The values of L_{max} , L_{∞} , and k estimated in this study for females (98 cm, 105.6 cm, and 0.54 year⁻¹, respectively) and males (94 cm, 122.18 cm, and 0.22 year⁻¹, respectively) are closer to those provided by Lombardi–Carlson et al. [31] for Florida Bay, which is the southernmost part of Florida (females 100 cm, 93.9 ± 58, and 0.29 ± 0.09 year⁻¹, respectively; males 85 cm, 85.8 ± 9.2, and 0.25 ± 0.12 year⁻¹), than for those reported from the Tampa Bay and northwest Florida. Florida Bay is geographically located at ~24°50′ N, while the study area of this paper is the coast of the municipalities of San Fernando and Soto La Marina in the state of Tamaulipas, Mexico, located at ~24°50′ N and ~23°78′ N, respectively. Tampa Bay and the northwest region of Florida are located at 28°10′ N and 29°40′ N, respectively.

Small samples are common in *S. tiburo* growth studies ($n \approx 100$). In growth research of *S. tiburo*, small samples are often obtained from both commercial fishing and scientific sampling. Parsons [29], in his study from July 1982 to December 1986, obtained samples of 144 (females = 96, males = 48) and 99 individuals (females = 45, males = 44) from Tampa Bay and Florida Bay, respectively; in northeastern Florida (San Andrés Bay System and an arm of the sea in San Andrés) Carlson and Parsons [30] observed 115 individuals (females = 65, males = 50) in the period from October 1992 to October 1995; and Lombardi–Carlson [47] from March 1998 to September 2000 obtained samples from 191 individuals (females = 99, males = 92) in northeast Florida, 164 individuals in Tampa Bay (females = 77, males = 84), and 145 organisms in Florida Bay (females = 76, males = 69). Castillo–Géniz [8], in a study aiming to determine the size structure of the species in Playa Bagdad, Tamaulipas, collected only 73 individuals over 12 consecutive months. This author reported that this species represents 14.66% of commercial fisheries in the GM and 0.71% in Playa Bagdad in the Municipality of Matamoros, Tamaulipas, leading to the suggestion that this species' low contribution to local fisheries production prevented them from estimating the catch per

unit effort. In this study, the sample size was 104 individuals collected discontinuously from September 2016 to April 2019 for reasons related to the abundance of the species.

5. Conclusions

In this study, the hypothesis of two phase growth of *S. tiburo* is confirmed for the first time, and the hypothesis of continuous growth (VB models) traditionally reported by the literature is discarded. In particular, this species grows through the increase in the growth rate as a function of age, rather than the infinite length, adjusting for length at birth. The VB1 model did not have any supporting evidence of fitting the data observed in the three datasets (females, males, and total), while the evidence supporting the model of Soriano et al. [27] (two-phase) was so strong (w_i = 100%) that it was not necessary to apply the MMI to any of the three datasets.

Taking the traditional approach of choosing VB1 a priori in this study would have yielded biased results, probably reflected as overestimated k values, which in turn would have led to an underestimation of longevity compared to what was obtained in this study and to that reported by the literature. The TL where the two growth phases overlap in females and both sexes is highly similar to the TL described by the scientific literature, where a dietary change occurs between the juvenile and adult stages, while in males this transition coincides more with the TLs reported by other studies, when reproductive maturity begins.

Now the challenge is to corroborate this hypothesis of two phase growth in the entire fishing stock of *S. tiburo* throughout the GM, mainly in southeastern Mexico and on both coasts of Florida, with published data and future data, and to verify this finding in the stocks of the rest of the small coastal sharks of the GM.

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