RESEARCH ARTICLE





Potential distribution and population trends of the smalltail shark *Carcharhinus porosus* inferred from species distribution models and historical catch data

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Abstract

- Updated distribution ranges are crucial for conservation status assessments.
 Comprehensive analyses combining published literature and available data on historical catches and species distribution models (SDMs) are effective tools that could improve the prediction of more realistic scenarios for some species, especially those with limited information available and facing multiple threats.
- 2. The present study aimed at generating an updated distribution for the smalltail shark *Carcharhinus porosus*, one of the most threatened and understudied shark species of the western Atlantic Ocean. Estimates of the key areas for this species conservation based on the SDMs, and trends in catch probabilities throughout its distribution range are provided.
- 3. Four algorithms (BIOCLIM, Domain, Mahalanobis, and Maximum Entropy) were used to model the distribution of *C. porosus* and calculate its habitat suitability based on marine environmental variables. To assess historical catch probability trends, we built a generalized linear model from published and grey literature data. This analysis was used to estimate catch probability as an indication of population trends.
- 4. SDMs suggest that the northern coast of South America (NCSA) harbours the most suitable habitats for *C. porosus* in the world, which was expected given its historically high catch rate in this region. In addition, there was a continuously declining catch probability trend starting in the 1970s. However, the decline was smaller for the NCSA as compared with the Gulf of Mexico and the eastern South America coast.
- 5. Results indicate that the NCSA should be considered the currently most important area in the world for this species conservation. Furthermore, the lack of data throughout Central and South American marine regions hampers the evaluation of extinction risk throughout its updated distribution. Thus, research in these areas is urgently required for a more comprehensive conservation status assessment.

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KEYWORDS

coastal, conservation evaluation, ecological niche models, fish, fishing, species distribution

1 | INTRODUCTION

Baseline information on species natural history and population trends are crucial for the development of effective conservation plans. For instance, good information on taxonomic resolution, distribution range, habitat use, abundance patterns, and reproductive behaviour can determine key areas for species survival (Cochrane, 2002). These data are, however, mostly incomplete or unavailable for most elasmobranch species (Dulvy et al., 2014). Data gaps prevent the International Union for the Conservation of Nature (IUCN) from having updated conservation status assessments on a species-specific level, thus hampering the implementation of effective conservation measures (O'Hara, Afflerbach, Scarborough, Kaschner, & Halpern, 2017). The most important data available on the smalltail shark (Carcharhinus porosus), a data deficient listed species in IUCN, comes from studies carried out in the waters around Brazil's northern coast (BNC; 4°11′40.58″N to 2°18′45.53″S) during the 1980s and 1990s (Lessa. 1986a, b; Lessa & Almeida, 1997; Lessa, Santana, Menni, & Almeida, 1999: Menni & Lessa, 1998).

Age and growth data show that males and females of *C. porosus* reach sexual maturity when 6 years old and a total length of 71 and 70 cm, respectively (Lessa & Santana, 1998). These animals grow 7 cm year⁻¹ until reaching maturity when growth reduces to 4 cm. year⁻¹ (Lessa & Santana, 1998). Therefore, even though this species is considered a small shark, its growth rate is similar to larger bodied species, which have longer lifespans and are particularly susceptible to fishing (Branstetter, 1993). Moreover, reproduction follows a biannual cycle with an average of six pups produced in an approximately 12-month gestation (Lessa et al., 1999). With all these features combined, *C. porosus* has an intrinsically low resilience to fishing, and a genetic bottleneck has already been recorded in the BNC population (Tavares et al., 2013).

During the 1980s and 1990s, C. porosus was the most abundant shark species in the drift gillnet fisheries at the BNC, comprising up to 43% of elasmobranch catches, 80% of those corresponding to juveniles (Menni & Lessa, 1998). However, in 2004, despite increased fishing effort, an 85% decrease in the total biomass landed occurred (ICMBIO, 2014). This suggested a strong population decline, from which there has been no recovery (Lessa, Repinaldo-Filho, Moro, Charvet, & Santana, 2018). Despite the inclusion of C. porosus in the Annex I of the Brazilian Red List of Threatened Species Ordinance 05/2004 (ICMBIO/MMA, 2004) and the prohibitions to its capture, recent data indicate that catches of C. porosus continue (Feitosa et al., 2018). Indeed, fisheries have had a severe impact on recruitment for several decades, despite being mostly artisanal, leading the smalltail shark and other closely related species, such as Isogomphodon oxyrhynchus, to suffer severe population declines (Lessa, Batista, & Santana, 2016).

Despite this regional decline, the northern coast of South America (NCSA), comprising the highly turbid and productive waters between Venezuela and the BNC, is still considered as the global centre of abundance for this species (Lessa, Almeida, Santana, Siu, & Perez, 2006). Furthermore, the most recent IUCN report considered C. porosus global distribution to range from the tropical and subtropical areas of the western Atlantic and eastern Pacific Oceans (Lessa et al., 2006). However, Castro (2011) performed a taxonomic review of C. porosus based on morphological characters and raised Carcharhinus cerdale, previously considered a synonym restricted to the tropical Pacific coast of the Americas, to a valid species. Further molecular analysis supported this finding (Naylor et al., 2012), and C. cerdale and C. porosus are currently considered to be separate species. Therefore, C. porosus is restricted to the coastal areas of the western Atlantic Ocean, although some studies still wrongly consider it to occur on both Mexican coasts (Ehemann, del Valle González-González, Chollet-Villalpando, & De La Cruz-Agüero, 2018), and provide catch data from the Pacific side of Mexico (Saldaña-Ruiz, Sosa-Nishizaki, & Cartamil, 2017).

An effective way to evaluate species distribution patterns is to combine occurrence records from international databases and published literature and incorporate them into species distribution models (SDMs). These models are especially important because they provide information on which areas have greater suitable habitats along a predicted distribution for a species (Elith & Leathwick, 2009). In general, SDMs are structured with species occurrence records and the application of mathematical models that evaluate the species' niche in different ways using environmental data as predictive variables (Araújo & Guisan, 2006; Carpenter, Gillison, & Winter, 1993; Elith & Leathwick, 2009; Phillips, Aneja, Kang, & Arya, 2006; Rangel & Loyola, 2012). More recently, global marine environmental datasets have been increasingly used to infer the geographic distributions of marine organisms (Tyberghein et al., 2012). However, due to the lack of large-scale studies on C. porosus throughout its previously predicted distribution, no accurate geographical range estimate currently exists for this species.

Another concerning factor is the lack of fisheries data for *C. porosus* throughout its distribution range. In fact, recent data only exist for northern Brazil, Guyana, and Mexico (Feitosa et al., 2018; Kolmann, Elbassiouny, Liverpool, & Lovejoy, 2017; Pérez-Jiménez & Mendez-Loeza, 2015). Worryingly, this species' population trends are unknown to IUCN and, without this information, it is almost impossible to have any assessment of its extinction risk at any geographical scale. However, generalized linear models (GLMs) are a powerful tool to estimate fisheries trends over time (Maunder & Punt, 2004). This is especially important when evaluating a data-poor species subjected to different types of fisheries (e.g. gillnets and longlines) over wide geographical areas.

In the present study, publicly available data from global species occurrence databases, SDMs, and historical fisheries catch data were used to: (1) provide an updated distribution of *C. porosus* across the coastal areas of the western Atlantic Ocean; (2) estimate where suitable habitats might still exist for this species; (3) identify the areas with most potential for this species conservation; and (4) estimate its historical catch probability trends based on fisheries catch data

2 | METHODS

2.1 | Species data

Occurrence data were used to build the SDMs and carry out the habitat suitability analysis. Data were obtained mostly through global online occurrence databases such as Global Biological Information Facility (GBIF), the Ocean Biogeographic Information System (OBIS), the Shorefishes of the Greater Caribbean (SGC), and FishNet2 (http:// fishnet2.net/aboutFishNet.html), but also by searching in scientific collection databases. Furthermore, to avoid misrepresenting areas without records in the online databases but with known occurrences in the literature, general coordinate points were established based on published studies with maps of the sampled area (Castillo-Géniz, Márquez-Farias, Rodriguez de la Cruz, Cortés, & Cid del Prado, 1998: Kolmann et al., 2017; Lessa & Santana, 1998; Stride, Batista, & Raposo, 1992). Although using occurrences estimated on general sampling locations increases the chance of error in the SDM, there is evidence that this approach still yields reliable distribution models (Graham et al., 2008), Finally, experts (Dr Rachel Graham and Dr Dean Grubbs) who carry out research on elasmobranch communities in both Central and North America were contacted to check for eventual unpublished records of C. porosus.

Geographic coordinates were filtered based on oceanographic basins, presence of vouchers deposited in museums, and studies carried out with reliable morphological or molecular identification methods. Moreover, *C. porosus* occurrences were carefully checked to avoid potential occurrences from falling within areas beyond its known distribution range (i.e. Africa, mid Atlantic Ocean, etc.). Further occurrence point quality checks were made based on the species' biology (e.g. preferred continental platform). Whilst museum misidentifications are recognized as a potential problem, no visits to collections were carried out due to the lack of funds. Nevertheless, collections such as the American Museum of Natural History provide pictures of each specimen, and their identifications were confirmed following Compagno (1984).

Finally, all occurrences were checked by Dr R. Lessa, who published the last IUCN assessment for this species, and occurrences considered as unreliable were removed from further analyses. Occurrence points were mapped on grid-cells at 5 arc-min resolution, and all duplicated points within the grid-cells were removed. In the end, 140 occurrence points were used to model the species' distribution (Supplementary File S1).

2.2 | Environmental data

The marine environmental data used in this study were obtained from the Bio-ORACLE database with a spatial resolution of 5 arc-min (Assis et al., 2017; Tyberghein et al., 2012). A subset of 13 environmental variables that are biologically meaningful for the distribution of C. porosus was selected for species' distribution modelling (Supplementary File S2). To avoid collinearity and model overfitting, the correlation between those variables were examined and only the uncorrelated ones were retained (correlation values <0.7) (Dormann et al., 2013). From the 13 initially selected variables, six were used as predictors to build the SDMs: (1) primary productivity (the mean primary production at mean depth); (2) dissolved oxygen (the mean dissolved oxygen concentration at mean depth); (3) seawater temperature (the mean seawater temperature at mean depth); (4) mean salinity values (the mean seawater salinity at mean depth); (5) range salinity values (the range of seawater salinity at mean depth); and (6) mean light at bottom.

These six marine variables were chosen due to their direct and indirect effects on shaping shark species distributions. Specifically, mean primary productivity contributes to shape marine food webs and affects the diversity and abundance of shark prev species (Brown et al., 2010). Dissolved oxygen is a key variable for species occurrences and behaviour (Carlson & Parsons, 2001), with high variability in estuarine and coastal areas. Water temperature is also a major factor affecting the distribution of sharks in general, but even more so for coastal sharks in tropical areas, since they are subjected to little seasonal temperature variation (Knip, Heupel, & Simpfendorfer, 2010). Furthermore, seawater salinity is a major factor driving shark distribution and occurrence patterns since it imposes a strong physiological constraint on most shark species, including C. porosus (Knip et al., 2010; Lessa, 1997). Finally, light at bottom was selected to evaluate C. porosus distribution due to its known association with turbid coastal waters throughout its distribution range (Lessa, 1997).

2.3 | Modelling description and evaluation

Considering that different modelling methods are naturally variable and may produce different species potential distributions (Araújo & New, 2007; Diniz-Filho et al., 2009), the ecological niche of *C. porosus* was modelled using four distinct algorithms: BIOCLIM, Domain, Mahalanobis, and Maximum Entropy (Maxent).

In BIOCLIM, presence-only records are used to estimate a species niche based on a simple bioclimatic envelope. The BIOCLIM algorithm calculates the suitability of a given grid-cell by comparing the predictor values at this grid-cell to the distribution percentiles of the values at the species' known occurrences. Therefore, predictor values closer to the 50th percentile (the median) are considered the most suitable (Elith et al., 2006). Both Domain and Mahalanobis use presence-only records to estimate a species niche based on environmental distances (Carpenter et al., 1993; Rangel & Loyola, 2012). The Domain algorithm calculates the Gower distance between

environmental variables at any location with those from known locations of species occurrence, while calculations with the mahal algorithm are based on the Mahalanobis distance (Carpenter et al., 1993). Bioclim models were fitted with the bioclim function, and Domain and Mahalanobis distance models with the domain and mahal functions, respectively, from the R package dismo (Hijmans, Phillips, Leathwick, & Elith, 2017). In contrast, Maxent is a more complex machine-learning technique that uses presence-background data to estimate a species niche based on the maximum entropy probability (Phillips et al., 2006; Rangel & Loyola, 2012). Maxent models were fitted with the maxent function from the R package dismo. The R package rJava (Urbanek, 2018) was used to install the Maxent species distribution model software.

All models were constructed based on species occurrences and environmental data. Considering that Maxent also requires background data, grid-cells for which the species were not recorded were randomly selected as background. For this, a prevalence equal to 0.5 was kept, thus generating a dataset in which the number of background points matched the number of species occurrences. For each model, 75% of presence/background data were randomly separated for training, and 25% for testing the model's predictability. This datasplitting process was repeated 20 times for each algorithm (i.e. crossvalidation), thus generating 80 models with a resolution of 5 arc-min. All models were created and evaluated for the American continent. Model evaluation was performed using the area under the curve (AUC) of the receiver operating characteristic plot (ROC), which is a threshold-independent metric varying from 0 to 1. AUC values >0.7 indicate models with acceptable predictive performance (Elith et al., 2006).

An ensemble forecasting approach was applied to combine the outputs from all models into the background area (Araújo & New, 2007; Diniz-Filho et al., 2009). The combination of different projections based on different conditions and methods is considered more robust than single model analysis and should therefore be used whenever possible (Araújo & New, 2007). In fact, model ensembles only keep the consensus-projected areas, thus decreasing variation among projections (Araújo & New, 2007; Diniz-Filho et al., 2009). This is especially important for conservation purposes, as model uncertainty may mislead conservational efforts (Araújo & New, 2007). Continuous predictions of habitat suitability derived from the four previously described algorithms were converted onto a single presence-absence map (binary distribution) according to a habitat suitability threshold. This was done by extracting ensemble habitat suitability values for all presence location points and calculating the 5% quantile. Only models with AUC values >0.7 were used in final models of potential distribution.

To evaluate the influence of each environmental variable in predicting species distribution, each of the 80 models was rerun removing one of the six predictor variables each time. Then, for each mode, seven AUC values were obtained: (1) removing mean salinity; (2) removing salinity range; (3) removing mean primary productivity; (4) removing mean light at bottom; (5) removing dissolved oxygen range; (6) removing mean seawater temperature; (7) including

all variables. Low values of AUC after variable removal indicate which variables are more important to predict the species distribution

2.4 | Historical catch probability trends

A GLM was built to estimate the catch probability of *C. porosus* from a historical perspective using data obtained from a published and grey literature review. Only papers describing the catch composition of gillnet and/or longline fisheries throughout the western Atlantic Ocean were considered for this analysis. The smalltail shark's predicted distribution was divided into three major areas based on the number of available studies from each and the highest habitat suitability scores obtained by the SDMs. These were the Gulf of Mexico ranging from the eastern Mexico coast to the Florida Big Bend area, NCSA, comprising the whole Amazon coast from Venezuela to Maranhão state, Brazil, and Eastern South America comprising Piauí to Santa Catarina states (Supplementary File S3). Historical catch probability trends were estimated on 5-year intervals (from the 1970s to the late 2010s).

A binomial model with a logistic distribution was built for the GLM. Year of the study, fishing gear, and region were used as explanatory variables, while smalltail shark's presence/absence was used as the response variable. Model fit was evaluated by calculating the Akaike information criterion (AIC), Cook's distance, and residual deviances. While both the AIC and the Cook's distance evaluate model parsimony, in which lower values represent more parsimonious and better-fitted models, residual analysis evaluates model homoscedasticity. Finally, the model that presented a better fit (AIC = 159.02) was: $M = \alpha + \beta$ year $+ \delta$ site $+ \gamma$ gear, in which M is the catch probability, α is the null parameter (intercept), and β , γ , δ are the parameters of the explanatory variables. Model fit graphs are presented in Supplementary File 4. All GLM analysis were performed in R software (version 3.6.1).

3 | RESULTS

3.1 | SDM

Analysing all the occurrence data obtained, records were found for 15 countries comprising literature, museum collections, and GBIF, OBIS, SGC, and FishNet2 databases. *Carcharhinus porosus* distribution models attained high AUC values, indicating acceptable model performances (Table 1). Overall, the variables with greatest contributions for predicting the species distribution were seawater temperature, light at bottom, and dissolved oxygen (Supplementary File 5). Seawater temperature was the most influential predictor in the Domain and Mahalanobis distance methods, while light at bottom was the most important predictor in Bioclim and Maxent (Table 1).

Previously, *C. porosus* distribution was considered to range from the south-eastern USA - Texas, Louisiana and southern Florida -

TABLE 1 Model performance related to the distribution of *Carcharhinus porosus* measured as the area under the curve of the receiver operating characteristic plot. Low values of area under the curve after variable removal indicate that this variable is important to predict the species distribution

Excluded variable	Modelling method							
	BIOCLIM		Domain		Mahalanobis		Maxent	
	Average	SD	Average	SD	Average	SD	Average	SD
Salinity mean	0.858523	0.074104	0.744628	0.048188	0.875413	0.034227	0.982128	0.020113
Salinity range	0.881973	0.041245	0.744835	0.069452	0.889153	0.033746	0.985847	0.019535
Primary productivity	0.834039	0.068471	0.73781	0.054571	0.865496	0.04455	0.972934	0.024131
Light at bottom	0.771643	0.044946	0.739876	0.034226	0.847521	0.038424	0.93657	0.02837
Dissolved oxygen	0.858781	0.079609	0.71219	0.080377	0.786054	0.054834	0.976756	0.019588
Temperature	0.797262	0.060418	0.435382	0.103645	0.665806	0.081893	0.987603	0.011878
None	0.840083	0.064215	0.743492	0.076054	0.87531	0.048056	0.987397	0.013899

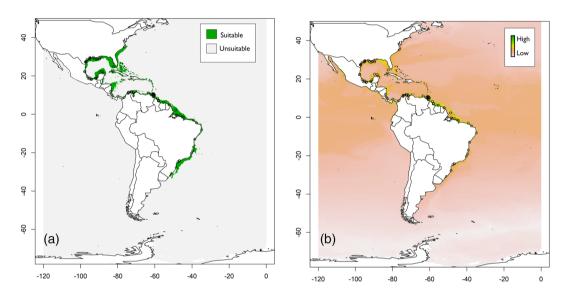


FIGURE 1 Prediction of *Carcharhinus porosus* distribution using an ensemble approach with four distinct algorithms (BIOCLIM, Domain, Mahalanobis and Maxent). (a) Predicted distribution based on a habitat suitability threshold; (b) habitat suitability levels. Dots represent occurrence records

through Central America and Southern Brazil to the Uruguay border (Compagno, 1984; Menni & Lucifora, 2007). However, the potential distribution obtained with the SDMs demonstrates that this species probably ranges from the eastern coast of the USA to south Brazil (Figure 1a). *C. porosus* is known to inhabit coastal areas within the continental platform, and the same pattern was obtained in the present study throughout the whole western Atlantic Ocean. For instance, the Caribbean islands (outside the continental platform) have very few suitable areas for *C. porosus* when compared to the estuaries and river mouths of the Mississippi, Orinoco, and Amazon rivers (Figures 1b and 2). Interestingly, areas with the narrowest suitable habitats for *C. porosus* also coincide with short continental platforms, such as in north-eastern Brazil and some portions of Central America and northern Mexico (Figure 1a).

The models predicted that the Amazon coastal areas, especially combining the Amazon-Orinoco estuarine system, which comprises

French Guyana, Suriname, and Guyana, have the highest habitat suitability for *C. porosus* (Figures 1b and 2a). However, within the Amazon coast, only the eastern portion has a somewhat high habitat suitability (Figure 2a). In Central and North America, suitable habitats are scarcer and occurrences are highly concentrated in estuarine and mangrove areas, especially within the Gulf of Mexico (Figure 2b). Although western Florida yielded a medium habitat suitability, there are no records of the smalltail shark in this region (Dr Dean Grubbs, personal communication September 2018).

3.2 | Catch probability trends

GLM results demonstrate a decreasing trend in catch probabilities for all regions presented. Overall, the NCSA had the highest historical catch probability followed by eastern South America and the Gulf of

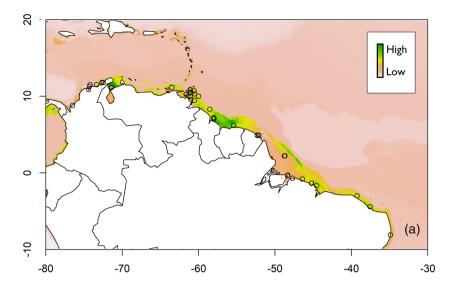
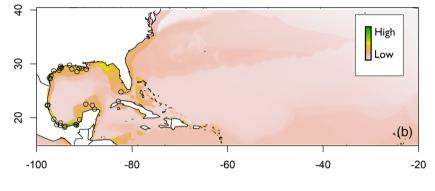


FIGURE 2 Expanded maps of the areas with the highest habitat suitability levels for *Carcharhinus porosus* along its predicted distribution. (a) Northern coast of South America; (b) Gulf of Mexico. Dots represent occurrence records



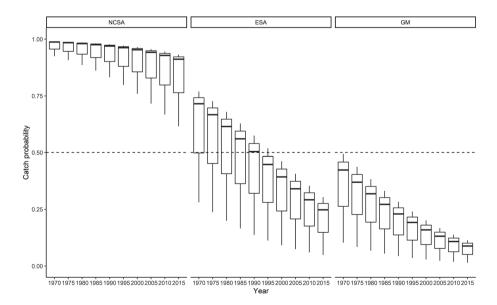


FIGURE 3 Catch probability distribution over time (1970–2015) for the regions analysed. NCSA, northern coast of South America; ESA, eastern South America, GM, Gulf of Mexico. Dashed line represents the 50% catch probability thresholds

Mexico. Furthermore, calculated catch probabilities yielded average values below 0.5 (50%) for all regions, except the NCSA (Figure 3). As a general trend, the Gulf of Mexico presented a small catch probability when compared to other regions analysed, with values below 50% since the 1970s. Eastern South America presented a nearly linear

decrease trend with a 3-fold decline from the 1970s to the late 2010s. Despite the historical decline trend, catch probabilities did not reach null values for any regions analysed. In fact, the decrease trend in the Gulf of Mexico shows a slight reduction between 2005 and 2010.

4 | DISCUSSION

Based on the results obtained, the current distribution of *C. porosus* is likely to be clumped in the NCSA, with decreasing habitat suitability as latitudeincreases. Furthermore, the northern coast of South America includes the areas of highest habitat suitability throughout its distribution range. This corroborates the results of previous studies showing that *C. porosus* represents a considerable proportion of the overall coastal shark catch composition in this region (Lessa, 1997) when compared to others. Furthermore, the GLM results demonstrated that the NCSA has the highest catch probability estimates among all studied areas for all years estimated (Figure 3). Therefore, SDM and GLM results provide comprehensive evidence of the importance of this region for the smalltail shark's conservation.

Indeed, the NCSA was considered its global centre of abundance in the latest IUCN assessment (Lessa et al., 2006). This conclusion is mostly based on the number of specimens caught in this area when compared to others throughout its distribution. In fact, it comprised an important portion of the bycatch in shallow (5-20 m depth) gillnet fisheries targeting the acoupa weakfish (Cynoscion acoupa, Sciaenidae) and the Brazilian Spanish mackerel (Scomberomorus brasiliensis, Scombridae), as well as the deeper (20-50 m depth) shrimp trawl fisheries (Furtado-Júnior, Tavares, & Brito, 2002) by artisanal and industrial fleets in the BNC. Furthermore, C. porosus was considered as a low value species due to its small body and fin sizes, but recent evidence places it as one of the most important species in apprehended fin shipments in Brazil (da Silva Ferrette et al., 2019). In addition, its fins have been found in Hong Kong markets among small, low-value fins of several species (Cardeñosa et al., 2019). Despite this information, most specimens are locally consumed since its meat is cheap (Martins et al., 2018).

During the 1980s, C. porosus comprised nearly half of all shark catches in Maranhão, with neonates and juveniles comprising almost 80% of all smalltail shark specimens caught (Lessa, 1997). However, C. porosus catches have sharply declined in the BNC since 2004 and its catch probability is in a decreasing trend throughout its distribution (Figure 3). It went from being the most caught shark in the area in the 1980s and 1990s (Menni & Lessa, 1998) to the third in the late 2010s (Feitosa et al., 2018). Declines in populations of C. porosus are, at least partially, due to life history features that contribute to its intrinsically low resilience to fishing pressure (Lessa et al., 1999; Lessa & Santana, 1998). C. porosus is a K strategist species with late sexual maturity, slow growth, and low fecundity. These biological features, together with an increasing fishing effort (Almeida, Santos, Carvalho-Neta, & Pinheiro, 2014) are the major causes for its decline. Furthermore, fishing fleets targeting C. acoupa and S. brasiliensis have increased in size, are using longer gills nets, and the stocks from the BNC are exploited by fleets from at least five Brazilian states (Amapá, Pará, Maranhão, Ceará, and Pernambuco) (Mourão et al., 2014). Therefore, the target species' populations are also on a decreasing trend (Almeida et al., 2014; Mourão et al., 2014), with evidence of reduced genetic variability and an observed 27% decline in landed weight between 2005 and 2015 for the acoupa weakfish (Chao et al., 2015; Rodrigues et al., 2008). When the target teleost populations are already decreasing, the populations of the bycaught sharks are probably in a much worse situation.

Since artisanal, unregulated, and under-reported fisheries with similar characteristics prevail in Mexico and both Central and South America (Salas, Chuenpagdee, Charles, & Seijo, 2011), there is the same declining catch probability for *C. porosus* in these areas. However, the declining trend for the smalltail shark in the NCSA is the smallest of all three areas evaluated. This somewhat slower decrease is likely to be related to the expected higher abundance of this species when compared to other areas of its known distribution (Lessa et al., 2006). Despite the slowly decreasing trend, the future scenarios are concerning when factors such as the lack of fisheries data, inspection, and growing fishing effort in the NCSA are considered. On a larger scale, expectations worsen since the species' actual distribution is much smaller than previously thought and suitable habitat is not continuous throughout its predicted distribution range (Figure 1b).

Since only environmental variables with current data were used to build this SDM, the predicted distribution might be affected by climate change. This is especially the case when considering which variables had a higher effect on the AUC values. Water temperature was the most important variable, followed by light at bottom (Table 1), which is a proxy for turbidity. Indeed, areas with the highest habitat suitability (i.e. NCSA and the southern Gulf of Mexico) have both warm temperatures and elevated turbidity in common. *Carcharhinus porosus* is considered highly associated to mangrove forests composed of *Rhizophora mangle* and *Avicennia germinans* and estuarine areas such as the NCSA and southern Gulf of Mexico (Day-Jr et al., 1996; Diniz, Cortinhas, Sadeck, & Adami, 2019). Leopold (2004) also correlated *C. porosus* occurrences to turbid coastal environments. Therefore, we consider that both fishing and essential habitat are key aspects that must be considered for this species conservation.

Since the most suitable area for C. porosus comprises five countries (Venezuela, French Guyana, Suriname, Guyana, and Brazil), a joint effort would be necessary to effectively evaluate the conservation status of populations and the establishment of measures to protect the remaining individuals. So far, only Brazil has advanced in that area, although modestly. Carcharhinus porosus has been listed as overexploited by the Normative Instruction 5 (IN 5/2004) from the Brazilian Ministry of Environment (MMA) since 2004 (ICMBIO/MMA, 2004). There, a management plan should have been developed and implemented by 2009 to establish a sustainable exploitation model. However, these requirements were not met and populations have not recovered since. In 2014, the Ordinance No. 445 listed C. porosus as critically endangered and prohibited its catch, landing, and trade in the country (ICMBIO/MMA, 2014). Although legislation aiming to protect this and other elasmobranchs exists, catch and trade of prohibited species continues to occur indiscriminately throughout Brazil (Almerón-Souza et al., 2018; Feitosa et al., 2018; Palmeira et al., 2013).

Such inefficiency in law enforcement also reflects the lack of fisheries data in Brazil, and throughout the species distribution range (Salas et al., 2011). The only somewhat updated data available from Mexico indicates *C. porosus* comprised 0.18% of shark catches in the country between 2011 and 2014 (Pérez-Jiménez & Mendez-Loeza,

2015). Furthermore, it currently comprises 8% of sharks caught in Colombia (García, 2017), 17.4% of all sharks caught by the artisanal fisheries of Guyana (Kolmann et al., 2017), and 9.8% in Brazil's northern coast (Feitosa et al., 2018). Furthermore, no catches have been recorded in the north-eastern Gulf of Mexico so far (R. Dean Grubbs, personal communication, September 2018), while the last *C. porosus* specimen captured in Pernambuco state was in 1994 (Hazin, Wanderley Junior, & Mattos, 2000).

When the smaller and clumped distribution, the decreasing trend in catch probability, and the species' biological features are combined, it is clear that the smalltail shark is under serious extinction threat. However, since there are no directed fisheries toward it, conservation measures focusing on mitigating its catches must be focused on the target species. Considering that most artisanal fishers have low income and depend on this economic activity for financial support (Martins et al., 2018; Salas et al., 2011), management strategies should focus on alternatives that enable fisheries to take place. However, the major step necessary is the collection of fisheries statistics from both industrial shrimp trawl and artisanal teleost fisheries. Although artisanal fisheries are considered to have little impact on populations, they still demand statistics, proper stock assessments, effective management, and inspections to be sustainable (Pauly & Zeller, 2016).

For that, a good relationship between inspection agencies, managers, and the fishing community is paramount to manage fisheries on a regional level. Another possibility could be decreasing the gillnet soak time to enable the release of live specimens, especially those below the size at maturity (>71 cm total length). Furthermore, we propose mangrove conservation to be included in the National Plans of Action for Sharks and Rays that countries eventually develop, since no effective conservation can be obtained if habitat quality decreases. Nevertheless, future research on habitat-use patterns and evaluating nursery grounds is crucial to establish potential fisheries exclusion zones to protect the most critical life stages for the species. Other distribution models projecting its future distribution in a climate change scenario could also be an interesting source of information on the species conservation for the near future.

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