

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Original research article

Close to extinction? The collapse of the endemic daggernose shark (*Isogomphodon oxyrhynchus*) off Brazil

Rosangela Lessa^{a,*}, Vandick S. Batista^b, Francisco M. Santana^c^a Laboratório de Dinâmica de Populações Marinhas (DIMAR), Departamento de Pesca e Aquicultura (DEPAq), Universidade Federal Rural de Pernambuco (UFRPE), R. Dom Manoel de Medeiros, S/N, Dois Irmãos, Recife-PE, CEP 52171 – 900, Brazil^b Instituto de Ciências Biológicas e da Saúde, Campus A. C. Simões - Av. Lourival Melo Mota, s/n - Tabuleiro do Martins - Maceió, AL - CEP: 57072-970, Brazil^c Unidade Acadêmica de Serra Talhada (UAST), Universidade Federal Rural de Pernambuco (UFRPE), Av. Gregório Ferraz Nogueira, S/N, Serra Talhada-PE, CEP 56909-535, Brazil

HIGHLIGHTS

- The demography of *Isogomphodon oxyrhynchus* indicates a sharp decline in population.
- The juveniles were the most important for the sustainability of the species.
- The daggernose shark was one of the least resilient shark of northern Brazil.
- Fishing mortality was the cause of the daggernose shark collapse.
- The species is considered well on the way of extinction.

ARTICLE INFO

Article history:

Received 29 December 2015

Received in revised form 26 April 2016

Accepted 26 April 2016

Available online 25 May 2016

Keywords:

Chondrichthyes

Elasmobranch conservation

Extinction risk

IUCN Red List

Equatorial Atlantic

Amazonian estuary

ABSTRACT

The daggernose shark, *Isogomphodon oxyrhynchus* is endemic to the northern of South America from Trinidad and Tobago to Tubarão bay in Maranhão state (Brazil) where collapsed since the 1990's, due to several gillnet fisheries for teleost fishes, fisheries targeting sharks, including the daggernose shark, itself, and trawling for shrimp. Based on gillnets with meshes 80–>200 mm, we analyzed the intrinsic and extrinsic vulnerabilities of the species through different scenarios investigating the species' resilience. Samples were collected from December 1989 to September 1991, off the coast of Maranhão. Mortalities were $M = 0.188$ and $Z = 0.653$ for males and 0.725 in females. Only a scenario without fishing allowed for the population to remain in equilibrium. The survival of young specimens between 1 to 6 years was critical to sustainability according to elasticities that exceeded 70%. The intrinsic rebound (r_z) of 0.039, demonstrated the species low resilience. An unsustainable exploitation was revealed for different ages at first capture (t_c) when the maximal yield per recruit (YPR) provided F_{max} (0.15), below the actual $F = 0.47$ in 1991 when an exploitation rate $E = 0.72$ was obtained. Using data collected in 1980/1990 the species was globally categorized in 2006 as critically endangered (CR) similar to assessments in Brazil in 2004. After a three-generation period the species, which did not recover, is now collapsed matching the predicted quasi-extinction condition which claims for urgent and effective conservation measures.

© 2016 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

* Corresponding author.

E-mail address: rptlessa@gmail.com (R. Lessa).

1. Introduction

The daggernose shark (*Isogomphodon oxyrinchus*, Müller and Henle 1839) occurs along the northern coast of South America, in an area limited in the North by Trinidad and Tobago and in the South by the Tubarão bay in the Brazilian state of Maranhão (2°30'S/43°30'W), where the species has its southern most confirmed registration. The distribution area also includes Suriname, the Guyanas and the states of Amapá and Pará in Brazil (Bigelow and Schroeder, 1948; Lessa and Araújo-Filho, 1984; Barthem, 1985; Lessa et al., 1999; Léopold, 2004). Along the area the daggernose shark is also named “quati” or “pato” (Brazil) and “bécune” or “demoiselle” (French Guyane) (Fig. 1).

The species dwells in an area with a hot humid climate, in shallow and highly turbid waters derived from the drainage of numerous large rivers composing the Amazonian Estuary where muddy bottoms, covered by mangroves dominate along a well indented coastline with tides attaining a height of 7 m (Lessa et al., 1999; Léopold, 2004).

The range of distribution of the daggernose shark situated this species among the living sharks which occupy the narrowest areas in the world (Lessa et al., 2000) with records of occurrence to the south of Maranhão state in Brazil and to the north/west of Trinidad and Tobago, never confirmed (Casselberry and Carlson, 2015).

In the study area, the daggernose shark ranked fourth and first most abundant by-catch species in gillnets, the main gear targeting the Brazilian Spanish mackerel, *Scomberomorus brasiliensis* Collette, Russo and Zavalla-Camin (1978), and the weakfish *Cynoscion acoupa*, (Lacepède, 1801), respectively, during the 1980's and 1990's. Overall, the species corresponded to about 10% of shark captures of the first quoted exploitation, reaching 71 kg/km⁻¹ in the second (Lessa, 1986; Stride et al., 1992). The daggernose shark was also caught as a bycatch species in gillnets targeting the gillbacker-sea-catfish (*Sciades parkeri*), as a target in gillnets fisheries off the Amapá (Brazil) (Nascimento and Asano-Filho, 1999), in trawlings directed to *Penaeus* spp and in longlines all over the area (Frédou and Asano-Filho, 2006). In consequence, since the 1990's, catches have decreased in abundance by 90% (Lessa et al., 2006; Rodrigues-Filho et al., 2009; Almeida et al., 2014) leading the daggernose shark to be assessed by the IUCN as Critically Endangered-CR in 2006.

Although population data is lacking for Trinidad and Tobago, in the Guyanas and Suriname, the decline of the species in these countries should be similar to what happened in Brazil due to high fishing pressure over the targeted species. Also, the high value of by-products of teleosts (Almeida et al., 2014) and fins of sharks boosted gillnet fisheries.

The available information on the daggernose shark, apart from the taxonomic descriptions (Bigelow and Schroeder, 1948; Compagno, 1984) and paleontological records (Bassedick et al., 1984), is restricted to the northern Brazilian coast focusing on abundance (Lessa, 1986; Stride et al., 1992; Frédou and Asano-Filho, 2006), community studies (Lessa and Menni, 1994), reproduction (Stride et al., 1992; Lessa et al., 1999), age and growth (Lessa et al., 2000) and genetic studies by Rodrigues-Filho et al. (2009). Despite them, information about the resilience of the species is limited, not allowing the identification of the actual conservation status.

In the current study we analyzed the collapse of the daggernose shark in a large part of its habitat, off northern Brazil. For this, we proposed likely scenarios built using different levels of natural mortality with the aim of estimating intrinsic susceptibility. By employing age-based approaches (catch-curves and YPR) we analyzed the fishing mortality in the 1990's.

2. Material and methods

Data on the biology of *I. oxyrinchus* was obtained on the west coast of Maranhão state (46°W to 43°40'00"W) (Fig. 1) where 1135 individuals were collected using gillnets from December 1989 to September 1991. Overall, data came from fisheries surveys, aimed at developing shark fishing, which was common place at that time (Stride et al., 1992). Also, data collected from 1987 to 1989 in artisanal fishing operations for *Scomberomorus brasiliensis* were used (Lessa et al., 1999).

Length frequency distributions using total length (TL) were established by sex with overall sexual proportion of 1 male: 1.26 females. Males ($n = 503$) were between 60.6 and 127 cm, the mean length (\bar{x}) being 98.7 cm, with standard deviation (SD) = 1.4 cm, and median size (\tilde{x}) 99 cm; whereas females ($n = 632$) measured from 58 to 160 cm, with the mean length $\bar{x} = 121.8$ cm, with standard deviation (SD) of 2.5 cm, and median size $\tilde{x} = 128$ cm.

Information on age and growth was provided through vertebral analysis (Lessa et al., 2000). The growth model was combined as there was no difference between sexes. The von Bertalanffy growth parameters were obtained: $L_{\infty} = 171.4$ cm; $K = 0.121$ and $t_0 = -2.612$ years. Maximal age (t_{max}) in the study sample was 12 years, with first maturity achieved (t_{mar}) at 6.6 years. Furthermore, the ratio of embryos by sex was 1:1 and the size at maturity was estimated at 115 cm TL for females (Lessa, 1987; Stride et al., 1992; Lessa et al., 1999).

Stride et al. (1992) analyzing 53 pregnant females observed fecundity ranging from 1 to 8 embryos, leading to the mean of 4.85 embryos ($SD = 1.56$ embryos). The gestation period extends over one year, with a resting period seeming to occur between two successive cycles (Lessa et al., 1999). Thus, as for several species of the Carcharhinidae family, the reproductive cycle in the current study was 2 years. The fertility (m_x) of the species (i.e.: females embryos born of each pregnant female per year) resulted in a mean value of 1.21.

The instantaneous rate of mortality (Z) allowed for the estimation of intrinsic susceptibility and to infer the vulnerability of the population without fishing exploitation. For natural mortality (M), nine age-independent and two age-dependent methods were considered, all based on parameters of life history of the species. Weight-length relationship of females, used for obtaining (M) through the Peterson and Wroblewski approach was: $W = 0.0022TL^{3.1514}$ ($r^2 = 0.9692$; $n = 110$) (Lessa et al., 1999).

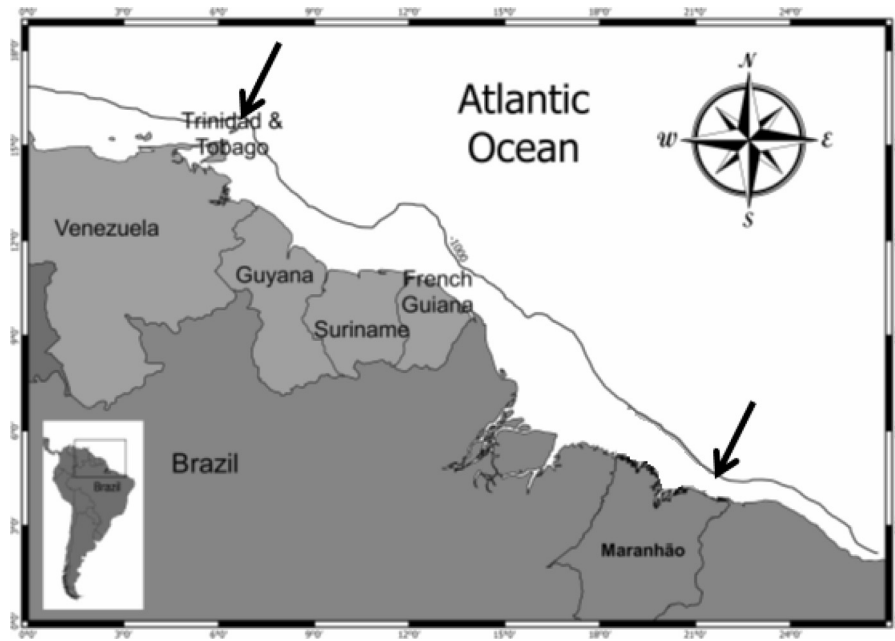


Fig. 1. Geographic range area (between arrows) of *Isogomphodon oxyrinchus*.

The rate of total mortality (Z) estimated by using the catch-curve (Ricker, 1975) took into account different sexes. The total mortality (Z) was split into natural mortality rate (M) and fishing mortality rate (F); survival values (S) for each mortality rate were estimated using: $S = e^{-Z}$ (Ricker, 1975).

Additionally, aiming at analyzing the fishing levels to which the daggenose shark was subjected we calculated $E = F/Z$ (Pauly, 1980), which allowed the rough assessment of whether the stock was overfished or not—on the assumption that the optimal is $E \approx 0.5$, which provides a reference point for sustainability.

The age-based Leslie matrix of the PopTools program (Hood, 2006) of the Microsoft Excel software was employed. The age-based matrix (L) was a Leslie population projection matrix, adopting a pre-breeding census (reproduction first, then survival):

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

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.

On the basis of Leslie matrix (L), the population parameters were obtained employing the formula by Simpfendorfer (2005): 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) (Mollet and Cailliet, 2002).

The matrix L , to estimate the stable age distribution and elasticities (e_{ij}), corresponding to the survivorship by age and fertility were used. For elasticity estimations of λ (proportional change in λ for proportional changes in matrix L , denominated a_{ij}), the values of each age and fertility are additive. Thus, the sum of these elasticities values define the proportional contribution of a_{ij} to the overall population λ . Elasticity is calculated as:

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

Also, the intrinsic rebound potential or intrinsic rate of increase (r_z) for *I. oxyrinchus* was estimated according to Smith et al. (1998).

For female abundance in the exploited population of Maranhão, the methods by Krebs (1998) were used. The Eberhardt's removal method allowed inferences on population size, considering the removal (before and after) of a given number of individuals, and the use of indices to estimate absolute density. Thus, the population size for both sexes was worked out. The formula for population size (\hat{N}) was: $\hat{N} = \frac{x_1 R}{x_1 - x_2}$, where x_1 and x_2 were the index at time 1 and 2, and R was the number of animals removed.

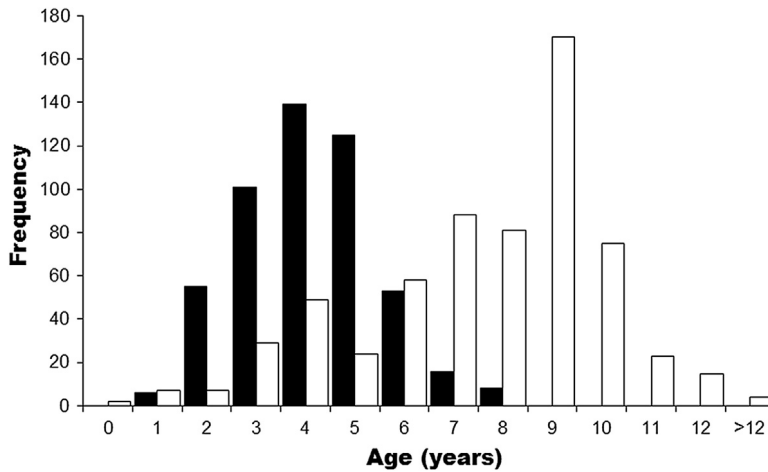


Fig. 2. Age frequency distribution of males (black bars) and females (white bars) of *Isogomphodon oxyrhynchus* off northern Brazil (Maranhão).

The information on abundance was used to estimate the quasi-extinction (Q_t) rate. According Otway et al. (2004), Q_t is defined as the time necessary for the population to be reduced fitting the IUCN criterion for species classified as Critically Endangered.

$$Q_t = \frac{\ln\left(\frac{N_t}{\hat{N}_1}\right)}{\ln \lambda} \quad \text{and} \quad N_t = \hat{N}_1 e^{rt}$$

where t is the time of quasi-extinction (Q_t), N_t is the final population size (250 females) and \hat{N}_1 is the initial population size (abundance).

The fishing mortality rate necessary to drive the species to extinction ($F_{extinct}$) was estimated according to Garcia et al. (2008). This mortality rate is equivalent to the maximum intrinsic rate of population increase (r_{max}), which is a standard measure of population productivity (Dulvy et al., 2004) and of extinction risk. The estimated $F_{extinct}$ was obtained from interactions using the equation:

$$m_x = e^{\left\{F_{extinct} \times [t_{mat} - t_c + 1] \times \left[1 - e^{-(M + F_{extinct})}\right]\right\}}$$

where t_c is the age at first capture or the age at which fishes enter the fishery.

Moreover, through the yield per recruit model (YPR) we considered strategies of exploitation for age at first capture t_c , determined from the age frequency distribution—ages 3–6 years. The intention was to estimate the fishing mortality (F_{max}) that would guarantee the stock replacement, allowing comparisons between (F_{max}) and the actual value of F . In this way, we inferred how much the level of sustainability had been extrapolated. Using this approach our aim was to explain the declines experienced by the stock.

The yield per recruit (YPR) was estimated following the model by Gulland (1983):

$$YPR = F \times \exp^{-M \times (t_c - t_r)} \times W_\infty \times \left(\frac{1}{Z} - \frac{3S}{Z + k} + \frac{3S^2}{Z + 2k} - \frac{S^3}{Z + 3k} \right)$$

where t_r is the age of recruitment to fisheries; W_∞ is the asymptotic weight and S corresponds to the equation $\exp^{-k \times (t_c - t_0)}$.

3. Results

Age distribution of males and females sampled showed significant differences (Mann–Whitney U -test, $P < 0.001$) ranging from 1.0 to 8.6 years for males ($\bar{x} = 4.6$ years, $\tilde{x} = 4.5$ years, $s = 1.4$ years) of which 89.9% were juveniles. On the other hand, the majority of females (76.3%) were adults, aged from 0.8 to >12 years ($\bar{x} = 8.0$ years, $\tilde{x} = 8.7$ years, $s = 2.5$ years) (Fig. 2) (see Table 1).

Mortality rates (M) ranged from 0.447 for age 0 to 0.062 for age 12, according to the Chen and Watanabe’s method. Considering age independent approaches the estimated M ranged from 0.182 using Jensen 2 to 0.384 using the Mollet and Cailliet’s method (Table 2). The average rate of natural mortality and rate of survival for all ages and all methods were 0.266 ($SD = 0.081$) and 0.769 ($SD = 0.063$), respectively. The rate of total mortality estimated from the catch curve for females was 0.653, whereas for males it was 0.725 (Fig. 3), corresponding to survival rates of 0.520 and 0.484 respectively. Taking into account the natural mortality of 0.188, fishing mortality rates (F) for males and females were 0.537 and 0.465 respectively, resulting in exploitation rates (E) of 0.741 and 0.712, indicating overexploitation.

Table 1

Methods and formulae used to estimate natural mortality (M) of *Isogomphodon oxyrhynchus*. L_{∞} —asymptotic length, K —growth coefficient, T —mean annual water temperature (28 °C), t_{mat} —Age at female maturity, t_{max} —maximal age observed, W_t —weight (in grams) of the specimen at age t and t_0 —theoretical age at zero length.

Method	Equation
<i>Age-independent</i>	
Pauly (1980)	$\ln M = -0.0152 - [0.279 \ln(L_{\infty})] + [0.6543 \ln(K)] + [0.463 \ln(T)]$
Jensen (1996) 1	$M = 1.6K$
Jensen (1996) 2	$M = 1.5K$
Jensen (1996) 3	$M = \frac{1.65}{t_{mat}}$
Rikhter and Efanov (1976)	$M = \left(\frac{1.521}{t_{mat}^{0.72}}\right) (-0.155)$
Hoinig (1982) for teleosts	$\ln M = 1.46 - 1.01 [\ln(t_{max})]$
Hoinig (1982) for cetaceans	$\ln M = 0.941 - 0.873 [\ln(t_{max})]$
Hewitt and Hoinig (2005)	$M = \frac{4.22}{t_{max}}$
Mollet and Cailliet (2002)	$M = \frac{\ln(0.01)}{t_{max}}$
<i>Age-dependent</i>	
Peterson and Wroblewski (1984)	$M = 1.92 W_t^{-0.25}$
Chen and Watanabe (1989)	$M_{(t)} = \left[\frac{K}{1 - e^{-k(t-t_0)}}\right], M_{(t, t_{max})} = \left[\frac{1}{(t_{max} - t)}\right] \times \ln \left[\frac{(e^{K t_{max}} - e^{K t_0})}{(e^{K t} - e^{K t_0})}\right]$

Table 2

Demographic parameters and elasticities by M method (e_1 , e_2 and e_3 = sum of elasticities of fertility, juvenile survival and adult survival, respectively) of *Isogomphodon oxyrhynchus*.

Method	M value	λ	r (year ⁻¹)	R_0	T (years)	e_1	e_2	e_3
Peterson and Wroblewski (1984)	0.431–0.179	0.950	−0.053	0.667	9.184	0.110	0.662	0.227
Chen and Watanabe (1989)	0.447–0.066	0.987	−0.014	0.932	9.406	0.108	0.647	0.245
Pauly (1980)	0.275	0.941	−0.062	0.624	8.907	0.112	0.674	0.213
Rikhter and Efanov (1976)	0.237	0.976	−0.026	0.852	8.965	0.112	0.674	0.214
Hewitt and Hoinig (2005)	0.352	0.870	−0.140	0.319	8.959	0.113	0.676	0.211
Hoinig (1982) for teleosts	0.350	0.872	−0.138	0.323	8.961	0.113	0.676	0.211
Hoinig (1982) for cetaceans	0.293	0.923	−0.081	0.525	8.974	0.112	0.675	0.213
Jensen (1996) 1	0.194	1.018	0.016	1.243	8.987	0.112	0.673	0.215
Jensen (1996) 2	0.182	1.034	0.032	1.430	8.934	0.112	0.672	0.216
Jensen (1996) 3	0.251	0.960	−0.042	0.743	9.974	0.112	0.674	0.214
Mollet and Cailliet (2002)	0.384	0.842	−0.173	0.244	8.958	0.113	0.677	0.210

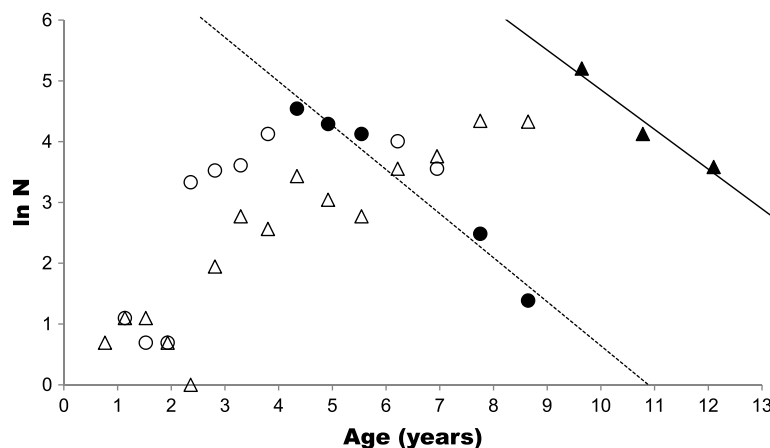


Fig. 3. Catch curve of males (circles) and females (triangles) of *Isogomphodon oxyrhynchus* caught off northern Brazil (Maranhão). Black points were used for the regression to estimate Z .

If we consider scenarios built using natural mortality rates, obtained through distinct approaches, there were not large variations between demographic parameters, with a λ around the mean of 0.943 ($SD = 0.062$). The majority of scenarios displayed values below the equilibrium ($\lambda < 1$) and the fertility elasticity (e_1), and survival elasticities of juveniles (e_2) and adults (e_3) showing also narrow ranges (Table 2).

Table 3

Demographic parameters (with lower/upper approximate confidence limits) and elasticities by scenario 1 ($M = 0.188$ constant for age class), 2 ($Z = 0.653$ from the fishing recruitment age of nine years-old for females) and 3 ($Z = 0.391$ between age classes four and nine years-old, corresponding to proportion of Z for males) of *Isogomphodon oxyrinchus*.

Scenario	λ	r (year ⁻¹)	R_0	T (years)	e_1	e_2	e_3
1	1.029	0.028	1.288	8.926	0.113	0.675	0.212
2	1.003	0.003	1.030	8.424	0.119	0.713	0.169
3	0.909	-0.095	0.453	8.305	0.119	0.715	0.166

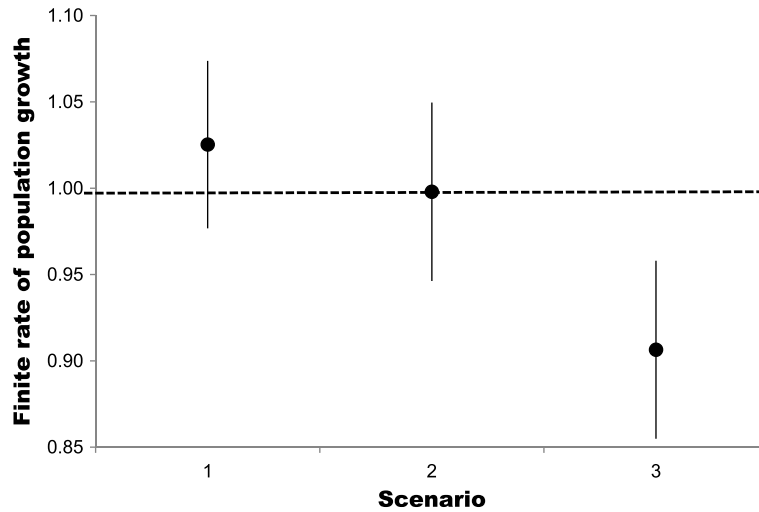


Fig. 4. Finite rate of population growth (λ) values (mean – point and standard deviation – bars) for different scenarios of *Isogomphodon oxyrinchus* population caught off northern Brazil (Maranhão). The dashed line corresponds to the population equilibrium ($\lambda = 1$).

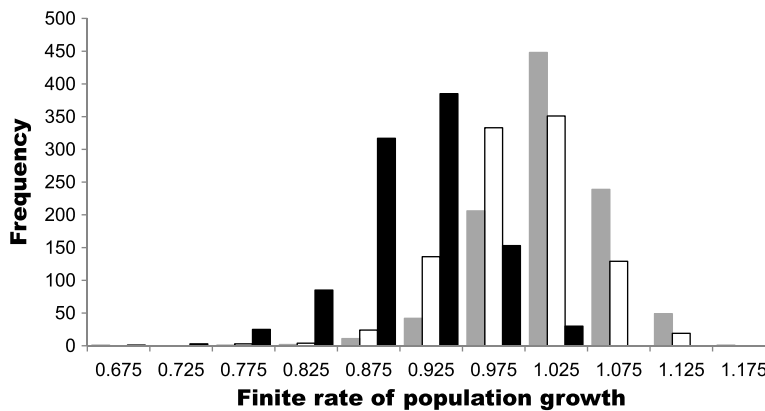


Fig. 5. Frequency distributions of simulations by scenario of life-history table (1000 finite rate of population growth– λ) of *Isogomphodon oxyrinchus* captured off northern Brazil (Maranhão). Histograms are presented for scenarios simulating constant M by age class (gray bars); F starting from the age of fishery recruitment for females (white bars) and the current scenario (F starting from the age of recruitment for males and females—black bars).

Although there was little variation in demographic parameters and in elasticities, for most natural mortality rates, λ were smaller than 1, indicating natural declines of the population, which explains why they were not considered. Instead, only the mean natural mortality obtained through Jensen 1 and 2 were chosen, leading to $M = 0.188$ ($S = 0.829$).

Three scenarios were deemed for the demography of *I. oxyrinchus*. In the first one, the median natural mortality rate through the method of Jensen 1 and 2 for all ages, replicated a hypothetical scenario of absence of fishing exploitation. As expected, this scenario led the population near the equilibrium, with annual increase of population of 2.8% (Table 3) and $\lambda > 1$ (Figs. 4 and 5). When analyzing the stable age distribution and elasticities by age class in this scenario, the importance of the survival of the young (<7 years) in this population is evident, with proportion of stable age distribution and elasticity for this phase corresponding to 78.5 and 67.5% (Figs. 6 and 7).

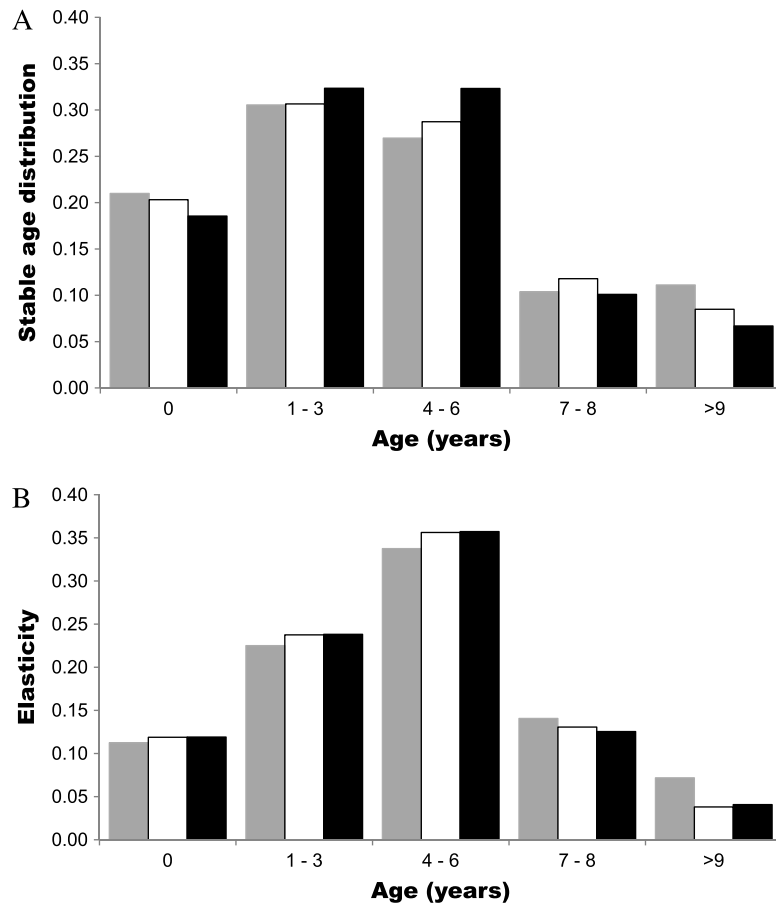


Fig. 6. Stable age distribution (A) and elasticity (B) by stages of life cycle (0 = Neonates, 1–3 years = juveniles; 4–6 years = large juveniles–subadults; 7–8 years = adults and >9 years = large adults). Scenarios are represented by gray (1), white (2) and black columns (3).

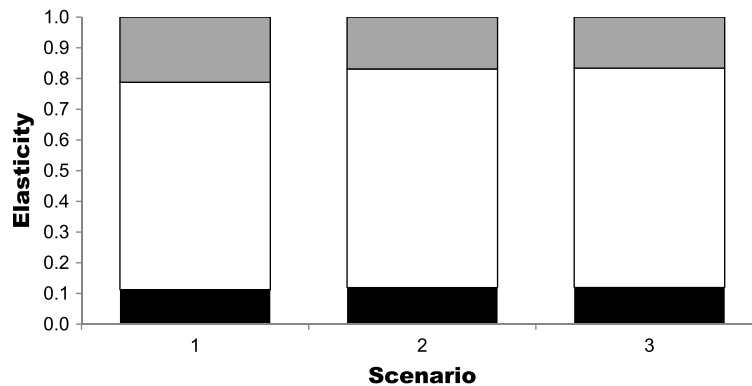


Fig. 7. Elasticity for each scenario; bars represent fertility elasticity (black) and survival elasticity for juveniles (white) and adults (gray).

In scenario two a total mortality rate of (0.653) was estimated for females from the fishing recruitment age of 9 years, which led the population close to the equilibrium (Table 3, Fig. 4)—with 50% of λ values greater than 1 (Fig. 5). The highest importance of the survival was estimated for young totaling 79.7% and the elasticity of 71.3% (Figs. 6 and 7).

The third scenario was considered the most plausible and accurate, as it took into account total mortality of males, starting with 4 years of age. Some females were also captured before fishing recruitment at 9 years. On the base of total mortality rate for males ($Z = 0.725$), the proportional value of Z to the number of females in age classes 4–8 years led to $Z = 0.391$. For this scenario, the mortality rate M (0.188) was used for age classes between 0 and 3 years, $Z = 0.391$ was used for age classes between 4 and 8 years, and 0.653 for ages 9 and older. The population decline was more important, with an annual population decrease of about 10% (Table 3, Fig. 4), and only 3% of λ values greater than 1 (Fig. 5). Furthermore, it is clear

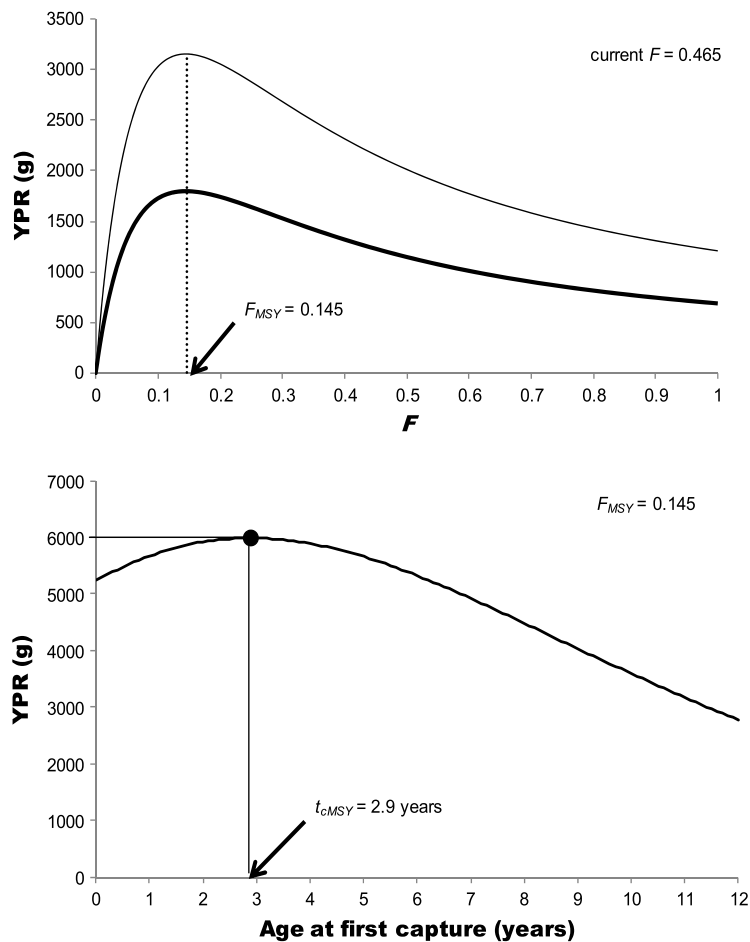


Fig. 8. Yield per recruit (YPR) curves by fishing mortality (F) for age at first capture (t_c) of 3 (simple line) and 6 (bold line) years (A) and with different values of t_c when applying a value of F_{MSY} (B) of *Isogomphodon oxyrinchus*. t_{cMSY} corresponding to age at first capture to maximum sustainable yield.

that the survival of young aged between 1 and 6 years was critical to the population (Fig. 6), with about the same values of elasticity as in scenario 2 (Fig. 7).

The population size of 4252 individuals was estimated. Thus, we considered 4000 as the number of females in the population, which would become extinct in 29 years (Q_t), when that number would be reduced to 250 females, thus leading the taxon to be included into Critically Endangered category according to Criteria of IUCN (Standards and Petitions Subcommittee, 2014).

The three scenarios show the importance of the survival of young females. The elasticities and age distribution reveal that the females in the younger classes were the most important, since they represented more than 70% of elasticities (Fig. 5). The intrinsic rebound (r_z) was 0.039, confirming the low resiliency of the species.

The $F_{extinct}$ which was 0.535 for *I. oxyrinchus*, higher than the fishing mortality rate (F) for females (0.465) and near to the F value of males (0.537), constitutes a mortality close to the level that could drive the species to extinction.

Regarding the YPR, we assumed that the age of first capture was 3–6 years, implying that 50% of the fishing stock would be in that range. The F_{max} ($F \approx 0.15$) attained the maximal MSY, for a t_c of 2.9 years, declining soon after, as F increased (Fig. 8).

4. Discussion

4.1. Intrinsic and extrinsic susceptibilities

In the current assessment, daggernose sharks are assumed to be a single population along the area from Trinidad and Tobago to Maranhão at Tubarão Bay ($2^{\circ}30'S/43^{\circ}30'W$), which is supported by consistent population parameters and seasonal movements. In the current study we showed that juveniles dominate in catches of different mesh sizes. Overall, fishing nets employed to catch the Brazilian Spanish mackerel, the weakfish, the gillbacker-sea-catfish, captured the entire range of sizes of the studied species. However, size composition in shrimp trawls and in bottom longlines targeting the

Table 4

Comparative finite rate of population growth (λ), generation time (T) and elasticities (e_1 = sum of elasticities of fertility, e_2 = sum of juvenile survival and e_3 = sum of adult survival) values for coastal carcharhinid sharks. All values were estimated using only natural mortality by Peterson and Wroblewski (1984) method, in Cortés (2002) (except for *Isogomphodon oxyrinchus* of present study).

Species	λ	T (years)	e_1	e_2	e_3
<i>Carcharhinus acronotus</i>	0.847	4.2	0.191	0.472	0.336
<i>Isogomphodon oxyrinchus</i>	0.950	9.2	0.110	0.662	0.227
<i>Carcharhinus limbatus</i>	0.974	10.0	0.093	0.600	0.306
<i>Carcharhinus leucas</i>	0.998	21.6	0.044	0.774	0.181
<i>Carcharhinus plumbeus</i>	1.022	19.8	0.048	0.693	0.259
<i>Carcharhinus obscurus</i>	1.030	26.2	0.037	0.679	0.285
<i>Carcharhinus brevipinna</i>	1.037	10.4	0.088	0.614	0.298
<i>Rhizoprionodon terraenovae</i>	1.056	4.9	0.169	0.475	0.356
<i>Negaprion brevirostris</i>	1.064	16.4	0.057	0.700	0.242
<i>Rhizoprionodon taylori</i>	1.073	2.9	0.261	0.227	0.512
<i>Carcharhinus porosus</i>	1.086	8.4	0.107	0.582	0.312
<i>Galeocerdo cuvier</i>	1.246	10.9	0.084	0.699	0.217

weakfish throughout the area remains still unknown (Frédou and Asano-Filho, 2006). The combined effect of several gear fishing on a highly threatened species render possible the access to shelter areas thus exceeding the growth capacity of the already reduced population (Vooren and Klippel, 2005).

Among biological traits that resulted in low intrinsic population growth rates for the daggernose shark [low fecundity, 2–8 embryos, one year gestation period and an assumed biennial reproductive cycle], the average natural mortality rate (M) of 0.266 (ranging from 0.447 for age 0 to 0.062 for age 12) was consistent with findings for the Carcharhinidae family (Smith et al., 1998; Santana et al., 2009). Also, small coastal sharks may have M , equal to or higher than 0.2, as happens to *Squatina californica* (Cailliet et al., 1992), *Rhizoprionodon terraenovae* (Cortés, 1995). In the case of *I. oxyrinchus*, M higher than 0.2, implied population decrease, which is compatible with large coastal sharks, demonstrating the species low resilience. Thus, when using only the Jensen (1996) 1 and 2 models, the resulting $M = 0.188$ ($S = 0.829$) allowed the population to increase to close to the equilibrium, justifying the choice of such an approach.

Different methods provided varying M values for *I. oxyrinchus*, as those obtained for coastal sharks like *C. isodon* (Carlson et al., 2003). However, there is no consensus on methods for M estimations, due to the uncertainties and performance of each method.

A mean λ around 0.943 (SD = 0.062) led for most scenarios to values below the equilibrium ($\lambda < 1$), while fertility elasticities (e_1), and elasticities of juveniles (e_2) and adult survival (e_3) showed small variations. Furthermore, the daggernose shark's low resilience is corroborated by its productivity (r_z) that is close to that of large coastal sharks, the most vulnerable group among all sharks. This productivity is inversely proportional to the age of sexual maturation (Smith et al., 1998), which in *I. oxyrinchus* starts from 7 years, leading to a low r_z , which reinforces the species vulnerability to overexploitation.

According to the stable age distribution and elasticities, young females between 1 and 6 years accounted for 65%–70% of the population. Elasticities corresponding to the survival of young individuals were most significant for *I. oxyrinchus*, identical to species studied by Cortés (2002) (Table 4). These results imply that gillnets with smaller meshes caused the most damage, since catches of younger individuals occurred in higher numbers.

In all, prevalence of juveniles in catches was considered to be determinant for the collapse of the daggernose shark, since results demonstrated that they were the most important for the sustainability. Overall, the elasmobranchs have low fertility, a trait that is particularly important in the present study. Low fertility of *I. oxyrinchus*, combined with high catchability of young individuals, determined a low λ , revealing that the species was one of the least resilient of coastal sharks (Table 4).

The high mortality rates of young individuals caused a significant decrease in the reproductive stock, leading the number of new recruits to diminish, thus contributing to population reduction.

Among the extrinsic causes of risk, fishing mortality (F) appears as the main stressor when the species displays high catchability (Dulvy et al., 2004). Thus, among methods for assessing population vulnerability, the yield per recruit model provides a reference point for the limits of declines beyond which populations are at risk (Cortés, 2002).

In this regard, total mortality rate $Z = 0.653$ for females, led to a fishing mortality of $F = 0.47$ and to an exploitation rate (Gulland, 1983) $E = 0.72$, indicating that the daggernose shark capture was unsustainable. Furthermore, when YPR was analyzed, unsustainable exploitation was also revealed for any age at first capture (t_c) since the estimated F value ($F = 0.47$) was far beyond the F_{\max} , which would guarantee the stock replacement. In most elasmobranch studies, the predicted maximum YPR was considered unlikely to be sustainable (Cortés, 2001). Thus, Waring (1984), obtaining Z from age-based catch curves concluded that the F value which maximized YPR, could lead to overexploitation due to low fertility of *Raja erinacea*. On the contrary, the current study, F_{\max} being quite low, showed low productivity of the population that led to the daggernose shark's collapse, since the ability to withstand that level of mortality was exceeded.

In addition, the YPR model showed important declines for each (t_c) soon after the F_{\max} was attained, corroborating with results of scenarios above, built for estimating the intrinsic susceptibility that led the population to drop—meaning that the species was only able to put up with very low fishing mortality.

Furthermore, the most likely scenario ($M = 0.188$) for age classes 0–3 years, $Z = 0.391$ for age classes 4–8 years, and 0.653 for ages 9 and older, in which an annual estimate of population decreased of 17%, with a λ well below 1, provided elasticities of quasi-extinction condition of 26 years. The context of the collapse for the daggernose shark corroborated with results indicating that about 27 years after data collection, a period of time equivalent to three generations (see Table 4) – a temporal window generally admitted in IUCN assessments – the daggernose shark has not recovered from the collapse and the condition now matches the predicted quasi-extinction. Moreover, fishing mortality (F) which is due to intensive fisheries, directly caused the collapse of *I. oxyrinchus*. Such results agree with Garcia et al. (2008) who demonstrated that the coastal chondrichthyan species have higher $F_{extinct}$.

It is worth mentioning that the daggernose shark's started to decline in the 1990's, however, during the last 26 years high fishing efforts continued to affect the population. Thus, is plausible to consider that threats, having not ceased and considering the vulnerability of the species to exploitation in the area, the daggernose shark may have already been extirpated from areas of northern Brazil where it was abundant (Casselberry and Carlson, 2015).

4.2. Conservation perspectives for the daggernose shark in northern Brazil

Based on data analyzed in the current study (collected from 1987 to 1991) the species was assessed in Brazil as threatened by extinction, in 2004 (Brasil, IN 05, Annexe 1, 21/05/2004), and critically endangered globally (CR) in 2006 (Lessa et al., 2006), later in 2014, it was again assessed as critically endangered (CR) by the Brazilian Environment Ministry (MMA, Directive No 445). In consequence of those assessments, Brazilian legislation determined that this species (CR) should have captures prohibited. However, these norms and regulations have never been enforced in northern Brazil. Also, the institutions of Brazil's Marine Protected Areas (MPAs) along the range of the daggernose shark distribution have never restricted artisanal fisheries (Lessa et al., 1999). Overall, the existing set of regulatory mechanisms did not bring any protection to the daggernose shark from fishing mortality. Deterrent measures to impede their decline are not in place due to the high value of target species (and their by-products) – in relation to the lower commercial value of the daggernose shark – which explains the inability to provide the necessary protection.

Overall, problems in fisheries management in Brazil, such as the canceling of fishing statistics since 2008, the lack of monitoring programs for fisheries and fisheries inspection deficiencies, impede ascertaining the current state of the species (Chao et al., 2015; Di Dario et al., 2015). However, the absence from gillnet catches observed in the last decades in areas where the species was abundant (Almeida et al., 2014; Mourão et al., 2014), suggests that the species collapse may be even more stringent than that found in the data collected 26 years ago. The fact that the species is sporadically caught by other fisheries, such as trawling and longline, exceeds the population's reduced capacity to grow.

Gillnet exploitation in the whole area developed in an uncontrolled, unrecorded and unmanaged manner, leading the main target species *Cynoscion acoupa* and *Sciaedes parkeri*, to be currently assigned to the Near Threatened (NT) and Vulnerable (VU) categories, respectively (Mourão et al., 2014; Betancur et al., 2015; Chao et al., 2015). Moreover, other common bycatch species declined as well in the 1990's, such as the yellow hammerhead (*Sphyrna tudes*), the bonnethead shark (*S. tiburo*), the smalltail shark (*Carcharhinus porosus*) and the sawfish (*Pristis* spp)– (Lessa, 1986; Stride et al., 1992; Lessa and Menni, 1994; Menni and Lessa, 1998; Brasil, 2004; Lessa et al., 2006; Brasil, 2014).

The sizes of gillnets have in average augmented three-fold since 1990 throughout the daggernose distribution range (Brasil, 2011), incrementing fishing efforts to compensate losses of productivity of target species (Brasil, 2011). Currently, 3–9 km-long gillnets were reported for *Scomberomorus brasiliensis* (Almeida et al., 2014; Mourão et al., 2014) and 3–15 km-long gillnets for *Cynoscion acoupa* and *Sciaedes parkeri* fisheries (Matos and Lucena, 2006; Brasil, 2011; Almeida et al., 2014). Furthermore, the gillnet fishery directed to the daggernose shark off of Amapá state (Nascimento and Asano-Filho, 1999), which employed 6 km-long nets with 180–200 mm mesh, may have been discontinued due to productivity losses.

The collapse of the daggernose shark in the 1990's fits the context of multispecies fisheries, where by-catch are the first to decline due to differences in resilience, when compared to the targeted species (Camhi et al., 1998). The daggernose species was unable to endure fishing mortality, meaning that a compromise between the resilience of this species and the intensity of fisheries would have been critical for their sustainability when the daggernose shark was still commonly captured.

Because of its limited distribution, complexities of its life cycle and dramatic population decline, the results in the current study pointed out a high risk of extinction, urging for effective conservation action. As this shark species is endemic gillnets have to be banned from its main living grounds and marine territories around its nursery areas must be protected.

5. Conclusion

In summary, based on data collected during the 1980's and 1990's, the daggernose shark ended up recognized as critically endangered-CR (Brasil, 2004; Lessa et al., 2006; Brasil, 2014). Such a condition entailed the prohibition of landing, commercializing and transporting threatened species (Brasil, 2004). However, the daggernose shark, in fact, continued being freely caught and commercialized (Lessa et al., 2006) due to the lack of enforcement of regulations. Hence, the daggernose shark, after three decades of data collection (or 3 generations) is currently deemed to be on its way to extinction, claiming for urgent effective measures for their conservation.

Acknowledgments

Authors thank Universidade Federal do Maranhão (UFMA) where the “Artisanal Fisheries Project” was developed, the Overseas Development Administration, the British Council and Financiadora de Estudos e Projetos (FINEP) which provided the funds. Authors owe deep gratitude to Richard K. Stride who made data available. Research grants (303251/2010-7) were provided to RPL and to VSB (303469/2013-7) by CNPq.

References

- Almeida, Z.S., Santos, N.B., Carvalho-Neta, R.N.F., Pinheiro, A.L., 2014. Análise multidisciplinar das pescarias de emalhe da pescada amarela, de camarão de muruada e da catação do caranguejo uça em três municípios do Maranhão. In: Haimovici, M., Andrigueto, J.M., Sunyé, P.S. (Eds.), *A Pesca Marinha e Estuarina no Brasil: Estudos de Caso Multidisciplinares*. Editora FURG, Rio Grande, pp. 161–170.
- Barthem, R.B., 1985. Ocorrência, distribuição e biologia dos peixes da Baía de Marajó, Estuário Amazônico. *Bol. Mus. Para. Emilio Goeldi, Sec. Zool.* 2, 49–69.
- Bassedick, N., Aguilier, J.P., Capetta, H., Micaux, J., 1984. Le climat du Néogène dans le sud de la France, d’après l’analyse des faunes (Rongeurs et Sélaciens) et des flores polliniques. *Paléobiol. Cont. (Montp.)* 14 (2), 181–190.
- Betancur, R., Marceñik, A.P., Giarrizzo, T., Frédou, F.L., 2015. *Sciaed parkeri*. The IUCN Red List of Threatened Species. Version 2015.2. <http://www.iucnredlist.org> (Downloaded on 21 July 2015).
- Bigelow, H.B., Schroeder, W.C., 1948. *Sharks. In: Fishes of the Western North Atlantic, Part I. Mem. Sears. Found. Mar. Res.* pp. 53–546.
- Brasil, 2004. Ministério do Meio Ambiente, MMA. Instrução Normativa No 05. http://www.icmbio.gov.br/sisbio/images/stories/instrucoes_normativas/IN05_2004_MMA_Aquaticosamecados.pdf (Downloaded 02 July 2015).
- Brasil, 2011. Relatório do Grupo Técnico de Trabalho sobre a Gestão da Pesca de Emalhe no Brasil—GTT/Emalhe. Portaria Interministerial no. 2, 14/9/2010. Ministério da Pesca e Aquicultura e Ministério do Meio Ambiente, MPA/MMA.
- Brasil, 2014. Ministério do Meio Ambiente, MMA. Portaria MMA 445. http://www.icmbio.gov.br/cepsul/images/stories/legislacao/Portaria/2014/p_mma_445_2014_lista_peixes_amecados_extincao_altrd_p_98_2015.pdf (Downloaded 05 July 2015).
- Cailliet, G.M., Mollet, H.F., Pittenger, G.G., Bedford, D., Natanson, L.J., 1992. Growth and demography of the Pacific Angel Shark (*Squatina californica*), based upon tag returns off California. *Aust. J. Mar. Freshw. Res.* 43, 1313–1330.
- Camhi, M., Fowler, S.L., Musick, J.A., Bräutigam, A., Fordham, S.V., 1998. *Sharks and their Relatives—Ecology and Conservation*. IUCN/SSC Shark Specialist Group, IUCN, Gland, Switzerland and Cambridge, Oxford.
- Carlson, J.K., Cortés, E., Bethea, D.M., 2003. Life history and population dynamics of the finetooth shark (*Carcharhinus isodon*) in the northeastern Gulf of Mexico. *Fish. Bull.* 101, 281–292.
- Casselberry, G.A., Carlson, J.K., 2015. Endangered species act review of the daggenose shark (*Isogomphodon oxyrinchus*). Report to the National Marine Fisheries Service, SFD Contribution PCB-15-05. Office of Protected Resources.
- Chao, L.N., Frédou, F.L., Haimovici, M., Peres, M.B., Polidoro, B., Raseira, M., Subirá, R., Carpenter, K., 2015. A popular and potentially sustainable fishery resource under pressure-extinction risk and conservation of Brazilian Sciaenidae (Teleostei: Perciformes). *Glob. Ecol. Conserv.* 4, 117–126.
- Chen, S., Watanabe, S., 1989. Age dependence of natural mortality coefficient in fish population dynamics. *Nipp. Suis. Gakk.* 55, 205–208.
- Compagno, L.J.V., 1984. *Sharks of the World, Part 2: Carcharhiniformes*. FAO Fisheries Synopsis, Rome.
- Cortés, E., 1995. Demographic analysis of the Atlantic sharpnose shark, *Rhizoprionodon terranova*, in Gulf of Mexico. *Fish. Bull.* 93, 57–66.
- Cortés, E., 2001. Life history patterns, demography and population dynamics. In: *Biology of Sharks and their Relatives*. pp. 449–469. Chap. 15.
- Cortés, E., 2002. Incorporating uncertainty into demographic modeling: Application to shark populations and their conservation. *Conserv. Biol.* 16, 1–15.
- Di Dario, F., Alves, C.B.M., Boos, H., Frédou, F.L., Lessa, R.P., Mincarone, M.M., Pinheiro, M.A.A., Polaz, C.N.M., Reis, R., Rocha, L.A., Santana, F.M., Santos, R.A., Santos, S.B., Vianna, M., Vieira, F., 2015. A better way forward for Brazil’s fisheries. *Science* 347 (6226).
- Dulvy, N.K., Ellis, J.R., Goodwin, N.B., Grant, A., Reynolds, J.D., Jennings, S., 2004. Methods of assessing extinction risk in marine fishes. *Fish. Fish.* 5, 255–276.
- Frédou, F.L., Asano-Filho, M., 2006. Recursos pesqueiros da região norte. In: Ministério do Meio Ambiente, (Ed.), *Secretaria de Qualidade Ambiental. In: Programa REVIZEE: Avaliação do Potencial Sustentável de Recursos Vivos na Zona Econômica Exclusiva: Relatório Executivo/MMA, Ministério do Meio Ambiente, Brasília, Brazil*, pp. 121–152.
- García, V., Lucifora, L.O., Myers, R.A., 2008. The importance of habitat and life history to extinction risk in sharks, skates, rays and chimaeras. *Proc. R. Soc. B* 275, 83–89.
- Gulland, J.A., 1983. *Fish Stock Assessment: A Manual of Basic Methods*. FAO/Wiley Series on Food and Agriculture, Rome.
- Hewitt, D.A., Hoening, J.M., 2005. Comparison of two approaches for estimating natural mortality based on longevity. *Fish. Bull.* 103, 433–437.
- Hoening, J.M., 1982. A compilation of mortality and longevity estimates for fish, mollusks and cetaceans with a bibliography of comparative life history studies. *Tech. Rep., Ref. 82-2*. University of Rhode Island, Grad. School Oceanogr.
- Hood, G.M., 2006. PopTools version 2.7.5. www.cse.csiro.au/poptools (Downloaded 28 Jan 2015).
- IUCN Standards and Petitions Subcommittee, 2014. Guidelines for Using the IUCN Red List Categories and Criteria. Version 11. <http://www.iucnredlist.org/documents/RedListGuidelines.pdf> (Downloaded 20 July 2015).
- Jensen, A.L., 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Can. J. Fish. Aquat. Sci.* 53, 820–822.
- Krebs, C.J., 1998. *Ecological Methodology*. Addison Wesley Longman ed., New York.
- Léopold, M., 2004. *Poissons de Mer de Guyane: Guide Illustré*. Ifremer, Paris.
- Lessa, R.P., 1986. Levantamento faunístico dos elasmobrânquios (Pisces, Chondrichthyes) do litoral ocidental do estado do Maranhão, Brasil. *Bol. Lab. Hidro.* 7, 27–41.
- Lessa, R.P., 1987. Aspectos da biologia do cação-quati, *Isogomphodon oxyrinchus* (Müller and Henle, 1839) (Chondrichthyes: Carcharhinidae), das Reentrâncias Maranhenses. *Bol. Ciênc. Mar.* 44, 1–18.
- Lessa, R.P., Araújo-Filho, J.B., 1984. Sobre os elasmobrânquios da Baía de Cumã e Araóca—Maranhão. In: Abstract of XI Congresso Brasileiro de Zoologia, Belém—PA, pp. 184–185.
- Lessa, R., Batista, V., Almeida, Z., 1999. Occurrence and biology of the daggenose shark *Isogomphodon oxyrinchus* (Chondrichthyes: Carcharhinidae) off the Maranhão coast (Brazil). *Bull. Mar. Sci.* 64, 115–128.
- Lessa, R., Charvet-Almeida, P., Santana, F.M., Almeida, Z., 2006. *Isogomphodon oxyrinchus*. The IUCN Red List of Threatened Species. Version 2014.3. www.iucnredlist.org (Downloaded 14 May 2015).
- Lessa, R.P., Menni, R.C., 1994. The Chondrichthyan Community off Maranhão. In: Fourth Indo-Pacific Fish Conference. Systematics and Evolution of Indo-Pacific Fishes. Bangkok, Thailand, pp. 138–172.
- Lessa, R., Santana, F.M., Batista, V., Almeida, Z., 2000. Age and growth of the daggenose shark, *Isogomphodon oxyrinchus*, from northern Brazil. *Mar. Freshw. Res.* 51, 339–347.
- Matos, I.P., Lucena, F., 2006. Descrição da pesca da pescada-amarela, *Cynoscion acoupa*, da costa do Pará. *Arq. Ciênc. Mar.* 39, 66–73.
- Menni, R.C., Lessa, R.P., 1998. The chondrichthyan community off Maranhão (northeastern Brazil). II. Biology of species. *Acta Zool. Lilloana* 44, 69–89.
- Mollet, H.F., Cailliet, G.M., 2002. Comparative population demography of elasmobranchs using life history tables, Leslie matrices and stage-based matrix models. *Mar. Freshw. Res.* 53, 503–516.
- Mourão, K.R.M., Espírito-Santo, R.V., Silva, B.B., da, Almeida, M.C., Isaac, V., Frédou, T., Frédou, F., 2014. A pesca da Serra *Scomberomorus brasiliensis* e alternativas para o seu manejo no litoral do Nordeste do Pará, Brasil. In: Haimovici, M., Andrigueto, J.M., Sunyé, P.S. (Eds.), *A Pesca Marinha e Estuarina no Brasil: Estudos de Caso Multidisciplinares*. Editora FURG, Rio Grande, pp. 171–179.

- Nascimento, R., Asano-Filho, M., 1999. Descrição e Caracterização da Pescaria Artesanal de Cação Pato *Isogomphodon oxyrhynchus* (Muller and Henle, 1841) na Região Norte do Brasil. In: Anais do I Congresso Latinoamericano de Engenharia de Pesca CONLAEP, Recife, Brazil (1), pp. 996–1002.
- Otway, N.M., Bradshaw, C.J.A., Harcourt, R.G., 2004. Estimating the rate of quasi-extinction of the Australian grey nurse shark (*Carcharias taurus*) population using deterministic age- and stage-classified models. *Biol. Conserv.* 119, 341–350.
- Pauly, D., 1980. A Selection of Simple Methods for the Assessment of Tropical Fish Stocks. FAO Fisheries Circular, Rome.
- Peterson, I., Wroblewski, J.S., 1984. Mortality rate of fishes in the pelagic ecosystem. *Can. J. Fish. Aquat. Sci.* 41, 1117–1120.
- Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* 191.
- Rikhter, V.A., Efanov, V.N., 1976. On one of the approaches to estimation of natural mortality of fish populations. ICNAF Research Document, IG/VVS, 1–12.
- Rodrigues-Filho, L.F.S., Rocha, T.C., Rêgo, P.S., Schneider, H., Sampaio, I., Vallinoto, M., 2009. Identification and phylogenetic inferences on stocks of sharks affected by the fishing industry off Northern coast of Brazil. *Genet. Mol. Biol.* 32, 405–413.
- Santana, F.M., Duarte-Neto, P., Lessa, R., 2009. Demographic analysis of the night shark (*Carcharhinus signatus*, Poey, 1868) in the equatorial southwestern Atlantic Ocean. *Fish. Res.* 100, 210–214.
- Simpfendorfer, C.A., 2005. Demographic models: Life tables, matrix models and rebound potential. In: Musick J.A., Bonfil R. (Eds.), Elasmobranch Fisheries Management Techniques FAO Fisheries Technical Paper, Rome.
- Smith, S.E., Au, D.W., Show, C., 1998. Intrinsic rebound potentials of 26 species of Pacific sharks. *Mar. Freshw. Res.* 49, 663–678.
- Stride, R.K., Batista, V.S., Raposo, L.A., 1992. Pesca experimental de tubarão com redes de emalhar no litoral maranhense. Projeto desenvolvimento da pesca artesanal marinha do Maranhão. ODA/FINEP/UFMA, São Luís, Brazil.
- Vooren, C.M., Klippel, S., 2005. Diretrizes para a conservação de espécies ameaçadas de elasmobrânquios. In: Vooren, C.M., Klippel, S. (Eds.), Ações Para a Conservação de Tubarões e Raias no Sul do Brasil. Igaré, Porto Alegre, pp. 213–228.
- Waring, G.T., 1984. Age, growth, and mortality of the little skate off the northeast coast of the United States. *Trans. Am. Fish. Soc.* 113, 314–321.