RESEARCH ARTICLE

From plentiful to critically endangered: Demographic evidence of the artisanal fisheries impact on the smalltail shark (*Carcharhinus porosus*) from Northern Brazil

Francisco Marcante Santana[1,2]☯*, Leonardo Manir Feitosa[2,3]☯, Rosângela Paula Lessa[2,3]☯

1 Laboratório de Dinâmica de Populações Aquáticas (DAQUA), Universidade Federal Rural de Pernambuco (UFRPE), Unidade Acadêmica de Serra Talhada (UAST), Serra Talhada, PE, Brazil, 2 Laboratório de Dinâmica de Populações Marinhas (DIMAR), Universidade Federal Rural de Pernambuco (UFRPE), Departamento de Pesca e Aqüicultura (DEPAq), Recife, PE, Brazil, 3 Programa de Pós-Graduação em Biologia Animal, Universidade Federal de Pernambuco (UFPE), Recife, PE, Brazil

☯ These authors contributed equally to this work.
* framarsantana@yahoo.com.br

Abstract

The smalltail shark, *Carcharhinus porosus*, was the most abundant elasmobranch species in fisheries off Brazil's northern coast (BNC) in the 1980s, but its population has been declining since the 1990s. For this reason, a demographic analysis is necessary to determine the extent of this decline and the fishing effect on the BNC's population. Therefore, we performed a stochastic demographic analysis of the population in the BNC, and considered its global center of abundance. Smalltail shark specimens ($n = 937$) were collected with gillnets in Maranhão state, eastern BNC, in the 1980s with sizes ranging between 29.6 and 120.0 cm total length. Most of the individuals (90.6%) caught were juveniles (< 6 years-old), and the mortality and exploitation rates showed that the species was overexploited (92.3% above the fishing mortality corresponding to the population equilibrium threshold). The smalltail shark's biological characteristics, such as slow growth and low fecundity, demonstrate that it is one of the least resilient species among similar sized coastal sharks in the region. All these factors yielded an annual decrease of 28% in the intrinsic population growth rate, resulting in a population decline of more than 90% in only 10 years, and much higher for the current period. This set of features comprising fishing recruitment occurring upon juveniles, overfishing, and intrinsically low resilience make the population unable to sustain fishing pressure and severely hamper biological recruitment, thus causing this drastic population decline. Furthermore, several local extinctions for this species in the northeastern and southeastern regions of Brazil highlight its concerning conservation scenario. Therefore, since similar fisheries characteristics occur throughout its distribution range, *C. porosus* fits the criteria E of the IUCN Red List for a critically endangered species and urgent conservation measures are needed to prevent its extinction in the near future.

Introduction

Basic studies on elasmobranch populations are crucial for conservation status assessments and the establishment of management measures. These studies are particularly important for Data Deficient (DD) species for which little or no information is available, but populations might be under extinction risk [1,2]. An effective way to provide this information is to perform demographic analysis based on species-specific biological data. This has been done for several shark species to identify the major threats they face [3–5] employing stochastic demographic analysis and Monte Carlo simulations [3,6,7]. Consequently, this has enabled the incorporation of uncertainty and elasticity into population parameters, thus increasing the robustness of demographic analysis and enabling researchers to evaluate how populations would behave under different fishing scenarios.

However, demographic analyses are typically performed for highly fished species, especially those subjected to intense industrial fishing by developed countries' fishing fleets [3,8]. Brazil, on the other hand, has an intense artisanal and semi-industrial fishery with elevated elasmobranch bycatch levels, and little to no regulation for almost ten years now [9]. In this context, only a handful of coastal shark species (*Isogomphodon oxyrhynchus* [4], *Carcharhinus signatus* [3]) were studied through demographic analyses and elasticities testing different exploitation scenarios. Nevertheless, 27 shark species are under some level of threat in Brazil even with population trends mostly unknown [10].

One of these is *Carcharhinus porosus* (Ranzani, 1839), a coastal shark that inhabits tropical waters, common in mud bottoms and near estuaries, not exceeding 150 cm total length (TL) [11]. It was considered to occur from the Gulf of Mexico to southern Brazil and from the Gulf of California to Peru [11,12]. However, a recent taxonomic review by Castro [13] resurrected its Pacific Ocean synonym, *C. cerdale*, as a valid species, thus restricting the distribution of *C. porosus* to the Western Atlantic Ocean. In fact, both are part of the *Carcharhinus dussumieri-sealei* group with similar sized sharks mentioned by Garrick [14] known to occur all over the world in coastal tropical waters and with recent taxonomic revisions [15–17]. Furthermore, *C. obsolerus*, a recently described species from this group is one of the few sharks already considered to be extinct [16], thus raising concerns regarding *C. porosus* conservation prospects in both short and long-term scenarios. In Brazil, *C. porosus* original area of distribution ranged from the northern coast to Cananeia beach in São Paulo, Southeastern Brazil [18–20]. Recent studies demonstrated that this occurrence pattern has changed dramatically with a significant decrease in the species' distribution area throughout Brazil's coast [21–23]. These declines caused by possible local extinctions restricted *C. porosus* occurrence to the northern coast of Brazil between Maranhão and Amapá states [21]. This area is considered its global center of abundance for the high proportion of individuals caught when compared to other regions where it occurs [24]. Recent data estimates show that the Amazon coast is likely the most important area for its conservation along its geographical distribution [23]. Notwithstanding, it was the dominant species of shark landed during the 1980s and 1990s in the Brazilian Northern coast (BNC), but it is now only the third most caught shark species in the region [22].

The BNC is considered one of the major fishing grounds for several highly exploited marine crustacean, teleost, and elasmobranch species, with two states in the region among the largest fish producers in Brazil. Pará state was the largest producer in 2011 with around 87,000 tons and Maranhão was the third with over 45,000 tons [25]. Three main types of fisheries exist in the area and cause major bycatch for *C. porosus* in different types of habitat. First, the artisanal gillnet fisheries targeting the Brazilian Spanish mackerel, *Scomberomorus brasiliensis*, and the acoupa weakfish, *Cynoscion acoupa*, which is characterized by a large artisanal fleet composed of wood boats with little fishing autonomy employing surface and midwater gillnets [20,26]. Second, the bottom trawl shrimp fishing operated mostly in an industrial scale targeting the

pink shrimp *Farfantepenaeus subtilis* [27]. This fishery operates over long periods (40 to 90 days) with large metal boats (< 20 m long) with refrigerators [27,28]. Ships use single or double-rig otter trawl nets for five to seven hours employed between the 20 and 50 m isobaths within the continental platform outside the Amazon River mouth [27–29]. Third, industrial generalist fisheries targeting several teleost species, which uses similar settings to the bottom trawl shrimp fisheries, but employ gillnets ranging from 1 to 9 km in extension targeting large teleosts in general, especially the Laulao catfish *Brachyplatystoma vaillantii* [29,30].

Little information exists on the impacts these fisheries have had on the *C. porosus* population in the area, especially for the trawl and large teleost gillnet fisheries. During the 1980s, it corresponded up to 70% of the total catch weight and 43% of the number of individuals caught in the artisanal gillnet fisheries [19,20]. *Carcharhinus porosus* catches decreased from a CPUE of 2.87 kg/hour in 1990 to 0.43 kg/hour in the early 2000s [21,26]. Regarding the shrimp trawl fisheries, no catch data at the species level exists, but sharks were considered to be frequently caught and corresponding to 35.1% of the bycatch, including *C. porosus* [27,31]. The only data with identification at the species level points out that *C. porosus* corresponded to roughly 1.5% of the catch in the shrimp trawl fisheries prospections in the early 2000s [28].

Due to the great portion of juvenile individuals in the artisanal gillnet fisheries and the 85% biomass decrease observed in 2004, *C. porosus* was considered initially as threatened with extinction by the Normative Instruction 05/2004 [32]. In 2005, the species was considered overexploited, but not under extinction threat [33]. In 2014, the Brazilian government started to apply the International Union for the Conservation of Nature (IUCN) Red List Categories and Criteria to evaluate the national species, and their conservation statuses. Then, *C. porosus* was classified as critically endangered (CR) in Brazil due to the recent increase in fishing effort with the use of longer gillnets spanning over 10 km [34], its occurrence in several different large scale fisheries for shrimp and teleosts [30], and its decreased national occurrence area, and lack of population increase [21]. However, even though a few studies investigating *C. porosus* biological features such as age and growth [35], diet [36], reproduction [37,38], sexual dimorphism [39], distribution [23], and habitat use [40] exist, it remains DD according to the IUCN. Furthermore, genetic diversity data obtained from specimens in the Amazon coast point to a low allele diversity, which potentially indicates the effects of overfishing in the population [41]. Therefore, new data, especially considering the effects of fishing on its population, are paramount for *C. porosus* classification as a species of high risk of extinction and for the development of effective science-based conservation strategies.

To provide a population assessment for *C. porosus*, this study aims to estimate its demographic parameters in its global center of abundance. We also tested population responses to different fishing scenarios by calculating survival and fertility elasticities. Furthermore, we analyzed the *C. porosus* population's recovery potential against other related species with similar total lengths by comparing published demographic parameters. We hypothesize that fishing recruitment on the second year of life, thus well before individuals reach sexual maturity and reproduce, is the most important cause for the observed decline of *C. porosus*. To demonstrate that, we expect to obtain negative values of population growth rate under the realistic fishing scenario, and positive population growth rate for the no fishing scenario. Finally, we applied the IUCN criteria to the data obtained for an accurate assessment of *C. porosus* conservation status.

Materials and methods

Ethics statement

Although we report data obtained with field research and animal sampling, no permit for this research was issued because no ethics committee existed at the time (early 1980s in Brazil)

sampling took place. Furthermore, no field work was carried out nor animals were killed specifically for this study.

Species biological information

Data analyzed herein only corresponds to the written sample files from the experimental gillnet fisheries study carried out by Rosangela Lessa in the 1980s in Maranhão state. These data were collected with gear on the same settings as the one employed in the artisanal fishery targeting *S. brasiliensis* and *C. acoupa* in Maranhão state's coast. *C. porosus* specimens analyzed were caught with 900 m long and 7.5 m high gillnets, with 8.0 cm stretched mesh between June 1984 and November 1987 in the BNC (46ºW to 43º40'00"W) (Fig 1). Sex and TL (cm) were registered for each individual and the biological data were retrieved from published literature [20,35,37,38]. Since there are no data on the specimens captured by the shrimp trawl fisheries, all conclusions drawn in this study are specifically applied to the artisanal gillnet fishery.

Carcharhinus porosus reproductive biology in Maranhão state is well known [26,37,38], with males and females reaching sexual maturity at 70 cm and 71 cm total length, respectively.
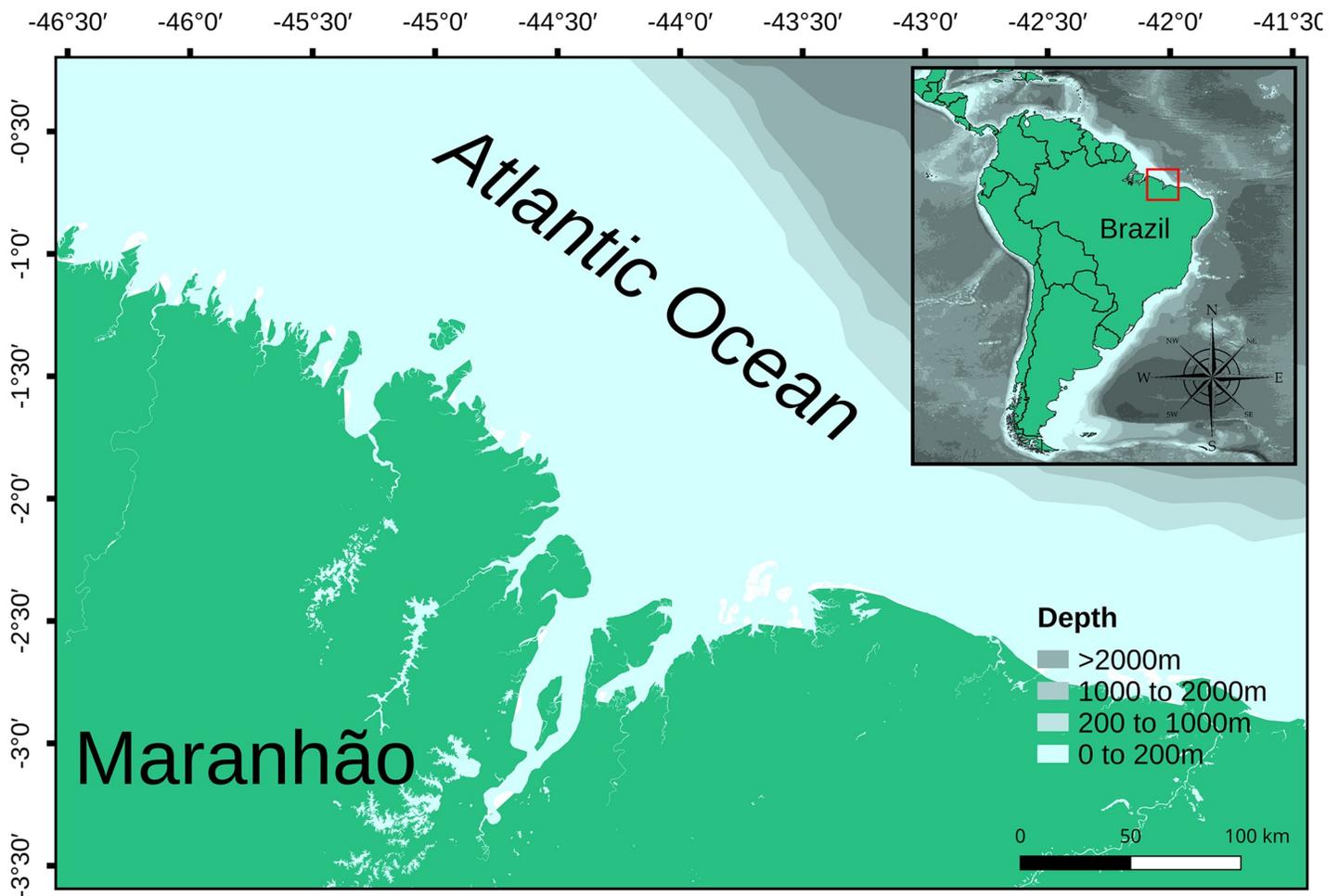

Fig 1. Location of *Carcharhinus porosus* catches in Maranhão state's coast. Light blue areas correspond to the 200 m isobaths followed by the 1000 m, 2000 m and above 2000 m depth.

Furthermore, the embryo sex ratio is 1:1, fecundity varies from 1 to 10 embryos (average = 5.94 ± 2.26) with a biennial reproductive cycle. These values yielded an average fecundity of 1.48 (SD = ±0.57) female embryos per pregnant individual per year. We used a normal distribution with this mean and standard deviation as uncertainties for the stochastic demographic analysis.

Growth parameters and population structure were estimated for *C. porosus* in Maranhão by Lessa & Santana [35]. Their results showed no significant age and growth differences between sexes, thus yielding the following von Bertalanffy growth function (VBGF) growth parameters: L_∞ = 136.4 cm TL; k = 0.077 yr^{-1}, and t_0 = -3.27 years. The maximum observed age (t_{max}) was of 12 years, with sexual maturity (t_{mat} converting the length at maturity of 71 cm for females in age through the inverted VBGF equation) occurring at 6 years of age. We used discrete probability distributions of both ages as uncertainties in the stochastic analysis, with probability (p) of 0.50 for the ages t_{max} and t_{mat}, and p = 0.25 for a year prior to t_{mat} or t_{max}, and other p = 0.25 for a year after t_{mat} or t_{max}.

Demographic analysis

Natural mortality rates (M) were estimated by nine age-independent and two age-dependent methods, based on several life cycle parameters for the species (Table 1). Furthermore, total mortality rates (Z) were calculated by catch curves (one using total lengths converted to age by the inverted VBGF and other based on the sample age structure), and by the methods of Beverton & Holt [42] by length and age. The stochastic analysis was estimated as uncertainties from both the eleven values of M and the four values of Z obtained, with discrete probability distributions of 0.0909 for each M value and 0.250 for each Z value. Although we understand the limitations of demographic analysis to estimate extinction risk due to density-dependent factors on population dynamics [43], we use it as a tool to unravel the effects of fisheries in the *C. porosus* population at the BNC.

Table 1. Methods and formulae used to estimate natural mortality (M) of *Carcharhinus porosus* in Northern Brazil.

Method	Equation
Pauly [44]	$\ln M = -0.0152 - [0.279\ln(L_\infty)] + [0.6543\ln(k)] + [0.463\ln(Temp)]$
Jensen [45]	$M = 1.6k$
Jensen [45] 2	$M = 1.5k$
Jensen [45] 3	$M = \frac{1.65}{t_{mat}}$
Rikhter & Efanov [46]	$M = \left(\frac{1.521}{t_{mat}^{0.72}}\right)(-0.155)$
Hoenig [47] for Teleosts	$\ln M = 1.46 - 1.01[\ln(t_{max})]$
Hoenig [47] for Cetaceans	$\ln M = 0.941 - 0.873[\ln(t_{max})]$
Hewitt & Hoenig [48]	$M = \frac{4.22}{t_{max}}$
Mollet & Cailliet [49]	$M = \frac{\ln(0.01)}{t_{max}}$
Peterson & Wroblewski [50]	$M = 1.92W_t^{-0.25}$
Chen & Watanabe [51]	$M_{(t)} = \frac{k}{[1 - e^{-k(t-t_0)}]}$ for ages up to 1—t_{mat} (6 years), and $M_{(t,t_{max})} = \left[\frac{1}{(t_{max}-t)}\right] \times \ln\left[\frac{(e^{k\,t_{max}} - e^{k\,t_0})}{(e^{k\,t} - e^{k\,t_0})}\right]$ for $t \geq 7$ years

L_∞ - asymptotic length, k—growth coefficient, *Temp*—mean annual water temperature (28˚C), t_{mat}—age of female maturity, t_{max}—maximal age observed, and t_0—theoretical age at zero length.

We averaged total (Z) and natural mortality (M) estimates solely to calculate fishing mortality (F), which is the difference between the former and the latter. On the other hand, we calculated survival (S) for each of the estimated total mortalities from the equation described by Ricker [52]:

$$S = e^{-Z}$$

In addition, we calculated the exploitation rate (E), which enables the observation of over (when > 0.5) or under (< 0.5) exploitation, with the equation: $E = F/Z$ [44]. All calculations were done in Microsoft Excel.

We employed the age-based Leslie matrix (L) from the PopTools program [53] in Microsoft Excel to calculate population elasticities. L was a Leslie population projection matrix, adopting a pre-breeding census (reproduction first, then survival):

$$L = \begin{bmatrix} f_0 & f_1 & f_2 & \cdots & f_x \\ s_0 & 0 & 0 & 0 & 0 \\ 0 & s_1 & 0 & 0 & 0 \\ 0 & 0 & \ldots & 0 & 0 \\ 0 & 0 & 0 & s_{x-1} & 0 \end{bmatrix}$$

In which $f_x = s_x \times m_x$ and s_x are the annual survivorship term for age x, and f_x represents age-specific fecundity rate per capita. This method employs matrix algebra to calculate λ values for each age in the population [54]. Furthermore, this method enables us to calculate elasticities, which are defined as the proportional sensitivities of the population to a given matrix element (i. e. fishing recruitment) [55].

From this Leslie matrix, we calculated the population parameter values of R_0 (expected number of replacements or net reproductive rate), T (generation time or time for increase in R_0), r (intrinsic rate of population growth or rate of increase), and λ (finite rate of population growth) [54,56]. Furthermore, Monte Carlo simulations were used to estimate these parameters and the used elasticities (e_{ij}) corresponding to the survivorship by age and fertility. For elasticity estimates of λ (proportional change in λ for proportional changes in matrix L, denominated a_{ij}), the values of each age and fertility are additive. Therefore, the sum of these elasticities defines the proportional contribution of a_{ij} to the overall population λ. Elasticity was calculated as:

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}$$

From these results, we created three scenarios to estimate demographic parameters. First, a no-fishing hypothesis with a constant M value was used for the age classes. In the second, the closest to reality, the F value was included through the fishing recruitment age (highest number of individuals from the same age caught by the fishery). Third, we analyzed the influence of juvenile captures on the species' demography with a hypothetical scenario, in which fisheries only catch adult individuals. Therefore, fishing mortality rates are used only for age classes above six years.

For scenarios with negative r values, we estimated the number of survivors for age t (N_t), corresponding to 10 years in the population (N_{10}) and three times the generation time (N_{3T}), considering an initial survival (N_0) of 1 through the equation described by Otway et al. [57]: $N_t = N_0 e^{rt}$. This calculation enables us to estimate the population decline ($D_t = 1 - e^{rt}$) according

to the scenarios employed and their comparison with criterion E of the IUCN conservation status assessment protocol: Quantitative analysis showing the probability of extinction in the wild is at least 50% in three generations [58].

In addition, the intrinsic rebound potential of productivity (r_Z) was estimated according to Smith et al. [59], and the fishing mortality rate necessary to drive the species to extinction ($F_{extinct}$) was calculated according to Garcia et al. [60]. This mortality rate is equivalent to the maximum intrinsic rate of population increase (r_{max}), which is a standard measure of population productivity and of extinction risk [1]. All these calculations were performed in Microsoft Excel.

Results

We analyzed catch and biological information for 937 individuals of *Carcharhinus porosus*. Since no significant differences exist in the frequency distributions between sexes by length and age [37], both sexes were analyzed together. Total lengths varied from 29.6 to 120.0 cm TL, with a larger frequency between 45 and 55 cm (Fig 2A). Ages estimated according to the inverted VBGF varied between 0 and >14 years with the mode indicating fishing recruitment at 2 years-old with a juvenile frequency (< 6 years) of 90.6% (Fig 2B).

The smaller value estimated for M was established by the Jensen [45] 2 method and the greatest by the Mollet & Cailliet [49] method, resulting in an average of 0.261 ($S = 0.770$) from the eleven methods (Table 2). Total average mortality rate (Z) was 0.656 ($S = 0.519$) and, when subtracted by M, yielded a fishing mortality $F = 0.395$ and an exploitation rate $E = 0.602$, thus indicating overexploitation.

The mortality rate corresponding to population equilibrium (Z'), which is the constant total mortality Z that would be enough to keep the population under sustainable levels (corresponding to a value of $r = 0$ and $\lambda = 1$), was estimated at 0.271 ($S = 0.763$). Considering $M = 0.239$, the equilibrium fishing mortality rate (F') would be equal to 0.032. When compared to the estimated F value (0.417), we obtain an overexploitation degree of 92.3%.

In the first scenario of the elasticity analysis (no fishing exploitation), *C. porosus* population would be close to equilibrium ($\lambda = 1$, $r = 0$), with a slight annual increase of 0.3%, thus indicating the intrinsic natural vulnerability of the population. The greatest elasticity corresponded to juvenile survival (e_2), which demonstrates the importance of this life stage for the population demography (Table 3). The 1,000 simulations performed in this scenario reveal a similarity in the proportions of the λ values, with 51.1% of it indicating population increase ($\lambda > 1$) and a decrease for the rest ($\lambda < 1$) (Figs 3 and 4).

When the fishing exploitation is evaluated from the age of fishing recruitment (2 years) (Scenario 2), the inclusion of F yields a population decrease of around 28% per year with all simulations resulting in λ values smaller than 1. Therefore, in these conditions, there is no perspective of population increase nor equilibrium (Table 3; Figs 3 and 4). In addition, this scenario evidences that the catch of juvenile individuals and the high fishing mortality rate starting at 2 years old caused a major population decline in *C. porosus*. The estimated value of r in this scenario reveals that only 5.8% of the population survives for the first 10 years of life and, in three generations, there are only 0.1% of the initial cohort left, resulting in population declines of almost 100% during these periods (Table 3).

Considering the hypothesis that fishing recruitment started at the age of maturity (6 years) (Scenario 3), the population would continue to decline, but at a much lower rate (approximately 6.8% per year) (Table 3). The population decline at this scenario would be much smaller than in scenario 2, with a decline of 49.5% for the first 10 years, and 77.1% for three generations (Table 3). Of the 1,000 simulations performed for λ, 71.6% reveal population
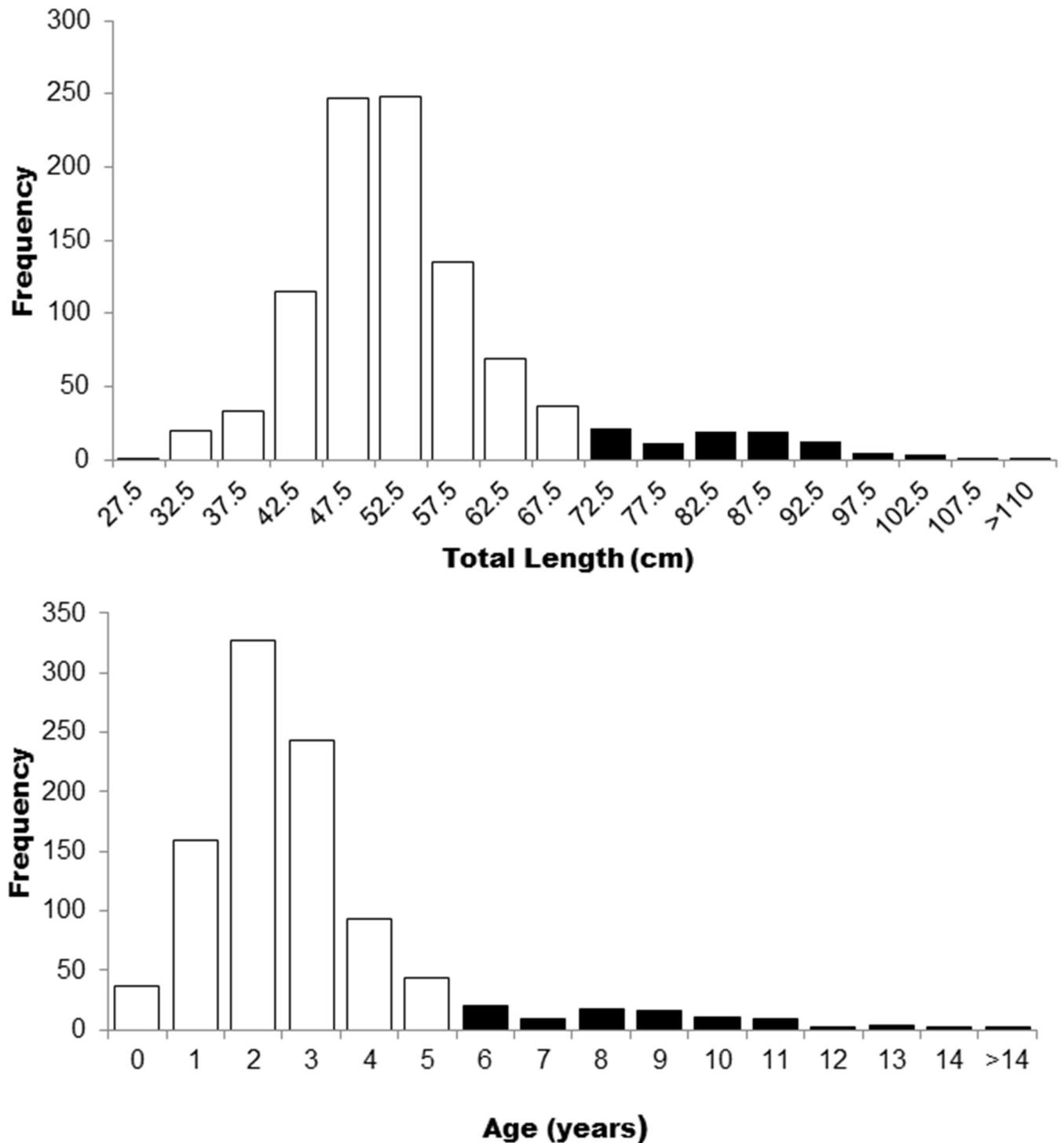
Fig 2. Total length (a) and age (b) frequency distributions of juvenile and adult individuals of *Carcharhinus porosus* from Northern Brazil. White columns correspond to juveniles and black columns to adults.

declines (Figs 3 and 4), thus indicating that the fishing mortality in scenario 2 is so high that, even capturing only adult individuals, the population would still decline.

Table 2. *Carcharhinus porosus* natural and total mortalities, as well as survival rates estimated by several methods.

Method	Mortality	Survival
Natural (*M*)		
Pauly	0.222	0.801
Rikhter & Efanov	0.250	0.779
Hewitt & Hoenig	0.301	0.740
Hoenig–teleosts	0.300	0.741
Hoenig–cetaceans	0.256	0.774
Jensen 1	0.123	0.884
Jensen 2	0.116	0.891
Jensen 3	0.263	0.769
Mollet & Cailliet	0.329	0.720
Peterson & Wroblewski	0.540–0.247	0.583–0.781
Chen & Watanabe	0.346–0.062	0.708–0.940
Total (*Z*)		
Catch curve by length	0.677	0.508
Catch curve by age	0.749	0.473
Beverton & Holt by length	0.519	0.595
Beverton & Holt by age	0.681	0.506

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For the three scenarios, the most important age classes for *C. porosus* demography were between 1 and 5 years. These classes represent more than 50% of the stable age distribution and survival elasticities (Fig 5), since survival of these individuals is fundamental for the reproductive stock. Furthermore, the intrinsic rebound (r_z) estimated for *C. porosus* was of 0.048, and the $F_{extinct}$ value of 0.254, which is inferior to the estimated *F* value, thus indicating the species overexploitation.

Discussion

Demographic inferences

Based on the demographic analysis, *C. porosus* decline in the BNC was caused by intense overfishing. All the information obtained by this study points toward a sharp decline in *C. porosus* population in its global center of abundance and the most important region for this species conservation in the world [23,24]. In the BNC, gillnet fisheries in the 1980s caught essentially juvenile *C. porosus*, especially those with 2 years old, who accounted for 37.8% in these fisheries (Fig 2B). Catching individuals 4 years before they reach sexual maturity causes a significant decline in the reproductive stock, also reducing biological recruitment levels in the population, which would help to maintain its sustainability. This pattern can be found in the same area for similar-sized species such as *I. oxyrhynchus* [4], causing significant declines in their populations.

In the smalltail shark's case, we estimated the fishing mortality rate for this species to be almost 100% higher than the population could withstand. Furthermore, we obtained an exploitation rate greater than sustainability ($E > 0.5$), which is also corroborated by the *F* value above $F_{extinct}$. Therefore, fisheries overexploitation magnified the population decline already caused by the fishing recruitment of juveniles. Indeed, several demographic studies with sharks reveal overfishing as one of the main causes for population declines [3,4,7,59]. This scenario is worsened if we consider the existence of the shrimp and teleost trawl fisheries, which have not

Table 3. Demographic analysis for *C. porosus* with extrapolations for the next three generations and 10 years.

Scenario	λ	r (year^{-1})	R_0	T (years)	e_1	e_2	e_3	$3T$ (years)	N_{3T}	D_{3T}	N_{10}	D_{10}
1	1.011 (0.780/1.254)	0.003 (-0.248/0.226)	1.588 (0.123/5.720)	8.030 (6.750/9.264)	0.126	0.628	0.246	24.090	-	-	-	-
2	0.756 (0.624/0.910)	-0.285 (-0.472/0.095)	0.163 (0.022/0.525)	7.737 (6.537/8.891)	0.131	0.654	0.215	23.211	0.001	0.999	0.058	0.942
3	0.940 (0.756/1.161)	-0.068 (-0.279/0.149)	0.809 (0.111/2.578)	7.207 (6.004/8.601)	0.140	0.701	0.158	21.620	0.229	0.771	0.505	0.495

Demographic parameters (λ, r, R_0, and T) with respective 95% confidence intervals between parenthesis (lower/upper), elasticities (e_1 = sum of elasticities of fertility, e_2 = sum of juvenile survival and e_3 = sum of adult survival), three times the generation time ($3T$); proportion of survivals at the age corresponding to three generations (N_{3T}) and 10 years (N_{10}), and respective declines (D_{3T} and D_{10}) by scenario 1 (constant M for age classes), 2 (Z from the fishing recruitment age at two years old), and 3 (Z from the hypothetical fishing recruitment age equal to the age at maturity of six years old).

been analyzed here but likely cause severe negative impacts on the *C. porosus* population as well [27,28,30].

In addition to overfishing and the high incidence of juveniles in the catches, *C. porosus* is an intrinsically low resilient species and highly vulnerable to fishing exploitation, mainly due to its biological characteristics. Even though Branstetter [61] classified *C. porosus* as a species with small size ($L_{max} \sim 100$ cm TL) and fast growth ($> 30\%$ of birth length in the first year of life), its life history traits are actually the opposite. *Carcharhinus porosus* has one of the longest juvenile phases when compared to several species of small coastal sharks, thus taking longer to reach sexual maturity. Indeed, when we added its high longevity and slow growth to its low fecundity, we obtained a small productivity value ($r_z = 0.051$) (Table 4). Furthermore, *C. porosus* productivity was closer to that of large coastal sharks ($r_z < 0.04$), which are generally low
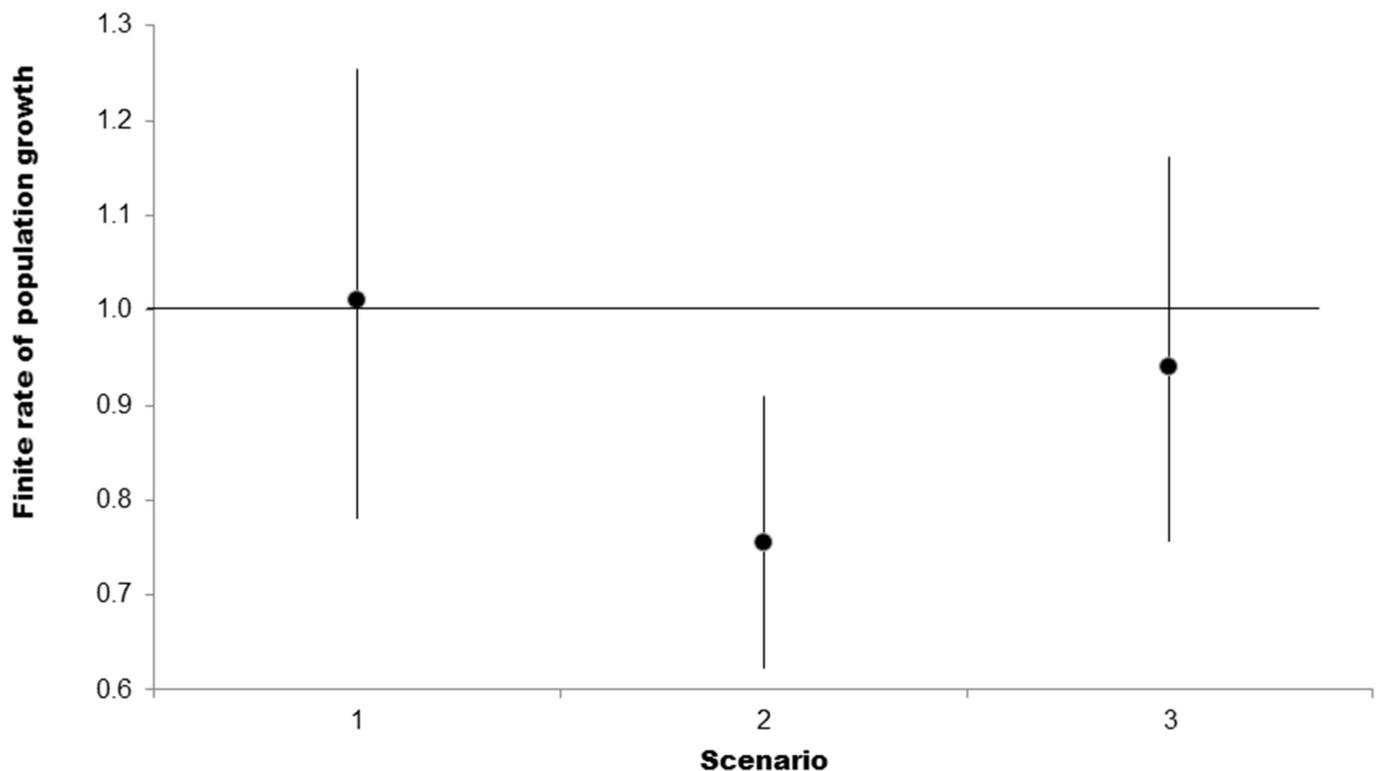

Fig 3. Finite rate of population growth (λ) mean (points) and 95% confidence intervals (bars) for different scenarios of *C. porosus*. Dashed line corresponds to the population equilibrium ($\lambda = 1$).
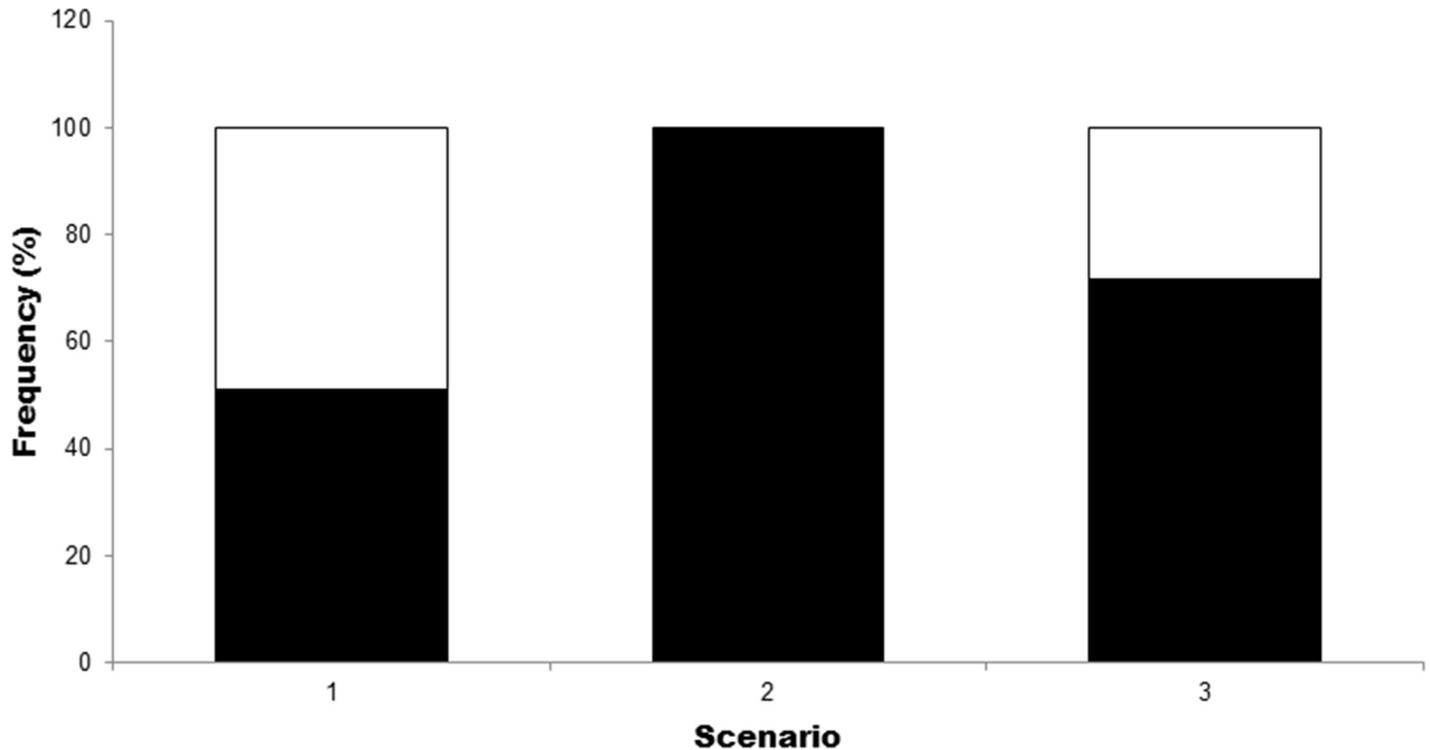
Fig 4. Proportions of finite rate of population growth (λ). Smaller values (black) and larger (white) than 1 of the 1000 simulations by scenario for *Carcharhinus porosus*.

[59]. In fact, its r_z value is much inferior to the one expected for similar-sized coastal sharks (Table 4).

Smith et al. [59] estimated the yield for 26 Pacific shark species and determined that small coastal sharks tend to have r_Z values higher than 0.08, denoting their high resilience. Indeed, Cortés [75] and Brewster-Geisz & Miller [76] describe the strong relationship between the vulnerability and the survival of juveniles, age at maturity, and other life history traits in the population parameters of shark species. Furthermore, Liu et al. [77] and Branstetter [61] argue that sharks with an earlier sexual maturity tend to maintain the population in equilibrium more easily even with a somewhat high fishing effort. This is the case because specimens are usually fished after the first reproduction, thus ensuring their contribution to the population. Therefore, there is a direct relationship between the duration of the juvenile phase and the vulnerability of a shark species.

As demonstrated by the mortalities and exploitation rate results, the BNC's *C. porosus* population was already heavily overfished in the 1980s. Furthermore, the higher elasticity values for all scenarios tested point that the juvenile phase (1 to 5 years of age) is the most important stage for this species maintenance and individuals between these ages represent 86.9% of the population in these fisheries. Further analyzing the species' resilience to fisheries, we calculated its intrinsic rebound potential ($r_z = 0.051$) and generation time ($T = 7.9$ years). Both values are similar to the ones found by Cortés [75] for *C. porosus* and, when compared to other similar-sized species, demonstrate how susceptible it is to fisheries exploitation. In fact, species already globally endangered such as *Sphyrna lewini* and *C. longimanus*, have smaller generation times than *C. porosus*, thus reproducing faster. On the other hand, r_z was a little higher than the one obtained for *I. oxyrhynchus* ($r_z = 0.039$) [4], but still confirming its low resilience to fisheries.
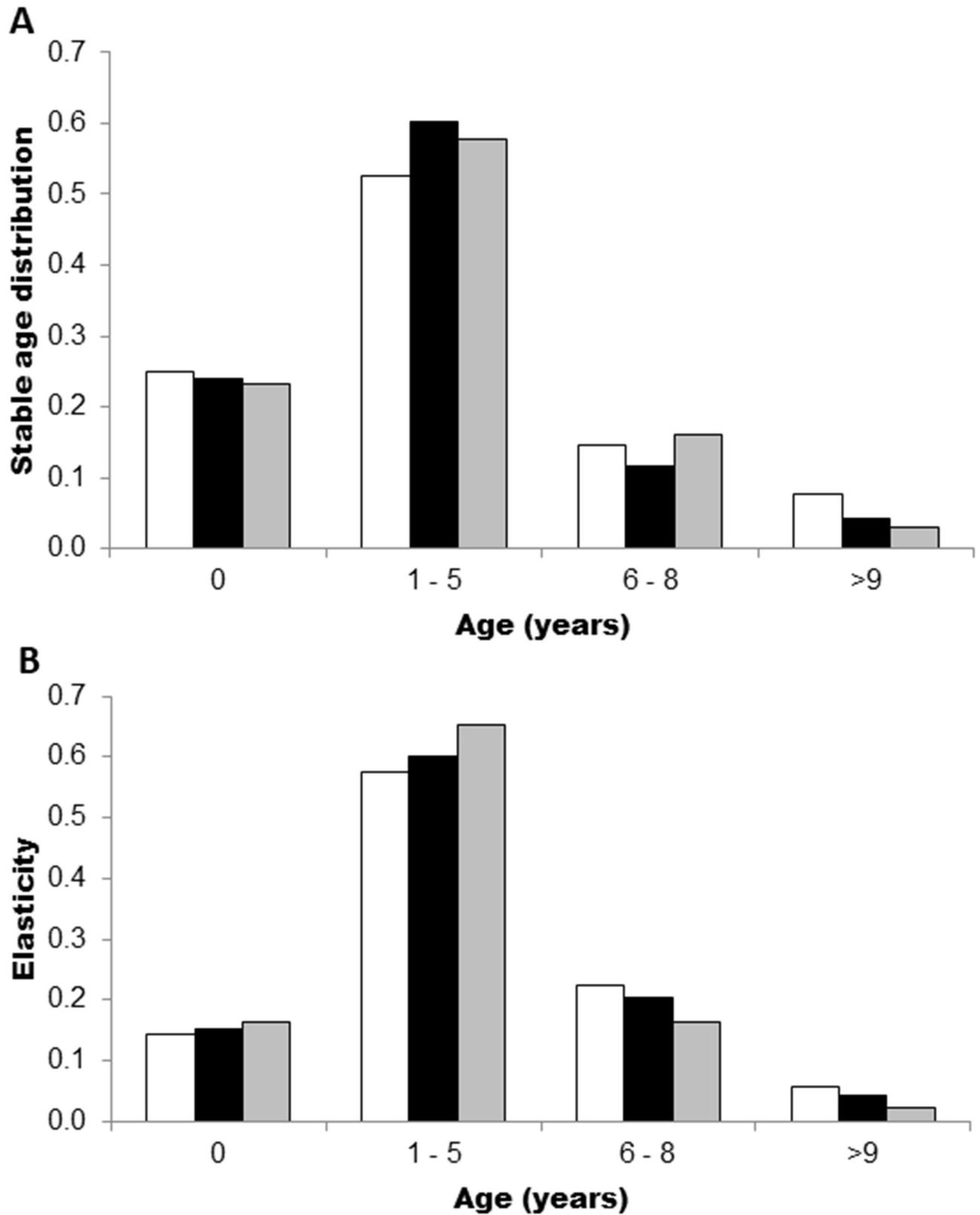
Fig 5. Stable age distribution (a) and elasticity (b) by stage of life cycle of *C. porosus*. Scenarios are represented by gray (1), white (2) and black (3) columns. Life stages are separated in neonates: 0; juveniles: 1–5 years; adults: 6–8 years, and large adults: >9 years).

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Table 4. Life history characteristics estimated for coastal shark species by different authors.

Species	TL_{max}	k	t_{max}	t_{mat}	m_x	r_Z	References
Isogomphodon oxyrhynchus	141.0	0.121	12	6.6	1.21	0.053	Lessa et al. [62,63]
Carcharhinus acronotus	132.0	0.120	16	7.1	1.00	0.053	Hazin et al. [64]; Barreto et al. [65]
Carcharhinus porosus	120.5	0.077	12	6.1	1.48	0.051	Lessa & Santana [35]; Lessa et al. [37]
Rhizoprionodon terranovae	115.0	0.359	10	4.2	1.33	0.080	Cortés [56]
Rhizoprionodon porosus	110.0	0.171	10	3.3	2.50	0.098	Machado et al. [66]; Lessa et al. [67]
Rhizoprionodon lalandii	76.5	0.301	6	2.6	1.20	0.108	Lessa et al. [67]; Lessa [68]
Sphyrna tiburo	103.0	0.340	7	2.2	4.50	0.130	Parsons [69]
Carcharhinus leucas	285.0	0.076	27	15	3.25	0.027	Smith et al [59]; Branstetter & Stiles [70]; Pirog et al [71]
Negaprion brevirostris	320.0	0.057	25	12.7	4.25	0.034	Smith et al [59]; Feldheim et al [72]
Galeocerdo cuvier	430	0.202	28	11	5.6	0.043	Smith et al [59]; Winter & Dudley [73]; Whitney & Crow [74]

Maximum total length in cm–TL_{max}, von Bertalanffy growth coefficient by year–k, Age at maturity—t_{mat} and maximum observed—t_{max} in years, average fertility of pregnant females from female embryos per year–m_x, and intrinsic rebound potential of productivity (r_Z). All data regard females.

Unlike other small to medium-sized coastal shark species (i.e. *Rhizoprionodon* spp.), *C. porosus* follows the same trends regarding life history features present in other *Carcharhinus* species such as *C. acronotus* and *C. brevipinna* [75], and the closely related *I. oxyrhynchus* [4]. When compared to other similar-sized species, the population parameters of *C. porosus* are concerning (Table 5). For example, its estimated maximum size is the smallest, but its generation time is higher and its survival rates are smaller than the ones of larger species such as *C. acronotus*, *C. sorrah*, and *C. tilstoni*. In addition, when the elasticity results are compared, the dependence on the juvenile life stage is similar to large coastal species such as *C. leucas* and *Galeocerdo cuvier*. Therefore, *C. porosus* is one of the most naturally at-risk species of *Carcharhinus* in the world, and the fishing pressure has deteriorated its population.

Table 5. Comparative finite rate of population increase (λ), generation time (T, in years) and elasticities (e_1 = sum of elasticities of fertility, e_2 = sum of juvenile survival and e_3 = sum of adult survival) for coastal Carcharhinidae sharks used only natural mortality.

Species	λ	T	e_1	e_2	e_3
Carcharhinus acronotus	0.847	4.2	0.191	0.472	0.336
Carcharhinus amblyrhynchus	0.941	9.6	0.094	0.609	0.297
Isogomphodon oxyrhynchus	0.950	9.2	0.110	0.662	0.227
Carcharhinus limbatus	0.974	10.0	0.093	0.600	0.306
Carcharhinus leucas	0.998	21.6	0.044	0.774	0.181
*Carcharhinus porosus**	1.013	8.0	0.126	0.628	0.246
Carcharhinus plumbeus	1.022	19.8	0.048	0.693	0.259
Carcharhinus obscurus	1.030	26.2	0.037	0.679	0.285
Carcharhinus brevipinna	1.037	10.4	0.088	0.614	0.298
Rhizoprionodon terranovae	1.056	4.9	0.169	0.475	0.356
Negaprion brevirostris	1.064	16.4	0.057	0.700	0.242
Rhizoprionodon taylori	1.073	2.9	0.261	0.227	0.512
Carcharhinus porosus	1.086	8.4	0.107	0.582	0.312
Carcharhinus sorrah	1.093	4.3	0.194	0.370	0.435
Carcharhinus tilstoni	1.145	6.0	0.145	0.419	0.436
Galeocerdo cuvier	1.246	10.9	0.084	0.699	0.217

All values were obtained from Cortés [75], except for *Isogomphodon oxyrhynchus* [4] and *Carcharhinus porosus* in the present study (*).

Conservation problems and future strategies

Our results are strong evidence for the deleterious effect of fishing on *C. porosus* BNC population, thus being responsible for its decline. Furthermore, recent studies demonstrate that the shark community in the BNC seems to have also suffered significant changes. The once most abundant species *I. oxyrhynchus* and *C. porosus* are now severely depleted [78], and were substituted by others with a higher resilience to fisheries such as *R. porosus* and *C. acronotus* [22]. Since fishing recruitment occurred at two years old (Fig 2B), the population could not sustain this fishing pressure and biological recruitment was severely hampered, thus evidencing its sharp population decline. In addition, the perspective worsens with the estimates of local extirpations in the Southeast and Northeastern regions of Brazil where catches have not been reported for decades [21].

Even though legislation has tried to follow along the conservation needs to manage this species' populations by prohibiting its catches since 2004, no effective actions have been taken so far. In fact, the management plans that should have been developed when the species was listed in Annex I of the Normative Instruction No. 5 from 2004 [32] were never implemented and no population recovery has been observed so far. This led *C. porosus* to be considered as critically endangered in the current Brazilian Red List of endangered fishes and aquatic invertebrates (Ordinance 445/2014) [21,79]. Therefore, it is clear that the necessary information to apply management strategies already existed since the early 2000s, but the overall inaction of the environmental agencies and the Brazilian government were key to the current state of *C. porosus* populations in Brazil.

Despite the existence of catch and trade prohibitions, recent studies have demonstrated that several highly endangered species, including *C. porosus*, are continually caught in the BNC [22,80,81]. Furthermore, fishers report the lack of dialogue between the environmental agencies and their communities, as well as the virtually complete absence of inspections in the largest fishing ports of the region [78]. Since the fisheries in the area are mainly artisanal with traditional communities being an important factor in this equation, fishing ports are scattered throughout the area, thus making inspections and the reporting of endangered species extremely difficult. Furthermore, the lack of data on the semi-industrial and industrial shrimp and general teleost trawl fisheries that operate in the continental platform of the Amazon coast are extremely concerning and a key aspect that needs to be addressed by the responsible authorities.

Overall, fisheries management in Brazil is extremely flawed with the statistics program being discontinued since 2011, and no reliable information for any type of fishing activity exists ever since [9]. The only updated information on fishing activities in the area come from Mourão et al. [34] and Almeida et al. [82], who identified an average three-fold increase in the length of gillnets used in the BNC to overcome the decreased productivity of the target species [83]. Gillnets targeting *S. brasiliensis* now range from 3 to 9 km long [34], while the ones used in the *C. acoupa* and *Sciades parkeri* fisheries range from 3 to 15 km long [82]. Furthermore, artisanal fishers operate in vessels with little autonomy to fish for a long time and there is little use of vessel tracking systems [78], thus making it virtually impossible to monitor where fishing takes place. In the case of the industrial and semi-industrial fisheries, the boats have an autonomy of roughly three months at sea, and the use of satellite boats is common, with the large one operating as storage for the catch [30].

As a result of this complex scenario, several elasmobranch species commonly bycaught by the gillnet fisheries previously mentioned such as *Sphyrna tudes*, *S. tiburo*, *I. oxyrhynchus*, *Pristis pristis* and *P. pectinata* are now considered to be critically endangered in Brazil [10]. These species have the common feature of neonate and juvenile specimens being consistently found

in the BNC's coastal and estuarine waters [4,84–86], which has been highlighted in previous studies as a potential communal nursery for elasmobranchs [87]. In fact, most of the BNC has been considered as a global conservation hotspot for elasmobranchs due to its high degree of irreplaceability as a crucial habitat for these animals [88].

Recent data using vertebrae microchemistry has demonstrated that the BNC might actually be an essential habitat, especially for species that fulfill their entire life cycle in the area [40]. Indeed, habitat use data indicate that *C. porosus* likely uses the waters of the Amazon coast during all life stages, with some level of sexual segregation. This habitat use pattern fits the description provided by Knip et al [89] of how small coastal shark species tend to use their habitat. Therefore, *C. porosus* is much more vulnerable to the fishing activity than other migrating coastal species such as *Galeocerdo cuvier* [90]. Despite this, species distribution modelling and historical catch data estimated that the Amazon coast is the area where the species has the highest catch and occurrence probability throughout its distribution range [40]. Therefore, the Amazon coast is likely the most important area for this species throughout its distribution, but is also where fisheries exposure are likely the highest [91].

Conservation status recommendation

Considering all the data shown and the published information regarding the level of the threats for *C. porosus*, including the exposure to different fisheries within the BNC, we applied the IUCN criteria for conservation status assessments [58]. Overexploitation and the elevated juvenile captures, together with an intrinsically low resilience to fisheries, caused a significant decline in *C. porosus* population. The demographic analyses in the present study and the exploitation scenarios showed over 90% declines in the population over thirty years ago. Since its generation time is approximately 8 years, at least four generations have passed since the data presented herein was collected. Therefore, *C. porosus* fits Criterion E (Quantitative analysis showing the probability of extinction in the wild is at least 50% in three generations) of the IUCN. Even though this study is restricted to the BNC, the species faces similar threats throughout its geographic distribution [92], and thus should be considered as CR globally.

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Author Contributions

Conceptualization: Francisco Marcante Santana, Leonardo Manir Feitosa, Rosângela Paula Lessa.

Data curation: Francisco Marcante Santana, Leonardo Manir Feitosa, Rosângela Paula Lessa.

Formal analysis: Francisco Marcante Santana.

Investigation: Leonardo Manir Feitosa, Rosângela Paula Lessa.

Methodology: Francisco Marcante Santana, Leonardo Manir Feitosa, Rosângela Paula Lessa.

Supervision: Rosângela Paula Lessa.

Visualization: Leonardo Manir Feitosa.

Writing – original draft: Francisco Marcante Santana, Leonardo Manir Feitosa.

Writing – review & editing: Francisco Marcante Santana, Leonardo Manir Feitosa, Rosângela Paula Lessa.

References

1. Dulvy NK, Ellis JR, Goodwin NB, Grant A, Reynolds JD, Jennings S. Methods of assessing extinction risk in marine fishes. Fish and Fisheries 5. 255–276. Fish Fish. 2004; 5:255–76.

2. Walker TI. The state of research on chondrichthyan fishes. Mar Freshw Res. 2007; 58(1):1.

3. Santana FM, Duarte-Neto P, Lessa R. Demographic analysis of the night shark (*Carcharhinus signatus*, Poey, 1868) in the equatorial Southwestern Atlantic Ocean. Fish Res. 2009; 100(3):210–4.

4. Lessa R, Batista VS, Santana FM. Close to extinction? The collapse of the endemic daggernose shark (*Isogomphodon oxyrhynchus*) off Brazil. Glob Ecol Conserv. 2016; 7:70–81. Available from: http://dx.doi.org/10.1016/j.gecco.2016.04.003

5. Smart JJ, Punt AE, Espinoza M, White WT, Simpfendorfer CA. Refining mortality estimates in shark demographic analyses: A Bayesian inverse matrix approach. Ecol Appl. 2018; 28(6):1520–33. https://doi.org/10.1002/eap.1687 PMID: 29345743

6. Beerkircher L, Cortés E, Shivji M. A Monte Carlo demographic analysis of the silky shark (*Carcharhinus falciformis*): implications of gear selectivity. Fish. 2003; 101:168–74.

7. Carlson JK, Cortés E, Bethea DM. Life history and population dynamics of the finetooth shark (*Carcharhinus isodon*) in the northeastern Gulf of Mexico. Fish Bull. 2003; 101(2):281–92.

8. Grant MI, Smart JJ, Rigby CL, White WT, Chin A, Baje L, et al. Intraspecific demography of the silky shark (*Carcharhinus falciformis*): implications for fisheries management. ICES J Mar Sci. 2020; 77 (1):241–55.

9. Barreto RR, Bornatowski H, Motta FS, Santander-Neto J, Vianna GMS, Lessa R. Rethinking use and trade of pelagic sharks from Brazil. Mar Policy. 2017; 85:114–22. Available from: http://dx.doi.org/10.1016/j.marpol.2017.08.016

10. ICMBio/MMA. Livro Vermelho da Fauna Brasileira Ameaçada de Extinção. 1 ed. Vols. VI-Peixes. Brasília: ICMBIO/MMA; 2018. 1235 p.

11. Compagno LJ V. FAO species catalogue. Vol. 4 Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2. Carcharhiniformes. Vol. 125, FAO Fisheries Synopsis. Rome; 1984.

12. Ebert DA, Stehman MF. Sharks, batoids, and chimaeras of the North Atlantic. Vol. 7, FAO Species Catalogue for Fishery Purposes. 2013. 56–66 p.

13. Castro JI. Resurrection of the name Carcharhinus cerdale, a species different from *Carcharhinus porosus*. aqua, Int J Ichthyol. 2011; 17(1):1–10.

14. Garrick J. Sharks of the genus *Carcharhinus*. NOAA Tech. Rep. NMFS, Circular, 1982; 445:1–194.

15. White W. A redescription of *Carcharhinus dussumieri* and *C. sealei*, with resurrection of *C. coatesi* and *C. tjutjot* as valid species (Chondrichthyes: Carcharhinidae). Zootaxa. 2012; 3241:1–34.

16. White WT, Kyne PM, Harris M. Lost before found: A new species of whaler shark *Carcharhinus obsolerus* from the Western Central Pacific known only from historic records. PLoS One. 2019; 14(1): e0209387. https://doi.org/10.1371/journal.pone.0209387 PMID: 30601867

17. White WT, Weigmann S. *Carcharhinus humani* sp. nov., a new whaler shark (Carcharhiniformes: Carcharhinidae) from the western Indian Ocean. Zootaxa. 2014; 3821:71–87. https://doi.org/10.11646/zootaxa.3821.1.5 PMID: 24989727

18. Sadowsky V. Selachier aus dem Litoral von Sao Paulo, Brasilien. Beitrage zur Neotropischen Fauna. 1967; 5(2):71–88.

19. Lessa RP. Levantamento faunístico dos elasmobrânquios (Pisces, Chondrichthyes) do litoral ocidental do estado do Maranhão, Brasil. Bol do Laboratório Hidrobiol. 1986; 7:27–41.

20. Lessa RP. Sinopse dos estudos sobre elasmobrânquios da costa do Maranhão. Bol do Laboratório Hidrobiol. 1997; 10:19–36.

21. Lessa RPT, Repinaldo-Filho FPM, Moro G, Charvet P, Santana FM. *Carcharhinus porosus*. In: Livro Vermelho da Fauna Brasileira Ameaçada de Extinção: Volume VI—Peixes. 1 ed. Brasília: ICMBIO/MMA; 2018. p. 950–3.

22. Feitosa LM, Martins APB, Giarrizzo T, Macedo W, Monteiro IL, Gemaque R, et al. DNA-based identification reveals illegal trade of threatened shark species in a global elasmobranch conservation hotspot. Sci Rep. 2018; 8(1):1–11. https://doi.org/10.1038/s41598-017-17765-5

23. Feitosa LM, Martins LP, Souza-Junior LA, Lessa RP. Potential distribution and population trends of the smalltail shark *Carcharhinus porosus* inferred from species distribution models and historical catch data. Aquat Conserv Mar Freshw Ecosyst. 2020; 31:1–10.

24. Lessa R, Almeida Z, Santana FM, Siu S, Perez M. *Carcharhinus porosus*, Smalltail Shark. IUCN Red List Threat Species. 2006;8235.

25. Brasil. Relatório do Grupo Tecnico de Trabalho sobre a Gestão da Pesca de Emalhe no Brasil–GTT/ Emalhe. 2011.

26. Stride RK, Batista VS, Raposo LA. Pesca experimental de tubarão com redes de emalhar no litoral maranhense. 3rd ed. São Luís: Universidade Federal do Maranhão; 1992. 160 p.

27. Paiva K de S, Aragão JAN, Silva KC de A, Cintra IHA. Fauna acompanhante da pesca industrial do camarão-rosa na plataforma norte brasileira. Bol Técnico Científico CEPNOR. 2009; 9:25–42.

28. Furtado-Júnior I, Tavares MC da S, Brito CSF. Avaliação do potencial da produção de peixes e camarões, com rede-de-arrasto de fundo na plataforma continental da região norte do Brasil (área de pesca do caramão-rosa). Bol Técnico Científico CEPNOR. 2002; 3(1):147–61.

29. Aragão JAN, Cintra IHA, Silva KCA, Vieira IJA. A explotação camaroeira na costa norte do Brasil. Bol Técnico Científico CEPNOR. 2001; 1:7–32.

30. Isaac VJ, Santo RVE, Bentes B, Frédou FL, Mourão KRM, Frédou T. An interdisciplinary evaluation of fishery production systems off the state of Para in North Brazil. J Appl Ichthyol. 2009; 25:244–55.

31. Marceniuk AP, Barthem RB, Wosiacki WB, Klautau AGC de M, Junior TV, Rotundo MM, et al. Sharks and batoids (Subclass Elasmobranchii) caught in the industrial fisheries off the Brazilian North coast. Rev Nord Biol. 2019; 27(1):120–42.

32. MMA. Instrução Normativa 05/2004. Brasília: Ministério do Meio Ambiente; 2004.

33. MMA. Instrução Normativa 52. Brasília: Ministério do Meio Ambiente; 2005.

34. Mourão KRM, Espírito-Santo RV do, Silva BB, Almeida MC, Isaac VJ, Frédou T, et al. A pesca de *Scomberomorus brasiliensis* e alternativas para o seu manejo no litoral nordeste do Pará - Brasil. In: Haimovici M, Andriguetto Filho JM, Sunye PS, editors. A pesca marinha e estuarina no Brasil: estudos de caso multidisciplinares. Rio Grande: Editora da FURG; 2014. p. 171–80.

35. Lessa R, Santana FM. Age determination and growth of the smalltail shark, *Carcharhinus porosus*, from northern Brazil. Mar Freshw Res. 1998; 49:705.

36. Lessa R, Almeida Z. Analysis of stomach contents of the smalltail shark *Carcharhinus porosus* from northern Brazil. Cybium. 1997; 21(2):123–33.

37. Lessa R, Santana F, Menni R, Almeida Z. Population structure and reproductive biology of the smalltail shark (*Carcharhinus porosus*) off Maranhão (Brazil). Mar Freshw Res. 1999; 50:383–8.

38. Lessa RP. Contribuição ao conhecimento da biologia de *Carcharhinus porosus* Ranzani, 1839 (PISCES, CHONDRICHTHYES) das Reentrâncias Maranhenses. Acta Amaz. 1986; 16/17:73–86.

39. Martins APB, da Silva Filho E, Feitosa LM, Nunes E Silva LP, de Almeida Z da S, Nunes JLS. Sexual dimorphism of sharks from the amazonian equatorial coast. Univ Sci. 2015; 20(3):297–304.

40. Feitosa LM, Dressler V, Lessa RP. Habitat Use Patterns and Identification of Essential Habitat for an Endangered Coastal Shark With Vertebrae Microchemistry: The Case Study of *Carcharhinus porosus*. Front Mar Sci. 2020; 7:1–12.

41. Tavares W, da Silva Rodrigues-Filho LF, Sodré D, Souza RFC, Schneider H, Sampaio I, et al. Multiple substitutions and reduced genetic variability in sharks. Biochem Syst Ecol. 2013 Aug; 49:21–9. http://www.sciencedirect.com/science/article/pii/S0305197813000379

42. Beverton RJ, Holt SJ. On the dynamics of exploited fish populations. 11th ed. Springer Science & Business Media; 2012.

43. Gedamke T, Hoenig JM, Musick JA, DuPaul WD, Gruber SH. Using Demographic Models to Determine Intrinsic Rate of Increase and Sustainable Fishing for Elasmobranchs: Pitfalls, Advances, and Applications. North Am J Fish Manag. 2007; 27(2):605–18. http://www.tandfonline.com/doi/abs/10.1577/M05-157.1

44. Pauly D. A selection of simple methods for the assessment of tropical fish stocks. Rome; 1980.

45. Jensen AL. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Can J Fish Aquat Sci. 1996; 53(4):820–2. http://www.nrcresearchpress.com/doi/abs/10.1139/f95-233

46. Rikhter VA, Efanov VN. On one of the approaches to estimation of natural mortality of fish populations. ICNAF Research Document, 1976; 76/VI/8:1–12.

47. Hoenig JM. A compilation of mortality and longevity estimates for fish, mollusks and cetaceans with a bibliography of comparative life history studies. University of Rhode Island, Graduate School of Oceanography, Technical Report Reference No. 1982;82–2:14 pp.

48. Hewitt DA, Hoenig JM. Comparison of two approaches for estimating natural mortality based on longevity. Fish Bull. 2005; 437:433–7.

49. Mollet HF, Cailliet GM. Comparative population demography of elasmobranchs using life history tables, Leslie matrices and stage-based matrix models. Mar Freshw Res. 2002; 53(2):503–16.

50. Peterson I, Wroblewski JS. Mortality Rate of Fishes in the Pelagic Ecosystem. Can J Fish Aquat Sci. 1984; 41:1117–20.

51. Chen S, Watanabe S. Age Dependence of Natural in Fish Population Mortality Coefficient Dynamics. Nippon Suisan Gakkaishi. 1989; 55(2):205–8.

52. Ricker WE. Calcul et Interprétation des Statistiques Biologiques des Populations de Poissons. Ottawa; 1980.

53. Hood GM. PopTools. 2006. http://www.cse.csiro.au/poptools

54. Simpfendorfer CA. Demographic models: life tables, matrix models and rebound potential. In: Musick J, Bonfil R (Eds.). Management Techniques for Elasmobranch Fisheries. FAO Fisher. Rome: Food and Agriculture Organization of the United Nations; 2005:143–53.

55. Kroon H de, Groenendael J Van, Ehrlen J. Elasticities: A Review of Methods and Model Limitations. Ecology. 2000; 81(3):607–18.

56. Cortés E. Demographic analysis of the Atlantic sharpnose shark, *Rhizoprionodon terranovae*, in Gulf of Mexico. Fish Bull. 1995; 93:57–66.

57. Otway NM, Bradshaw CJA, Harcourt RG. Estimating the rate of quasi-extinction of the Australian grey nurse shark (*Carcharias taurus*) population using deterministic age- and stage-classified models. Biol Conserv. 2004; 119(3):341–50.

58. IUCN. IUCN Red List Categories and Criteria: Version 3.1. 2nd ed. Gland, Switzerland and Cambridge, UK; 2012. 32 p.

59. Smith SE, Au DW, Show C. Intrinsic rebound potential of 26 species of Pacific sharks. Mar Freshw Res. 1998; 49:663–78.

60. García VB, Lucifora LO, Myers RA. The importance of habitat and life history to extinction risk in sharks, skates, rays and chimaeras. Proc R Soc B Biol Sci. 2008; 275(1630):83–9.

61. Branstetter S. Early Life-History Implications of Selected Carcharhinoid and Lamnoid Sharks of the Northwest Atlantic. 1990.

62. Lessa R, Batista V, Almeida Z. Occurence and biology of the daggernose shark *Isogomphodon oxyrhynchus* (Chondrichtyes: Carcharinidae) off the Maranhao coast (Brazil). Bull Mar Sci. 1999; 64 (1):115–28.

63. Lessa R, Santana FM, Batista V, Almeida Z. Age and growth of the daggernose shark, *Isogomphodon oxyrhynchus*, from northern Brazil. Mar Freshw Res. 2000; 51:339–47.

64. Hazin FH V, Oliveira PG, Broadhurst MK. Reproduction of the blacknose shark (*Carcharhinus acronotus*) in coastal waters off Northeastern Brazil. Fish Bull. 2002; 148(July 2001):143–8.

65. Barreto RR, Lessa RP, Hazin FH, Santana FM. Age and growth of the blacknose shark, *Carcharhinus acronotus* (Poey, 1860) off the northeastern Brazilian Coast. Fish Res. 2011; 110(1):170–6.

66. Machado MRB, Almeida Z da S, Castro ACL. Estudo da biologia reprodutiva de *Rhizoprionodon porosus* Poey, 1861 (Chondrychthyes: Carcharhinidae) na plataforma continental do estado do Maranhão, Brasil. Bol do Laboratório Hidrobiol. 2000; 13:51–65.

67. Lessa R, Santana FM, De Almeida ZDS. Age and growth of the Brazilian sharpnose shark, *Rhizoprionodon lalandii* and Caribbean sharpnose shark, *R. porosus* (Elasmobranchii, carcharhinidae) on the northern coast of Brazil (Maranhão). Panam J Aquat Sci. 2009; 4(4):532–44.

68. Lessa RP. Premières observations sur la biologie reproductive de *Rhizoprionodon* lalandei (Valenciennes, 1839) (Pisces, Carcharhinidae) de la côte nord du Brésil–Maranhão. Rev Bras Biol. 1988; 48:721–30.

69. Parsons GR. Age determination and growth of the bonnethead shark *Sphyrna tiburo*: a comparison of two populations. Mar Biol. 1993; 117(1):23–31.

70. Branstetter S, Stiles R. Age and growth estimates of the bull shark, *Carcharhinus leucas*, from the northern Gulf of Mexico. Environ Biol Fishes. 1987; 20(3):169–81.

71. Pirog A, Magalon H, Poirout T, Jaquemet S. Reproductive biology, multiple paternity and polyandry of the bull shark *Carcharhinus leucas*. J Fish Biol. 2019; 95:1195–206. https://doi.org/10.1111/jfb.14118 PMID: 31393599

72. Feldheim KA, Gruber SH, Ashley M V. Reconstruction of parental microsatellite genotypes reveals females polyandry and philopatry in the lemon shark, *Negaprion brevirostris*. Evolution. 2004; 58 (10):2332–42. https://doi.org/10.1111/j.0014-3820.2004.tb01607.x PMID: 15562694

73. Winter SP, Dudley SFJ. Age and growth estimates for the tiger shark, Galeocerdo cuvier, from the east coast of South Africa. Mar Freshw Res. 2000; 51:43–53.

74. Whitney NM, Crow GL. Reproductive biology of the tiger shark (Galeocerdo cuvier) in Hawaii. Mar Biol. 2007; 151:63–70.

75. Cortés E. Incorporating uncertainty into demographic modeling: Application to shark populations and their conservation. Conserv Biol. 2002; 16(4):1048–62.

76. Brewster-Geisz KK, Miller TJ. Management of the sandbar shark, *Carcharhinus plumbeus*: Implications of a stage-based model. Fish Bull. 2000; 98(2):236–49.

77. Liu KM, Chin CP, Chen CH, Chang JH. Estimating finite rate of population increase for sharks based on vital parameters. PLoS One. 2015; 10(11):1–20.

78. Martins APB, Feitosa LM, Lessa RP, Almeida ZS, Heupel M, Silva WM, et al. Analysis of the supply chain and conservation status of sharks (Elasmobranchii: Superorder Selachimorpha) based on fisher knowledge. PLoS One. 2018; 13(3):1–15.

79. ICMBIO/MMA. Portaria Nº 125. Brasília: Ministério do Meio Ambiente; 2014.

80. Palmeira CAM, Rodrigues-Filho LF da S, Sales JB de L, Vallinoto M, Schneider H, Sampaio I. Commercialization of a critically endangered species (largetooth sawfish, *Pristis perotteti*) in fish markets of northern Brazil: Authenticity by DNA analysis. Food Control. 2013; 34(1):249–52. http://dx.doi.org/10.1016/j.foodcont.2013.04.017

81. Rodrigues-Filho LF, Feitosa LM, Nunes JLS, Palmeira ARO, Martins APB, Giarrizzo T, et al. Molecular identification of ray species traded along the Brazilian Amazon coast. Fish Res. 2020; 223:105407. https://doi.org/10.1016/j.fishres.2019.105407

82. Almeida Z da S de, Santos NB, Carvalho-Neta RNF, Pinheiro A de LR. Análise multidisciplinar das pescarias de emalhe da pescada-amarela, de camarão de puçá de muruada e da catação de caranguejo uçá em três municípios costeiros do Maranhão. In: Haimovici M., Andriguetto Filh JM, Sunye PS, editors. A pesca marinha e estuarina no Brasil: estudos de caso multidisciplinares. Rio Grande: Editora da FURG; 2014. p. 161–70.

83. IBAMA—Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis. Proposta de Plano de Gestão para o uso sustentável de Elasmobrânquios sobre-expotados ou ameaçados de sobre-explotação no Brasil. In: Ibama; MMA. 2011. p. 154.

84. Menni RC, Lessa RP. The chondrichthyan community off Maranhão (northeastern Brazil) II. Biology of species. Acta Zool Lilloana. 1998; 44(1):69–89.

85. Feitosa LM, Martins APB, Nunes JLS. Sawfish (Pristidae) records along the Eastern Amazon coast. Vol. 34, Endangered Species Research. 2017. p. 229–34.

86. Feitosa LM, Martins APB, Lessa RP, Barbieri R, Nunes JLS. Daggernose Shark: An Elusive Species from Northern South America. Fish. 2019; 44(3):144–7.

87. Lessa R, Santana FM, Rincón G, Gadig OBF, El-Deir ACD. Biodiversidade de elasmobrânquios do Brasil. Recife: Ministério do Meio Ambiente; 1999. 1–154 p.

88. Dulvy NK, Fowler SL, Musick J a, Cavanagh RD, Kyne PM, Harrison LR, et al. Extinction risk and conservation of the world's sharks and rays. Elife. 2014; 3:e00590. https://doi.org/10.7554/eLife.00590 PMID: 24448405

89. Knip DM, Heupel MR, Simpfendorfer CA. Sharks in nearshore environments: Models, importance, and consequences. Mar Ecol Prog Ser. 2010; 402:1–11.

90. Hazin FHV, Afonso AS, De Castilho PC, Ferreira LC, Rocha BCLM. Regional movements of the tiger shark, *Galeocerdo cuvier*, off Northeastern Brazil: inferences regarding shark attack hazard. An Acad Bras Cienc. 2013; 85(3):1053–62. https://doi.org/10.1590/S0001-37652013005000055 PMID: 24068092

91. Oliver S, Braccini M, Newman SJ, Harvey ES. Global patterns in the bycatch of sharks and rays. Mar Policy. 2015; 54:86–97.

92. Salas S, Chuenpagdee R, Charles A, Seijo JC. Coastal fisheries of Latin America and the Caribbean. Rome: FAO; 2011. 430 p.