



ORIGINAL ARTICLE

Age and growth of the sailfish *Istiophorus platypterus* (Istiophoridae) in the Gulf of Tehuantepec, Mexico

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Abstract

We analysed the recreational-dependent and the commercial fishery data of *Istiophorus platypterus* from the Gulf of Tehuantepec, Mexico. We estimated the age and growth of sailfish in our study based on growth rings in the cross-sections of the fourth dorsal fin spine. We sampled 4976 individuals, with length and weight data collected from 2000 to 2008. We analysed the ages of 535 sailfish, with their individual growth estimated by using two models. The first was the Schnute generalized-growth model and the second was the von Bertalanffy growth function. The parameters in each model and their confidence intervals (CI) were computed. The best candidate model was selected using Akaike's information criterion. We found the growth curve for sailfish from the Gulf of Tehuantepec is based on the three-parameter model rather than the generalized Schnute model. The parameters estimated and confidence intervals were (1) mean asymptotic eye-fork length = 180.6 cm (CI = 176–186 cm), (2) Brody growth coefficient = 0.36 (CI = 0.34–0.39), and (3) hypothetical age at length zero = –0.24 (CI = –0.30 to –0.18). Consequently, we believe that the von Bertalanffy growth function adequately described the individual mean growth for this species in the region.

Key words: Ageing, AIC, fin spines, *Istiophorus platypterus*, sailfish

Introduction

The sailfish is a member of the family Istiophoridae and is highly regarded by the recreational fishery industry for its spectacular game-fish characteristics. Its distribution is in tropical and subtropical waters and it inhabits the pelagic realm of the Pacific and Indian Ocean (Nakamura 1985). The species *Istiophorus platypterus* (Shaw & Nodder, 1792) is part of the well-known sport fishery in the Mexican Pacific. The Mexican government allows sailfish to be taken with sport fishing gear only. The legal protocol for this is the National Fisheries Chart (Álvarez-Torres et al. 2002), which seeks to avoid the overexploitation of this species in the Mexican Pacific. The federal government controls the number of licences and limits the catch to one billfish (marlin, sailfish, spearfish, or swordfish) per boat per day. The main

fishing grounds for sailfish are along the coast of Colima and Sinaloa, although the species is also distributed along the coast of Jalisco, Nayarit, Baja California Sur, Guerrero, Oaxaca, and Chiapas (Figure 1). According to the National Fisheries Chart, the catch-per-unit effort (CPUE) in the central and south Mexican Pacific declined from 2.7 sailfish/fishing day in 1957 to 0.5 sailfish/fishing day in 1999. The area with highest CPUE is in waters off Colima. Presently, there are no biological reference points indicating the level of fishing mortality or the biomass; consequently the status of the stock of the sailfish sport fishery off Sinaloa and Colima is assumed at risk (DOF 2000).

For successful fishery management, elements of reproduction, recruitment, age, and growth must be understood. For sailfish in the Mexican Pacific, the reproductive period is in summer and autumn

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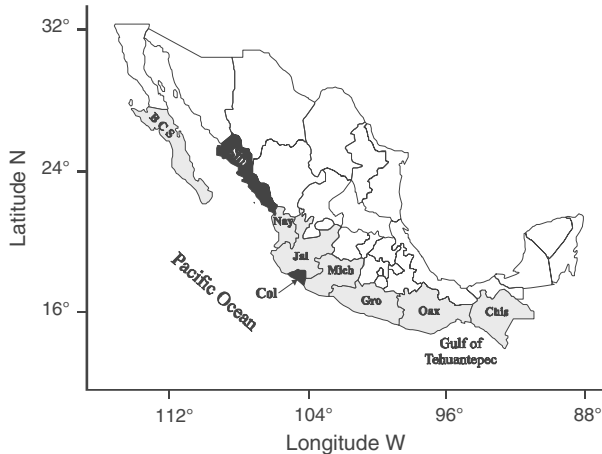


Figure 1. Study zone in the Gulf of Tehuantepec, Mexico. The dark areas of the figure show the coast of the Mexican states with the main fishing grounds off Colima (Col) and Sinaloa (Sin). In grey, the coast of the Mexican states where *Istiophorus platypterus* is commonly distributed; Baja California Sur (BCS), Nayarit (Nay), Jalisco (Jal), Michoacán (Mich), Guerrero (Gro), Oaxaca (Oax), and Chiapas (Chis).

when the sea surface temperature is between 27 and 30°C (Hernández & Ramírez 1998). The available data for *I. platypterus* are often biased because the information is obtained from the sport fishery in the central Mexican Pacific, where only the largest individuals are targeted. Thus, crucial biological information on smaller individuals of the population is often lacking. The models only describe the population dynamics of the adult individuals (Alvarado-Castillo & Felix-Uraga 1998; Hernández & Ramírez 1998). Studies using the length frequency data, estimated age, and growth from the Atlantic sport-fishery data reported that sailfish grow rapidly over the first 4 years (De Silva 1957). Jolley (1977) and Hedgepeth & Jolley (1983) used dorsal fin spines to report eight age-classes of sailfish. In the Mexican Pacific, the sport-fishery-dependent data showed that the migration of *I. platypterus* in the region modifies the length structure of the population, with the length structure varying according to the season (Macías-Zamora et al. 2001; Alvarado-Castillo & Felix-Uraga 1996). In these studies the von Bertalanffy growth curve has been fitted using recreational-dependent fishery data, assuming normal distribution and unequal variances of the residuals per age class, with the results showing overestimation of the sizes of the younger individuals (Alvarado-Castillo & Felix-Uraga 1998; Macías-Zamora et al. 2001).

In our work we analysed the recreational-dependent and the commercial fishery data of *I. platypterus* from the Gulf of Tehuantepec, Oaxaca, Mexico (Figure 1). In our study, we had access to a broad length-structure of sailfish. Although the

National Fisheries Chart recommends the species be reserved for recreational fishery, there is an illegal catch of this species, principally due to the absence of surveillance in areas difficult to access. According to Uosaki & Bayliff (1999), the Gulf of Tehuantepec is a core area for sailfish distribution in the tropical Pacific. The ability to collect sailfish samples of different sizes and ages in the region allowed us to update biological information for this species in the southern zone of its Mexican Pacific distribution. The objectives of our study were to determine age, growth, and stock structure for sailfish from the southeastern Mexican Pacific.

Materials and methods

Sailfish *Istiophorus platypterus* ($n=4976$) were sampled from the commercial and recreational catch during 2000–2008 from five locations in the Gulf of Tehuantepec, Oaxaca, Mexico (Figure 1). For each fish the total body weight (TW) was measured to the nearest 0.1 kg and the eye-fork length (EFL) was measured to the nearest cm. To estimate the relationship between the eye-fork length and the body weight we used the power equation $TW = \alpha \times EFL^\beta$, where α is a coefficient related to the body form and β is an exponent indicating isometric growth when equal to 3 and allometric growth when significantly different from 3 (Esmacili & Ebrahimi 2006; Aguirre et al. 2008). The estimated value of β was analysed with Student's t -test (Zar 1999) to determine whether growth was isometric or allometric.

The ages of 535 sailfish were interpreted from the fourth dorsal fin spine. We used this calcified structure because it provides more precise age estimates and are easier to collect and process than the sagittal otoliths (Hill et al. 1989). In addition, the spines have been used extensively and successfully to age the swordfish *Xiphias gladius* (Ehrhardt 1992; Tserpes & Tsimenides 1995), sailfish *Istiophorus platypterus* (Alvarado-Castillo & Félix-Uraga 1996; Chiang et al. 2004), and black marlin *Makaira indica* (Speare 2003). The spines were cut to obtain a cross-section, each about 0.4 mm thick. The cross-sections were taken at a distance of one-half the length of the condyle base with a Buehler Isomet low-speed saw. The sections were submerged in water in a Petri dish and viewed with a stereoscopic microscope by transmitted light. The annuli were counted based on the recognition of paired opaque and translucent growth bands (Figure 2). According to Jolley (1977) and Chiang et al. (2004), the direct reading was based on the count of the annuli. An annual period was assumed for each adjoining pair of opaque and translucent bands. Alvarado-Castillo & Félix-Uraga

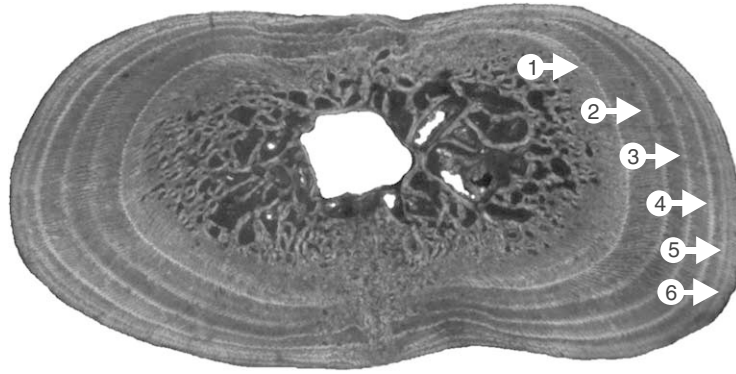


Figure 2. Cross-section of the fourth dorsal fin spine of *Istiophorus platypterus*. The translucent (arrows) and opaque bands are shown.

(1996, in the Gulf of California) and Chiang et al. (2004, in Taiwan) both reported that the presence of one opaque and one translucent band showing one year of growth. The spine sections were interpreted three times by one person; additional readings were made when some counts did not agree (Santamaria et al. 2009). The precision in the identification of ages was analysed with the coefficient of variance proposed by Chang (1982) as

$$CV_j = \frac{\sqrt{\frac{\sum (X_{ij} - X_j)^2}{R - 1}}}{X_j} 100\%, \quad (1)$$

where CV_j represents the variation coefficient to the j th fish, R is the number of times that the age was estimated for each fish, X_{ij} represents the i th estimation of age of the j th fish, and X_j is the mean value of the annulus of the j th fish.

Back-calculation of fish length

We selected younger individuals with at least four visible radii. The nucleus of the spine section to the outer edge and the distance between each growth ring were measured. The mean value and variance of each ring were estimated. Using these estimates we applied a final correction of age estimates for the rest of the spine samples, and assigned this to the spine samples that were missing early bands by comparing the radii of the first four bands to the mean and 95% confidence limits (Hill et al. 1989). Consequently, the correction of age estimates was made to coincide with the maximum number of length measurements for each age group, using the spine with the first annulus visible as a pattern. The number of empty cells was related to the number of missing rings, and thus it was possible to estimate the real age for each fish sampled (Freire et al. 1998).

To infer length at an earlier age from each fish, the distance from the nucleus of the spine section to the outer edge (R_T) and distance between each growth

ring (R_n) were measured in microns with the Image-Pro software, after calibration against an optical micrometer. This was done because the nucleus of the spine is reabsorbed in older individuals and the first annuli disappeared as the spine radius increases its length. Consequently, there is an underestimation of the age for older fish. The back-calculation allows for estimating the fish length in earlier life and thus estimate the correct age (Drew et al. 2006). Two approaches were used in this study. The first was that the relationship between the *EFL* at capture and R_T is linear, and the back-calculation function is (Fraser 1916; Lee 1920):

$$L_i = a + (L_c - a) \times \left(\frac{R_i}{R_T} \right), \quad (2)$$

where L_i = *EFL* at age i , L_c = *EFL* at capture, R_i = spine radius at age i , R_T = total radius, and a the L -intercept of the regression line $L_c = a + b \cdot R_T$.

The second approach was that the relationship between L_c and R_T is nonlinear, $L_i = c \times R_T^d$ in the back-calculation function is according to Monastyrsky (Bagenal & Tesch 1978)

$$L_i = \left(\frac{R_i}{R_T} \right)^d \times L_c. \quad (3)$$

To determine which equation best describes the relationship between the *EFL* at capture (L_c) and spine radius (R_T) we used the r^2 criterion.

Periodicity of growth increments

The marginal increment ratio (MIR) was used to validate the periodicity of growth increments in the spine (Chiang et al. 2004). The equation used was

$$MIR = \frac{(R_T - R_n)}{R_n - R_{n-1}}, \quad (4)$$

where R_T = spine total radius, R_n = radius of ring n , and R_{n-1} = radius of ring $n - 1$. The mean monthly MIR and its standard error were computed. When

those were minimum values we consider this as the formation time.

Growth function

The eye-fork to length-at-age data were fitted to the von Bertalanffy (1938) growth model

$$\hat{L}(t) = L_{\infty} [1 - \exp^{-K(t-t_0)}], \quad (5)$$

where L_{∞} is the mean asymptotic eye-fork length, t is age (years), t_0 is the hypothetical age at length 0, and k is the Brody growth coefficient (Ricker 1975; Chiang et al. 2004).

The sampling size distribution and age structure of the sailfish population are usually biased. This condition is commonly seen because the data are obtained from sport fishing, where the catch is reported for only the largest individuals. Consequently, the von Bertalanffy growth model is difficult to fit. An alternative is the Schnute (1981) growth model, a generalized growth model allowing parameter estimation in the absence of very young or old individuals. The model is:

$$L(t) = \left[l^{\rho} + (\delta^{\rho} - l^{\rho}) \frac{1 - \exp^{-\lambda(t-\tau_1)}}{1 - \exp^{-\lambda(\tau_2-\tau_1)}} \right]^{\frac{1}{\rho}}, \quad (6)$$

where l and δ are the sizes at time τ_1 and τ_2 observed in the biological samples of sailfish and are the younger and older individuals, λ is the constant of relative growth (equivalent to k in the von Bertalanffy model), and ρ is the rate of relative growth (Schnute 1981). The parameters to be estimated in the model are l , δ , λ , and ρ .

We assumed a multiplicative error in the estimation of $L(t)$ and the expression was $L_t = \hat{L}_t \exp^{\varepsilon_i}$, where $\varepsilon_i \sim N(0, \sigma^2)$. The θ parameters in the von Bertalanffy model were L_{∞} , t_0 , and k (Equation (5)). For the Schnute model the θ parameters were l , δ , λ and ρ (Equation (6)). The parameters were estimated by minimizing the negative log-likelihood estimator (Hilborn & Mangel 1997) with the Newton algorithm (Neter et al. 1996).

$$-\ln L(\theta|data) = \sum_i \left[-\frac{1}{2} \ln(2\pi) \right] - \left[\frac{1}{2} \ln(\sigma^2) - \left(\frac{\ln L(t) - \ln \hat{L}(t)^2}{2\sigma^2} \right) \right]. \quad (7)$$

For the standard deviation (σ) the analytical solution was proposed as

$$\sigma = \sqrt{\frac{1}{n} \sum_{i=1}^n [\ln L(t) - \ln \hat{L}(t)]}, \quad (8)$$

where n represents the number of ages observed in the sailfish samples.

For the Schnute growth function, when the parameters l , δ , λ and ρ were estimated, the estimation of L_{∞} and t_0 (defined by Schnute as τ_0) were from the equations (Schnute 1981)

$$\tau_0 = \tau_1 + \tau_2 - \frac{1}{\lambda} \ln \left[\frac{\exp^{\lambda \tau_2} \delta^{\rho} - \exp^{\lambda \tau_1} l^{\rho}}{\delta^{\rho} - l^{\rho}} \right] \quad (9)$$

and

$$L_{\infty} = \left[\frac{\exp^{\lambda \tau_2} \delta^{\rho} - \exp^{\lambda \tau_1} l^{\rho}}{\exp^{\lambda \tau_2} - \exp^{\lambda \tau_1}} \right]^{\frac{1}{\rho}}. \quad (10)$$

The solutions for Equations (9) and (10) assume that $\lambda \neq 0$, $\rho \neq 0$ (Schnute 1981).

Confidence intervals

To estimate the confidence intervals (CI) for the parameters in Equations (5) and (6), we used the likelihood-profile method (Venzon & Moolgavkar 1988; Hilborn & Mangel 1997) because it can be used to determine confidence intervals for the parameters either jointly or individually. The confidence intervals for the θ parameters were estimated based on the χ^2 distribution with m degrees of freedom (Zar 1999). The confidence interval was defined as all values of θ that satisfy the inequality

$$2[L(Y|\theta) - L(Y|\theta_{best})] < \chi_{1,1-\alpha}^2, \quad (11)$$

where $L(Y|\theta_{best})$ is the negative log-likelihood of the most likely value of θ and $\chi_{1,1-\alpha}^2$ are the values of the χ^2 distribution with 1 degree of freedom at a confidence level of $1 - \alpha$. Thus, the 95% confidence interval for θ encompasses all values of θ that are twice the difference between the negative log-likelihood and the negative log-likelihood of the best estimate of θ that is less than 3.84 for one parameter (Haddon 2001; Pawitan 2001). The likelihood profile shape was estimated for the θ_i that generates a negative log-likelihood equal to the maximum negative log-likelihood $L(Y|\theta_{best})$ minus half the required χ^2 value (3.84/2). The estimator is (Haddon 2001)

$$L(Y|\theta) = L(Y|\theta_{best}) - \frac{\chi_{1,1-\alpha}^2}{2}. \quad (12)$$

When considering more than one parameter, the confidence intervals become wider. This only occurs if there is any correlation (covariance) between parameters because if there were no parameter correlation then there would be no interference between the parameters and the confidence intervals would be unbiased (Haddon 2001). Welch & McFarlane (1990) explained that the von Bertalanffy growth model has the parameters correlated. An alternative solution is to compute the likelihood-based confidence region estimated from contours of

constant log-likelihood over the objective surface. This procedure was applied to the L_{∞} and k parameters jointly to avoid the problem of parameter correlation. In this case, Equation (11) must satisfy the inequality associated with the χ^2 distribution with 2 degrees of freedom, where the reference value is less than 5.99 for two parameters (Haddon 2001; Pawitan 2001). The values of 3.84 or 5.99 are obtained from statistical tables of χ^2 distribution (Zar 1999).

Akaike's information criterion

We solved two candidate growth-models with a different number of θ parameters. The comparison between candidate models was analysed with Akaike's information criterion (AIC). The smallest AIC is for the best model (Haddon 2001; Chiang et al. 2004). The von Bertalanffy and Schnute functions were analysed as:

$$AIC = (2 \times -\ln L) + (2 \times \theta), \quad (13)$$

where $-\ln L$ was the negative log-likelihood estimated in Equation (7) and θ is the number of parameters in each model.

Results

The eye-fork length frequency and total body-weight frequency distributions for the 4976 individuals are shown in Figure 3. The eye-fork length frequency distribution for 4976 individuals is 55–240 cm, mean = 159.8 cm, and standard deviation (s) = 13.4 cm. The weight frequency distribution, based on 3344 individuals, is 1.6–69.6 kg, mean = 27.9 kg, and s = 6 kg. The eye-fork length to body weight relationship was expressed as $TW = 5 \times 10^{-5} \times EFL^{2.6}$ ($r^2 = 0.7$, $P < 0.05$) (Figure 4). According to the Student's t -test, the β parameter was significantly different from 3 (t -test, $P < 0.05$), thus indicating allometric growth of *Istiophorus platypterus*.

From 535 spines sampled we could only successfully read 477 spines. The age estimation precision between readings varied by 11%, but a chi-squared test revealed no significant differences between them (χ^2 test, $P < 0.05$). The first four rings were visible in 79% of the spine samples. We corrected 21% of the spine samples adding a maximum of three missing rings. The corrected age groups and the mean and standard error of rings for each age group are in Figure 5. A maximum of nine age groups were estimated by direct reading. After the correction of missing rings, 11 age groups were evident in our analysis (Figure 6). The age-length key for *I. platypterus* is shown in Table I. Our samples showed that age-class 5 was the most abundant (32%),

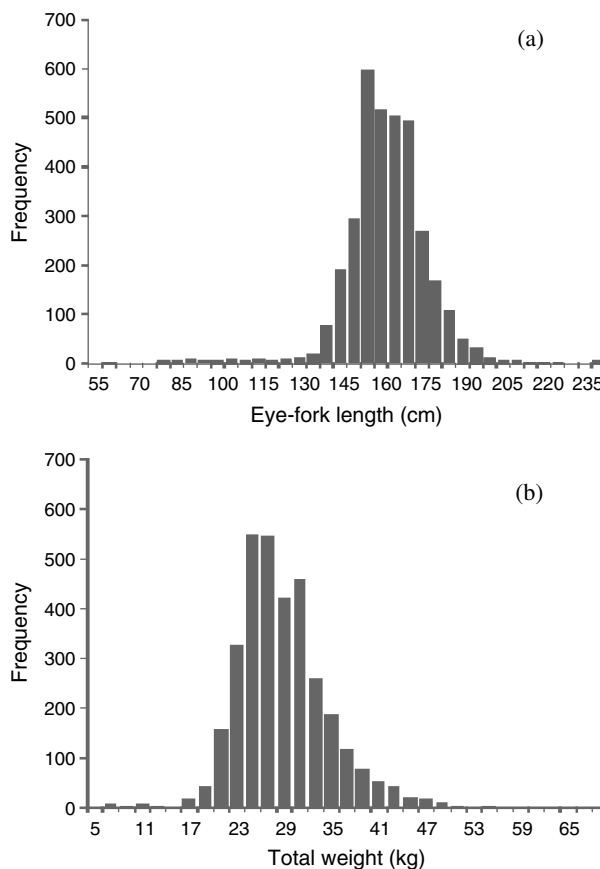


Figure 3. Eye-fork length-frequency distribution; $n=4976$ (a) and total body weight frequency distribution; $n=3344$ (b) of *Istiophorus platypterus* in the Gulf of Tehuantepec, Mexico.

followed by age-class 6 (24%) and age-class 4 (14%).

The relationships between the *EFL* and radius ring were analysed assuming a linear and power function. Figure 7 shows the models fitted to the data. According to the r^2 criterion the better fit was the power function expressed as $y = 47.6x^{0.81}$ ($r^2 = 0.82$, $P < 0.05$, $n = 480$), the linear function

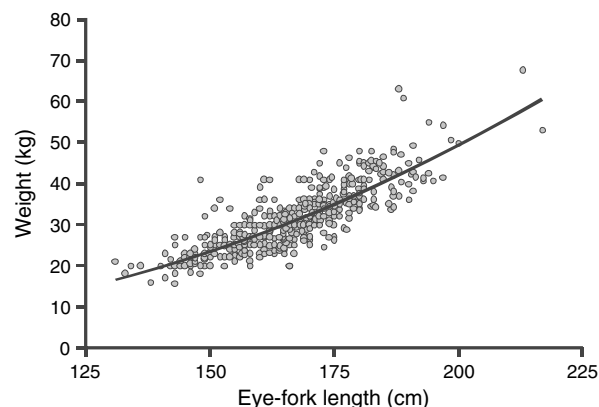


Figure 4. Total body weight and eye-fork length relationship for *Istiophorus platypterus* in the Gulf of Tehuantepec, Mexico.

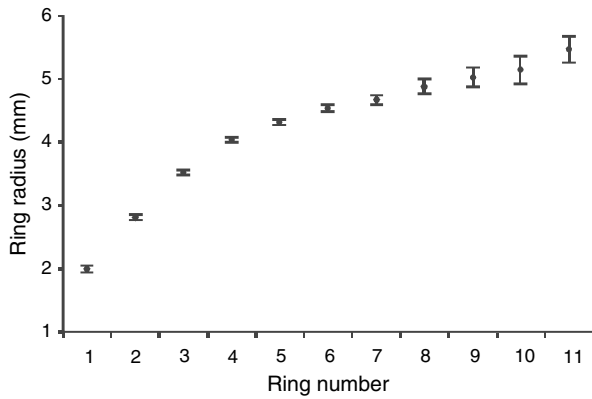


Figure 5. Number of growth rings and their ring radius for sailfish *Istiophorus platypterus* from the Gulf of Tehuantepec, Mexico. Means (\pm SE) are shown.

was $y = 25.5x + 43.9$, and it had a correlation of $r^2 = 0.76$ ($P < 0.05$, $n = 480$). For both functions the mean length-at-age from each relationship, linear or power, are shown in Table I. The comparison between the mean length-at-age showed a significant difference (t -test: $P < 0.05$). Consequently, we used the power function for back-calculation, because these values did not show overestimation of the mean length-at-age back-calculated in comparison with the linear function (Table II).

The monthly means of the marginal increment ratio were higher during March and August, with the mean value of the MIR during this time period was 0.64 (Figure 8). In this period, we did not estimate a significant difference among the MIR values (ANOVA: $P < 0.05$). After August the MIR declined with the MIR mean value of 0.45 from September to December (Figure 8). The ANOVA test did not show a significant difference during this period (ANOVA: $P < 0.05$). During January the species is not available in the zone and February shows the transition between formations of growth rings. From these estimates of the MIR we concluded that one

Table I. Age length key for *Istiophorus platypterus* from the Gulf of Tehuantepec, Mexico.

| EFL (cm) | Age group (year) | | | | | | | | | | |
|-------------|------------------|-----|-----|------|------|------|------|-----|-----|-----|-----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
| 80 | 1 | | | | | | | | | | |
| 85 | | 2 | | | | | | | | | |
| 90 | | | | | | | | | | | |
| 95 | | | | | | | | | | | |
| 100 | | | | | | | | | | | |
| 105 | | | | | | | | | | | |
| 110 | 1 | | | | | | | | | | |
| 115 | | 2 | | | | | | | | | |
| 120 | | 1 | 1 | | | | | | | | |
| 125 | | | | | | | | | | | |
| 130 | | | 2 | 1 | 1 | | | | | | |
| 135 | | | | 1 | 1 | | | | | | |
| 140 | | | 2 | 5 | 6 | 2 | | | | | |
| 145 | | | 4 | 2 | 9 | 7 | 2 | | | | |
| 150 | | | 1 | 7 | 12 | 9 | 5 | 1 | | 1 | |
| 155 | | | 3 | 10 | 27 | 10 | 7 | 2 | | 1 | |
| 160 | | | 1 | 18 | 30 | 11 | 4 | 3 | 3 | 1 | |
| 165 | | | 2 | 8 | 28 | 21 | 5 | 4 | 5 | | |
| 170 | | | | 3 | 28 | 23 | 18 | 4 | 3 | | |
| 175 | | | | 5 | 8 | 11 | 6 | 5 | 2 | | 2 |
| 180 | | | | 4 | 4 | 9 | 7 | 2 | 3 | 2 | 1 |
| 185 | | | | 2 | | 7 | 2 | 2 | 1 | 1 | 1 |
| 190 | | | | 1 | | | 2 | 2 | | | 1 |
| 195 | | | | | | | 3 | | | 1 | 1 |
| 200 | | | | | | | | | | 1 | |
| 205 | | | | | | | | | 1 | 1 | |
| 210 | | | | | | | | | | | |
| 215 | | | | | | | | | | 1 | |
| 220 | | | | | | | | | | | 1 |
| n | 2 | 5 | 16 | 67 | 154 | 115 | 58 | 26 | 21 | 6 | 7 |
| Percent (%) | 0.4 | 1.0 | 3.3 | 14.0 | 32.3 | 24.1 | 12.1 | 5.4 | 4.4 | 1.2 | 1.5 |

growth ring is formed annually. This occurs during September to December.

The value of the mean asymptotic eye-fork length had similar values and the same was estimated for the Brody growth coefficient. However, the value of the hypothetical age at length 0 was different between models. The Schnute growth model fitted

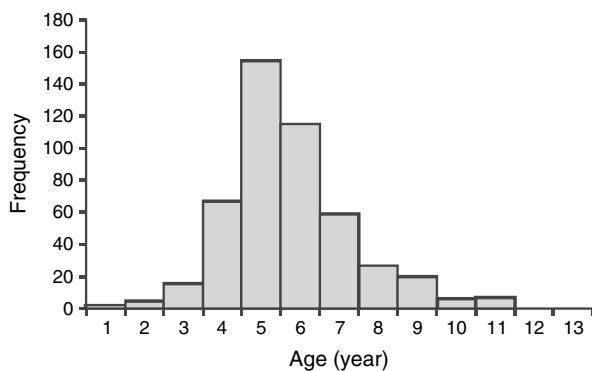


Figure 6. Age composition of *Istiophorus platypterus* in the Gulf of Tehuantepec, Mexico.

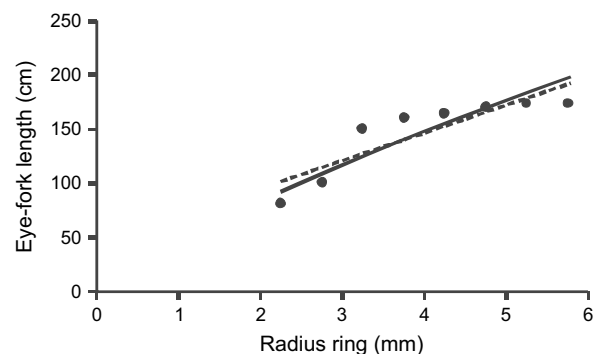


Figure 7. Linear (dashed line) and power (solid line) relationship between eye-fork length (cm) and spine radius (mm) of *Istiophorus platypterus* from the Gulf of Tehuantepec, Mexico.

Table II. Estimates of mean eye-fork length back-calculated for *Istiophorus platypterus* from the Gulf of Tehuantepec, Mexico.

| Age | Linear model (cm) | Power model (cm) |
|-----|-------------------|------------------|
| 1 | 88.5 | 65.1 |
| 2 | 124.8 | 102.8 |
| 3 | 148.3 | 125.4 |
| 4 | 167.3 | 142.4 |
| 5 | 176.0 | 151.8 |
| 6 | 187.8 | 161.3 |
| 7 | 194.4 | 164.8 |
| 8 | 199.0 | 168.7 |
| 9 | 206.5 | 172.8 |
| 10 | 212.4 | 173.8 |
| 11 | 223.9 | 187.5 |

to the data is shown in Figure 9 and the likelihood profiles of the θ parameters are in Figure 10. The values were $\iota = 65.1$ cm (CI = 63.2–67.2 cm, $P < 0.05$), $\delta = 180.5$ cm (CI = 178.5–182.6 cm, $P < 0.05$), $\lambda = 0.21$ (CI = 0.19–0.23, $P < 0.05$), $\rho = 2.14$ (CI = 1.97–2.32, $P < 0.05$). The negative log-likelihood was estimated as -29.93 . For the von Bertalanffy growth model the fitted data are shown in Figure 11. The joint confidence contour for L_∞ and k parameters are in Figure 12. The estimated values were $L_\infty = 180.6$ cm (CI = 176–186 cm, $P < 0.05$), $k = 0.36$ (CI = 0.34–0.39, $P < 0.05$), $t_0 = -0.24$ (CI = -0.30 to -0.18 , $P < 0.05$). The negative log-likelihood was estimated as -27.31 . The AIC = 60.62 showed the von Bertalanffy function to be the best candidate model, whereas Schnute growth model showed an AIC = 67.86.

Discussion

Our samples of sailfish included a wide range of eye-fork lengths (55–240 cm). The back-calculation was estimated using two models, defined as linear and power functions. We found that the power model

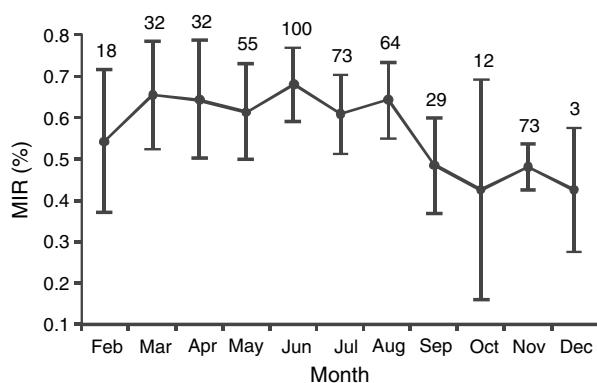


Figure 8. Monthly means of the marginal increment ratio (MIR) for the sailfish *Istiophorus platypterus* in the Gulf of Tehuantepec, Mexico. Vertical bars are $\pm 95\%$ confidence intervals, numbers above the vertical bars are sample sizes.

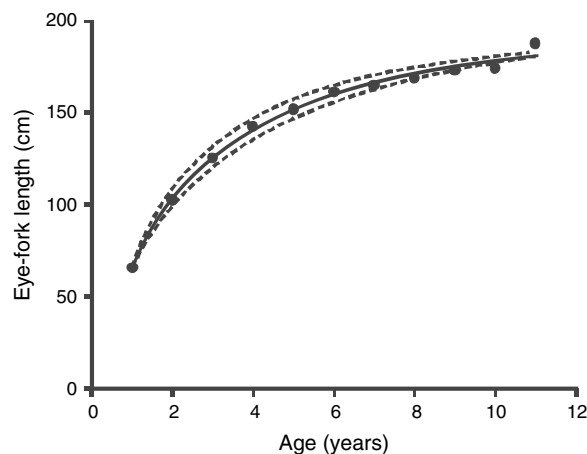


Figure 9. The Schnute growth model (solid line) fitted to eye-fork length (points) of *Istiophorus platypterus* in the Gulf of Tehuantepec, Mexico. The upper and lower dashed lines are $\pm 95\%$ confidence intervals.

was better than the linear model by using the r^2 criterion. This procedure allows us to correct the number of ages from the direct reading. With the ages corrected from 9 to 11 age groups, for both linear and power functions the mean length-at-age estimated were different. Ehrhardt (1992), analysing growth of *Xiphias gladius*, explained that the linear formulation proposed by Lee (1920) overestimates the back-calculated length at age in small individuals (ages 1 and 2), and simultaneously the linear model underestimates the back calculated length-at-ages 3–8 years (large individuals). Our estimates of the back calculated length at age showed an overestimation for all ages with the linear model. Tserpes & Tsimenides (1995) for *X. gladius* and Chiang et al. (2004) for *Istiophorus platypterus* also recommended the power model for the back-calculation. The back-calculation may avoid the problems associated with false rings and the presence of the vascularized core which can obscure the early growth rings in the larger fish.

The analysis of the marginal increment ratio showed two periods, the first from March to August, characterized by the higher MIR, and the second had a low increment from September to December. In the second period a new ring begins its formation; consequently the MIR analysis showed that one growth ring is formed annually for *I. platypterus*. Ehrhardt (1992) comments that if the rings seen on spine sections are valid indicators of age, then they should be formed over a short time, and at the same time every year. Chiang et al. (2004) showed for *I. platypterus* off Taiwan the minimum MIR values during September to November for males, and minimum MIR values during October–November for females. In the Gulf of California, Alvarado-Castillo & Félix-Uraga (1996) found an annual

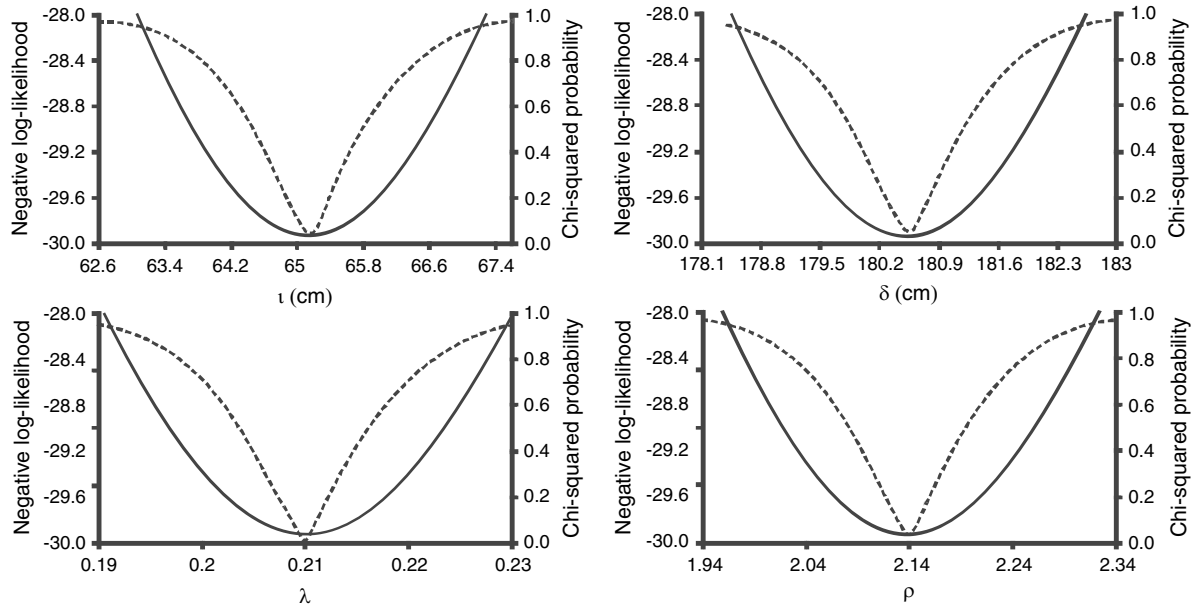


Figure 10. Likelihood profiles of parameters of t , δ , λ and ρ estimated for the Schnute growth model. The solid line represents the negative log-likelihood profile and the dashed line is the χ^2 probability.

pattern of growth for *I. platypterus*. They used a monthly analysis of the type of edge (opaque and hyaline) in the fourth dorsal fin spine. The annual growth was found during the summer months. Comparatively, we found a similar pattern of annuli formation for this species and confirmed the annual pattern in growth of *I. platypterus* in the Gulf of Tehuantepec.

We estimated 11 age-classes (1–11 years). Age-classes five and six were predominant in the samples. In the Mexican Pacific, Alvarado-Castillo & Félix-Uraga (1996) observed seven and Macías-Zamora et al. (2001) observed 10 age-classes, with age-classes three and four the most abundant. Chiang et al. (2004) found, in the waters off eastern Taiwan,

11 age-classes in males and 12 in females of *I. platypterus*. Freire et al. (1998) reported 10 age-classes for sailfish from off northeastern Brazil, whereas Prince et al. (1986) reported the estimated maximum age of Atlantic sailfish at 13–15 years based on a single mark-recapture fish.

We noted that *I. platypterus* showed a rapid growth, reaching 100 cm during the second age-class, which is more than 50% of the mean asymptotic eye-fork length. This pattern of growth has been documented in different areas (De Silva 1957; Jolley 1977; Hedgepeth & Jolley 1983; Chiang et al. 2004). Rapid growth may be an advantage adapted for predator avoidance. Our estimates of the mean asymptotic eye-fork length in the Gulf of Tehuantepec were $L_{\infty} = 190.6$ with the Schnute growth model, and $L_{\infty} = 180.6$ with the von Bertalanffy growth function. These values of the mean asymptotic eye-fork length

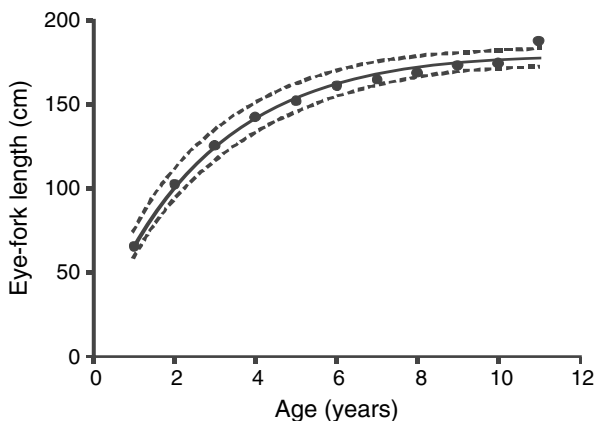


Figure 11. The von Bertalanffy growth model (solid line) fitted to eye-fork length (points) of *Istiophorus platypterus* in the Gulf of Tehuantepec, Mexico. The upper and lower dashed lines are \pm 95% confidence intervals.

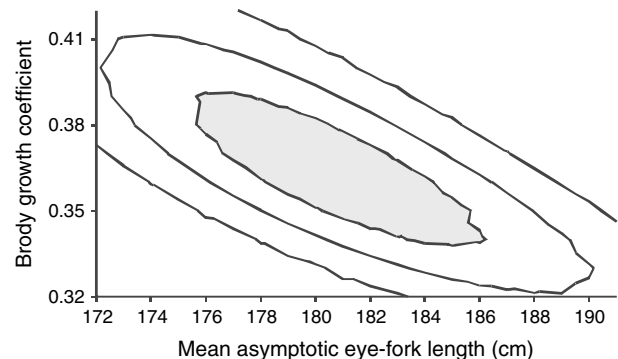


Figure 12. Negative log-likelihood contour for parameters L_{∞} and k , estimated from the von Bertalanffy growth model. The area in grey denotes joint confidence intervals (χ^2 test, $p < 0.05$).

were less than those estimated by Chiang et al. (2004) in the waters off Taiwan. They reported 257.3 cm for males and 289.9 for females using the lower-jaw fork length. The values for this variable from Arabian Gulf sailfish were 191 cm (females) and 160 cm (males) using the lower-jaw fork length (Hoolihan 2006). Freire et al. (2006) report a L_{∞} of 179.6 using the eye-keel length off northeastern Brazil.

In previous reports the uncertainties in the growth parameters of the *Istiophorus platypterus* were not estimated and the parameters themselves were estimated with an algorithm based on ordinary least squares (Hedgepeth & Jolley 1983; Alvarado-Castillo & Félix-Uraga 1998; Freire et al. 1998; Hoolihan 2006). Table III shows a comparison among growth models and parameters from different regions. Usually the main problem is that the data for age-classes are estimated using individuals caught by the sport fishery, where the targets are the older and larger individuals. The absence of the younger and smaller individuals does not yield the best fit of the growth model to the data. Consequently, alternative models must be solved to confront the models with data and adequately estimate the individual growth pattern (Richards 1959; Schnute 1981; Katsanevakis 2006). Chiang et al. (2004) estimated the growth of *I. platypterus* in waters off eastern Taiwan. They analysed the performance of the von Bertalanffy and Richards functions using a likelihood-ratio test. They found that the Richards model was better. The model fitted the observed data of the 0 age-class, and the theoretical growth curve showed that the general growth-model of Richards was more flexible when younger individuals were scarce in the biological samples.

In previous studies of individual growth, some general models have been used, such as the Chapman model (1961) applied to the swordfish *Xiphias gladius* (Ehrhardt 1992; Tserpes & Tseminides 1995), which is a general form model of the von Bertalanffy growth function (VB). The comparison between the Chapman and VB models did not show differences in the performance of the models based on the estimation of r^2 , which was reported by Tserpes & Tseminides (1995), and they recommended using the VB for growth for studies of *X. gladius*, because the Chapman model overestimated the asymptotic length. Ehrhardt (1992), analysing the individual growth of this species, recommended the Chapman model as the best in comparison with the VB. This conclusion was supported in over-estimations of expected values at younger and older ages, and underestimation for expected lengths at intermediate ages. Another general model applied to

Table III. Estimates of individual growth parameters for in different geographical zones. The table shows the growth model for females (♀) and males (♂), parameters and confidence intervals (CI) if these were reported, and the algorithm for the parameter estimation defined as the sum of squares (SSQ), In likelihood (ln L), or not reported (NR).

| Site | n | Model | L_{∞} | k | K | t_0 | m | IC | Algorithm | Reference |
|---------------------|-------|-----------------|--------------|------|-------|---------|-------|----------------|-----------|--|
| Florida | 310 ♀ | Von Bertalanffy | 183 | 0.15 | | -3.31 | | NR | SSQ | Hedgepeth & Jolley (1983) |
| Florida | 259 ♂ | Von Bertalanffy | 147 | 0.30 | | -1.95 | | NR | SSQ | Hedgepeth & Jolley (1983) |
| Gulf of California | 754 | Von Bertalanffy | 207.3 | 0.75 | | -0.0016 | | NR | SSQ | Alvarado-Castillo & Félix-Uraga (1998) |
| Brazil | 126 | Von Bertalanffy | 179.6 | 0.14 | | -1.24 | | NR | SSQ | Freire et al. (1998) |
| Mexican Pacific | 1216 | Von Bertalanffy | 177.16 | 2.97 | | -0.016 | | NR | SSQ | Macias-Zamora et al. (2001) |
| Taiwan | 436 ♀ | Richards | 343.8 | | 0.011 | -0.46 | -1.63 | Standard error | SSQ | Chiang et al. (2004) |
| Taiwan | 699 ♂ | Richards | 294 | | 0.023 | -0.70 | -1.28 | Standard error | SSQ | Chiang et al. (2004) |
| Arabian Gulf | 35 ♀ | Von Bertalanffy | 191 | 0.29 | | -4.31 | | NR | SSQ | Hoolihan (2006) |
| Arabian Gulf | 50 ♂ | Von Bertalanffy | 160 | 0.42 | | -4.92 | | NR | SSQ | Hoolihan (2006) |
| Gulf of Tehuantepec | 477 | Von Bertalanffy | 180.6 | 0.36 | | -0.24 | | Likelihood | -ln L | This study |
| Gulf of Tehuantepec | 477 | Schnute | 190.6 | 0.21 | | 0.49 | | Likelihood | -ln L | This study |

the sailfish *Istiophorus platypterus* is the Richards growth function (Richards 1959). This model was used by Chiang et al. (2004). They compared the Richards and VB models and concluded that the general model showed the best fit to the data of *I. platypterus* off Taiwan. The criterion for the selection model was the likelihood-ratio test. The advantages of the Richards model is that it contains the common form of the VB, with the VB allometric, VB isometric, including logistic, and Gompertz models as special cases.

In our study, the Schnute model showed near values of the negative log-likelihood in comparison with the VB model. Our results also showed that the VB function was the best candidate model. Given this result, we assumed that the age data are sufficiently informative to describe the growth pattern of *Istiophorus platypterus* according to the VB function. For the Schnute growth model (Schnute 1981) the general procedure is to begin by locating an optimum four-parameter model. Then one can inspect the parameter estimates for λ and ρ in the context of the general model. It may happen that the estimated curve lies close to a three-parameter (or even two-parameter) submodel. In this case, one might estimate the parameters for the submodel and compare them. The VB model is a special case of the Schnute model if the parameter $\rho = 1$; however, our estimation of this parameter showed that it is different from 1.

We compared the Schnute and VB models rather than any others because the Schnute model shows a differential equation forming eight different curve patterns depending on the parameter values. The advantage of the Schnute model is that the Richards growth curve is a special case within the alternative solutions. The Schnute model is a general four-parameter growth model that contains most of the preceding growth models as special cases. Rather than modelling the instantaneous rate of change, Schnute concentrates on the relative rate of change. Additionally, Schnute showed a parameterization approach that is statistically stable. The convergence of the nonlinear least squares can be successful when other parameterizations failed to converge. As two of the four parameters in Schnute's model are expected value parameters (t , δ), one would expect a greater stability than for either the VB allometric or Richards parameterizations (Quinn & Deriso 1999).

The confrontation among candidate models, data, and the criteria of selection for the best model is the main source of uncertainty. In the study of fish growth some criteria as r^2 (Tserpes & Tseminides 1995), the likelihood-ratio test for nested models (Hilborn & Mangel 1997; Chiang et al. 2004), and Akaike's information criterion (AIC) (Akaike 1973) have been used. The model

selection based on information theory has been recommended as a better and more robust alternative than traditional approaches to hypothesis testing or inference from the r^2 values (Burnham & Anderson 2002; Katsanevakis 2006; Katsanevakis & Maravelias 2008). Additionally, the best fit of the models to the data depend on the objective function. It can be residual sum squares, likelihood, or log-likelihood. Katsanevakis (2006) and Katsanevakis & Maravelias (2008) used a multi-model inference to model selection for the study of fish growth. The criterion was the AIC where the objective function was the residual sum squares. The advantage of this approach is that the models are hierarchically ordered considering the fit to the data, and the parameters of the candidate models may be averaged. For this procedure it is necessary to estimate the weighted average from the estimation of the Akaike weights (Burnham & Anderson 2002). In our study we compared only two candidate models (VB and Schnute). The comparison with a multimodel inference was not used in this study, but the model selection was based on the AIC criterion. Thus the model selection was based on the principle of parsimony according to Akaike's information criterion, with the best candidate model the VB.

Conclusions

We assumed that the frequency of young and old individuals in the biological samples was sufficient to avoid a failure in the iterative procedure, where the consequences are either overestimation or underestimation in the growth parameters. The Schnute model is a general growth model similar to Richard's model and its parameters are statistically stable and have a biological interpretation (Schnute 1981). However, in our study the von Bertalanffy growth function was the best candidate. We analysed a broad size-range for *Istiophorus platypterus* in the Gulf of Tehuantepec, Mexico and compared two candidate growth models. Their performances were measured with Akaike's information criterion and we found that the growth curve for this species is based on the three-parameter model rather than generalized Schnute model. Consequently, we believe that the von Bertalanffy growth function adequately describes the individual growth for this species in the region.

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