



Age, growth and demography of the silky shark *Carcharhinus falciformis* from the southwestern Atlantic

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ABSTRACT: The silky shark *Carcharhinus falciformis* is considered one of the least productive pelagic shark species. The estimation of growth and demographic parameters presented here is fundamental to a sound knowledge of population status of the species in the Atlantic Ocean. Data was collected through an onboard observer program of the Brazilian chartered pelagic longline fishing fleet that operates in the Equatorial Southwestern Atlantic. Vertebral analysis produced the von Bertalanffy growth parameters for pooled sexes $L_{\infty} = 283.05$ cm; $k = 0.0987$ yr⁻¹ and $t_0 = -3.47$ yr. Males reached sexual maturity at 8.6 yr and females at 9.9 yr. Longevity was estimated at 27.2 yr. Age structure analysis indicated that 80.5% of the catch was composed of juveniles, with recruitment to the fishery from the first year of life (age 1+). These biological parameters are responsible for the species' low resistance to fishing pressure, and our demographic analysis (Leslie Matrix) shows an annual population decline of 12.7% yr⁻¹ under the current fishing scenario for the period analyzed. Therefore, conservation measures must be enacted to reestablish the population of silky sharks to safe levels for the maintenance of this species in the South Atlantic.

KEY WORDS: Conservation · Life history · Fisheries · Population dynamics · Chondrichthyes

1. INTRODUCTION

The silky shark *Carcharhinus falciformis* is an epipelagic species captured in both coastal and oceanic waters of tropical regions. It is more frequently found near oceanic sea mounts and islands at maximum depths of 500 m (Compagno et al. 2005, Bonfil 2008, Ebert et al. 2013). In the western Atlantic Ocean, it is distributed from Massachusetts (USA) to southern Brazil, including the Gulf of Mexico, Caribbean Sea, and Saint Peter and Saint Paul Archipelago (Rigby et al. 2017).

Ecological risk assessments have indicated that *C. falciformis* is the most vulnerable species to overexploitation among the Atlantic Ocean pelagic elasmobranchs (Cortés et al. 2010), and it is currently among the least productive stocks (Cortés et al. 2015). Although the incidental catch of *C. falciformis* in several important fisheries is well known (Rice & Harley 2013, Oliver et al. 2015, Barreto et al. 2016a), the current population status and the effect of these fisheries on the species are still unclear. In a study carried out with pelagic longlines in the Atlantic Ocean, *C. falciformis* represented less than 1% of the total of elas-

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mobranch species by number of individuals, with a catch per unit effort of less than 1 individual per 1000 hooks (Coelho et al. 2012). According to fishing logbooks of longline vessels, *C. falciformis* represented only about 3% of all sharks caught in the South Atlantic between 1979 and 2011 (Barreto et al. 2016a).

An abundance analysis of *C. falciformis* in the Atlantic Ocean indicated declines of 91% in the Gulf of Mexico between 1950 and 1990 (Baum & Myers 2004) and 50% in the central west portion of the North Atlantic (western North Atlantic) between 1992 and 2005 (Cortés et al. 2007). Recently, an analysis of pelagic shark catch rates in the South Atlantic between 1979 and 2011 indicated capture declines of 61 and 90% for *C. falciformis* in different exploration phases, aside from the 96% decline reported for the 'grey sharks' category (Barreto et al. 2016a), which includes *C. falciformis* among other carcharhinids (Hazin et al. 1990, Barreto et al. 2016a). An analysis of the 'grey shark' category conducted by Baum & Blanchard (2010) between 1992 and 2005 in the Northern Atlantic revealed a 76% decline (Baum & Blanchard 2010).

Life history aspects of *C. falciformis* have been evaluated in all oceans. A large number of studies have reported the species' age and growth (Branstetter 1987a, Bonfil et al. 1993, Oshitani et al. 2003, Joung et al. 2008, Sánchez-de Ita et al. 2011, Hall et al. 2012, Grant et al. 2018), but these parameters are quite variable between regions (Grant et al. 2020). In the West Atlantic, Domingues et al. (2018) detected significant differences in population structure between the Northwest and Southwest Atlantic. In the Northern Atlantic, reproductive and growth parameters were investigated by Branstetter (1987a) and Bonfil et al. (1993), while Hazin et al. (2007) and Lana (2012) analyzed reproductive aspects in the Equatorial Atlantic. However, age and growth information from the South Atlantic remain unavailable. Such parameters are of great importance for population dynamics and demography. In this sense, growth and maturity parameters that are key for the calculation of growth and mortality rates, longevity, and age of maturity (Cailliet & Goldman 2004, Cailliet et al. 2006, Goldman et al. 2012) are also important for the stock evaluations that are used by different agencies involved in fishing management and conservation (Barreto et al. 2016b). Therefore, accurate estimates of growth parameters are crucial for stock assessments and, consequently, sustainable management.

Demographic analysis is increasingly being used to evaluate the susceptibility to fisheries and recovery potential of species with scarce catch data, as is the

case with most sharks (Cortés 2002a, Simpfendorfer 2005). In this kind of analysis, susceptibility to over-exploitation and recovery potential are directly correlated with life history parameters (Hutchings 2002, Frisk et al. 2005, García et al. 2008). The methods used in demography allow for estimation of rates of population increase and recovery potential, in addition to providing a better understanding of when and how species are most vulnerable to changes in their vital rates, such as through fishing mortality (F) (Galagher et al. 2012).

In the Atlantic Ocean, the National Marine Fisheries Service (NMFS) implemented a recommendation from the International Commission for the Conservation of Atlantic Tuna (ICCAT) prohibiting the retention, transshipment, and landing of *C. falciformis* (ICCAT 2011). Although this restriction is not currently in place, following this recommendation in 2014 the capture of *C. falciformis* was prohibited in Brazilian waters (Brasil 2014). Currently, *C. falciformis* is classified as Vulnerable (VU) globally, with a trend of population decline (Rigby et al. 2017).

The present study aimed to evaluate whether *C. falciformis* fisheries can be sustainable in the southwestern Atlantic through examination of demographic parameters and respective responses in terms of population growth rates under different fishing scenarios and growth parameters estimated through multi-model inference.

2. MATERIALS AND METHODS

2.1. Sampling

Onboard observers sampled *Carcharhinus falciformis* specimens caught by the Brazilian pelagic longline of the chartered fishing fleet from Spain, Panama, Honduras, Morocco, Portugal, and the UK fishing off northeastern Brazil between 2004 and 2011. This fleet operated in the Atlantic between 10 and 35° W and 5° N to 30° S, and fishing logbooks were filled between 2004 and 2010.

From each specimen, sex and total length (TL, cm) were recorded. When TL was not available, fork length (FL, cm), pre-caudal length (PCL, cm), and inter-dorsal distance (ID, cm) were converted to TL through existing relationships (Bonfil et al. 1993, Joung et al. 2008). Thus, when we refer to length throughout the study, we are referring to TL. From some specimens ($n = 106$) caught by this fleet, a block of 5 vertebrae was retrieved from below the first dorsal fin for aging analysis. Furthermore, lengths ($n =$

553) from the fishing logbooks of this fleet were also used to convert *C. falciformis* sizes to age in order to establish the age structure of sampled individuals.

2.2. Age and growth

After removal of excess tissue, vertebrae were fixed in 4% formaldehyde for 24 h and preserved in 70% ethanol (Gruber & Stout 1983). Subsequently, one of the vertebrae was embedded in polyester resin and sectioned using a low-speed diamond saw. A 0.3 mm thick longitudinal section was taken through the focus of each vertebra. Following standard protocols (i.e. Cailliet et al. 2006), 2 types of growth bands were examined in the section: one larger translucent band and another narrow opaque band, which together make a band pair that can be considered a growth band.

Band pair counts were carried out under a stereoscopic microscope using magnification (1 micrometric unit = 1 mm) and reflected light. Band pairs were counted and the distances from the focus of the vertebra to the outer margin of each band pair and to the vertebrae edge were measured with a micrometric ocular lens (Cailliet et al. 1983). The relationships between vertebrae radius and TL were calculated for each sex separately and compared using ANCOVA ($\alpha = 0.05$).

The index of average percentage error (IAPE) (Beamish & Fournier 1981) was calculated to compare the reproducibility of the reads between readers:

$$\text{IAPE} = \frac{1}{N} \sum_{j=1}^R \frac{1}{R} \left[\sum_{i=1}^R \left(\frac{|X_{ij} - X_j|}{X_j} \right) \right] 100 \quad (1)$$

where N is the number of vertebrae, R is the number of readings for the same individuals, X_{ij} . When the estimated IAPE of an age group was greater than 10%, a third reading was carried out seeking consensus.

To evaluate the formation periodicity of age groups, a marginal increment ratio (MIR) analysis was performed (Natanson et al. 1995) to estimate the period in which a new band pair starts to be formed:

$$\text{MIR} = \frac{\text{VR} - R_n}{R_n - R_{n-1}} \quad (2)$$

where VR is the vertebral radius, R_n is the radius of the ultimate band pair formed, and R_{n-1} is the radius of the penultimate band pair formed.

Significant differences between months were analyzed with the Kruskal-Wallis test and a post hoc Dunn test (Sokal & Rohlf 1995), with a significance level of 0.05.

Since the first growth band radius after the birth-mark is, for most individuals, smaller than the radius between the first and second bands, as suggested by Harry et al. (2010), we assumed an average age of 6 mo for the first band pair and that the following band pairs were formed 1 yr after the previous band pair.

We employed the maximum likelihood that uses a chi-square distribution for comparing growth curves between sexes, as proposed by Kimura (1980).

Specimen lengths were back-calculated to the last age through measurements between the vertebrae focus and each translucent band for each individual, using the Fraser-Lee equation (Francis 1990). This was done regardless of the observed lengths, as back-calculated lengths improved model adjustment, and as estimated birth size is closer to the observed birth size of *C. falciformis* in this region:

$$\text{TL} = \left(\frac{R_t}{\text{VR}} \right) (L_c - a) + a \quad (3)$$

where TL is the specimen length when band pair t was formed, R_t is the distance between the vertebrae focus and each band pair at age t , L_c is the specimen length at the moment of capture, and a is the linear coefficient of $\text{VR} \times \text{TL}$.

A multimodel inference using Akaike's information criterion (AIC; Burnham & Anderson 2002) was used to select the model that shows the best fit. Four models were selected *a priori* and applied to the back-calculated length-at-age data. The models chosen were the von Bertalanffy growth model (VBGM; von Bertalanffy 1938), von Bertalanffy growth model with birth size (VBGM-2; von Bertalanffy 1938), logistic (Schnute 1981), and Gompertz (Gompertz, 1825) (See Table S1 in the Supplement at www.int-res.com/articles/suppl/n045p237_supp.pdf). Model parameters were obtained using the Solver function of Microsoft Excel. The likelihood tool and the bootstrap iteration function of the PopTools software (Hood 2006) were used to generate confidence intervals for each parameter based on minimum likelihood. AIC (Akaike 1974) was evaluated as follows:

$$\text{AIC} = -2\log(\theta) + 2K \quad (4)$$

where Δ is the maximum likelihood and K is the number of parameters.

The model with the lowest AIC value (AIC, min) was selected as the most appropriate representation of the length-at-age data. Differences in AIC values (ΔAIC) were calculated for subsequent models as follows: ($\Delta\text{AIC}_i = \text{AIC}_i - \text{AIC, min}$), whereby a ΔAIC of 0–2 had the highest statistical support, ΔAIC of 4–7 had considerably less statistical support, and $\Delta\text{AIC} >$

10 had no statistical support (Burnham & Anderson 2002). Additionally, AIC weights (w_i) were calculated from AIC values, which described the probability of selecting the most suited model as follows:

$$w_i = \frac{e^{(-0.5\Delta_i)}}{\sum_{i=1}^n e^{(-0.5\Delta_i)}} \quad (5)$$

Through the model selected, the age at maturity was estimated from maturity lengths of 197.5 and 207.5 cm (Lana 2012) for males and females, respectively.

Longevity (ω) was estimated using the equation proposed by Ricker (1979) and suggested by Cailliet et al. (2006) for elasmobranchs:

$$t_x = \frac{1}{k} \ln\{(L_\infty - L_0) / [L_\infty(1 - 0.95)]\} \quad (6)$$

where t_x is the time in which the species reaches 95% of its L_∞ (L_∞ is theoretical maximum growth), k is the growth constant, and L_0 is size at birth.

2.3. Life history parameters

We used reproductive biology data for *C. falci-formis* obtained from the same area as the present study (Hazin et al. 2007, Lana 2012). Uterine fecundity ranged from 4–25 embryos (estimated fecundity average \pm SD: 11.7 ± 3.1 embryos female⁻¹), and an embryo sex ratio of 1.3 females for each male. A 2 yr reproductive cycle (one for gestation and the other for resting and starting a new cycle) was assumed in this analysis, which coincides with what was found for the species (Branstetter 1987a, Hoyos-Padilla et al. 2012, Galván-Tirado et al. 2015). Taking this data into account, we considered that the estimated average annual fecundity of female embryos for the pregnant female (m_x) was 3.3 ± 0.9 , and this value varied in accordance with normal distribution for stochastic analysis. This analysis also considered the age at first maturity (t_{mat}) and the maximum age estimated (t_{max}). We used discrete probability distributions of both ages as uncertainties in the stochastic analysis, with probability (p) of 0.50 for t_{mat} and t_{max} , $p = 0.25$ for 1 yr prior to t_{mat} and t_{max} , and $p = 0.25$ for 1 yr after t_{mat} and t_{max} .

2.4. Mortality and survival rates

We used several age-independent methods for the estimates of natural mortality rates (M) (see Table S2); all of these methods were used in stochastic analysis

from a discrete probability distribution with $p = 0.111$. We estimated the population age structure of lengths from fishing logbooks through the best-fitted model and parameters from this study. Subsequently, we estimated the total mortality rate (Z) through the catch curve method (Simpfendorfer et al. 2005). F and the exploitation rate (E) were obtained through $F = Z - M$ and $E = F / Z$, respectively (Sparre & Venema 1997, Simpfendorfer et al. 2005). Survival values (S) for each mortality rate were obtained through the formula by Ricker (1975):

$$S = e^{-Z} \quad (7)$$

2.5. Demographic analysis

PopTools (Hood 2006) in Excel software was used to build a deterministic matrix based on age. The Solver subroutine, also in Excel, was used to perform 1000 iterations with t_{mat} , t_{max} , m_x , and the number of survivors by age, varying according to their distributions. The pre-breeding census was used (first reproduction, then survival), enabling the calculation of elasticity matrices and projection analysis. The matrix based on age (\mathbf{A}) is the population projection Leslie matrix:

$$\mathbf{A} = \begin{bmatrix} f_0 & f_1 & f_2 & \dots & f_x \\ s_0 & 0 & 0 & 0 & 0 \\ 0 & s_1 & 0 & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & s_{x-1} & 0 \end{bmatrix} \quad (8)$$

where $f_x = s_x \times m_x$; f_x represents the fertility rate for an individual at a specific age and s_x is the annual survival to the end of age x .

The initial parameters estimated by the demographic analysis according to Simpfendorfer (2005) are the intrinsic population growth rate (r , yr⁻¹) and the finite rate of population growth (λ), which are related as follows:

$$\lambda = e^r \quad (9)$$

We also estimated the net reproductive rate (R_0), which is the number of females produced by an individual in a single cohort and generation time (T , in years), which is the median time between parental and offspring births (Simpfendorfer 2005).

For the λ elasticity estimates (proportional change of λ for proportional changes in matrix \mathbf{A} , named a_{ij}), values for each age and fertility are additive. Therefore, adding these elasticity values defines a propor-

tional contribution of a_{ij} for any population value of λ . Since elasticities are proportions, their sum equals one. Elasticity is calculated as follows:

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{v_j w_i}{\langle w, v \rangle} \quad (10)$$

where e_{ij} is elasticity, a_{ij} represents transition matrix elements, and v and w are left (reproductive value for specific age) and right (age structure) auto-vector elements.

Finally, we created 4 scenarios to estimate demographic parameters. The first (S1: the no-fisheries hypothesis) was simulated, thus using only the constant value of M for the age classes. In the second scenario (S2), the equilibrium mortality rate (Z') was constantly applied for all age classes. The third scenario (S3) was closest to the real situation of the *C. falciformis* population because it uses fishing mortality; the F value was from fishing recruitment age (1+). In the fourth scenario (S4), fisheries only capture adult individuals, thus F rates are used only for the age classes above 10 yr.

3. RESULTS

3.1. Sampling

In total, 106 individuals were sampled for vertebrae (36 males, 33 females, and 37 with unregistered sex); TL ranged from 99–270 cm for males, 85–272 cm for females, and 73–258 cm for unregistered sex (Fig. 1).

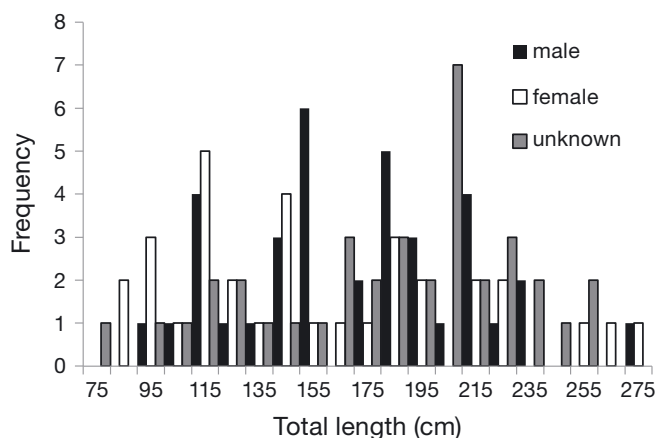


Fig. 1. Length–frequency distribution of the silky shark *Carcharhinus falciformis* captured in the tropical southwestern Atlantic. Only individuals with analyzed vertebrae are shown

3.2. Age and growth

We did not find any significant differences between sexes in the regressions between VR and TL (angular coefficient, $p = 0.9367$; linear coefficient, $p = 0.0596$) using ANCOVA. The relationship between VR and TL for the total sample showed the linear relationship $TL = 15.402VR + 21.026$ ($R^2 = 0.945$, $n = 61$).

The IAPE initially calculated was 5.61% but the classes with relative reading errors above 10% were read again. Their values after the consensus reading were 3.88% for the whole sample, and the variation throughout the classes was 0% for age 0+ (only birth-mark) and 7.69% for age 13+ (14 band pairs). Even though a few classes had to be read again, the level of reading precision obtained was considered acceptable.

The monthly relative marginal increment (RMI) analysis carried out with 103 individuals did not reveal significant differences between months with respect to smaller and larger values ($H_{11,103} = 9.8295$, $p = 0.5458$). However, June had the lowest RMI value. Therefore, as with other species already studied from the Carcharhinidae family such as *C. longimanus*, *C. signatus*, and *C. plumbeus* (Lessa et al. 1999, Santana & Lessa 2004, Romine et al. 2006), as well as *C. falciformis* (Bonfil et al. 1993, Oshitani et al. 2003, Joung et al. 2008), an annual band pair deposition was assumed.

No significant differences were found in the comparison between VBGM model parameters for males and females ($\chi^2 = 3.19$, $df = 3$, $p = 0.3632$); thus, data were combined into a single-sex model.

The lowest AIC value and highest w_i was estimated for VBGM, which is thus considered the best model to describe the growth of *C. falciformis*. VBGM-2 followed with less support, and the Gompertz and logistic models had no support (Table 1).

The growth curve obtained for VBGM (Fig. 2) had the following parameters: $L_\infty = 283.05$ cm TL (95% CI: 261.81–304.30); $k = 0.0987$ yr⁻¹ (95% CI: 0.0782–0.1191), and $t_0 = -3.47$ yr (95% CI: -4.14 to -2.81) (Table 1).

C. falciformis in the study area range from ages 0+ to 21+, reaching maturity around 8.6 and 9.9 yr for males and females, respectively. Their average lifespan is 27.2 yr of age.

We estimated the age distribution for the sample from length data in fishing logbooks ($n = 553$) and from this analysis determined that 80.5% of the individuals are immature, with fishing recruitment (modal class) occurring in the first year of age (Fig. 3).

Table 1. Growth models and parameters estimated for the length-at-age data of the silky shark *Carcharhinus falciformis* from the southwestern Atlantic. Models: VBGM: von Bertalanffy; VBGM-2: modified von Bertalanffy with birth size; Gompertz (with $a = 0.94$); Logistic. MLL: minimal likelihood; K : number of parameters; AIC: Akaike's information criterion; Δ : difference in AIC values between models; w : AIC weight. L_{∞} : asymptotic length; k : growth parameter; t_0 : time at length zero with their respective lower and upper confidential intervals in parentheses

Model	MLL	K	AIC	Δ	w	L_{∞}	k	t_0
VBGM	394.02	4	796.03	0.00	78.41	283.05 (261.81, 304.30)	0.099 (0.078, 0.119)	-3.47 (-4.14, -2.81)
VBGM-2	396.31	3	798.62	2.59	21.45	270.36 (256.49, 284.23)	0.116 (0.101, 0.131)	
Gompertz	400.35	4	808.70	12.67	0.14	262.84 (247.79, 277.90)	0.157 (0.132, 0.183)	
Logistic	406.58	4	821.16	25.13	0.00	252.72 (239.99, 265.45)	0.217 (0.185, 0.248)	2.65 (2.13, 3.17)

3.3. Mortality and survival rates

Rates of M estimated by several empirical methods (see Table S3) ranged from 0.137 (Rikhter & Efanov 1976) to 0.219 (Mollet & Cailliet 2002), with an aver-

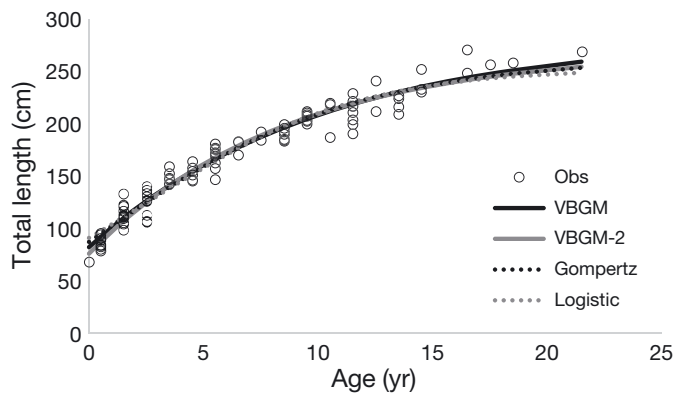


Fig. 2. Estimated growth curves using 4 different models with data back-calculated to the last ring for the silky shark *Carcharhinus falciformis* captured in the southwestern Tropical Atlantic. VBGM: von Bertalanffy growth model; VBGM-2: von Bertalanffy growth model with birth size. Obs: observed data

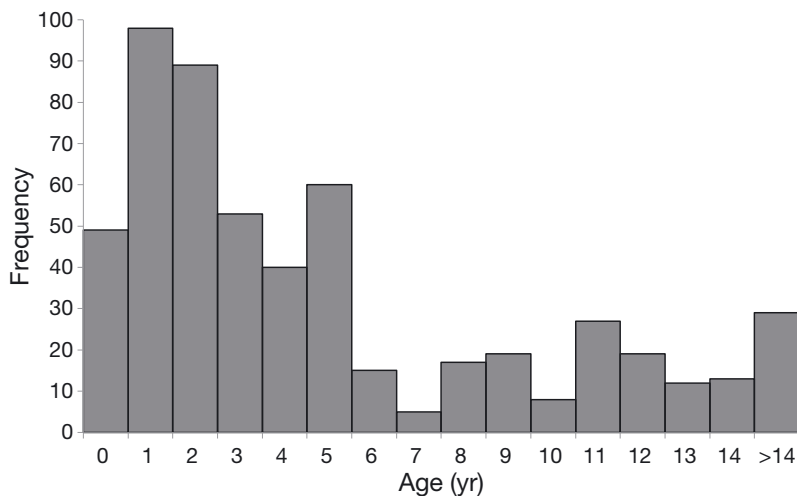


Fig. 3. Age frequency distribution of silky sharks *Carcharhinus falciformis* captured in the southwestern Tropical Atlantic between 2004 and 2010

age of 0.180 (± 0.029), corresponding to a survival rate of 0.836 (± 0.024). On the other hand, Z , estimated through the catch curve (Fig. 4), resulted in a value of 0.387, equivalent to a survival rate of 0.679.

From the values of M and Z , we estimated F at 0.207, which results in an E of 0.536, thus indicating a tendency for overfishing (>0.5). Z' , that is, mortality rate without population increase or decline, was estimated to be 0.261. Considering the M value estimated (0.180), the rate of F needed for the maintenance of population equilibrium ($F' = Z' - M$) would be 0.081. Therefore, our analyses show evidence that the level of F currently inflicted on *C. falciformis* ($F = 0.207$) is 60.9% above the level supported by the population to maintain equilibrium.

3.4. Demographic analysis

For scenario S1, using only a constant value of M (from all 9 methods) for all age classes, our analyses indicated $\lambda > 1$, and an annual population increase of around 4.3% (Table 2). The second scenario (S2), with a constant Z' rate for all age classes, indicated population equilibrium ($\lambda = 1$) as expected, demonstrating that in addition to M , the population could have a maximum fishing exploitation of 0.081 while maintaining equilibrium.

Scenario S3, which is closer to the current real-world situation of the *C. falciformis* population, indicated $F = 0.207$ from the first year of life, resulting in a population decline of 12.7% yr^{-1} and $\lambda < 1$ (Table 2).

Scenario S4 is a hypothetical situation in which fisheries capture only adult individuals (i.e. $>9+$ yr). This scenario would lead to an annual population growth of 2.3%, which is corroborated by elasticity values corresponding to juvenile survival

Table 2. Demographic parameters (with lower and upper confidence intervals) and elasticities (e_1 : fecundity; e_2 and e_3 : juvenile and adult phase survivals, respectively) of *Carcharhinus falciformis* from the southwestern Atlantic for each scenario: S1: only natural mortality (M); S2: using equilibrium mortality rate (Z'); S3: using fishing mortality (F) from recruitment age; S4: using fishing mortality after maturity age (t_{mat}). λ : finite rate of population growth; r : intrinsic rate of population growth (yr^{-1}), R_0 : net reproductive rate; T : generation time (in years)

Scenario	λ	r	R_0	T	e_1	e_2	e_3
S1: M	1.045 (0.952, 1.131)	0.043 (-0.049, 0.123)	1.803 (0.556, 3.791)	11.200 (10.444, 11.896)	0.078	0.762	0.160
S2: Z'	1.000 (0.927, 1.064)	0.000 (-0.076, 0.062)	1.068 (0.411, 1.926)	11.210 (10.450, 11.899)	0.078	0.762	0.160
S3: F from recruitment	0.881 (0.819, 0.947)	-0.127 (-0.200, -0.055)	0.266 (0.097, 0.570)	11.168 (10.364, 11.873)	0.079	0.769	0.152
S4: F from t_{mat}	1.024 (0.934, 1.120)	0.023 (-0.068, 0.114)	1.434 (0.452, 3.249)	11.019 (10.200, 11.788)	0.085	0.818	0.097

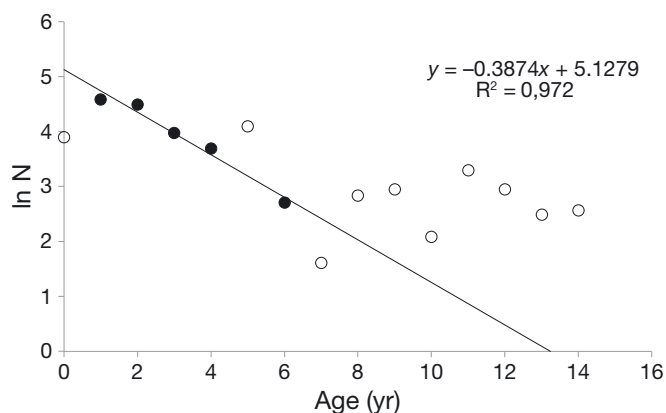


Fig. 4. *Carcharhinus falciformis* catch curve from the Southwestern Tropical Atlantic between 2004 and 2010. Filled circles correspond to the values used in the regression to estimate total mortality (Z)

(e_2) higher than 70% for the 4 scenarios (Table 2). The greatest demographic impact is mainly on juveniles between 1 and 6 yr of age, according to age distribution and survival elasticity calculations (e_2 and e_3) (Fig. 5).

4. DISCUSSION

Carcharhinus falciformis is a coastal and oceanic species globally exploited by multiple fisheries (Poisson et al. 2014, Oliver et al. 2015). Consequently, there is a great need for management measures based on regional life history parameters (Grant et al. 2018). The results of the present study provide the first estimation of age and growth parameters of the species in the southwestern Atlantic Ocean. Compared with previous length-at-age studies in the Atlantic, our findings are similar to those from the Campeche Bank (Bonfil et al. 1993) but differ from those from the Gulf of Mexico (Branstetter 1987a) in that the sharks grow more slowly and live longer. The demographic analysis shows that *C. falciformis* can not support current levels of F and indicates that the only sce-

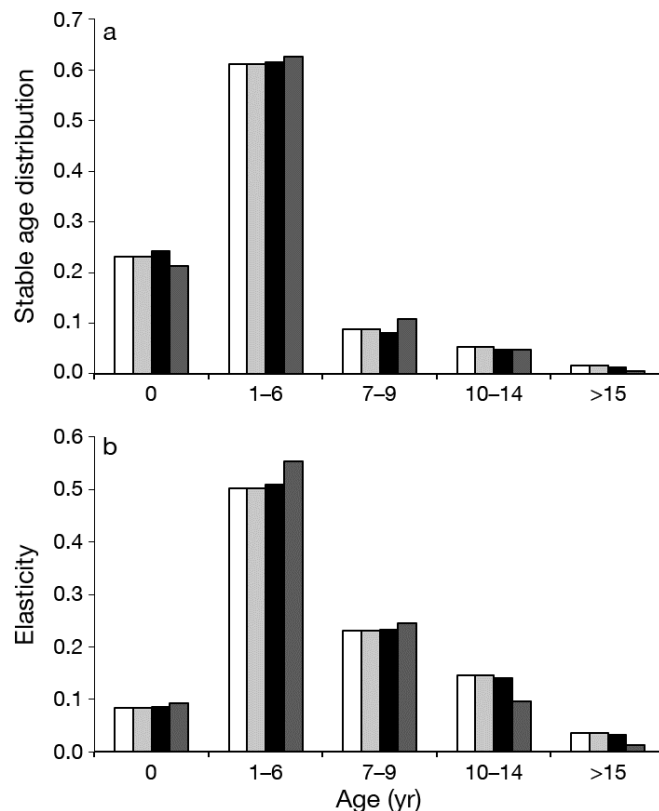


Fig. 5. (a) Stable age distribution and (b) elasticity corresponding to survival for life cycle phases (age 0: newborn; 1–6 : juveniles; 7–9 yr: pre-adults; 10–14: adults; >15: large adults) of *Carcharhinus falciformis* in the Southwestern Atlantic. The scenarios (see Section 2.5 for details) are represented by white columns (1), light grey (2), black (3), and dark grey (4)

nario of possible sustainable exploitation is when F begins only after t_{mat} .

4.1. Age and growth

The multimodel inference suggested for age and growth estimates was used to select the model providing the best fit for length-at-age data (Katsanevakis 2006, Smart et al. 2016) of *C. falciformis*. The

von Bertalanffy models provided the best fit for *C. falciformis* as expected for viviparous sharks, although this may not always be the case (Smart et al. 2016). Despite criticism of the t_0 parameter (Cailliet et al. 2006), the model using it provided the best fit among all tested models.

The average size-at-birth for *C. falciformis* in the area was estimated at 76 cm TL based on the mean of the sizes of the largest embryo and the smallest free-living individual (Hazin et al. 2007). This size-at-birth is close to that observed for the species in most studies (63–82 cm TL; Bonfil et al. 1993, Oshitani et al. 2003, Joung et al. 2008, Grant et al. 2018). The sample ranged from neonates to large individuals close to the larger specimens used in most *C. falciformis* studies of age and growth (Branstetter 1987a, Joung et al. 2008, Sánchez-de Ita et al. 2011, Hall et al. 2012, Grant et al. 2018). This size variation reduces the possibility of bias due to a lack of specific age classes.

C. falciformis growth parameters estimated in the present study did not differ between sexes, which aligns with other studies on the species (Branstetter 1987a, Bonfil et al. 1993, Oshitani et al. 2003, Joung et al. 2008, Sánchez-de Ita et al. 2011, Hall et al. 2012, Grant et al. 2018), suggesting that similar growth parameters for the different sexes may be a pattern for the species.

Growth parameters estimated for *C. falciformis* did not agree in most studies (Table 3). Variations in growth parameters have implications for stock assessments since life history parameters may cause the species to be considered more or less resilient. Therefore, knowledge of the species' population parameters within the whole area is crucial for man-

agement in order to guarantee resource sustainability. In the case of *C. falciformis*, these differences may be due to (1) natural variations between populations (Clarke et al. 2015, Domingues et al. 2018), even when not yet known (Grant et al. 2018); (2) sampling design leading to a lack of or emphasis on specific age classes (Bonfil et al. 1993, Grant et al. 2018); (3) body location where vertebrae were removed (Joung et al. 2008 versus all other studies); (4) differences in the interpretation of growth bands through time; (5) differences in methodological approaches defining age (Oshitani et al. 2003 versus all other studies); and (6) improvement of methodological approaches and recommendations for elasmobranch growth parameter estimation (Cailliet et al. 2006, Smart et al. 2016).

Despite presenting these possibilities, it is difficult to state which one caused the difference in the parameters. In the Atlantic Ocean, for example, Domingues et al. (2018) raised the hypothesis that there are at least 2 separate populations in the northern and southern regions of the western Atlantic. For the Gulf of Mexico region (Branstetter 1987a), *C. falciformis* presented a high growth coefficient and younger ages (both observed and estimated) compared to the present study (Table 3). These differences may be due to samples from this locality being composed of few large individuals, as pointed out by Bonfil et al. (1993), age underestimation (Harry 2018), or natural variation among populations. In Campeche Bank (Bonfil et al. 1993), however, parameters such as growth coefficient, maximum observed age, and maximum estimated age were close to those presented here. Differences detected in maximum observed length and asymptotic length may be due to the absence of large

Table 3. Comparisons of growth-related parameters for *Carcharhinus falciformis* in several regions. TL: total length; L_{∞} : asymptotic length; k : growth coefficient (von Bertalanffy); g : growth coefficient (logistic); t_0 : age-at-length zero; n : number of individuals. Adapted from Grant et al. (2018)

Region	Max. observed age (yr)	Max. estimated age (yr)	Max. observed TL (cm)	L_{∞} (cm)	k (yr^{-1})	g (yr^{-1})	t_0 (yr)	n	Reference
Indian Ocean									
Indonesia	20	40	260	299	0.066	–	–	200	Hall et al. (2012)
Pacific Ocean									
Central west Pacific	28	42	271	268	–	0.14	–	526	Grant et al. (2018)
Northeast Taiwan	14	33	256	332	0.084	–	–2.76	250	Joung et al. (2008)
Central Pacific	13	18	292	288	0.148	–	–1.76	298	Oshitani et al. (2003)
East Pacific	16	18	260	240	0.14	–	–2.98	145	Sánchez-de Ita et al. (2011)
Atlantic Ocean									
Campeche Bank	22+	27	314	311	0.101	–	–2.72	83	Bonfil et al. (1993)
Gulf of Mexico	13+	18	267	291	0.153	–	–2.2	100	Branstetter (1987a)
Southwestern Atlantic	21+	27	272	283	0.099	–	–3.47	106	Present study

individuals either because they are currently rare or due to the selectivity of the fishing gear.

C. falciformis from the southwestern Atlantic presented a k value near the intermediate level for sharks (0.1 yr^{-1} ; Branstetter 1987b), which was higher than other large *Carcharhinus* species such as *C. obscurus* ($k = 0.043$ and 0.045 yr^{-1}) (Simpfendorfer 2000, Simpfendorfer et al. 2002) and *C. leucas* ($k = 0.042 \text{ yr}^{-1}$) (Neer et al. 2005).

4.2. Demography

The rates of M found for *C. falciformis* were low, similar to other larger carcharhinids species (Cortés 2002a, Mollet & Cailliet 2002, Smith et al. 2008). In general, the methods that generated the highest values of M were those that used t_{max} as a parameter (see Tables S2 & S3). The Pauly (1980) method, which uses the parameters of growth and temperature, also generated a high value for M . The methods that used age of maturity and growth rate generated medium to low values. The M values estimated from the methods of Jensen (1996) were similar to those calculated from the Campeche Bank (Beerkircher et al. 2003, Grant et al. 2020) due to similarities in the age and growth parameters between Bonfil et al. (1993) and the present study.

Values of M associated with life history aspects generated an estimated intrinsic rate of population growth ($r = 4.3\% \text{ yr}^{-1}$) at the lower end of the range of variation already found for the species ($r = 4.3\text{--}8.6\% \text{ yr}^{-1}$) in several regions (Smith et al. 1998, Cortés 2002a, 2008, Beerkircher et al. 2003, Grant et al. 2020), indicating reasonable results. Since these rates (finite and intrinsic) are closely related to life history parameters such as late maturity, low fecundity, slow growth, and high longevity, they are similar to those of other large carcharhinids such as *C. plumbeus* (~240 cm TL), *C. obscurus* (~400 cm TL), and *C. signatus* (~280 cm TL) (Sminkey & Musick 1996, Simpfendorfer 1999, Santana et al. 2009).

Despite the small variation in the finite and intrinsic rates of population growth between regions, other demographic parameters showed wide variations between the southwestern Atlantic (this study) and other regions (Grant et al. 2020). The net reproductive rate found in the southwestern Atlantic ($R_0 = 1.803$) is close to but below that found in other regions, which ranges from 2.05 in the East Pacific to 4.14 in the Central West Pacific (Beerkircher et al. 2003, Grant et al. 2020). The generation time found in the present study ($T = 11.2 \text{ yr}$) is within the range

of variation seen in other regions, which ranges from 9.54 yr in the Central Pacific to 19.34 yr in Indonesia (Beerkircher et al. 2003, Grant et al. 2020).

The main source of variation in the demographic attributes of *C. falciformis* between regions is related to the different parameters of the species' life history, such as growth rate, longevity, and age of maturity (Grant et al. 2020). These parameters had a direct influence on the estimates of M in the present study due to the varying methods used. The present study showed a relatively low growth rate and age of maturity, which may have been reflected in T values being closer to the lower limit of variation found by Beerkircher et al. (2003) and Grant et al. (2020). T data for the Central Pacific, East Pacific, Taiwan, Gulf of Mexico, and the southwestern Atlantic (present study) were less than the 15 yr defined in the IUCN silky shark assessment (Rigby et al. 2017). This underscores the importance of regional Red List assessments (Grant et al. 2020) for *C. falciformis*, where distinct populations throughout the distribution of the species (Clarke et al. 2015, Domingues et al. 2018) are reflected in different life history parameters.

The elasticities corresponding to juvenile survival (Fig. 5) revealed the importance of this life stage, with a high juvenile/adult ratio. Thus, the capture of juvenile individuals causes a decline in the reproductive stock and, consequently, reduces the number of new recruits that can enter the population. The species' sexual maturation is late and, due to the predominantly juvenile and sub-adult individuals being captured, the replacement rate is hampered. This reduced survival during the juvenile phase for this shark species has a direct relationship with its greater vulnerability and lower productivity (Cortés 2002b, Liu et al. 2015, Pardo et al. 2016). Several studies have shown an abundance of *C. falciformis* juveniles in global captures (Beerkircher et al. 2003, Amandè et al. 2008, Hall et al. 2012, Poisson et al. 2014, Galván-Tirado et al. 2015, Grant et al. 2018), including in the Atlantic Ocean (Hazin et al. 2007, Coelho et al. 2012, Lucena Frédou et al. 2015). This vulnerability to fisheries due to their life history characteristics is evident in the demographic analysis.

Demographic models that do not include F generate estimates of r that only represent the probability of increase or decrease in population growth rates under the value of F to which the population is subjected (Cortés 1998, Gedamke et al. 2007). F values that guarantee the maintenance of the southwestern Atlantic population ($F = 0.081$) also seem unrealistic for most large shark species such as *Sphyrna lewini*,

C. obscurus, *C. signatus*, *C. plumbeus*, *C. longimanus*, *Alopias superciliosus*, *A. pelagicus*, and *Isurus oxyrinchus* (Sminkey & Musick 1995, Liu & Chen 1999, Romine et al. 2009, Santana et al. 2009, Tsai et al. 2010) because they cannot support $F > 0.1$. Thus the high degree of vulnerability of these species when subjected to any real levels of F , as observed for *C. falciformis* in the present and previous studies (Beerkircher et al. 2003, Grant et al. 2020).

This species can withstand F in a scenario (S4) in which capture occurs after the age of maturity, reinforcing the need to guarantee the survival of juveniles as observed for *S. lewini* (Liu & Chen 1999). Indeed, this observation corroborates the results found for *C. plumbeus* and *C. signatus* in which scenarios of Z above M during the juvenile stage led to stock declines (Sminkey & Musick 1996, Santana et al. 2009). As λ seems to be more sensitive to juvenile survival than fecundity and adult survival for most shark populations (Cortés 2002a), it is important to protect this life stage to prevent population declines. However, although management of longline fisheries is possible using size limits for sharks, this strategy is not realistic due to problems such as selectivity of the fishing gear used, post-capture mortality, economic viability, and illegal, unreported, and unregulated fisheries (Smart et al. 2020). It is important to mention that in a recent study with *C. albimarginatus* and *C. limbatus* (Smart et al. 2017), a scenario was tested in which juveniles were harvested but the breeding stock was protected, and this study showed that those species could support some level of F without experiencing a population decline. However, this scenario would not be adequate for *C. falciformis* in the southwestern Atlantic due to the already scarce adult stock and the difficulty in implementing this measure for pelagic sharks considering the characteristics of longline fishing in this area.

The low resilience of *C. falciformis* along with the high capture of juveniles and overfishing has caused significant declines in its populations, resulting in the species' inclusion in several threatened or priority-for-management species lists worldwide. The probability of a decrease in population growth under a fishing scenario (S3) corroborates results from the South Atlantic, where declines of up to 90% were estimated (Barreto et al. 2016a).

Recommendations prohibiting *C. falciformis* fishing in Brazilian jurisdictional waters and in the national territory (Brasil 2014), which covers most of the southwestern Atlantic, are in place but the lack of inspections has caused it to be overfished. A recent study showed that, when safely landed aboard, post-

release survival rates for *C. falciformis* can be high (Schaefer et al. 2021), indicating that it is possible to implement measures to recover silky shark populations. Therefore, focused conservation management measures must be maintained and enhanced (i.e. prohibition of the use of steel lines in longliners and cut the line to release the catch) due to their important contribution to reestablishing populations back to safe levels for the maintenance of this species in the South Atlantic.

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