HELOÍSA DE CIA CAIXETA

DNA barcoding of the western South Atlantic deep-sea fishes (Actinopterygii:Teleostei)

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A simplified version of the master's thesis submitted to the Oceanographic Institute of the University of Sao Paulo as part of the requirements for the degree of Master of Science, program of Oceanography, Biological Oceanographic area.

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RESUMO

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O oceano profundo é o maior e mais extremo ecossistema da Terra, e abriga aproximadamente 15% de todas as espécies de peixes que possuem uma variedade de adaptações às condições extremas de luminosidade incipiente ou ausente, altíssima pressão hidrostática, zonas de mínimo oxigênio e baixas temperaturas, dentre outros fatores bióticos e abióticos. A dificuldade para obtenção de amostras faz com que existam grandes lacunas geográficas de conhecimento e diversos grupos ainda são carentes de estudos taxonômicos mais robustos. Durante o projeto DEEP-OCEAN, foram realizados dois cruzeiros oceanográficos a bordo do N/Oc *Alpha Crucis* para coletar peixes de oceano profundo entre 250 e 1.520 m, no talude continental do Sul e Sudeste do Brasil. Foram coletados 1.400 amostras de tecido para análise molecular de peixes-ósseos (Actinopterygii). Desta forma, tornou-se possível a utilização da ferramenta molecular de DNA barcoding para a identificação das espécies de peixes de oceano profundo do Atlântico Sul Ocidental. A extração do DNA foi feita utilizando kits de extração e fragmentos do gene citocromo c oxidase I foram amplificados utilizando primers universais. Os produtos foram sequenciados bidirecionalmente, e as sequências foram comparadas com sequências disponíveis em bancos de dados digitais, confrontando a identificação morfológica realizada em laboratório. Árvores filogenéticas de máxima verossimilhança e bayesianas foram construídas utilizando os softwares RAxML e MrBayes, respectivamente. Para acessar a diversidade de peixes de oceano profundo na região foram calculadas a riqueza de espécies e a diversidade filogenética alpha e beta entre os estratos de profundidade. Foram geradas 144 sequências de 82 espécies pertencentes a 41 famílias e 18 ordens, sendo uma espécie incertae sedis in Epercaria. Os resultados contribuíram para as primeiras sequências disponíveis de 15 espécies; para o Atlântico Sudoeste de 29 espécies, Atlântico Sul de 16 espécies e para o Atlântico as primeiras sequências de 12 espécies. Foi identificada uma nova espécie de *Polymixia* (Polymixiidae: Polymixiiformes) apresentada aqui, além de três possíveis novas espécies dos gêneros *Bassozetus* (Ophidiidae: Ophidiiformes), *Aristostomias* e *Photonectes* (Stomiidae: Stomiiformes) que estão sob investigação. Adicionalmente, foi realizado os primeiros registros de ocorrência de *Coryphaenoides subserrulatus* Makushok, 1976 na Zona Econômica Exclusiva brasileira e de *Coryphaenoides striaturus* Barnard, 1925 (Macrouridae:

Gadiformes) no Atlântico. Profundidades intermediárias apresentaram tanto uma alta riqueza de espécies como uma alta diversidade filogenética, observadas por três picos de diversidade de acordo com o aumento da profundidade, sendo o primeiro em 400–500 m seguido de 700–800 e 900–1,000 m. A maior diversidade de peixes foi encontrada em 900–1,000 m de profundidade, composta principalmente por espécies pelágicas de Stomiiformes e bentopelágicas de Gadiformes e Anguilliformes. O DNA barcoding revelou uma alta diversidade de peixes de oceano profundo para o Atlântico Sudoeste, possíveis novas espécies e sinonímias e novas ocorrências; como também indicou uma alta diversidade filogenética em torno de 1,000 m de profundidade.

Palavras–chave: citocromo c oxidase I. diversidade de oceano profundo. taxonomia. delimitação de espécies. Zona Econômica Exclusiva Brasileira.

ABSTRACT

CAIXETA, Heloísa D.C. **DNA barcoding of the western South Atlantic deep-sea fishes (Actinopterygii: Teleostei).** 2023. 138 p. Master's thesis – Oceanographic Institute of University of São Paulo, São Paulo, 2023

The deep sea is the largest and most extreme ecosystem on Earth, and harbors approximately 15% of all fishes which have a variety of adaptations to extreme conditions of incipient or absent light, high hydrostatic pressure, low temperatures, among other biotic and abiotic factors. The difficulty to obtain samples makes there exist large geographical gaps and several groups still lacking extensive taxonomic revisions. During the DEEP-OCEAN project, two oceanographic cruises were conducted aboard the N/Oc *Alpha Crucis* to collect deep-sea fish between 250 and 1,520 m on the continental slope of Southern and Southeastern Brazil, including 1,400 tissue samples for molecular analysis of bony fish (Actinopterygii). Thus, it became possible to use the molecular tool of DNA barcoding for the identification of deep-sea fishes of the western South Atlantic. DNA extraction was performed using extraction kits and fragments of the cytochrome c oxidase I gene were amplified using universal primers. The products were sequenced bidirectionally, and the sequences were compared with sequences available in digital databases, confronting the morphological identification performed in the laboratory. Phylogenetic trees of maximum likelihood and bayesian were constructed using the RAxML and MrBayes software, respectively. To access the diversity of deep-sea fishes in the region were calculated the species richness, alpha and beta phylogenetic diversity between the depth range. A total of 144 sequences of 82 species belonging to 41 families and 18 orders were generated, including a species insertae sedis in Epercaria. The results contributed to the first available sequences of 15 species, for the western South Atlantic of 29 species, South Atlantic of 16 species and for the Atlantic the first sequences of 12 species. A new species of *Polymixia* (Polymixiidae: Polymixiiformes) was identified, presented here, in addition to three putative new species of the genera *Bassozetus* (Ophidiidae: Ophidiiformes), *Aristostomias* e *Photonectes* (Stomiidae: Stomiiformes), under investigation. Additionally, the new occurrences of *Coryphaenoides subserrulatus* Makushok, 1976 in the Brazilian Exclusive Economic Zone and of *Coryphaenoides striaturus* Barnard, 1925 (Macrouridae: Gadiformes) in the Atlantic were recorded. Intermediate depths presented both a high species richness and a high phylogenetic diversity, observed by three peaks of diversity according to the increase in depth, beiging with 400–500 m, followed by 700–800, and 900–1,000 m. The greatest diversity of fish was found between 900–1,000 m deep, composed mainly by pelagic stomiiforms and the benthopelagic gadiforms and anguilliforms. The DNA barcoding revealed a high diversity of deep-sea fish for the western South Atlantic, possible new species and synonyms and new occurrences; as well as indicated a high phylogenetic diversity around 1,000 m deep.

Keywords: citocromo c oxidase I. deep-sea diversity. taxonomy. species delimitation. Brazilian Exclusive Economic Zone.

1. Introduction

Fishes are the most diversified group of vertebrates, including 36,584 valid species among which 18,010 species, or 49% of the total, are marine (FRICKE; ESCHMEYER; FONG, 2023). Although the number of marine fishes is remarkable, representing almost one half of the total valid species, the diversity of marine fishes from the deep sea is still underestimated; especially considering that most studies focus on shallow-water species, which are easier to collect and more well represented in scientific collections (COSTELLO; CHAUDHARY, 2017; ESCHMEYER *et al*., 2010). It is estimated that about 10% and 15% of the total fish diversity inhabits the deep sea, including different most groups, such as the hagfishes (Myxini), cartilaginous fishes (Chondrichthyes), bony fishes (Actinopterygii) and the coelacanths (Sarcopterygii) (PRIEDE, 2017; WEITZMAN, 1997). In this context, the deepest record of Actinopterygii is the scorpaeniform *Pseudoliparis belyaevi* Andriashev & Pitruk, 1993 found in 8,336 m (JAMIESON *et al*., 2023).

The deep sea is the largest ecosystem on Earth and usually defined as oceanic waters, off the break of the continental shelf, at depths greater than 200 m (RAMIREZ-LLODRA *et al*., 2010; THISTLE, 2003). The deep-sea ecosystems can be divided into the pelagic and demersal (or benthopelagic). The pelagic is divided into vertical zones according to light penetration and hydrostatic pressure: the epipelagic zone, or photic zone, varies from 0 to 200 m; the mesopelagic or twilight zone, from 200 m to 1,000 m; the bathypelagic zone, from 1,000 m to 3,500 m; the abyssopelagic zone, from 3,500 m to the ocean floor at about 5,000 m; and hadalpelagic zone, in trenches that may reach up to 11,000 m. The benthopelagic ecosystems, in turn, are distributed along a depth gradient that extends from the continental shelf (0–200 m), through the continental slopes, rises and sea floor to the hadal zone (COLAÇO *et al*., 2017). HAEDRICH; MERRET (1998) classified the deep-demersal zones into upper slope (200 to 750 m), middle slope (750 to 1,500 m), lower slope (1,500 to 2,250 m), upper rise (2,250 to 3,000 m), middle rise (3,000 to 3,750 m), lower rise (3,750 to 4,250 m), and the abyss (4,250 to 5,000 m).

The zonation of deep-sea ecosystems by depth affects the patterns of fish diversity. Even though the fish diversity decreases by increasing depth from the epipelagic zone, influenced by the decrease of food available due to the absence of primary photosynthetic production (LEATHWICK *et al*., 2006; PRIEDE; FROESE, 2013; SMITH; BROWN, 2002). Looking at the deep-sea ecosystems, the number of benthopelagic fish species increases by increasing depth, with a peak around 1,600m depth, and then, at deeper depths the diversity decreases

(PRIEDE *et al*., 2010). Additionally, the described pattern is also reported for other deep-sea benthic groups (HAEDRICH; ROWE; POLLONI, 1980; VINOGRADOVA, 1961).

The deep sea hosts some of the most extreme environments for life, including zones where the sunlight is dim or completely absent, extremely high hydrostatic pressure caused by the increase of 1 ATM each 10 meters, low temperatures that may reach below 0ºC in some regions, zones of minimum oxygen, hydrothermal vents, and deep-sea trenches (PRIEDE, 2017; RAMIREZ-LLODRA *et al*., 2010; THISTLE, 2003). Such extreme environments are home to some of the most unique species, with marvelous adaptations to produce their own source of light through bioluminescent organs, capable of swallowing enlarged preys, eyes that can capture minimum light, efficient swimming facilitated by high hydrostatic pressure and even highly developed lateral-line systems to detect any kind of movement (COCKER, 1978; FALCUCCI *et al*., 2021; RAMOS *et al*., 2023; WANG *et al*., 2019; MARTINEZ *et al*., 2021; MELO, 2008). Despite being the largest and extreme environment on Earth, the deep sea is still largely unexplored (DANOVARO *et al*., 2017). Indeed, the study of deep-sea species is limited by high-cost of the cruises, technological restrictions, research funding, and availability of research vessels (BELL *et al*., 2022, 2023).

For a long time, it was believed that the first record of deep-sea biodiversity would have been the Echinodermata collected by John Ross on the North-West Passage Expedition in 1818. However, ETTER; HESS (2015) suggested that the first records were made in the mid-18th century, based on echinoderms obtained from the Caribbean Sea. And then, the first oceanographic expedition to collect deep-sea organisms occurred in the 19th century, the British Challenger Expedition, between 1873 and 1876 (THOMSON, 1878). The HMS Challenger traveled around the globe including the Brazilian margin and passed through the Fernando de Noronha and São Pedro and São Paulo archipelagos, and off the coast of Pernambuco and Bahia in Northeastern Brazil (THOMSON, 1878). Additional explorations in the Brazilian deep sea only occurred again after eight decades, with the incentive to the exploitation of fishing resources carried out by the North American ships MIV *Oregon II* between 1957 and 1976, German R/V *Ernst Haeckel* in 1966, and French R/V *Marion Dufresne* in 1987 (MELO; CAIRES; SUTTON, 2020).

The Brazilian Exclusive Economic Zone (EEZ) was established in 1993 expanding the territorial sea to 200 nautical miles (ca. 370 km) off the coast, becoming one of the largest areas of territorial sea in the world (SUMIDA; DE LEO; BERNARDINO, 2020). The Brazilian EEZ, mostly located in the Western Atlantic, is such an extensive and important area from economic, social, and ecological factors (SILVA, 2013). Noteworthy, it was only after the establishment of the EEZ that most deep-sea biomes, such as the continental slopes and rises, were added to Brazilian territory. As a consequence, the coastal areas and continental shelf are relatively well studied, but more than 90% of the vast marine Brazilian area is largely unexplored.

Accordingly, MELO; CAIRES; SUTTON (2020) from the 2000s onwards, there was a significant increase in data on the ichthyofauna from Brazilian waters due to the efforts of the company Petróleo Brasileiro S.A. – PETROBRAS, with the vessels OSV *Astro Garoupa* in 2001 and 2007, R/V *Luke Thomas* in 2009 and R/V *Seward Johnson* in 2011; and the program Programa de Avaliação do Potencial Sustentável de Recursos Vivos na Zona Econômica Exclusiva - REVIZEE, which started in 1995 and remained active for ten years, being one of the most extensive surveys of information on marine biodiversity, with the R/V *Thalassa* in 1999 and 2000, R/V *Atlântico Sul* between 1996 and 1999 and the FVs *Diadorim* and *Solancy Moura* between 1996 and 2002. As of 2012, contributions from Brazilian ships such as FV *Transmar I* and MS *Tehapoo* also appear, with the most recent explorations in the context of the Acoustics along the Brazilian Coast – ABRACOS projects with the French R/V *Antea* in 2015 and 2017 and the project Diversidade e Evolução de Peixes de Oceano – DEEP OCEAN with the Brazilian ship N/Oc *Alpha Crucis* from 2019, whose results will be discussed in this study.

In the knowledge of Brazilian EEZ biodiversity, 712 species from 145 families and 37 orders of deep-sea fishes have already been registered (MELO; CAIRES; SUTTON, 2020). The greatest of the diversity of fishes is benthopelagic inhabiting deep waters, where Actinopterygii is the most diverse group with 237 species from 51 families and 18 orders being Gadiformes, Ophidiiformes and Anguilliformes the most diverse (MELO; CAIRES; SUTTON, 2020). Actinopterygii also is the most diverse group in pelagic ecosystems, with Myctophiformes and Stomiiformes the most diverse in mesopelagic zone and Aulopiformes and Stomiiformes in bathypelagic zone (MELO; CAIRES; SUTTON, 2020).

Among this diversity, some species are target resources in the Brazilian commercial fisheries: the gadiforms *Merluccius hubbsi* MARINI, 1933 and *Urophycis mistacea* MIRANDA–RIBEIRO, 1903; the lophiform *Lophius gastrophysus* MIRANDA–RIBEIRO, 1915; the ophidiiform *Genypterus brasiliensis* REGAN, 1903; the zeiform *Zenopsis conchifer* (LOWE, 1852), and the incertae sedis in Eupercaria *Lopholatilus villarii* MIRANDA–RIBEIRO, 1915 (PEREZ *et al*., 2003, 2020). Despite being a remote and challenging-to-access environment, some deep-sea species are threatened with extinction due to fishing, oil and gas exploration, mining, climate change, and pollution. (ANGEL, 1997; CHIBA *et al*., 2018;

RAMIREZ-LLODRA *et al*., 2011). Indeed, in Brazil, 16 deep-sea species are at risk of extinction (ICMBIO/MMA, 2018).

Scientific contributions to the knowledge of deep-sea fish in the Brazilian margin include taxonomic studies based on morphology, biological and ecological aspects, and marine pollution (EDUARDO *et al*., 2019; FERREIRA *et al*., 2023; KLAUTAU *et al*., 2020; MELO *et al*., 2021; NUNES *et al*., 2016). However, advances in taxonomic studies have established DNA barcoding as a popular and effective tool for identifying deep-sea fish species. (TERAMURA *et al*., 2021). Due to the standardized application for animal species, the technique facilitates identifying species and accelerated alpha taxonomy in the discovery of new species (DESALLE; GOLDSTEIN, 2019; HAJIBABAEI *et al*., 2007).

Although species identification through DNA sequencing has been used since 1980, the technique has become popular since 2003, with HEBERT *et al*. (2003) who proposed a short and standardized region based on 650 base pairs of the COI gene for species identification. The COI gene is ideal due to its mutation rate combined with gene conservation in conspecifics, lack of introns (non-coding sequences), large copy number, and maternal inheritance. (TRIVEDI *et al*., 2016). Since then, various studies about and using DNA barcoding have been developed. (DESALLE; GOLDSTEIN, 2019).

A database with reference sequences combined with morphological identification and audiovisual resources, such as photos, becomes essential for species identification based on DNA fragments (WARD; HANNER; HEBERT, 2009). Genbank (http://www.ncbi.nlm.nih.gov), distributed by the National Center for Biotechnology Information (NCBI), is an open-access database that stores nucleotide sequences, biological information, and bibliography. (CLARK *et al*., 2016). NCBI also distributes the BLASTn platform (blast.ncbi.nlm.nih.gov), where it is possible to detect a sequence's similarity level with the sequences available in the Genbank database. (ALTSCHUL *et al*., 1990). Currently, the Barcode of Life Data System (BOLD) acts as an open-access database and analytical platform for the COI gene sequences of species (RATNASINGHAM; HEBERT, 2007).

DNA barcoding has become an efficient method for characterizing marine fishes (XU *et al*., 2019, 2021) and assessing biodiversity and its conservation status (MIR *et al*., 2021). DNA barcoding can identify species from muscle tissue, eggs, and larvae (WARD; HANNER; HEBERT, 2009). The method has been promising in revealing new species (SU; LIN; HO, 2022), resolving synonyms (BAÑÓN *et al*., 2021), identifying cryptic species, and providing different taxonomic hypotheses (STEINKE *et al*., 2009).

In addition to solving taxonomic problems, DNA barcoding can help monitor illegal trade in some species (BERNARDO *et al*., 2020), fraud verification (CHEN *et al*., 2020), fisheries and aquaculture management (PAVAN-KUMAR *et al*., 2020), feed studies (PRASANNAKUMAR *et al*., 2020), eggs and larvae taxonomy (KERR *et al*., 2020), and understanding the evolutionary and phylogenetic history of biodiversity (SCHANDER; WILLASSEN, 2005).

The survey of fish diversity in remote and deep environments through DNA barcoding has been recorded in different regions of the ocean, such as the Mediterranean Sea (PAZ *et al*., 2018), North and South Pacific (ROBERTSON *et al*., 2017; SMITH *et al*., 2011), Indian (WILLIAMS *et al*., 2018), and North Atlantic (KENCHINGTON *et al*., 2017). However, studies involving DNA barcoding of deep-sea fishes in the South Atlantic are rare and restricted to extreme latitudes (GORDEEVA, 2014; SMITH *et al*., 2011). This results in the region's tenuous and sparse deep-sea fish genetic information. In this context, despite the efforts made since the 2000s and the significant contribution of specimens in ichthyological collections, there has not yet been an assessment of the biodiversity of deep-sea fishes using DNA barcoding in one of the largest territorial sea areas in the world located in the western South Atlantic, the Brazilian Exclusive Economic Zone (EEZ).

1.1. The DEEP–OCEAN Project

This present contribution is a part of the project Diversidade e Evolução de Peixes de Oceano Profundo – DEEP-OCEAN Project (FAPESP 2017/12909–4). The project aims to understand the diversity and evolution of Brazilian deep-sea fish, generating data to better understand the impacts/disturbances caused by anthropic activities in this environment. Through collections at depths of 200 to 1,520 meters with bottom trawls on the southeastern Brazil continental slope, the project collected new samples of fish and invertebrates to understand the evolution of substances that produce bioluminescence and carry out integrative taxonomic studies using morphology and genetics. The work fits into this last goal, based on the molecular identification of the species, using the mitochondrial cytochrome c oxidase I (COI) gene.

Using techniques of DNA barcoding to deepen the taxonomy of Brazilian EEZ deep-sea fish, this work is established as a pioneering study in the Western South Atlantic. DNA barcoding is an essential step of the DEEP-OCEAN project, which intends to study Brazilian deep-sea species thoroughly, identify new species and genetic variability, and solve possible taxonomic problems, such as synonymy and homonymy. Furthermore, building a sequence library through DNA barcoding is essential for more complex analyses, such as species phylogeny, phylogeography, and population analyses.

2. Conclusion

While DNA barcoding has been applied to access the diversity and taxonomy of deep-sea fish around the world, regions like the Brazilian EEZ deal in darkness when it comes to this data. This work provides the successful identification of a high diversity of deep-sea fish from the Brazilian margin. In addition to some taxonomic insights by one new and three putative new species, new occurrences, putative synonyms and species complex. Looking for database contributions, we provide the first barcode sequence for 15 species; and the first sequences from the Western South Atlantic of 29 species, from the South Atlantic of 16 species, and from the Atlantic Ocean of 12 species.

The DNA barcoding was an effective and powerful technique; however we emphasize the importance of analysis based on characters to analyze barcode sequences and provide conclusions based on phylogenetic relationship between species instead of divergence rate. Moreover, this analysis helps to identify misidentification on databases and mitigates the loop of erroneous identifications. In addition, is the extreme importance of the conference and revision of database sequences frequently.

The assessment of deep-sea fish diversity by DNA barcoding data together with collection data proved to be a powerful approach to measure species richness and phylogenetic diversity and examine how the taxonomic levels hold the deep-ocean depths. Our results provide a pattern of depth zonation for deep-sea fishes from western South Atlantic, by three main peaks of diversity. The peak of diversity on intermediate depths suggests a zone of fauna transition, a pattern reported for benthic fauna. Results of phylogenetic diversity show intermediate depths inhabit for species phylogenetically distant, and 900–1,000 m deep a distinct zone corroborating with the transition zone hypothesis.

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