UNIVERSIDADE FEDERAL DE PERNAMBUCO

CENTRO DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA ANIMAL

LEONARDO MANIR FEITOSA

USO DE HABITAT E DISTRIBUIÇÃO GEOGRÁFICA DE *CARCHARHINUS POROSUS* (RANZANI, 1839) (CARCHARHINIDAE) NO OCEANO ATLÂNTICO OESTE

RECIFE

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Dissertação apresentada ao Programa de Pós-graduação em Biologia Animal, área de concentração Ecologia, da Universidade Federal de Pernambuco, como requisito parcial para obtenção do título de Mestre em Biologia Animal.

Orientadora: **Profa. Dra. Rosangela Paula Teixeira Lessa**

RECIFE

2019

Catalogação na fonte
Elaine C Barroso (CRB4/1728)

Feitosa, Leonardo Manir

Uso de habitat e distribuição geográfica de *Carcharhinus porosus* (Ranzani,1839) (Carcharhinidae) no Oceano Atlântico Oeste / Leonardo Manir Feitosa- 2019.

70 folhas: il., fig., tab.

Orientadora: Rosângela Paula Teixeira Lessa

Dissertação (mestrado) – Universidade Federal de Pernambuco. Centro de Biociências. Programa de Pós-Graduação em Biologia Animal. Recife, 2018.
Inclui referências
1. Tubarão 2. Conservação de tubarões 3. Pesca I. Lessa, Rosângela Paula Teixeira (orient.) II. Título

597.3 CDD (22.ed.) UFPE/CB-2019-403

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Aprovado em: 29/07/2019

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Aos meus pais, Antonio e Márcia, que despertaram em mim o amor por conhecer o mundo e conservar a Natureza como ela é.

AGRADECIMENTOS

Meus agradecimentos aqui proferidos vêm no sentido de expressar minha gratidão e admiração às pessoas que participaram da minha jornada até esse momento tão importante e gratificante.

Primeiramente, agradeço à minha família, em especial minha mãe Márcia e meu pai Antônio pelo apoio, incentivo, pelos ensinamentos de dedicação ao estudo e pelo entendimento de nosso papel social enquanto acadêmicos. Cresci tendo esse exemplo dentro de casa e agora entendo todo o esforço que eles me cobravam durante minha educação escolar. Essa gratidão vai além de qualquer titulação acadêmica que eu receba.

Agradeço agora à pessoa que tem um significado imenso para mim desde o momento em que eu decidi me mudar pra Recife. Rafael Brandão, meu grande amigo e o irmão mais velho que eu nunca tive, me deu todo o apoio possível que alguém pode receber. Rafa fez o mudar de cidade e ficar longe da minha família parecer fácil. Esse trabalho não teria saído como saiu sem você, irmão.

À Profa. Rosangela Lessa por topar o desafio desse trabalho e por depositar em mim a confiança de que eu seria capaz de realiza-lo. Além disso, obrigado pelo exemplo constante de perseverança e pelo incentivo para prosseguir pesquisando.

À Renata Albertim que se tornou um alicerce imprescindível para mim. Obrigado pela parceria, pela torcida positiva, pelo apoio e pelos papos cabeça de sempre. Minhas vitórias também passam por você e é um grande prazer dividir meus sonhos, planos e angústias com você. Agradeço também à família da Renata pelo acolhimento e por, definitivamente, fazer Recife parecer a minha segunda casa.

À Mariana Bonfim, minha grande amiga e confidente diária sobre praticamente tudo que acontece, o tempo todo. Obrigado pela ajuda com esse trabalho, pelos debates científicos à distância, pelo incentivo e por acreditar em mim sempre.

À Carol Pessoa, minha companheira de moradia por mais de um ano e que me ensinou muita coisa sobre a vida nos cafés da manhã e nas mesas de bar.

À Lucas Martins a Leandro Souza, dois grandes amigos que tiveram participação direta na elaboração do capítulo 1 aqui apresentado.

Aos amigos do DIMAR que dividiram a labuta, os momentos de estresse e os horários de almoço regados a debates político-sociais e sobre elasmobrânquios. Obrigado, principalmente,

pela atmosfera descontraída e de amizade que existe em nosso laboratório. Agradeço especialmente a Jonas, Leandro, Philippe, Laís e Priscila pelo auxílio durante esses dois anos de mestrado.

Aos amigos da graduação, em especial Elias, Thayrine, Clarisse, Diego, Marco, Fernanda, Leila, Mairla e Emily que, apesar de longe, sempre se fazem presentes nas minhas voltas para casa.

Aos amigos do PPGBA, em especial Letícia, Alexsandra, Rodrigo, Kata, Sérgio, Aninha e Radharanne pela parceria desde o começo do mestrado e pelo compartilhamento das mágoas e angústias da vida acadêmica.

Aos amigos que fiz em Recife, em especial Borba, Gabi, Camila Monteiro, Sabino, Osvaldo, Marx, Arthur, Camila Miranda, Lara, Rebeca, Ricardo, Ítalo e Babi que se tornaram grandes parceiros e foram responsáveis por momentos incríveis ao longo desses dois anos que moro aqui. Vocês fizeram o mestrado parecer mais leve do que realmente foi.

Aos amigos da turma da praia, obrigado também pelos momentos inesquecíveis de conversas, viagens, incentivos e, talvez o mais importante, por me ajudarem a sair da bolha acadêmica que, muitas vezes, engole os alunos de pós-graduação.

Aos mentores passados e que ainda se fazem presentes, especialmente Ana Paula, Jorge e Luís Fernando, obrigado pela parceria de sempre e pelo incentivo contínuo.

À Clarissa, minha psicóloga, por ter feito milagres e ter me ajudado a atingir a saúde mental que tenho hoje.

Finalmente, agradeço à Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco (FACEPE) pela bolsa de mestrado sob o processo IBPG 0089-2.05/17 e à Coordenação de Aperfeiçoamento de Pessoal do Ensino Superior (CAPES) pelo financiamento ao Programa de Pós-Graduação em Biologia Animal (PPGBA/UFPE). Além disso, agradeço à UFPE e à UFRPE pela estrutura proporcionada para a realização deste trabalho.

“Educar é impregnar de sentido o que fazemos
a cada instante”.

Paulo Freire (1996)

“Nós somos uma maneira do Cosmos conhecer
a si mesmo”.

Carl Sagan (1980)

RESUMO

Tubarões estão entre os animais mais ameaçados globalmente, com 25% de todas as espécies sob risco de extinção. Dentre elas, *Carcharhinus porosus* é uma das espécies mais ameaçadas do Brasil devido à sobrepesca. Os objetivos deste trabalho, dividido em dois capítulos, são investigar sua ocorrência e as tendências históricas de captura, bem como avaliar seu uso de habitat a partir de microquímica de vértebras no litoral norte brasileiro. Sua ocorrência foi estimada através da construção de modelos de distribuição de espécies. As tendências de captura foram avaliadas por modelos lineares generalizados para a costa norte da América do Sul (NCSA) e Golfo do México. Na microquímica, quatro elementos foram estudados: Ba, Mg, Mn e Sr. Diferenças foram avaliadas entre estágios de vida, sexos e décadas de coleta. Os resultados demonstraram o declínio generalizado da espécie e evidenciaram a NCSA como sendo o habitat mais favorável para sua ocorrência. Diferenças significativas foram encontradas entre os sexos para o uso de habitat. Dentre neonatos, evidenciou-se a ocorrência de pelo menos quatro grupos, apontando a existência de diferentes berçários para a população. Ademais, assinaturas químicas similares foram encontradas para espécimes coletados com 30 anos de diferença, indicando um provável comportamento filopátrico. Portanto, os resultados apontam a NCSA como a região mais importante para a conservação de *C. porosus* no mundo por ser uma zona de berçário e com habitats altamente favoráveis para sua ocorrência.

Palavras-chave: Áreas prioritárias. Carcharhinidae. Conservação de tubarões. Elementos-traço. Pesca.

ABSTRACT

Sharks are among the animals most threatened with extinction in the world, with at least 25% of all species under some level of threat. Among them, *Carcharhinus porosus* is one of the most threatened sharks in Brazil due to overfishing. Divided in two chapters, the present study aimed at investigating its occurrence and historical catch trends, as well as its habitat use through vertebrae microchemistry in Brazil's Northern coast. Occurrence was estimated through species distribution models. Historical catch trends were evaluated with generalized linear models for the northern coast of South America (NCSA) and the Gulf of Mexico. Four elements were used for the microchemistry analysis: Ba, Mg, Mn, and Sr. Differences between life stages, sexes, and decades of capture were evaluated in a multi-element setting. Results demonstrated the generalized decline of *C. porosus*, and evidenced that the NCSA has the highest habitat suitability for its occurrence. Moreover, the habitat use analysis only yielded significant differences between sexes. Among neonates, results showed the existence of, at least, four groups within the samples, thus providing evidence of different nurseries in the region. Furthermore, similar chemical signatures were found for specimens sampled 30 years apart, indicating a likely philopatric behavior. Therefore, the data presented herein suggests that Brazil's Northern coast is the most important region for its conservation due to its greatest habitat suitability and presence of nurseries for this species.

Keywords: Priority areas. Carcharhinidae. Shark conservation. Trace elements. Fisheries.

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LISTA DE ABREVIATURAS

AIC - Akaike Information Criterion

ANOVA - Analysis of variance

AUC - Area under the Curve

BNC - Brazil’s northern coast

CR - Critically Endangered

DD - Data Deficient

GBIF - Global Biological Information Facility

IUCN - International Union for the Conservation of Nature

LA-ICP-MS - Laser ablation inductively coupled plasma mass spectrometry

LOD - Limit of Detection

MMA - Ministério do Meio Ambiente

MS - Mean Squares

NCSA - Northern coast of South America

NIST - National Institute of Standards and Technology

NPOA-Sharks - National Plan of Action for Sharks and Rays

OBIS - Ocean Biogeographic Information System

ONU - Organização das Nações Unidas

PCA - Principal Component Analysis

PERMANOVA - Permutational Analysis of Variance

ROC - Receiver Operating Characteristic

SDM - Species Distribution Model

SGC - Shorefishes of the Greater Caribbean

SUMÁRIO

1 INTRODUÇÃO

Tubarões são membros da classe Chondrichthyes, sub-classe Elasmobranchii que se dividem em duas superordens: Squalomorphi e Galeomorphi (COMPAGNO 1984). São vertebrados predominantemente marinhos, de hábitos bentônicos e pelágicos. Caracterizam-se por serem consumidores de níveis elevados nas teias tróficas costeiras e oceânicas (MYERS *et al*., 2007) e, desse modo, influenciam direta e indiretamente na densidade populacional de inúmeras espécies de organismos marinhos do mundo todo (FERRETI *et al*., 2010).

Atualmente, 509 espécies de tubarões são consideradas como *taxa* válidos, distribuindo-se ao redor do mundo em ambientes marinhos, dulcícolas, costeiros, oceânicos e de profundidade (WEIGMANN, 2016). A sub-classe Elasmobranchii é composta por nove ordens de tubarões, sendo Carcharhiniformes a mais diversa (WEIGMANN, 2016). Dentro desta ordem, a família Carcharhinidae é a mais especiosa com 57 *taxa* com elevada diversidade de estratégias de história de vida e milhões de anos de evolução. Dentre essas, 35 são do gênero *Carcharhinus*, sendo esse o mais abundante entre os tubarões no Brasil (ROSA; GADIG, 2014; WHITE *et al*., 2019). Os membros dessa família estão entre as principais espécies de tubarões pescadas local, regional e mundialmente e, portanto, estão sob constante ameaça de extinção devido às atividades antrópicas (DULVY *et al*., 2014). De forma geral, a grande maioria das espécies de Carcharhinidae são classificadas como *k* estrategistas devido à sua baixa fecundidade, crescimento lento e longo ciclo de vida (COMPAGNO, 1984; CAMHI *et al*., 1998).

Globalmente, a pesca de tubarões movimenta, desde 2000, entre 306 a 409 milhões de dólares anualmente (WORM *et al*., 2013). Desse modo, Worm *et al*. (2013) estimam que, em 2010, a produção total de tubarões tenha sido em torno de 1.412.000t. No Brasil, a pesca de Chondrichthyes alcançou sua menor produtividade em 2012 com apenas 400 toneladas (FAO Fishstat 2012). Entretanto, entre 2001 e 2011, mais de 115 mil toneladas de peixes cartilaginosos foram pescadas no país (FAO Fishstat 2012). Com as medidas de conservação adotadas pelo Ministério do Meio Ambiente, a pesca de várias espécies de tubarões é terminantemente proibida. Entretanto, ela continua em vários estados brasileiros, dentre eles o Maranhão, onde a fiscalização é falha e não há uso de técnicas que evitem o *bycatch* dessas espécies (FEITOSA *et al*., 2018; MARTINS *et al*., 2018).

No Brasil, a região Norte/Nordeste é a responsável pelos maiores índices de *bycatch* de tubarões (OLIVER *et al*., 2015). Além disso, espécies que habitam as zonas rasas da porção ocidental do oceano Atlântico Central são mais ameaçadas de extinção do que as de zonas profundas (>200m), como na região Norte/Nordeste do Brasil (DULVY *et al*., 2014). Ademais, a região da costa Amazônica é considerada um dos *hotspots* globais para a conservação de tubarões devido à elevada diversidade de espécies e da ocorrência de espécies endêmicas na região (DULVY *et al*., 2014). De modo geral, o padrão climático da costa amazônica é definido com duas estações do ano obedecendo o ciclo hídrico da região, com a estação chuvosa ocorrendo de janeiro a junho e a estação de seca de agosto a dezembro e o mês de julho correspondendo ao período de transição (SOUZA-FILHO, 2005). Este ciclo hídrico altera as características do ambiente costeiro com um elevado aporte de água doce advindo da vazão dos rios da região, o que está diretamente ligado ao aumento considerável na turbidez da água das regiões costeiras. Por conta desses fatores, a região possui a maior quantidade de manguezais da região neotropical (DINIZ et al., 2019).

Apesar do conhecimento de que várias espécies da região estão ameaçadas de extinção, é necessário conhecer a biologia de cada uma e estimar o nível de degradação populacional em que se encontram para que estratégias de conservação sejam elaboradas. Para isso, avaliações de *status* de conservação que levam em conta os dados publicados acerca da história de vida, distribuição, tendências de declínio populacional e as ameaças para cada espécie são realizadas periodicamente nas escalas estadual, federal e internacional. No entanto, a maioria dos tubarões está classificada como deficiente de dados e, portanto, não possui um *status* de conservação que possa justificar a tomada de decisões visando sua preservação (DULVY *et al*., 2014). Dentre essas espécies, *Carcharhinus porosus*, popularmente conhecido como cação-junteiro na costa norte do Brasil, configura-se como uma das mais importantes dos pontos de vista pesqueiros e de conservação (LESSA *et al*., 2006) (Figura 1).

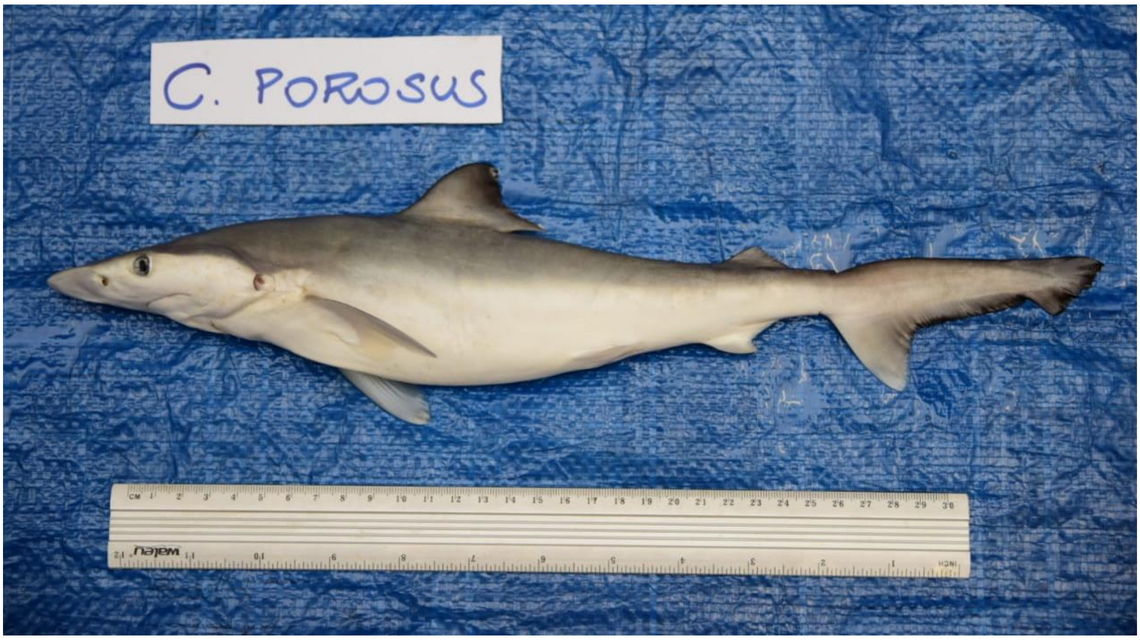

Figura 1. Espécime jovem de *Carcharhinus porosus* Foto: Keyton Kylson, São Luís – MA.

Filogeneticamente, *C. porosus* é considerado um dos tubarões mais derivados de Carcharhinidae (VÉLEZ-ZUAZO; AGNARSSON, 2011). Ele é membro do grupo *Carcharhinus dussumieri-sealei* cunhado por Garrick (1982), que compõe espécies de *Carcharhinus* de pequeno e médio portes distribuídas mundialmente. Entretanto, Garrick (1982) não resolveu a taxonomia de seus membros, levantando a suspeita de que *Carcharhinus porosus* era na verdade uma espécie presente nas zonas tropicais de todos os oceanos. Atualmente, o grupo *dussumieri-sealei* é um dos que tem passado por mais mudanças taxonômicas, com a descrição de duas espécies novas e a ressurreição taxonômica de vários sinônimos como *C. coatesi*, *C. tjutjot*, and *C. cerdale* (WHITE *et al*., 2019). Este último ocorre na zona tropical da costa americana no Oceano Pacífico e era considerado sinônimo de *C. porosus* até 2011 quando Castro (2011) revisou a taxonomia e separou *C. porosus* em duas espécies. Desde então, a ocorrência de *C. porosus* é considerada restrita à região costeira do Oceano Atlântico Oeste.

1.1 PROBLEMATIZAÇÃO

Segundo relatório recente da Organização das Nações Unidas (ONU), tubarões e raias são os peixes mais ameaçados de extinção do mundo, além de terem uma das maiores proporções de espécies sem dados suficientes para definição de seus *status* de conservação (IBPES, 2019). Dentro deste cenário, o Brasil tem um papel de destaque, sendo o maior importador mundial de carne de tubarão (DENT; CLARKE, 2015). Além disso, 33% das espécies de tubarões e raias do Brasil sofrem de alguma ameaça de extinção, o que é mais do que a média global para esse grupo taxonômico (BARRETO *et al.* 2017).

Dentre as ameaças antrópicas para a conservação desses animais, as pescarias direcionadas e não-direcionadas são os principais fatores, seguidos pelas mudanças climáticas (IBPES, 2019). Apesar de uma alarmante ausência de dados pesqueiros desde 2011 em ambas as escalas industriais e artesanais (BARRETO *et al.*, 2017), sabe-se que a pesca incidental (*bycatch*) é mais comum na costa norte do país, afetando principalmente tubarões e raias (OLIVER *et al.*, 2015). Além disso, a região é um dos principais *hotspots* globais de conservação para tubarões e raias devido à quantidade de espécies endêmicas e a existência de berçários para várias dessas espécies (LESSA *et al.*, 1999a; DULVY *et al.* 2014). Como resultado deste cenário, várias espécies já tiveram seus declínios documentados para essa região, como é o caso do tubarão-quati *Isogomphodon oxyrhynchus* (LESSA *et al.*, 2016), do espadarte *Pristis pristis* (FEITOSA *et al.*, 2017) e outros tubarões de pequeno porte como *Sphyrna tudes*, *Sphyrna tiburo* e *Carcharhinus porosus* (MARTINS *et al.*, 2018).

Dentre as 19 espécies de tubarões registradas para a costa do estado do Maranhão, 13 encontram-se em algum nível de ameaça de extinção (ICMBIO/MMA, 2018). Mais especificamente, o cação junteiro (*Carcharhinus porosus*) que configurava-se como a espécie mais abundante dentre as capturas incidentais da pescaria para pescada-amarela *Cynoscion acoupa* (Lacepéde, 1801) e o peixe serra *Scomberomorus brasiliensis* Colette, Russo & Zavala-Camin, 1978, agora é apenas a terceira espécie mais importante nesta pescaria (FEITOSA *et al.*, 2018). Além disso, um declínio de 85% na biomassa capturada dessa espécie foi registrado em 2004 e os índices têm permanecido baixos desde então (MMA, 2004). Por isso, *C. porosus* foi listado como ameaçado no Anexo II da Instrução Normativa 05/2004 do Ministério do Meio Ambiente, que previa a elaboração de um plano de manejo para a recuperação dos estoques desta espécie. Tal plano de manejo nunca foi elaborado e, devido aos baixos índices de captura e do aumento do esforço de pesca na região, a espécie atualmente considerada como Criticamente em Perigo (CR) no Brasil (ICMBIO/MMA, 2018).

Por conseguinte, *C. porosus* continuou sendo pescado no país e, atualmente, encontra-se com sua distribuição consideravelmente reduzida, com a existência de registros recentes exclusivamente na costa Norte do Brasil (ICMBIO/MMA, 2018). Apesar das informações existentes para a espécie no Brasil, a falta de dados para outras regiões do mundo onde essa espécie ocorre faz com seu status de conservação global seja dado como Dados Deficientes

(DD). De fato, considerava-se que o cação-junteiro ocorria nas duas regiões costeiras tropicais e sub-tropicais do continente americano (COMPAGNO, 1984). Porém, Castro (2011) realizou uma revisão taxonômica entre as duas populações de *C. porosus* (oceanos Atlântico e Pacífico) e descobriu que a população da costa oeste da América se tratava, na verdade, de uma espécie diferente. Ao descobrir isso, Castro (2011) ressuscitou o antigo sinônimo *Carcharhinus cerdale* como uma espécie válida, portanto restringindo a área de distribuição de *C. porosus* apenas para o Oceano Atlântico. Porém, seu status de conservação mundial ainda não foi atualizado (LESSA *et al*., 2006).

Com base no conhecimento biológico já existente, pode-se inferir sua baixa resiliência à pressão pesqueira, mesmo que em níveis baixos. Assim, destaca-se sua baixa fecundidade (média de 6 embriões por gestação), maturação sexual tardia (6 anos de idade), reprodução bienal e crescimento lento (LESSA, 1986; LESSA; SANTANA, 1998; LESSA *et al.* 1999b). Além disso, grande parte da captura observada durante as décadas de 1980 e 1990 consistia de juvenis, o que causou um impacto significativo na população prejudicando o recrutamento populacional por várias gerações (MENNI; LESSA, 1998; LESSA *et al*., 2018). Além disso, estudos de genética populacional da costa norte do Brasil demonstram a sua já diminuta diversidade de alelos, o que evidencia a ocorrência de gargalos populacionais causados pelo recrutamento pesqueiro dos juvenis antes da primeira reprodução (TAVARES et al., 2013b).

A ausência de informações atualizadas sobre sua ocorrência, distribuição geográfica em larga escala e padrões de uso de habitat são lacunas cruciais para o melhor entendimento de suas populações e para as avaliações de status de conservação mundial da espécie. Desta forma, o presente trabalho, dividido em dois capítulos complementares, tem como objetivo fornecer informações atualizadas acerca de sua ocorrência e distribuição em larga escala, bem como elucidar os padrões de uso de habitat.

1.2 OBJETIVOS

1.2.1 Manuscrito I

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

1.2.1.1 Objetivo Geral

- Fornecer a distribuição atual de *Carcharhinus porosus* através de revisão de literatura e análise de dados públicos em bases de dados de ocorrências.

1.2.1.2 Objetivos Específicos

- Estimar os habitats favoráveis ao longo de sua distribuição global através de modelos de distribuição de espécies.

1.2.2 Manuscrito II

Habitat use of the smalltail shark *Carcharhinus porosus* (Ranzani, 1839) from northern Brazil inferred from vertebrae microchemistry analysis

1.2.2.1 Objetivo Geral

- Identificar padrões de uso de habitat da espécie *Carcharhinus porosus* (Ranzani, 1839) na região Norte do Brasil, através da análise microquímica de vértebras.

1.2.2.2 Objetivos Específicos

- Identificar padrões de uso de habitat nas diferentes classes de idade da população, e nas diferentes fases do ciclo de vida (recém-nascidos, jovens, sub-adultos e adultos), através da comparação dos dados obtidos com os dados já existentes sobre a idade e crescimento da espécie na região;

- Identificar padrões de uso de habitat entre os sexos na população, através da comparação dos resultados da microquímica para cada sexo;

- Verificar a existência de áreas prioritárias para conservação da espécie na região através da identificação de padrões de uso de habitat;

- Subsidiar com informações as futuras avaliações de *status* de conservação da espécie.

1.3 PROCEDIMENTOS METODOLÓGICOS

Para os primeiros dois objetivos, são apresentados um modelo de distribuição de espécie construído a partir de dados de presença com pontos georreferenciados ao longo da distribuição geográfica atualizada de *C. porosus*. O modelo de distribuição foi desenvolvido com o uso de quatro algoritmos aplicados a análises de nicho ecológico para a predição de habitats favoráveis ao longo da distribuição da espécie estudada. Foram esses: BIOCLIM (ELITH et al. 2006), Mahalanobis (RANGEL; LOYOLA 2012), Domain (CARPENTER et al. 1993) e Maxent (PHILLIPS et al. 2006). Desta forma, apresenta-se a distribuição global atualizada da espécie, bem como as áreas principais onde novas pesquisas avaliando o status populacional em caráter regional devem ser realizadas.

Para o último objetivo, aplicou-se a análise de microquímica de vértebras, uma técnica amplamente usada para estudos de uso de habitat para peixes teleósteos e que vem ganhando notoriedade entre os elasmobrânquios. De modo geral, esta técnica baseia-se no princípio de que a composição química do ambiente é afetada pelas variáveis ambientais (salinidade, temperatura, proximidade de estuários) (PONTUAL; GEFFEN 2002). Dessa forma, certos elementos são característicos de determinados ambientes e seus padrões de concentração ambiental são refletidos nas vértebras dos elasmobrânquios (McMILLAN et al. 2017). Por exemplo, estrôncio (Sr) é característico de ambientes marinhos, enquanto que bário (Ba) é característico de ambientes fluviais (SMITH et al. 2013; McMILLAN et al. 2017). Apesar destas informações, este tipo de análise é bastante incipiente para elasmobrânquios, o que faz com que este trabalho seja o primeiro avaliando uso de habitat através de microquímica para tubarões na América do Sul. Com isso, objetivamos investigar a existência de diferenças nos padrões de uso ambiental entre os estágios de vida, entre os sexos, entre as décadas de coleta das amostras e avaliar a existência de possíveis berçários na região Norte do Brasil, uma das mais importantes para a conservação do cação-junteiro no mundo.

2 MANUSCRITO I

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

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Abstract

1. Updated distribution ranges are crucial for conservation status assessments. Comprehensive analyses combining published literature and available data on historical catch trends 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 *Carcharhinus porosus*, providing estimates for the key areas for its conservation based on the SDMs, and estimate population trends from published historical catch data from Mexico, Guyana, and northern Brazil.

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.

4. The SDM results suggest that the 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, the GLM demonstrated a continuous decline trend starting in the 1980s in all areas presenting historical data, with higher abundances likely existing in the NCSA.

5. Therefore, 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 and research in these areas is urgently needed for a more comprehensive assessment.

Keywords: coastal; conservation evaluation; distribution; fish; fishing; modelling.

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 *et al.*, 2017). The most important data available on the smalltail shark (*Carcharhinus porosus*, Carcharhinidae) comes from studies carried out in Brazil's Northern coast (BNC) (4°11'40.58"N to 2°18'45.53"S) during the 1980s and 1990s (LESSA, 1986; LESSA; ALMEIDA, 1997; LESSA *et al.*, 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). 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). Similarly, reproduction follows a biennial cycle with an average of 6 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.*, 2013b).

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 (LESSA *et al.* 2018). This suggested a strong population decline, from which there has been no recovery (LESSA *et al.*, 2018). Furthermore, this decline led to the inclusion of *C. porosus* in the Annex I of the Brazilian Red List of Threatened Species Ordinance 05/2004 (ICMBIO/MMA, 2004) prohibiting its capture, but recent data proved that catches continue (Feitosa et al., 2018). Indeed, fisheries had a severe impact on recruitment for several decades, despite being mostly artisanal. This has led the smalltail shark and other closely related species, such as *Isogomphodon oxyrhynchus* to severe population declines (LESSA *et al.*, 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 *et al.*, 2006). 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 (LESSA *et al.*, 2006). However, Castro (2011) performed a taxonomic review along the *C. porosus* geographical occurrence based on morphological data 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 and *C. cerdale* and *C. porosus* are now considered to be separate species (NAYLOR *et al.*, 2012). Therefore, *C. porosus* is now restricted to the coastal areas of the western Atlantic Ocean, although some studies still wrongly consider it to occur in both Mexican coasts (EHEMANN *et al.*, 2018), and provide catch data from the Pacific side of Mexico (SALDAÑA-RUIZ *et al.*, 2017).

An effective way to evaluate species distribution and occurrence patterns is to combine records from internationals, published catch data, and the use of species distribution models (SDMs). The latter is especially important because they provide information on which habitats are more suitable 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 with environmental data as predictive variables (ARAÚJO; GUISAN, 2006; CARPENTER *et al.*, 1993; ELITH; LEATHWICK, 2009; PHILLIPS *et al.*, 2006; RANGEL; LOYOLA, 2012). More recently, global marine environmental datasets have been 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 currently exists for this species.

Therefore, the present study aimed to provide an updated distribution map of *C. porosus* based on literature review and publicly available data from global species occurrences, and to estimate the location of suitable habitats for the species using SDMs. The results obtained are key to direct future research and conservation efforts throughout the species distribution.

2 METHODS

2.1 Species data

Occurrences were used to build the SDMs and carry out the habitat suitability analysis. Data were obtained mostly through global online occurrences such as Global Biological Information Facility (GBIF), the Ocean Biogeographic Information System (OBIS), the Shorefishes of the Greater Caribbean (SGC), and the FishNet2 database (http://fishnet2.net/aboutFishNet.html), but also by searching directly in scientific collection databases. Furthermore, to avoid misrepresenting areas without records in the online, but with known occurrences in the literature, general coordinates were established points based on published studies in which maps of the sampled area were available (STRIDE *et al.*, 1992; CASTILLO-GENIZ *et al.*, 1998; LESSA; SANTANA, 1998; KOLMANN *et al.*, 2017). 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, we contacted experts (Dr. Rachel Graham and Dr. Dean Grubbs) who carry out research on elasmobranch communities in both Central and North Americas to check eventual unpublished records of *C. porosus*.

Coordinates were filtered based on oceanographic basins, presence of vouchers deposited in museums, and gone through reliable taxonomic identification. Moreover, the occurrence data were carefully checked to avoid potential occurrences out of its known distribution range (e.g. Africa, mid Atlantic Ocean, etc.). Occurrence points were mapped on grid-cells 10 km wide and all duplicated points within the grid-cells were removed. In the end, 140 occurrence points were used to model the species distribution (Supplementary Table S1).

2.2 Environmental data

The marine environmental data used in this study are from the present and were obtained from Bio-ORACLE with a spatial resolution of 10 km (TYBERGHEIN *et al*., 2012; ASSIS *et al*., 2017). A subset of 14 environmental variables that are biologically meaningful for the distribution of *C. porosus* were selected (Supplementary Table 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 14 initially selected variables, six were used as predictors to build the SDMs, which comprised mean productivity, mean dissolved oxygen, mean seawater temperature, mean and range salinity values, and mean light at bottom (Table 1).

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 *et al.*, 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 as background were randomly selected. 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 for training, and 25% for testing the model's predictability were randomly separated. This data-splitting process was repeated 20 times for each algorithm (i.e. cross-validation), thus generating 80 models that had a 10km resolution and were created and evaluated for the American continent. Models were evaluated 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 above 0.7 indicate models with acceptable predictive performance (ELITH *et al.*, 2006).

Ensemble forecasting approach was applied to combine the outputs from all models into a 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.

3 RESULTS

Analysing all the data obtained, records were found in 15 countries comprising literature, museum collections, and GBIF, OBIS, SGC, and FishNet2 databases. *Carcharhinus porosus* distribution models attained high AUC values (BIOCLIM: mean ± SD = 0.840 ± 0.064; Domain: mean ± SD = 0.743 ± 0.076; Mahalanobis: mean ± SD = 0.875 ± 0.048; Maxent: mean ± SD = 0.987 ± 0.013), indicating acceptable model performances (Supplementary Table S3). Previously, *C. porosus* distribution was considered to range from the south-eastern USA –

Texas, Louisiana and southern Florida – through Central America and Southern Brazil until Uruguay (COMPAGNO, 1984; MENNI; LUCIFORA, 2007). However, the current distribution obtained with the SDMs demonstrates that this species likely ranges from the eastern coast of the United States of America to south Brazil (Figure 1A). In fact, *C. porosus* is known to inhabit coastal areas within the continental platform. The same pattern was obtained in the present study throughout the whole western Atlantic Ocean, since the Caribbean islands have very little suitable areas when compared to estuaries and river mouths such as the Mississipi, Orinoco and the Amazon rivers (Figure 1B).

Indeed, the areas with the thinnest suitable occurrence coincide with short continental platforms such as in Northeastern Brazil and some portions of Central America and northern Mexico (Figure 1A). Furthermore, the models predicted that the Amazon coastal areas, especially combining the Amazon-Orinoco estuarine system, which comprises French Guyana, Surinam, 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 the Central and North Americas, suitable habitat is scarcer and occurrences are highly concentrated in estuarine and mangrove areas (Figure 2B). Although western Florida yielded a medium habitat suitability, there are no records of the smalltail shark in this region (Dr. Dean Grubbs, pers. comm.).

Table 1. List of marine environmental variables selected to build the SDMs and their conceptual rationale explanations.

Variables	Explanation
Primary productivity (mean)	Productivity affects the distribution of shark species due to its importance in shaping food webs, thus directly affecting the diversity, abundance, and distribution of sharks (BROWN *et al.*, 2010).

Dissolved oxygen (mean)	Dissolved oxygen is one of the most important environmental variables involved in shark distributions and behaviour (CARLSON; PARSONS, 2001), and is highly variable between estuarine and coastal areas.
Water temperature (mean)	Water temperature affects the distribution of coastal sharks (KNIP *et al.*, 2010). Its mean values enable us to predict where specimens could be found seasonally.
Salinity (mean and range)	Salinity affects the distribution of coastal sharks due to species specific physiological tolerances to salinity changes (KNIP *et al.*, 2010).
Light at bottom (mean)	*C. porosus* is known to be associated to highly turbid estuarine waters (LESSA, 1997), thus a higher probability of occurrence is expected in the Atlantic ocean's turbid coastal waters.

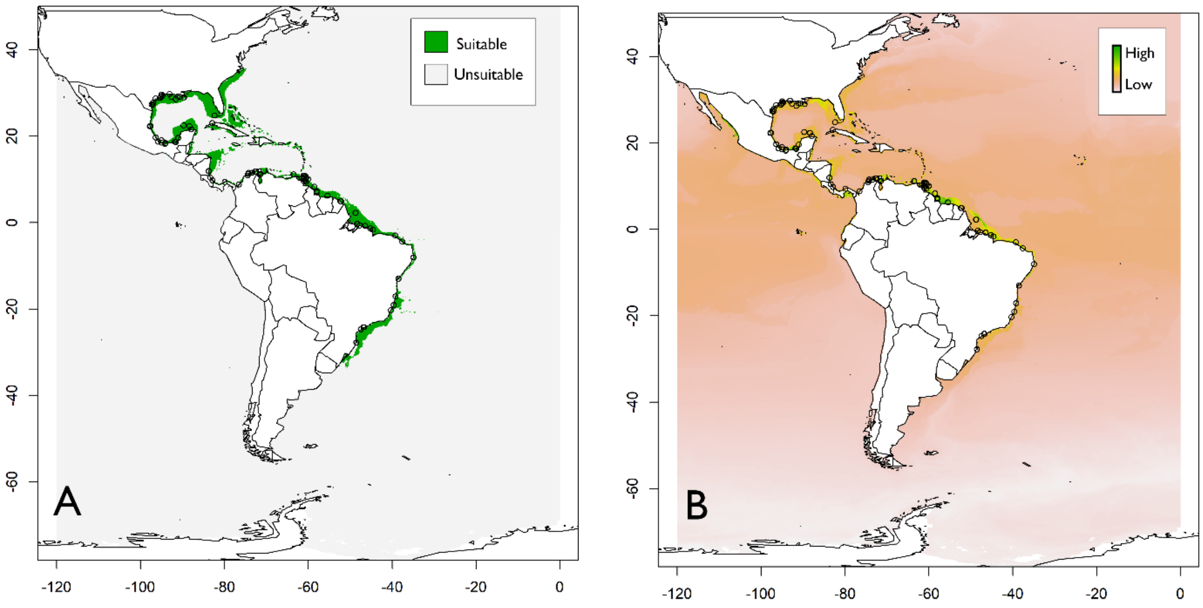

Figure 1. Prediction of *Carcharhinus porosus* distribution using an ensemble approach with four distinct algorithms (BIOCLIM, Domain, Mahalanobis and Maxent). A – Presence-absence map, B – Habitat suitability map. Circles represent occurrence records.

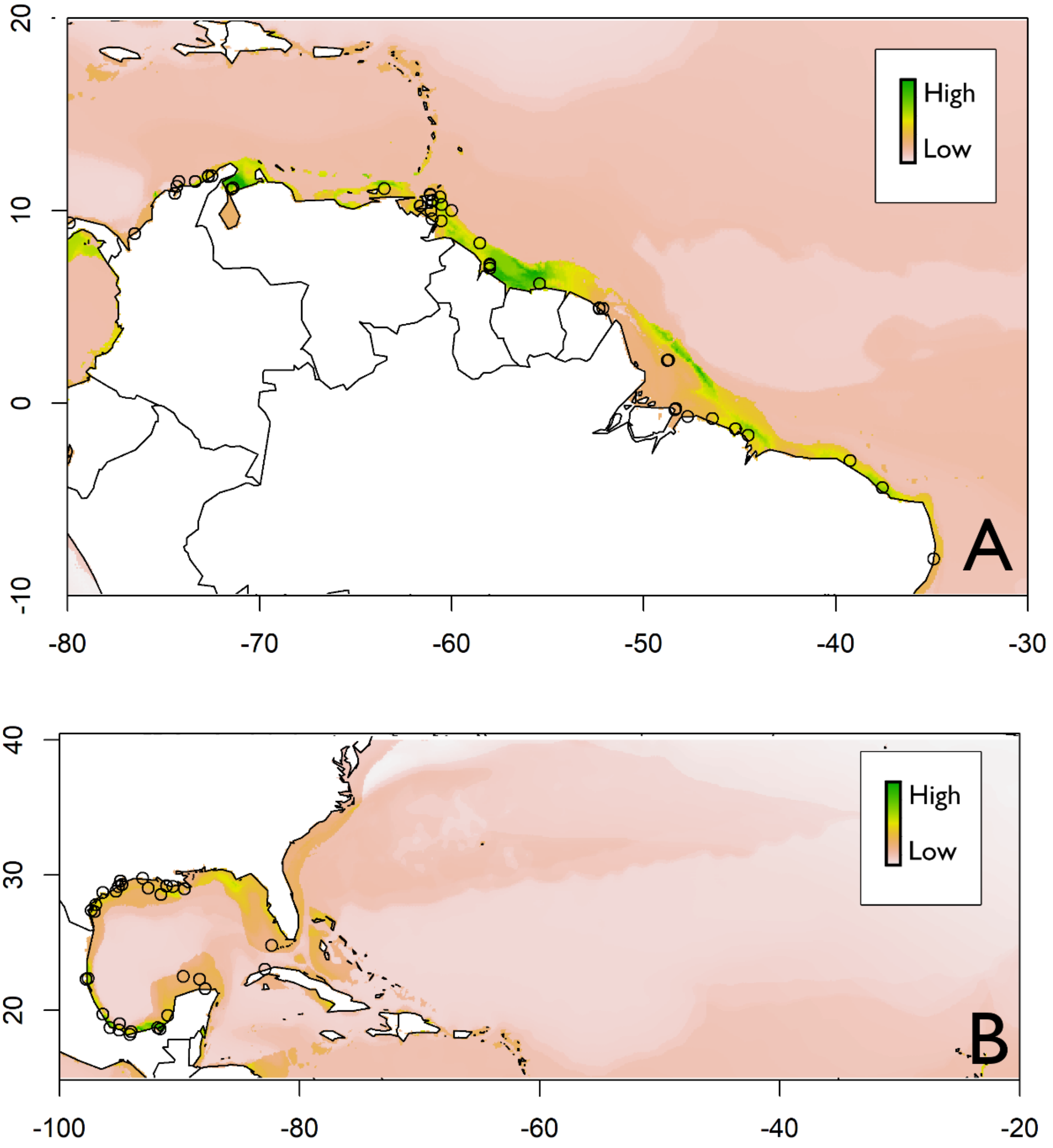

Figure 2. Fine scale habitat suitability predictions. A – Northern coast of South America, B - Gulf of Mexico and Caribbean. Circles represent occurrence records.

4 DISCUSSION

The results obtained demonstrate that *C. porosus* current distribution is likely clumped in the northern coast of South America, with decreasing habitat suitability as latitudes increase (Figure 1B). Furthermore, the northern coast of South America (NCSA) includes the areas of higher habitat suitability throughout its distribution range, which 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).

However, habitat suitability is not constant throughout the NCSA, with low suitability in the Amazon River estuary (Figure 2A). Even though *C. porosus* is known to be highly associated with turbid waters (LEOPOLD, 2004), we argue that this low suitability is caused by the strong freshwater discharge caused by the Amazon River, since the decreased suitability extends to northern Brazil, following the Northern Brazil superficial current flow (COLES *et al.*, 2013). Nevertheless, the eastern Amazon coast comprised by areas in eastern Pará and western Maranhão states yielded high suitability.

In fact, Maranhão state was considered as *C. porosus* global centre of abundance in the last conservation assessment carried out by IUCN (LESSA *et al.*, 2006). This species comprised an important portion of the bycatch in shallow (5-20m depth) gillnet fisheries targeting the acoupa weakfish (*Cynoscion acoupa*, Sciaenidae) and the Brazilian Spanish mackerel (*Scomberomorus brasiliensis*, Scombridae), as well as the deeper (20-50m depth) trawl shrimp fisheries (FURTADO-JÚNIOR *et al.*, 2002) explored by artisanal fishers in the Brazilian Amazon coast. During the 1980s, *C. porosus* composed nearly half of all shark catches in Maranhão, thus figuring as the most important shark for fisheries, with neonates and juveniles comprising almost 80% of all smalltail shark specimens caught. However, it is now considered only the third most important shark species in this fishery and has been substituted by *Rhizoprionodon porosus*, which is a morphologically similar shark, but more resilient to fisheries impacts (CORTÉS, 2002; FEITOSA *et al.* 2018).

Carcharhinus porosus declined due to its life history features that explain its intrinsically low resilience to fishing pressure (LESSA; SANTANA, 1998; LESSA *et al.*, 1999). Since artisanal, unregulated and under-reported fisheries with similar characteristics prevail in Mexico and both Central and South Americas (SALAS *et al.*, 2011), the same pattern likely has occurred in these areas for decades. Therefore, recruitment could have been dramatically impaired on a wider level. Even though Central America and the Gulf of Mexico were not considered highly suitable by the models (Figure 2B), both areas are included in the predicted distribution of the smalltail shark (Figure 1A). It is then reasonable to suppose that viable populations might still exist in these areas, but further research is necessary to elucidate this assumption.

Since the most suitable area for *C. porosus* comprises five countries (Venezuela, French Guyana, Surinam, 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 topic, although modestly. *C. 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 carried out until 2009 to ensure sustainable exploitation. 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, landings, and trade in the country (ICMBIO/MMA, 2014). Although legislation aiming to protect this and other elasmobranchs exists, catch and trade of prohibited species continue to occur indiscriminately throughout Brazil (PALMEIRA *et al*., 2013; ALMERÓN-SOUZA *et al*., 2018; FEITOSA *et al*., 2018).

Such inefficiency in law enforcement also reflects the lack of fisheries data in Brazil, which is also a constant throughout the species distribution range (SALAS *et al*., 2011). The only somewhat updated data available from Mexico pose *C. porosus* as comprising 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 the Brazilian Amazon coast (FEITOSA *et al*., 2018). No specific published studies citing this species in French Guyana, Surinam, Panama, Costa Rica, Nicaragua, USA, Belize, and Cuba were found as of May 2019. Out of those, French Guyana and Surinam are the key countries from where fisheries catch data for this species need to be imperatively obtained for a better understanding of its conservation status.

The higher habitat suitability and abundance of *C. porosus* in the NCSA makes it the most important area in the world for this species conservation. The habitat suitability analysis demonstrated that the most important areas throughout its distribution are where mangrove forests thrive (GIRI *et al*., 2011; SHI; WANG, 2010). In fact, the largest abundances of neonates and juveniles occur within coastal turbid tropical waters near mangrove-rich areas (LESSA, 1986). The NCSA has the largest continuous mangrove forest in the world and its Brazilian portion represents ~77% of the mangrove cover in the Neotropical portion of the Southern Hemisphere (DINIZ *et al*., 2019).

Therefore, all the data presented herein highlights the NCSA as the most critical area for *C. porosus* conservation along its geographical distribution. Furthermore, mangrove conservation should be included in the National Plans of Action for Sharks and Rays (NPOA-Sharks) that countries eventually develop, since no effective conservation can be obtained if habitat quality decreases. Besides protecting the environment, artisanal fisheries are the greatest threat for its conservation despite the smaller impact it causes when compared to industrial fishing. Therefore, artisanal fisheries still require statistics, proper stock assessments, effective management, and inspections to be sustainable. Although inspections have never sufficed the needs to effectively implement legislations, a good relationship between inspection agencies, managers, and the fishing community is paramount to obtain positive results on a regional level. These aspects need to be urgently addressed in order to improve population numbers and promote the species' recovery.

ACKNOWLEDGMENTS

Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco (FACEPE) provided a scholarship to LMF under the process IBPG-0089-2.05/17. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nivel Superior – Brasil (CAPES) – Finance code 001. Comissão Interministerial para os Recursos do Mar (CIRM) funded the data collection along the Maranhão Coast (1984/1988) and Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq provided Research Grants (301048/1986 and 303251/2010) to RPTL. Furthermore, the Mariana Bonfim and Cleber Ten Caten’s comments were essential for the elaboration of this research, and the help of Clarisse Éleres Figueiredo, Patrício Getúlio Garcia Neto, and Rafael Antonio Brandão with figure editing is herein acknowledged.

APPENDICES

S1 File. Georeferenced records obtained from GBIF, OBIS, SGC, FishNet2 and bibliographical sources used to build the SDMs.

Longitude	Latitude
-96.4	28.7
-91	19.6
-76.5	8.8
-46.8	-24.2
-61	10.5
-95	19
-61.1	10.8
-60.6	10.7
-95.3	28.8
-83.7	11.9
-52.3	4.9
-97.8	22.3
-95.8	18.7
-97	27.8
-96.4	19.7
-58	7.2
-60	10
-91.1	29.2
-40.3	-20.3
-38.5	-13
-91.8	18.7
-34.9	-8.1
-72.67	11.8
-72.66	11.75
-72.48	11.8
-74.2	11.5
-74.31	11.25
-73.35	11.5
-83.33	10.41
-82.81	9.73
-828,873	23,025
-52,133	4,917
-58	7
-8,234,069,061	2,478,056,526
-9,261,405,182	2,901,935,005
-97,369,133	2,737,338,638
-9,413,179,779	1,821,105,766
-970,777,359	2,728,079,605
-8,834,420,776	223,022,728

-9,402,115,631	1,839,526,176
-8,788,371,277	2,157,045,364
-9,763,271,332	2,233,607,483
-9,308,989,716	2,974,850,845
-58.52	8.31
-799,014	93,592
-60.54	9.45
-61.01	9.56
-61.08	10
-616,333	10.25
-60.51	10.3
-744,149	108,751
-71.47	11.11
-63.5	11.14
-71.39	11.17
-950,247	185,186
-91.6	18.6
-89.7	22.49
-915,628	285,675
-896,075	289,723
-95,107	29,139
-90.56	29.14
-910,817	291,853
-948,134	292,877
-949,364	295,694
-3,958,333,333	-1,908,333,333
-47.7	-0.7
-39,182,222	-171,130,556
-4,673,444,444	-2,420,416,667
-4,833,138,889	-0.29166667
-4,745,777,778	-2,473,694,444
-3,756,722,222	-439,805,556
-3,923,916,667	-299,333,333
-48,704,833	2,237,667
-48,759	22,111,667
-48,361,389	-0.353611
-44,547,778	-1,669,722
-45,226,389	-1,347,778
-46,431,389	-0.805
-4,851,194,444	-2,779,027,778
-58	7.15
-83,749,313	11,932,675
-5,231,062	4,932,294
-61,016,667	10,516,667
-61,124,764	10,845,215
-554,166,667	6.2

-61,617,517	10,253,551

S2 File. List of the 14 environmental variables chosen for the SDM analysis.

Variables
Light at bottom (maximum)
Light at bottom (range)
Light at bottom (mean)
Chlorophyll (mean)
Chlorophyll (range)
Dissolved oxygen (range)
Dissolved oxygen (mean)
Primary productivity (range)
Primary productivity (mean)
Salinity (mean)
Salinity (range)
Sea water temperature (mean)
Sea water temperature (range)

S3 File. AUC values for each SDM algorithm used.

Bioclim	Gower	Maha	Maxent
0.852272727	0.761363636	0.824380165	0.991735537
0.742768595	0.681818182	0.845041322	1
0.923553719	0.849173554	0.904958678	0.995867769
0.830578512	0.734504132	0.820247934	0.987603306
0.808884298	0.659090909	0.814049587	0.964876033
0.830578512	0.723140496	0.921487603	0.995867769
0.815082645	0.659090909	0.83677686	0.977272727
0.839876033	0.691115702	0.824380165	0.977272727
0.897727273	0.803719008	0.917355372	0.993801653
0.805785124	0.725206612	0.931818182	1
0.816115702	0.76446281	0.814049587	1
0.813016529	0.716942149	0.900826446	0.969008264
0.741735537	0.603305785	0.834710744	0.969008264
0.933884298	0.820247934	0.892561983	0.966942149
0.862603306	0.75	0.911157025	1
0.930785124	0.82231405	0.886363636	1
0.892561983	0.851239669	0.933884298	0.993801653
0.940082645	0.888429752	0.958677686	1
0.79338843	0.690082645	0.826446281	1
0.730371901	0.674586777	0.907024793	0.964876033
Average			
0.840082645	0.743491736	0.875309917	0.987396694
Standard deviation			
0.064214768	0.076053725	0.048055573	0.013898776

3 MANUSCRITO II

Habitat use of the smalltail shark *Carcharhinus porosus* (Ranzani, 1839) from northern Brazil inferred from vertebrae microchemistry analysis

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Abstract

Sharks are among the most endangered and data poor vertebrates in the world. The lack of information regarding their habitat use is especially concerning since these are crucial for the elaboration of management measures and establishment of priority areas for species conservation. Investigating the trace elements present in shark vertebrae has become an interesting tool to analyze species habitat use patterns over individual's lifetimes. Therefore, the present study aimed at using vertebrae microchemistry to investigate the habitat use patterns of *Carcharhinus porosus* in Brazil's Northern Coast (BNC) – its global center of abundance. Vertebrae from seventeen individuals sampled in the 1980s (n=8) and in between 2017 and 2018 (n=9) were analyzed through laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS). Five elements known to reflect environmental characteristics (Ba, Ca, Mg, Mn, and Sr) were read and analyzed by sex and life stages. Significant differences in element concentration were found solely between sexes. Furthermore, when evaluating the neonate signature between individuals, four major clusters were obtained, thus suggesting that the species has at least four birthing grounds in the area. Despite the occurrence of individuals of all sizes, adults show a more distinct occurrence pattern. Females are more frequently caught in the rainy season, while males are more abundant on the dry season. In addition, the occurrence of adult individuals with different neonate signatures throughout Maranhão state's coast corroborates the existence of a single population in the area. Finally, the results reinforce the hypothesis that the BNC is likely a nursery for the species, and thus a critical area for its conservation.

Keywords: Carcharhinidae; Brazil’s Northern Coast; movement ecology; vertebrae trace elements.

1 INTRODUCTION

Basic biological data such as demographic parameters, life history traits, reproductive patterns, and habitat use are crucial for species management and conservation (COCHRANE, 2002). However, sharks are among the taxonomic groups with less basic information available, thus hampering proper conservation actions in all geographical scales (DULVY *et al*., 2014). Furthermore, most shark populations are subjected to overfishing and an overall decreasing habitat quality due to water pollution, which raises concern for their sustainability in the near future.

Sharks in Brazil are facing similar problems, and legislation aiming at mitigating them has not followed along (BARRETO *et al*., 2017). In addition, several nationally and internationally endangered species are consistently caught as bycatch of shrimp and teleost fisheries (PALMEIRA *et al*., 2013; ALMERÓN-SOUZA *et al*., 2018; FEITOSA *et al*., 2018). The northern coast, which includes the Amazon estuary, is the main region in Brazil where sharks experience bycatch (OLIVER *et al*., 2015). Brazil’s Northern Coast is one of the main fishing areas of the country and harbors a great diversity of elasmobranchs, including endemic species (LESSA *et al*., 1999). Furthermore, it is considered a global conservation hotspot for these *taxa* and several portions are or should be protected areas (DAVIDSON; DULVY, 2017; DULVY *et al*., 2014).

Nevertheless, gillnet fisheries targeting large teleost species such as the Acoupa Weakfish *Cynoscion acoupa* and the Brazilian Spanish Mackerel *Scomberomorus brasiliensis* have caused severe population collapses on sharks such as *Isogomphodon oxyrhynchus* in Brazil’s northern coast (LESSA *et al.*, 2016). These fisheries use drift gillnets soaked for up to 12 hours with 170 mm meshes between knots, 4 to 6 m in height extending for at least 3 km for *Cynoscion acoupa* (ALMEIDA *et al*., 2014) and 60 mm meshes for *S. brasiliensis* reaching more than 5,000 m in extension (MOURÃO *et al*., 2014). The smalltail shark *Carcharhinus porosus* is another shark species that has suffered severe declines, but its collapse has been under documented. Nevertheless, an 85% biomass decrease in the region considered its global center of abundance was recorded in 2004 and evidence of low genetic diversity in this population already exists (LESSA *et al*., 2006; TAVARES *et al*., 2013).

Since this species corresponded to 43% of the sharks caught by gillnets in the region during the 1980s and 1990s (LESSA, 1997), this dramatic decline is of particular concern. Despite its small size (150 cm estimated maximum length), its life history traits make it easily susceptible to overfishing since its fecundity is low (average of 6 pups per gestation), the reproductive cycle is biannual, and both sexes reach sexual maturity with six years old (LESSA; SANTANA, 1998; LESSA *et al.*, 1998). It is highly associated to turbid and dynamic areas with mangrove rich coasts and juveniles were consistently caught within estuaries in Maranhão state's coast (MENNI; LESSA, 1998). Despite this information, its habitat use patterns are still poorly understood.

Several techniques such as acoustic and satellite telemetry have been recently applied to study habitat use of several shark species (HAZIN *et al.*, 2013; TAYLOR *et al.*, 2017). However, these methods are expensive, require the capture, tagging, and release of live specimens, and only gather data within a limited timeframe of the animal's life (FRASER *et al.*, 2018). As a counterpart, the evaluation of trace element composition in fish hard parts provides a glimpse of how an animal uses its habitat during its lifetime (WALTHER, 2019), thus being a promising technique that has been widely used for teleost fishes (PONTUAL; GEFFEN, 2002; GILLANDERS, 2005; ELSDON *et al.*, 2008; PAILLON *et al.*, 2014), and is being increasingly applied on sharks and rays (TILLETT *et al.*, 2011; IZZO *et al.*, 2016; McMILLAN *et al.*, 2017, 2018). Several elements such as Strontium (Sr), Barium (Ba), Manganese (Mn), and Magnesium (Mg) have been considered to be reliable proxies for environmental tracers of species habitat use, since their concentration in the vertebrae has been shown to reflect their environmental concentrations (McMILLAN *et al.*, 2017).

More specifically, Sr and Ba are related to changes in salinity, in which the former is more abundant in saltwater and the latter in freshwater (McMILLAN *et al.*, 2017). On the other hand, both Mn and Mg are associated with large variations in water temperature, but Mn concentration changes are also believed to reflect proximity of mangrove areas (PAILLON *et al*, 2014; SMITH *et al.*, 2016). Since these variations are stored in the vertebrae and no evidence of element reabsorption by the body, evaluating their concentration changes in hard parts enables the understanding of changes in trace element composition throughout an individual's lifetime. With these, key information on the type of habitat a species uses during each life stage (MCMILLAN et al., 2017), and even potential nursery areas (TILLETT *et al.*, 2011; LEWIS *et al.*, 2016; SMITH *et al.*, 2016; HEUPEL *et al.*, 2018) can be obtained. However, several aspects of this methodology need to be addressed to improve the robustness of conclusions, especially in areas with little environmental variation.

Unraveling the habitat use patterns of a species according to age, together with other biological information can provide enough information to establish key areas for a species conservation such as nurseries. Thus, this study aimed at investigating these patterns across life stages and between sexes for one of the most heavily fished shark species in the Brazilian northern coast through vertebrae trace elements. We also used the vertebrae microchemistry data to investigate eventual changes in habitat use when the species was abundant (1980s) and after population collapse (2010s), as well as investigating eventual chemical differences between seasons. Furthermore, we tested the data obtained to the criteria developed by Heupel et al (2007) that define the assumptions for an area to be considered an elasmobranch nursery. Finally, we briefly discuss knowledge gaps that need to be filled by future elasmobranch vertebrae microchemistry studies carried out with species endemic to low latitude areas.

2 METHODS

2.1 Sampling area

Brazil’s northern coast (4°11'40.58"N to 2°18'45.53"S) is a highly indented area subjected to the Amazon River’s estuary of which Maranhão state is part (Figure 1). Temperatures suffer little variation during the year (average water temperature 28ºC), but the region experiences two marked seasonal pluviometry cycles. The rainy season extends from January to June and the dry season from August to December, with a transition period in July. In addition, daily tidal cycles pose a great level of dynamism to the coastal areas with spring tides reaching up to 7 m in amplitude from high to low. The vast amount of estuaries and the tropical climate grant the region the unique characteristics of its mangrove forests, with trees reaching 30 m in height and extending for over 5,000 km^2 (SOUZA-FILHO, 2005). Due to its highly productive and turbid water’s, diversity and endemism levels are high, thus making it one of the most important areas for shark conservation in the world.

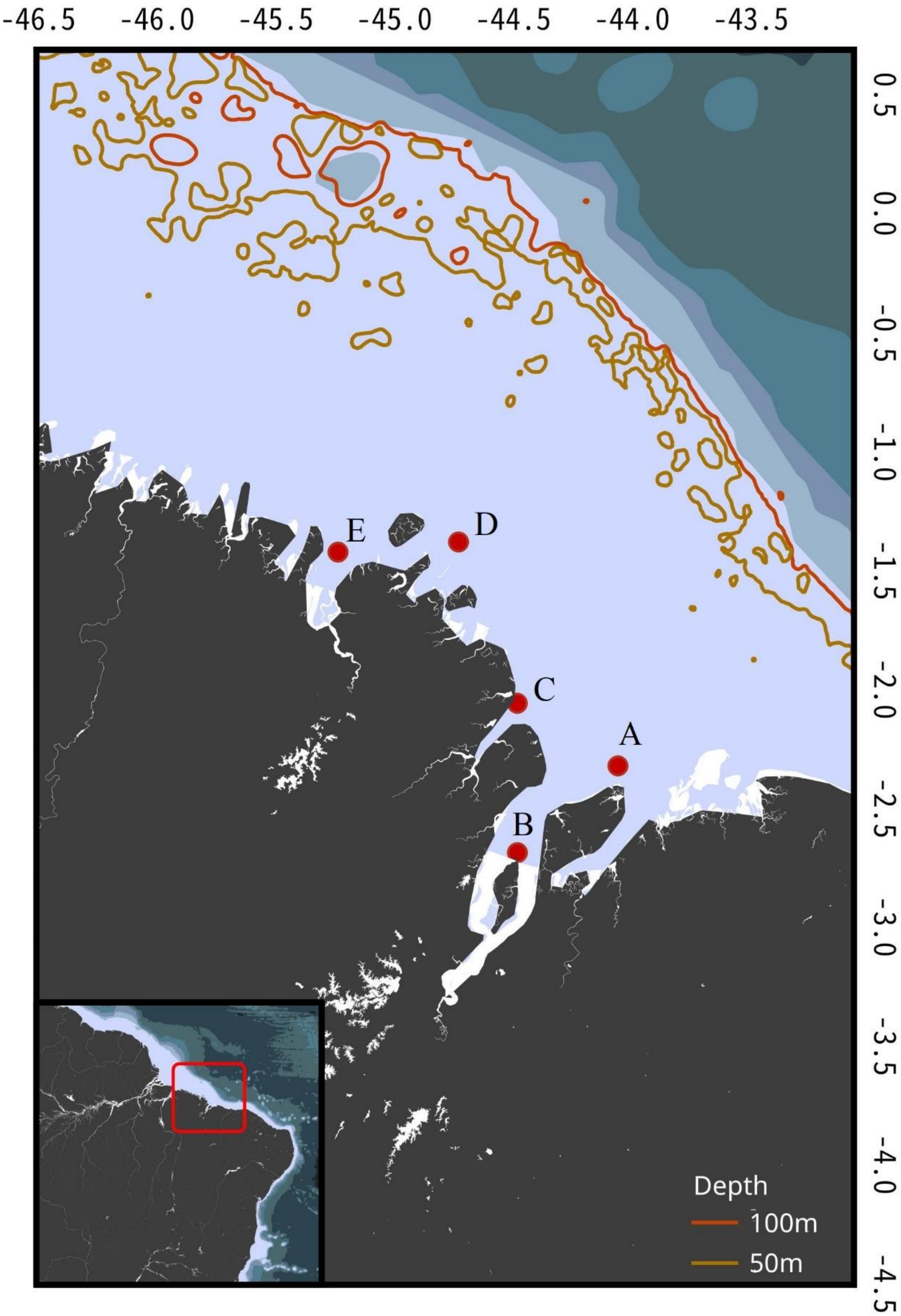

Figure 1. Brazil's Northern Coast (area within the red square) with sampling locations, and 50 and 100 m depth isobaths. A – Canal do Navio; B – Ilha dos Caranguejos; C – Araoca; D – Farol São João; E – Turiaçu.

2.2 Sampling design

Smalltail shark vertebrae were sampled from specimens landed in the Raposa municipality in Maranhão state (0º59’0.88”S to 2°18'45.53"S). Blocks of five vertebrae were retrieved from seventeen specimens. Since carcasses were already processed (headed and gutted), identification followed the field remarks pointed by Compagno (1984), such as the origin of the second dorsal fin over the midbase of a strongly notched anal fin. Samples were collected according to the Brazilian environmental laws under the license (License SISBIO, 49663-1). The relationship between vertebrae radius and TL was calculated through the equation by Lessa; Santana (1998).

2.3 Vertebrae processing

For the vertebrae microchemistry analysis, frozen samples were thawed and two vertebrae from each block were retrieved. The connecting tissue was removed and vertebrae were air dried for 48 hours (n=9). Samples collected by R. Lessa and V. Batista in the 1980s were also included in the analysis (n=8). Although these were subjected to formaldehyde 4% treatment, it does not impair our analysis since there is no evidence of this kind of procedure affecting microchemistry results - other than sodium concentration (MOHAN *et al*., 2017).

For processing, all vertebrae were embedded in polyester resin and air dried for 48 hours. Vertebrae were transversely sectioned with low speed diamond Isomet™ (Buehler) saw. Translucent and opaque rings of band pairs were considered to be formed annually (LESSA; SANTANA, 1998). Prior to analysis by laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS), vertebrae, sections were polished with silicon carbide paper (no 8000), washed ultrasonically with ultrapure water (Milli-Q, Millipore) and dried in sterilized vials for 48 hours before analysis. Cleaned samples were stored individually in hermetic plastic bags until laser ablation.

Analytical measurements were taken at the *Departmento de Química* (UFSM) with a Q-switched pulsed 213 nm Nd:YAG laser ablation system (NWR 213, ESI – New Wave Research) coupled to an Agilent 7500 inductively coupled plasma mass spectrometer. The laser was operated with a pulse frequency of 20 Hz, a scan speed of 30 $\mu m\ s^{-1}$, and an energy output of 0.2 to 0.3 mJ per pulse. Under these conditions, the crater width was approximately 25 µm. The ablated material was conducted through a Teflon-coated tube into the ICP-MS using argon as a carrier gas (0.85 $dm^3\ min^{-1}$). The ICP was operated at 1,300 W nominal powers with outer and intermediate gas flows of 15.0 and 1.1 $dm^3\ min^{-1}$, respectively. Quantification was performed using element:Calcium ratios as internal standard for each element. The NIST 612 certified reference material was employed to obtain counts per second (CPS), which were later transformed into concentrations (ppm) by the equation formulated by Longerich *et al.* (1996). The limit of detection (LOD) was calculated following Longerich *et al.* (1996) and elements that did not meet this standard were excluded from the analysis.

2.4 Fisheries-independent data

Finally, we have gathered log book data from the fisheries-independent sampling carried out and published by Lessa & Santana (1998) between 1984 and 1987. All specimens sampled (n=930) were computed, together with the sampling location, month, year, total length, and depth. The inverted von Bertalanffy growth function was calculated to obtain an estimate of age based on individual size. However, we only used the season, month, and depth information to evaluate eventual occurrence patterns based on such abiotic factors (Table 1).

Table 1. Sex ratio (M:F) of catch data published by Lessa *et al.* (1999) discriminated by season, month, and depth range. Bolded values correspond to female biased occurrence, while underlined values correspond to male biased occurrence.

Factor		Sex ratios (M:F)				
Season		Neonate	Juvenile	Subadult1	Subadult2	Adult
	Rainy	0.67	1.02	1.36	1.00	**0.54**
	Transition	0.75	2.13	0.88	**0.88**	1.00
	Dry	0.70	0.88	1.59	3.20	6.00
Month						
	January	0	0.88	1.00	0	**0.60**
	February	0	1.00	2.00	1.00	0
	March	0	0	3.00	**0.40**	**0.42**
	May	4.00	1.33	1.00	1.00	1.00
	June	0.29	0.76	6.00	0.13	2.00
	July	0.75	2.13	0.88	0.13	1.00
	August	1.30	0.84	1.10	**0.75**	**0.17**
	September	0.67	1.00	1.00	0	0
	October	0.29	0.94	0.75	13.00	6.50
	November	0	1.67	0.67	0	0
	December	0	0	0	0	1.00
Depth (m)						
	0 to 10	0.33	0.50	0.38	0	**0.50**
	10 to 20	0.88	0.98	1.10	3.00	2.67
	20 to 35	0	0	16.00	6.75	1.67

2.5 Data analysis

The distance from the nucleus to each band was measured to estimate the exact positioning of the element concentration counts provided by the LA-ICP-MS. This enabled the establishment of the profile for each element analyzed for each year of life. Since specimens had different ages and the information on habitat use per life stage is much more meaningful than on annual basis, life stages were chosen following the age and growth data for both sexes (LESSA; SANTANA, 1998). The neonate portion of vertebrae was considered to range from the birth-mark to the end of the first year of life, followed by the juvenile phase between the start of the second year of life to the end of the third. The sub-adult stage was subdivided in two groups: sub-adult1 that ranges from the third year to the end of the fourth, and sub-adult2 ranging from the start of the fifth to the end of the sixth year of life. The adult stage was considered from the sixth year to the end of the vertebra. Furthermore, fisheries-independent data published by Lessa *et al.* (1999) and Stride *et al.* (1992) were used to establish potential relationships of habitat use patterns with the elemental signature results.

Seventeen individuals (Table 2) were analyzed in a multi-element LA-ICP-MS for ^{24}Mg, ^{43}Ca, ^{55}Mn,^{86}Sr, ^{138}Ba,^{112}Cd,^{206}Pb, and ^{208}Pb. Element:Ca ratios were calculated for each element with raw concentration counts (CPS) already transformed to ppm and were then either log(x+1) transformed (for the PERMANOVA or scaled with the Z transformation (for the cluster and PCA analysis) to obtain results on the same scale for all elements analyzed. Only elements that have already been validated to represent proxies for environmental features such as salinity and temperature changes were used in further analysis. Average reads for each life stage and each element were calculated and used on the subsequent statistical analysis. A PERMANOVA with an Euclidian distance resemblance matrix and 1000 permutations was carried out with sex, age, season, and decade of capture as fixed factors to evaluate multi and single-elemental differences in habitat use for the species. We also performed a cluster analysis with average distances to check if certain individuals would form groups based on their neonate multi-element chemical signature, thus signaling the repetitive use of certain areas. Finally, to obtain which elements were most important for sexes, seasons and decades, a similarity percentages analysis (SIMPER) was carried out with the average values for each factor using Euclidian distances. All statistical analysis were performed in R version 3.5.1 (R CORE TEAM, 2013) except for SIMPER which was performed in PRIMER. All statistical tests considered a significance level of 0.05.

3 RESULTS

Out of the elements analyzed, only Ca, Mg, Mn, Sr, and Ba were used for the habitat use analysis due to their reliability as proxies for environmental tracers in elasmobranchs. Cd and Pb isotopes were excluded from the final analysis because they were below the limit of detection (LOD). No significant statistical differences between life stages were found in any of the PERMANOVAs performed. However, significant differences were found between sexes, seasons, and decades in the multi-element analysis, as well as for sexes in all element:Ca analysis for sexes. Furthermore, significant differences were found between decades for Sr:Ca, and between seasons for Mg:Ca and Ba:Ca (Table 3).

Table 2. Description of the total length (TL), sex, location, date of capture, and source for each individual sampled and analyzed with LA-ICP-MS.

Sample	TL (cm)	Age (years)	Sex	Sampling station	Season	Month	Year	Source
CP A4 37	85.3	9	Male	Canal do Navio	Dry	October	1984	Lessa (1986)
CP A39 01	85.6	12	Male	Caranguejos	Rainy	March	1986	Lessa (1986)
CP A39 09	87.5	9	Female	Caranguejos	Rainy	March	1986	Lessa (1986)
CP A50 09	73	7	Female	Araoca	Dry	October	1987	Lessa (1986)
CP A50 12	80	7	Female	Araoca	Dry	October	1987	Lessa (1986)
CP A50 16	101	11	Female	Araoca	Dry	October	1987	Lessa (1986)
CP B4 02	90	15	Male	Farol São João	Rainy	March	1989	Stride et al. (1992)
CP B4 06	97	12	Male	Farol São João	Rainy	March	1989	Stride et al. (1992)
CP101	85.94	8	Male	Canal do Navio	Dry	October	2017	Present study
CP103	67.09	7	Male	Canal do Navio	Dry	October	2017	Present study
CP104	64.49	7	Male	Canal do Navio	Dry	October	2017	Present study
CP105	63.84	7	Male	Canal do Navio	Dry	October	2017	Present study
CP106	65.14	8	Male	Canal do Navio	Dry	October	2017	Present study
CP108	56.04	5	Male	Canal do Navio	Dry	October	2017	Present study
CP109	61.89	6	Female	Canal do Navio	Dry	October	2017	Present study
CP110	65.2	7	Female	Turiaçu	Rainy	April	2018	Present study
CP111	115	18	Female	Canal do Navio	Dry	October	2018	Present study

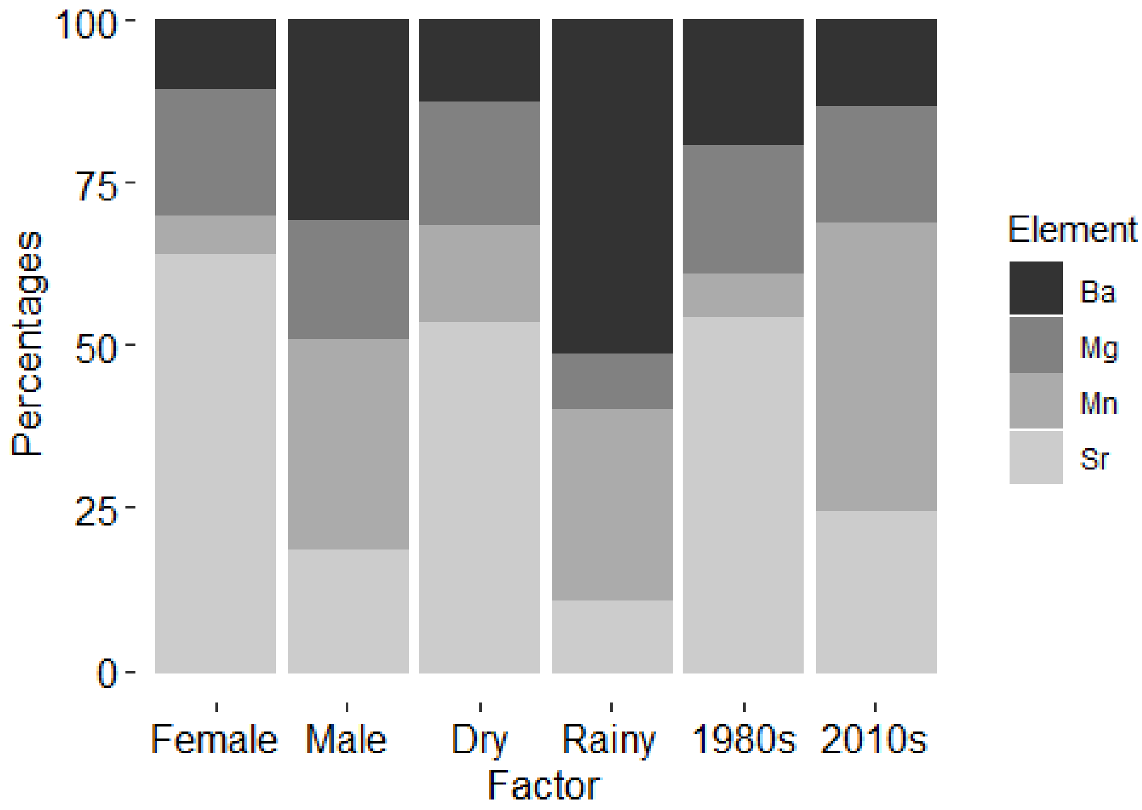

Figure 2. Similarity percentages (SIMPER) demonstrating the chemical signatures for the factors analyzed. Total n = 17 (sex – female: n = 7; male: n = 10), (seasons – dry: n = 12; rainy: n = 5), (sampling decades – 1980: n = 8; 2010: n = 9).

SIMPER results demonstrate the clear signal of Ba in the rainy season, and elevated percentage of Sr in the dry season. As expected based on the PERMANOVA results, chemical signatures were different for sexes, with Sr being much more abundant in females than in males, and Ba following the inverse pattern in males. Regarding the decades of the samples analyzed, the major differences were found in Sr and Mn, with the former being much more abundant in the 1980s and the later sharply increasing in the 2010s. Overall, the element with the smallest variation in all factors evaluated was Mg.

Table 3. Results for the one-step PERMANOVAs calculated for the multi and single-element analysis with life stage, decade, season, and sex of individuals as factors. df – degrees of freedom; MS – Mean Square values; *p* – probability of results being due to random factors. Statistically significant measures are in bold.

Element	Life Stage			Decade			Season			Sex		
	df	MS	*p*	df	MS	*p*	df	MS	*p*	df	MS	*p*
Multi	4	0.1638	0.9930	1	2.9047	**0.0299**	1	3.8046	**0.0119**	1	12.4393	**0.0009**
Residuals	78	0.7473		81	0.7472		81	0.6807		81	0.5741	
Mg:Ca	4	0.0062	0.9950	1	0.2419	0.1748	1	1.2927	**0.0023**	1	2.3744	**0.0009**
Residuals	78	0.1326		81	0.1347		81	0.1217		81	0.1084	
Mn:Ca	4	0.1188	0.3916	1	0.0463	0.5495	1	0.0406	0.5924	1	1.9551	**0.0009**
Residuals	78	0.1091		81	0.1103		81	0.1104		81	0.0867	
Sr:Ca	4	0.0016	1.0000	1	2.1345	**0.0129**	1	0.8638	0.1339	1	5.9686	**0.0009**
Residuals	78	0.3665		81	0.3267		81	0.3424		81	0.2794	
Ba:Ca	4	0.0371	0.9001	1	0.4818	0.0519	1	1.6072	**0.0009**	1	2.1411	**0.0009**
Residuals	78	0.1289		81	0.1200		81	0.1061		81	0.0995	

Cluster results demonstrated that the multi-element signatures for the neonate phase demonstrated that individuals have different birthplaces. Indeed, the cluster analysis evidenced at least three birthing grounds based on the average chemical similarities between individuals with cophenetic distance of 0.93671 (Figure 4). Furthermore, since the locations in Figure 5 reflect the collection places of the adults instead of the actual birth areas, and the localities are intermingled among the clusters, the birthing grounds seem to be specific.

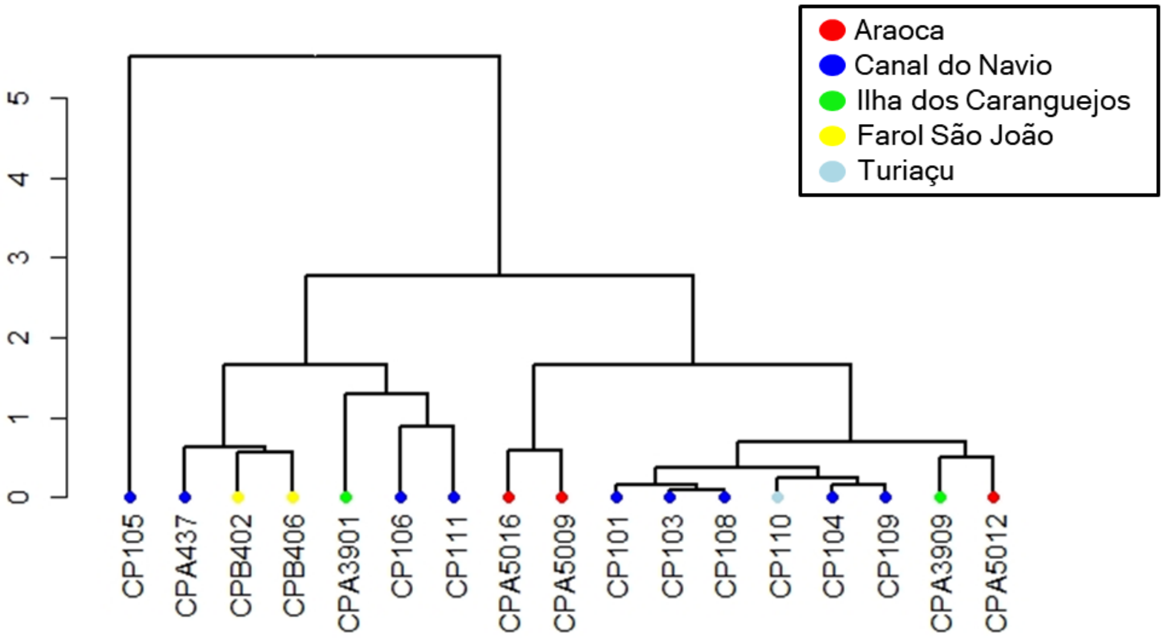

Figure 3. Cluster analysis for neonate multi-element chemical signatures. Sample codes are in the x-axis. Sites are the sampling points where adults were captured. Each branch tip color represents a sampling location: red = Araoca, blue = Canal do Navio, light blue = Turiaçu, green = Ilha dos Caranguejos, yellow = Farol São João.

4 DISCUSSION

4.1 Patterns of habitat use and suggestions for effective species management

Results demonstrated that the smalltail shark does not undertake habitat partitioning throughout its ontogeny (Table 3). However, multi and single-element PERMANOVAs separately testing differences between seasons, sex, and decades yielded statistically significant differences. Overall, the PERMANOVA results point that all life stages of the *C. porosus* population uses the whole area in a constant manner. However, the differences obtained demonstrate that the smalltail shark likely presents sex segregation, which is a somewhat widespread behavior among shark species (WEARMOUTH; SIMS, 2010). Nevertheless, it is not clear if the specimens move further away from the coast or to deeper areas where salinity is expected to be higher in the rainy seasons.

Seasonality in the region is strong and the sex differences in multi-element signatures shown by the SIMPER analysis (Figure 2) seem to reinforce this argument, since Ba is much more representative for males. Indeed, Ba is an element known as a proxy for proximity to freshwater runoff areas (SMITH *et al*., 2013). However, our fisheries-independent catch data point to a greater percentage of Ba for males instead of females. Moreover, the lack of differences in the single-element results for Mn indicates that the species remains near the coast subjected to influences from mangrove habitat, since Mn is considered to be more abundant in coastal areas with mangrove forests nearby (PAILLON *et al*., 2014). Even though the SIMPER results demonstrate a drastic change in Sr percentages between the dry (higher) and rainy (lower) seasons, its single-element results yielded no significant differences between them. In fact, the incongruence between analyses is likely related to the higher variance for Ba, which was indeed statistically significant in the single-element analysis between seasons (Table 2).

On the other hand, Mg was also significant between seasons in the single-element analysis. Since its concentration is considered to be negatively affected by temperature variations (SMITH *et al*., 2013), we tested it to investigate potential dives for deeper areas in which water temperature would be significantly lower than in coastal waters. This behavior has been shown for several shark species (AFONSO; HAZIN, 2015), but never for a small coastal one. Indeed, no evidence of such dives were obtained for *C. porosus*, which is in accordance with the known biology of the species, thus reinforcing that its distribution is likely restricted to the surface waters within the continental platform (LESSA *et al*. 1999). However, there is also evidence pointing that Mg may suffer biological influences from diet and physiology on a species-specific basis (McMILLAN *et al*., 2017), thus its results must be taken cautiously and further laboratory validation for each organism analyzed.

4.2 Evaluation of nursery criteria

Nurseries have long been considered as one of the most critical areas for elasmobranch conservation since they provide key habitat for neonates and juveniles to grow and thus guarantee recruitment for the next generations (LESSA *et al*., 1999). However, there have been several attempts to define what would be considered as a nursery, since these areas should be preserved and there it is impossible to guarantee the conservation of each one (BECK *et al.*, 2001; HEUPEL *et al.*, 2007; HEUPEL *et al.*, 2018). Therefore, Heupel *et al.* (2007) developed three testable criteria to designate a given area as a nursery, which are: (1) newborns and young-of-year specimens must by more commonly found in the studied area than elsewhere, (2) must remain in that area for longer periods of time, and (3) the area must be repeatedly used across years. Furthermore, Heupel *et al.* (2018) have considered that the statement by Beck *et al.* (2001) that juveniles and adults should not coexist in a nursery to be true.

Recently, Heupel *et al.* (2018) revised the existing literature testing the criteria and stated that small-bodied coastal sharks tend not to have specific nursery areas. However, applying those criteria to the gillnet capture and microchemistry data presented herein, the smalltail shark could be a different case for four reasons. First, the BNC has the highest occurrence of newborns and young-of-year specimens known in any other area along its geographical distribution (LESSA *et al.*, 1999; LESSA *et al.*, 2006). The only other areas with juvenile captures are Sergipe and São Paulo state's coasts (SADOWSKY, 1967; MENESES *et al.*, 2005), but numbers are still much lower than in the BNC.

Second, they seem to stay in the same area until reaching sexual maturity as shown by the fisheries independent data. Comparing the microchemistry results and the fisheries-independent data (Table 1), adult females are more abundant during the rainy season, especially in March when they correspond to double the number of adult males. On the other hand, the sex ratio is skewed towards adult males in October (Table 1). Interestingly, the sex ratio between adult males and females becomes less skewed during June and July when the transition between the rainy and dry seasons occur. We argue that these differences in occurrence between adult individuals, together with the microchemistry results, are strong evidence that a seasonal habitat partitioning between sexes likely occurs in the BNC population.

However, fishing gear might also be responsible for this catch patterns. Fisheries-independent surveys carried out in the BNC with different gillnet sizes during the 1980s and 1990s have conflicting results. Lessa *et al.* (1999), using gillnets 900m long (7.5m in height and 80mm mesh size between knots) caught 1,128 specimens between 1984 and 1987 from which ~80% comprised neonates or juveniles. On the other hand, Stride *et al.* (1992) only caught adult individuals (N=78) on the same areas using gillnets with larger mesh sizes (200 mm between knots, 400 m long, and 6 m height) than the ones used by Lessa *et al.* (1999). Furthermore, increasing mesh sizes resulted in a decrease in capture of *C. porosus* from 14%

in the 200mm mesh to 0.8% in the 300mm mesh size (STRIDE *et al*., 1992). Thus, gear selectivity is an important source of bias for the life stage occurrences observed. In addition, specimens were most commonly caught in areas where salinity tended to be higher, but no information on seasonal changes in capture are provided (STRIDE *et al*., 1992).

Nevertheless, Stride *et al*. (1992) caught a larger number of pregnant females (n=10). Among those samples, six were caught in May and most had near-term embryos (size at birth at 30cm TL). This information, together with the existing reproductive, catch, and habitat use data for the species led us to argue that most *C. porosus* females likely give birth in the second trimester (rainy season), and copulation likely takes place in October with females that are resting from gestation from the previous year. Further evidence for that is the capture of an adult female used in the present study (individual CP111) with fresh mating scars in October 2018 (Figure S1). In addition, this is further evidence that *C. porosus* whole life cycle (birth, growth, copulation, reproduction, and death) occurs within the continental platform and little dispersion exists.

Third, the existence of at least two groups in the cluster analysis (Figure 3), as well as the grouping of samples captured in the 1980s and 2017/2018 point towards the existence of historically used nursery areas and philopatry behavior. Future research should focus on catching neonates and juveniles and evaluating the vertebral edge microchemistry signature to compare with the ones obtained in the present study and accurately mark each nursery area. However, molecular studies through genotype reconstruction or long-term telemetry of adult females are needed to effectively prove this hypothesis. Furthermore, the coexistence of adults born in areas with diverging chemical signatures (Figure 3) reinforces the hypothesis that the BNC’s smalltail sharks comprise a single population and thus should be managed as a single unit.

Fourth, although adults and juveniles overlap, clear differences in occurrences exist (Table 1), especially considering the depth range with neonates and juveniles completely absent from areas deeper than 20m, thus reinforcing the little overlap of different ontogenetic phases. Therefore, we argue that the BNC, especially the eastern Amazon coast in Maranhão state, fulfills the majority of the elasmobranch nursery criteria, and that the species spends its whole life cycle within the continental platform, but with habitat partitioning between sexes and several different birthing grounds. Since this species seems to have a restricted dispersion capacity, it is likely that several nurseries exist throughout its geographical distribution and these different cohorts might actually have little connectivity, thus being an important information for stock management and species conservation.

4.3 Improvement suggestions for future microchemistry studies at low latitudes

Although elasmobranch vertebrae microchemistry has proven to be a robust technique to evaluate habitat use patterns (McMILLAN *et al*., 2017), there is not enough information on the physiological processes involved in element uptake by the vertebrae. Indeed, there are only two studies carried out in controlled environments evaluating the effects of biotic (diet, physiology) and abiotic factors (salinity, temperature, pH) on element concentrations (SMITH *et al*., 2013; PISTEVOS *et al*., 2019). In addition, elasmobranch microchemistry studies are mostly carried out with temperate species subjected to a much more variable environment, with strong seasonality. Therefore, the published literature is not always in accordance with the environmental characteristics of the tropics. Consequently, it is a lot harder for researchers studying tropical species to draw strong conclusions about their results based on literature specialized in temperate species.

Regardless, it is clear that a lot more research is necessary to fill the major elasmobranch microchemistry knowledge gaps pointed by McMillan *et al*. (2017). Indeed, most of the assumptions used in elasmobranch trace element studies are based on otolith microchemistry (McMILLAN *et al*., 2017), a much more solid field of research (PANFILI *et al*., 2002). This is likely a result of the difficulty in maintaining elasmobranchs in aquaria (MCMILLAN *et al*., 2017). Therefore, we discuss what the next frontiers for elasmobranch vertebrae microchemistry studies carried out with tropical sharks and rays are. We also raise two major questions regarding the main knowledge gaps for elasmobranch microchemistry based on the published literature and our data.

First, which elements are capable of assessing finer-scale changes in habitat use for species subjected to little environmental variation? The smalltail shark might indeed have little variation in habitat use and, since the habitat environmental characteristics are generally stable over time, the trace elements we analyzed were not capable of detecting fine scale changes, such as salinity differences detected by Tillett *et al*. (2011). However, this could also be a methodological feature that requires further information. Therefore, we reinforce the need to study element uptake physiology in depth and to validate the environmental signal each element provides, especially for species occurring in low latitudes. A potential candidate might be sulfur, which could be a successful element to evaluate horizontal migrations and distance from the coast (see RUBENSTEIN; HOBSON, 2004 and DOUBLEDAY *et al.*, 2018 for further information), since it seems to reflect organic matter concentration in the water. Another potential candidate could be manganese that, even though validation tests have already investigated its potential as an environmental tracer, conflicting results were obtained and its information might be more useful on a species-specific basis (SMITH *et al*., 2013; PISTEVOS *et al*., 2019). Paillon *et al*. (2014) found it to be representative of the *Lutjanus fulviflamma* (Perciformes: Lutjanidae) population collected near mangrove forests in New Caledonia, but no tests have been carried out to test this assumption in the laboratory, and this conclusion might be site specific rather than general.

Second, what is the effect of metabolic rate on the time it takes for a given water chemistry signature to be marked on the vertebrae? To our knowledge, the only study ever carried out investigating how growth and environmental history affected elemental concentration in the vertebrae was done by Smith *et al*. (2013). As expected, specimens in higher temperatures had a significantly higher growth rate when compared to those as lower temperatures, as well as the deposition rate, but growth rates did not have an effect on elemental composition (SMITH *et al*., 2013). Therefore, it is expected that specimens occurring in low latitudes have higher growth and vertebrae deposition rates. However, the question of how much time is necessary for the chemistry of a given water mass to have a distinct signature on the vertebrae remains. In fact, this is such a difficult topic that the same question exists for otoliths, even though some data point to a time frame between 25 and 40 days for a signature to be formed (WALSH; GILLANDERS, 2018).

Another important factor to consider is the difference in growth rate during ontogenetic development (WALTHER; LIMBURG, 2012). Indeed, *C. porosus* is expected to grow 7 cm.year^{-1} on the first four years of life, and decreasing to 4 cm.year^{-1} (LESSA *et al*., 1999). Therefore, it is likely that the chemical signals from the subadult2 phase further are subjected to different metabolic and growth rates. Furthermore, this pattern is likely to be species-specific, since each one have different growth rates and life histories. Perhaps a good alternative to overcome this problem would be to choose a model species of relatively easy rearing in controlled environments for each major taxonomic group of sharks (family Carcharhinidae, Lamnidae, etc.). Studying these models would potentially enable researchers to extrapolate the results obtained to the other species from the same group, thus obtaining more reliable interpretations from the data.

5 CONCLUSIONS

The results obtained demonstrate the elevated importance the BNC has for the maintenance of *C. porosus*. Since its greatest threat is the bycatch in fisheries targeting two of the most important Brazilian fishing resources, the release of live specimens, especially those under 70cm TL could be a short-term feasible practice. It is worth noting that it is impossible to ban the target fisheries, since several communities depend on them for subsistence, although their productivity has been declining quickly. Therefore, managing the target fisheries will likely have a positive effect on *C. porosus* populations. However, since elasmobranchs have a longer life cycle, these management strategies would require a longer time to rebuild the stocks. Another feasible and perhaps more crucial action would be to effectively implement the existing conservation areas throughout the BNC, especially in Maranhão state. Finally, the legal framework, especially to enable *in situ* inspections, adequate punishment for prohibited catches, and the existence of fisheries statistic programs along the BNC are crucial to monitor trends in geographical occurrence and stock size.

ACKNOWLEDGMENTS

We appreciate FACEPE and CNPq under the projects APQ 10.11-2015 and 306672/15, respectively, for covering the costs of the LA-ICP-MS analysis in both laboratories used. Furthermore, we thank FACEPE for providing a scholarship to LMF under the process IBPG 0089-2.05/17. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nivel Superior – Brasil (CAPES) – Finance code 001. Comissão Interministerial para os Recursos do Mar (CIRM) funded the data collection along the Maranhão Coast (1984/1988) and Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq provided Research Grants (306672/2015-4 and 302276/2017-3) to RPTL and VD, respectively. In addition, acknowledge the help of Vinicius M Neves in the LA-ICPMS processing, and Mariana Bonfim in the data analysis. Furthermore, we thank Leandro Augusto Junior and Clarisse Éleres Figueiredo for the help with figure editing and elaboration and Maylis Labonne (IRD, France) for critically readings. Finally, we thank Jorge Nunes and the fishermen from Raposa for the help with sample collection.

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APPENDICES

Figure S1. Female *Carcharhinus porosus* with fresh mating scars on the right pectoral fin.

4 CONSIDERAÇÕES FINAIS

Os resultados obtidos e apresentados nos dois manuscritos aqui inseridos demonstram, de forma robusta, a importância que a Costa Norte do Brasil possui para a conservação de *Carcharhinus porosus*, tanto nas escalas nacional como internacional. Além disso, este trabalho foi capaz de demonstrar as regiões prioritárias para a conservação da espécie analisada em caráter regional e ao longo de sua distribuição global, identificando o Golfo do México como uma provável região chave para sua conservação no Oceano Atlântico Norte. A partir da distribuição aqui apresentada, será possível melhor avaliar o seu status de conservação global, visto que a última avaliação contava com informações de distribuição desatualizadas e irá ajudar em ações de conservação mais efetivas.

No estudo de uso de habitat, demonstrou-se que a espécie em questão possui hábitos de segregação sexual, diferentes zonas de parto na área de estudo, ciclo de vida completo na região, além de se inferir as prováveis épocas de cópula, nascimento e a existência de comportamento filopátrico. Com o fornecimento de todos esses dados, as próximas avaliações de status de conservação, tanto nacionais quanto internacionais, serão mais fidedignas ao real risco de extinção que a espécie corre, bem como serão capazes de formular estratégias de manejo e conservação mais eficazes. Os dados aqui apresentados demonstram que o litoral maranhense é crucial para a conservação de *Carcharhinus porosus* por configurar-se como uma zona de berçário para essa espécie. Além disso, é a primeira vez que uma área deste tipo, com uso de múltiplas fontes de dados e amplas evidências, é identificada para a região norte do Brasil. Ademais, este é o primeiro trabalho realizado no Brasil avaliando padrões de uso de habitat de tubarões através de microquímica de vértebras, consequentemente sendo um marco científico. Portanto, o presente trabalho traz grandes avanços científicos e de informação sobre uma das espécies de tubarão mais ameaçadas do Brasil e que se sabia muito pouco.

REFERÊNCIAS

AFONSO, A. S.; HAZIN, F. H. V. Vertical movement patterns and ontogenetic niche expansion in the tiger shark, *Galeocerdo cuvier*. **PLoS ONE**, v. 10, n. 1, p. 1–26, 2015.

ALMEIDA, Z. S.; SANTOS, N. B.; CARVALHO-NETA, R. N F.; PINHEIRO, A. L .R. 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 FILHO, J. M.; SUNYE, P. S. (Eds.). **A pesca marinha e estuarina no Brasil: estudos de caso multidisciplinares**. Rio Grande: Editora da FURG, 2014. p. 161–170.

ALMERÓN-SOUZA, F.; SPERB, C.; CASTILHO, C. L.; FIGUEIREDO, P. I. C. C.; GONÇALVES, L. T.; MACHADO, R.; OLIVEIRA, L. R. VALIATI, V. H.; FAGUNDES, N. J. R. Molecular identification of shark meat from local markets in Southern Brazil based on DNA barcoding: Evidence for mislabeling and trade of endangered species. **Frontiers in Genetics**, v. 9, p. 1–12, 2018.

ARAÚJO, M. B.; GUISAN, A. Five (or so) challenges for species distribution modelling. **Journal of Biogeography**, v. 33, n. 10, p. 1677–1688, 2006.

ARAÚJO, M. B.; NEW, M. Ensemble forecasting of species distributions. **Trends in Ecology and Evolution**, v. 22, n. 1, p. 42–47, 2007.

ASSIS, J. TYBERGHEIN, L.; BOSCH, S.; VERBRUGGEN, H.; SERRÃO, E. A.; CLERCK, O. Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. **Global Ecology and Biogeography**, v. 27, n. 3, p. 277–284, 2017.

BARRETO, R. R. BORNATOWSKI, H.; MOTTA, F. S.; SANTANDER-NETO, J.; VIANNA, G. M. S. LESSA, R. P. Rethinking use and trade of pelagic sharks from Brazil. **Marine Policy**, v. 85, p. 114–122, 2017.

BECK, M. W.; HECK, K. L.; ABLE, K. W.; CHILDERS, D. L.; EGGLESTON, D. B.; GILLANDERS, B. M.; HALPERN, B.; HAYS, C.; TISTHAMMER, K.; MINELLO, T. J.; ORTH, R. J.; SHERIDAN, P. F. The Identification, Conservation, and Management of Estuarine and Marine Nurseries for Fish and Invertebrates. **BioScience**, v. 51, n. 8, p. 633, 2001.

BRANSTETTER, S. Conservation Biology of Elasmobranchs. **NOAA Technical Report NMFS 115**, v. 115, 1993.

BROWN, C. J.; FULTON, E. A.; HOBDAY, A. J.; MATEAR, R. J.; POSSINGHAM, H. P.; BULMAN, C.; CHRISTENSEN, V.; FORREST, R. E.; GEHRKE, P. C.; GRIFFITHS, N. A.; LOZANO-MONTES, H.; MARTIN, J. M.; METCALF, S.; OKEY, T. A.; WATSON, R.; RICHARDSON, A. J. Effects of climate-driven primary production change on marine food webs: Implications for fisheries and conservation. **Global Change Biology**, v. 16, n. 4, p. 1194–1212, 2010.

CAMHI, M.; FOWLER, S.; MUSICK, J. BRÄUTIGAM, A.; FORDHAM, S. Sharks and Their Relatives: Ecology and Conservation. **IUCN/SSC Shark Specialist Group**. IUCN, Gland, Switzerland and Cambridge, UK. v. 3, 1998.

CARLSON, J. K.; PARSONS, G. R. The effects of hypoxia on three sympatric shark species: Physiological and behavioral responses. **Environmental Biology of Fishes**, v. 61, n. 4, p. 427–433, 2001.

CARPENTER, G.; GILLISON, A. N.; WINTER, J. Domain - a Flexible Modeling Procedure for Mapping Potential Distributions of Plants and Animals. **Biodiversity and Conservation**, v. 2, n. 6, p. 667–680, 1993.

CASTILLO-GÉNIZ, J. L.; MÁRQUEZ-FARIAS, J. F.; CRUZ, M. C. R.; CORTÉS, E.; PRADO, A. C. The Mexican artisanal fishery in the Gulf of Mexico: towards a regulated fishery. **Marine Freshwater Research**, v. 49, p. 611–620, 1998.

CASTRO, J. I. Resurrection of the name *Carcharhinus cerdale*, a species different from *Carcharhinus porosus*. **aqua, International Journal of Ichthyology**, v. 17, n. 1, p. 1–10, 2011.

COCHRANE, K. L. **A fishery manager’s guide book: management measures and their applications** (K. L. Cochrane, Ed.). [s.l.] FAO, 2002.

COLES, V. J. et al. The pathways and properties of the Amazon River Plume in the tropical North Atlantic Ocean. **Journal of Geophysical Research: Oceans**, v. 118, p. 6894–6913, 2013.

COMPAGNO, L. J. V. Sharks of the World. Vol . 4 , Part 2, Carcharhiniformes. Fao Species Catalogue. **Food and Agriculture Organisation of the United Nations Fisheries Synopsis**, v. 4, n. 125, p. 249, 1984.

CORTÉS, E. Incorporating uncertainty into demographic modeling: Application to shark populations and their conservation. **Conservation Biology**, v. 16, n. 4, p. 1048–1062, 2002.

DAVIDSON, L. N. K.; DULVY, N. K. Global marine protected areas to prevent extinctions. **Nature Ecology & Evolution**, v. 1, n. 2, p. 0040, 2017.

DENT, F.; CLARKE, S. State of the global market for shark products. **FAO Fishereis and Aquaculture Technical paper No. 590.**, p. 187, 2015.

DINIZ-FILHO, J. A. F.; BINI, L. M.; RANGEL, T. F.; LOYOLA, R. D.; HOF, C.; NOGUÉS-BRAVO, D.; ARAÚJO, M. B. Partitioning and mapping uncertainties in ensembles of forecasts of species turnover under climate change. **Ecography**, v. 32, n. 6, p. 897–906, 2009.

DINIZ, C.; CORTINHAS, L.; SADECK, L.; ADAMI, M. Brazilian Mangrove Status: Three Decades of Satellite Data Analysis. **Remote Sensing**, v. 11, 2019.

DORMANN, C. F.; ELITH, J.; BACHER, S.; BUCHMAN, C.; CARL, G.; CARRÉ, G.; MARQUÉZ, J. R. G.; GRUBER, B.; LAFOURCADE, B.; LEITÃO, P. J.; MÜNKEMÜLLER, T.; McCLEAN, C.; OSBORNE, P. E.; REINEKING, B.; SCHRÖDER, B.; SKIDMORE, A. K.; ZURELL, D.; LAUTENBACH, S. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. **Ecography**, v. 36, n. 1, p. 027–046, 2013.

DOUBLEDAY, Z. A.; CLIFF, J.; IZZO, C.; GILLANDERS, B. M. Untapping the potential of sulfur isotope analysis in biominerals. **Marine Ecology Progress Series**, v. 598, n. June, p. 159–166, 2018.

DULVY, N. K.; M.; HARRISON, L. R.; CARLSON, J. K.; DAVIDSON, L. N. K.; FORDHAM, S. V.; FRANCIS, M. P.; POLLOCK, C. M.; SIMPFENDORFER, C. A.; BURGESS, G. H.; CARPENTER, K. E.; COMPAGNO, L. J. V.; EBERT, D. A.; GIBSON, C.; HEUPEL, M. R.; LIVINGSTONE, S. R.; SANCIANGO, J. C.; STEVENS, J. D.; VALENTI, S.; WHITE, W. T. Extinction risk and conservation of the world's sharks and rays. **eLife**, v. 3, p. e00590, jan. 2014.

EHEMANN, N. R.; N. R.; GONZÁLEZ-GONZÁLEZ, L. V.; CHOLLET-VILLALPANDO, J. G.; CRUZ-AGÜERO, J. Updated checklist of the extant chondrichthyes within the exclusive economic zone of Mexico. **ZooKeys**, v. 2018, n. 774, p. 17–39, 2018.

ELITH, J.; GRAHAM, C. H.; ANDERSON, R. P.; DUDÍK, M.; FERRIER, S.; GUISAN, A.; HIJMANS, R. J. Novel methods improve prediction of species' distributions from occurrence data. **Ecography**, v. 29, n. 2, p. 129–151, 2006.

ELITH, J.; LEATHWICK, J. R. Species Distribution Models: Ecological Explanation and

Prediction Across Space and Time. **Annual Review of Ecology, Evolution, and Systematics**, v. 40, n. 1, p. 677–697, 2009.

ELSDON, T.; WELLS, B.; CAMPANA, S.; GILLANDERS, B.; JONES, C.; LIMBURG, K.; SECOR, D.; THORROLD, S.; WALTHER, B. Otolith Chemistry To Describe Movements And Life-History Parameters Of Fishes. In: GIBSON, R. N.; ATKINSON, R. J. A.; GORDON, J. D. M. (Eds.). **Oceanography and Marine Biology: An Annual Review**. 46. ed. Boca Raton: CRC Press, 2008. p. 297–330.

FEITOSA, L. M.; MARTINS, A.P.B.; GIARRIZZO, T.; MACEDO, W.; MONTEIRO, I.L., GEMAQUE, R.; NUNES, J.L.S.; GOMES, F.; SCHNEIDER, H.; SAMPAIO, I.; SOUZA, R.; SALES, J.B.; RODRIGUES-FILHO, L.F.; TCHAICKA, L.; CARVALHO-COSTA, L.F. DNA-based identification reveals illegal trade of threatened shark species in a global elasmobranch conservation hotspot. **Scientific Reports**, v. 8, n. 1, p. 1–11, 2018.

FEITOSA, L. M.; MARTINS, A. P. B.; NUNES, J. L. S. Sawfish (Pristidae) records along the Eastern Amazon coast. **Endangered Species Research**, v. 34, p. 229-234, 2017.

FRASER, K. C.; DAVIES, K. T.A.; DAVY, C. M.; FORD, A. T.; FLOCKHART, D. T. T.; MARTINS, E. G. Tracking the conservation promise of movement ecology. **Frontiers in Ecology and Evolution**, v. 6, n. October, p. 150, 2018.

FURTADO-JÚNIOR, I.; TAVARES, M. C. DA S.; BRITO, C. S. F. 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). **Boletim Técnico Científico CEPNOR**, v. 3, n. 1, p. 147–161, 2002.

GARCÍA, C. B. What do we know about soft-bottom elasmobranch species richness in the Colombian Caribbean and of its spatial distribution? **Regional Studies in Marine Science**, v. 9, p. 62–68, 2017.

GARRICK, J. Sharks of the genus *Carcharhinus*. **NOAA Technical Reports NMFS No. 445.** 1982.

GILLANDERS, B. M. Otolith chemistry to determine movements of diadromous and freshwater fish. **Aquatic Living Resources**, v. 18, n. 3, p. 291–300, 2005.

GIRI, C.; OCHIENG, E.; TIESZEN, L. L.; ZHU, Z.; SINGH, A.; LOVELAND, T.; MASEK, J.; DUKE, N. Status and distribution of mangrove forests of the world using earth observation satellite data. **Global Ecology and Biogeography**, v. 20, n. 1, p. 154–159, 2011.

GRAHAM, C. H.; ELITH, J.; HIJMANS, R. J.; GUISAN, A.; PETERSON, A. T.; LOISELLE, B. A.; ANDERSON, R. P. The influence of spatial errors in species occurrence data used in distribution models. **Journal of Applied Ecology**, v. 45, n. 1, p. 239–247, 2008.

HAZIN, F. H. V.; AFONSO, A. S.; CASTILHO, P. C.; FERREIRA, L. C.; ROCHA, B. C. L. M. Regional movements of the tiger shark, Galeocerdo cuvier, off Northeastern Brazil: inferences regarding shark attack hazard. **Anais da Academia Brasileira de Ciências**, v. 85, n. 3, p. 1053–1062, 2013.

HEUPEL, M. R.; KANNO, S. B. C.; MARTINS, A. P. B., SIMPFENDORFER, C. A. Advances in understanding the roles and benefits of nursery areas for elasmobranch populations. **Marine and Freshwater Research**, 2018.

HEUPEL, M. R.; CARLSON, J. K.; SIMPFENDORFER, C. A. Shark nursery areas: Concepts, definition, characterization and assumptions. **Marine Ecology Progress Series**, v. 337, n. Nmfs 2006, p. 287–297, 2007.

HIJMANS, R. J.; PHILLIPS, S.; LEATHWICK, J. R.; ELITH, J. dismo: Species Distribution Modelin. **R CRAN Project**, p. 55, 2017.

IBPES. Nature’s Dangerous Decline ‘Unprecedented’ Species Extinction Rates ‘Accelerating’ 2019. Disponível em: https://www.ipbes.net/news/media-release-global-assessment#_by_the_numbers.

ICMBIO/MMA. **Instrução Normativa Nº5.** Brasília, Ministério do Meio Ambiente, 2004.

ICMBIO/MMA. **Portaria 445/2014.** Brasilia, Ministério do Meio Ambiente, 2014.

ICMBIO/MMA. **Livro Vermelho da Fauna Brasileira Ameaçada de Extinção**. 1 ed. Brasília: ICMBIO/MMA, 2018. v. VI-Peixes.

IZZO, C.; HUVENEERS, C.; DREW, M.; BRADSHAW, C. J. A.; DONNELLAN, S. C.; GILLANDERS, B. M. Vertebral chemistry demonstrates movement and population structure of bronze whaler. **Marine Ecology Progress Series**, v. 556, p. 195–207, 2016.

KNIP, D. M.; HEUPEL, M. R.; SIMPFENDORFER, C. A. Sharks in nearshore environments: Models, importance, and consequences. **Marine Ecology Progress Series**, v. 402, p. 1–11, 2010.

KOLMANN, M. A.; ELBASSIOUNY, A. A.; LIVERPOOL, E. A.; LOVEJOY, N. R. DNA barcoding reveals the diversity of sharks in Guyana coastal markets. **Neotropical Ichthyology**, v. 15, n. 4, p. 1–8, 2017.

LESSA, R.; SANTANA, F.; MENNI, R.; ALMEIDA, Z. Population structure and reproductive biology of the smalltail shark (*Carcharhinus porosus*) off Maranhão (Brazil). **Marine and Freshwater Research**, v. 50, p. 383–388, 1999a.

LESSA, R.; SANTANA, F. M.; RINCÓN, G.; GADIG, O. B. F.; EL-DEIR, A. C. A. **Biodiversidade de elasmobrânquios do Brasil**. Recife: Ministério do Meio Ambiente, 1999b.

LESSA, R.; ALMEIDA, Z.; SANTANA, F. M.; SIU, S.; PEREZ, M. *Carcharhinus porosus*, Smalltail Shark. **The IUCN Red List of Threatened Species**, v. 8235, 2006.

LESSA, R.; ALMEIDA, Z. Analysis of stomach contents of the smalltail shark *Carcharhinus porosus* from northern Brazil. **Cybium**, v. 21, n. 2, p. 123–133, 1997.

LESSA, R.; BATISTA, V. S.; SANTANA, F. M. Close to extinction? The collapse of the endemic daggernose shark (*Isogomphodon oxyrhynchus*) off Brazil. **Global Ecology and Conservation**, v. 7, p. 70–81, 2016.

LESSA, R. P. Contribuição ao conhecimento da biologia de *Carcharhinus porosus* Ranzani, 1839 (PISCES, CHONDRICHTHYES) das Reentrâncias Maranhenses. **Acta Amazonica**, v. 16/17, p. 73–86, 1986a.

LESSA, R. P. Levantamento faunístico dos elasmobrânquios (Pisces, Chondrichthyes) do litoral ocidental do estado do Maranhão, Brasil. **Boletim do Laboratório de Hidrobiologia**, v. 7, p. 27–41, 1986b.

LESSA, R. P. Sinopse dos estudos sobre elasmobrânquios da costa do Maranhão. **Boletim do Laboratório de Hidrobiologia**, v. 10, p. 19–36, 1997.

LESSA, R. P. T.; REPINALDO-FILHO, F. P. M.; MORO, G.; CHARVET, P.; SANTANA, F. M. *Carcharhinus porosus*. In: **Livro Vermelho da Fauna Brasileira Ameaçada de Extinção: Volume VI - Peixes**. 1 ed. Brasília: ICMBIO/MMA, 2018. p. 950–953.

LESSA, R.; SANTANA, F. M. Age determination and growth of the smalltail shark, Carcharhinus porosus, from northern Brazil. **Marine and Freshwater Research**, v. 49, p. 705, 1998.

LEWIS, J. P.; PATTERSON, W. F.; CARLSON, J. K.; McLACHLIN, K. Do vertebral chemical signatures distinguish juvenile blacktip shark (*Carcharhinus limbatus*) nursery regions in the northern Gulf of Mexico? **Marine and Freshwater Research**, v. 67, n. 7, p. 1014–1022, 2016.

LONGERICH, H. P.; JACKSON, S. E.; GÜNTHER, D. Inter-laboratory note. Laser ablation inductively coupled plasma mass spectrometric transient signal data acquisition and analyte concentration calculation. **J. Anal. At. Spectrom.**, v. 11, n. 9, p. 899–904, 1996.

MARTINS, A. P. B., FEITOSA, L. M.; LESSA, R. P.; ALMEIDA, Z. S.; HEUPEL, M.; SILVA, W. M.; TCHAICKA, L.; NUNES, J. L. S. Analysis of the supply chain and conservation status of sharks (Elasmobranchii: Superorder Selachimorpha) based on fisher knowledge. **PLoS ONE**, v. 13, n. 3, p. 1–15, 2018.

MCMILLAN, M. N.; IZZO, C.; WADE, B.; GILLANDERS, B. M. Elements and elasmobranchs: hypotheses, assumptions and limitations of elemental analysis. **Journal of Fish Biology**, v. 90, n. 2, p. 559–594, 2017.

MCMILLAN, M. N.; HUVENEERS, C.; SEMMENS, J. M.; GILLANDERS, B. M. Natural tags reveal populations of conservation dependent school shark use different pupping areas. **Marine Ecology Progress Series**, v. 599, p. 147–156, 2018.

MENESES, T. S.; SANTOS, F. N.; PEREIRA, C. W. Fauna De Elasmobrânquios Do Litoral Do Estado De Sergipe, Brasil. **Arquivos de ciências do mar**, n. 38, p. 79–83, 2005.

MENNI, R. C.; LESSA, R. P. The chondrichthyan community off Maranhão (northeastern Brazil) II. Biology of species. **Acta Zoologica Lilloana**, v. 44, n. 1, p. 69–89, 1998.

MENNI, R. C.; LUCIFORA, L. O. **Contrictios de la Argentina y Uruguay.** ASFA C.S.A., 2007.

MOHAN, J. A.; TINHAN, T. C.; MILLER, N. R.; WELLS, R. J. D. Effects of sample cleaning and storage on the elemental composition of shark vertebrae. **Rapid Communications in Mass Spectrometry**, v. 31, n. 24, p. 2073–2080, 2017.

MOURÃO, K. R. M.; ESPÍRITO-SANTO, R. V.; SILVA, B. B.; ALMEIDA, M. C.; ISAAC, V.; FRÉDOU, T.; FRÉDOU, F. L. A pesca de *Scomberomorus brasiliensis* e alternativas para o seu manejo no litoral nordeste do Pará - Brasil. In: HAIMOVICI, M.; ANDRIGUETTO FILHO, J. M.; SUNYE, P. S. (Eds.). **A pesca marinha e estuarina no Brasil: estudos de caso**

multidisciplinares. Rio Grande: Editora da FURG, 2014. p. 171–180.

NAYLOR, G. J. P.; CAIRA, J. N.; JENSEN, K.; ROSANA, K. A. M.; WHITE, W. T.; LAST, P. R. A DNA sequence-based approach to the identification of shark and ray species and its implications for global elasmobranch diversity and parasitology. **Bulletin of the American Museum of Natural History**, v. 367, n. 5, p. 262, 2012.

O'HARA, C. C.; AFFLERBACH, J. C.; SCARBOROUGH, C.; KASCHNER, K.; HALPERN, B. S. Aligning marine species range data to better serve science and conservation. **PLoS ONE**, v. 12, n. 5, p. 1–15, 2017.

OLIVER, S.; BRACCINI, M.; NEWMAN, S. J.; HARVEY, E. S. Global patterns in the bycatch of sharks and rays. **Marine Policy**, v. 54, p. 86–97, 2015.

PAILLON, C.; WANTIEZ, L.; KULBICKI, M.; LABONNE, M.; VIGLIOLA, L. Extent of mangrove nursery habitats determines the geographic distribution of a coral reef fish in a South-Pacific Archipelago. **PLoS ONE**, v. 9, n. 8, p. 1–10, 2014.

PALMEIRA, C. A. M.; RODRIGUES-FILHO, L. F.; SALES, J. B. 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**, v. 34, n. 1, p. 249–252, 2013.

PÉREZ-JIMÉNEZ, J. C.; MENDEZ-LOEZA, I. The small-scale shark fisheries in the southern Gulf of Mexico: Understanding their heterogeneity to improve their management. **Fisheries Research**, v. 172, p. 96–10, 2015.

PHILLIPS, S. B.; ANDERSON, R. P.; SCHAPIRE, R. E. Modelling and analysis of the atmospheric nitrogen deposition in North Carolina. **International Journal of Global Environmental Issues**, v. 6, n. 2–3, p. 231–252, 2006.

PISTEVOS, J. C. A.; REIS-SANTOS, P.; IZZO, C.; GILLANDERS, B. M. Element composition of shark vertebrae shows promise as a natural tag. **Marine and Freshwater Research**, v. 3, 2019.

PONTUAL, H. DE; GEFFEN, A. J. Otolith microchemistry. In: PANFILI, J. et al. (Eds.). . **Manual of fish sclerochronology**. [s.l.] Éditions Ifremer, 2002. p. 245–307.

RANGEL, T. F.; LOYOLA, R. D. Labeling Ecological Niche Models. **Natureza & Conservação**, v. 10, n. 2, p. 119–126, 2012.

ROSA, R. S.; GADIG, O. B. F. Conhecimento da diversidade dos Chondrichthyes marinhos no Brasil: a contribuição de José Lima de Figueiredo. **Arquivos de Zoologia**, v. 45, n. esp, p. 89, 2014.

RUBENSTEIN, D. R.; HOBSON, K. A. From birds to butterflies: Animal movement patterns and stable isotopes. **Trends in Ecology and Evolution**, v. 19, n. 5, p. 256–263, 2004.

SADOWSKY, V. Selachier aus dem Litoral von Sao Paulo, Brasilien. **Beitrage zur Neotropischen Fauna**, v. 5, n. 2, p. 71–88, 1967.

SALAS, S.; CHUENPAGDEE, R.; CHARLES, A.; SEIJO, J. C. **Coastal fisheries of Latin America and the Caribbean**. Rome: FAO, 2011.

SALDAÑA-RUIZ, L. E.; SOSA-NISHIZAKI, O.; CARTAMIL, D. Historical reconstruction of Gulf of California shark fishery landings and species composition, 1939–2014, in a data-poor fishery context. **Fisheries Research**, v. 195, n. July, p. 116–129, 2017.

SHI, W.; WANG, M. Characterization of global ocean turbidity from moderate resolution imaging spectroradiometer ocean color observations. **Journal of Geophysical Research: Oceans**, v. 115, n. 11, p. 1–14, 2010.

SMITH, W. D.; MILLER, J. A.; MÁRQUEZ-FARIAS, F.; HEPPELL, S. S. Elemental signatures reveal the geographic origins of a highly migratory shark: Prospects for measuring population connectivity. **Marine Ecology Progress Series**, v. 556, p. 173–193, 2016.

SMITH, W. D.; MILLER, J. A.; HEPPELL, S. S. Elemental Markers in Elasmobranchs: Effects of Environmental History and Growth on Vertebral Chemistry. **PLoS ONE**, v. 8, n. 10, p. 1–19, 2013.

SOUZA-FILHO, P. W. M. Costa de Manguezais de Macromaré da Amazônia: cenários morfológicos, mapeamento e quantificação de áreas usando dados de sensores remotos. **Revista Brasileira de Geofísica**, v. 23, n. 4, p. 427–435, 2005.

STRIDE, R. K.; BATISTA, V. S.; RAPOSO, L. A. B. **Pesca experimental de tubarão com redes de emalhar no litoral maranhense**. São Luís: CORSUP/EDUFMA, 1992a.

TAVARES, W.; RODRIGUES-FILHO, L. F.; SODRÉ, D.; SOUZA, R. F. C.; SCHNEIDER, H.; SAMPAIO, I.; VALLINOTO, M. Multiple substitutions and reduced genetic variability in sharks. **Biochemical Systematics and Ecology**, v. 49, p. 21–29, 2013.

TAYLOR, M. D.; BABCOCK, R. C.; SIMPFENDORFER, C. A.; CROOK, D. A. Where technology meets ecology: Acoustic telemetry in contemporary Australian aquatic research and management. **Marine and Freshwater Research**, v. 68, n. 8, p. 1397–1402, 2017.

TEAM, R. C. **R: A language and environment for statistical computing.**Vienna, AustriaR Foundation for Statistical Computing, , 2013. Disponível em: <http://www.r-project.org/>

TILLETT, B. J.; MEEKAN, M. G.; PARRY, D.; MUNKSGAARD, N.; FIELD, I. C.; THORBURN, D.; BRADSHAW, C. J. A. Decoding fingerprints: Elemental composition of vertebrae correlates to age-related habitat use in two morphologically similar sharks. **Marine Ecology Progress Series**, v. 434, p. 133–142, 2011.

TILLETT, B. J.; MEEKAN, M. G.; FIELD, I. C.; THORBURN, D. C.; OVENDEN, J. R.; Evidence for reproductive philopatry in the bull shark *Carcharhinus leucas*. **Journal of Fish Biology**, v. 80, n. 6, p. 2140–58, 2012.

TYBERGHEIN, L.; VERBRUGGEN, H.; PAULY, K.; TROUPIN, C.; MINEUR, F.; CLERCK, O. Bio-ORACLE: A global environmental dataset for marine species distribution modelling. **Global Ecology and Biogeography**, v. 21, n. 2, p. 272–281, 2012.

URBANEK, S. **rJava: Low-Level R to Java Interface**, 2018. Disponível em: <https://cran.r-project.org/package=rJava>

VÉLEZ-ZUAZO, X.; AGNARSSON, I. Shark tales: A molecular species-level phylogeny of sharks (Selachimorpha, Chondrichthyes). **Molecular Phylogenetics and Evolution**, v. 58, n. 2, p. 207–217, 2011.

WALSH, C. T.; GILLANDERS, B. M. Extrinsic factors affecting otolith chemistry – implications for interpreting migration patterns in a diadromous fish. **Environmental Biology of Fishes**, v. 101, n. 6, p. 905–916, 2018.

WALTHER, B. D. The art of otolith chemistry: interpreting patterns by integrating perspectives. **Marine and Freshwater Research,** 2019.

WALTHER, B. D.; LIMBURG, K. E. The use of otolith chemistry to characterize diadromous migrations. **Journal of Fish Biology**, v. 81, p. 796–825, 2012.

WEARMOUTH, V. J.; SIMS, D. W. Sexual segregation in Elasmobranchs. **Biologia Marina Mediterranea**, v. 17, n. 1, p. 236–239, 2010.

WEIGMANN, S. Annotated checklist of the living sharks, batoids and chimaeras (Chondrichthyes) of the world, with a focus on biogeographical diversity. **Journal of Fish Biology**, v. 88, n. 3, p. 837–1037, 2016.

WHITE, W. T.; KYNE, P. M.; 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**, v. 14, n. 1, p. e0209387, 2019.