UNIVERSIDADE FEDERAL DO CEARÁ
CENTRO DE CIÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM SISTEMÁTICA, USO E CONSERVAÇÃO DA BIODIVERSIDADE

LILIAN GLÓRIA XAVIER DE SOUZA

DISTRIBUIÇÃO GEOGRÁFICA, MORFOLOGIA DOS DENTÍCULOS DÉRMICOS E NÍVEIS DE CONTAMINAÇÃO POR METAIS EM ELASMOBRÂNQUIOS DO ATLÂNTICO SUDOESTE: A RAIA COSTEIRA *Zapteryx brevirostris* E O TUBARÃO PELÁGICO *Megachasma pelagios*

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Tese de Doutorado apresentada ao Programa de Pós-graduação em Sistemática, Uso e Conservação da Biodiversidade da Universidade Federal do Ceará, como requisito parcial à obtenção do título de Doutora. Área de concentração: Taxonomia, sistemática e evolução biológica.

Orientador: Prof. Dr. Vicente Vieira Faria

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Aprovada em: 19 / 12 / 2024.

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A minha querida filha Helena Xavier.

AGRADECIMENTOS

O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Código de Financiamento 001

Ao Dr. Vicente Vieira Faria pelo apoio e valiosa orientação ao longo da minha caminhada acadêmica.

Aos coautores do primeiro capítulo Dr. Nelson D. Bovcon, Dr. Thiago H. Basílio, Dr. João Eduardo P. Freitas, Dra. Patricia Charvet, e Dr. Vicente V. Faria pela valorosa participação e suporte durante todo o processo da pesquisa desempenhada até a publicação.

À Dra. Georgia Maria de Oliveira Aragão pela amostragem do exemplar de tubarão-boca-grande do Piauí, pelo compartilhamento da amostra e por toda confiança.

Ao Dr. Gustavo Henrique Gonzaga da Silva, coordenador do Laboratório de Limnologia e Qualidade de Água – LIMNOAQUA, UFERSA, pela permissão no uso da infraestrutura do laboratório para a pesagem e encapsulamento das amostras de isótopos estáveis. À Dra. Cyntia Moraes pelo auxílio no processamento das amostras de isótopos estáveis, assim como pelas valiosas contribuições na análise de isótopos estáveis.

À Dra. Rachel Hauser-Davis, coordenadora do Laboratório de Avaliação e Promoção da Saúde Ambiental, Instituto Oswaldo Cruz, e sua equipe pela determinação dos metais e metaloides do tubarão-boca-grande.

Ao Dr. Salvatore Siciliano, coordenador do Grupo de Estudos de Mamíferos Marinhos da Região dos Lagos – GEMM-Lagos, Instituto Oswaldo Cruz, pela disponibilidade das amostras do espécime de tubarão-boca-grande do Rio de Janeiro.

Ao Dr. Luiz Drude de Lacerda pela participação na interpretação e validação dos resultados de metais e metaloides.

Ao Dr. Emílio de Castro Miguel e Dra. Ana Kamila Medeiros Lima pelo preparo das amostras de dentículos dérmicos no Laboratório de Biomateriais da UFC e obtenção das imagens dos dentículos no microscópio eletrônico de varredura na Central Analítica da UFC.

Ao Me. Jules Soto, diretor e curador do setor de ictiologia, do Museu Oceanográfico Univali – MOVI, Universidade do Vale do Itajaí – Univali, pelas amostras de tecido concedidas para análise de escamas placoides e informação sobre o registro mais ao sul do tubarão-boca-grande em águas brasileiras.

Aos Dr. Daniel Cassiano Lima, coordenador do Museu de História Natural Dias da Rocha – MHNCE, Dra. Raquel Caminha Rocha, diretora do Museu do Ceará, por me

concederem acesso ao acervo de peixes do naturalista cearense Francisco Dias da Rocha, e Dr. Marco Crosariol, curador da coleção de ornitologia MHNCE, e Dra. Karla Janaísa Gonçalves Leite, curadora do acervo Dias da Rocha – Museu do Ceará, por me apoiarem durante todo o processo.

Ao Prof. Dr. Paulo Cascon pelo uso das instalações do Laboratório de Zoologia Experimental da UFC, espaço compartilhado pelo Laboratório de Evolução e Conservação de Vertebrados Marinhos – EvolVe, para o processamento das amostras do tubarão-boca-grande.

Aos membros da banca da defesa da tese de doutorado, Dra. Maria Cristina Oddone, Dr. Getúlio Rincon, Dr. Moisés Fernandes Bezerra e Dr. Emílio de Castro Miguel, pelo tempo, pelas valiosas colaborações e sugestões.

À Dra. Vânia Melo, coordenadora do Programa de Pós-graduação em Sistemática, Uso e Conservação da Biodiversidade – PPGSis, pela presteza e atenção em todas as demandas endereçadas a ela durante o período de doutorado.

Aos meus colegas de doutorado do PPGSis e aos membros do Laboratório de Evolução e Conservação de Vertebrados Marinhos – EvolVe que estiveram presentes em momentos de muito aprendizado.

Ao meu núcleo familiar, Victor e Helena, que tanto me fortaleceu nessa caminhada de aprendizado acadêmico e pessoal. À valiosa rede de apoio que construí junto aos meus familiares e amigos, mesmo sendo pequena em número é grandiosa em apoio mútuo e confiança.

RESUMO

Tubarões e raias desempenham um papel crucial na estruturação dos ecossistemas marinhos, atuando em diversos níveis tróficos. No entanto, o grupo enfrenta ameaças crescentes, como a sobrepesca e a degradação de habitat, tornando urgentes as estratégias de conservação baseadas em dados biológicos precisos. O objetivo desta tese foi revisar os limites de distribuição da raia endêmica *Zapteryx brevirostris* e caracterizar a ocorrência e a ecologia do tubarão-boca-grande, *Megachasma pelagios*, no Atlântico Sudoeste. O estudo foi dividido em três abordagens principais. Primeiramente, a revisão da distribuição de *Z. brevirostris*, baseada em coleções científicas e literatura, redefiniu seus limites geográficos desde a foz do Rio Doce, Espírito Santo (19ºS), até as Ilhas Falkland/Malvinas (53ºS). Este novo limite meridional amplia a distribuição conhecida da espécie em mais de 2.000 km, sugerindo influências de fatores bióticos ao norte e abióticos ao sul. Em relação ao tubarão *M. pelagios*, foi descrito o terceiro registro no Brasil (Piauí), baseado a partir de identificação molecular do gene *ND2*. A análise de microscopia eletrônica de varredura revelou que os dentículos dérmicos deste espécime (neonato) apresentam morfologia distinta da observada em adultos, indicando modificações ontogenéticas. Por fim, a composição isotópica do neonato foi investigada via isótopos estáveis de $\delta^{13}C$ e $\delta^{15}N$. Contrariando a alimentação independente, as assinaturas isotópicas refletiram o investimento nutricional materno proveniente de águas oligotróficas do Oceano Atlântico Tropical. A baixa concentração de mercúrio corrobora o estágio neonatal, enquanto níveis elevados de alumínio e chumbo indicam que ouve transferência materna (*maternal offloading*) desses elementos. Estes resultados estabelecem uma linha de base crítica para o monitoramento de espécies raras e deficientes de dados no Oceano Atlântico Sudoeste.

Palavras-chave: Elasmobranchii; DNA mitocondrial; Escamas placoides; Isótopos estáveis; Metais e Metaloides.

ABSTRACT

Sharks and rays play a crucial role in structuring marine ecosystems, occupying diverse trophic levels. However, this group faces increasing threats, such as overfishing and habitat degradation, necessitating urgent conservation strategies based on accurate biological data. The aim of this thesis was to review the distribution limits of the endemic ray *Zapteryx brevirostris* and to characterize the occurrence and ecology of the Megamouth Shark, *Megachasma pelagios*, in the Southwestern Atlantic. The study was divided into three main approaches. First, the distribution review of *Z. brevirostris*, based on scientific collections and literature, redefined its geographic limits from the Doce River mouth, Espírito Santo (19ºS), to the Falkland/Malvinas Islands (53ºS). This new southern limit extends the species' known distribution by over 2,000 km, suggesting the influence of biotic factors in the north and abiotic factors in the south. Regarding the shark *M. pelagios*, the third record in Brazil (Piauí) was described based on molecular identification using the *ND2* gene. Scanning electron microscopy analysis revealed that the dermal denticles of this specimen (a neonate) exhibit a morphology distinct from that observed in adults, indicating ontogenetic changes. Finally, the isotopic composition of the neonate was investigated via $\delta^{13}C$ and $\delta^{15}N$ stable isotopes. Contradicting independent feeding, the isotopic signatures reflected maternal nutritional investment originating from oligotrophic waters of the Tropical Atlantic Ocean. The low mercury concentration corroborates the neonatal stage, while elevated levels of aluminum and lead indicate maternal offloading of these elements. These results establish a critical baseline for monitoring rare and data-deficient species in the Southwest Atlantic Ocean.

Keywords: Elasmobranchii; Mitochondrial DNA; Placoid scale; Stable isotopes; Metals and Metalloids.

SUMÁRIO

1 APRESENTAÇÃO GERAL

Os elasmobrânquios, grupo que compreende tubarões e raias, desempenham papéis cruciais na manutenção e estruturação dos ecossistemas aquáticos. Embora historicamente associados ao topo das teias alimentares, estes animais ocupam uma variedade de níveis tróficos, atuando não apenas como predadores de topo, mas também como mesopredadores e filtradores planctófagos. Essa diversidade funcional permite que conectem fluxos energéticos entre diferentes ambientes, como o bentônico e o pelágico. No entanto, características de história de vida como baixa fecundidade e crescimento lento, associadas a ameaças crescentes — incluindo a sobrepesca, perda de habitat e mudanças climáticas — tornam este um dos grupos de vertebrados mais ameaçados do planeta. Nesse sentido, a construção de conhecimento biológico e ecológico sobre essas espécies é o ponto de partida fundamental para a elaboração de estratégias de conservação eficazes. Assim, a presente pesquisa teve por objetivo revisar os limites de distribuição geográfica de uma raia costeira ameaçada e caracterizar a ocorrência, morfologia e ecologia trófica de um dos tubarões mais raros do mundo no Oceano Atlântico Sudoeste. Este documento de tese está estruturado em três capítulos, descritos a seguir:

O primeiro capítulo apresenta uma revisão da distribuição geográfica da raia-viola-de-focinho-curto, *Zapteryx brevirostris*, com foco na delimitação dos seus extremos latitudinais norte e sul. Comumente, a distribuição desta espécie é reportada do sudeste do Brasil até o norte da Argentina, porém, inconsistências e imprecisões nos registros históricos exigiram uma reavaliação. Essa investigação foi realizada por meio da consulta a coleções científicas (via plataformas SpeciesLink e GBIF e contato direto com curadores), revisão sistemática da literatura e incorporação de dados de observação de bordo. Ao todo, 1.363 espécimes foram analisados neste levantamento, com registros datando desde 1865 *(Artigo publicado na Revista Ocean and Coastal Research. http://doi.org/10.1590/2675-2824072.23119).*

O segundo capítulo sumariza os registros de ocorrência do tubarão-boca-grande, *Megachasma pelagios*, no Atlântico Sudoeste, com ênfase na caracterização morfológica e molecular. O estudo destaca o terceiro registro da espécie na região — um espécime neonato e o menor já registrado nesta área geográfica — cuja identificação foi confirmada através do gene mitocondrial *nd2*. Além disso, os três exemplares conhecidos para a região (um adulto, um juvenil e o referido neonato) foram caracterizados quanto à morfologia dos dentículos dérmicos. As amostras foram examinadas por microscopia eletrônica de varredura (MEV) para avaliar a existência de variações morfológicas ontogenéticas *(Artigo publicado na Revista Environmental Biology of Fishes. https://doi.org/10.1007/s10641-025-01668-w).*

O terceiro capítulo identifica a composição isotópica de carbono e nitrogênio e os níveis de metais e metaloides do espécime neonato de *Megachasma pelagios* (terceiro registro no Atlântico Sudoeste). O conhecimento sobre a dieta desta espécie é escasso, baseando-se majoritariamente em análises de conteúdo estomacal de adultos, com uma lacuna completa de informações sobre os estágios iniciais de vida. Neste estudo, utilizou-se a análise de isótopos estáveis de carbono ($\delta^{13}C$) e nitrogênio ($\delta^{15}N$) para investigar qual a composição isotópica de um exemplar neonato. Adicionalmente, foi realizada a determinação de metais e metaloides, preenchendo uma lacuna de conhecimento sobre esta espécie enigmática, anteriormente estudada apenas em adultos e juvenis. A baixa concentração de mercúrio corrobora o estágio neonatal, enquanto níveis elevados de alumínio e chumbo indicam que ouve transferência materna (*maternal offloading*) desses elementos *(Manuscrito elaborado de acordo com as normas do periódico Marine Pollution Bulletin).* Por fim, os achados de cada capítulo são sintetizados ao final desta tese na seção de conclusões.

2 CAPÍTULO I: Distributional limits of the Shortnose Guitarfish, *Zapteryx brevirostris* (Rhinopristiformes, Trygonorrhinidae) – An update

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Abstract

The Shortnose Guitarfish, *Zapteryx brevirostris*, is endemic to the Southwest Atlantic and its geographic range is commonly reported from southeastern Brazil to northern Argentina. However, range limits are imprecise or inconsistent in some cases. These inconsistencies were solved in this study based on 1,363 specimens collected since 1865. These records were obtained from scientific collections, a systematic review of literature, and an on-board observation database. According to the data collected in this study, the known northernmost distributional limit of the species lies at the mouth of the Doce River, northern Espírito Santo State, in Southeastern Brazil (19ºS). As for the other extreme of its range, the known southernmost distribution limit refers to the Falkland Islands (Malvinas) (53°S). This represents more than 2,000 km of coastline geographic range extension — in comparison to the previous known southernmost range limit for this species. The geographical range of *Z. brevirostris* seems to follow biogeographic patterns operating at an ecosystem level in which biotic (especially in the north) and abiotic factors (especially in the south) play a role in imposing limits to its distribution range.

Keywords: Batoid, Chondrichthyes, Distribution range, Range boundaries, Southwest Atlantic Ocean

2.1 Introduction

Distributional limits of species are influenced by many factors in a complex interaction system (Brown and Lomolino, 1998, Lomolino et al., 2010). These include ecological and environmental factors, such as biotic interactions and abiotic conditions (Dobzhansky, 1950, MacArthur, 1972), as well as evolutionary responses to biotic and abiotic gradients (Hardie and Hutchings, 2010, Willi and Van Buskirk, 2019, Alexander et al., 2022). Besides being an issue of biological interest due to connecting species range to ecology and evolution, understanding species boundaries may also be crucial information considering global environmental changes (Thomas, 2010). As global temperatures fluctuate and habitats undergo transformations, certain species may migrate or adapt, whereas others may face higher extinction risks (Gervais et al., 2021). Furthermore, understanding the geographic range of a species and shifts on its boundaries is fundamental for conservation planning (Franklin, 2010). For instance, a well-defined geographic range may help establish priority conservation areas, appropriate monitoring of range reduction, and overlapping threats (Chan et al., 2021, Becerril-García et al., 2022). Therefore, establishing well-defined geographic range and distributional limits of species at risk of extinction can be considered a pressing issue.

Currently, one of the most threatened groups of species in the world is the Elasmobranchii, which includes sharks and rays (Díaz et al., 2019). Bycatch, overexploitation, and finning have led to population declines of dozens of species (Dulvy et al., 2014, Dent and Clarke, 2015, Charvet et al., 2021, Dulvy et al., 2021). Many elasmobranchs are characterized by slow growth, late maturity, and low fecundity, which make this group much more susceptible to threats (Dulvy et al., 2014). Among them, shark-like batoids (Rhinopristiformes) are one of the most threatened groups (Faria et al., 2013, Moore, 2017, Jabado, 2018, Dulvy et al., 2021). The genus *Zapteryx* Jordan and Gilbert, 1880 comprises three batoid species of the order Rhinopristiformes (Last et al., 2016, Weigmann, 2016). One of them, the Shortnose Guitarfish *Zapteryx brevirostris* (Müller and Henle, 1841), is endemic to the Southwest Atlantic, from Southeastern Brazil to Northern Argentina (Weigmann, 2016, Gomes et al., 2019).

This trygonorrhinid batoid has a short cuneiform-shaped snout, which is the main morphological character to differ it from other guitarfishes from the Southwest Atlantic (Last et al., 2016). The only somewhat similar guitarfishes in this region include two rhinobatid species, *Pseudobatos horkelii* (Müller and Henle, 1841) and *P. percellens* (Walbaum, 1792), which differ from *Z. brevirostris* because they have an elongated snout (Bigelow and

Schroeder, 1953). The Shortnose Guitarfish is commonly caught as bycatch throughout its geographic range (Costa and Chaves, 2006, Chiaramonte et al., 2011, Colonello et al., 2011, Wosnick et al., 2019). This led to a population reduction of 85% in Brazil and 25% in Uruguay in the last three generations period (Pollom et al., 2020). Consequently, this species is currently listed as Endangered (EN) by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Pollom et al., 2020). Its current conservation status suggests a trend of increased extinction risk given that in its previous IUCN Red List assessment this species was assigned to a lower threat category (Vulnerable - VU; Vooren et al., 2006).

Within the geographic range of *Z. brevirostris*, there currently exists some confusion about its distributional limits. Historically, the northernmost limit has been mentioned as the oceanic Fernando de Noronha Archipelago (Northeastern Brazil) (Batista, 1987a, 1987b, Castello, 1971, Santos et al., 2006; but not in Soto et al., 2001), Bahia State (Northeastern Brazil) (Bigelow and Schroeder, 1953, Menni and Stehmann, 2000), Espírito Santo State (Southeastern Brazil) (Pinheiro et al., 2015, Pollom et al., 2020), and Rio de Janeiro State (Southeastern Brazil) (Miranda-Ribeiro, 1904; 1907). On the other hand, the southernmost limit has more consistently been mentioned as Mar del Plata (Argentina) in the literature (Menni and Stehmann, 2000, Wosnick and Freire, 2013, Gomes et al., 2019, Wosnick et al., 2019), although one online database (i.e., FishBase) reports one specimen collected as south as the Falkland Islands (Malvinas) (Froese and Pauly, 2022). [The Falkland Islands (Malvinas) are listed as a Non- Self-Governing Territory by the United Nations, which also recognizes the dispute concerning the sovereignty of these islands (UN, 2024).] This study reviewed the occurrence records of *Z. brevirostris* along its geographic range, focusing on its distributional limits.

2.2 Methods

Occurrence records of *Z. brevirostris* were first compiled from two sources. Specimens deposited in scientific collections were accessed by (1) online database search made on SpeciesLink (Specieslink, 2022) and Global Biodiversity Information Facility-GBIF (GBIF, 2022); and (2) inquiries to curators and collection managers from museums and scientific collections (Table 1). The taxonomic identification associated with specimen records obtained from online databases was considered reliable since *Z. brevirostris* is the only species of the family present in the Atlantic Ocean (Weigmann, 2016). In one case, additional information and photographs from a female specimen from the Falkland Islands (Malvinas) (ISH 591-

1978, a specimen from the Zoologisches Museum, Universität Hamburg, - ZMH collection) was obtained to verify the species identity and associated locality information.

Table 1: Museums and scientific collections used as source of occurrence records of the Shortnose Guitarfish, *Zapteryx brevirostris*. The left column indicates how the locality information associated with specimens were accessed. The right column shows the collections that served as source of information; codes follow Fricke and Eschmeyer (2022), Sabaj (2022), and Faria et al. (2021).

Access to specimen	**Collection**
Online database	**BMNH** – Natural History Museum, London, United Kingdom **CAS** – California Academy of Sciences, San Francisco, USA **CENPAT** – Centro Nacional Patagónico, Puerto Madryn, Argentina **CIUFES** – Ichthyological Collection of Universidade Federal do Espírito Santo, Vitória, Brazil **ColBIO** – Coleção Biológica "Prof. Edmundo F. Nonato" do Instituto Oceanográfico, Universidade de São Paulo, Cidade Universitária, São Paulo, Brazil **LIRP** – Laboratório de Ictiologia de Ribeirão Preto, Departamento de Biologia, Universidade de São Paulo, Ribeirão Preto, Brazil **MBML** – Museu de Biologia Professor Mello Leitão, Instituto Nacional da Mata Atlântica, Santa Teresa, Brazil **MCP** – Museu de Ciências e Tecnologia – MCT, Pontifícia Universidade Católica do Rio Grande do Sul - PUCRS, Porto

	Alegre, Brazil **MCZ** – Museum of Comparative Zoology, Cambridge, USA **MHNCI** – Museu de História Natural do "Capão da Imbuia", Curitiba, Brazil **MNHN** – Muséum national d'Histoire naturelle, Paris, France **MOVI** – Museu Oceanográfico Univali, Universidade do Vale do Itajaí, Balneário Piçarras, Brazil **MZUSP** – Museu de Zoologia da Universidade de São Paulo, SãoPaulo,_Brazil **MZUEL** – Museu de Zoologia, Universidade Estadual de Londrina, Londrina, Brazil **MZFS** – Museu de Zoologia da Universidade Estadual de Feira de Santana, Feira de Santana, Brazil **NPM** – Núcleo em Ecologia e Desenvolvimento Sócio-Ambiental, Universidade Federal do Rio de Janeiro, Macaé, Brazil **NRM** – Naturhistoriska Riksmuseet [Swedish Museum of Natural History], Sweden **SMF** – Senckenberg Naturmuseum Frankfurt, Frankfurt, Germany **ZUEC** – Museu de Zoologia da Universidade Estadual de Campinas "Adão José Cardoso", Campinas, Brazil
Direct enquiry to curator and/or collection manager	**ANSP** – The Academy of Natural Sciences of Philadelphia, Philadelphia, USA **CIDRO** – Coleção Ictiológica Dias da

Rocha, Universidade Federal do Ceará, Fortaleza, Brazil

INIDEP – Instituto Nacional de Investigaciones y Desarrollo Pesquero, Mar del Plata, Argentina

MACN – Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina

MHNM – Museo Nacional de Historia Natural, Montevideo, Uruguay

MNRJ – Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

ZMH – Zoologisches Museum, Universität Hamburg, Hamburg, Germany

ZMB – Museum für Naturkunde, Berlin, Germany

Another source of information of occurrence records of *Z. brevirostris* was a systematic review of literature. For this, the PICO Strategy (acronym for patient/population, intervention, comparison, and outcome) was applied to the bibliographic search, according to a previously described methodology (Richardson et al., 1995). The terms 'population' and 'intervention' were used to choose keywords (O'Dea et al., 2021). In the search, under 'population' the term searched was '*Zapteryx brevirostris*' and, under 'intervention', the term 'Atlantic' was applied in three languages (English, Portuguese, and Spanish). The Boolean operator AND was applied to combine the terms 'population' and 'intervention'. The term 'Atlantic' (three languages) was separated by the Boolean operator OR.

The Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) is a set of guidelines and a structured framework for planning and conducting systematic reviews and meta-analyses in research (O'Dea et al., 2021). The PRISMA Protocol approach was used as the criteria for research article selection. Searches using the online databases Scopus, ScienceDirect, and Web of Science were carried out on May 15, 2023.

Additional searches in Google Scholar using the term ‘*Zapteryx brevirostris*’ as keyword were carried out for further information about geographic range and distributional limits of *Z. brevirostris*. Only research articles and one technical note that provided primary occurrence data of *Z. brevirostris* were included in the analysis. Conversely, articles providing only secondary or incomplete occurrence data of *Z. brevirostris* and those providing occurrence data of other *Zapteryx* species were excluded.

One last source of information was the ‘On-Board Observer Program’ of the Fisheries Secretariat of the Province of Chubut, Argentina. This program monitors bycatch in the *Pleoticus muelleri* (Bate, 1888) shrimp fishery. This database has been kept unpublished but was accessed by the second author of this study (N. Bovcon).

For map preparation, the geographic range of *Z. brevirostris*, geographic coordinates, and shapefiles were converted to WGS84. Then, occurrence records with inaccuracies or missing coordinates were removed from the dataset. Records without geographic coordinates but with detailed information about the sampling locality had the coordinates estimated and were included in the dataset used for map construction. Once the dataset was considered suitable, the geographic coordinates were plotted on Qgis, version 3.10.8 (QGIS, 2020).

2.3 Results

Data collection resulted in 1,363 specimens of *Zapteryx brevirostris*: one from on-board observation, 257 from scientific collections, and 1,105 from the literature review (30 research articles and one technical note) from 1865 to 2022 (Table S1; Supplementary Material). These specimens were collected from 107 localities - each considered an occurrence point – from Brazil, Uruguay, and Argentina (Figure 1). The 107 occurrence points had the following sources: collection managers (n = 16), online databases (n = 80), published research articles (n= 9), onboard observation (n = 1), and a technical note (n = 1).

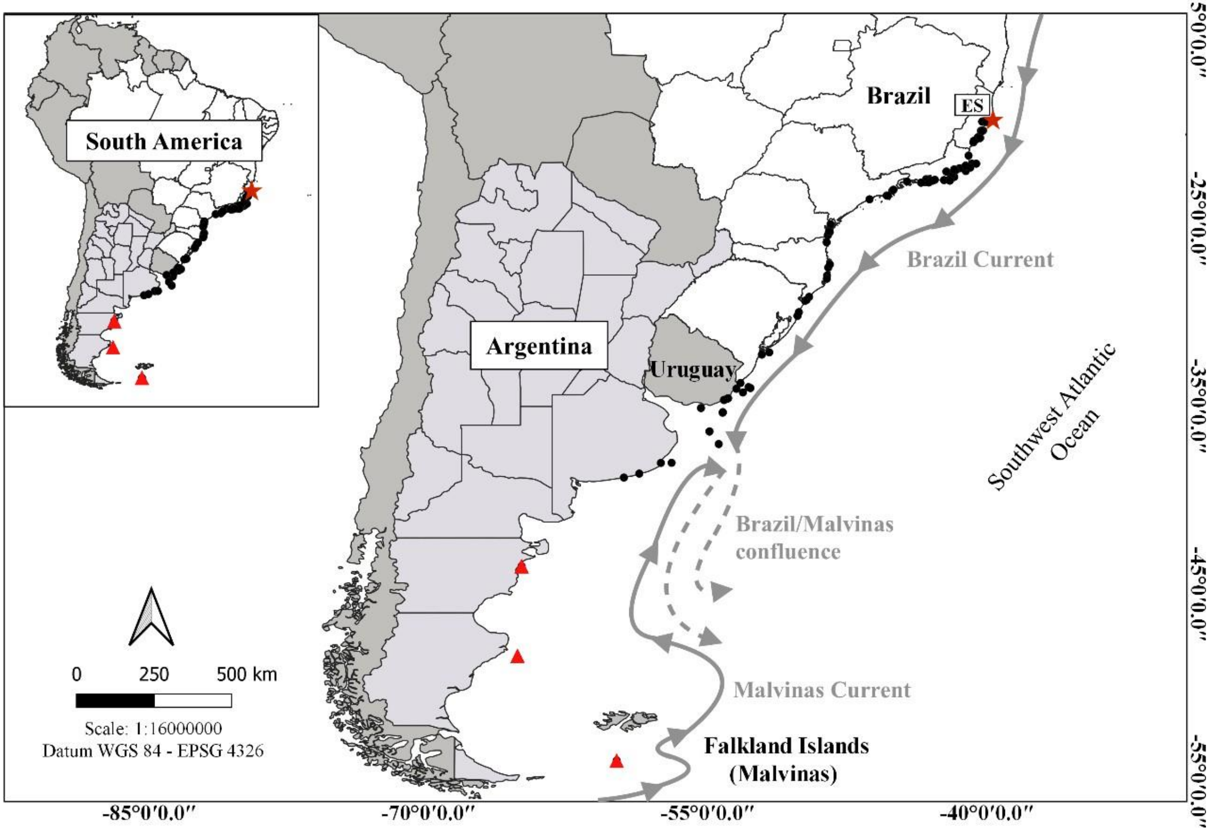

Figure 1. Dot map of the geographic range of the Shortnose Guitarfish, *Zapteryx brevirostris*. Each black dot represents a locality in which the species has been documented by either a voucher deposited in museums and scientific collections or a specimen mentioned in a scientific article. The red star represents the species northernmost occurrence: Linhares, in 2016 (voucher specimen MBML–PEIXES 120490). Red triangles represent the species southernmost occurrence: (1) upper triangle: Chubut, in 2010 (on-board observation; N. D. Bovcon, unpubl. data); (2) the triangle in between the other two: Santa Cruz Province, in 1997 (technical note; Wohler et al., 1999) and (3) the lower triangle: south of the Falkland Islands (Malvinas), in 1978 (voucher specimen ISH 591-1978). Oceanographic currents follow Piola and Matano (2019). ES: Espirito Santo State.

The search for *Z. brevirostris* on the three databases (Scopus, ScienceDirect, and Web of Science) resulted in 42 research articles that mentioned the occurrence of this species, 25 of which were excluded from this study due to duplicates and lack of precise occurrence data, which resulted in 17 research articles being considered suitable. Moreover, 13 research articles were incorporated after a complementary search (i.e., Google Scholar). Therefore, 30 research articles were effectively included in this study (references in Table 2 and as follows: Jaureguizar et al., 2003, 2004, Colonello et al., 2014, Loto et al., 2018, Alvarenga et al., 2021, Gatts et al., 2021, Karlovic et al., 2021, Lucena et al., 2021, Martins et al., 2021, Takatsuka et al., 2022). These 30 research articles reported data from each country as follows: Brazil only (n = 23); Brazil, Uruguay, and Argentina (n = 1); Argentina and Uruguay (n = 3); and Argentina only (n= 3) (Table S1). All studies included provided information on geographic range or distributional limits or information, such as sampling location and/or number of individuals.

Table 2. List of publications that included specific remarks on the geographic range or distributional limits associated with the Shortnose Guitarfish, *Zapteryx brevirostris*.

Geographic range or distributional limit	Source
Ilha Rasa, Rio de Janeiro Coast, Brazil	Miranda-Ribeiro (1904)
Rio de Janeiro and Bahia, Brazil	Miranda-Ribeiro (1907)
Near to Bahia and near to Rio de Janeiro, Brazil	Bigelow and Schroeder (1953)
Fernando de Noronha Archipelago, Brazil to Mar del Plata, Argentina	Batista (1987a, b); Castello (1971); Santos et al. (2006)
Western South Atlantic (northeast of Brazil to Argentina)	Batista (1991); Figueiredo (1977);
Bahia, Brazil to Bonaerensean District, Argentina	Menni and Stehmann, (2000)
Southeast Brazil to Mar del Plata, Argentina	Gomes et al. (2019); Wosnick and Freire (2013); Wosnick et al. (2019)
Brazil to Northern Argentina	Colonello et al. (2011)
Western South Atlantic Ocean, from Southeastern Brazil to Northern Argentina	Caltabellotta et al. (2019); Barbini et al. (2011); Pasquino et al. (2016)
Espírito Santo coast (Brazil) to Argentina	Alexandre de-Franco et al. (2012); Pinheiro et al. (2015, 2018)

The northernmost records for *Z. brevirostris* refer to three specimens captured at the mouth of the Doce River, Regência, in the Municipality of Linhares, Northern Espírito Santo State, Southeastern Brazil (19º44'57" S 39º41'51" W; MBML – PEIXES 12049). Other northernmost records of *Z. brevirostris* include an adult female from Aracruz, Espírito Santo State (19º49'49" S 40º03'09" W; CIDRO-B-38; Figure 2A) and a juvenile male from Piúma, Espírito Santo State (20º50' 58"S 40º43'56" W; CIDRO-B-39; Figure 2B).

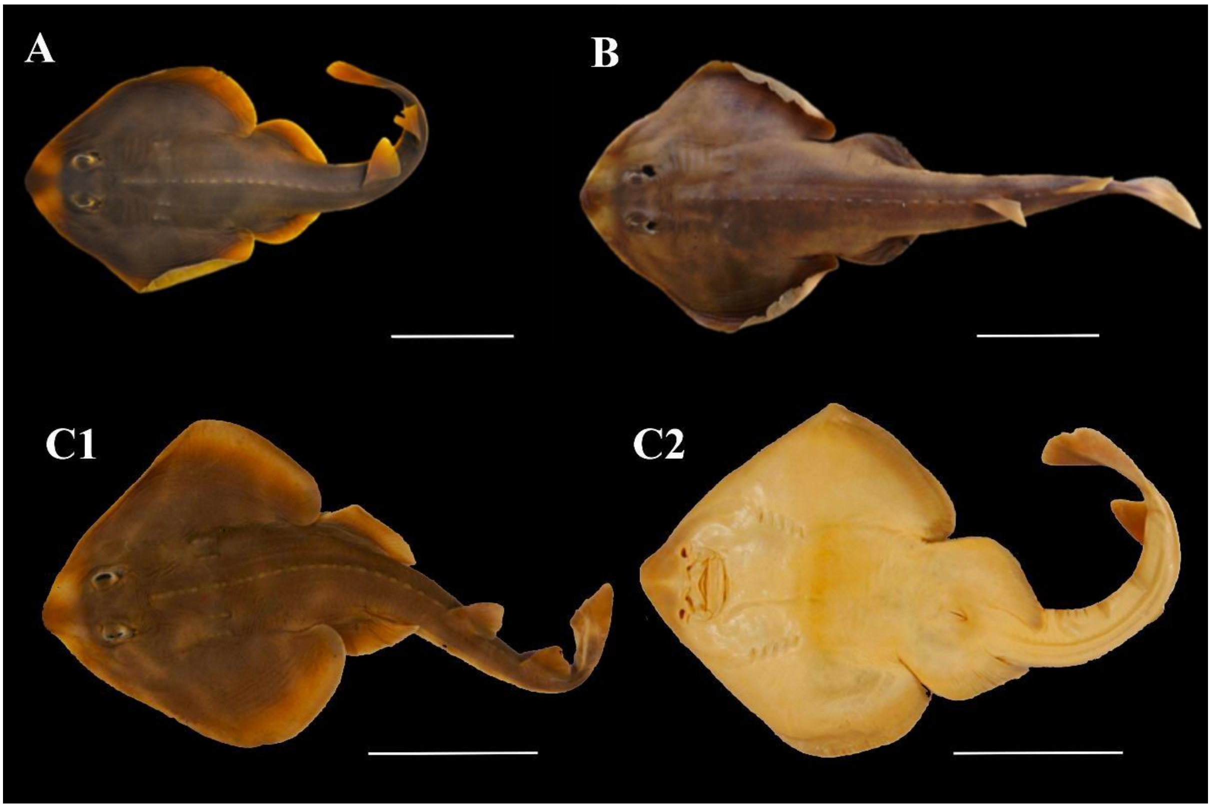

Figure 2. Three voucher specimens of the Shortnose Guitarfish, *Zapteryx brevirostris*, collected at the species' distributional limits. Figure 2A: dorsal view of an adult female from Aracruz, Espírito Santo State, Southeastern Brazil (CIDRO-B-38; photo by Lilian Xavier). Figure 2B: dorsal view of a juvenile male from Piúma, Espírito Santo State, Southeastern Brazil (CIDRO-B-39; photo by Lilian Xavier). Figure 2 - C1 and Figure 2 - C2: dorsal and ventral views, respectively, from an adult female from the Falkland Islands (Malvinas) (ISH 591-1978; photos by Irina Eidus). Scale bar: 10 cm.

The southernmost records for *Z. brevirostris* were as follows: (1) one specimen captured in the coastal area of the Province of Chubut, Argentina (43º30'S 65º12'W; 34 m depth, December 26, 2010) as part of the 'On-Board Observer Program' of the Fisheries Secretariat of the Province of Chubut, which monitors bycatch in the *Pleoticus muelleri* (Bate, 1888) shrimp fishery (Bovcon, unpubl. data); (2) one specimen captured in the Province of

Santa Cruz, Argentina (48º28.3’S 65º24.5’W; from 50 - 100 m depth isobaths) in 1997 during research campaigns for southern demersal fisheries carried out in the summer on the continental shelf of the Argentine Sea by the National Institute for Fisheries Research and Development - INIDEP) (Wöhler et al., 1999); and (3) one specimen captured south of the Falkland Islands (Malvinas) (53°52’S 59°55’W; 205 m depth) as part of the Argentine Expedition 1978 (ISH 591-1978, this specimen is currently deposited at the Zoologisches Museum, Universität Hamburg; Figure 2 - C1 and C2 - Table S1).

2.4 Discussion

The geographic distribution of species is often associated to patterns delimited as biogeographic provinces (Briggs, 1974). Delimiting a biogeographic province follows distinct criteria in different approaches; as a result, its limits and names fail to necessarily coincide (e.g. Spalding et al., 2007, Toonen et al., 2016). Furthermore, the distributional limits of species fail to be always restricted to a single biogeographic province (Spalding et al., 2007, Briggs and Bowen, 2012). This seems to be the case regarding the distribution of Z*apteryx brevirostris*, which can be associated with various provinces: (a) Indian (Indias Occidentales), Temperate Western South Atlantic (Argentina), and Magellanic (Magallanica) (sensu Lopez, 1963, Menni and Stehmann, 2000, Menni et al., 2010, Cousseu et al., 2019); (b) also Brazilian, Argentinian, Southern Argentina, and Falkland Islands (sensu Floeter et al., 2008, Briggs and Bowen, 2012, Toonen et al., 2016); (c) and Tropical Southwestern Atlantic, Warm Temperate Southwestern Atlantic, and Magellanic (sensu Spalding et al., 2007). Regardless of which approach is followed, in all cases, this species crosses different biogeographical limits and its distribution range comprises at least three biogeographical provinces.

Zapteryx brevirostris uses multiple marine habitats (Barbini et al., 2011), including estuaries (Wosnick and Freire, 2013), which may favor its dispersion from its core distribution area. Therefore, as for any organism, biotic and abiotic factors will play a role in imposing its distribution range limits. The distribution of this species appears to follow biogeographic patterns operating at an ecosystem level. In the northern limit, biotic factors such as species higher diversity seem to affect *Z. brevirostris* distribution, whereas, in the southern border, abiotic factors such as water temperature seem to play a role in imposing its limits.

2.4.1 Northernmost range limit

Previous reports of *Z. brevirostris* further north than Espirito Santo State should be viewed with caution. The mention of Ilha Rasa for the Fernando de Noronha Archipelago (Castello, 1971; followed by Batista, 1987a, 1987b and Santos et al., 2006, but not in Soto, 2001) is doubtful and should be disregarded. This mistake is possibly due to a misinterpretation of Miranda- Ribeiro's (1904) records of *Z. brevirostris* for Ilha Rasa, Guanabara Bay, Rio de Janeiro State. Mentions of *Z. brevirostris* for the coastal region of Bahia State (Northeastern Brazil) lack support of museum specimens or detailed locality records. Miranda-Ribeiro (1907) mentioned Bahia State as part of this species habitat despite the absence of locality data. Other subsequent studies (Bigelow and Schroeder, 1953, Figueiredo, 1977, Batista, 1991) based their accounts on Miranda-Ribeiro (1907). This study found no additional evidence of *Z. brevirostris* for Bahia State. Nonetheless, Bahia and Espirito Santo States have been considered a part of an ecotone area that enables the occurrence of fauna from different subdivisions of the Brazilian Biogeographic Province (Cord et al., 2022, Anderson et al., 2023). Moreover, the distribution of a species is dynamic and influenced by environmental factors associated with its life history, migration patterns, colonization, and even local extinction (Brown and Lomolino, 1998, Luiz et al., 2012). It is possible that migrants of *Z. brevirostris* once reached southern Bahia State but fluctuations occurred temporally and the presence of this species currently remains uncertain.

Oceanographic features possibly play an important role on the northernmost range limit of *Z. brevirostris*. The South Equatorial Current bifurcates in Northeastern Brazil from 10°S to 15°S, generating the Brazil Current, which influences conditions in Southeastern Brazil (Peterson and Stramma, 1991, Piola and Matano, 2019). The Brazil Current, along with upwellings from the south, generates a transition zone of tropical and subtropical waters in Espirito Santo State (Schmid et al., 1995, Floeter et al., 2001, 2007). Moreover, freshwater discharge from the Sao Francisco River (Pinheiro et al., 2018) and the Abrolhos Archipelago, which is characterized as a topographic barrier to the Brazil Current (Schmid et al., 1995), possibly influence oceanographic conditions to the north of Espirito Santo along the southeast shelf. It is already known that variations in environmental conditions strongly affect reef fish species occurrence in the area (Pinheiro et al., 2018). These environmental features have established Espirito Santo State as the northernmost range limit for some species (Floeter et al., 2001, Barroso et al., 2016, Pinheiro et al., 2018). Besides *Z. brevirostris* (Pinheiro et al., 2015), examples of other elasmobranches that have Espirito Santo State as their northern range limit include the Brazilian Guitarfish, *P. horkelii*, the Groovebelly Stingray, *Dasyatis hypostigma*

Santos and Carvalho, 2004, and the Angular Angel Shark, *Squatina guggenheim* Marini, 1936 (Last et al., 2016, Pinheiro et al., 2015, 2018). The northernmost range limit of *Z. brevirostris* is in a tropical area and may also be affected by biotic factors. In the tropics, biotic conditions may be drivers capable of limiting the abundance and distribution of species (Dobzhansky, 1950, MacArthur et al., 1972). Commonly, these areas have a higher species richness (Brown and Lomolino, 1998), which might be the case for the northern range limit of *Z. brevirostris* since other authors (Pinheiro et al., 2018) have suggested a relatively high reef fish species richness.

2.4.2 Southernmost range limit

The southernmost range limit of *Z. brevirostris* is most often set as the continental shelf off Mar del Plata, in northeastern coast of Argentina (Castello, 1971, Last et al., 2016, Menni and Stehmann, 2000, Santos et al., 2006, Gomes et al., 2019). However, records further south in Argentina have also been mentioned, such as Puerto Quequen (Tamini et al., 2006, Chiaramonte et al., 2011, Barbini and Cousseau, 2015; see also MACN-Ict 9664) and the Gulf of San Matias (Pollom et al., 2020). The three occurrence records highlighted in this study [Chubut Province, Santa Cruz Province, and the Falkland Islands (Malvinas)] further extend the known distribution range for *Z. brevirostris* (more than 2,000 km further south than the Gulf of San Matias).

These occurrence records, reaching the Central Coast of Patagonia, may be facilitated by the Brazil Current, which could have its greatest influence in the region during summer months (Boschi, 1989, Caille and Maldonado, 1993). Accordingly, the records for Chubut and Santa Cruz provinces both refer to warm months (December and February, respectively). In this region, several other species from temperate warm waters have been recorded at higher latitudes during summer months (e.g., the Dusky Grouper, *Epinephelus marginatus*, Irigoyen et al., 2005; the Silver Porgy, *Diplodus argenteus*, Galvan et al., 2005; the Namorado Sandperch, *Pseudopercis numida*, Venerus et al., 2007; the Spotback Skate, *Atlantoraja castelnaui*, the Eyespot Skate, *Atlantoraja cyclophora*, the Atlantic Moonfish, *Selene setapinnis*, the Cochero, *Dules auriga*, the Argentine Goatfish, *Mullus argentinae*, the Brazilian Codling, *Urophycis brasiliensis*, the Red Porgy, *Pagrus pagrus* and the Largehead Hairtail, *Trichiurus lepturus*, Gongora et al., 2009, Bovcon et al., 2011; the Snowy Grouper, *Hyporthodus niveatus*, Trobbiani et al., 2014; the Tope, *Galeorhinus galeus*, Chiaramonte et al., 2016; the Striped Smoothhound, *Mustelus fasciatus*, and the Shortnose Eagle Ray, *Myliobatis ridens*, Chiaramonte et al., 2023).

In turn, the record of *Z. brevirostris* in the Falklands Islands (Malvinas) suggests a physiological plasticity for the species given the low water temperature in the region (4 to 10° C, influenced by cold waters from the Malvinas Current - Piola and Matano, 2019). Possibly, factors other than water temperature, such as salinity, depth, and bottom substrate type, further allow the occurrence of this species in the region. For instance, *Z. brevirostris* is intimately related to ocean floors that are flat and composed of sand, mud, and gravel (Barbini et al., 2011). All these conditions are present in the Patagonian Continental Shelf of Argentina, in which the Falklands Islands (Malvinas) are located (Violante et al., 2014).

Overall, biotic factors may influence the distribution of a species, affecting its range limit on one side (usually at low latitudes), whereas abiotic conditions might be the limiting factors on the other extreme of its range (usually at high latitudes) (Dobzhansky, 1950, Brown and Lomolino, 1998, MacArthur et al., 1972, Paquette and Hargreaves, 2021). This seems to apply to *Z. brevirostris*, which may have its southernmost range limit affected by abiotic factors. This area is influenced by the Malvinas Current and the Brazil/ Malvinas confluence (Piola and Matano, 2019). Environmental conditions such as bottom type, decreasing water temperature, increasing salinity, dissolved oxygen, and latitude affect the spatial distribution of many other species in this region (Menni et al., 2010, Barbini et al., 2011, Lucifora et al., 2012). Water temperature influences the geographical distribution of fish (Menni et al., 2010, Sunday et al., 2012, Rutterford et al., 2023). Water temperature (which is related to latitude) and depth are the abiotic factors that most influence (working as ecological drivers) the geographic distribution of Chondrichthyes in the Southwest Atlantic (Menni et al., 2010). For instance, influence of water temperature may even result in the splitting of the Chola Guitarfish, *Pseudobatos percellens*, into distinct genetic lineages (Cruz et al., 2023).

It is unknown if *Z. brevirostris* has established a population at its southernmost limit or if its presence in the region is due to occasional migrants. In fact, it is unclear if *Z. brevirostris* completes its life cycle throughout its entire geographic distribution range. Movements of Chondrichthyes further south of their distribution are mostly considered to be occasional or seasonal in the Southwestern Atlantic (Menni et al., 2010). This may explain a relatively sparser occurrence of *Z. brevirostris* at its southernmost limit when compared to its northernmost limit.

Acknowledgments

L.G.X. is thankful to M. Stehmann (ICHTHYS), R. Thiel and I. Eidus (ZMH), E. V. Silva and M. R. Britto (MNRJ/UFRJ), R. Robins (FLMNH), R. de Ruiter (RMNH), B. Brown (AMNH), P. Bartsch (ZMB), J. Williams (USNM), G. Chiaramonte (MACN - CONICET), A. Gosztonyi (CENPAT), S. Barbini (INIDEP), E. Giácomo (IBMPAS), and M. Loureiro (MHNM) for museum specimen information. L.G.X. and V.V.F. are also thankful to J. González (MHNM), J. Astarloa (UNMdP), M. Estalles (CONICET), C. Sampaio (UFAL), C. Ferreira (UFF), S. Floeter (UFSC), and J. Santander-Neto (IFES) for information on *Z. brevirostris* occurrence. CAPES provided a PhD fellowship to L.G.X. and postdoctoral fellowship (Programa Nacional de Pós-Doutorado - PNPD) to J.E.P.F. FUNCAP provided a visiting researcher grant to P.C. We are thankful for the comments provided by two anonymous reviewers, which improved the manuscript.

Author contribution

L.G.X.: Conceptualization; Investigation; Data Curation; Methodology; Writing – original draft; Writing – review & editing.

N.D.B.; T.H.B.: Investigation; Methodology; Writing – review & editing.

J.E.P.F.: Conceptualization; Supervision; Investigation; Writing – review & editing.

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2.6 Supplementary material

Table S1: Database of occurrence records of *Zapteryx brevirostris* between 1865 and 2021 years.

individual count	source	institution code	collection code	catalog number	identified by	collector	year collected	month collected	day collected	country	state province	county	locality	latitude	longitude	depth (m)	References
1	collection manager	ZMB	ZMB	ZMB 4544						Brazil							
2	collection manager	ANSP	ANSP	ANSP 103955		J. Baskins & N. A. Menezes	1964	03-04	03-09	Brazil	Rio de Janeiro	São João da Barra	Praia de Atafona	-21.631459	-41.007741		
1	collection manager	MNRJ	MNRJ	MNRJ 19138	J.L.Gasparini	J.L.Gasparini				Brazil	Espírito Santo	Guarapari	Ilha Escalvada	-20.700151	-40.406528		
1	collection manager	MNRJ	MNRJ	MNRJ 555	P.Miranda Ribeiro					Brazil	Rio de Janeiro	Baia de Guanabara	ilha Rasa, D.F.	-23.064549	-43.146290		
1	collection manager	MNRJ	MNRJ	MNRJ 6665		Rego Barros	1944	1	2	Brazil	Rio de Janeiro	Maricá		-22.919824	-42.819804		
3	collection manager	MNRJ	MNRJ	MNRJ 8972	P. M. Ribeiro	Haroldo Campos & Sérgio Ypiranga [Pinto]				Brazil	Rio de Janeiro	Rio de Janeiro	Barra de Guaratiba	-23.071308	-43.562512		
3	collection manager	MNRJ	MNRJ	MNRJ 8973	P. M. Ribeiro	Haroldo Campos & Sérgio Ypiranga [Pinto]				Brazil	Rio de Janeiro	Rio de Janeiro	Barra de Guaratiba	-23.071308	-43.562512		
1	collection manager	MNRJ	MNRJ	MNRJ 17706	A. Afonso	GWN, DFM, A.Thurler, G.Marcondes	1998	02	07	Brazil	Rio de Janeiro	Arraial do Cabo	Prainha	-22.961106	-42.024093		
5	collection manager	MNRJ	MNRJ	MNRJ 17762	A. Thurler	D.F.Moraes Jr. & A.Thurler	1998	05	08	Brazil	Rio de Janeiro	Macaé		-22.387318	-41.785662		
1	collection manager	MNRJ	MNRJ	MNRJ 21886	C.Amorim	S.Sicciliano				Brazil	Rio de Janeiro	Araruama	Praia Seca	-22.936405	-42.327976		
1	collection manager	MNRJ	MNRJ	MNRJ 38312	M.Senna		2003	7	24	Brazil	Rio de Janeiro	Macaé		-22.387318	-41.785662		
4	collection manager	MNRJ	MNRJ	MNRJ 38317	M.Senna	D.F.Moraes				Brazil	Rio de Janeiro	Arraial do Cabo	Praia do Forno	-22.965543	-42.015766		
1	collection manager	MNRJ	MNRJ	MNRJ 38543	S.Santos	M.Vianna,S.Santos,M.Macedo	2010	2	10	Brazil	Rio de Janeiro	Macaé		-22.966667	-42.933333		
1	collection	MNRJ	MNRJ	MNRJ		Rubens da Silva	1944	11	23	Brazi	Santa	Florianópol	Praia de	-	-		

	manager			7511						l	Catarina	is	Canasvieiras	27.429299	48.461641
1	collection manager	MNRJ	MNRJ	MNRJ 32339	M.L.V.Senna	W.D.Bandeira	2008			Brazil	Rio de Janeiro				
1	collection manager	MNRJ	MNRJ	MNRJ 32346	M.L.V.Senna	W.D.Bandeira	2008			Brazil	Rio de Janeiro				
1	collection manager	MNRJ	MNRJ	MNRJ 32503		D.F. de Moraes Junior	2007			Brazil	Rio de Janeiro				
1	collection manager	MNRJ	MNRJ	MNRJ 32504		D.F. de Moraes Junior	2007			Brazil	Rio de Janeiro				
1	collection manager	MNRJ	MNRJ	MNRJ 32505		D.F. de Moraes Junior	2007			Brazil	Rio de Janeiro				
1	collection manager	MNRJ	MNRJ	MNRJ 32531		D.F. de Moraes Junior	2007			Brazil	Rio de Janeiro				
5	collection manager	MNRJ	MNRJ	MNRJ 32593		D.F. de Moraes Junior	2007			Brazil	Rio de Janeiro				
1	collection manager	MNRJ	MNRJ	MNRJ 25	M.Senna					Brazil	Rio de Janeiro	Rio de Janeiro	Rio de Janeiro		
2	collection manager	MNRJ	MNRJ	MNRJ 32615		D.F. de Moraes Junior	2007	09	18	Brazil	Rio de Janeiro		Saquarema e Ponta Negra.		
1	collection manager	MNRJ	MNRJ	MNRJ 33233		F.Augusto	2008			Brazil	Rio de Janeiro	Rio de Janeiro	Rio de Janeiro		
1	collection manager	MHNM	MHNM	MHNM 1872		M. Cachés	1971	4		Uruguay	Rocha		Bahía grande frente a la isla, La Paloma	-34.658483	-54.150017
1	collection manager	MHNM	MHNM	MHNM 1873		M. Cachés	1971	4		Uruguay	Rocha		Bahía grande frente a la isla, La Paloma	-34.658483	-54.150017
1	collection manager	MHNM	MHNM	MHNM 1988		M. Cachés	1973	2	5	Uruguay	Rocha		Océano Atlántico, Playa Puerto de La Paloma	-34.649850	-54.149567
1	collection manager	MHNM	MHNM	MHNM 1989		M. Cachés	1973	2		Uruguay	Rocha		Océano Atlántico, Playa Puerto de La Paloma	-34.649850	-54.149567
1	collection manager	MHNM	MHNM	MHNM 1995		C. M. Martínz	1973	2	19	Uruguay	Maldonado	Pirinópolis		-35.082616	-55.3869694

2	collection manager	INIDEP	INIDEP	INIDEP:PECES:38	H. Castello		1970	10		Argentina	Mar Del Plata			-38.007340	-57.542523	
1	collection manager	MACN	MACN-Ict	MACN-Ict-9664	Chiaramonte, Gustavo	Tamini, Leo et al.	1999	2	25	Argentina	Puerto Quequén			-38.576146	-58.702791	
1	collection manager	UFC	CIDRO	CIDRO-B-38	T H Basilio	Tiago H Basilio	2006			Brazil	Espírito Santo	Aracruz	Barra do Riacho	-19.830361	-40.052417	
1	collection manager	UFC	CIDRO	CIDRO-B-39	T H Basilio	Tiago H Basilio	2013			Brazil	Espírito Santo	Piúma		-20.849397	-40.732250	
1	collection manager	ZMH	ZMH	ISH 591-1978	Dr. M. Stehmann	Unknown collector	1978	10	27	Falkland Islands (Malvinas)				-53.866667	-59.916667	205
1	database online	MACN	MACN-Ict	MACN-Ict-ct-376		Ruben Dellacasa (Don Curano)	2003	1	22	Argentina	Buenos Aires		Quequén	-38.7861	-59.5288	
1	database online	MACN	MACN-Ict	MACN-Ict-ct-372		Ruben Dellacasa (Don Curano)	2003	1	22	Argentina	Buenos Aires		Quequén	-38.7861	-59.5288	
1	database online	ZMH	ZMH	ISH 562-1978	Dr. M. Stehmann		1978	09	27	Uruguay				-36.333333	-54.933333	44
1	database online	ZMH	ZMH	ZMH 562-1978			1978	09	27	Argentina	Buenos Aires			-36.330000	-54.930000	
1	database online	MHNCI	MHNCI-PEIXES	MHNCI-PEIXES 9502		Gerhardinger, L. C. & Godoy, E.				Brazil	Santa Catarina	Bombinhas	Reserva Biológica Marinha do Arvoredo	-25.285278	-48.425	
1	database online	MHNCI	MHNCI-PEIXES	MHNCI-PEIXES 125	C. F. Haluch	Excursão zoológica	1965	09		Brazil	Paraná	Matinhos	Matinhos	-25.8175	-48.5428	
1	database online	MHNCI	MHNCI-PEIXES	MHNCI-PEIXES 10135						Brazil	Paraná	Guaratuba	Brejatuba	-25.8828	-48.5747	
1	database online	USP	MZUSP	MZUSP 72775	J.L.Figueiredo	Prof. W. Besnard				Brazil	Rio de Janeiro	Cabo Frio	Cabo Frio	-22.8794	-42.0186	
1	database online	USP	MZUSP	MZUSP 72778	J.P.Carvalho	W.Besnard				Brazil	Espírito Santo		Banco de São Tomé			
1	database online	USP	MZUSP	MZUSP 69285	RLMoura	Moura, Francini-Filho, Flesh et al.	2000	03	20	Brazil	Rio de Janeiro	Búzios	Ilha da Âncora	-22.766666	-41.783333	
1	database online	USP	MZUSP	MZUSP 72777	J.L.Figueiredo		1966	07	26	Brazil	Rio de Janeiro	Angra dos Reis	Angra dos Reis	-23.0067	-44.3181	

1	database online	USP	MZUSP	MZUSP 72774	J.L.Figueiredo	C.Jesus	1962	05	18	Brazil	São Paulo	Santos	Proximidades da Ilha da Moela	-23.96	-46.33	
1	database online	USP	MZUSP	MZUSP 3192	J.L.Figueiredo/1972	A.Campos				Brazil	Rio de Janeiro		Rio de Janeiro			
1	database online	USP	MZUSP	MZUSP 47018	RLMoura	A. Carvalho Filho				Brazil	São Paulo	São Sebastião	Praia de Toque-Toque, ii-iii.1987, S. Sebastião, SP	-23.76	-45.41	
1	database online	USP	MZUSP	MZUSP 48199	JLFigueiredo		1975	02	20	Brazil			N.Oc.'Prof. W.Besnard': Estação 2204.	-22.166666	-41.166668	
1	database online	USP	MZUSP	MZUSP 69284	RLMoura	Moura, Francini-Filho, Flesh et al.	2000	03	20	Brazil	Rio de Janeiro	Búzios	Ilha da Âncora	-22.766666	-41.783333	
1	database online	USP	MZUSP	MZUSP 72779		Gilda de Quadros Benvegnú	1972	10	29	Uruguay				-35.316666	-54.216667	
1	database online	IOUSP	OBIS_BR	382			1972			Brazil	Rio Grande do Sul		offshore	-34.5616	-53.9253	23
1	database online	IOUSP	OBIS_BR	383			1972			Brazil	Rio Grande do Sul		offshore	-34.0536	-53.4872	21
1	database online	IOUSP	OBIS_BR	375			1972	4		Brazil	Rio Grande do Sul		offshore	-33.9667	-52.8333	29
1	database online	IOUSP	OBIS_BR	377			1972	8		Brazil	Rio Grande do Sul		offshore	-34.5833	-53.9667	22
1	database online	IOUSP	OBIS_BR	378			1972	8		Brazil	Rio Grande do Sul		offshore	-34.25	-53.1333	31
1	database online	IOUSP	OBIS_BR	379			1972	8		Brazil	Rio Grande do Sul		offshore	-34.0167	-52.7333	28
1	database online	IOUSP	OBIS_BR	374			1972	1		Brazil	Rio Grande do Sul		offshore	-34.1833	-52.3167	58
1	database online	IOUSP	OBIS_BR	376			1972	8		Brazil	Rio Grande do Sul		offshore	-35.3	-54.2167	27

1	database online	IOUSP	OBIS_BR	381			1972			Brazil	Rio Grande do Sul		offshore	-35.3309	-54.222	
1	database online	IOUSP	OBIS_BR	380			1972	8		Brazil	Rio Grande do Sul		offshore	-33.75	-53.2667	16
1	database online	UFES	CIUFES	CIUFES 3038	L. R. Bonesi	L. R. Bonesi	2013	11	20	Brazil	Espírito Santo	Aracruz	Barra do Sahy	-19.82	-40.273	
1	database online	UFES	CIUFES	CIUFES 3039	L. R. Bonesi	L. R. Bonesi	2013	11	20	Brazil	Espírito Santo	Aracruz	Barra do Sahy	-19.82	-40.273	
1	database online	UFES	CIUFES	CIUFES 3040	L. R. Bonesi	L. R. Bonesi	2013	11	20	Brazil	Espírito Santo	Aracruz	Barra do Riacho	-19.829	-40.061	
1	database online	UFES	CIUFES	CIUFES 3041	L. R. Bonesi	L. R. Bonesi	2013	11	20	Brazil	Espírito Santo	Aracruz	Barra do Sahy	-19.82	-40.273	
1	database online	UFES	CIUFES	CIUFES 3049	L. R. Bonesi	L. R. Bonesi	2013	11	20	Brazil	Espírito Santo	Aracruz	Barra do Riacho	-19.829	-40.061	
1	database online	UFES	CIUFES	CIUFES 3050	L. R. Bonesi	L. R. Bonesi	2013	11	20	Brazil	Espírito Santo	Aracruz	Barra do Riacho	-19.829	-40.061	
1	database online	UFES	CIUFES	CIUFES 3051	L. R. Bonesi	L. R. Bonesi	2013	11	20	Brazil	Espírito Santo	Aracruz	Barra do Riacho	-19.829	-40.061	
3	database online	UFES	CIUFES	CIUFES 3055	L. R. Bonesi	L. R. Bonesi				Brazil	Espírito Santo	Aracruz	Barra do Riacho	-19.829	-40.061	
1	database online	UFES	CIUFES	CIUFES 3060	L. R. Bonesi	L. R. Bonesi	2013	08	22	Brazil	Espírito Santo	Aracruz	Barra do Riacho	-19.829	-40.061	
1	database online	UFES	CIUFES	CIUFES 3062	L. R. Bonesi	L. R. Bonesi				Brazil	Espírito Santo	Aracruz	Barra do Riacho	-19.829	-40.061	
1	database online	UFES	CIUFES	CIUFES 3207	L. R. Bonesi	L. R. Bonesi	2014	02	17	Brazil	Espírito Santo	Aracruz	Barra do Riacho	-19.829	-40.061	
1	database online	UFES	CIUFES	CIUFES 3208	L. R. Bonesi	L. R. Bonesi	2014	02	17	Brazil	Espírito Santo	Aracruz	Barra do Riacho	-19.829	-40.061	
4	database online	UFES	CIUFES	CIUFES 3215	L. R. Bonesi	L. R. Bonesi	2014	02	17	Brazil	Espírito Santo	Aracruz	Barra do Riacho	-19.829	-40.061	
1	database online	UFES	CIUFES	CIUFES 394	J.-C. Joyeux	J-C. Joyeux et al. (turma de Recursos Vivos 1)	2002	09	17	Brazil	Espírito Santo	Vitória	Baía do Espírito Santo	-20.31	-40.34	
1	database online	UFES	CIUFES	CIUFES 397	J.-C. Joyeux	J-C. Joyeux et al. (turma de Recursos Vivos 1)	2002	09	17	Brazil	Espírito Santo	Vitória	Baía do Espírito Santo	-20.31	-40.34	
2	database online	UFES	CIUFES	CIUFES 824	C. R. Pimentel & H. T. Pinheiro	C. R. Pimentel, C. E. Stein & H. T. Pinheiro	2007	08	16	Brazil	Espírito Santo	Vitória	Praia de Camburi	-20.31	-40.34	
1	database online	UFES	CIUFES	CIUFES 882	C. R. Pimentel & L. B. Stocco	H. T. Pinheiro	2008	03	07	Brazil	Espírito Santo	Itapemirim	Ilha dos Franceses	-20.926	-40.752	

1	database online	BMNH	ZOO (Zoology)	1953.8.10.12						Brazil						
1	database online	BMNH	ZOO (Zoology)	1870.7.16.4						Brazil						
1	database online	BMNH	ZOO (Zoology)	1923.7.30.2						Brazil	Rio de Janeiro	Niterói	Sacco Sao Francisco	-22.9235	-43.1107	
1	database online	UEFS	MZFS	MZFS 2645	C.L.S. Sampaio	J.L. Gasparini	1998	06	26	Brazil	Espírito Santo	Guarapari	Arquipélago das 3 Ilhas	-20.689346	-40.387261	
1	database online	PUCRS	MCP-PEIXES	MCP-PEIXES-1520	C.A.S.Lucena Z.M.Lucena	L.C.C.Faleiro & L.Borsato	1969	07	21	Brazil	Santa Catarina	Florianópolis	unspecified	-27.5967	-48.5492	
1	database online	PUCRS	MCP-PEIXES	MCP-PEIXES-3601	C.A.S.Lucena Z.M.Lucena	A.Mafisoni, C.R.Poli & F.D'Incao	1970	01	15	Brazil	Santa Catarina	Garopaba	arrasto de pescadores	-28.0233	-48.6133	
1	database online	PUCRS	MCP-PEIXES	MCP-PEIXES-5334	C.A.S.Lucena Z.M.Lucena	T.Lema, L.C.Faleiro & Lenio	1969	07	04	Brazil	Rio Grande do Sul	Rio Grande	Arrasto do barco 'Apolo' na praia do Cassino	-32.2333335876	-52.1166648865	
1	database online	PUCRS	MCP-PEIXES	MCP-PEIXES-21581	J. Pezzi da Silva	A.Braum & D.Lewis	1997	12	01	Brazil	Rio Grande do Sul	Cidreira	Plataforma de Cidreira.	-30.1666660309	-50.2000007629	
1	database online	PUCRS	MCP-PEIXES	MCP-PEIXES-21582	J. Pezzi da Silva	A.Braum & D.Lewis	1997	12	01	Brazil	Rio Grande do Sul	Cidreira	Plataforma de Cidreira.	-30.1666660309	-50.2000007629	
2	database online	PUCRS	MCP-PEIXES	MCP-PEIXES-33524	A. Kruger	Eduardo Eli de Souza	2003	02	21	Brazil	Rio Grande do Sul	Torres	Arrasto em frente a praia de Torres.	-29.3666667938	-49.7999992371	20
17	database online	UFRJ	NPM	NPM 1513	Michael M. Mincarone	Michael M. Mincarone et al.	2008	04	13	Brazil	Rio de Janeiro		Bacia de Campos.	-22.45528	-41.16139	46,4-48,2
7	database online	UFRJ	NPM	NPM 1518	Michael M. Mincarone	Paulo A. S. Costa et al.	2008	04	19	Brazil	Rio de Janeiro		Bacia de Campos.	-22.30778	-41.49556	17,2-17,2
6	database online	UFRJ	NPM	NPM 1551	Michael M. Mincarone	Paulo A. S. Costa et al.	2008	04	19	Brazil	Rio de Janeiro		Bacia de Campos.	-22.21611	-41.13167	15,3-17,1
1	database online	UFRJ	NPM	NPM 1560	Michael M. Mincarone	Michael M. Mincarone et al.	2008	04	14	Brazil	Rio de Janeiro		Bacia de Campos. .	-22.76389	-41.77722	45,9-48,2
2	database online	UFRJ	NPM	NPM 1579	Michael M.	Paulo A. S. Costa et al.	2008	04	20	Brazil	Rio de Janeiro		Bacia de Campos.	-22.0616	-40.82722	18,8-19,5

					Mincarone									7		
17	database online	UFRJ	NPM	NPM 1580	Michael M. Mincarone	Paulo A. S. Costa et al.	2008	04	20	Brazil	Rio de Janeiro		Bacia de Campos.	-22.06417	-40.59722	47,7-48,2
16	database online	UFRJ	NPM	NPM 1581	Michael M. Mincarone	Paulo A. S. Costa et al.	2008	04	20	Brazil	Rio de Janeiro		Bacia de Campos.	-22.26917	-40.91667	45,4-46,7
1	database online	UFRJ	NPM	NPM 2627	Arthur de Barros Bauer	Arthur de Barros Bauer et al.	2014	09	30	Brazil	Rio de Janeiro	Macaé	Arquipélago de Santana, ao sul do Ilhote Sul.	-22.42667	-41.72222	15
3	database online	UFRJ	NPM	NPM 2649	Arthur de Barros Bauer	Arthur de Barros Bauer et al.	2014	12	18	Brazil	Rio de Janeiro	Macaé	Arquipélago de Santana, Ilha de Santana, Praia Principal.	-22.40722	-41.70806	
1	database online	UFRJ	NPM	NPM 2651	Arthur de Barros Bauer	Arthur de Barros Bauer et al.	2014	12	18	Brazil	Rio de Janeiro	Macaé	Arquipélago de Santana, Ilha de Santana, Praia Principal.	-22.40722	-41.70806	
2	database online	UFRJ	NPM	NPM 2653	Arthur de Barros Bauer	Arthur de Barros Bauer et al.	2014	12	18	Brazil	Rio de Janeiro	Macaé	Arquipélago de Santana, Ilha de Santana, Praia Principal.	-22.40722	-41.70806	
3	database online	UFRJ	NPM	NPM 2819	Arthur de Barros Bauer	Arthur de Barros Bauer & Luciano Gomes Fischer	2015	07	17	Brazil	Rio de Janeiro	Macaé	Arquipélago de Santana	-22.40861	-41.71056	5,5-6,9
5	database online	UFRJ	NPM	NPM 2820	Arthur de Barros Bauer	Arthur de Barros Bauer et al.	2015	08	17	Brazil	Rio de Janeiro	Macaé	Arquipélago de Santana, próximo a Ilha de Santana.	-22.40417	-41.705	5-8,8
4	database online	UFRJ	NPM	NPM 2821	Arthur de Barros Bauer	Arthur de Barros Bauer et al.	2015	08	17	Brazil	Rio de Janeiro	Macaé	Arquipélago de Santana,	-22.40806	-41.71056	6,8-8,8

4	database online	UFRJ	NPM	NPM286	FDD & MMP	Fabio Di Dario & André Carrara Morandini	2008	07	12	Brazil	Rio de Janeiro	Casimiro de Abreu	próximo a Ilha de Santana. Barra de São João.	-22.64083	-41.90417	30
2	database online	UFRJ	NPM	NPM 2999	Arthur de Barros Bauer	Arthur de Barros Bauer & Luciano Gomes Fischer	2014	12	18	Brazil	Rio de Janeiro	Macaé	Arquipélago de Santana.	-22.40667	-41.70833	5
2	database online	UFRJ	NPM	NPM 3001	Arthur de Barros Bauer	Arthur de Barros Bauer & Luciano Gomes Fischer	2014	12	18	Brazil	Rio de Janeiro	Macaé	Arquipélago de Santana.	-22.40556	-41.70639	5
2	database online	UFRJ	NPM	NPM 3002	Arthur de Barros Bauer	Arthur de Barros Bauer & Luciano Gomes Fischer	2014	12	18	Brazil	Rio de Janeiro	Macaé	Arquipélago de Santana, Laje da praia principal.	-22.40722	-41.70917	5
1	database online	UFRJ	NPM	NPM 3806	Arthur de Barros Bauer	Arthur de Barros Bauer	2017	1	30	Brazil	Rio de Janeiro	Macaé	Arquipélago de Santana.	-22.3708	-41.7868995666504	
1	database online	UFRJ	NPM	NPM 424	Matheus Maia S. Pereira	Júlio Agostinho	2008	07	23	Brazil	Rio de Janeiro	Macaé	Arredores do Arquipélago de Sant' Anna	-22.3708	-41.7869	
1	database online	UFRJ	NPM	NPM 686	Fabio Di Dario	Fabio Di Dario & Bruna P. S. Di Dario	2011	04	22	Brazil	Espírito Santo	Anchieta		-20.8058	-40.6456	
3	database online	UFRJ	NPM	NPM 73	Fabio Di Dario	Fabio Di Dario & Bruna P. S. Di Dario	2008	12	13	Brazil	Rio de Janeiro	Casimiro de Abreu	Barra de São João.	-22.4806	-42.2042	10-30
4	database online	UFRJ	NPM	NPM 92	Fabio Di Dario	André Carrara Morandini & Sérgio Stampar	2008	08	16	Brazil	Rio de Janeiro	Casimiro de Abreu	Barra de São João.	-22.4806	-42.2042	30
1	database online	UEL	MZUEL-PEIXES	MZUEL-PEIXES 13889	José Birindelli	Gilberto Ougo	2015	09	03	Brazil	Paraná	Pontal Do Parana	Balneário Shangri-la	-25.6985833333	-48.4680555556	
4	database online	UEL	MZUEL-PEIXES	MZUEL-PEIXES 7607	Wanessa Carmo	Zé do Zuca	2013	07	01	Brazil	Paraná	Pontal Do Parana	Balneário Shangri-lá	-25.6736	-48.5111	
1	database online	MCZ	HU-ZOO	HU-ZOO S-429	Ledger					Brazil	Rio de Janeiro			-23.047718	-43.349847	
1	database online	MCZ	HU-ZOO	HU-ZOO S-536	Ledger	Hassler Expedition	1872			Brazil	Rio de Janeiro	Rio de Janeiro and environs		-22.8916	-43.29166	

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1	database online	MBML	MBML-PEIXES	MBML-PEIXES 113	J.L.Gasparini	D.A.Jório	1995	01	01	Brazil	Espírito Santo	Guarapari	Enseada de Perocão	-20.657778	-40.510833	
3	database online	MBML	MBML-PEIXES	MBML-PEIXES 12049	Luisa maria Sarmento Soares	Lauana S. Fadini	2016	04	18	Brazil	Espírito Santo	Linhares	Regência.	-19.749167	-39.6975	
1	database online	MBML	MBML-PEIXES	MBML-PEIXES 170	J.L.Gasparini	J.L.Gasparini	1987	02	07	Brazil	Espírito Santo	Guarapari	Arquipélago das Três Ilhas	-20.657778	-40.510833	
1	database online	MBML	MBML-PEIXES	MBML-PEIXES 2190	J.L.Gasparini	J.L.Gasparini	1997	03	01	Brazil	Espírito Santo	Guarapari	Arquipélago das Três Ilhas	-20.657778	-40.510833	
1	database online	MBML	MBML-PEIXES	MBML-PEIXES 6109	L.M.Sarmento-Soares	G.I.Almeida	2001	01	01	Brazil	Espírito Santo	Vitória	Praia Camburiu em frente a CST - Arrastão de balão - Barco São Nicolau	-20.3	-40.233333	
1	database online	UNICAMP	ZUEC-PIS	ZUEC-PIS 183	V. S. Uieda	J. Oliveira	1977	11		Brazil	São Paulo	Ubatuba		-23.5	-45.1	
1	database online	UNICAMP	ZUEC-PIS	ZUEC-PIS 3726		J. Oliveira	1977	10		Brazil	São Paulo	Ubatuba		-23.5	-45.1	
1	database online	UNICAMP	ZUEC-PIS	ZUEC-PIS 4639		J. L. Gasparini & J. Caçador	2000	11	01	Brazil	Espírito Santo	Guarapari	Arquipélago das Três Ilhas	-20.658	-40.511	
1	database online	UNICAMP	ZUEC-PIS	ZUEC-PIS 6546	Natália Cristina Fidelis Bahia	Natália Cristina Fidelis Bahia	2010	07	10	Brazil	São Paulo	Ilhabela		-23.77	-45.35	
1	database online	CAS	CAS	CAS 52836						Brazil	Espírito Santo	Vitória	Praia de Maruípe	-20.301083	-40.288806	
1	database online	CAS	CAS	CAS 52837			1944	11	15	Brazil	Espírito Santo	Vitória	Enseada de Vitória	-20.321500	-40.290611	
1	database online	MNHN	MNHN-IC	MNHN-IC-1984-0015	Roux	N. O. Calupso & Roux	1961	12		Brazil	Rio Grande do Sul			-32.117000	-51.717000	21
1	database online	MNHN	MNHN-IC	MNHN-IC-0000-1258		Castelnau				Brazil	Rio de Janeiro	Rio de Janeiro		-23.000000	-43.283000	

3	database online	NRM	NRM	NRM 9053	Bod & Eia		1865-1868			Brazil	Rio de Janeiro						
1	database online	SMF	SMF	SMF 3923						Brazil	Rio de Janeiro						
1	database online	MOVI	MOVI	MOVI 05943	J.M.R.Soto		1991			Brazil	Santa Catarina		Praia das Gaivotas, Balneário das Gaivotas	-29.157576	-49.575840		
1	database online	MOVI	MOVI	MOVI 15099	J.M.R.Soto	M.Hostim-Silva	1995			Brazil	Santa Catarina		Baía da Babitonga, São Francisco do Sul	-26.250087	-48.63575		
1	database online	MOVI	MOVI	MOVI 08926	J.M.R.Soto	E.Santos	1996			Brazil	Santa Catarina			-28.193334	-48.628613	19-41	
1	database online	MOVI	MOVI	MOVI 24487	J.M.R.Soto	J.M.R.Soto et al.	2002	07	27	Brazil	Santa Catarina		Passo de Torres, Sombrio	-29.320941	-49.712440		
1	database online	MOVI	MOVI	MOVI 24597	J.M.R.Soto		1980			Brazil	Rio Grande do Sul						
1	database online	MOVI	MOVI	MOVI 111	J.M.R.Soto	J.M.R.Soto	1990			Brazil	Rio Grande do Sul	Imbé		-29.976378	-50.127440		
4	database online	USP	LIRP	LIRP 15344	André Esguícero	Flávio Bockmann	2017	10	4	Brazil	São Paulo	Ubatuba	Praia do Itaguá	-23.4463888889	-45.045		
1	database online	CENPAT	OBIS_AR	CNP-P-4238			1978	04	12	Argentina	Buenos Aires			-37	-54.433	135	
1	database online	CENPAT	OBIS_AR	CNP-P-4237			1978	03	12	Argentina				-32.6667	-45.75	120	
1	database online	CENPAT	OBIS_AR	CNP-P-4239			1978	04	15	Argentina	Buenos Aires	Mar Chiquita		-38	-56.9667	47	
1	on-board observation				Maria Vuccica	Maria Vuccica	2010	12	26	Argentina	Chubut		Restricted Effort Zone of the Province of Chubut	-43.50695	-65.0262166666666	34,1	
1	technical note	INIDEP					1997	2	between 15 and 28	Argentina	Santa Cruz	Provincia de Santa Cruz	Territorial waters	-48.285	-65.245	50-100	Wöhler et al. 1999

-	published research article		Brazil	Rio de Janeiro						Miranda-Ribeiro, 1904
-	published research article		Brazil	Rio de Janeiro						Miranda-Ribeiro, 1907
5	published research article		Brazil							Bigelow and Schroeder, 1953
10	published research article		Argentina	Mar Del Plata						Castello, 1971
-	published research article		Brazil							Figueiredo, 1977
210	published research article	1982-1984	Brazil	Rio de Janeiro	Itaipu		-22.96666666667	-43.05	10	Batista, 1987a
-	published research article	1982-1984	Brazil	Rio de Janeiro	Itaipu		-22.96666666667	-43.05	10	Batista, 1987b
-	published research article	1982-1984	Brazil	Rio de Janeiro	Itaipu		-22.96666666667	-43.05	10	Batista, 1991
-	published research article	1996	Argentina			Rio de la Plata estuary				Jaureguizar et al., 2003
-	published research article	1993 - 1996	Argentina			Rio de la Plata estuary				Jaureguizar et al., 2004
106	published research article	2000-2001	Brazil	Paraná						Santos et al., 2006
-	published research article		Brazil, Uruguay and Argentina							Menni and Stehmann, 2000
-	published research article		Brazil	Rio de Janeiro						Gomes et al., 2010
332	published research article	2001 and 2006	Uruguay and Argentina							Barbini et al., 2011

-	published research article		Uruguay and Argentina					Colonello et al., 2011
19	published research article	2008 - 2009	Brazil	São Paulo and Rio Grande do Sul				Alexandre de-Franco et al., 2012
48	published research article	2011	Brazil	Paraná	Shangrilá			Wosnick and Freire, 2013
-	published research article	2003 and 2005	Uruguay and Argentina					Colonello et al., 2014
-	published research article		Brazil	Espírito Santo				Pinheiro et al., 2015
-	published research article		Brazil	São Paulo		-25,166667	-47.866667	Pasquino et al., 2016
-	published research article		Brazil	Rio de Janeiro				Loto et al., 2018
7	published research article		Brazil					Pinheiro et al., 2018
90	published research article	2012 and 2014	Brazil	Paraná				Wosnick et al., 2019
-	published research article	2007 - 2009	Brazil	São Paulo	São Sebastião, Bertioga, Santos, Iguape, Cananeia			Caltabellotta et al., 2019
-	published research article		Brazil	Rio de Janeiro				Alvarenga et al., 2021
257	published research article	2011	Brazil	São Paulo	Arquipélago dos Alcatrazes			Karlovic et al., 2021
13	published research article	2015 - 2017	Brazil	Rio de Janeiro	in front of Cabo de São Tomé			Gatts et al., 2021
-	published research article		Brazil	Rio de Janeiro	Arraial do Cabo Marine Extractive Reserve			Lucena et al., 2021
6	published research article	2019	Brazil	São Paulo				Martins et al., 2021

1	published research article	2022	Brazil	São Paulo	Ubatuba	-23,7355556	-45,004444	Takatsuka et al., 2022

3 CAPÍTULO II: New occurrence record and dermal denticles of megamouth sharks stranded on the Southwest Atlantic Coast

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Abstract

The megamouth shark, *Megachasma pelagios*, is a rare circumtropical species with a distinctive appearance. To date, only 273 confirmed occurrence records have been documented globally. This study reports the third occurrence of a mega mouth shark on the Brazilian coast and provides descriptions of the dermal denticles of all three specimens recorded in the country. On September 10, 2018, a megamouth shark was found floating off Pedra do Sal Beach, Parnaíba, Piauí, Northeastern, Brazil. A mitochondrial ND2 sequence was obtained from this specimen, confirming its identity. Skin samples from this specimen, as well as from the two other previously recorded individuals from Southeastern Brazil (an adult stranded in Arraial do Cabo, Rio de Janeiro, and a juvenile captured off the coast of São Paulo), were analyzed to describe the dermal denticles using scanning electron microscopy and stereomicroscopy. The dermal denticles from the Brazilian specimens exhibited distinct shapes depending on body region. The specimen from São Paulo showed differences in the dermal denticles to those of adults, with an increase in the ridges and a reduction of cusps, particularly in the caudal peduncle, cheek, and pelvic fin regions. Furthermore, the dermal denticles of the two juvenile megamouth sharks exhibit, in general, a distinct arrangement pattern, appearing more closely spaced and slightly imbricated when compared to the adult from Arraial do Cabo and those reported in the literature.

Keywords Brazil · Megachasmidae · mtDNA · Placoid scale · Scanning electron microscopy

3.1 Introduction

The megamouth shark, *Megachasma pelagios* Taylor et al. 1983, is the only extant representative of the Lamniform shark family Megachasmidae, caught for the first time accidentally in 1976 off Hawaii, USA (Taylor et al. 1983; Compagno 1990). With its unmistakable appearance, this large planktivorous species (about 800 cm in total length) has a broad, large head with a short, rounded snout, and a terminal mouth with numerous small teeth (Taylor et al. 1983; Martínez-Ortiz et al. 2017; Ebert et al. 2021). Given its external morphological characteristics, taxonomic identification is relatively straightforward. Still, genetic markers such as the mitochondrial genes COI (Moura et al. 2015; Rodriguez-Ferrer et al. 2017; Liu et al. 2018; Kelez et al. 2020) and ND2 (Martin and Naylor 1997; Naylor et al. 2012a, b) have been used to confirm species identification and to describe pat terns of haplotype sharing for the megamouth shark across different ocean basins. Additionally, the complete mitochondrial genome has been sequenced for one specimen of this species (Chang et al. 2014).

Since its discovery, 273 confirmed occurrences of megamouth sharks have been documented (Florida Museum of Natural History 2024; Yu et al. 2021; present study). In most cases, these occurrence records result from stranding or accidental captures (Watanabe and Papastamatiou 2019). Despite its rarity, the species has a circumtropical distribution, with occurrence records in the Atlantic, Indian, and Pacific Oceans (Florida Museum of Natural History 2024), and it may be a long-distance migrant across these three oceans (Watanabe and Papastamatiou 2019). Most occurrence records are concentrated in the Pacific Ocean, with significantly fewer records in the Indian and Atlantic Oceans (Yu et al. 2021).

Currently, eight records of the megamouth shark have been documented in the Atlantic Ocean (Fig. 1). Four of these records are from the East Atlantic: Senegal (Séret 1995), Liberia (Environmental Jus tice Foundation 2020), Gabon, and Mauritania (Diez et al. 2022). The records of the West Atlantic include one in Puerto Rico, USA (Rodriguez-Ferrer et al. 2017), and three in Brazil. In Brazil, the first record was a juvenile male measuring 190 cm total length, accidentally caught off the State of São Paulo (27°08′00.0″S 43°55′00.0″W) in September 1995 (Amorim et al. 2000). The second record was of an adult male measuring 539 cm TL found stranded on Grande Beach, Arraial do Cabo, in the State of Rio de Janeiro (22°57′00.0″S 42°04′00.0″W), in July 2009 (Moura et al. 2015). The third record, a neonate or juvenile male, was found floating off Pedra do Sal Beach, Parnaíba, in the State of Piauí, in September 2018 and is here described.

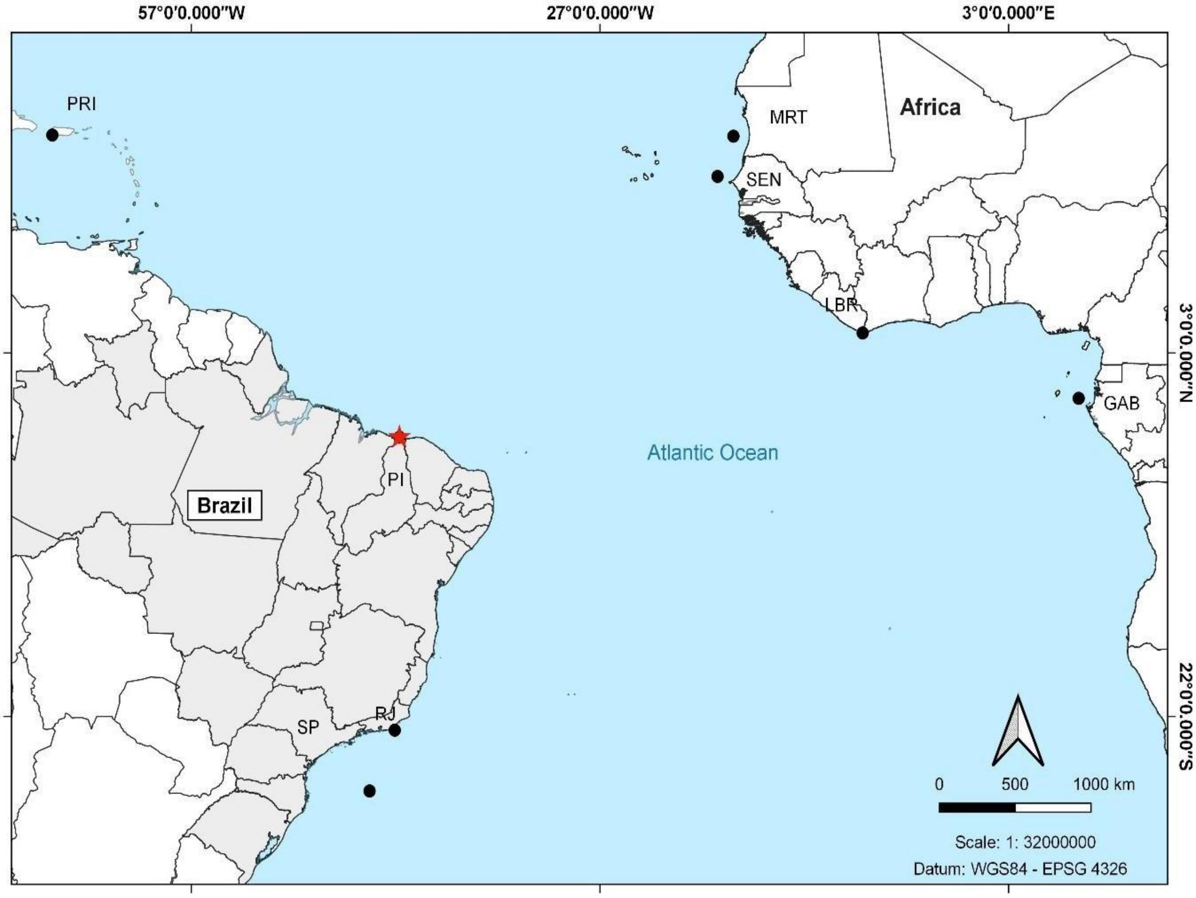

Fig. 1 Records of the megamouth shark in the Atlantic Ocean. The red star indicates the third occurrence record in Brazil, as reported here. Black dots refer to other records in the Atlantic Ocean. PI, Piauí; RJ, Rio de Janeiro; SP, São Paulo; PRI, Puerto Rico; MRT, Mauritania; SEN, Senegal; LBR, Liberia; GAB, Gabon

Many biological aspects of the megamouth shark remain poorly understood or require further description (Watanabe and Papastamatiou 2019), and the species' dermal denticles have been described only for seven adults (Taylor et al. 1983; Yano et al. 1997; Tomita et al. 2014; Duchatelet et al. 2020; Frumkin and Shimada 2020). The dermal denticles on the body of this species were first described by Taylor et al. (1983) as small and flattened (non-erect), with similarities between those on the lateral trunk and the dorsal surfaces of pelvic fins. In most areas, dermal denticles were loosely spaced, but displayed a closely imbricated arrangement on the pelvic fins and gill rakers (Taylor et al. 1983). The megamouth shark has a white band on the upper jaw, visible when the jaw protrudes (Nakaya 2001). In this region, dermal denticles were described by Duchatelet et al. (2020) as "highly joined," with the edges of each denticle positioned close to those of its neighbors.

Although the dermal denticles of the megamouth shark exhibit distinct features, such as their flattened and non-erect nature, their morphology and arrangement are subject to significant variation. These variations in shark dermal denticles, influenced by factors such as species, sex, ontogeny, and body location, encompass differences in size, shape, thickness, and patterns (Reif 1985; Dillon et al. 2017; Macías-Cuyare and Oddone, 2022; Vaz et al. 2023). In general, these structural variations are common across shark species and are essential for understanding taxonomic, evolutionary, and ecological questions (Dillon et al. 2017). These structures provide insights into various aspects of shark biology, including species identification, adaptations to different environmental conditions, and developmental changes throughout its life history (Reif 1985; Raschi and Tabit 1992; Cooper et al. 2023). Thus, this study provides the first description of dermal denticles in juvenile mega mouth sharks and documents the third occurrence of this species in the Southwest Atlantic Ocean, contributing to a better understanding of the life history of this enigmatic shark.

3.2 Methods

3.2.1 The third occurrence record for Brazil

A megamouth shark was found floating by local fishers off Pedra do Sal Beach, in Parnaíba, State of Piauí, on September 10, 2018. The animal was accurately measured before being distributed among the fishers for meat consumption. A portion of the animal’s trunk, approximately 6 kg in weight, containing skin, muscle, and cartilage, was donated for research purposes. The remaining portion of skin, muscle, and cartilage was deposited at the Dias da Rocha Ichthyological Collection, Department of Biology, Federal University of Ceará (specimen catalog number: CIDRO-B-669; Fig. S1).

3.2.2 DNA analysis for the third occurrence record

Muscle tissue samples were taken from the specimen. DNA extraction was performed using the QIAamp DNA Mini Kit (QIAGEN) following the manufacturer’s instructions (Qiagen Inc., Valencia, CA, USA). The quality of the extracted DNA was assessed using a NanoDrop 2000 spectrophotometer. The polymerase chain reaction (PCR) was conducted using the primers Ilem-Mustelus 5′-AAG GAC CAC TTT GAT AGA GT-3′ and Asn-Mustelus 5′-AAC GCT TAG CTG TTA ATT AA-3′ (Naylor et al. 2012b) (0.5μM of each primer), 50ng of extracted DNA, 12.5μl of AmpliTaq Gold 360 Master Mix (Life Technologies, Paisley, UK), and ultrapure water to a total volume of 25μl. PCR cycling conditions were as follows: an initial denaturation step at 94 C (2min), followed by 39 denaturation cycles at 95 C (30s each), primer ligation at 48°C (30s), extension at 72 C (90s), and a final extension step at 72 C (7min). The PCR was performed using a Veriti 96-Well Thermal cycler (Applied Biotech, Inc., Cambridge, UK). PCR products were purified using ExoSAP-IT (Affymetrix, Inc., Santa Clara, CA, USA) according to the manufacturer's protocol. Subsequently, the genetic mate rial was sequenced using a capillary sequencer (EZ Seq service, Macrogen, Inc., Seoul, South Korea). In addition to Ilem-Mustelus and Asn-Mustelus, an internal primer, ND2-batoids-IFA5′-CAC TTY TGA CTW CCA GAA GT-3′ (Naylor et al. 2012b), was also used for DNA sequencing. The partial mtDNA ND2 gene sequences obtained were edited and aligned using the megamouth shark mitochondrial genome as a reference (GenBank: KC702506; Chang et al. 2014) using Geneious 7.1.9 software. The resulting full ND2 1043 bp sequence was submitted to GenBank (accession number: PQ115089).

Two approaches were adopted to test for the identity of the specimen. First, the ND2 mtDNA sequence was submitted to the Basic Local Alignment Search Tool (BLAST) (Altschul et al. 1990) in GenBank. Then, this same sequence was used to assemble a dataset spanning 1043 bp, along with six homologous sequences for this gene sourced from GenBank for phylogenetic analysis. The GenBank sequences included in the dataset as ingroup taxa were as follows: *Megachasma pelagios* (n = 2) [GenBank KC702506 (Chang et al. 2014) and JQ518736 (Naylor et al. 2012b)]; *Odontaspis ferox* (Risso, 1810) (n = 1) [MT702386 (Vella and Vella 2020)]; *Pseudocarcharias kamoharai* (Matsubara, 1936) (n = 1) [KM597489 (Chang et al. 2016)]; *Alopias vulpinus* (Bonnaterre, 1788) (n = 1) [MF374733 (Doane et al. 2018)]; and *Mitsukurina owstoni* Jordan, 1898 (n = 1) [JQ519120 (Naylor et al. 2012b)]. Conversely, the sequence treated as the outgroup taxon was from *Mitsukurina owstoni* (n = 1) [JQ519120 (Naylor et al. 2012b)]. For Bayesian inference (BI) analysis, PartitionFinder (Lanfear et al. 2012) was employed to select the model of evolution, considering codon positions for the protein-coding ND2 gene. Based on the corrected Bayesian information criterion (BIC), the following evolutionary models were cho sen: HKY + I, HKY + I, and HKY for three partitions of ND2. The HKY model assumes that nucleotides occur at different frequencies for each base and have different substitution rates for transitions and trans versions (Hasegawa et al. 1985). The HKY + I model includes a parameter for invariant sites, which helps to model positions in DNA that do not change over time (Shoemaker and Fitch 1989). BI was performed using MrBayes software (Ronquist et al. 2012), running the dataset for 3 × 107 generations, with Markov chains sampled every 1000 generations, and discarding the initial 25% of generations as burn-in. Convergence and effective sample size (ESS) values were assessed using a plugin in Geneious version 7.1.9. The dataset was also subjected to maximum likelihood (ML) analysis using Randomized Accelerated Maximum Likelihood (RAxML) (Stamatakis 2006), with the GTR + G model of evolution and 10,000 bootstrap pseudoreplicates. In this model (GTR + G), the frequency of each nucleotide, as well as any substitutions, are specifically rated, taking into account the rate of variation across sites (Arenas 2015). Trees generated from analyses conducted in Geneious were edited using FigTree (http://tree.bio.ed.ac.uk/software/figtree).

3.2.3 Dermal denticles of all three megamouth sharks from Brazil

Skin samples were obtained from the three megamouth shark specimens from the Brazilian coast. The first record refers to a juvenile male captured off the coast of the State of São Paulo (MOVI 50260). A total of 16 skin sample points were collected following the methodology of Yano et al. (1997). The second record refers to an adult male that was stranded on the coast of the State of Rio de Janeiro. One skin sample was taken from the dorsal trunk, close to the head. The third record refers to the juvenile male described above. Five skin samples were taken from the trunk (the precise location of the samples could not be determined, as they were obtained from a portion of the specimen). Two points were designated as dorsal (blue-black) and ventral (white), based on skin coloration and the presence of a vertebral column fragment. The other three points were obtained from intermediate-colored skin zones with a gradient of light gray and one point with patches of light brown (Fig. S1). The samples were analyzed using scanning electron microscopy (SEM) to examine the surface morphology of the dermal denticles. To prepare the samples for analysis, they were dehydrated in an increasing ethanol series (70%, 90%, and 100%) for 40min at each step, followed by critical point drying using a K850 Critical Point Dryer. The dried samples were fixed onto aluminum stubs with double sided carbon tape and sputter covered with 20nm of gold using a Quorum Q150T ES instrument. Images were obtained with a Quanta FEG 450 SEM (Thermo Fisher) and an Inspect S50 SEM (FEI) at 20 kV. Additionally, the dermal denticles of the megamouth shark from Rio de Janeiro were visualized under a stereomicroscope (Stemi 508-Zeiss).

Morphological identification and nomenclature of dermal denticles were based on Reif (1985), Taylor et al. (1983), Yano et al. (1997), Dillon et al. (2017), and Duchatelet et al. (2020). Dermal denticle morphometric measurements were performed using ImageJ software (Schneider et al. 2012), including crown length and width, cusp length and width, denticle density, and surface coverage percentage. All measurements were taken from denticles with preserved features.

3.3 Results

The third occurrence record for Brazil On the afternoon of September 10, 2018, fishers found a megamouth shark specimen floating off Pedra do Sal Beach, Parnaíba, in the State of Piauí, Brazil (2°48′28.4″S 41°43′19.8″W). The juvenile male megamouth shark measured 170 cm in total length. Reddish patches were visible on ventral side of the specimen, which may have appeared either before or after death; however, no signs of swelling were observed (Fig. 2a, b). Overall, the specimen appeared relatively “fresh,” suggesting a recent death, with the skin coloration and eyes remaining well-preserved (Fig. 2c–f). According to the fishers, the animal had been dead for only a few hours and showed bite marks of cookiecutter sharks, *Isistius brasiliensis* (Quoy and Gaimard, 1824).

Fig. 2 Juvenile male megamouth shark found floating off Pedra do Sal Beach, Parnaíba, Piauí, Brazil, on September 10, 2018. Dorsal (**a**) and ventral views (**b**), an overview of the opened mouth with the upper jaw protruding (**c** - **d**), and lateral view of the specimen (**e** - **f**). Images reproduced from Costa (2018) and Pereira (2018)

3.3.1 DNA analysis for the third occurrence record

The ND2 sequence obtained (1043 bp) exhibited BLAST identities ranging from 97.3 to 100% with three other megamouth shark DNA sequences deposited in GenBank [U91430.1, 97.3%; LC647029.1, 99.9%; and NC_021442.1, 100%]. The match between the specimen examined in the current study and the megamouth shark sequences from GenBank, as indicated by BLAST analyses, were further supported by both Bayesian and maximum likelihood phylogenetic analyses. Specifically, the examined specimen clustered within a clade consisting exclusively of megamouth shark individuals (Fig. 3).

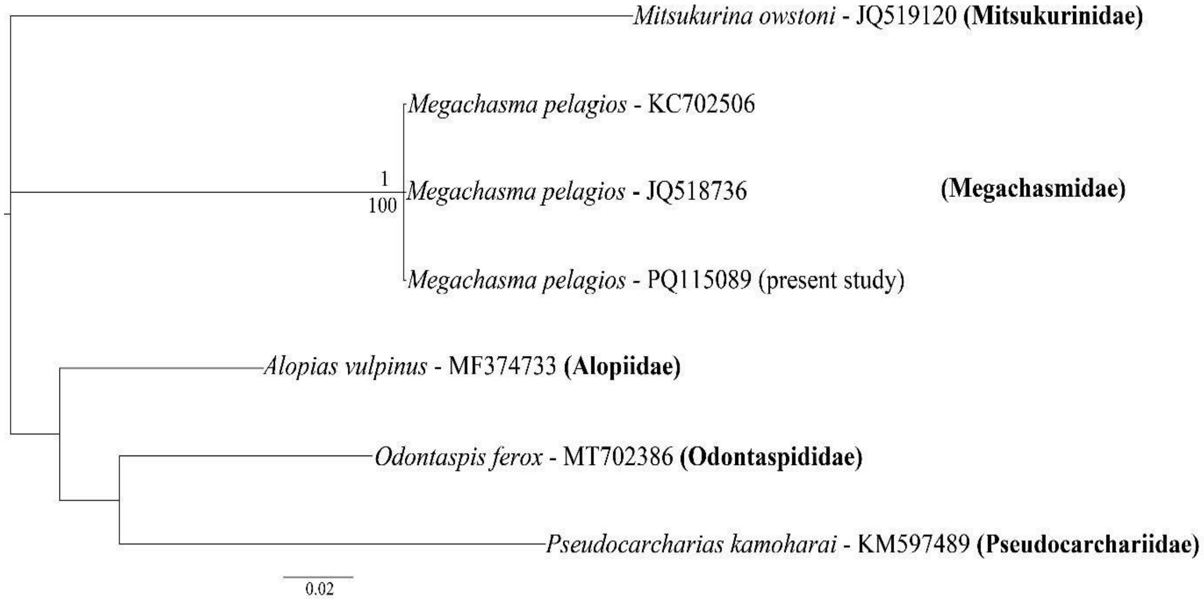

Fig. 3 Clade consisting of conspecific mtDNA ND2 gene sequences retrieved from GenBank for the megamouth shark, supplemented by a sequence from a single specimen collected off the coast of Piauí, Northeastern Brazil, Equatorial Southwest Atlantic, obtained in this study. The Bayesian tree was constructed from a dataset of mtDNA ND2 (1043 bp) sequences using the following evolutionary models: HKY+I, HKY+I, and HKY for the three ND2 partitions. A Posterior Bayesian probability (BP) is indicated above the branch with sufficient support. The same topology was obtained through maximum likelihood (ML) analysis using the GTR+G model of evolution. A bootstrap value for ML is displayed below the branch with sufficient support.

3.3.2 Dermal denticles of all three megamouth sharks from Brazil

The five skin samples from the trunk areas of the megamouth shark from the coast of Piauí presented five different dermal denticle shapes (Fig. 4; Table S1). All denticles were imbricated, with two specific degrees of overlap: (a) closely imbricated denticles show the entire cusps or posterior portion overlapping the anterior portion of adjacent denticles and (b) slightly imbricated show the tips of central or lateral cusps or a combination of them. On the dorsal view of the specimen, the dermal denticles were slightly imbricated, with moderate density (17.78 denticles/mm^2) and coverage (67.16%). The denticles displayed lanceolate-shaped crowns featuring a central longitudinal ridge and two lateral longitudinal ridges. Each ridge extended from the base towards well-defined cusps: one central and two laterals (Fig. 4a). The central cusp was larger (length, 95.02 ± 14.61 µm; width, 130.60 ± 8.73 µm) than the lateral ones (length, 8.13 ± 2.53 µm; width, 26.57 ± 5.52 µm). On the ventral view, the denticles were slightly imbricated, with a density of 11.8 denticles/mm^2 and a coverage of 62.18%. These denticles featured lanceolate-shaped crowns showing a central longitudinal ridge and two lateral longitudinal ridges. The central and lateral ridges extending from the base to the apex connect, forming a single cusp (Fig. 4b). Other dermal denticles, obtained from three intermediate-colored skin zones, exhibited four crown shapes. The first type consisted of slightly imbricated denticles, with a density of 9.65 denticles/mm^2 and a coverage of 71.63%. The denticles featured a drop shaped crowns with a central cusp and a central longitudinal ridge, along with two lateral longitudinal ridges originating at the base and extending towards the apex (Fig. 4c). The second type consisted of slightly imbricated denticles, with a density of 7.75 denticles/mm^2 and a coverage of 88.76%. The denticles displayed rounded, knob-shaped crowns without cusps, and either four poorly defined ridges or none. When present, the ridges originated at the base of the crown, radiating outward, ending before reaching the posterior margin (Fig. 4d). The third type consisted of closely imbricated denticles, with a density of 19.72 denticles/mm^2 and a coverage of 75.37%. The denticles exhibited lanceolate-shaped crowns, similar to the dermal denticles on the dorsal view of the specimen. These crowns featured a central longitudinal ridge and two lateral longitudinal ridges extending from the base to the apex, each ending in one central cusp and two lateral cusps, with the central cusp larger than the lateral ones (Fig. 4e). The central cusp was significantly larger (length, 112.54 ± 15.75 µm; width, 118.92 ± 13.09 µm) than the lateral ones (length, 11.54 ± 2.74 µm; width, 21.89 ± 12.56 µm). The fourth type consisted of slightly imbricated denticles with a density of 17.73 denticles/mm2 and a coverage of 43.99%. The denticles displayed a rounded, knob-shaped crowns without cusps. These crowns featured a central longitudinal ridge and two lateral longitudinal ridges or four radiating ridges. The ridges originate at the base of the crown, ending before reaching the posterior margin (Fig. 4f).

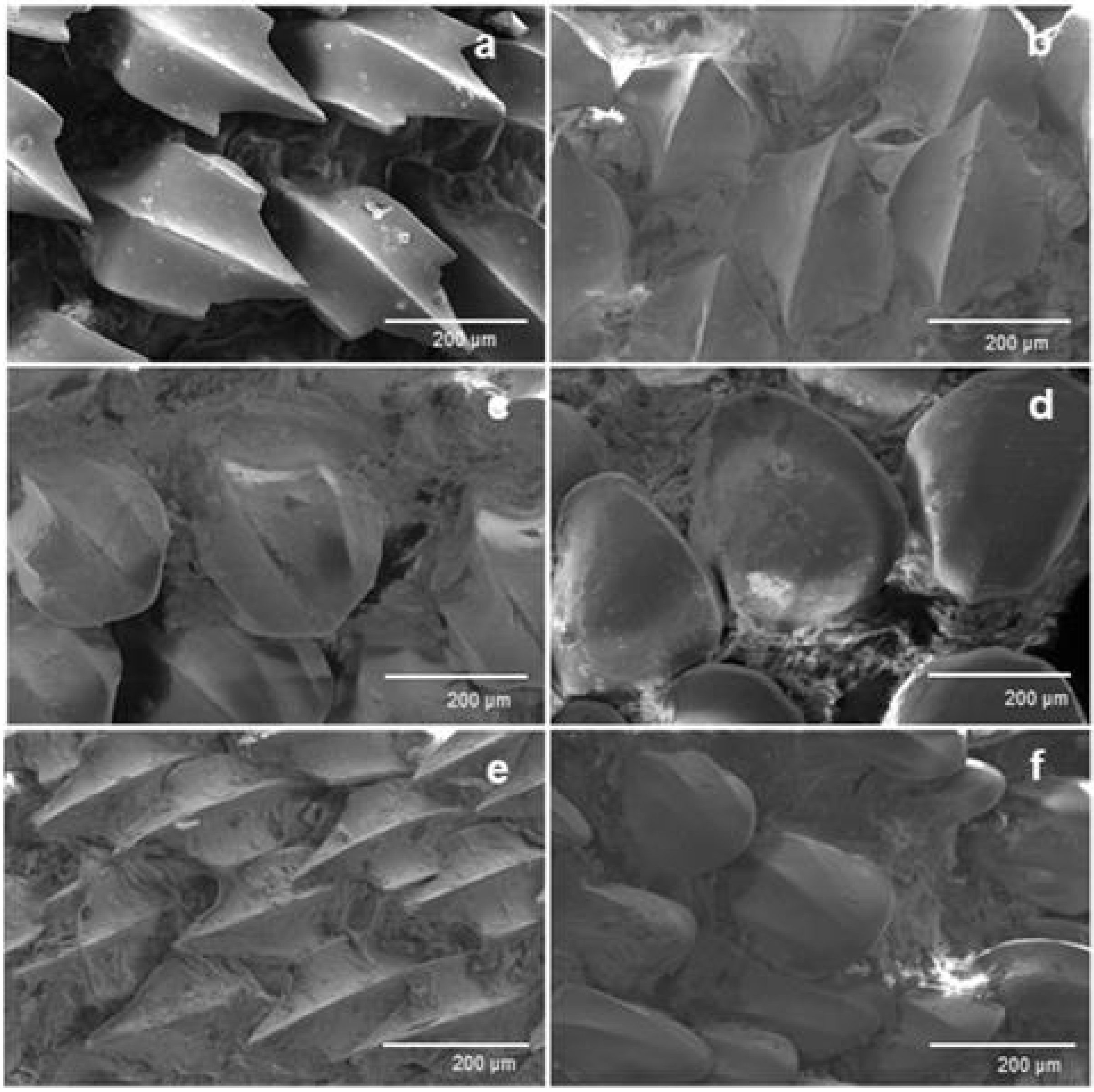

Fig. 4 Scanning electron microscopy images of dermal denticles from a juvenile male megamouth shark (170 cm TL) found floating off the coast of the State of Piauí, Brazil, on September 10, 2018. Dermal denticles from the dorsal (**a**) and ventral (**b**) sides. Dermal denticles from intermediate-colored skin zones are displayed in **c**, **d**, **e**, and **f**.

The juvenile specimen from the coast of São Paulo exhibited six distinct areas of dermal denticles with morphological differences compared to those previously described (Fig. 5; Table S1). The der mal denticles of the caudal peduncle were loosely spaced, without contact with neighboring denticles, with a density of 7.49 denticles/mm^2 and a cover age of 53.52% from upper side, and density of 12.86 denticles/mm^2, and a coverage of 45.12% from lower side. The denticles featured rounded and drop-shaped crowns with a central longitudinal ridge and two lateral longitudinal ridges, originating at the base of the crown, ending before reaching the posterior margin, without cusps (Fig. 5a, b). The dermal denticles on the dorsal and ventral sides of the pelvic fin were slightly imbricated, with some overlaps between the crowns, similar to those on the trunk. The density on the dorsal surface was 25.54 denticles/mm2 and a coverage of 52.87%. The crowns had a central longitudinal ridge and two lateral longitudinal ridges, with three well-defined cusps (Fig. 5c, d). The central cusp was larger (length, 80.85 ± 7.13 µm; width, 52.13 ± 7.88 µm) than the lateral ones (length, 18.57 ± 10.43 µm; width, 19.83 ± 6.10 µm). The dermal denticles' on the head were closely spaced, with neighboring denticles nearly touching at their edges. The denticles on the left cheek (Fig. 5e) and the center of the lower jaw (Fig. 5f) featured drop-shaped crowns with a central cusp, a central longitudinal ridge and two lateral longitudinal ridges, originating at the base and extending towards the apex. Oral denticles inside the mouth were closely spaced, at the center of the palate, with a density of 50.58 denticles/ mm^2 and a coverage of 63.86%. The denticles exhibited two shapes, distributed variably across the palate (Fig. 5g). One crown exhibited a rounded shape without ridges or cusps, while the other had a central ridge and two lateral longitudinal ridges, with both a central and lateral cusp. The central cusp was larger (length, 46.37 ± 11.11 µm; width, 72.90 ± 11.04 µm) than the lateral ones (length, 23.98 ± 12.31 µm; width, 32.31 ± 9.89 µm). The cusps were broader than tall, with the central cusp remaining longer than the lateral cusps. The rounded crown was less numerous than the tricuspid crown. An epithelial pore was observed on the palate (Fig. 5h). The dermal denticles from the other ten areas observed in the juvenile from São Paulo did not differ from the descriptions for adults (Fig. S2; Table S1).

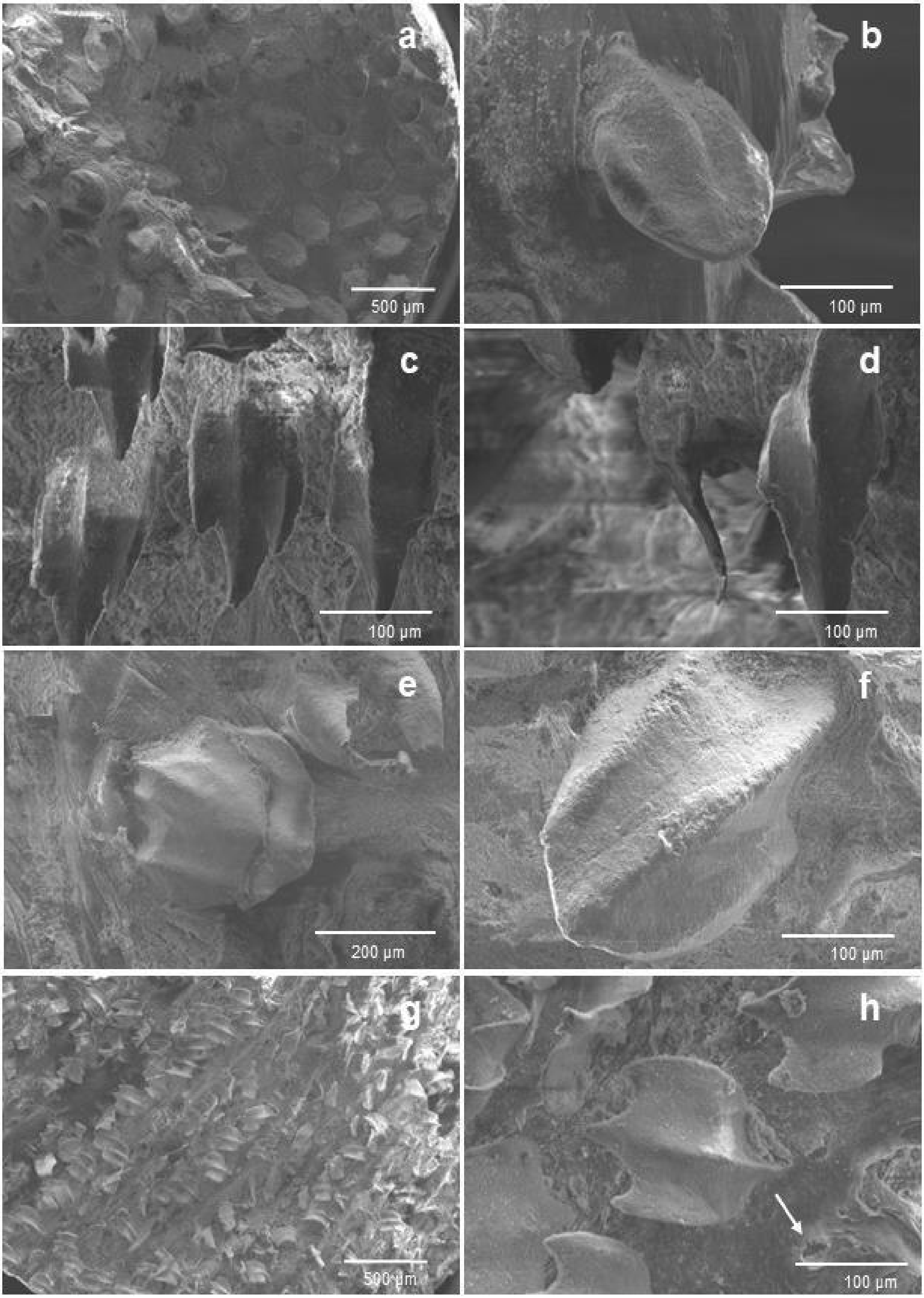

Fig. 5 Scanning electron microscopy images of six sample points of a juvenile male megamouth shark (190 cm TL) captured off the coast of the State of São Paulo, Brazil, on September 18, 1995. Dermal denticles from the upper (**a**) and lower (**b**) caudal peduncle of

the trunk, and the dorsal surface of the pelvic fin (**c** and **d** - lateral view). Dermal denticles from the head: left cheek (**e**) and center of the lower jaw (**f**). Oral denticles from the center of the palate are shown in (**g**) and (**h**). The detail indicated by the arrow highlights an epithelial pore on the palate.

The specimen from Arraial do Cabo, Rio de Janeiro exhibited dermal denticles similar to those described for the lateral trunk and fin regions (Figs. 6a, 7a; Table S1). The dermal denticles were grouped in patches, which were separated by skin lines without denticles located on the dorsal trunk (Fig. 6b, 7b). The dermal denticles were loosely spaced, with tri angular crowns featuring central and lateral longitudinal ridges that connected posteriorly, forming a single cusp (Fig. 7c, d). The crowns of this specimen were larger than the other two specimens (length, 452.88 ± 40.09 µm; width, 273.63 ± 24.07 µm). The density of denticles was 7.77 denticles/mm^2, with coverage reaching 74.58%. Additionally, pigment cells were observed within the denticles (Fig. 6c, d). Signs of wear, such as broken or worn cusp tips, were noted in some denticles of all three megamouth shark specimens, but their characteristics remained identifiable. Although no conclusive evidence of denticle replacement was observed, further analysis is needed to confirm or clarify this aspect.

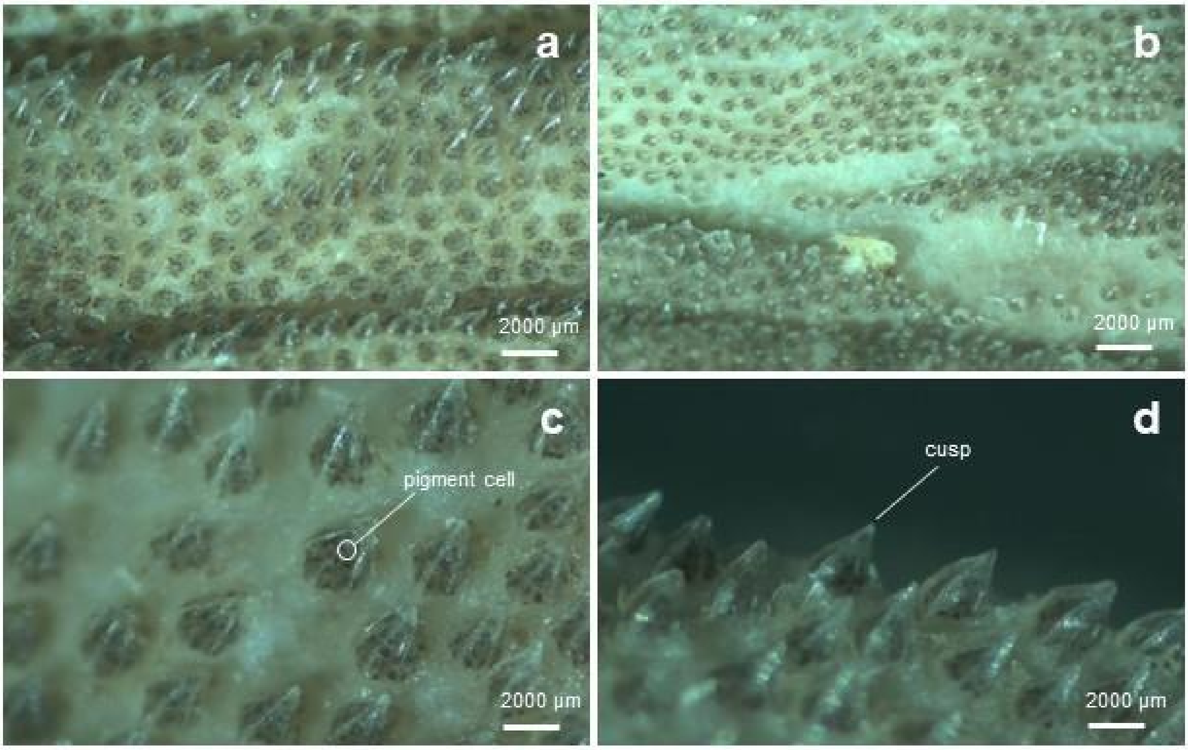

Fig. 6 Stereomicroscope images of dermal denticles from an adult male megamouth shark (539 cm TL) stranded on the coast of Rio de Janeiro, Brazil, on July 9, 2009. Overview of dermal denticles (**a**), showing areas without denticles (**b**). Presence of pigment cells within

the dermal denticles (**c**). Detail of the crown of a dermal denticle with a single cusp (**d**).

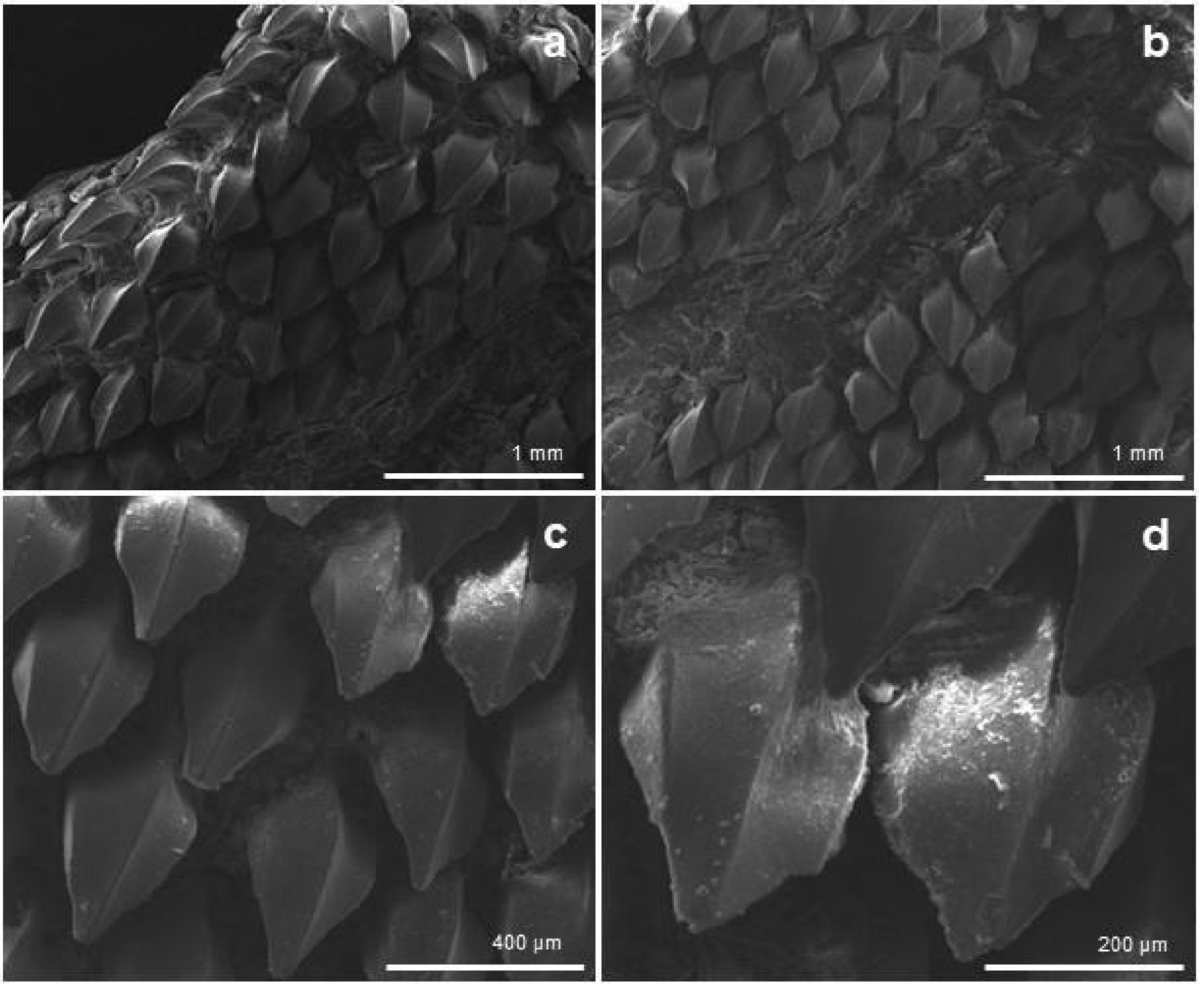

Fig. 7 Scanning electron microscopy images of the dermal denticles of an adult male megamouth shark (539 cm TL) stranded on the coast of Rio de Janeiro, Brazil, on July 9, 2009. Overview of dermal denticles on the dorsal trunk, near the first dorsal fin, close to the head (**a**), and a skin line without denticles in the center (**b**). Close-up of denticle crowns, highlighting their morphology (**c**) and surface texture (**d**).

3.4 Discussion

3.4.1 The third occurrence record for Brazil

The megamouth shark specimen from Piauí, Brazil, described in the present study, is the small est for the Atlantic Ocean. Measuring 170 cm in total length, this specimen was likely a neonate. A relatively recent record (November 14, 2023) of a pregnant female megamouth shark washed ashore in the Philippines carrying seven presumably near-term embryos measuring between 165 and 183 cm TL (Roberts 2023), therefore supporting this species' suggested birth size (>170 cm; Ebert et al. 2021). Prior to this study, the smallest specimen recorded in the Atlantic was 190 cm TL and was considered a juvenile (Amorim et al. 2000), as the smallest mature males measured ~ 400 cm TL (Watanabe and Papastamatiou 2019). Although this specimen is not a neonate, its total length suggests it is a juvenile in the early stages of growth. The megamouth shark occurrences in the Atlantic (Séret 1995; Amorim et al. 2000; Diez et al. 2022; present study) and the Indian Ocean (White et al. 2004; Fernando et al. 2015; van Beuningen et al. 2023) predominantly comprise individuals smaller than 200 cm TL (Yu et al. 2021). According to these authors, the presence of free-swimming individuals below this size in certain areas of the oceans may indicate potential nursery grounds. However, further studies are needed to better understand the ecological significance and extent of such potential nursery areas. There are only three records of adult and subadult megamouth shark in the Atlantic Ocean, one of which refers to a male from Arraial do Cabo, Rio de Janeiro, measuring 539 cm TL (Moura et al. 2015). This specimen can be considered sexually mature, as sexual maturity for this species is reached at approximately 400 cm TL for males and 500 cm TL for females (Nakaya 2010; Watanabe and Papastamatiou 2019). The other specimens—a male measuring 380 cm TL from Liberia (Environmental Justice Foundation 2020) and a female measuring 457 cm TL from Cabo Rojo, Puerto Rico (Rodriguez-Ferrer et al. 2017)— were considered subadults.

While records of the megamouth shark south of 27°S are rare (Watanabe and Papastamatiou 2019; Yu et al. 2021), there is anecdotal evidence of a ninth occurrence of this species in the Southwest Atlantic Ocean. On June 2007, the fishing crew of the FV "Yamaya III" reported an approximately 3–4 m TL specimen that was incidentally caught by a pelagic longline off the State of Santa Catarina, Southern Brazil (28°58′17″ S 46°26′12″ W) (J. Soto, unpublished data). The fishers described the specimen as notably soft, flexible, and lightweight, characteristics that led them to call it a "soft shark," with dorsal blueish and ventral white coloration, and undeveloped teeth. When shown images of a megamouth shark, they confirmed the species identification (J. Soto, unpublished data). The specimen was reported to have been released alive, without being photographed or having samples collected (J. Soto, unpublished data). Although this record is based solely on anecdotal data, it could represent the southernmost occurrence of the species in the Atlantic Ocean, underscoring the need for attention to this region.

3.4.2 DNA analysis for the third occurrence record

The megamouth shark has a distinctive appearance, making it relatively easy to identify visually, which combined with molecular identification confirms the record from Pedra do Sal Beach, Parnaíba, Piauí, Brazil, in 2018 as a megamouth shark. It is worth highlighting that, despite the disparate geo graphical origins of the analyzed megamouth shark specimens [KC702506 from the Western Pacific/Tai tung, Taiwan (Chang et al. 2014); JQ518736 from the Eastern Pacific/California, USA (Naylor et al. 2012b); and PQ115089 from the Southwest Atlantic/Piauí, Brazil (present study)], they showed 100% identity in the BLAST analysis for the complete ND2 gene. This is consistent with the sharing of mitochondrial haplotypes between the latitudinal extremes of the Pacific and the Atlantic Oceans (Liu et al. 2018).

3.4.3 Dermal denticles of all three megamouth sharks from Brazil

The dermal denticles of the specimen from Piauí differ slightly on arrangement from those of adults. The denticles in the skin sample from the trunk of this specimen are less spaced in comparison to adults, as in Taylor et al. (1983), Yano et al. (1997), and Duchatelet et al. (2020), and to the specimen from Arraial do Cabo. The transition to a loosely spaced arrangement could be related to increased age. An opposite pattern has been observed in the denticles from the trunk of an ontogenetic series of the Portuguese dog fish, *Centroscymnus coelolepis* Barbosa du Bocage and de Brito Capello, 1864 (Vaz et al. 2023). Dermal denticles' arrangement can differ during development (Reif 1978, 1985), and several studies have identified variations in their arrangement and shape throughout ontogeny (Hubbs and Taylor 1969; Paig-Tran et al. 2013; Ferrón et al. 2018; Popp et al. 2020; Macías-Cuyare and Oddone 2022; Vaz et al. 2023).

In the present study, dermal denticle morphology in certain areas of the juvenile megamouth shark specimen from São Paulo differed from that of adults. These differences may be associated with specific morphological transformations of dermal denticles that occur during ontogeny (Reif 1985; Vaz et al. 2023). Although the crowns of the dermal denticles on the caudal peduncle are rounded, simi lar to those in adults, the shape and number of ridges differ. In adults, the crowns are knob-shaped with 5 to 9 radial ridges (Yano et al. 1997), whereas in the juvenile, they are drop-shaped, with a reduction to 3 ridges arranged longitudinally (present study). The crowns of the denticles on the cheek and the center of the lower jaw have fewer ridges. In adults, the crowns may have 5 to 8 lateral ridges, including a cusp on the crowns at the center of the lower jaw (Yano et al. 1997). Furthermore, the crowns on the cheek of the left side of the head are knob-shaped in adults (Yano et al. 1997), while those of juvenile are drop-shaped (present study). The crowns on the dorsal and ventral sides of the pelvic fin are very similar to those of adults, except for the cusps, which are well-developed with three elongated tips.

Dermal denticle morphology is related to various body functions in sharks. Reif (1985) identified five functions: drag reduction, abrasion strength, defense, bioluminescence, and generalized functions. Dillon et al. (2017) further subdivided the morphotype of abrasion strength into “abrasion strength” and “ridged abrasion strength” considering the hydrodynamic function attributed to ridged crowns, as proposed by Raschi and Tabit (1992). Among these functions, the megamouth shark has been noted to exhibit abrasion strength on the head, possibly associated with feeding behavior (Yano et al. 1997). Duchatelet et al. (2020) identified other potential functions for megamouth shark denticles, such as abrasion or ectoparasite protection (on the white band, dorsal side, and pectoral fin), hydrodynamic properties (on the tongue, pectoral fin, dorsal and ventral sides), and drag reduction (on the oral floor and palate). Dermal denticles associated with ridged abrasion strength exhibit well-defined ridges that enhance their ability to resist physical wear and may also provide hydrodynamic benefits (Dillon et al. 2017; Raschi and Tabit 1992). Although the dermal denticles of the megamouth shark are not specialized as those of fast-swimming sharks (e.g., mako sharks), the increased number of ridges observed in the denticles of the caudal peduncle, center of lower jaw, and cheek from juvenile to adult may suggest a functional hydrodynamic adaptation. Even in a slow-swimming species (Nelson et al. 1997; Feld et al. 2019), this difference may reflect a role in optimizing hydrodynamic efficiency and resistance to physical wear, as noted as interbranchial dermal denticles of other shark species (Gabler-Smith et al. 2021). The observations reported here suggest a transition in the dermal denticles of the megamouth shark, characterized by a simplification in denticle shape and increase in number of ridges from juvenile to adults. Such changes may be linked to a shift in the function of the denticles, combining characteristics that influence both swimming efficiency and protection. The relatively uniform cover age and spacing of dermal denticles in juveniles may enhance protection against ectoparasites and create controlled turbulence, which could reduce drag and optimize swimming efficiency at moderate speeds (Wen et al. 2015). These characteristics, alongside the shark’s slow-swimming nature and vertical migrations, suggest that its denticles morphology and arrangement serve multiple functional roles, balancing hydrodynamic and protective demands.

Acknowledgments We would like to thank the fishers who donated the megamouth shark sample for research purposes. Our gratitude also extends to Paulo Cascon for providing infra structure support at the Experimental Zoology Lab at the Federal University of Ceará (UFC) including specimen handling and storage; to the Analytical Center (Central Analítica) at UFC for scanning electron microscopy; to the Embrapa Tropical Agroindustry for granting permission to conduct all DNA analyses; and to Bibiana Lessa from Museu Oceanográfico Univali (MOVI) for her assistance in taking tissue samples. We also thank the Graduate Program in Systematic Use and Conservation of Biodiversity (PPGSis) for all the necessary support to conduct this research. We would like to express our sincere gratitude to Victor Távora for his insights and assistance with the morphometric analyses of dermal denticles. We also thank Getulio Rincon (UFMA), Maria Cristina Oddone (FURG), and two anonymous reviewers for their invaluable comments and suggestions to the manuscript version.

Author contributions

LGX: Conceptualization, Investigation, Data Curation, Methodology, Writing – original draft, Writing – reviewing and editing.
AKML: Methodology, Writing – reviewing and editing.
ECM: Conceptualization, Methodology, Writing – reviewing and editing.
SS: Methodology, Writing – reviewing and editing.
RAH-D: Methodology, Writing – reviewing and editing.
PNB: Methodology, Writing – reviewing and editing
GMOA: Methodology, Writing – reviewing and editing.
JMRS: Methodology, Writing – reviewing and editing.
JEPF: Conceptualization, Methodology, Writing – reviewing and editing.
PC: Conceptualization, Supervision, Investigation, Writing – reviewing and editing.
VVF: Conceptualization, Supervision, Investigation, Methodology, Writing – reviewing and editing.

Funding This research was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Brazilian Ministry of Education, through a PhD student fellowship awarded to LGX and a postdoctoral fellowship awarded to JEPF (PNPD process number

88887.466769/2019–00); and by the Fundação Cearense de Apoio ao Desenvolvimento Científico e Tecnológico (FUNCAP) through a visiting researcher grant to PC.

Data availability The dataset generated in this research is available within the article and its electronic supplementary materials.

Declarations

Ethical approval Specimen sampling complied with the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) animal welfare laws, guidelines, and policies (SISBio license - number 69746/1).

Conflict of interest The authors declare no competing interests.

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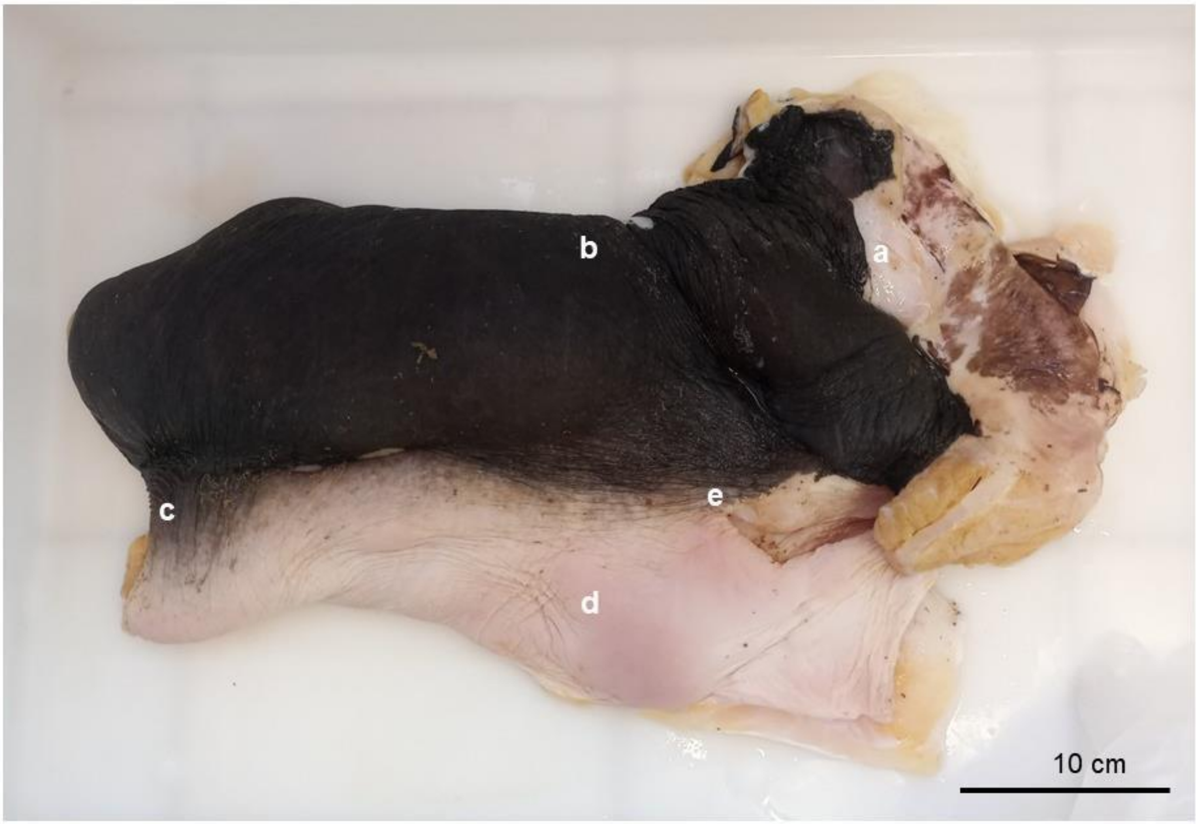
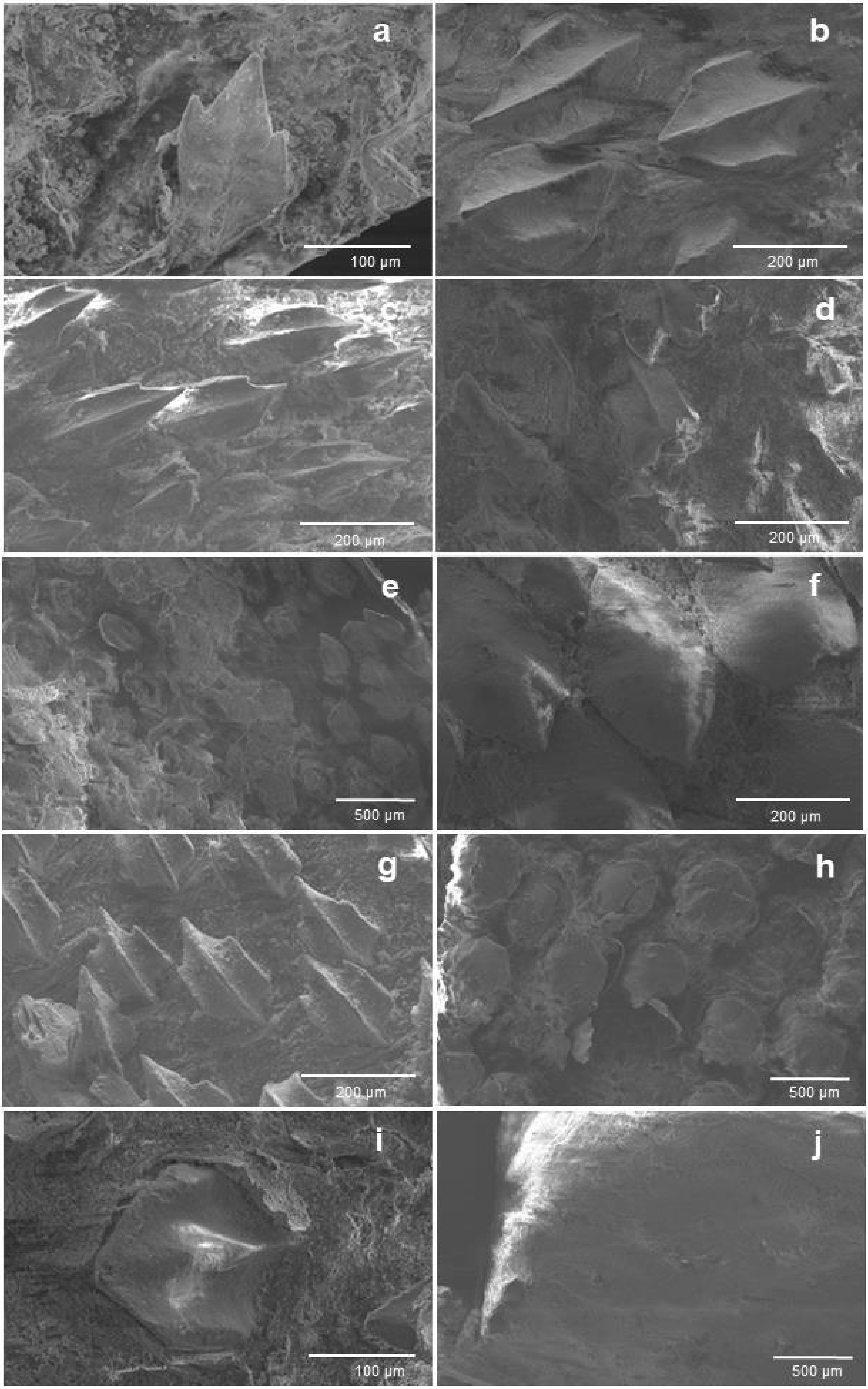
3.6 Supplementary material



FigS1. Five skin samples of a megamouth shark (*Megachasma pelagios*) (male, 170 cm TL) found floating off the coast of the state of Piauí, Brazil, on September 10, 2018. The samples include dorsal side (**b**), ventral side (**d**), and intermediate coloration zones of the skin (**a**, **c** and **e**). Scale bar: 10 cm


a
100 µm
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FigS2. Dermal denticles from ten areas of the juvenile megamouth shark from São Paulo, Brazil. Trunk areas: below the first dorsal fin (**a**), abdomen between the pectoral fins (**b**), and abdomen before the pelvic fins (**c**). Fin areas: dorsal surface of the pectoral fin (**d**), ventral surface of the pectoral fin (**e**), anterior margin of pelvic fin (**f**), and ventral surface of the pelvic fin (**g**). Head areas: interorbital region (**h**) and before the first gill opening (**i**). Inside the mouth area: upper side of the center of tongue (**j**). Scale bar: a, i (100 µm); b, c, d, f, g (200 µm); e, h (500 µm)

4 CAPÍTULO III: Stable isotopes, metals, and metalloids of the youngest Megamouth Shark, *Megachasma pelagios*, from the Western Tropical Atlantic Ocean

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Abstract

This study presents the first stable isotope analysis and evaluation of metals and metalloids in a neonate Megamouth Shark from the Western Tropical Atlantic Ocean. Muscle tissue analysis revealed low values of $\delta^{15}N$ (5.93‰) and $\delta^{13}C$ (-18.66‰), possibly reflecting maternal nutritional investment and foraging in oligotrophic tropical waters. Among the 65 elements evaluated, 41 were reported for the first time for the species. Mercury levels were low (0.015 $mg \cdot kg^{-1}$), indicating the early life stage of the specimen and minimal environmental bioaccumulation. On the other hand, high concentrations of aluminum (116.32 $mg \cdot kg^{-1}$) and lead (0.109 $mg \cdot kg^{-1}$) suggest maternal transfer via yolk or uterine fluids. Essential elements (Fe, Ca, K, Mg, and Zn) showed elevated levels, corroborating rapid neonatal growth. Arsenic level (4.57 $mg \cdot kg^{-1}$) was close to the specimen from the Subtropical Atlantic Ocean and higher compared to the population from the Pacific Ocean, indicating a possible regional variation. This study provides the first comprehensive metal and metalloid assessment and $\delta^{13}C$ and $\delta^{15}N$ stable isotope signature for a Megamouth Shark neonate in the Tropical Atlantic Ocean, filling a significant gap in knowledge about filter-feeding elasmobranchs.

Keywords Ecotoxicology, Brazil, Filter-feeding, Chondrichthyes, Elasmobranch, Megachasmidae

4.1 Introduction

The Megamouth Shark (*Megachasma pelagios* Taylor, Compagno and Struhsaker 1983) is a large and enigmatic elasmobranch that was discovered relatively recently in 1976 off the coast of Hawaii (Taylor et al., 1983). Although the species exhibits a circumtropical distribution, with more than 273 documented occurrences of this species across three oceans (Florida Museum of Natural History, 2024, Bueno et al., 2025; Tian et al., 2025), sightings remain rare, particularly in the Atlantic Ocean. Currently, there are only eight recorded sightings in this basin, which include occurrences in Senegal, Liberia, Gabon, Mauritania, Puerto Rico, and three in Brazil (Séret, 1995; Amorim et al., 2000; Moura et al., 2015; Rodriguez-Ferrer et al., 2017; Environmental Justice Foundation, 2020; Diez et al., 2022; Xavier et al., 2025). Most of these records are of stranded animals or accidental captures, which limits our understanding of the species' biology (Watanabe and Papastamatiou, 2019).

The Megamouth Shark is pelagic and filter-feeding (Taylor et al., 1983; Nakaya et al., 2008; Tomita et al., 2011), just like the Whale Shark, *Rhincodon typus* Smith, 1828, and the Basking Shark, *Cetorhinus maximus* (Gunnerus, 1765). Nevertheless, little is known about the Megamouth Shark's feeding behavior (Watanabe and Papastamatiou, 2019). Stomach content analyses have identified the presence of euphausiids, copepods, and gelatinous organisms (Lavenberg and Seigel, 1985; Yano et al., 1997; Nakaya et al., 2008; Tomita et al., 2011; Sawamoto and Matsumoto, 2012) as part of its diet. The shark functions as a primary or secondary consumer of planktonic prey items (Yu et al., 2025). This species exhibits a daily vertical migration pattern, remaining in mesopelagic waters (400 – 700 m) during the day and emerging to the epipelagic zone (0 – 50 m) at night, following the movement of zooplankton (Nelson et al., 1997; Clerkin et al., 2024).

Due to its elusive deep-water nature, the study of the trophic ecology of this species is challenging, which in turn demands the use of alternative research techniques. One such technique is stable isotope analysis (SIA), which is currently considered an alternative tool for studying trophic ecology. Stable isotope ratios of nitrogen ($^{15}N/^{14}N$) can be used to study diet, foraging ecology, trophic position, and food webs in various elasmobranch species. Stable isotope ratios of carbon ($^{13}C/^{12}C$) on the other hand, can be used to assess habitat use and movement patterns in these animals (Hussey et al., 2012). In contrast, only one study has described isotopic composition of carbon and nitrogen in the Megamouth Shark. This study was based on an adult individual male found stranded in Arraial do Cabo, Rio de Janeiro, Southeastern Brazil, and showed that isotopic composition corroborates with previous stomach content analysis (Berra and Hutchins, 1990; Yano et al., 1997; Nakaya et al., 2008; Tomita et al., 2011; Sawamoto and Matsumoto, 2012) describing this species as a deep water zooplanktivore (Moura et al., 2015).

The trophic ecology of an organism is important because feeding is the main incorporation route for many trace elements, including mercury, arsenic and other lipophilic contaminants. Therefore, SIA is often used as complementary data in metal contamination assessments (Madgett et al., 2021; Fragoso et al., 2024; Hauser-Davis et al., 2024; Campos et al., 2024). Still, only two studies have quantified metal and metalloid levels in the Megamouth Shark worldwide. The first one (Moura et al., 2015) described contamination level profile of 21 trace elements in the stranded adult individual from Southeastern Brazil. The other study (Ju et al., 2021) described the contamination profile of 24 trace elements in 27 individuals from Taiwan showing that feeding behavior could be associated with contamination levels of Hg, As, Cu, Ti, Al, and Fe. Interestingly, both studies focused on adult and sub-adults and, thus, information on metal accumulation and isotopic composition of juvenile and neonate individuals remains lacking. Given this is a viviparous species, aspects of feeding ecology, through stable isotope analysis, and ecotoxicology, based on the determination of metals and metalloids, obtained from neonates may reflect maternal characteristics. Moreover, it may reflect the characteristics of the environment where the mother was and fed, given that the species may exhibit resident behavior (Clerkin et al., 2024). Furthermore, filter-feeding elasmobranchs are increasingly recognized as bioindicator species for marine pollution on a global scale (Fossi et al., 2014; Boldrocchi et al., 2020, 2022). Despite this relevance, data on metal and metalloid levels in filter-feeders from the Tropical Atlantic remain scarce compared to the North Pacific (Boldrocchi et al., 2023).

In 2018, a dead male Megamouth Shark was found by fishers floating off Pedra do Sal beach, Parnaíba, Piauí, Brazil (Xavier et al., 2025). This specimen was the smallest Megamouth Shark found in the Atlantic Ocean and could be a neonate based on its length (170 cm). This rare specimen opened an opportunity to investigate gaps of knowledge involving this species. In this context, the goal of the present study was to quantify the stable isotope of carbon and nitrogen and metal and metalloids composition of the youngest individual of the Megamouth Shark from the Atlantic Ocean. Considering the absence of an established diet in neonates, we hypothesize that the isotopic composition of this individual reflects the diet and feeding location of its mother, indicating potential maternal transfer of chemical elements and providing an isotopic signature of the species' reproductive area.

4.2 Material and Methods

The specimen showed no signs of advanced decomposition, with the skin and eye color well-preserved. A portion of the animal's trunk (~ 6 kg), donated for research, was stored in a freezer and posteriorly transported to the Marine Vertebrate Evolution and Conservation laboratory, Universidade Federal do Ceará, in an insulated container with ice to ensure sample integrity. From this portion of the trunk, two muscle tissue samples were collected from the same region, one to assess the stable isotope of $\delta^{13}C$ and $\delta^{15}N$ and one for metal and metalloid compositions. The samples were washed with distilled water, dehydrated at 50º C for 48 hours.

The sample for stable isotope analysis was ground into a fine powder stored in tin capsules and weighed on a precision analytical balance (17.81×10^3 µg). (Laboratório de Limnologia e Qualidade de Água, UFERSA, BR). The sample was analyzed in triplicate using an isotope ratio mass spectrometer (VisION IRMS) (Elementar Analysensysteme GmbH, Langenselbold, Germany) coupled to an elemental analyzer (vario EL cube) (Stable Isotope Facility service, UC Davis, USA). The isotopic ratio for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) is expressed using the standard delta notation (δ) in parts per thousand (‰) according to the equation: $\delta X=[(Rsample/Rstandard) -1]x1000$, where R is the ratio of the heavy to light isotopes for carbon (^{13}C:^{12}C) and nitrogen (^{15}N:^{14}N). The stable isotope ratio of C and N are reported relative to the Vienna Pee Dee Belemnite and atmospheric N_2 for ^{13}C and ^{15}N, respectively. The analytical errors for reference materials were ±0.06 ‰ for $\delta^{13}C$ and ±0.03 ‰ for $\delta^{15}N$. Lipid extraction was not performed because the C:N ratio (3.14) was below the recommended threshold (3.5, Post et al., 2007).

A Bayesian mixing model (Moore and Semmens, 2008; Moraes and Henry-Silva, 2018) MixSIAR (Parnell et al., 2013; Stock and Semmens, 2016) was used to estimate isotopic relative contribution of the potential prey of the Megamouth Shark. Since stomach content data was not available, $\delta^{13}C$ and $\delta^{15}N$ values were compiled for from the scientific literature ensuring geographical and temporal data correspondence (Table S1). Potential prey groups were selected based on previous analyses of the stomach contents of the Megamouth Shark (e.g., Taylor et al., 1983; Berra and Hutchins, 1990; Yano et al., 1997; Nakaya et al., 2008; Tomita et al., 2011; Sawamoto and Matsumoto, 2012). The diet-tissue discrimination factors (DTDF) for elasmobranch muscle tissue ($\Delta^{13}C$: 0.90‰ ± 0.33 and $\Delta^{15}N$: 2.29‰ ± 0.22) proposed by Hussey et al. (2010) were used. Model convergence was confirmed by ensuring that the Gelman-Rubin diagnostic values for all parameters were below 1.05 (See Table S2). The mixing models were performed with R version 4.4.3 (R Core Team, 2025).

The sample for metal and metalloid analysis, approximately 4 mg, was mixed with 1.0 mL of bidistilled nitric acid (HNO3 - 67% v/v, grade P.AA, Hexis, São Paulo, Brazil) in sterile polypropylene tubes with a capacity of 15 mL. The sample was prepared and left overnight to react (~ 12 hours). After that, the sample was heated at 100ºC for 4h in closed polypropylene tubes to complete decomposition at high pressure and temperature (USP, 2013). After cooling to room temperature, the sample was made up to 10 mL with ultrapure water and analyzed in quintuplicate using an inductively coupled plasma mass spectrometer - NexION 300 ICP- MS (PerkinElmer, USA) (Laboratório de Espectrometria Atômica, PUC-Rio, BR). The instrumental operating conditions of the equipment are presented in Table S3. Furthermore, procedural blanks and two Certified Reference Materials (CRM) such as BCR-668 (mussel tissue) and DORM-2 (fish tissue) were prepared in the same way as sample for control and certification of method accuracy and determined in triplicate. Observed and certified metal and metalloid values and recoveries (%) are depicted in Table 1, expressed as mg.kg^{-1} d. w. (dry weight).

External calibration was performed using a mixed standard solution (Merck IV, multielemental) and rhodium (103 Rh) was added as the internal standard from a concentration of 20 mg L^{-1}. The correlation coefficients of the calibration curves were only accepted when above 0.995. The limit of quantification (LOQ) for each element was calculated according to the National Institute of Metrology, Quality and Technology (Inmetro, 2016), as follows: LOQ = 10 (SD / s), where: SD is the standard deviation of the blank response and *s* is the slope (slope) of the analytical curve. The metal and metalloid concentrations were expressed as wet weight (mg.kg-^{1} w.w.), considering a water loss of 75%.

Table 1 Observed and certified metal and metalloid values and recoveries (%). Data are expressed as mg.kg^{-1} (d. w.).

Element	**EMR-BB422**			**BCR-668**			**DORM-2**		
	Certified value	Observed value	Recovery (%)	Certified value	Observed value	Recovery (%)	Certified value	Observed value	Recovery (%)
Ag	-	-	-	-	-	-	0.041 ± 0.013	0.034 ± 0.008	83.3
As-total	12.7 ± 0.7	12.14 ± 1.73	95.6	7.1 ± 0.5	6.63 ± 152.11	93.37	18 ± 1.1	14.52 ± 1.19	80.7
Cd	0.008 ± 0.002	0.006 ± 0.002	92.5	0.275 ±0.011	0.24 ± 0.01	87.28	0.043 ± 0.008	0.034 ± 0.008	79.5
Co	-	-	-	0.31-0.36	0.34 ± 0.15	94.6 - 109.88	-	-	-
Cu	1.67 ± 0.16	1.40 ± 0.01	84.0	-	-	-	-	-	-
Fe	9.4 ± 1.4	9.98 ± 0.79	106	84.7-93.5	86.09 ± 41.48	92 - 101.63	-	-	-
Hg-total	0.601 ± 0.03	0.55 ± 0.09	91.2	-	-	-	4.64 ± 0.26	4.038 ± 0.96	87
Mn	0.37 ± 0.03	0.33 ± 0.04	91	-	-	-	-	-	-
Mo	-	-	-	1.99 ± 0.15	2.15 ± 0.32	108.1	-	-	-
Pb	-	-	-	-	-	-	0.065 ± 0.007	0.053 ± 0.11	82.46
Se	1.33 ± 0.13	1.12 ± 0.31	84.3	-	-	-	1.4 ± 0.09	1.103 ± 0.09	78.8
Zn	16 ± 1.1	13.02 ± 2.32	81.4	70.7 ± 0.4	56.17 ± 4.76	79.44	25.6 ± 2.3	18.05 ± 2.16	70.5

4.3 Results

The stable isotope values in the muscle tissue of the Megamouth Shark specimen were $\delta^{13}C$ = -18.66‰ and $\delta^{15}N$ = 5.93‰. The isotopic mixing model (MixSIAR) estimated a diet dominated by zooplankton. The primary contributor was the <64–100µm size class (mean contribution = 19.7%), followed by the 100–200µm size class (16.4%). The 200–500µm size class, which comprised two model groups, showed contributions of 10.1% and 9.9. Contributions from the remaining zooplankton size classes (500µm to >2000µm) were lower, ranging from 5.6% to 6.3%. The euphausiid and gelatinous prey groups were minor contributors, with mean contribution ranges of 2.6–3.9% and 2.7–3.3%, respectively. The proportional contributions of all potential prey are detailed in Table 2, and the model's isospace is shown in Figure 1.

Table 2 Proportional contribution of each potential prey group to the diet of the Megamouth Shark found floating on Pedra do Sal Beach, PI, BR, estimated by the Bayesian isotope mixing model (MixSIAR). Values are presented as mean contribution ± standard deviation (SD), and 95% Credibility Interval (CI).

Potential prey	Taxon Code	N	Size Class/Length	Mean ± SD (%)	95% CI (%)
Zooplanckton	ZOO2	19	<64–100µm	19.7±12.4	0.9 – 44.6
	ZOO3	19	100–200µm	16.4±12.3	0.4 – 43.7
	ZOO1	19	200–500 µm*	9.9±9.3	0.2 – 35.5
	ZOO4	19	200–500µm	10.1±9.5	0.3 – 36.1
	ZOO5	18	500–1000µm	6.3±6.0	0.2 – 21.6
	ZOO6	17	1000–2000µm	6.2±5.5	0.2 – 20.4
	ZOO7	13	>2000µm	5.6±5.0	0.2 – 18.4
Thysanopoda sp.	EUP1	6	4.40 ± 0.64 cm	3.6±3.7	0.1 – 13.7
Euphausiacea	EUP2	50	-	2.6±2.4	0.1 – 9.1
Euphausia gibboides	EUP3	6	1.50 ± 0.11 cm	3.6±3.4	0.1 – 12.1
Euphausia sp.	EUP4	3	1.43 ± 0.13 cm	3.9±4.3	0.1 – 15.4
Euphasiidae sp. 1	EUP5	4	1.5 ± 0.1 cm	2.7±2.6	0.1 – 9.6
Euphasiidae sp. 2	EUP6	3	1.4 ± 0.1 cm	3.4±3.3	0.1 – 11.9
Abylopsis tetragona	GEL1	3	-	3.3±3.2	0.1 – 11.4

Siphonophorae sp.	GEL2	3	-	2.7±2.5	0.1 – 9.4

*mainly copepods

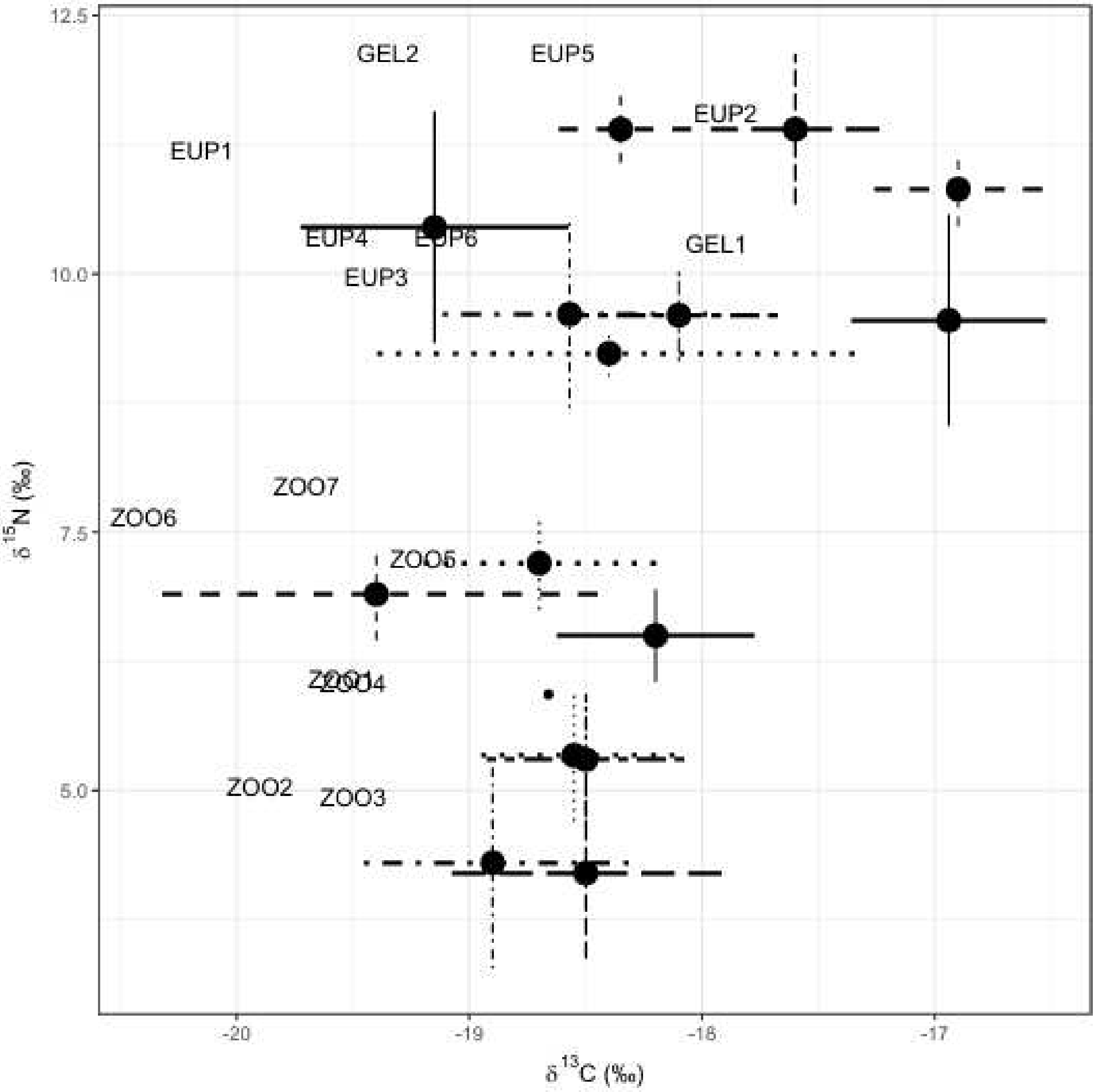

Figure 1. Isospace plot of muscle $\delta^{13}C$ versus $\delta^{15}N$ for the neonate Megamouth Shark and its potential prey sources.

The concentrations of sixty-five metals and metalloids in the muscle tissue of the Megamouth Shark specimen were assessed. Forty-one elements were evaluated for the first time for this species (Au, Be, Br, Ce, Cs, Dy, Er, Eu, Gd, Ge, Ho, I, In, La, Lu, Mo, Nb, Nd, P, Pd, Pt, Pr, Rb, Re, S, Sb, Sc, Si, Sm, Sn, Ta, Tb, Th, Tl, Tm, U, V, W, Y, Yb and Zr). Among the detected elements, the other twenty-four elements, the highest concentrations were K > Ca > Mg

> Al > Fe ranging from 802.895 mg.kg^{-1} to 51.328 mg.kg^{-1}. The middle concentrations were Zn > Sr > As > Ti > Mn ranging from 10.924 mg.kg^{-1} to 1.6 mg.kg^{-1}. The lowest concentrations were Cr > Ba > B > Cu > Se > Ni > Pb > Li > Ga > Co > Hg > Ag > Bi ranging from 0.915 mg.kg^{-1} to 0.004 mg.kg^{-1} (Table 3). The concentrations of Au, Cd, Ge, In, Nd, Re, Si, and W were below the limits of quantification (LOQ) of < 0.00025, < 0.001, < 0.00125, < 0.00025, < 0.0625, < 0.0001, < 0.0005, and < 0.03 mg.kg^{-1}, respectively (Table S4).

Table 3 Concentrations of twenty-four metals and metalloids of the Megamouth Shark. Data are expressed as mg.kg^{-1} (wet weight).

Metal and metalloids	**LOQ**	**Brazil**	**Brazil**		**Taiwan**
		muscle	**muscle**	**liver**	**muscle**
		Present study (n=1)	**Moura et al. (2015) (n=1)**		**Ju et al. (2020) (n=27)**
Ag	0.0008	0.006	0.05	0.21	0.027 ± 0.036
Al	1.550	116.317	4.60	4.40	58.8 ± 46.8
As	0.0035	4.574	5.57	13.93	1.37 ± 0.95
B	0.175	0.522	362.50	2.62	1.63 ± 0.60
Ba	0.375	0.635	-	-	0.49 ± 0.42
Bi	0.0018	0.004	0.03	0.06	0.042±0.031
Ca	473.80	766.85	41.10	106.72	51.1 ± 20.3
Cd	0.0015	< 0.0015	0.05	7.46	0.075 ± 0.101
Co	0.0055	0.015	0.01	0.05	0.071 ± 0.055
Cr	0.010	0.916	0.67	0.76	1.63 ±1.25
Cu	0.150	0.494	0.23	2.6	5.47 ± 3.53
Fe	3.950	51.327	5.18	13.52	20.0 ± 14.8
Ga	0.010	0.028	-	-	0.008 ± 0.006
Hg*	0.0035	0.015	0.09958	0.0264	0.058 ± 0.075
K	1.575	802.895	1102.74	313.39	133 ± 93.1
Li	0.0018	0.064	0.02	0.04	0.034 ± 0.018
Mg	17.50	287.16	275.53	933.79	153 ± 84.5
Mn	1.500	1.598	0.10	0.70	0.68 ± 0.45
Ni	0.0325	0.131	0.09	0.08	1.02 ± 0.74
Pb	0.0425	0.109	0.01	0.07	0.25 ± 0.23
Se	0.0225	0.310	0.76	1.61	-
Sr	0.675	9.142	0.85	1.42	2.96 ± 1.26
Ti	0.025	2.193	-	-	547 ± 276
Zn	3.200	10.924	18.37	19.57	7.82 ± 5.18

* total Hg

4.4 Discussion

The $\delta^{15}N$ value of the Megamouth Shark specimen (5.93‰) is notably low, compared to the adult specimen from the Subtropical Atlantic Ocean ($\delta^{15}N$ = 8.2‰; Moura et al., 2015) and falls below the minimum range recorded for the species in the Northwestern Pacific (6.83 to 11.67‰; Yu et al., 2025). Regarding $\delta^{13}C$, the value (-18.66‰) differs from other regions: it is lower than the range observed in the Pacific (-18.14‰ to -14.99‰; Yu et al., 2025) but enriched compared to the Subtropical Atlantic specimen (-19.8‰; Moura et al., 2015), highlighting distinct regional baselines.

Furthermore, the $\delta^{13}C$ and $\delta^{15}N$ value of the neonate contrasts with the isotopic values reported for other large filter-feeding elasmobranchs, such as the Whale Shark from India ($\delta^{13}C$ = -17.9‰ to -14.7‰; $\delta^{15}N$ = 11.0‰ to 15.5‰; Borrell et al., 2011), from Mexico ($\delta^{13}C$ = -15.4 ± 0.5‰ [La Paz Bay] and $\delta^{13}C$ = - 14.2 ± 0.1‰ [Yucatan Peninsula]; $\delta^{15}N$ = 13.5 ± 0.1‰ [La Paz Bay] and 8.3 ± 0.1‰ [Yucatan Peninsula]; Whitehead et al., 2020), and from the Northwestern Pacific ($\delta^{13}C$ = -15.7 ± 0.8‰; $\delta^{15}N$ = 9.0 ± 1.8‰; Yu et al., 2025); the Basking Shark from Northwestern Atlantic Ocean ($\delta^{13}C$ = -22.5‰; $\delta^{15}N$ = 10.4‰; Estrada et al., 2003); and the Reef Manta Ray from Australia and Mozambique ($\delta^{13}C$ = -17.4 ± 0.1‰; $\delta^{15}N$ = 8.9 ± 0.3‰; Couturier et al., 2013).

The diet of elasmobranchs can vary with ontogeny, geographic region, and seasonality (Wetherbee et al., 2004), reflecting differences in the isotopic composition of their tissues (Hussey et al., 2012). The isotopic values of the neonate from the present study (Tropical Atlantic) differed by 1.14‰ for $\delta^{13}C$ and 2.27‰ for $\delta^{15}N$ from those reported for the adult specimen from the Subtropical Atlantic (Moura et al., 2015). These differences may suggest that the regional isotopic baseline acts as a geographic tracer for this species, a pattern identified in other elasmobranchs (e.g., Carlisle et al., 2012; Bird et al., 2018; Madigan et al., 2021). Recent evidence of potential residency in Megamouth Sharks (Clerkin et al., 2024) lends further support to this hypothesis. Alternatively, given that the specimen analyzed in this study is likely a neonate (see Xavier et al., 2025), its tissue's isotopic composition could also reflect maternal isotopic transfer, a phenomenon already documented in other shark species (e.g., Olin et al., 2011; Bourg et al., 2014; Niella et al., 2020; Rangel et al., 2020).

The Bayesian mixing model analysis revealed the dominance of the smallest zooplankton size classes (predominantly <500µm) in the diet of the neonate Megamouth Shark. The predominance of <500µm zooplankton may be related to the region where the specimen was recorded: the Tropical Atlantic, an oceanographic region characterized as oligotrophic and dominated by smaller-sized plankton (Armengol et al., 2019). Furthermore, factors such as swimming speed, morphology and anatomy of the gills and buccal cavity can directly influence filter-feeding during early life stages (Paig-Tran et al., 2011).

The metal and metalloids assessment of 41 new elements for the Megamouth Shark contributes to improving an ecotoxicological database for this species and other filter-feeding elasmobranchs. The present study provides the first assessment of metal and metalloids in a neonate Megamouth Shark. The observed Hg value (0.015 $mg \cdot kg^{-1}$) seems to follow an ontogenetic trend when compared to literature data: it is lower than the average for the Pacific population (Hg: 0.058 ± 0.075 $mg \cdot kg^{-1}$; Ju et al., 2021), composed of juveniles and adults, and about six times lower than the value recorded for the South Atlantic adult (Hg: 0.099 $mg \cdot kg^{-1}$; Moura et al., 2015). Maternal transfer of mercury and other nonessential elements has been documented in shark species (Frías-Espericueta et al., 2014; Dutton and Venuti, 2019; Hauser-Davis et al., 2020). A recent occurrence of a pregnant female Megamouth Shark confirmed the hypothesis that the species is aplacental viviparous (Bueno et al., 2025). Sharks with an aplacental viviparity strategy, maternal transfer of mercury is limited via yolk, resulting in minimal body burdens at birth (Pethybridge et al., 2010; Dutton et al., 2023). Consequently, the minimal Hg burden observed confirms that the neonate had negligible environmental exposure post-birth. Furthermore, the molar ratio between selenium and mercury (Se:Hg) was calculated at approximately 52:1, far exceeding the 1:1 threshold required for protection against mercury toxicity (Adams and Duguay, 2025).

The total arsenic concentration (4.574 $mg \cdot kg^{-1}$) was slightly lower than that reported for the adult specimen from the Southwestern Atlantic (5.57 $mg \cdot kg^{-1}$; Moura et al., 2015), but notably higher than the mean observed for the specimens in the Northwestern Pacific (1.37 ± 0.95 $mg \cdot kg^{-1}$; Ju et al., 2021). This regional difference implies a basin-specific geochemical potentially driven by the oligotrophic conditions of the Tropical Atlantic. In this environment phosphate depletion promotes the uptake of arsenate as a chemical substitute by primary producers, thereby increasing arsenic bioavailability at the base of the food web (Wurl et al., 2015). On the other hand, the substantial concentration found in this early life stage aligns with recent global findings indicating that, unlike mercury, total arsenic accumulation in sharks does not strictly correlate with body size, and likely comprises predominantly non-toxic organic species (e.g., arsenobetaine) (Hauser-Davis et al., 2024; Maciel et al., 2025). The neonate's arsenic level exceeded those of other giants filter-feeders from the Atlantic Ocean, such as the Whale Shark (*Rhincodon typus*: 0.52 ± 0.44 $mg \cdot kg^{-1}$), the Basking Shark (*Cetorhinus maximus*:

0.77 ± 0.28 mg·kg^{-1}), and the Oceanic Manta Ray (*Mobula birostris*: 0.27 ± 0.18 mg·kg), although lower than that of smaller rays, such as *Mobula mobular* (15.8 ± 8.14 mg·kg^{-1}) and *Mobula munkiana* (10.5 ± 0.35 mg·kg^{-1}) (Boldrocchi et al., 2023).

The Pb concentration (0.109 mg·kg^{-1}) was approximately eleven times higher than that found in the adult individual from the Southwestern Atlantic Ocean (0.01 mg·kg^{-1}; Moura et al., 2015) yet remained about half the concentration observed in the Pacific population (0.25 ± 0.23 mg·kg^{-1}; Ju et al., 2021). Measurable Pb levels in the neonate likely reflect maternal transfer that occurred during vitellogenesis (Reinero et al., 2022; Veron et al., 2022). Lead mimic calcium biological pathways entering biological cells through calcium transportation mechanisms (Generalova et al., 2025). Therefore, the high calcium demand for skeletogenesis can facilitate the inadvertent transport of lead from the mother to the embryo. With growth, Pb concentrations may decrease due to metabolic processes, as identified for the Lesser Spotted Dogfish, *Scyliorhinus canicula* (Reinero et al., 2022). Despite the ontogenetic difference, the recorded concentration is comparatively low within the Chondrichthyes, falling below the global mean reported for batoids (0.31 ± 0.24 mg·kg^{-1}; Bezerra et al., 2019).

The Al concentration (116.32 mg·kg^{-1}) was notably higher than in the adult from the Southwestern Atlantic Ocean (4.60 mg·kg^{-1}; Moura et al., 2015). However, this value falls well within the wide range reported for the species in the Pacific Ocean, where concentrations reached up to 187 mg·kg^{-1} (Ju et al., 2020). Given that the specimen is from a neonate and rigorous sampling was performed, this elevated burden can indicate maternal transfer. Previous studies have confirmed the presence of aluminum in the uterine fluids of sharks, exposing embryos during development (Naidoo et al., 2017; Souza-Araujo et al., 2020). In contrast, titanium levels (2.19 mg·kg^{-1}) were two orders of magnitude lower than the extremely high values reported for specimens from Taiwan (547 ± 276 mg·kg^{-1}; Ju et al., 2020). These high Ti levels were attributed to the ingestion of specific planktonic prey rich in lithogenic minerals (Ju et al., 2020).

Regarding essential elements, concentrations of Fe, Ca, K, Mg, and Zn were found in high concentrations in the neonate. Ca and Fe were high when compared to adults and subadults of the species (Moura et al., 2015; Ju et al., 2021). These elements may reflect metabolic processes crucial to the biology and health of sharks (Lall and Kaushik, 2021). The elevated levels of these elements in the muscles of the Megamouth Shark could be related to its developmental stage, as juvenile sharks have higher requirements for these elements to support growth and development (Lall and Kaushik, 2021).

This study provides the first comprehensive inorganic element profile and $\delta^{13}C$ and $\delta^{15}N$ isotopic signature for a Megamouth Shark neonate in the Tropical Atlantic Ocean, filling a significant gap in knowledge about filter-feeding elasmobranchs. Simultaneously, the stable isotope values reflect maternal nutritional investment rather than independent postpartum feeding. Specifically, the observed isotopic profile aligns with the Tropical Atlantic isotopic maps described by Graham et al. (2010), indicating that the mother fed in these oligotrophic waters during gestation.

4.5 References

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4.6 Supplementary material

Table S1 Stable isotopic composition of carbon and nitrogen in the Megamouth Shark and its potential prey from the Atlantic Ocean.

Category	Group	Specie	Code	N	δ13C (‰)	δ15N (‰)	C:N	lipidic extraction	lipid correction	carbonate removal	Sampling site	Ocean	Sampling date	Source*	Observation
Predator	Elasmobranch	*Megachasma pelagios*	ELA1	1	−18.66	5.93	3.14	No	No	No	Pedra do Sal beach, PI, Brazi; 2°48′28.4″S 41°43′19.8″W	Western Tropical Atlantic	September 10, 2018	Present study	total length: 170cm
Predator	Elasmobranch	*Megachasma pelagios*	ELA2	1	−19.8	8.2	2.41	No	No	No	Arraial do Cabo, RJ, Brazil; 22°57S 42°04W	Western Subtropical Atlantic	July 9, 2009	Moura et. al., 2015	total length: 539 cm
Potential prey	Euphausiids	*Thysanopoda* sp.	EUP1	6	−20.05 ± 0.49	8.15 ± 1.10	2.47 ± 0.41	No	No	No	Areia Branca, RN, Brazil	Western Tropical Atlantic	April and June, 2018	Moraes, 2021	size: 4.40 ± 0.64 (cm)
Potential prey	Euphausiids		EUP2	50	−17.80 ± 0.2	8.52 ± 0.3	2.08	No	No	No	Areia Branca, RN, Brazil	Western Tropical Atlantic	April and June, 2018	Moraes, 2021	Bulk isotopic values (50 pooled individuals); SDs represent analytical error.
Potential prey	Euphausiids	*Euphausia gibboides*	EUP3	6	−19.30 ± 1.01	6.93 ± 0.09	3.28 ± 0.04	No	No	No	Surrounding Rocas Atol and Fernando de Noronha Archipelago and adjacent seamounts, Brazil	Western Tropical Atlantic	April 9 - May 6, 2017	Eduardo et al., 2020	size: 1.50 ± 0.11 (cm)
Potential prey	Euphausiids	*Euphausia* sp.	EUP4	3	−19.47 ± 0.51	7.31 ± 0.88	3.26 ± 0.09	No	No	No	Surrounding Rocas Atol and Fernando de Noronha Archipelago and adjacent seamounts, Brazil	Western Tropical Atlantic	April 9 - May 6, 2017	Eduardo et al., 2020	size: 1.43 ± 0.13 (cm)

Potential prey	Gelatinous organism	*Abylopsis tetragona*	GEL1	3	−17.84 ± 0.29	7.25 ± 1.00	3.31 ± 0.09	No	No	No	Surrounding Rocas Atol and Fernando de Noronha Archipelago and adjacent seamounts, Brazil	Western Tropical Atlantic	April 9 - May 6, 2017	Eduardo et al., 2020	
Potential prey	Gelatinous organism	*Siphonophorae* sp.	GEL2	3	−19.25 ± 0.04	9.10 ± 0.25	3.48 ± 0.11	No	No	No	Surrounding Rocas Atol and Fernando de Noronha Archipelago and adjacent seamounts, Brazil	Western Tropical Atlantic	April 9 - May 6, 2017	Eduardo et al., 2020	
Potential prey	Zooplanckton		ZOO1	19	−19.45 ± 0.31	3.04 ± 0.60	4.52 ± 0.51	No	No	Yes	Surrounding Rocas Atol and Fernando de Noronha Archipelago and adjacent seamounts, Brazil	Western Tropical Atlantic	April 9 - May 6, 2017	Eduardo et al., 2020	size class: 200–500 µm (mainly copepods)
Potential prey	Zooplanckton		ZOO2	19	−19.8 ± 0.5	2.0 ± 1.0	4.7 ± 0.2	No	Yes	No	Fernando de Noronha Archipelago and adjacent seamounts, Brazil	Western Tropical Atlantic	April and May, 2017	Eduardo et al., 2023	size class: <64–100µm
Potential prey	Zooplanckton		ZOO3	19	−19.4 ± 0.5	1.9 ± 0.8	4.6 ± 0.7	No	Yes	No	Fernando de Noronha Archipelago and adjacent seamounts, Brazil	Western Tropical Atlantic	April and May, 2017	Eduardo et al., 2023	size class: 100–200µm
Potential prey	Zooplanckton		ZOO4	19	−19.4 ± 0.3	3.0 ± 0.6	5.6 ± 1.2	No	Yes	No	Fernando de Noronha Archipelago and adjacent seamounts, Brazil	Western Tropical Atlantic	April and May, 2017	Eduardo et al., 2023	size class: 200–500µm
Potential prey	Zooplanckton		ZOO5	18	−19.1 ± 0.3	4.2 ± 0.4	4.2 ± 0.4	No	Yes	No	Fernando de Noronha Archipelago and adjacent	Western Tropical Atlantic	April and May, 2017	Eduardo et al., 2023	size class: 500–1000µm

											seamounts, Brazil				
Potential prey	Zooplanckton		ZOO6	17	−20.3 ± 0.9	4.6 ± 0.4	4.8 ± 0.6	No	Yes	No	Fernando de Noronha Archipelago and adjacent seamounts, Brazil	Western Tropical Atlantic	April and May, 2017	Eduardo et al., 2023	size class: 1000–2000µm
Potential prey	Zooplanckton		ZOO7	13	−19.6 ± 0.4	4.9 ± 0.4	4.5 ± 0.3	No	Yes	No	Fernando de Noronha Archipelago and adjacent seamounts, Brazil	Western Tropical Atlantic	April and May, 2017	Eduardo et al., 2023	size class: >2000µm
Potential prey	Euphausiids	Euphasiidae sp. 1	EUP5	4	−18.5 ± 0.2	9.1 ± 0.7	3.21 ± 0.1	No	No	Yes	Fernando de Noronha Archipelago and adjacent seamounts, Brazil	Western Tropical Atlantic	April and May, 2017	Eduardo et al., 2023	size: 1.5 ± 0.1 (cm)
Potential prey	Euphausiids	Euphasiidae sp. 2	EUP6	3	−19.0 ± 0.3	7.3 ± 0.4	3.28 ± 0.1	No	No	Yes	Fernando de Noronha Archipelago and adjacent seamounts, Brazil	Western Tropical Atlantic	April and May, 2017	Eduardo et al., 2023	size: 1.4 ± 0.1 (cm)
Potential prey	Euphausiids	Euphausiids	EUP7	31	−20.30 ± 0.50	5.11 ± 2.31	4.10 ± 1.54	No	No	No	15°N to 5°S at 23°W and 20 to 27°W at 18°N	Eastern Tropical Atlantic	October 24 - November 23, 2012	Hauss, 2015	juveniles (mainly Euphausia gibboides and Thysanopoda tricuspidata); size class: <200µm
Potential prey	Copepods	*Miracia efferata*	COP1	15	−20.06 ± 0.64	1.89 ± 0.35	10.64 ± 1.37	No	No	No	15°N to 5°S at 23°W and 20 to 27°W at 18°N	Eastern Tropical Atlantic	October 24 - November 23, 2012	Hauss, 2015	size class: <200µm
Potential prey	Copepods	*Scolecithrix danae*	COP2	54	−19.97 ± 0.52	5.11 ± 1.40	4.10 ± 1.03	No	No	No	15°N to 5°S at 23°W and 20 to 27°W at 18°N	Eastern Tropical Atlantic	October 24 - November 23, 2012	Hauss, 2015	size class: <200µm
Potential prey	Copepods	*Undinula vulgaris*	COP3	56	−19.74 ± 0.58	5.19 ± 1.59	3.63 ± 0.72	No	No	No	15°N to 5°S at 23°W and 20 to 27°W at 18°N	Eastern Tropical Atlantic	October 24 - November 23, 2012	Hauss, 2015	size class: <200µm

Potential prey	Copepods	*Euchaeta marina*	COP4	33	−20.61 ± 0.48	6.33 ± 1.23	3.17 ± 0.88	No	No	No	15°N to 5°S at 23°W and 20 to 27°W at 18°N	Eastern Tropical Atlantic	October 24 - November 23, 2012	Hauss, 2015	size class: <200µm
Potential prey	Copepods	*Candacia* sp.	COP5	26	−20.08 ± 0.77	4.72 ± 1.94	5.33 ± 1.56	No	No	No	15°N to 5°S at 23°W and 20 to 27°W at 18°N	Eastern Tropical Atlantic	October 24 - November 23, 2012	Hauss, 2015	size class: <200µm
Potential prey	Copepods	*Macrosetella gracilis*	COP6	11	−21.33 ± 0.73	2.50 ± 0.54	8.16 ± 1.89	No	No	No	15°N to 5°S at 23°W and 20 to 27°W at 18°N	Eastern Tropical Atlantic	October 24 - November 23, 2012	Hauss, 2015	size class: <200µm
Potential prey	Copepods	*Pontella* sp.	COP7	12	−19.28 ± 0.43	5.04 ± 1.03	4.06 ± 0.72	No	No	No	15°N to 5°S at 23°W and 20 to 27°W at 18°N	Eastern Tropical Atlantic	October 24 - November 23, 2012	Hauss, 2015	size class: <200µm
Potential prey	Amphipods		AMP1	8	−20.4 ± 1.1	4.2 ± 0.8	6.1 ± 1.0	No	Yes	No	North of Cape Santa Marta-shelf break; 28°S-24°S	Subtropical Western South Atlantic	spring and autumn (2012–2015)	Troina et al., 2020	
Potential prey	Chaetognaths		CHT1	9	−19.4 ± 0.6	5.6 ± 1.3	6.0 ± 1.8	No	Yes	No	North of Cape Santa Marta-shelf break; 28°S-24°S	Subtropical Western South Atlantic	spring and autumn (2012–2015)	Troina et al., 2020	
Potential prey	Copepods		COP8	12	−20.4 ± 1.1	4.3 ± 1.7	6.4 ± 2.9	No	Yes	No	North of Cape Santa Marta-shelf break; 28°S-24°S	Subtropical Western South Atlantic	spring and autumn (2012–2015)	Troina et al., 2020	
Potential prey	Euphausiids		EUP8	5	−19.6 ± 0.5	3.8 ± 1.2	6.4 ± 2.2	No	Yes	No	North of Cape Santa Marta-shelf break; 28°S-24°S	Subtropical Western South Atlantic	spring and autumn (2012–2015)	Troina et al., 2020	
Potential prey	Amphipods		AMP2	11	−18.9 ± 1.4	1.8 ± 1.3	6.2 ± 1.0	No	Yes	No	North of Cape Santa Marta-offshore; 28°S-24°S	Subtropical Western South Atlantic	spring and autumn (2012–2015)	Troina et al., 2020	
Potential prey	Chaetognaths		CHT2	9	−18.5 ± 1.1	3.6 ± 1.5	5.2 ± 0.9	No	Yes	No	North of Cape Santa Marta-offshore; 28°S-24°S	Subtropical Western South Atlantic	spring and autumn (2012–2015)	Troina et al., 2020	
Potential prey	Copepods		COP9	16	−19.8 ± 1.1	1.3 ± 2.0	5.7 ± 1.2	No	Yes	No	North of Cape Santa Marta-	Subtropical Western South	spring and autumn (2012–2015)	Troina et al., 2020	

										offshore; 28°S-24°S	Atlantic		
Potential prey	Euphausiids	EUP9	17	−19.1 ± 0.6	3.2 ± 1.5	4.4 ± 1.0	No	Yes	No	North of Cape Santa Marta-offshore; 28°S-24°S	Subtropical Western South Atlantic	spring and autumn (2012–2015)	Troina et al., 2020
Potential prey	Amphipods	AMP3	19	−19.6 ± 1.3	6.0 ± 2.5	5.9 ± 0.8	No	Yes	No	South of Cape Santa Marta-shelf break; 34°S-28°S	Subtropical Western South Atlantic	spring and autumn (2012–2015)	Troina et al., 2020
Potential prey	Chaetognaths	CHT3	16	−19 ± 1.0	6.9 ± 2.7	5.4 ± 1.0	No	Yes	No	South of Cape Santa Marta-shelf break; 34°S-28°S	Subtropical Western South Atlantic	spring and autumn (2012–2015)	Troina et al., 2020
Potential prey	Copepods	COP10	21	−20.2 ± 1.1	6.1 ± 2.3	5.7 ± 1.5	No	Yes	No	South of Cape Santa Marta-shelf break; 34°S-28°S	Subtropical Western South Atlantic	spring and autumn (2012–2015)	Troina et al., 2020
Potential prey	Euphausiids	EUP10	15	−19.5 ± 1.0	6.9 ± 2.0	5.2 ± 1.1	No	Yes	No	South of Cape Santa Marta-shelf break; 34°S-28°S	Subtropical Western South Atlantic	spring and autumn (2012–2015)	Troina et al., 2020
Potential prey	Amphipods	AMP4	20	−19.4 ± 0.9	3.7 ± 1.6	5.7 ± 0.6	No	Yes	No	South of Cape Santa Marta-offshore; 34°S-28°S	Subtropical Western South Atlantic	spring and autumn (2012–2015)	Troina et al., 2020
Potential prey	Chaetognaths	CHT4	19	−19 ± 0.5	5.3 ± 1.2	4.8 ± 0.5	No	Yes	No	South of Cape Santa Marta-offshore; 34°S-28°S	Subtropical Western South Atlantic	spring and autumn (2012–2015)	Troina et al., 2020
Potential prey	Copepods	COP11	27	−20.8 ± 0.4	3.9 ± 1.6	5.2 ± 0.6	No	Yes	No	South of Cape Santa Marta-offshore; 34°S-28°S	Subtropical Western South Atlantic	spring and autumn (2012–2015)	Troina et al., 2020
Potential prey	Euphausiids	EUP11	30	−19.6 ± 0.7	4.9 ± 1.3	4.8 ± 0.8	No	Yes	No	South of Cape Santa Marta-offshore; 34°S-28°S	Subtropical Western South Atlantic	spring and autumn (2012–2015)	Troina et al., 2020

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Table S2 Gelman-Rubin diagnostic values for the Bayesian Isotopic Mixing Model (MixSIAR) applied to the Megamouth Shark neonate diet. The p.global[1-15] parameters correspond to the proportional contribution of each of the 15 potential prey sources included in the model. All "Point Estimate" values are below the recommended threshold of 1.05, indicating successful model convergence.

Parameter	**Point Estimate (PRSF)**	**Upper C.I. (95%)**
deviance	1.0051	1.0127
loglik	1.0051	1.0127
p.global[1]	1.0040	1.0075
p.global[2]	1.0014	1.0017
p.global[3]	1.0022	1.0081
p.global[4]	1.0078	1.0118
p.global[5]	1.0026	1.0051
p.global[6]	1.0024	1.0050
p.global[7]	1.0040	1.0067
p.global[8]	0.9993	1.0001
p.global[9]	1.0016	1.0028
p.global[10]	0.9992	0.9995
p.global[11]	0.9999	1.0022
p.global[12]	0.9995	0.9999
p.global[13]	1.0008	1.0019
p.global[14]	0.9992	0.9994
p.global[15]	1.0004	1.0025

Table S3: Instrumental operating conditions of ICP-MS.

Instrumental parameter	**Condition**
Radio frequency (Rf) power	1100 W
Plasma flow rate	17.0 L min^{-1}
Auxiliary gas flow rate	1.2 L min^{-1}
Carrier gas flow rate	0.98 L min^{-1}
Composition of sampling cones and skimmer	Pt
Dwell time	50 ms per isotope
Number of readings	5

Table S4 Sixty-five metal and metalloid concentrations of the neonate Megamouth Shark from Pedra do Sal beach, Piauí, Brazil. Data are expressed as mg.kg-^{1} w. w.

Metal and metalloids	LOQ	Concentrations
Ag	0.0008	0.006
Al	1.550	116.317
As	0.0035	4.574
Au	0.0003	< 0.0003
B	0.175	0.522
Ba	0.375	0.635
Be	0.0005	0.001
Bi	0.0018	0.004
Br	0.275	87.721
Ca	473.800	766.850
Cd	0.0015	< 0.0015
Ce	0.010	0.077
Co	0.0055	0.015
Cr	0.010	0.916
Cs	0.0008	0.017
Cu	0.150	0.494
Dy	0.0003	4.729
Er	0.0001	0.002
Eu	0.0003	0.002
Fe	3.950	51.327
Ga	0.010	0.028
Gd	0.0005	0.007
Ge	0.0013	< 0.0013
Hg	0.0035	0.015
Ho	0.0001	0.001
I	0.040	0.435
In	0.0003	< 0.0003
K	1.575	802.895
La	0.0013	0.035
Li	0.0018	0.064
Lu	0.0001	0.0003
Mg	17.500	287.160
Mn	1.500	1.598
Mo	0.0008	0.006
Nb	0.0023	0.008
Nd	0.0625	< 0.0625
Ni	0.0325	0.131
P	4.250	2,132.821
Pb	0.0425	0.109
Pd	0.0063	0.007
Pr	0.0003	0.009

Pt	0.0000	0.000
Rb	0.0073	0.408
Re	0.0001	< 0.0001
S	33.750	1.218.947
Sb	0.0005	0.006
Sc	0.100	0.209
Se	0.0225	0.310
Si	0.0005	< 0.0005
Sm	0.0005	0.006
Sn	0.0043	< 0.0043
Sr	0.675	9.142
Ta	0.0003	0.001
Tb	0.0003	0.001
Th	0.0020	0.007
Ti	0.025	2.193
Tl	0.0001	0.001
Tm	0.0001	0.0003
U	0.0005	0.006
V	0.0025	0.332
W	0.030	< 0.030
Y	0.0008	0.027
Yb	0.0003	0.003
Zn	3.200	10.924
Zr	0.0058	0.092

5 CONCLUSÕES

Os limites de distribuição geográfica da raia-viola-de-focinho-curto, *Zapteryx brevirostris*, estão compreendidos entre as áreas do Rio Doce, norte do Espírito Santo, no Sudeste do Brasil (19ºS), ao norte, e nas Ilhas Falkland (Malvinas) (53°S) ao sul. O limite mais ao sul estende a distribuição geográfica em mais de 2.000 Km de linha de costa.

O espécime encontrado boiando em 10 de setembro de 2018 em Praia Grande, Parnaíba, Piauí, Nordeste do Brasil é um exemplar neonato do tubarão-boca-grande.

O espécime neonato do tubarão-boca-grande apresenta diferenças na forma e espaçamento dos dentículos dérmicos em algumas áreas do corpo, diferindo do que já é documentado para o adulto da espécie. Isso indica uma relação de modificação dos dentículos dérmicos a partir dos estágios ontogenéticos da espécie.

As assinaturas isotópicas de $\delta^{13}C$ e $\delta^{15}N$ do exemplar neonato do tubarão-boca-grande refletem investimento nutricional materno, indicando forrageamento em águas oligotróficas do Oceano Atlântico Tropical.

Os níveis de metais e metaloides como o mercúrio corroboram o estágio inicial de vida do espécime neonato do tubarão-boca-grande. Além disso, os níveis elevados de chumbo e alumínio sugerem transferência materna (maternal *offloading*) via vitelo ou fluidos uterinos. O nível de arsênio pode estar relacionado a uma possível variação regional.

6 CONSIDERAÇÕES FINAIS

Este estudo fornece a primeira evidência de variação ontogenética de dentículos dérmicos na espécie, assim como fornece os primeiros valores de isotópicos de $\delta^{13}C$ e $\delta^{15}N$ e de metais e metaloides para um neonato de tubarão-boca-grande no Oceano Atlântico Tropical, preenchendo uma lacuna significativa no conhecimento sobre elasmobrânquios filtradores.

A elucidação da distribuição latitudinal da raia costeira, *Zapteryx brevirostris*, levanta novas questões sobre a conectividade populacional ao longo da sua faixa de distribuição geográfica. Estudos futuros de filogeografia e genética de populações são recomendados para investigar a estrutura populacional da espécie tanto nos extremos latitudinais quanto ao longo da faixa de distribuição a fim de identificar se o fluxo gênico é mantido com a população central ou se representam unidades evolutivas distintas. Tais dados teriam implicações diretas para o manejo e a conservação da espécie frente às mudanças climáticas e à pressão pesqueira.

A confirmação de um neonato de tubarão-boca-grande, *Megachasma pelagios*, no

Oceano Atlântico Tropical Oeste reconfigura o entendimento sobre o ciclo de vida da espécie nesta bacia, sugerindo que a região atua como área de residência e berçário. A variação ontogenética dos dentículos dérmicos, identificada nesta tese, suscita questões ecomorfológicas fundamentais sobre as adaptações funcionais necessárias à transição do nado em diferentes estágios de vida. Além disso, aprofundar o conhecimento sobre as estratégias reprodutivas e a dinâmica trófica em ambientes oligotróficos é crucial para compreender como grandes filtradores maximizam a sobrevivência de sua prole nesses ambientes.

Por fim, os achados desta pesquisa reforçam o valor inestimável das coleções científicas e da integração da ciência cidadã (amostra do tubarão-boca-grande doado à pesquisa por pescadores locais) como fontes primárias de dados. A continuidade do monitoramento no Oceano Atlântico Sudoeste é fundamental para expandir e consolidar o conhecimento sobre a biodiversidade de elasmobrânquios, preencher lacunas biogeográficas e subsidiar políticas de conservação em escalas local e global.

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