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DA GINGA À SARDINHA: ETNOICTIOLOGIA E SISTEMÁTICA MOLECULAR DE PEQUENOS PEIXES DE VALOR CULTURAL DA COSTA BRASILEIRA

THAIS FERREIRA PINTO DE ARAÚJO

Dissertação de Mestrado
Natal/RN, Abril de 2020

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Dissertação apresentada ao Programa de Pós-graduação em Sistemática e Evolução, Universidade Federal do Rio Grande do Norte como requisito para obtenção do título de Mestre em Sistemática e Evolução.

Orientador: Sergio Maia Queiroz Lima
Co-orientador: Pedro Hollanda Carvalho

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“*Olhe, meu trabalho pode tá uma merda, mas meu cabelo tá lindo!*”

(V. Vale, 2019)

“*Se você quiser, se você se esforçar, se você treinar, se você entrar de cabeça, se você se concentrar... nada garante que você vai conseguir*”

(Craque Daniel, personagem do ator/comediante Daniel Furlan)

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RESUMO

A avaliação de estoques pesqueiros para o manejo sustentável e medidas conservacionistas são feitas através da estatística pesqueira, que demanda dados confiáveis e é, na maioria dos casos, baseada em nomes populares. Entretanto, dados básicos como taxonomia, nomes populares, distribuição geográfica e delimitação de estoques, por exemplo, muitas vezes não estão disponíveis comprometendo o manejo pesqueiro. Assim, esse trabalho une etnoictiologia e análises filogeográficas dos clupeídeos *Opisthonema oglinum* e *Harengula* spp. com o objetivo de identificar seus nomes populares e investigar seus padrões filogeográficos, no intuito de delimitar estoques pesqueiros na costa brasileira. No primeiro capítulo, descrevemos a percepção dos pescadores e dos consumidores locais acerca da ginga, que são pequenos peixes costeiros que compõem o prato típico "ginga com tapioca", patrimônio imaterial do Estado do Rio Grande do Norte. Através de entrevistas e obtenção de espécimes em feiras ou mercados de peixe de seis localidades, em três estados do Nordeste brasileiro, detectamos que ginga consiste em indivíduos juvenis de algumas espécies de sardinhas e arenques, e que a única diferença entre ginga e sardinha é o tamanho, representando a ginga os peixes menores e a sardinha os maiores, às vezes da mesma espécie. O termo é basicamente restrito à região metropolitana de Natal. Além disso, a ginga pode ser considerada uma "espécie culturalmente importante" e, consequentemente, deve estar entre as espécies-alvo para conservação e manejo local. No segundo capítulo, comparamos os padrões filogeográficos dos dois grupos mais representativos da ginga, *O. oglinum* e *Harengula* spp., ao longo de suas supostas distribuições no Atlântico Oeste, dos EUA até o sul do Brasil, usando o marcador mitocondrial CO1. Além disso, investigamos quantas populações existem desses táxons na costa brasileira e no arquipélago oceânico de Fernando de Noronha. Nesse arquipélago, as sardinhas são usadas como isca para pesca artesanal, e tem gerado um conflito entre os pescadores e os órgãos ambientais. A carência de informações básicas, como por exemplo, a identidade taxonômica das espécies, é fundamental para o manejo sustentável. Nossos resultados apontam *O. oglinum* como sendo uma única linhagem em todo o Atlântico Oeste, mas que possui estruturação populacional entre Brasil, EUA+México e Bermudas, e *Harengula* como sendo duas espécies, *Harengula clupeola* e *H. jaguana* na América do Norte e Caribe e uma distinta linhagem no Brasil, que possivelmente possa se tratar de uma nova espécie. Ao avaliar esses táxons em um contexto temporal, revelam que a separação entre as espécies de *Harengula* do hemisfério norte e do Brasil coincide com o aumento do fluxo da descarga dos rios Amazonas e Orinoco. Com esses resultados é possível observar que, apesar

da biologia similar, *O. oglinum* e *Harengula* spp. não apresentam o mesmo padrão filogeográfico e devem ser manejadas de maneiras distintas.
Palavras-chave: Recursos pesqueiros, Clupeidae, Etnozoologia, Espécies culturalmente importantes, DNA mitocondrial, Diversidade críptica

ABSTRACT

The assessment of fishery stocks for sustainable management and conservation measures are made using fishery statistics, which requires reliable data and is, in most cases, based on popular names. However, basic data such as taxonomy, popular names, geographical distribution, and delimitation of stocks, for example, often are not available, which compromise fishery management. Thus, this project combines ethnoichthyology and phylogeographic analyses of the clupeids *Opisthonema oglinum* and *Harengula* spp. to identify their popular names and investigate their phylogeographic patterns, and then delimit fish stocks on the Brazilian coast. In the first chapter, I describe the perception of fishers and local consumers of what is “ginga”, which are small coastal fish and are part of the typical dish “ginga com tapioca”, an intangible cultural heritage of the Rio Grande do Norte state. Through interviews and specimens at fish markets in six locations in three states of Northeastern Brazil, we found that “ginga” consists of juvenile individuals of some sardine and anchovy species, and that the only difference between “ginga” and sardine is the size, “ginga” representing the smaller fishes and sardines the larger, sometimes of the same species. The popular name is basically restricted to the metropolitan region of Natal city. In addition, the “ginga” can be considered a "culturally important species" and, therefore, should among the target species for conservation and local management. In the second chapter, we compare the phylogeographic patterns of the two most representative groups of “ginga”, *O. oglinum* and *Harengula* spp., along their supposed Western Atlantic distributions using the mitochondrial marker CO1. Additionally, we investigate how many stocks of these taxa are on the Brazilian coast and in the oceanic archipelago of Fernando de Noronha. In this archipelago, sardines are used as bait for artisanal fishing, and this have been generating a conflict between fishers and environmental agencies. The lack of basic information, such as the taxonomic identity of species, is essential for sustainable management. Our results indicate *O. oglinum* as a single lineage in the entire Western Atlantic, but shows population structure between Brazil, USA+Mexico, and Bermuda, and *Harengula* as two species, *Harengula clupeola* and *H. jaguana* in North America and the Caribbean and one distinct lineage in Brazil, which might be a new species. When evaluating these taxa in a temporal context, revealed that the separation between the *Harengula* species in the northern hemisphere and Brazil coincides with the increased discharge of the Amazon and Orinoco rivers. With these results it is possible to observe that, despite the similar biology, *O. oglinum* and *Harengula* spp. do not have the same phylogeographic pattern and must be handled differently.

Keywords: Fishery resources, Clupeidae, Ethnozoology, Culturally important species, Mitochondrial DNA, Cryptic diversity

INDÍCE DE ANEXOS, FIGURAS E TABELAS

SUMÁRIO

1. INTRODUÇÃO GERAL

1.1 Estatística pesqueira e etnotaxonomia

Sobrepesca é uma das principais causas do declínio de populações marinhas e estoques pesqueiros no mundo inteiro (Coleman and Williams 2002; Diamond 1984; Pauly et al. 2003). Ademais, várias espécies que estão sendo sobre-explotadas podem não ter informações básicas disponíveis, como identificação taxonômica correta, distribuição geográfica e delimitação de estoques (Carvalho and Hauser 1995), o que pode comprometer o manejo sustentável dessas espécies.

Incertezas taxonômicas diminuem e impedem a confiabilidade dos dados estatísticos da pesca (FAO 2016). Isso é mais evidente para alguns recursos pesqueiros de pequeno porte e abundantes, onde apenas os seus nomes comuns são considerados, como sardinha e anchova, embora possam abrigar vários táxons sob a mesma denominação. Essa riqueza de nomes populares que correspondem a um maior número de espécies biológicas é conhecida na literatura de etnotaxonomia como sub-diferenciação tipo II (Berlin 1973). Em outros casos, as pessoas podem atribuir nomes diferentes para fases distintas da vida de uma espécie. Por exemplo, *Caranx crysos* (Mitchill 1815) é conhecido em algumas partes do Brasil como "Manequinho", "Carapau" ou "Xerelete", dependendo do tamanho (sobre-diferenciação tipo I) (Seixas and Begossi 2001). A avaliação do conhecimento ecológico local (Local Ecological Knowledge – LEK) dos pescadores é uma alternativa para associar corretamente os nomes comuns às espécies científicas as quais correspondem (Begossi et al. 2008; Freire and Pauly 2005; Previero et al. 2013).

Os peixes da família Clupeidae são considerados de grande importância e bastante explorados pela pesca, visto que além de servirem como alimento, também são utilizados como isca para a pesca de peixes maiores (Whitehead 1985). Apesar de formarem grandes cardumes, em alguns casos, estoques de clupeídeos foram sobre-explotados, resultando no colapso da pesca (Clark 1976; Cushing 1992; Dickey-Collas et al. 2010; Jablonski 2007). Em alguns lugares, esses peixes, geralmente pequenos, também são uma parte significativa da cultura, como é o caso das sardinhas em Portugal (Instituto Nacional de Estatística 2012) ou em partes do Brasil, principalmente na região nordeste. Nesses locais, o valor cultural desses clupeídeos ultrapassa sua importância socioeconômica, fazendo parte, por exemplo, de pratos tradicionais (Dantas 2015; Lima et al. 2016).

No nordeste do Brasil, além do popular sardinha, o nome ginga também é usado como sinônimo do primeiro, mas algumas informações anedóticas apoiam a ideia de que ginga engloba múltiplos peixes juvenis da família Clupeidae. A própria ginga foi declarada Patrimônio

Cultural Imaterial do Estado do Rio Grande do Norte, através da Lei Estadual nº 10.481, de 30/01/2019 (Rio Grande do Norte 2019) por fazer parte do que talvez seja o prato local mais tradicional, a "ginga com tapioca", que consiste em pequenos peixes fritos dentro de uma massa frita de mandioca. Ainda assim, não foi realizado um estudo etnoictiológico para identificar quais espécies são realmente consumidas. Nos dias anteriores à existência da "ginga com tapioca" (criada entre 1950-1960), esses pequenos peixes costumavam ser descartados pelos pescadores (Dantas 2015; Lima et al. 2016).

1.2 Conservação e filogeografia

Aliada às incertezas taxonômicas, a falta de conhecimento sobre a distribuição geográfica e delimitação de estoques pesqueiros compromete o manejo, tendo em vista que a estruturação populacional de uma espécie é um dos aspectos mais importantes para sua conservação (Frankham 2010). A Filogeografia pode ser definida como o estudo dos princípios e processos que governam a distribuição geográfica de linhagens genealógicas próximas, especialmente aquelas em um nível intraespecífico (Avise et al. 1987). Recentemente, com o estabelecimento da "teoria da coalescência" e o desenvolvimento de uma série de métodos analíticos nela baseados, o campo da Filogeografia Estatística (Knowles 2009), ganhou o poder de gerar e testar hipóteses evolutivas através de análises probabilísticas. Por isso, a Filogeografia vem sendo empregada para subsidiar políticas conservacionistas através do estabelecimento de parâmetros genéticos e demográficos, como o grau de conectividade entre populações, índices de diversidade e tamanho populacional (Garrick et al. 2006). Considerando que a Genética da Conservação consiste no uso de ferramentas genéticas aplicadas à conservação de espécies em seu ambiente natural (Frankham 2010), acreditamos que este trabalho representa um ponto de encontro entre a Filogeografia, um ramo de ciência de base focado na microevolução, e sua aplicação prática em medidas conservacionistas.

Membros da família Clupeidae, os táxons *Opisthonema oglinum* (Lesueur 1818) e *Harengula* spp. são peixes marinhos de pequeno porte, encontrados no Atlântico Oeste, que formam grandes cardumes, apresentam desova pelágica (forma larval com duração de 19-25 dias) e usam regiões de estuários como berçário e área de recrutamento (Finucane and Shaffer 1986; Martinez and Houde 1975; Pierce et al. 2001; Vega-Cendejas et al. 1997; Whitehead 1985). A sardinha-bandeira/sardinha-azul, *Opisthonema oglinum* é a única espécie do gênero que ocorre no Atlântico Oeste, com distribuição geográfica do norte dos Estados Unidos até o norte da Argentina, e possui o último raio da nadadeira dorsal prolongado, o que facilita sua identificação (Whitehead 1985). Para as sardinhas-cascudas do gênero *Harengula* Valenciennes 1847, *H.*

humeralis (Cuvier 1829), *H. clupeola* (Cuvier 1829) e *H. jaguana* Poey 1865 são as espécies que ocorrem no Atlântico Oeste (Fricke et al. 2019; Whitehead 1985). Enquanto *H. humeralis* tem sua distribuição restrita ao hemisfério norte, *H. clupeola* e *H. jaguana* são sintópicas e ocorrem do sul dos Estados Unidos até o sul do Brasil (Whitehead 1985). Além disso, essas espécies são confundidas entre si pois um dos únicos caracteres diagnósticos apresenta sobreposição e o outro apresenta diferenças sutis. O número de rastros branquiais inferiores no primeiro arco branquial, em que *H. clupeola* possui de 28 a 34 (normalmente de 30 a 32) rastros, e *H. jaguana* possui de 30 a 40 (normalmente de 32 a 39) rastros (Whitehead 1985). Já as diferenças nas placas dentígeras no assoalho bucal são bem sutis entre essas espécies. Isso tudo dificulta a identificação morfológica dessas espécies, resultando em incertezas taxonômicas. Embora não sejam o principal alvo da pesca de sardinhas, essas espécies são usadas como isca para peixes maiores, ou na alimentação de subsistência (Whitehead 1985). Ademais, os estoques pesqueiros de *H. clupeola* e *H. jaguana* na Zona Econômica Exclusiva do Brasil estão sobre-explotados e *O. oglinum* está totalmente explotado (Verba et al. 2019).

Algumas espécies que apresentavam ampla distribuição no Atlântico Oeste e com pouca ou nenhuma variação morfológica visível, foram identificadas como complexos de espécies crípticas (Colborn et al. 2001; Dias et al. 2019; Floeter et al. 2008; Leite et al. 2008; Rocha 2003; Rodríguez-Rey et al. 2017). Se por um lado os longos períodos larvais de *O. oglinum* e *Harengula* spp. podem permitir o fluxo gênico entre localidades distantes, a reprodução associada aos estuários pode resultar na estruturação populacional (Baggio et al. 2017), que exigiria um manejo pesqueiro diferenciado para cada estoque. Assim, podemos estabelecer uma hipótese para explicar os padrões filogeográficos desses táxons, baseada nos aspectos oceanográficos do Atlântico Oeste.

A estruturação genética de clupeídeos pode estar relacionada com variações de temperatura, salinidade e profundidade, tendo em vista que essas características oceanográficas são conhecidas por influenciarem a estruturação de outras espécies marinhas que possuem larvas pelágicas (Floeter et al. 2008; Luiz et al. 2011; Palumbi 1994; Rocha and Bowen 2008). O deságue dos rios Amazonas e Orinoco (AOP) é uma conhecida barreira biogeográfica intermitent para alguns organismos marinhos (Floeter et al. 2008; Luiz et al. 2011; Rocha 2003; Rocha et al. 2008). O seu deságue de água doce cria uma região de baixa salinidade e alta turbidez no Atlântico Oeste (Luiz et al. 2011). Além disso, essa barreira separa as províncias marinhas Carolinian+Greater Caribbean e Brazilian (Floeter et al. 2008). Considerando que os táxons abordados nesse estudo possuem distribuição geográfica e aspectos biológicos similares, como duração do estágio larval e reprodução em áreas estuarinas, podemos esperar que eles apresentem os mesmos padrões filogeográficos (Lukoschek 2018). O efeito da AOP como barreira biogeográfica intermitente já foi testado por Luiz et al. (2011) em peixes recifais, e se mostrou como uma barreira efetiva para algumas espécies. Todavia, não podemos estipular que a AOP tenha o mesmo efeito sobre os táxons-alvo desse trabalho que são animais costeiros e pelágicos.

Ademais, cardumes de *Harengula* spp. são encontrados em Fernando de Noronha, que é um arquipélago oceânico de origem vulcânica, localizado a 360 km de distância da costa brasileira (Instituto Brasileiro de Geografia e Estatística - IBGE 2015). Essas sardinhas constituem fonte essencial para os pescadores locais, por serem utilizadas como isca para a pesca de grandes peixes pelágicos. No entanto, os cardumes nem sempre se encontram na área de uso sustentável da Área de Proteção Ambiental (APA), pois em algumas épocas do ano eles migram para a área de proteção integral, onde a pesca não é permitida. Isso acarretou um conflito que já dura, pelo menos, 12 anos entre os pescadores e as autoridades ambientais no arquipélago de Fernando de Noronha. Essa problemática já foi trazida à tona por Lopes et al. (2017), que, através de uma análise de cadeia de produtividade, concluiu que o consumo de grandes peixes por turistas e moradores locais, causam uma pressão econômica para a pesca de sardinhas. Informações sobre a identidade dessas sardinhas, e se as mesmas pertencem ao mesmo estoque ao longo da costa brasileira poderá auxiliar na tomada de decisões pelas autoridades a fim de resolver esse conflito.

Esse trabalho foi divido em dois capítulos, o primeiro aborda os aspectos etnográficos da ginga e o segundo identifica e compara os padrões filogeográficos de *O. oglinum* e *Harengula* spp., clupeídeos potencialmente comercializados como ginga. No primeiro capítulo, investigamos duas possíveis hipóteses sobre a identidade taxonômica e distribuição geográfica do nome ginga, podendo ser composta por uma única espécie com mais de um nome para diferentes classes de tamanho, ou composta por mais de uma espécie sob uma mesma denominação. No segundo capítulo, investigamos a estruturação genética entre as províncias Carolinian+Greater Caribbean e Brazilian de *O. oglinum* e *Harengula* spp. usando sequências de mtDNA, em um contexto filogenético temporal, visando entender padrões e processos que modulam a sua diversidade genética.

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2. CAPÍTULO I. SIZE IS DOCUMENT: THE ETHNOICHTHYOLOGY OF A CULTURALLY IMPORTANT SPECIES IN THE NORTHEASTERN BRAZIL

SIZE IS DOCUMENT: THE ETHNOICHTHYOLOGY OF A CULTURALLY IMPORTANT SPECIES IN THE NORTHEASTERN BRAZIL

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Abstract

Fishery statistics, when available, are mainly made by recording the popular name of the fish, which is later translated into scientific identification. Popular names often refer to a species group or, even worse, vary from place to place, increasing identification uncertainty. In addition, variations of local names may also reveal the role that certain species play in a culture. Species that have significant and unique cultural value for a particular traditional community are known as culturally important species (CIS). This cultural importance enhances the success of local conservation measures when a CIS is used as a target species. Herein, we assessed Fishers' Local Ecological Knowledge (LEK) to investigate a clupeid fish ("ginga"), recognized as a cultural heritage of Brazilian northeastern, possibly suggesting it is a CIS. Through 103 interviews, we were able to determine the taxonomic range of "ginga" and where this common name is used. "Ginga" is associated with at least three species of clupeid - *Opisthonema oglinum*, *Harengula* sp., and *Lile piquitinga* - and, although this name may be known elsewhere, its trade, as a set of species contained in a popular name, is unique to a metropolitan area of Natal, in Rio Grande do Norte state. This sort of clarification can support and refine fisheries reconstruction catch data. Also, while none of the clupeids included under the popular name of "ginga" are endangered, their CIS status is a potentially useful tool in fisheries management.

Keywords: Ethnozoology, Fisheries, Clupeidae, Folk Taxonomy, Ginga

Resumo

As estatísticas da pesca, quando disponíveis, são feitas principalmente registrando o nome popular dos peixes, que é posteriormente traduzido em uma identificação científica. Os nomes populares geralmente se referem a um grupo de espécies ou, pior ainda, variam de um lugar para outro, aumentando a incerteza de identificação. Além disso, variações de nomes locais também podem revelar o papel que determinadas espécies desempenham em uma cultura. As espécies que têm um valor cultural significativo e único para uma comunidade tradicional em particular são conhecidas como Espécies Culturalmente Importantes (CIS). Essa importância cultural aumenta o sucesso das medidas locais de conservação quando uma CIS é usada como espécie-alvo. Nesse estudo, avaliamos o Conhecimento Ecológico Local dos pescadores (LEK) para investigar um peixe clupeídeo (ginga), reconhecido como patrimônio cultural no nordeste do Brasil, possivelmente sugerindo que seja uma CIS. Por meio de 103 entrevistas, conseguimos determinar a abrangência taxonômica de ginga e onde esse nome comum é usado. Ginga está associado a, pelo menos, três espécies de clupeídeos - *Opisthonema oglinum*, *Harengula* sp. e *Lile piquitinga* - e, embora esse nome possa ser conhecido em outros lugares, seu comércio, como um conjunto de espécies contidas em um nome popular, é exclusivo da região metropolitana de Natal, no estado do Rio Grande do Norte. Esse tipo de esclarecimento pode auxiliar e refinar a reconstrução dos dados de captura da pesca. Além disso, embora nenhum dos clupeídeos incluídos sob o nome popular de ginga esteja em perigo, seu status de CIS é uma ferramenta potencialmente útil no gerenciamento da pesca.

Palavras-chave: Etnozoologia, Pesca, Clupeidae, Taxonomia popular, Ginga

2.1 Introduction

Overfishing is one of the leading causes of declining marine populations and fish stocks worldwide, together with habitat loss, invasive species, and climate change (Coleman and Williams 2002; Diamond 1984; Pauly et al. 2003). Yet, many species that are being overexploited or overfished may lack basic information, such as correct taxonomic identification, geographical distribution, and stock delimitation (Carvalho and Hauser 1995; Ward et al. 2005), without which proper management can be compromised.

Taxonomic uncertainties diminish and hamper the reliability of fishery statistical data (FAO 2016). This is most evident for some small and abundant fishery resources, for which only common names are considered, such as sardines and anchovies that may harbor several taxa under the same denomination. An example is the fish known as "pititinga" in Bahia state, northeast of Brazil, which includes several morphologically similar species (Rodrigues et al. 2016). This richness of biological species corresponding to fewer popular names is known in the ethnotaxonomy literature as under-differentiation Type II (Berlin 1973). There are two types of under-differentiation, type I, when a popular name corresponds to more than one species of the same genus, and type II, when a popular name corresponds to more than one species of different genera (Seixas and Begossi 2001). In other cases, people may consciously assign different names to distinct life phases of a given species. The blue runner *Caranx crysos* (Mitchill, 1815), for instance, is known in parts of Brazil as "Manequinho", "Carapau", or "Xerelete", depending on their life stage or size (over-differentiation Type I) (Berlin 1973; Seixas and Begossi 2001). Fishers' Local Ecological Knowledge (LEK) assessment is an alternative to correctly associate common names with the scientific species to which they correspond (Begossi et al. 2016; Costa-Neto and Marques 2000; Freire and Pauly 2005; Previero et al. 2013; Seixas and Begossi 2001).

Clupeid fishes are widely exploited worldwide for human consumption, fishmeal and fish oil, and as baitfish (Whitehead 1985). Although they tend to form large schools and have high fecundity and early maturity (Opportunistic, Kindsvater et al. 2016), some species have been overexploited in some localities in Atlantic and Pacific Ocean (Clark 1976; Cushing 1992; Dickey-Collas et al. 2010; Jablonski 2007; Verba et al. 2019). Recently, Verbal et al. (2019) assessed the exploitation status of fish species in the Brazilian Exclusive Economic Zone and of the six clupeid species analyzed, five are fully exploited, overexploited, or collapsed.

In some places, these usually small fish are also a significant part of a culture, such as sardines in Portugal (Instituto Nacional de Estatística 2012) or in northeastern Brazil (Lessa et al. 2004). In these places, the clupeid cultural value goes beyond their socio-economic importance, being, for example, part of signature dishes (Dantas 2015; Lima et al. 2016; Sobral 2008). These species with high significance for human culture can be considered “culturally important species” (CIS), which is a broader term compared to “cultural keystone species” (Freitas et al. 2020). While “cultural keystone species” are species whose existence are crucial to the survival and identity of human cultures (Cristancho and Vining 2004; Garibaldi and Turner 2004), the CIS are species that have significant importance in a culture, but are not necessarily essential for the survival of the culture (Freitas et al. 2020). Nonetheless, the decline or overexploitation of CIS may negatively affect the subsistence and traditional practices of a traditional community (Freitas et al. 2020).

In northeastern Brazil, in addition to the popular name “sardinha” (sardine), the name “ginga” is used for small clupeid fish, but it is not clear if it comprises juveniles of a single species (over-differentiation Type I) or individuals/juveniles of multiple species (under-differentiation Type I or II). “Ginga” itself was declared an Intangible Cultural Heritage under the Rio Grande do Norte State Law Nº 10.481 (Rio Grande do Norte 2019) as part of what may be the most important traditional local dish, the “ginga with tapioca” (small fried fish inside a cassava flour pancake). Still, an ethnoichthyological study has not been conducted to identify which species are actually consumed. In the days prior to the existence of “ginga with tapioca” (created between 1950-1960), these small fish juveniles/fry used to be discarded by fishers (Dantas 2015; Lima et al. 2016).

The trade of fry or juvenile fish under a single common name, such as “ginga”, precludes an accurate identity of the traded species and, thus, of the quantities regularly harvested and in which stages of their life cycle. This information would not only support future management, but also help in the effort made in recent years to reconstruct historical information on fisheries catch around the world, including Brazil (Freire and Oliveira 2007). Therefore, this study aims to combine the sampling of individuals in fish markets with the identification and description of the fish sold as “ginga”, according to fishers. Accordingly, this study has an ethnographic objective, in the sense that it describes the perception of fishers about what would be the fish known as “ginga”. Our hypothesis is that “ginga” comprehends more than one species (under-differentiation). Considering that a vernacular generic name is an impediment to the generation of reliable fishery statistics data, it is important to describe the “ginga” taxonomic range to direct the focus of fisheries management measures to this group

2.2 Material and Methods

2.2.1 Samplings

Interviews and fish sampling were conducted at six important fish landing sites on the northeast coast of Brazil (IBAMA 2006; Lessa et al. 2004; Silva 2010), which included three different states: Rio Grande do Norte (samplings in Macau, Natal, and Baía Formosa municipalities, in the north, east and southeast parts of the state, respectively), Paraíba (Cabedelo), and Pernambuco (Recife and Fernando de Noronha, the latter an oceanic island). Although "ginga" is a cultural heritage of Rio Grande do Norte, we included two neighboring states (Paraíba and Pernambuco) to assess the geographical range of this popular name. In each site, we searched for traditional fishing communities and local fish markets to conduct the interviews and purchase fish.

In five fish markets at each of the sampling sites, we bought 0.5 kg of fresh or frozen fish that were being sold as "ginga" and "sardinha". Individuals were measured (standard length) and identified to species level, whenever possible, using the "Manual de Peixes Marinhos do Sudeste do Brasil: Teleostei (1)" (Figueiredo and Menezes 1978) and the FAO Species Catalogue Vol. 7 Clupeoid fishes of the world (Whitehead 1985). All material was deposited in the ichthyological collection of the Federal University of Rio Grande do Norte (UFRN). Samplings were conducted under the permit SISBIO nº 67671-1.

2.2.2 Interviews and questionnaire

Prior to the interviews, we briefly explained the purpose of our study and asked if the fisher would like to participate. Those who accepted signed an informed consent form. The approaching procedure followed the recommendations of the Research Ethics Committee (CAAE 09901318.1.0000).

The semi-structured questionnaire was elaborated in two sections (Annex 1). The first consisted of an identification board with photos of nine species of small commercial coastal fishes, one photo per species, so that the fisher would provide the popular name of each fish s/he recognized (Annex 2). The photographs corresponded to the species or genus: *O. oglinum* (Lesueur, 1818), *Harengula* sp., *Sardinella brasiliensis* (Steindachner, 1879), and *Lile piquitinga* (Schreiner, Miranda & Ribeiro, 1903) of Clupeidae family, *Lycengraulis grossidens* (Spix & Agassiz, 1829), *Cetengraulis edentulus* (Cuvier, 1829), and *Anchoviella lepidentostole* (Fowler, 1911) of Engraulidae family, *Atherinella brasiliensis* (Quoy & Gaimard, 1825) of Atherinopsidae family, and *Mugil* spp. of Mugilidae family (*sensu* Fricke et al. 2019). These species were selected based on their characteristics, specifically small size, metallic silver body, and schooling behavior. The second section consisted of questions about fishing gear, purpose, and sale value of each fish species according to its popular name. This questionnaire was conducted at different localities to check for divergence or convergence of popular names for these commercial species and which species were sold as “ginga”.

2.2.3 Data analysis

First, the raw data from the interviews were tabulated and categorized. The processed information acquired in the interviews was organized and standardized in digital spreadsheets.

To determine the geographic range of the name “ginga”, we analyzed the processed ethnoichthyological data and searched for which localities fishers recognized any of the species shown in the questionnaire as “ginga”. For the “ginga” taxonomic range, we analyzed both the processed ethnoichthyological data and the species we identified and that were being sold as “ginga”. The distribution map was created using software QGIS 3.10.2 (QGIS Development Team 2020).

To establish if “ginga” were being sold below its size at first sexual maturity, we calculated the mean and median of the Standard Length (SL), from the snout tip to the beginning of the caudal fin, for individuals sold as “ginga” (N=293) and “sardinha” (N=57) using the software R (R Development Core Team 2019). We then calculated the frequency distribution of fish size using the Sturges’ equation (Sturges 1926): $K = 1 + 3.332 \log (N)$, where K is the number of classes and N is the number of individuals. The amplitude of each class was calculated using the formula: $A = (\max SL – \min SL) / K$, where A is amplitude, and max SL and min SL are the maximum and minimum SL sampled, respectively.. The size at first sexual maturity of the main species identified as “ginga” or “sardinha” were determined according to the literature (Martinez and Houde 1975; Trindade-Santos and Freire 2015).

2.3 Results

2.3.1 Fisher’s knowledge

A total of 103 interviews were conducted during the survey with the fishers at six localities (35 in Macau, 23 in Natal, 25 in Baía Formosa, four in Cabedelo, seven in Recife, and nine in Fernando de Noronha) (Figure 1a). Except for one female in Cabedelo, all fishers were male. These fishers were on average 50.4 ± 12.1 years old and had been fishing for 34.7 ± 14.1 years. About half (49%) of the fishers were born in the same place where they currently live and fish.

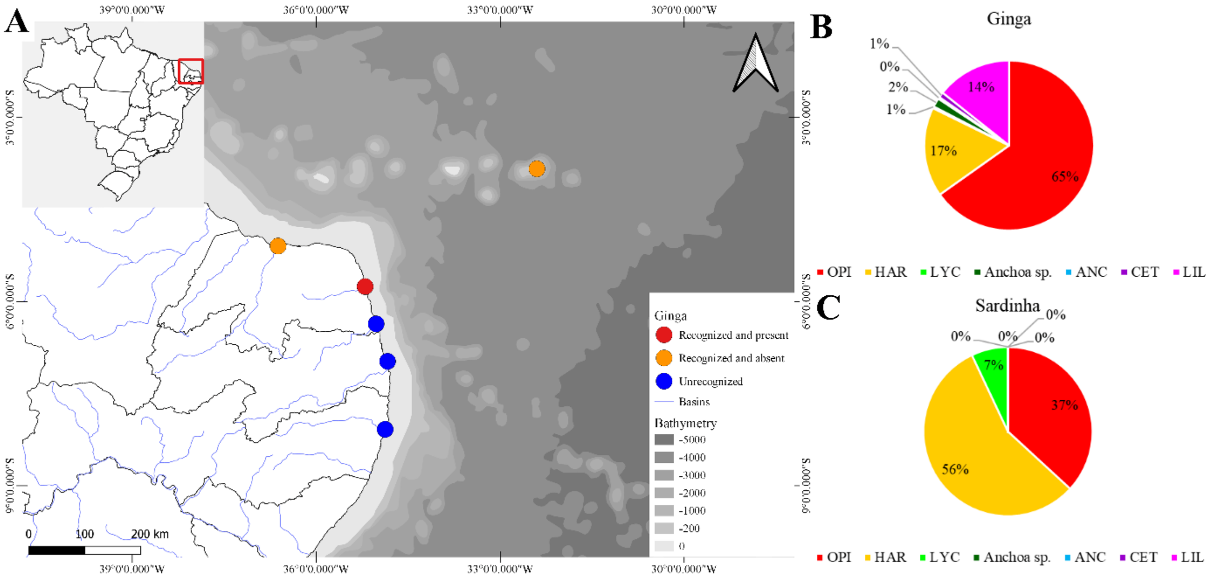


Figure 1. Map of sampling localities and graphs of species composition. A. Sampling localities of interviews and fish specimens, sites in different colors show where the popular name "ginga" was cited by fishers; B. Species composition of fish sold as "ginga" (n=293); C. Species composition of fish sold as "sardinha" (n=57). OPI = *Opisthonema oglinum*, HAR = *Harengula* spp., LYC = *Lycengraulis grossidens*, ANC = *Anchoviella lepidentostole*, CET = *Cetengraulis edentulus*, LIL = *Lile piquitinga*.

In the identification stage of the interview, fishers cited over 30 popular names for the nine species presented. The most cited were "sardinha" (sardine/herring), "arenque" (anchovy), "ginga", and "manjuba", respectively. The name "ginga" was cited in Natal, Macau, and Fernando de Noronha (20.3%). However, the fishers in Macau and Fernando de Noronha that cited "ginga" stated that this fish only occurs in Natal. The name "sardinha" was cited by all fishers in all localities, and "arenque" was the second most cited common name (79.6%), followed by "manjuba" (25.2%) (Table 1).

Table 1. Localities were the interviews were conducted and the common names that were cited by the local fishers.

Local (N of interviews)	Sardinha (%)	Arenque (%)	Ginga (%)	Manjuba (%)
Macau/RN (35)	35 (100%)	31 (88.5%)	6 (17.1%)	8 (22.8%)
Natal/RN (23)	23 (100%)	18 (78.2%)	14 (60.8%)	4 (17.3%)
Baía Formosa/RN (25)	25 (100%)	23 (92%)	0 (0%)	7 (28%)
Cabedelo/PB (4)	4 (100%)	1 (25%)	0 (0%)	2 (50%)
Recife/PE (7)	7 (100%)	7 (100%)	0 (0%)	4 (57.1%)
Fernando de Noronha/PE (9)	9 (100%)	2 (22.2%)	1 (11.1%)	1 (11.1%)
Total (103)	103 (100%)	82 (79.6%)	21 (20.3%)	26 (25.2%)

Legend: PB: Paraíba state, PE: Pernambuco state, RN: Rio Grande do Norte state.

According to the fishers' identifications, we were able to assess the species compositions of "ginga", "sardinha", "arenque" and "manjuba" (Figure 2). For the fishers, "ginga" was mainly composed by *Harengula* spp. (HAR) (44%), followed by *Anchoviella lepidentostole* (ANC) (24.8%), *Lile piquitinga* (LIL) (16%), and *Opisthonema oglinum* (OPI) (12%), all belonging to the family Clupeidae, except ANC which belongs to the family Engraulidae. The "sardinha" was mainly composed by OPI (25%) and HAR (24.4%), and, to a lesser extent, composed by *Sardinella brasiliensis* (SAR) (18.9%), *Cetengraulis edentulous* (CET) (15.9%), and LIL (9.3%) all belonging to Clupeidae, except CET that belongs to Engraulidae. Fish identified as "arenque" were mainly composed by *Lycengraulis grossidens* (LYC) (36.7%), followed by ANC (22.2%), CET (13.4%), SAR (9.3%), and *Atherinella brasiliensis* (ATH) (9.3%). LYC, ANC, and CET belong to Engraulidae, SAR belong to Clupeidae, and ATH is a presentative of the order Atheriniformes, family Atherinopsidae. Lastly, "manjuba" was composed of ANC (48.2%), SAR (13.8%), ATH (20.6%), and HAR (6.9%).

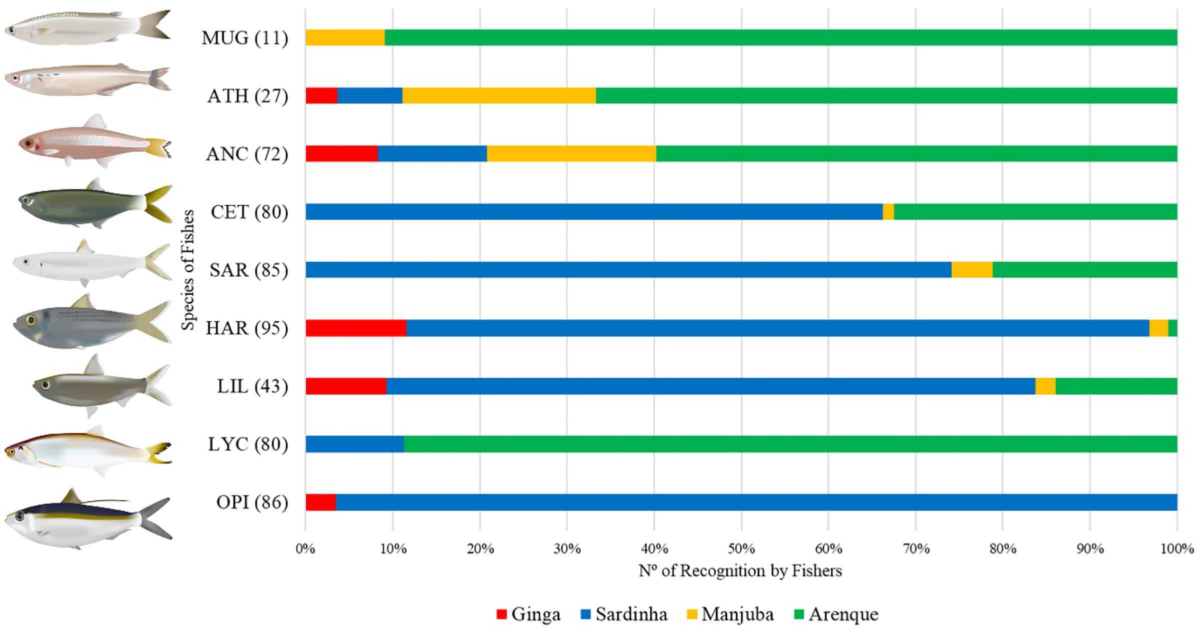
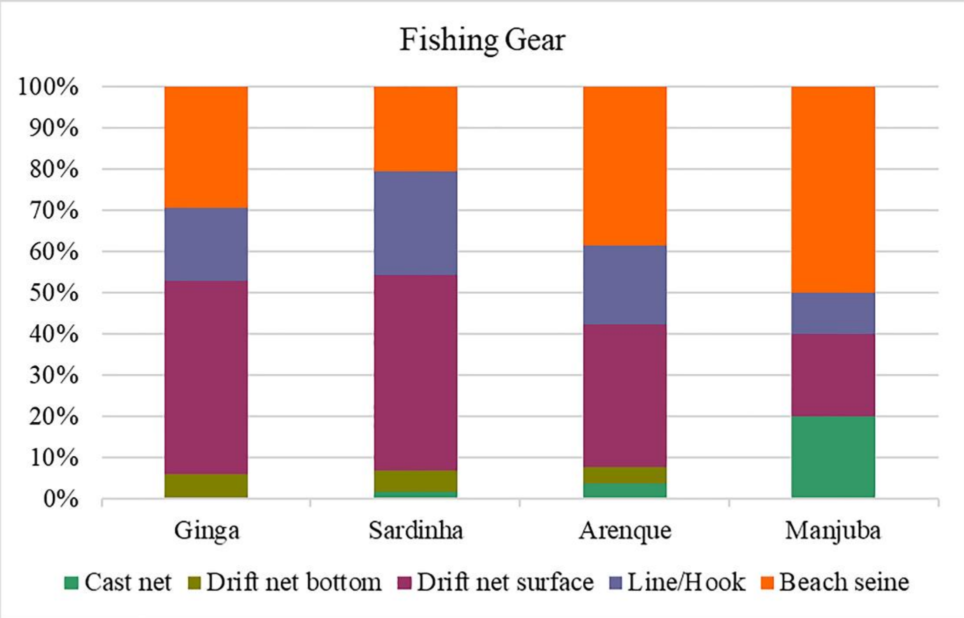
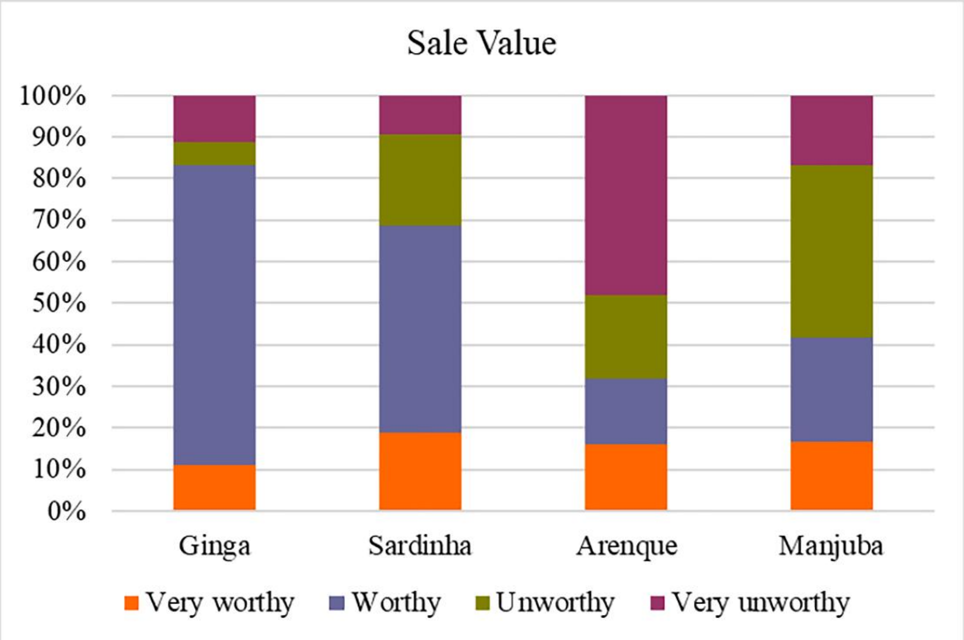


Figure 2. The common names assigned by northeastern Brazil fishers (n=103) according to photo plates. The values on the x axis correspond to how many times the species was recognized as that common name, the total value for each is between parenthesis. OPI = *Opisthonema oglinum*; LYC = *Lycengraulis grossidens*; LIL = *Lile piquitinga*; HAR = *Harengula* sp.; SAR = *Sardinella brasiliensis*; CET = *Cetengraulis edentulus*; ANC = *Anchoviella lepidentostole*; ATH = *Atherinella brasiliensis*; MUG = *Mugil* sp.

The fishing aspects of “ginga”, “sardinha”, “arenque”, and “manjuba” were assembled based on the fishers’ answers (Figure 3). For “ginga”, its fishing characteristics were drift net surface as fishing gear used (47%), worthy as sale value (72.2%), and sale for consumption as purpose of fishing (38.2%). “Sardinha” had the same characteristics: drift net surface as fishing gear used (47.4%), worthy as sale value (50%), and sale for consumption as purpose of fishing (33.6%). For “arenque”, the fishing characteristics were beach seine as fishing gear used (38.5%), very unworthy as sale value (48%), and own use for consumption as purpose of fishing (38.7%). And for “manjuba”, its fishing characteristics were beach seine as fishing gear used (50%), unworthy as sale value (41.6%), and sale for consumption as purpose of fishing (46.1%).


Fishing Gear
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Ginga
Sardinha
Arenque
Manjuba
Cast net
Drift net bottom
Drift net surface
Line/Hook
Beach seine


Sale Value
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Ginga
Sardinha
Arenque
Manjuba
Very worthy
Worthy
Unworthy
Very unworthy

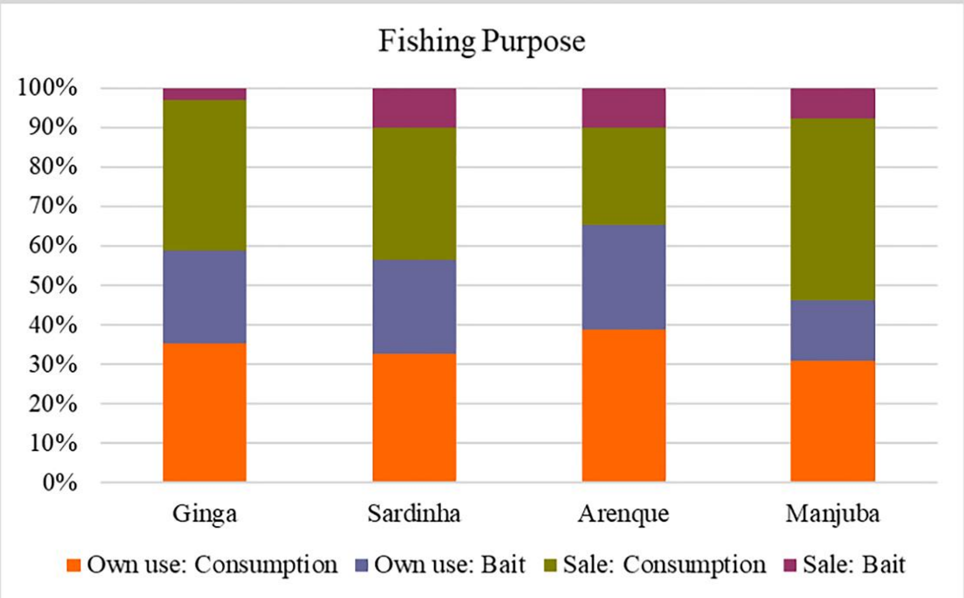

Fishing Purpose
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Ginga
Sardinha
Arenque
Manjuba
Own use: Consumption
Own use: Bait
Sale: Consumption
Sale: Bait

Figure 3. Fishing characteristics of fishes by their common names in northeastern Brazil.

2.3.2 Size is document, the "ginga" case

We acquired fish specimens from Natal, Macau, and Cabedelo to assess which species were being caught and sold as "ginga" and "sardinha" (Table 2). We did not purchase fish in Baía Formosa, Recife, and Fernando de Noronha because there were no "ginga" or "sardinha" being sold at the time of the sampling. We did not attempt to buy "arenque" and "manjuba" because they are not commercially valuable species, thus they are not sought or sold separately in fish markets

Table 2. List of the species and their common names used by local fishers and fish markets.

Species	Family	Common name	Locality	Catalog number
Opisthonema oglinum	Clupeidae	Ginga	Natal, RN	UFRN4786-5134-5547
Chloroscombrus chrysurus	Carangidae	Ginga	Natal, RN	UFRN4787-5135
Lile piquitinga	Clupeidae	Ginga	Natal, RN	UFRN5301
Harengula sp.	Clupeidae	Ginga	Natal, RN	UFRN5302-5309-5548
Anchoviella lepidentostole	Engraulidae	Ginga	Natal, RN	UFRN5133-5303-5549
Anchoa sp.	Engraulidae	Ginga	Natal, RN	UFRN5304
Cetengraulis edentulus	Engraulidae	Ginga	Natal, RN	UFRN5305-5550
Lycengraulis grossidens	Engraulidae	Ginga	Natal, RN	UFRN5132-5306
Opisthonema oglinum	Clupeidae	Ginga	Natal, RN	UFRN4790
Opisthonema oglinum	Clupeidae	Sardinha	Natal, RN	UFRN4791
Opisthonema oglinum	Clupeidae	Sardinha	Cabedelo, PB	UFRN4906
Harengula sp.	Clupeidae	Sardinha	Cabedelo, PB	UFRN4907
Opisthonema oglinum	Clupeidae	Sardinha	Macau, RN	UFRN5053
Opisthonema oglinum	Clupeidae	Sardinha	Macau, RN	UFRN5054
Lycengraulis grossidens	Engraulidae	Sardinha	Macau, RN	UFRN5055

Legend: RN: Rio Grande do Norte state, PB: Paraíba state.

Most specimens commonly known as "ginga" belonged to *O. oglinum*, followed by *Harengula* sp. and *L. piquitinga* (Figure 1b). Moreover, few additionally specimens belonged to Engraulidae were also named "ginga". Although "ginga" was recognized in Macau, Fernando de Noronha, and Natal, all 293 specimens of "ginga" were bought in Natal, since it was the only place where this fish was being sold. Individuals sold as "sardinha" were mainly *Harengula* sp. and *O. oglinum*, with few specimens of *L. grossidens* (Figure 1c). The 57 individuals sold as "sardinha" were bought in Natal, Macau, and Cabedelo.

We measured 350 individuals that were sold as "sardinha" and "ginga" in Natal, Macau, and Cabedelo (Figure 4). The mean and median for "sardinha" was 130.7 mm and 114.3 mm, respectively, and for "ginga" these values were 77.4 mm and 76.9 mm, respectively.

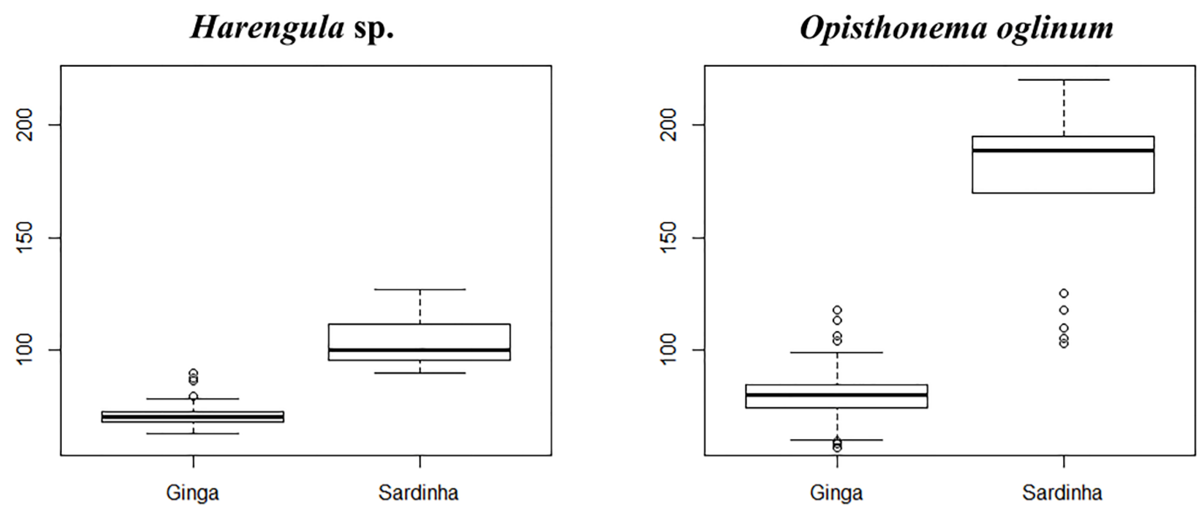


Figure 4. Boxplots of the standard length (SL) of *Harengula* sp. (n=82) and *Opisthonema oglinum* (n=212) sold as “ginga” and “sardinha” in Rio Grande do Norte and Paraíba states.

Most individuals of the main species sold as “ginga” were below the size at first sexual maturity, which are 78-85 mm of SL for *Harengula* sp. and 117-157 mm of SL for *Opisthonema oglinum* (Martinez and Houde 1975; Trindade-Santos and Freire 2015), (n=41, 82% for *Harengula* sp; n=190, 99.5% for *O. oglinum*) (Figure 5). For fish sold as “sardinha”, all individuals of *Harengula* sp. (n=32) were above the size at first sexual maturity and most individuals of *O. oglinum* (n=16) were above the size at first sexual maturity.

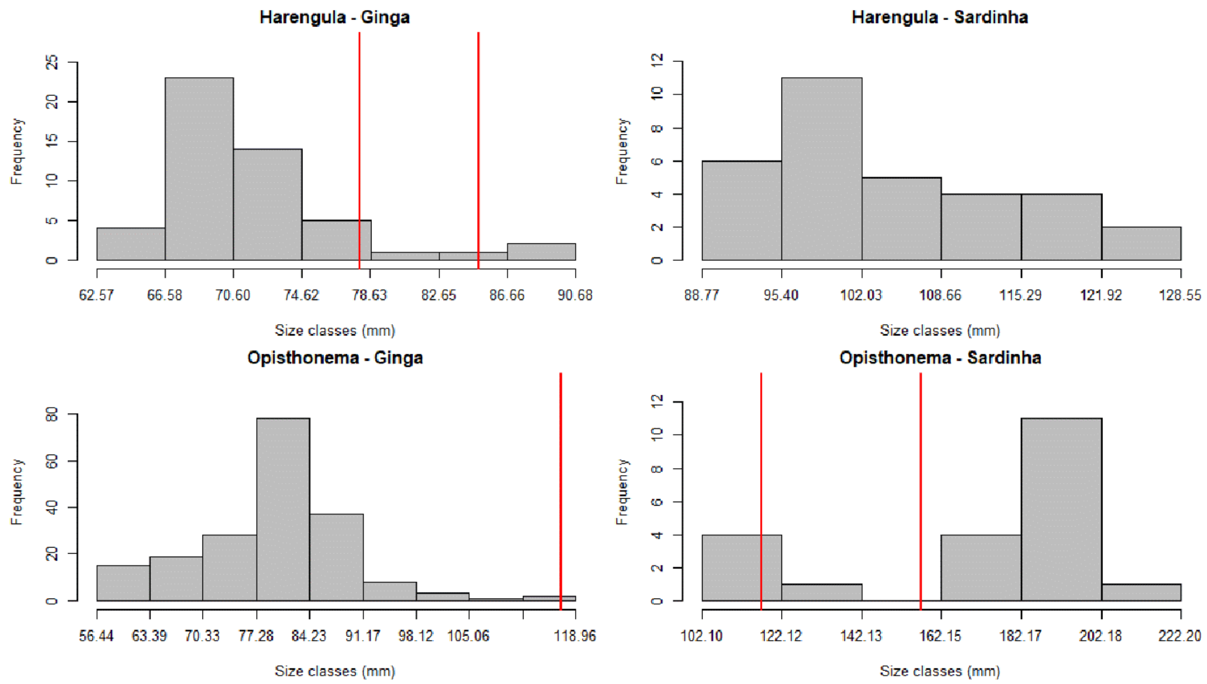


Figure 5. Frequency distribution of size of *Harengula* sp. (n=82) and *Opisthonema oglinum* (n=212) sold as "ginga" and "sardinha" in Rio Grande do Norte and Paraíba states. Red lines indicate the size at first sexual maturity.

Natal and "ginga"

All fishes purchased as "ginga" were bought in Natal, as it was the only place where this fish was being sold. We acquired 293 individuals in a total of six field trips to fish markets in March, October, and December of 2018 and January and March of 2019. On the first field in March, we acquired 116 specimens of *O. oglinum* and one specimen of *Chloroscombrus chrysurus*, the latter a member of the family Carangidae, Carangiformes. On the second, also in March, we acquired 10 individuals of *O. oglinum* and one Engraulidae individual. We were unable to identify this last specimen further because its head was missing. However, due to some specific characteristics such as body shape, longitudinal silver band on both sides of the body, and position of dorsal fin (Figueiredo and Menezes 1978; Whitehead 1985), we identified it as a possible member of Engraulidae. On October, we acquired 73 specimens of *O. oglinum*, eight specimens of *A. lepidentostole*, five specimens of *L. grossidens*, and one specimen of *C. chrysurus*. On December, we acquired 41 individuals of *L. piquitinga*, 20 individuals of *O. oglinum*, five individuals of *Anchoa* sp., four individuals of *L. grossidens*, three individuals of *Harengula* sp., three individuals of *C. edentulus*, and two individuals of *A. lepidentostole*. On January, we acquired 50 specimens of *Harengula* sp. On the last field trip in March, we acquired 30 specimens of *Harengula* sp., 29 specimens of *O. oglinum*, one specimen of *C. edentulus*, and one specimen of *A. lepidentostole*.

2.4 Discussion

Ethnotaxonomy or folk taxonomy is the labelling of organisms according to the perception of traditional communities. Understanding this knowledge is particularly important for organisms that are traded under a popular name, which is based on a set of criteria used by local communities (Johannes 1998; Johannes et al. 1999). One source of uncertainty that negatively affects catch statistics is a lack of knowledge of common names and corresponding fish species (Freire and Pauly 2005). Without this correspondence, it is difficult to know the species exploited by fisheries. Additionally, ethnotaxonomy is also a source of knowledge that can provide guidance for conservation efforts, as fishers' LEK can provide valuable insight into the diversity of species from locations lacking scientific knowledge (Begossi et al. 2008).

Our results showed that the common name "ginga" is not associated with a particular fish species, but with the small size of a few fish species. This kind of correspondence is an under-differentiation Type II. Small silver fishes that form schools and are associated with coastal environment are identified as "ginga" by the local community of Natal in Rio Grande do Norte state. The species with greater representativity as "ginga" were the clupeids *Opisthonema oglinum*, *Harengula* sp., and *Lile piquitinga*, respectively. Most individuals (94.6%) sold as "ginga" were under the size of first sexual maturity, which puts pressure on juveniles. Catching fish that have not reached sexual maturity may decrease future catches, recruitment of fish stocks, and lead to overexploitation (Crowder and Murawski 1998; Diamond et al. 1999; Najmudeen and Sathiadhas 2008). However, other studies suggest that due to the natural high mortality in juveniles of some species, targeting juveniles is "better" than fishing the adults to avoid overexploitation (e.g. Codling et al. 2005; Crouse et al. 1987). Even though *O. oglinum* and *Harengula* spp. (both *H. jaguana* and *H. clupeola*) are considered as Least Concern by IUCN (Munroe et al. 2015a, 2015b, 2019), their stocks in Brazil are fully exploited and overexploited, respectively (Verba et al. 2019). While *O. oglinum* is mainly exploited by industrial fishery, *Harengula* spp. is mainly exploited by small-scale fishery (Verba et al. 2019)

Fishers' perception of "ginga" is slightly different from what is actually sold in fish markets: individuals sold as "ginga" were mainly composed by *O. oglinum* in markets, whereas fishers recognize "ginga" mainly as *Harengula* sp. While five species (HAR, OPI, LIL, ANC, ATH) were indicated as "ginga" by fishers, seven species (HAR, OPI, LIL, ANC, CET, LYC, *Anchoa* sp.) were identified being sold as "ginga" in markets. Also, fishers indicated only one species of Engraulidae and one species of Atherinopsidae as "ginga", but among the fishes sold as "ginga" on markets, we identified four species of Engraulidae and none of Atherinopsidae. This disparity may have been caused by the fishes' pictures used in the interview, which are from adult individuals (adults of *O. oglinum* are larger than *Harengula* sp.) and fishers associate "ginga" with small sized fish (juveniles). Corroborating this idea is the fact that all specimens of the smaller of those species, such as *L. piquitinga*, were sold as 'ginga'. Additionally, "ginga" is a common name used exclusively in Natal's metropolitan area. Therefore, the "ginga" found in markets is the result of the artisanal fishing of juveniles of a few clupeid species that occur in coastal waters, which are captured by surface drift nets, have a medium sale value, and are mainly sold for consumption.

The association of "ginga" with the local and traditional dish "ginga com tapioca", makes "ginga" not only a food and economic resource but also a cultural asset of Natal. Therefore, the species associated to "ginga" could be considered CIS, meaning that they can play an important role in conservation and fisheries management, improving the odds of making conservation work in contrast to non-CIS (Cristancho and Vining 2004; Garibaldi and Turner 2004; Noble et al. 2016).

2.5 Conclusion

Using LEK as a tool for gaining taxonomic knowledge of locally marketed fishes is one way to tackle some of the most basic problems associated with fishing statistics: to actually know what is caught by fishers. Also, this source of knowledge is a valuable ally to conservation. Herein we identified that "ginga" is an assemblage of juveniles of different species (*O. oglinum*, *Harengula* sp., *L. piquitinga*, and few species of Engraulidae), caught in the city of Natal, Rio Grande do Norte state. Fishing pressure on juveniles may be a threat to the maintenance of fish stocks, which are already considered as fully exploited or overexploited, depending on the quantity caught and some eventual selection process by fishery on these juveniles. On the other hand, "ginga" could be considered a CIS, given its singular cultural importance to local communities, which could facilitate any eventual conservation measure. Additional studies should be done to evaluate the impacts of fishing on juveniles, while promoting the role of "ginga" as a CIS to ensure the maintenance of these stocks.

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2.7 Appendix

Annex 1. Semi-structured questionnaire used for fishers' interviews.

Nome do entrevistador: __________________ Data: _________
Cidade: __________________ Comunidade: __________________
Nome do pescador: _________________________________ Naturalidade: __________________
Idade: ___________ Gênero: ______________ Ano que começou a pescar: _________

Mostrar a prancha de ID e perguntar se o pescador conhece os peixes e por qual nome ele os conhece

- ⇨ **SE NÃO CONHECE:** Concluir entrevista.
- ⇨ **SE CONHECE:** Continue.

Qual peixe é a ginga? ❑OPI ❑LYC ❑LIL ❑HAR ❑SAR ❑CET ❑ANC ❑ATH ❑MUG ❑outro ❑não conhece

Qual peixe é a sardinha? ❑OPI ❑LYC ❑LIL ❑HAR ❑SAR ❑CET ❑ANC ❑ATH ❑MUG ❑outro ❑não conhece

Qual peixe é a manjuba? ❑OPI ❑LYC ❑LIL ❑HAR ❑SAR ❑CET ❑ANC ❑ATH ❑MUG ❑outro ❑não conhece

Qual peixe é a/o ____________________? ❑OPI ❑LYC ❑LIL ❑HAR ❑SAR ❑CET ❑ANC ❑ATH ❑MUG ❑outro ❑não conhece

Qual peixe é a/o ____________________? ❑OPI ❑LYC ❑LIL ❑HAR ❑SAR ❑CET ❑ANC ❑ATH ❑MUG ❑outro ❑não conhece

Gostaria que o senhor pensasse apenas sobre a pesca da GINGA:

Em que ano começou a pescar? ______ **Em que ano parou de pescar?** _____ *[❑ainda pesca]*

Qual tipo de pesca o senhor realiza?
Qual a quantidade normalmente pescada? ______________ ❑ kg *[❑ outra unidade: _________]*
Tempo de pesca: ❑horas ❑dias ________________________ Número de pescadores:________
Aparelho: ❑Rede espera: (❑Fundo❑Superfície) ❑Tarrafa ❑Rede arrasto: (❑Praia ❑Fundo) ❑Linha/Anzol ❑Outro: ___________

Época do ano: ❑Jan ❑Fev ❑Mar ❑Abr ❑Mai ❑Jun ❑Jul ❑Ago ❑Set ❑Out ❑Nov ❑Dez

Qual o destino do peixe pescado: ❑Uso próprio para consumo ❑Uso próprio como isca ❑Venda para consumo ❑Venda como isca ❑Outro: ____________________________

Para as próximas perguntas, considere a sua carreira de pesca inteira na pescaria.
Dada a sua experiência, o senhor diria que a quantidade de peixe (kg/ton):
❑ Aumentou ❑ Diminuiu ❑ Permaneceu igual ❑ Não sabe

Durante o seu tempo na pescaria, o senhor diria que o tamanho dos peixes:

- ❑ Aumentou
- ❑ Diminuiu
- ❑ Permaneceu igual
- ❑ Não sabe

Considere o custo de pescar, o tempo e esforço que leva para pescar, e o preço de venda dessa pescaria nos últimos anos em que pescou. O senhor diria que essa pescaria:

❑ Vale muito a pena
❑ Vale a pena
❑ Quase não vale a pena
❑ Com certeza não vale a pena

Gostaria que o senhor pensasse apenas sobre a pesca da SARDINHA:

Em que ano começou a pescar? ______ **Em que ano parou de pescar?** _____ *[❑ainda pesca]*

Qual tipo de pesca o senhor realiza?
Qual a quantidade normalmente pescada? _______________ ❑ kg *[❑ outra unidade: _________]*
Tempo de pesca: ❑horas ❑dias _________________________ Número de pescadores:________
Aparelho: ❑Rede espera: (❑Fundo❑Superfície) ❑Tarrafa ❑Rede arrasto: (❑Praia ❑Fundo) ❑Linha/Anzol ❑Outro: ___________

Época do ano: ❑Jan ❑Fev ❑Mar ❑Abr ❑Mai ❑Jun ❑Jul ❑Ago ❑Set ❑Out ❑Nov ❑Dez

Qual o destino do peixe pescado: ❑Uso próprio para consumo ❑Uso próprio como isca ❑Venda para consumo ❑Venda como isca ❑Outro: _____________________________

Para as próximas perguntas, considere a sua carreira de pesca inteira na pescaria.
Dada a sua experiência, o senhor diria que a quantidade de peixe (kg / ton):
❑ Aumentou ❑ Diminuiu ❑ Permaneceu igual ❑ Não sabe

Durante o seu tempo na pescaria, o senhor diria que o tamanho dos peixes:

❑ Aumentou
❑ Diminuiu
❑ Permaneceu igual
❑ Não sabe

Considere o custo de pescar, o tempo e esforço que leva para pescar, e o preço de venda dessa pescaria nos últimos anos em que pescou. O senhor diria que essa pescaria:

❑ Vale muito a pena
❑ Vale a pena
❑ Quase não vale a pena
❑ Com certeza não vale a pena

Gostaria que o senhor pensasse apenas sobre a pesca da MANJUBA:

Em que ano começou a pescar? ______ **Em que ano parou de pescar?** _____ *[❑ainda pesca]*

Qual tipo de pesca o senhor realiza?
Qual a quantidade normalmente pescada? _______________ ❑ kg *[❑ outra unidade: _________]*
Tempo de pesca: ❑horas ❑dias _________________________ Número de pescadores:________
Aparelho: ❑Rede espera: (❑Fundo❑Superfície) ❑Tarrafa ❑Rede arrasto: (❑Praia ❑Fundo) ❑Linha/Anzol ❑Outro: ___________

Época do ano: ❑Jan ❑Fev ❑Mar ❑Abr ❑Mai ❑Jun ❑Jul ❑Ago ❑Set ❑Out ❑Nov ❑Dez

Qual o destino do peixe pescado: ❑Uso próprio para consumo ❑Uso próprio como isca ❑Venda para consumo ❑Venda como isca ❑Outro: _____________________________

Para as próximas perguntas, considere a sua carreira de pesca inteira na pescaria.

Dada a sua experiência, o senhor diria que a quantidade de peixe (kg / ton):
❑ Aumentou ❑ Diminuiu ❑ Permaneceu igual ❑ Não sabe

Durante o seu tempo na pescaria, o senhor diria que o tamanho dos peixes:	❑ Aumentou ❑ Diminuiu ❑ Permaneceu igual ❑ Não sabe
Considere o custo de pescar, o tempo e esforço que leva para pescar, e o preço de venda dessa pescaria nos últimos anos em que pescou. O senhor diria que essa pescaria:	❑ Vale muito a pena ❑ Vale a pena ❑ Quase não vale a pena ❑ Com certeza não vale a pena

Gostaria que o senhor pensasse apenas sobre a pesca da _____________________:

Em que ano começou a pescar? ______ **Em que ano parou de pescar?** _____ *[❑ainda pesca]*

Qual tipo de pesca o senhor realiza?
Qual a quantidade normalmente pescada? _______________ ❑ kg *[❑ outra unidade: __________]*
Tempo de pesca: ❑horas ❑dias _________________________ Número de pescadores:_________
Aparelho: ❑Rede espera: (❑Fundo❑Superfície) ❑Tarrafa ❑Rede arrasto: (❑Praia ❑Fundo)
❑Linha/Anzol ❑Outro: ____________

Época do ano: ❑Jan ❑Fev ❑Mar ❑Abr ❑Mai ❑Jun ❑Jul ❑Ago ❑Set ❑Out ❑Nov ❑Dez

Qual o destino do peixe pescado: ❑Uso próprio para consumo ❑Uso próprio como isca ❑Venda para consumo ❑Venda como isca ❑Outro: _____________________________

Para as próximas perguntas, considere a sua carreira de pesca inteira na pescaria.
Dada a sua experiência, o senhor diria que a quantidade de peixe (kg/ton):
❑ Aumentou ❑ Diminuiu ❑ Permaneceu igual ❑ Não sabe

Durante o seu tempo na pescaria, o senhor diria que o tamanho dos peixes:	❑ Aumentou ❑ Diminuiu ❑ Permaneceu igual ❑ Não sabe
Considere o custo de pescar, o tempo e esforço que leva para pescar, e o preço de venda dessa pescaria nos últimos anos em que pescou. O senhor diria que essa pescaria:	❑ Vale muito a pena ❑ Vale a pena ❑ Quase não vale a pena ❑ Com certeza não vale a pena

Gostaria que o senhor pensasse apenas sobre a pesca da _____________________:

Em que ano começou a pescar? ______ **Em que ano parou de pescar?** _____ *[❑ainda pesca]*

Qual tipo de pesca o senhor realiza?
Qual a quantidade normalmente pescada? _______________ ❑ kg *[❑ outra unidade: __________]*
Tempo de pesca: ❑horas ❑dias _________________________ Número de pescadores:_________
Aparelho: ❑Rede espera: (❑Fundo❑Superfície) ❑Tarrafa ❑Rede arrasto: (❑Praia ❑Fundo)
❑Linha/Anzol ❑Outro: ____________

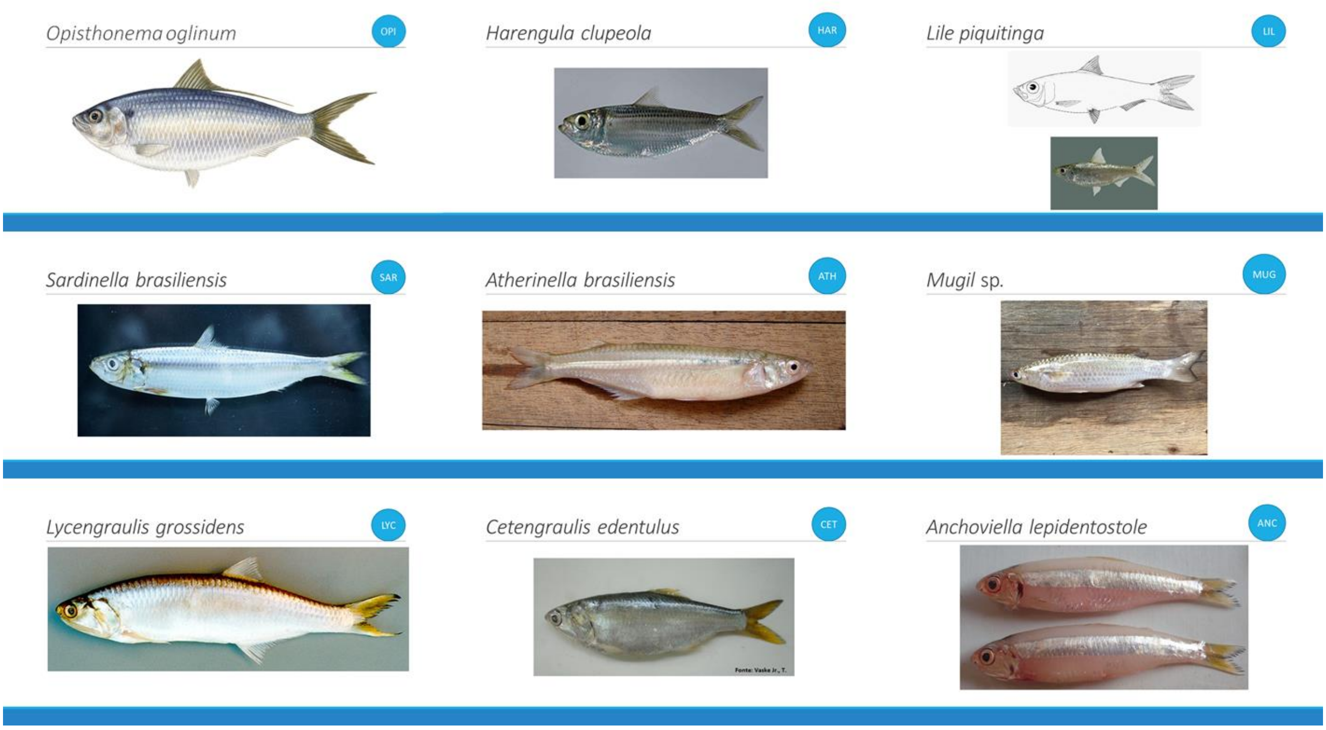
Época do ano: ❑Jan ❑Fev ❑Mar ❑Abr ❑Mai ❑Jun ❑Jul ❑Ago ❑Set ❑Out ❑Nov ❑Dez

Qual o destino do peixe pescado: ❑Uso próprio para consumo ❑Uso próprio como isca ❑Venda para consumo ❑Venda como isca ❑Outro: ___________________________

Para as próximas perguntas, considere a sua carreira de pesca inteira na pescaria.
Dada a sua experiência, o senhor diria que a quantidade de peixe (kg/ton):
❑ Aumentou ❑ Diminuiu ❑ Permaneceu igual ❑ Não sabe

Durante o seu tempo na pescaria, o senhor diria que o tamanho dos peixes:	❑ Aumentou ❑ Diminuiu ❑ Permaneceu igual ❑ Não sabe
Considere o custo de pescar, o tempo e esforço que leva para pescar, e o preço de venda dessa pescaria nos últimos anos em que pescou. O senhor diria que essa pescaria:	❑ Vale muito a pena ❑ Vale a pena ❑ Quase não vale a pena ❑ Com certeza não vale a pena

Annex 2. Identification boards with fish species photos. Each board was a photo, scientific name, and acronym for each species.



3. CAPÍTULO II. DIFFERENT PHYLOGEOGRAPHIC PATTERNS OF TWO CLUPEID FISH FROM THE WESTERN ATLANTIC OCEAN

DIFFERENT PHYLOGEOGRAPHIC PATTERNS OF TWO CLUPEID FISH FROM THE WESTERN ATLANTIC OCEAN

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***Esse capítulo está na mesma formatação do capítulo anterior com o intuito de padronização.**

Abstract

Harengula and *Opisthonema* belong to the family Clupeidae and both have species that co-occur in the Western Atlantic Ocean. Additionally, these species share some similar biological aspects. In this study, we investigated the phylogeographic patterns of *Harengula* spp. and *O. oglinum* throughout their entire distributions in the Western Atlantic using the CO1 gene. Based on the phylogeographic and lineage delimitation analyses, we assessed the different phylogeographic patterns of *Harengula* spp. and *O. oglinum*. For *Harengula* spp., we found two species in the Western Atlantic, *H. clupeola* and *H. jaguana* occurring in the Carolinian+Greater Caribbean province, and one distinct lineage in the Brazilian province with two structured populations. While for *O. oglinum*, our results indicated the presence of a single species for the entire Western Atlantic with two populations in the Carolinian+Greater Caribbean province and another one in the Brazilian province. Additionally, we recovered the divergence time of 2.4 Myr between the *Harengula* species from the Carolinian+Greater Caribbean province and *Harengula* sp. from the Brazilian province, which coincides with the greater discharge of the AOP. This suggests that the AOP might be what caused their separation, and that *Harengula* and *O. oglinum* are differently affected by this barrier. Furthermore, this distinct lineage of *Harengula* from the Brazilian province needs a further taxonomic investigation using both morphological and additional genetic data.

Keywords: Cryptic diversity, DNA barcode, Clupeidae, Amazon river plume, Pleistocene

Resumo

Harengula e *Opisthonema* são gêneros da família Clupeidae, ambos com espécies que coocorrem no Oceano Atlântico Oeste. Ademais, essas espécies possuem alguns aspectos biológicos similares. Neste estudo, investigamos os padrões filogeográficos de *Harengula* spp. e *O. oglinum* em toda sua distribuição no Atlântico Oeste usando o gene CO1. Com base nas análises filogeográficas e delimitações de linhagens, detectamos diferentes padrões filogeográficos de *Harengula* spp. e *O. oglinum*. Para *Harengula*, encontramos duas espécies, *H. clupeola* e *H. jaguana*, na província Carolinian+Greater Caribbean, e uma linhagem distinta na província Brazilian, com duas populações estruturadas. Enquanto para *O. oglinum*, nossos resultados indicaram uma única espécie para todo o Atlântico Oeste, com duas populações na província Carolinian+Greater Caribbean e uma na província Brazilian. Além disso, recuperamos o tempo de divergência de 2,4 Myr entre as espécies *Harengula* da província Carolinian+Greater Caribbean e *Harengula* sp. da província Brazilian, que coincide com a maior fluxo de desague da AOP. Isso sugere que a AOP pode ter sido o filtro que moldou essa separação e que *Harengula* e *O. oglinum* são diferentemente afetadas por essa barreira. Ademais, esta linhagem distinta de *Harengula* da província Brazilian precisa de uma investigação taxonômica usando ambos dados genéticos adicionais e morfológicos.

Palavras-chave: Diversidade críptica, Barcode DNA, Clupeidae, Pluma do rio Amazonas, Pleistoceno

3.1 Introduction

The lack of basic information, such as taxonomic uncertainty and stock delimitation can compromise the management of fisheries resources (Carvalho and Hauser 1995; Ward et al. 2005). When taxonomic identity is uncertain it is not possible to generate reliable fishery statistical data (FAO 2016). This is particularly difficult for small and numerous schooling fishes as the anchovies and sardines. One alternative to deal with this problematic is to integrate genetic data into taxonomic identifications (Waples et al. 2008), and several studies identified possible cryptic species using DNA barcode in commercial fishes (Durand et al. 2017; Jacobina et al. 2020; Mat Jaafar et al. 2012; Wu et al. 2016).

The sardines belong to the family Clupeidae, which consist a valuable commercial fishery, used as food or bait (Whitehead 1985). This family comprehends 55 genera and 198 valid species, most of them tropical marine and some freshwater or anadromous (Fricke et al. 2019a).

Opisthonema oglinum (Lesueur, 1818) is the only species of the genus that occurs in the Western Atlantic, from the north of the United States to the north of Argentina (IUCN - International Union for Conservation of Nature 2015a) (Figure 6). Its type locality is in Newport, Rhode Island, USA (Fricke et al. 2019b). Meanwhile, the genus *Harengula* Valenciennes, 1847 is represented by three species in the same area, *H. clupeola* (Cuvier, 1829), *H. humeralis* (Cuvier, 1829), and *H. jaguana* Poey, 1865 (Fricke et al. 2019b; Whitehead 1985). While *H. humeralis* distribution is from Florida (USA) to the Guianas, *H. clupeola* and *H. jaguana* co-occur from south of USA to south of Brazil (IUCN - International Union for Conservation of Nature 2015b, 2018; Whitehead 1985) (Figure 6). The type localities of *H. clupeola* and *H. jaguana* are Martinique Island and Cuba, both in Caribe, respectively (Fricke et al. 2019b). However, one of the only distinctive characters between them is the number of lower gill-rakers in the first branchial arch, in which *H. clupeola* has 28 to 34 (usually 30 to 32) and *H. jaguana* has 30 to 40 (usually 32 to 39) (Whitehead 1985). The other character is the different widths of tooth-plates on floor of mouth, which are quite subtle (Whitehead 1985). These make their species identification difficult, leading to taxonomic uncertainties, and hampers fisheries management of these species. Furthermore, Whitehead (1985) stated that specimens of *H. jaguana* show differences in morphological data over its distribution and some subspecies may eventually be recognized, suggesting population structuring or even cryptic species.

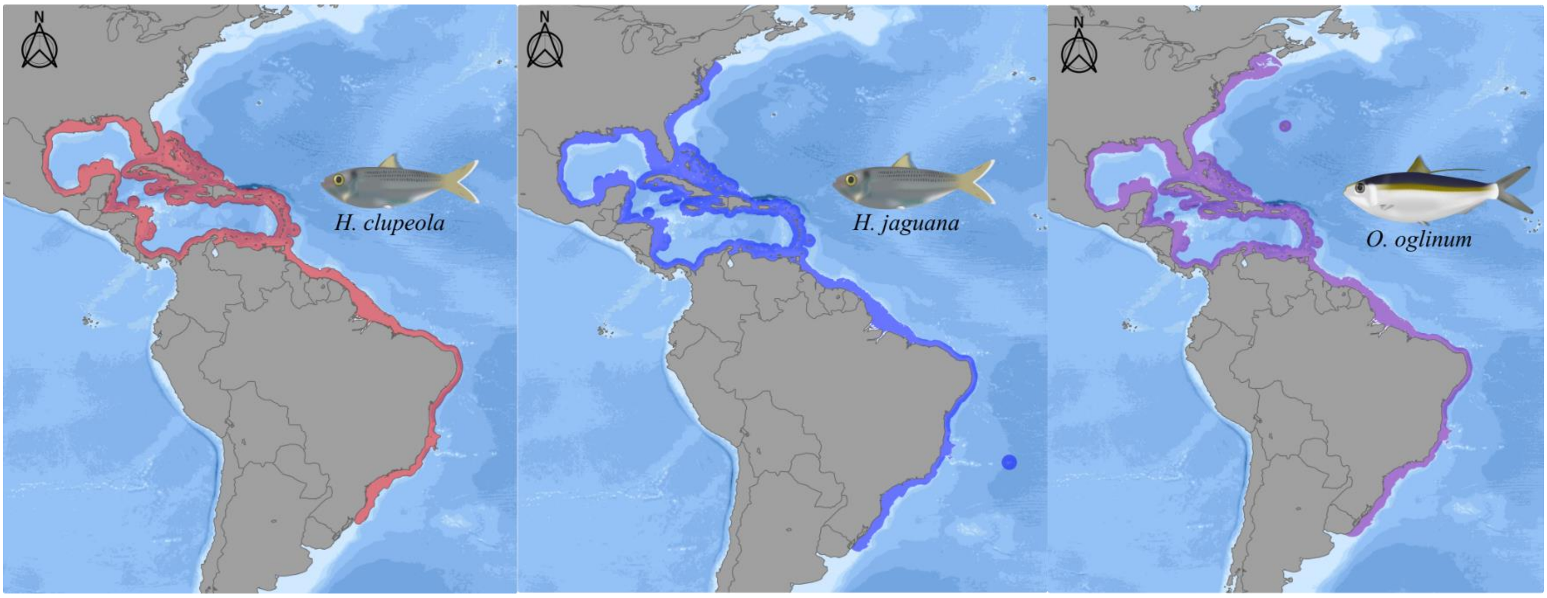


Figure 6. Distribution maps of *Harengula clupeola* (red), *H. jaguana* (blue), and *Opisthonema oglinum* (purple) according to IUCN.

In the last years, some species that putatively had wide distribution in the Western Atlantic were identified as cryptic species complexes (Colborn et al. 2001; Dias et al. 2019; Leite et al. 2008; Luiz et al. 2011; Rocha 2003; Rodríguez-Rey et al. 2017). These allopatric species are usually found on each side of the main oceanographic barriers, reducing their geographic distribution and increasing their richness.

Clupeid genetic structuring can be related to temperature, salinity, and depth variations, considering that these oceanographic characteristics are known to influence the population structure of other species with pelagic larvae (Floeter et al. 2008; Luiz et al. 2011; Palumbi 1994; Rocha and Bowen 2008). Although the long larval periods of *O. oglinum* (about 19 days) and *Harengula* spp. (about 25 days) (Finucane and Shaffer 1986; Martinez and Houde 1975; Pierce et al. 2001; Vega-Cendejas et al. 1997) can allow gene flow between distant locations, reproduction associated to estuarine regions can result in population structure (Baggio et al. 2017).

The Amazon-Orinoco plume (AOP) is a known intermittent biogeographic barrier for some marine organisms (Floeter et al. 2008; Jacobina et al. 2020; Luiz et al. 2011; Rocha 2003; Rocha et al. 2002, 2008). Its discharge of freshwater creates a region of low salinity and high turbidity in the Western Atlantic Ocean (Luiz et al. 2011). The intensity of this barrier varied with the sea-level fluctuations through the interglacial and glacial periods (Rocha 2003). Additionally, this barrier separates the Carolinian+Greater Caribbean and Brazilian provinces (Floeter et al. 2008). Considering that the taxa selected in this study have similar geographic distribution and biological aspects, such as larval stage duration and reproduction in estuarine areas, it is expected that they have the same phylogeographic patterns (Lukoschek 2018). By testing this barrier, we will be evaluating the effects of the freshwater intake (AOP) for coastal pelagic fishes.

These clupeids are important fishery and cultural resources in Brazilian coast (Freire and Pauly 2015; Pauly et al. 2020) and oceanic islands, since *Harengula* is found in Fernando de Noronha and Trindade and Martim Vaz archipelagos (Gasparini and Floeter 2001; Sazima et al. 2006). In Fernando de Noronha, this fish is the most important bait, and is involved in an ongoing conflict between local fishers and the environmental agency since most of the archipelago is a Marine Protected Area (Lopes et al. 2017). Furthermore, Verba et al. (2019) indicated that the exploitation status of both *H. clupeola* and *H. jaguana* are overexploited and *O. oglinum* is fully exploited in the Brazilian Exclusive Economic Zone.

In this study we tested the role of the AOP in structuring of coastal pelagic clupeids from the Western Atlantic Ocean based on the mitochondrial cytochrome c oxidase subunit 1 (CO1) gene. Specifically, we aim to answer these three questions: (1) Is there genetic differences between individuals from Carolinian+Greater Caribbean and the Brazilian provinces for *O. oglinum* and *Harengula* spp.? (2) If yes, these genetic differences originated around the same time as the AOP? (3) How many populations of *O. oglinum* and *Harengula* spp. are in the Brazilian coast? These results will help to identify which species are been exploited in Brazil, besides providing information on stock delimitation.

3.2 Material and methods

3.2.1 Samplings

Dataset consisted in both original and available DNA sequences. Original data is represented by individuals bought from fish markets and collected using a 5-meter-long beach seine (5 mm mesh) in five localities along the Brazilian coast: Macau, Natal, and Baía Formosa in Rio Grande do Norte state, Cabedelo in Paraíba state, and the oceanic archipelago of Fernando de Noronha in Pernambuco state (Annex 3 – Appendix). Samplings were conducted under the System Authorization and Information on Biodiversity permit (SISBIO nº 67671-1).

Morphological identification was based on the ‘Manual de Peixes Marinhos do Sudeste do Brasil’ (Figueiredo and Menezes 1978) and FAO’s Species Catalog Vol. 7 Clupeoid fishes of the world (Whitehead 1985). First, tissue samples were collected and stored in ethanol p.a. (98%). Then, voucher specimens were fixed in formaldehyde 4% and later transferred to an ethanol 70% solution, and then deposited in the ichthyological collection of the Universidade Federal do Rio Grande do Norte (UFRN).

3.2.2 DNA extraction, PCR, and sequencing

Tissue samples were submitted to DNA extraction by saline extraction, following protocol proposed by Bruford et al. (1992) with some modifications (Annex 4 - Appendix). Then, DNA amplification by PCR was performed using the GoTaq® Green Master mix (Promega, Madison, WI, USA) and the primers FISH-BCL (5'- TCAACYAATCAYAAAGATATYGG-CAC) and FISH-BCH (5'- TAAACTTCAGGGTGACCAAAAAATCA) for mitochondrial marker CO1. PCR steps consisted in a first cycle of 2 min at 95°C; 35 cycles of denaturation at 94°C for 30 sec, annealing at 54°C for 30 sec, and extension at 72°C for 1 min; and a final cycle of 10 min at 72°C (Baldwin et al. 2009). The amplicons were sequenced by the Macrogen Inc (https://dna.macrogen.com/).

Additional sequences from USA, Mexico, and Caribe were downloaded from Genbank database (https://www.ncbi.nlm.nih.gov/genbank/) and aligned with our sequences (Annex 3 – Appendix). Three different datasets were assembled: the first, sequences of all valid species of *Harengula* and *Opisthonema* with several other species of clupeids (Clupeidae dataset); the second, only species of *Harengula* from the Western Atlantic Ocean, except *H. humeralis* (See Results for explanation); and the third, only species of *Opisthonema* from the Western Atlantic Ocean. For the *Harengula* dataset, sequences of *H. humeralis* and *H. thrissina* (Jordan & Gilbert, 1882) were used as outgroups. For the *O. oglinum* dataset, sequences of *O. bulleri* (Regan, 1904), *O. medirastre* Berry & Barrett, 1963, and *O. libertate* (Günther, 1867) were used as outgroups. To verify the species identification of the sequences on Genbank, we used the comparative search tool BLASTn of NCBI to check the similarity of sequences by species.

3.2.3 Phylogenetic analysis and lineage delimitation

Forward and reverse sequences of *O. oglinum* and *Harengula* spp. were edited and consensus sequences of 555 bp were created in SeqTrace v. 0.9 (Stucky 2012). First, the Clupeidae dataset was aligned using the MUSCLE algorithm (Edgar 2004) and its best evolutionary model was calculated, both done in MEGA6 (Tamura et al. 2013). Then, the same was performed for *O. oglinum* and *Harengula* datasets. Following the Bayesian Information Criterion (BIC), the evolutionary model used for Clupeidae dataset was Kimura 2-parameter with invariant sites and gamma distribution (K2P+I+G) and for *O. oglinum* and *Harengula* datasets was the same, excluding I+G.

Bayesian Inference (BI) was performed in BEAST v. 1.10.2 (Suchard et al. 2018), using the following parameters: substitution model as Hasegawa–Kishono–Yano with I+G (HKY+I+G) for the Clupeidae dataset and HKY for the *Harengula* and *O. oglinum* datasets with base frequencies as all equal (since there is no K2P model in BEAST, the equivalent of it is HKY with base frequencies equal). The selected clock type was strict clock with normal distribution and mean of 0.01 mutations/Myr (substitution rate suggested for fish mtDNA (Bermingham et al. 1997; Thomaz et al. 2015)) and standard deviation of 0.001. The tree prior model was set as speciation with yule process for Clupeidae dataset and coalescent with constant size for *Harengula* and *O. oglinum* datasets. The Markov chain Monte Carlo (MCMC) was run with 20,000,000 generations and sampled every 2,000 generations. The other parameters were set as default. To ensure quality of the MCMC simulations, ESS values of at least 200 were checked using Tracer 1.77 (Rambaut et al. 2018). Then, TreeAnnotator v. 1.10.2 was used to summarize the BEAST results into a single tree with burn-in of 20% and a posterior probability limit of 0.5. The final tree was visualized and edited in FigTree v. 1.4.4 (Rambaut 2018).

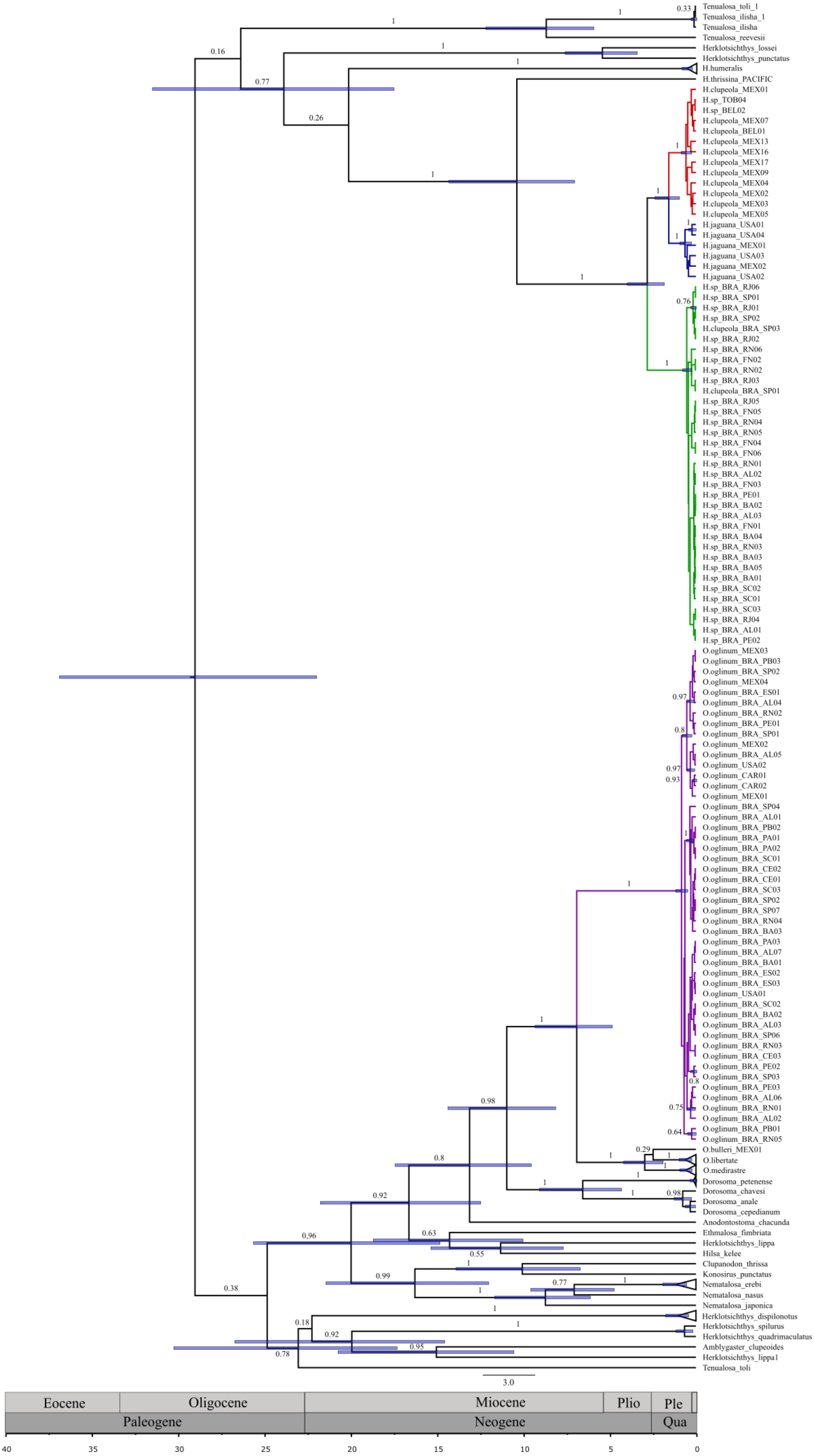
For the lineage delimitations, we only analyzed the *Harengula* and *O. oglinum* datasets. Four single-locus lineage delimitation analyses were performed to increase robustness in delimiting lineages for both datasets separately: Multi-rate Poisson Tree Processes (mPTP) (Kapli et al. 2017); single-threshold of Generalized Mixed Yule-Coalescent (sGMYC) and multiple-threshold GMYC (mGMYC) (Fujisawa and Barraclough 2013); and Automatic Barcode Gap Discovery (ABGD) (Puillandre et al. 2012). A ML tree generated on MEGA6 with 1,000 replications, Nearest-Neighbor-Interchange with branch swap filter as moderate, was used as input tree for mPTP. The mPTP was performed on the online server (https://mptp.h-its.org/#/tree) using the default parameters. Ultrametric trees generated on BEAST from both datasets were used as input file for sGMYC and mGMYC. Both analyses were performed on the online server (https://species.h-its.org/gmyc/). ABGD distance-based analyses were run through the online server (https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html), with the relative gap width of 1.0 and the remaining parameters as default for all the distances available (Jukes-Cantor, Kimura, and simple distance). For this analysis, the delineation considered was the one with P-value of ~ 0.01, as suggested by previously studies (Blair and Bryson Jr 2017; Puillandre et al.

2012). For the delimitation based on genetic distance, the genetic divergence (K2P) was calculated in MEGA6 and a threshold value was set using the cut-off values of 2% of divergence for CO1 (Ward 2009).

To detect population structure in the species from Brazil, we used GENELAND, which does not require the assignment of samples to potential species a priori (Guillot et al. 2005). The GENELAND analysis was based on an uncorrelated frequency model, which is used to delimit clusters of possible distinct lineages (Pavón-Vázquez et al. 2018), with minimum population number 1 and maximum population number 10. The spatial model was selected to infer the number of clusters in nine independent runs using 1,000,000 MCMC iterations, of which every 1,000 was retained. A burn-in of 200 was applied and the run with the highest mean logarithm of posterior probability was used to compute the posterior probabilities of population membership. Finally, a haplotype network was inferred using the TSC method in PopART software (Leigh and Bryant 2015) to highlight the degree of divergence and spatial distribution of the molecular diversity.

3.3 Results

A total of 32 and 33 CO1 sequences of *O. oglinum* and *Harengula* spp. (*Harengula* sp. and putative *H. clupeola*) from the Western Atlantic, respectively, were sequenced and edited, then aligned with 26 and 47 sequences from Genbank, respectively. The calibrated BI tree using the Clupeidae dataset indicated that both *Harengula* and *Opisthonema* are monophyletic genera (Figure 7). However, the posterior value for the whole *Harengula* clade is low (0.26), but the posterior value of *H. thrissina*, *H. clupeola*, and *H. jaguana* group is high (1). This suggests that *H. humeralis* is quite genetically distant from the other species of *Harengula*. Due to this genetic divergency, *H. humeralis* was excluded from the *Harengula* dataset.


Tenualosa_toli_1
Tenualosa_ilisha_1
Tenualosa_ilisha
Tenualosa_reevesii
Herklotsichthys_lossei
Herklotsichthys_punctatus
H.humeralis
H.thrissina_PACIFIC
H.clupeola_MEX01
H.sp_TOB04
H.sp_BEL02
H.clupeola_MEX07
H.clupeola_BEL01
H.clupeola_MEX13
H.clupeola_MEX16
H.clupeola_MEX17
H.clupeola_MEX09
H.clupeola_MEX04
H.clupeola_MEX02
H.clupeola_MEX03
H.clupeola_MEX05
H.jaguana_USA01
H.jaguana_USA04
H.jaguana_MEX01
H.jaguana_USA03
H.jaguana_MEX02
H.jaguana_USA02
H.sp_BRA_RJ06
H.sp_BRA_SP01
H.sp_BRA_RJ01
H.sp_BRA_SP02
H.clupeola_BRA_SP03
H.sp_BRA_RJ02
H.sp_BRA_RN06
H.sp_BRA_FN02
H.sp_BRA_RN02
H.sp_BRA_RJ03
H.clupeola_BRA_SP01
H.sp_BRA_RJ05
H.sp_BRA_FN05
H.sp_BRA_RN04
H.sp_BRA_RN05
H.sp_BRA_FN04
H.sp_BRA_FN06
H.sp_BRA_RN01
H.sp_BRA_AL02
H.sp_BRA_FN03
H.sp_BRA_PE01
H.sp_BRA_BA02
H.sp_BRA_AL03
H.sp_BRA_FN01
H.sp_BRA_BA04
H.sp_BRA_RN03
H.sp_BRA_BA03
H.sp_BRA_BA05
H.sp_BRA_BA01
H.sp_BRA_SC02
H.sp_BRA_SC01
H.sp_BRA_SC03
H.sp_BRA_RJ04
H.sp_BRA_AL01
H.sp_BRA_PE02
O.oglinum_MEX03
O.oglinum_BRA_PB03
O.oglinum_BRA_SP02
O.oglinum_MEX04
O.oglinum_BRA_ES01
O.oglinum_BRA_AL04
O.oglinum_BRA_RN02
O.oglinum_BRA_PE01
O.oglinum_BRA_SP01
O.oglinum_MEX02
O.oglinum_BRA_AL05
O.oglinum_USA02
O.oglinum_CAR01
O.oglinum_CAR02
O.oglinum_MEX01
O.oglinum_BRA_SP04
O.oglinum_BRA_AL01
O.oglinum_BRA_PB02
O.oglinum_BRA_PA01
O.oglinum_BRA_PA02
O.oglinum_BRA_SC01
O.oglinum_BRA_CE02
O.oglinum_BRA_CE01
O.oglinum_BRA_SC03
O.oglinum_BRA_SP02
O.oglinum_BRA_SP07
O.oglinum_BRA_RN04
O.oglinum_BRA_BA03
O.oglinum_BRA_PA03
O.oglinum_BRA_AL07
O.oglinum_BRA_BA01
O.oglinum_BRA_ES02
O.oglinum_BRA_ES03
O.oglinum_USA01
O.oglinum_BRA_SC02
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O.oglinum_BRA_AL03
O.oglinum_BRA_SP06
O.oglinum_BRA_RN03
O.oglinum_BRA_CE03
O.oglinum_BRA_PE02
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O.libertate
O.medirastre
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Dorosoma_chavesi
Dorosoma_anale
Dorosoma_cepedianum
Anodontostoma_chacunda
Ethmalosa_fimbriata
Herklotsichthys_lippa
Hilsa_kelee
Clupanodon_thrissa
Konosirus_punctatus
Nematalosa_erebi
Nematalosa_nasus
Nematalosa_japonica
Herklotsichthys_dispilonotus
Herklotsichthys_spilurus
Herklotsichthys_quadrimaculatus
Amblygaster_clupeoides
Herklotsichthys_lippa1
Tenualosa_toli
3.0
Eocene
Oligocene
Miocene
Plio
Ple
Paleogene
Neogene
Qua
40
35
30
25
20
15
10
5
0

Figure 7. Calibrated tree of Bayesian Inference of Clupeidae dataset to infer the identity of the species from the Western Atlantic. Clade colors represent the species/lineages focused in this study: *Harengula jaguana* (blue), *H. clupeola* (red), *Harengula* sp. (green), and *Opisthonema oglinum* (purple). Numbers on branches are posterior values. Blue bars over nodes are confidence intervals.

The clades with highest posterior values (1) of *Opisthonema* and *Harengula* from the Western Atlantic were *H. clupeola* from Carolinian+Greater Caribbean province (red), *H. jaguana* from Carolinian+Greater Caribbean province (blue), *Harengula* sp. from Brazilian province (green), and *O. oglinum* from the whole Western Atlantic (purple). Within the *Harengula* clade from the Western Atlantic, the separation time of the *Harengula* groups from Carolinian+Greater Caribbean province and from Brazilian province was, approximately, 2.5 Mya (3.5-1.5 Mya). Additionally, the only sub-clades with a relatively high posterior values were *H. jaguana* from USA (1), within the *H. jaguana* clade, and *Harengula* sp. from south-southeastern Brazilian province (0.76). Within the *O. oglinum* clade, there are few well supported sub-clades such as the Bermuda in Carolinian+Greater Caribbean province (0.93) and other with several individuals from the Brazilian province (1). Also, no clear geographic pattern is shown within this clade.

The lineage delimitation analyses of *Harengula* dataset showed different results (Figure 8). mPTP and genetic distance indicated three lineages, *H. clupeola* and *H. jaguana* from Carolinian+Greater Caribbean province, and *Harengula* sp. from Brazilian province (Annex 4 – Appendix). Both GMYC analyses recovered the delimitation between *H. clupeola*, *H. jaguana*, and *Harengula* sp., but they also sub-divided both *H. clupeola* and *H. jaguana*. These two analyses normally overestimate the number of lineages (Fujisawa and Barraclough 2013; Hamilton et al. 2014). Lastly, the ABGD indicated *Harengula* sp. from Brazilian province but delimitated *H. clupeola* and *H. jaguana* together. All analyses recovered the lineage of *Harengula* sp. from Brazilian province. For the *O. oglinum* dataset, the delimitation analyses were more congruent, with mPTP, ABGD, and genetic distance indicating a single lineage but sGMYC and mGMYC over-split it into few and several clusters without any geographic pattern, respectively **(**Figure 8).

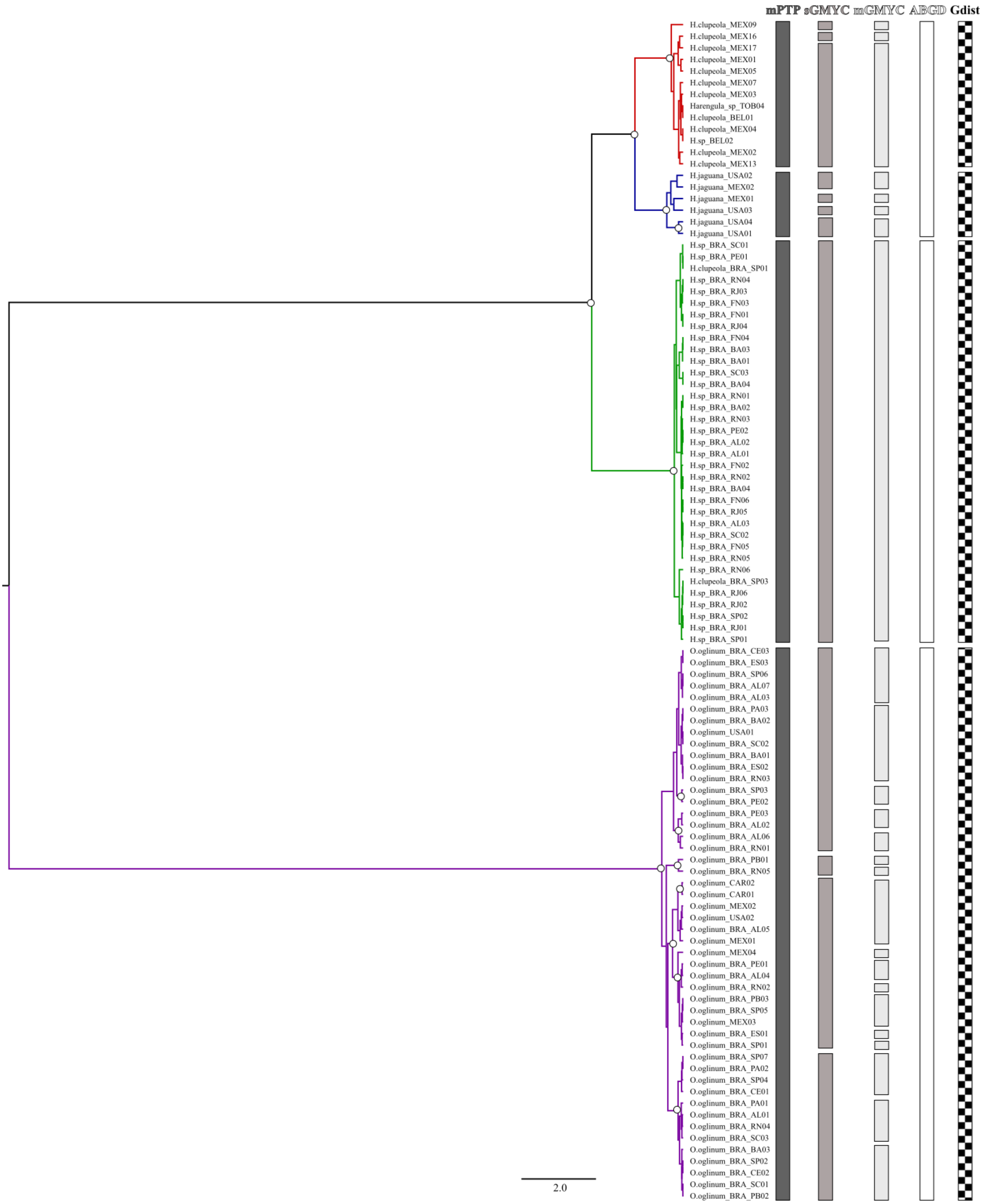

Figure 8. IB tree and lineage delimitation analyses of *Harengula* and *Opisthonema oglinum* datasets. Clade colors represent lineages: *H. jaguana* (blue), *H. clupeola* (red), *Harengula* sp. (green), and *Opisthonema oglinum* (purple). White circles over nodes indicate high posterior values (>0.85). Bars on the right side are clusters delimited by each lineage delimitation analyses. mPTP: multiple rate PTP;

sGMYC: single-threshold of Generalized Mixed Yule-Coalescent; mGMYC: multiple-threshold GMYC; ABGD: Automatic Barcode Gap Discovery; Gdist: Genetic distance (K2P).

The GENELAND for the whole *Harengula* dataset suggested two main lineages, one in Carolinian+Greater Caribbean province and other in the Brazilian province, separated by the AOP in agreement with the phylogenetics results (Figure 9a, b). Considering only the Brazilian lineage, two populations were indicated, one comprising specimens from the warm waters from northeastern Brazilian province (Brazil 1), and another of the temperate waters from south-southeastern Brazilian province (Brazil 2) (Figure 9c, d). For *O. oglinum*, three populations were recovered, one in the Brazilian province and two in the Carolinian+Greater Caribbean province (Figure 10), indicating a structure in the AOP area which was not identified in the previous analyses. However, one of the populations in Carolinian+Greater Caribbean province did not have a high posterior probability as the others (Figure 10c).

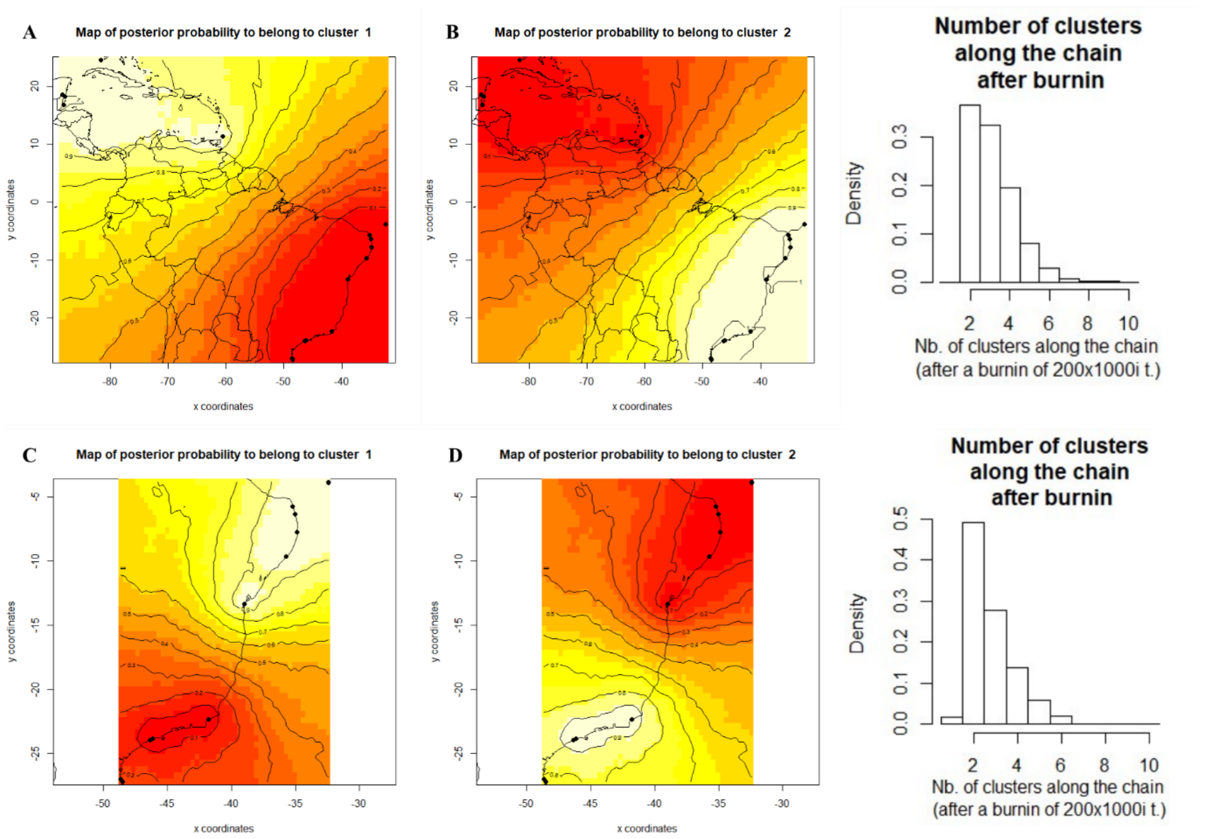

Figure 9. Map of posterior probability of population membership and spatial location of genetic discontinuities of *Harengula* dataset generated by GENELAND. Two main clusters (K = 2) can be visualized: A. *H. clupeola* and *H. jaguana* from Carolinian+Greater Caribbean province; B. *Harengula* sp. from

Brazilian province. Additionally, there are two sub-clusters in the Brazilian lineage (K = 2): C. *Harengula* sp. from northeastern Brazilian province (Brazil 1); D. *Harengula* sp. from south-southeastern Brazilian province (Brazil 2). Lightest colors indicate highest probabilities of membership and contour lines represent the spatial position of genetic discontinuities between populations.

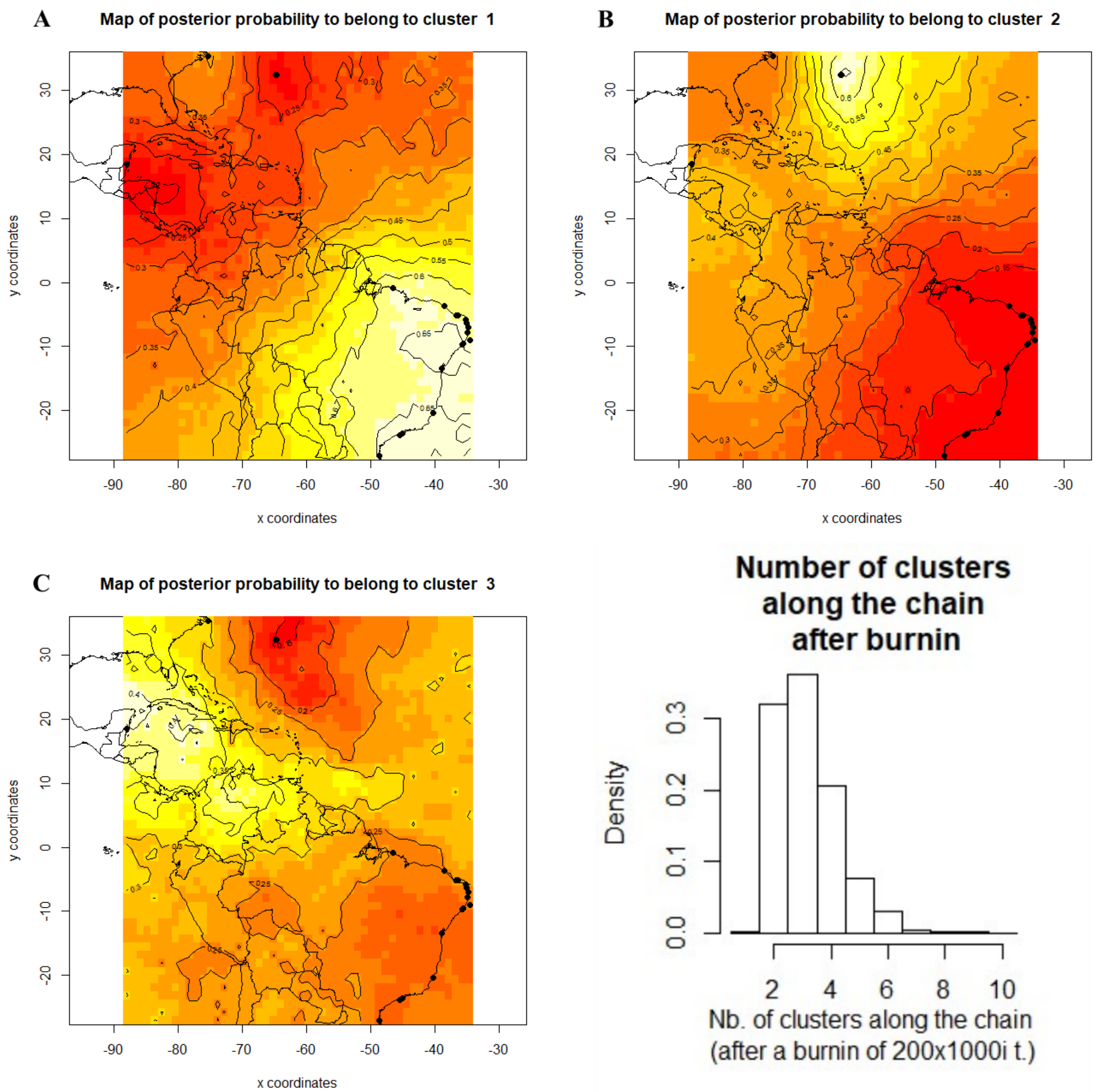

Figure 10. Map of posterior probability of population membership and spatial location of genetic discontinuities of *Opisthonema oglinum* dataset generated by GENELAND. Three main clusters (K = 3) can be visualized: A. *O. oglinum* from Brazilian province; B. *O. oglinum* from Bermuda, Carolinian+Greater Caribbean province; C. *O. oglinum* from USA and Mexico, Carolinian+Greater Caribbean province. Lightest colors indicate highest probabilities of membership and contour lines represent the spatial position of genetic discontinuities between populations.

The haplotype network of *Harengula* dataset showed a deep structure, with 18 mutational steps between the *Harengula* sp. from the Brazilian province and the *H. clupeola* + *H. jaguana* from the Carolinian+Greater Caribbean samples, and between *H. clupeola* and *H. jaguana* samples with 10 mutational steps (Figure 11). No structure is evident between *Harengula* sp. from northeastern (Brazil 1) and south-southeastern Brazilian province (Brazil 2). The haplotype network of *O. oglinum* dataset showed no clear genetic structure, besides two exclusive haplotypes from Bermuda (Carolinian+Greater Caribbean province) and some from Brazilian province.

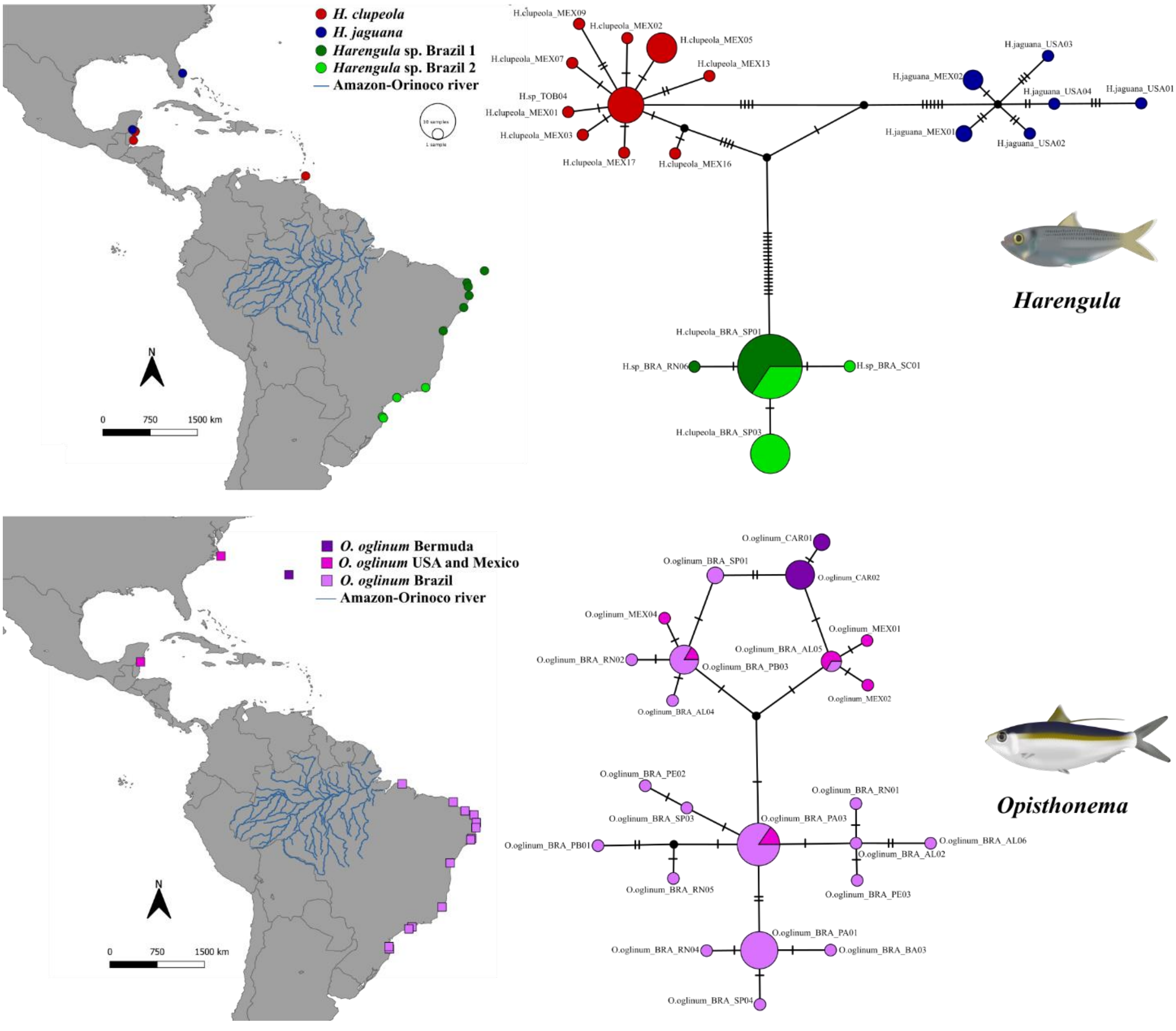

Figure 11. Map distribution and haplotype networks of *Harengula* spp. and *Opisthonema oglinum* for the molecular marker CO1. Bars over lines are mutational steps between haplotypes.

3.4 Discussion

With our results, we were able to answer our three questions formulated in the beginning of this study. We found different lineages of *Harengula* spp. and *O. oglinum* between the Carolinian+Greater Caribbean and Brazilian provinces (1). Additionally, the separation time of the *Harengula* lineages indeed match the time of the increased freshwater discharge of the AOP (2). Lastly, we identified two populations of *Harengula* sp. and one population of *O. oglinum* in the Brazilian province (3). Here we discuss these findings.

Two of the three lineages of *Harengula* we found in the Western Atlantic correspond to *H. clupeola* and *H. jaguana* in the Carolinian+Greater Caribbean province. The third is a very distinct lineage from the other two and is restricted to the Brazilian province. Additionally, *H. clupeola* and *H. jaguana* are more genetically similar between them than with the *Harengula* sp. from the Brazilian province. For *O. oglinum*, we detected three lineages: two in the Carolinian+Greater Caribbean province and one in the Brazilian province. However, the genetic differences between these lineages are way more subtle than the differences between the *Harengula* lineages. This suggests that even though both *Harengula* spp. and *O. oglinum* present different lineages between the Carolinian+Greater Caribbean and Brazilian provinces, these taxa responded differently to the probable biogeographic barriers in the Western Atlantic.

The separation between *H. clupeola* and *H. jaguana* from Carolinian+Greater Caribbean province and the different lineage from Brazilian province can be associated to the AOP. The AOP became a transcontinental river around 11 Mya, but its high sedimentation discharge only began around 2.4 Mya (Figueiredo et al. 2009), the latter date coinciding with the separation of the *Harengula* lineages from different provinces. Therefore, the distinct lineage from Brazilian province might be considered as a distinct species from the *Harengula* from Carolinian+Greater Caribbean province. This pattern also appears to be present in the *H. humeralis* distribution, which is restricted to Caribe, suggesting that the AOP is also an effective barrier to this species. Furthermore, the AOP also seems to influence the population structuring of *O. oglinum*, suggesting a stronger barrier role in *Harengula* than in *Opisthonema*. This supports the morphological data in previous studies that presented *O. oglinum* as a single species in its entire geographic distribution (Berry and Barrett 1963; Whitehead 1985). The distinct *Harengula* lineage could be a new species or a species that was synonymized in the past. For the latter, a taxonomic revision would be required considering the previous species described with its type locality in the Brazilian coast. Among the possibilities, *Harengula macrophthalma*

(Ranzani 1842), firstly described as *Clupea macrophthalma* (Fricke 2019b), would be a possible valid name for this species, according to the principle of priority.

When dealing with marine biogeographic patterns, life history traits are just as important as abiotic factors in shaping them (Luiz et al. 2011). Several studies showed that different biological traits can be related to a biogeographic barrier being effective or not for a species (Luiz et al. 2011; Rocha 2003). Our results indicated that these taxa do not present the same phylogeographic patterns. This disparity shows us that *Harengula* and *Opisthonema* might not have so similar biological characteristics as we previously thought. Apparently, *Opisthonema* can tolerate all oceanographic changes promoted by the AOP (e.g. salinity variation, and sediment and nutrient discharges), while these variations prevent *Harengula* of crossing this barrier. Additionally, the effectiveness of this barrier can change due to variations in sea-level, allowing or preventing dispersal through it (Rocha 2003), which can explain the population structuring in *O. oglinum*. On the other hand, depth or long distances, seem to be a barrier for *Opisthonema*, once *Harengula* sp. is present in oceanic islands, and Fernando de Noronha belongs to the same population of the coast (Brazil 1). The other population (Brazil 2) of *Harengula* is found in colder waters, and this structure might be related to the Cabo Frio Upwelling, which can be a dispersal barrier to some marine organisms (Maggioni et al. 2003; Peluso et al. 2018; Voloch and Solé-Cava 2005). Furthermore,

There are few limitations in our study regarding data limitation. Here, we only used one mtDNA gene and do not have access to the specimens from the sequences we used from Genbank. Using a broader genetic data, such as more variable genetic markers, could show us more subtle population structures that went undetected. Also, having the individuals from the Genbank sequences we used could help us in caring out a morphological study comparing the genetically different populations/species and see if they also show morphological differences.

In summary, we succeed in answering our three main questions: (1) There is indeed genetic differences between individuals of *Harengula* spp. and *O. oglinum* from Carolinian+Greater Caribbean and Brazilian provinces, but the genetic difference levels are distinct. For *Harengula* spp., we found a much deeper genetic distances between the *Harengula* lineages from Carolinian+Greater Caribbean and Brazilian provinces, to the point that the *Harengula* from Brazilian province could be regarded as a different species from *H. clupeola* and *H. jaguana*. Meanwhile, the genetic differences between *O. oglinum* from Carolinian+Greater Caribbean and Brazilian provinces are shallower and indicate population structure. (2) The divergence time between the *Harengula* from Carolinian+Greater Caribbean and Brazilian provinces coincide with the time of higher freshwater discharge of the AOP, suggesting that the AOP may be what cause this separation. (3) Within the Brazilian territory, there are two populations of *Harengula* sp. and one population of *O. oglinum*. Therefore, our study suggests that Pleistocene events influenced the diversification of Neotropical clupeids, promoting both speciation and population structuring in the AOP area.

3.5 Conclusion

Based on phylogenetic and phylogeographic analyses and lineages delimitations, we concluded that *H. clupeola* and *H. jaguana* are restricted to the Carolinian+Greater Caribbean province and a distinct lineage of *Harengula* is distributed through the Brazilian province. This different lineage has been isolated from the Carolinian+Greater Caribbean species for 2.4 Myr, this isolation was probably caused by the AOP. However, *O. oglinum* is formed by a single species with three populations through its entire distribution in the Western Atlantic Ocean. This goes against our expectation that, due to their apparently similar biology and geographic distribution, they would present the same phylogeographic pattern. One possible reason for this result could be that these fishes do not have a so similar biology as previously thought. Apparently, *O. oglinum* can tolerate all environmental changes caused by the AOP, while *Harengula* spp. cannot, making AOP an effective barrier for the latter. Additionally, the *Harengula* lineage from Brazilian province shows two structured populations and *O. oglinum* shows one possible structured population south of the AOP. The distinct lineage of *Harengula* from Brazilian province needs to be further investigated using morphological and additional genetic data to assess if it is a case of a new species or a species revalidation.

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3.7 Appendix

Annex 3. Samples from the ichthyological collection of Universidade Federal do Rio Grande do Norte and Genbank of CO1 used in the study. Borders delimit datasets. First dataset is *Harengula* and its outgroups, second is *O. oglinum* and its outgroups, and last is the Clupeidae. *Samples donated by Professor Claudio Oliveira from the Laboratório de Biologia e Genética de Peixes of the Universidade Estadual Paulista (UNESP-Botucatu).

Species	Sequence ID	Haplotype	Locality	Catalogue number	Genbank
Harengula sp.	H.sp_BRA_RN01	17	Natal, RN, Brazil	TIUFRN4754	-
Harengula sp.	H.sp_BRA_RN02	17	Natal, RN, Brazil	TIUFRN4780	-
Harengula sp.	H.sp_BRA_RN03	17	Baía Formosa, RN, Brazil	TIUFRN5098	-
Harengula sp.	H.sp_BRA_RN04	17	Natal, RN, Brazil	TIUFRN5006	-
Harengula sp.	H.sp_BRA_RN05	17	Natal, RN, Brazil	TIUFRN5023	-
Harengula sp.	H.sp_BRA_RN06	19	Natal, RN, Brazil	TIUFRN5030	-
Harengula sp.	H.sp_BRA_FN01	17	Fernando de Noronha, PE, Brazil	TIUFRN4956*	-
Harengula sp.	H.sp_BRA_FN02	17	Fernando de Noronha, PE, Brazil	TIUFRN4959*	-
Harengula sp.	H.sp_BRA_FN03	17	Fernando de Noronha, PE, Brazil	TIUFRN5201	-
Harengula sp.	H.sp_BRA_FN04	17	Fernando de Noronha, PE, Brazil	TIUFRN5220	-
Harengula sp.	H.sp_BRA_FN05	17	Fernando de Noronha, PE, Brazil	TIUFRN5221	-
Harengula sp.	H.sp_BRA_FN06	17	Fernando de Noronha, PE, Brazil	TIUFRN5244	-
Harengula sp.	H.sp_BRA_PE01	17	Itapissuma, PE, Brazil	TIUFRN4944*	-
Harengula sp.	H.sp_BRA_PE02	17	Itapissuma, PE, Brazil	TIUFRN4945*	-
Harengula clupeola	H.sp_BRA_AL01	17	Maceió, AL, Brazil	TIUFRN4946*	-
Harengula clupeola	H.sp_BRA_AL02	17	Maceió, AL, Brazil	TIUFRN4947*	-
Harengula clupeola	H.sp_BRA_AL03	17	Maceió, AL, Brazil	TIUFRN4948*	-
Harengula clupeola	H.sp_BRA_BA01	17	Valença, BA, Brazil	TIUFRN4950*	-
Harengula clupeola	H.sp_BRA_BA02	17	Valença, BA, Brazil	TIUFRN4951*	-
Harengula clupeola	H.sp_BRA_BA03	17	Valença, BA, Brazil	TIUFRN4953*	-
Harengula clupeola	H.sp_BRA_BA04	17	Valença, BA, Brazil	TIUFRN4954*	-
Harengula clupeola	H.sp_BRA_BA05	17	Valença, BA, Brazil	TIUFRN4955*	-
Harengula sp.	H.sp_BRA_RJ01	18	Macaé, RJ, Brazil	TIUFRN5314	-

Harengula sp.	H.sp_BRA_RJ02	18	Macaé, RJ, Brazil	TIUFRN5315	-
Harengula sp.	H.sp_BRA_RJ03	17	Macaé, RJ, Brazil	TIUFRN5316	-
Harengula sp.	H.sp_BRA_RJ04	17	Macaé, RJ, Brazil	TIUFRN5322	-
Harengula sp.	H.sp_BRA_RJ05	17	Macaé, RJ, Brazil	TIUFRN5323	-
Harengula sp.	H.sp_BRA_RJ06	18	Macaé, RJ, Brazil	TIUFRN5324	-
Harengula clupeola	H.sp_BRA_SP01	18	Bertioga, SP, Brazil	TIUFRN4932*	-
Harengula clupeola	H.sp_BRA_SP02	18	Santos, SP, Brazil	TIUFRN4938*	-
Harengula clupeola	H.sp_BRA_SC01	20	Balneário Camboriú, SC, Brazil	TIUFRN4942*	-
Harengula clupeola	H.sp_BRA_SC02	17	Balneário Camboriú, SC, Brazil	TIUFRN4943*	-
Harengula clupeola	H.sp_BRA_SC03	17	Bombinhas, SC, Brazil	TIUFRN4949*	-
Harengula jaguana	H.jaguana_USA01	2	Fort Pierce, Florida, USA	SMSA7110	JQ842517.1
Harengula jaguana	H.jaguana_USA02	3	Fort Pierce, Florida, USA	SMSA7091	JQ842516.1
Harengula jaguana	H.jaguana_USA03	4	Fort Pierce, Florida, USA	SMSA7090	JQ842515.1
Harengula jaguana	H.jaguana_USA04	5	Monroe, Florida, USA	KUT 6543	KF929959.1
Harengula jaguana	H.jaguana_MEX01	6	Chetumal, Quintana Roo, Mexico	ECO-CH-P5511A	GU225329.1
Harengula jaguana	H.jaguana_MEX02	7	Chetumal, Quintana Roo, Mexico	ECO-CH-P5511B	GU225328.1
Harengula jaguana	H.jaguana_MEX03	6	Chetumal, Quintana Roo, Mexico	ECO-CH-P5511C	GU225327.1
Harengula jaguana	H.jaguana_MEX04	7	Chetumal, Quintana Roo, Mexico	ECO-CH-P5511D	GU225326.1
Harengula jaguana	H.jaguana_MEX05	7	Chetumal, Quintana Roo, Mexico	ECO-CH-P5511E	GU225325.1
Harengula clupeola	H.clupeola_MEX01	8	Xcalak, Quintana Roo, Mexico	MX1267	GU225609.1
Harengula clupeola	H.clupeola_MEX02	9	Xcalak, Quintana Roo, Mexico	MX1264	GU225608.1
Harengula clupeola	H.clupeola_MEX03	10	Xcalak, Quintana Roo, Mexico	MX1265	GU225607.1
Harengula clupeola	H.clupeola_MEX04	1	Xcalak, Quintana Roo, Mexico	MX1266	GU225606.1
Harengula clupeola	H.clupeola_MEX05	11	Xcalak, Quintana Roo, Mexico	MFL312	GU224506.1
Harengula clupeola	H.clupeola_MEX06	11	Xcalak, Quintana Roo, Mexico	MFL313	GU224505.1
Harengula clupeola	H.clupeola_MEX07	12	Xcalak, Quintana Roo, Mexico	ECO-CH-P5491C	GU224504.1
Harengula clupeola	H.clupeola_MEX08	11	Xcalak, Quintana Roo, Mexico	ECO-CH-P5491D	GU224503.1
Harengula clupeola	H.clupeola_MEX09	13	Xcalak, Quintana Roo, Mexico	ECO-CH-P5491E	GU224502.1
Harengula clupeola	H.clupeola_MEX10	1	Xcalak, Quintana Roo, Mexico	ECO-CH-P5491B	GU224501.1
Harengula clupeola	H.clupeola_MEX11	1	Xcalak, Quintana Roo, Mexico	MFL279	GU224498.1
Harengula clupeola	H.clupeola_MEX12	11	Xcalak, Quintana Roo, Mexico	MFL280	GU224497.1

Harengula clupeola	H.clupeola_MEX13	14	Xcalak, Quintana Roo, Mexico	MFL276	GU224496.1
Harengula clupeola	H.clupeola_MEX14	1	Xcalak, Quintana Roo, Mexico	MFL277	GU224495.1
Harengula clupeola	H.clupeola_MEX15	11	Xcalak, Quintana Roo, Mexico	MFL260	GU224494.1
Harengula clupeola	H.clupeola_MEX16	15	Xcalak, Quintana Roo, Mexico	MFL254	GU224493.1
Harengula clupeola	H.clupeola_MEX17	16	Xcalak, Quintana Roo, Mexico	MFL245	GU224492.1
Harengula clupeola	H.clupeola_MEX18	1	Xcalak, Quintana Roo, Mexico	MFL243	GU224491.1
Harengula clupeola	H.clupeola_MEX19	11	Xcalak, Quintana Roo, Mexico	MFL244	GU224490.1
Harengula clupeola	H.clupeola_MEX20	11	Xcalak, Quintana Roo, Mexico	MFL241	GU224489.1
Harengula clupeola	H.clupeola_MEX21	1	Xcalak, Quintana Roo, Mexico	MFL242	GU224488.1
Harengula sp.	H.sp_BEL02	1	Dangriga, Stann Creek District, Belize	BZLW7159	JQ841218.1
Harengula clupeola	H.clupeola_BEL01	1	Dangriga, Stann Creek District, Belize	BZLW5362	JQ840530.1
Harengula clupeola	H.clupeola_BEL02	1	Dangriga, Stann Creek District, Belize	BZLW5361	JQ840529.1
Harengula sp.	H.sp_TOB04	1	Charlotteville, Tobago, Trinidad and Tobago	TOB9249	JQ842892.1
Harengula clupeola	H.clupeola_BRA_SP01	17	São Paulo, Brazil	HRCB:46931	JQ365382.1
Harengula clupeola	H.clupeola_BRA_SP02	17	São Paulo, Brazil	HRCB:40626	JQ365381.1
Harengula clupeola	H.clupeola_BRA_SP03	18	São Paulo, Brazil	HRCB:40549	JQ365380.1
Harengula clupeola	H.clupeola_BRA_SP04	18	São Paulo, Brazil	HRCB:46933	JQ365379.1
Harengula clupeola	H.clupeola_BRA_SP05	17	São Paulo, Brazil	HRCB:40623	JQ365378.1
Harengula clupeola	H.clupeola_BRA_SP06	18	São Paulo, Brazil	HRCB:40624	JQ365377.1
Harengula clupeola	H.clupeola_BRA_SP07	18	São Paulo, Brazil	HRCB:46934	JQ365376.1
Harengula clupeola	H.clupeola_BRA_SP08	18	São Paulo, Brazil	HRCB:40580	JQ365375.1
Harengula clupeola	H.clupeola_BRA_SP09	18	São Paulo, Brazil	HRCB:46932	JQ365374.1
Harengula clupeola	H.clupeola_BRA_SP10	17	São Paulo, Brazil	HRCB:40625	JQ365373.1
Harengula clupeola	H.clupeola_BRA_SP11	18	São Paulo, Brazil	HRCB:40548	JQ365372.1
Harengula clupeola	H.clupeola_BRA_SP12	17	São Paulo, Brazil	HRCB:40547	JQ365371.1
Harengula clupeola	H.clupeola_BRA_SP13	17	São Paulo, Brazil	HRCB:46930	JQ365370.1
Harengula sp.	H.sp_USA01	-	Fort Pierce, Florida, USA	SMSA7186	JQ842513.1
Harengula sp.	H.sp_TOB01	-	Mount Irvine Bay, Tobago, Trinidad and Tobago	TOBA9014	JQ842895.1
Harengula sp.	H.sp_BEL01	-	Dangriga, Stann Creek District, Belize	BZLW7160	JQ841219.1
Harengula thrissina	H.thrissina_PACIFIC	-	California, USA	SIO 08-16	HQ010050.1
Harengula humeralis	H.humeralis_CAR01	-	Bermuda, Caribe	HAHU_CO_6	MK871635.1

Harengula humeralis	H.humeralis_CAR02	-	Bermuda, Caribe	HAHU_BAMZ_86	MK871634.1
Harengula humeralis	H.humeralis_CAR03	-	Bermuda, Caribe	HAHU_BAMZ_86	MK871634.1
Harengula humeralis	H.humeralis_CAR04	-	Bermuda, Caribe	HAHU_CO_5	MK871636.1
Harengula humeralis	H.humeralis_CAR05	-	Bermuda, Caribe	HAHU_CO_3	MK871637.1
Harengula humeralis	H.humeralis_MEX01	-	Xcalak, Quintana Roo, Mexico	MX1273	GU225612.1
Harengula humeralis	H.humeralis_MEX02	-	Xcalak, Quintana Roo, Mexico	MX1271	GU225611.1
Harengula humeralis	H.humeralis_MEX03	-	Xcalak, Quintana Roo, Mexico	MX1269	GU225610.1
Harengula humeralis	H.humeralis_BEL01	-	Dangriga, Stann Creek District, Belize	BZLW7158	JQ841220.1
Harengula humeralis	H.humeralis_BEL02	-	Dangriga, Stann Creek District, Belize	BZLW5360	JQ840531.1
Opisthonema oglinum	O.oglinum_BRA_PA01	1	Bragança, PA, Brazil	TIUFRN4923*	-
Opisthonema oglinum	O.oglinum_BRA_PA02	1	Bragança, PA, Brazil	TIUFRN4924*	-
Opisthonema oglinum	O.oglinum_BRA_PA03	2	Bragança, PA, Brazil	TIUFRN4908*	-
Opisthonema oglinum	O.oglinum_BRA_CE01	1	Fortaleza, CE, Brazil	TIUFRN4887*	-
Opisthonema oglinum	O.oglinum_BRA_CE02	1	Fortaleza, CE, Brazil	TIUFRN4889*	-
Opisthonema oglinum	O.oglinum_BRA_CE03	2	Fortaleza, CE, Brazil	TIUFRN4891*	-
Opisthonema oglinum	O.oglinum_BRA_RN01	3	Macau, RN, Brazil	TIUFRN4419	-
Opisthonema oglinum	O.oglinum_BRA_RN02	4	Macau, RN, Brazil	TIUFRN4439	-
Opisthonema oglinum	O.oglinum_BRA_RN03	2	Natal, RN, Brazil	TIUFRN4342	-
Opisthonema oglinum	O.oglinum_BRA_RN04	5	Baía Formosa, RN, Brazil	TIUFRN5108	-
Opisthonema oglinum	O.oglinum_BRA_RN05	6	Baía Formosa, RN, Brazil	TIUFRN5139	-
Opisthonema oglinum	O.oglinum_BRA_PB02	7	Cabedelo, PB, Brazil	TIUFRN3658	-
Opisthonema oglinum	O.oglinum_BRA_PB02	1	Cabedelo, PB, Brazil	TIUFRN3664	-
Opisthonema oglinum	O.oglinum_BRA_PB03	8	Cabedelo, PB, Brazil	TIUFRN4406	-
Opisthonema oglinum	O.oglinum_BRA_PE01	8	Itapissuma, PE, Brazil	TIUFRN4900*	-
Opisthonema oglinum	O.oglinum_BRA_PE02	9	Itapissuma, PE, Brazil	TIUFRN4902*	-
Opisthonema oglinum	O.oglinum_BRA_PE03	10	Itapissuma, PE, Brazil	TIUFRN4904*	-
Opisthonema oglinum	O.oglinum_BRA_AL01	1	Paripueira, AL, Brazil	TIUFRN4910*	-
Opisthonema oglinum	O.oglinum_BRA_AL02	11	Paripueira, AL, Brazil	TIUFRN4911*	-
Opisthonema oglinum	O.oglinum_BRA_AL03	2	Maceió, AL, Brazil	TIUFRN4912*	-
Opisthonema oglinum	O.oglinum_BRA_BA01	2	Valença, BA, Brazil	TIUFRN4918*	-
Opisthonema oglinum	O.oglinum_BRA_BA02	2	Valença, BA, Brazil	TIUFRN4919*	-

Opisthonema oglinum	O.oglinum_BRA_BA03	12	Valença, BA, Brazil	TIUFRN4921*	-
Opisthonema oglinum	O.oglinum_BRA_ES01	8	Vila Velha, ES, Brazil	TIUFRN5299	-
Opisthonema oglinum	O.oglinum_BRA_ES02	2	Vila Velha, ES, Brazil	TIUFRN5301	-
Opisthonema oglinum	O.oglinum_BRA_ES03	2	Vila Velha, ES, Brazil	TIUFRN5303	-
Opisthonema oglinum	O.oglinum_BRA_SP01	13	Ubatuba, SP, Brazil	TIUFRN4882*	-
Opisthonema oglinum	O.oglinum_BRA_SP02	1	São Sebastião, SP, Brazil	TIUFRN4895*	-
Opisthonema oglinum	O.oglinum_BRA_SP03	14	São Sebastião, SP, Brazil	TIUFRN4896*	-
Opisthonema oglinum	O.oglinum_BRA_SC01	1	Balneário Camboriú, SC, Brazil	TIUFRN4892*	-
Opisthonema oglinum	O.oglinum_BRA_SC02	2	Balneário Camboriú, SC, Brazil	TIUFRN4894*	-
Opisthonema oglinum	O.oglinum_BRA_SC03	1	Barra Velha, SC, Brazil	TIUFRN4916*	-
Opisthonema oglinum	O.oglinum_USA01	2	North Carolina, USA	USNM:FISH:433061	KT075297.1
Opisthonema oglinum	O.oglinum_USA02	20	North Carolina, USA	USNM:FISH:433122	MH378477.1
Opisthonema oglinum	O.oglinum_USA03	2	North Carolina, USA	USNM:FISH:433234	MH378561.1
Opisthonema oglinum	O.oglinum_USA04	20	North Carolina, USA	USNM:FISH:433255	MH378577.1
Opisthonema oglinum	O.oglinum_MEX01	15	Chetumal, Quintana Roo, Mexico	ECO-CH-P5505A	GU225414.1
Opisthonema oglinum	O.oglinum_MEX02	16	Chetumal, Quintana Roo, Mexico	ECO-CH-P5505B	GU225415.1
Opisthonema oglinum	O.oglinum_MEX03	8	Chetumal, Quintana Roo, Mexico	ECO-CH-P5505C	GU225416.1
Opisthonema oglinum	O.oglinum_MEX04	17	Chetumal, Quintana Roo, Mexico	ECO-CH-P5505E	GU225417.1
Opisthonema oglinum	O.oglinum_CAR01	22	Bermuda, Caribe	OPIO_BAMZ_21	MK871654.1
Opisthonema oglinum	O.oglinum_CAR02	23	Bermuda, Caribe	OPIO_BAMZ_22	MK871648.1
Opisthonema oglinum	O.oglinum_CAR03	23	Bermuda, Caribe	OPIO_BAMZ_23	MK871649.1
Opisthonema oglinum	O.oglinum_CAR04	23	Bermuda, Caribe	OPIO_BAMZ_24	MK871650.1
Opisthonema oglinum	O.oglinum_CAR05	23	Bermuda, Caribe	OPIO_BAMZ_25	MK871651.1
Opisthonema oglinum	O.oglinum_CAR06	22	Bermuda, Caribe	OPIO_DEEP_115	MK871655.1
Opisthonema oglinum	O.oglinum_CAR07	23	Bermuda, Caribe	OPIO_DEEP_116	MK871652.1
Opisthonema oglinum	O.oglinum_CAR08	23	Bermuda, Caribe	OPIO_DEEP_117	MK871653.1
Opisthonema oglinum	O.oglinum_BRA_AL04	19	Alagoas, Brazil	MUFAL1931	KY402279.1
Opisthonema oglinum	O.oglinum_BRA_AL05	20	Alagoas, Brazil	MUFAL1833	KY402280.1
Opisthonema oglinum	O.oglinum_BRA_AL06	21	Alagoas, Brazil	MUFAL1834	KY402282.1
Opisthonema oglinum	O.oglinum_BRA_AL07	2	Alagoas, Brazil	MUFAL1900	KY402281.1
Opisthonema oglinum	O.oglinum_BRA_SP04	18	São Paulo, Brazil	LBP-41578	GU702345.1

Opisthonema oglinum	O.oglinum_BRA_SP05	8	São Paulo, Brazil	LBP-35116	GU702358.1
Opisthonema oglinum	O.oglinum_BRA_SP06	2	São Paulo, Brazil	HRCB:35119	JQ365473.1
Opisthonema oglinum	O.oglinum_BRA_SP07	1	São Paulo, Brazil	LBPV35118.1	JX034010.1
Opisthonema oglinum	O.oglinum_BRA_SP08	13	São Paulo, Brazil	LBPV35117.1	JX034011.1
Opisthonema oglinum	O.oglinum_BRA_SP09	8	São Paulo, Brazil	LBPV35120.1	JX034012.1
Opisthonema bulleri	O.bulleri_MEX01	-	Mexico	OB1	KU587814.1
Opisthonema medirastre	O.medirastre_MEX01	-	Mexico	OM1	KU587832.1
Opisthonema medirastre	O.medirastre_MEX02	-	Mexico	OM2	KU587833.1
Opisthonema medirastre	O.medirastre_MEX03	-	Mexico	OM3	KU587834.1
Opisthonema medirastre	O.medirastre_MEX04	-	Mexico	OM4	KU587835.1
Opisthonema medirastre	O.medirastre_MEX05	-	Mexico	OM5	KU587836.1
Opisthonema medirastre	O.medirastre_MEX06	-	Mexico	OM6	KU587837.1
Opisthonema medirastre	O.medirastre_USA01	-	California, USA	SIO 07-96	HQ010075.1
Opisthonema libertate	O.libertate_MEX01	-	Mexico	OL1	KU587822.1
Opisthonema libertate	O.libertate_MEX02	-	Mexico	OL2	KU587823.1
Opisthonema libertate	O.libertate_MEX03	-	Mexico	OL3	KU587824.1
Opisthonema libertate	O.libertate_MEX04	-	Mexico	OL4	KU587825.1
Opisthonema libertate	O.libertate_MEX05	-	Mexico	OL5	KU587826.1
Opisthonema libertate	O.libertate_MEX06	-	Mexico	OL6	KU587827.1
Opisthonema libertate	O.libertate_MEX07	-	Mexico	OL7	KU587828.1
Opisthonema libertate	O.libertate_MEX08	-	Mexico	OL8	KU587829.1
Opisthonema libertate	O.libertate_MEX09	-	Mexico	OL9	KU587830.1
Opisthonema libertate	O.libertate_MEX10	-	Mexico	OL10	KU587831.1
Opisthonema libertate	O.libertate_USA01	-	California, USA	SIO 98-37	HQ010071.1
Amblygaster clupeoides	Amblygaster_clupeoides	-	China	GD 9082029	EF607313.1
Anodontostoma chacunda	Anodontostoma_chacunda	-	Malaysia	KL023	MH673898.1
Clupanodon thrissa	Clupanodon_thrissa	-	South China Sea	SCS-ZH2	NC_018600.1
Dorosoma anale	Dorosoma_anale	-	Calackmul reserve, Campeche, Mexico	MX1350	GU225594.1
Dorosoma cepedianum	Dorosoma_cepedianum	-	Maryland, USA	USNM:FISH:425115	MH570220.1
Dorosoma chavesi	Dorosoma_chavesi	-	San Juan, Nicaragua	stri-14543	MG496137.1
Dorosoma petenense	Dorosoma_petenense	-	Bacalar, Quintana Roo, Mexico	BACQ-29	MG449869.1

Dorosoma petenense	Dorosoma_petenense1	-	La Conquista, Nuevo León, Mexico	MXIV0286	HQ991858.1
Ethmalosa fimbriata	Ethmalosa_fimbriata	-	-	-	AM911179.1
Herklotsichthys dispilonotus	Herklotsichthys_dispilonotus	-	Pendas, Johor, Malaysia	PK12K6_F2	KX223910.1
Herklotsichthys dispilonotus	Herklotsichthys_dispilonotus1	-	Pendas, Johor, Malaysia	PK1K2_F2	KX223911.1
Herklotsichthys lippa	Herklotsichthys_lippa	-	Australia	BW-A8556	HQ956377.1
Herklotsichthys lippa	Herklotsichthys_lippa1	-	Australia	BW-A8458	HM902702.1
Herklotsichthys lossei	Herklotsichthys_lossei	-	Saudi Arabia	CEW0005	KU508431.1
Herklotsichthys punctatus	Herklotsichthys_punctatus	-	Israel	HePu34N	KM538357.1
Herklotsichthys quadrimaculatus	Herklotsichthys_quadrimaculatus	-	Pomene, Mozambique	ADC11_54.4 #6	KF489612.1
Herklotsichthys spilurus	Herklotsichthys_spilurus	-	St Philippe, Réunion	ECOMAR<FRA>:REU1835	JQ350053.1
Hilsa kelee	Hilsa_kelee	-	Moheshkhali, Bangladesh	DUZM_MF_017.2	MN083113.1
Konosirus punctatus	Konosirus_punctatus	-	Taiwan Strait	hap2	KU302347.1
Nematalosa erebi	Nematalosa_erebi	-	Townsville, QLD, Australia	CES-275	KJ669557.1
Nematalosa erebi	Nematalosa_erebi1	-	Point Sturt, SA, Australia	SAMA:F-FISH 1_JP15	KJ669558.1
Nematalosa japonica	Nematalosa_japonica	-	China	GD 9082030	EF607513.1
Nematalosa nasus	Nematalosa_nasus	-	Karimanal, Tamil Nadu, India	FBRC_ZSI_F3110_DNA410	MK962521.1
Tenualosa ilisha	Tenualosa_ilisha	-	Barisal, Bangladesh	DU6026	MK572610.1
Tenualosa ilisha	Tenualosa_ilisha1	-	Barisal, Bangladesh	DU6025	MK572611.1
Tenualosa reevesii	Tenualosa_reevesii	-	Shanghai, China	-	MF123318.1
Tenualosa toli	Tenualosa_toli	-	Chittagong, Bangladesh	DUZM_FF_017.2	MH429339.1
Tenualosa toli	Tenualosa_toli1	-	South Korea	bf79	MK359931.1

Annex 4. DNA extraction protocol (modified from Bruford et al. 1992).

1. Add 410 µL of extraction buffer and 80 µL of 10% SDS (detergent) inside a tube. Take a small piece of tissue and put in the tube. Add 10 µL of Proteinase K. Then, incubate it in a dry heat block at 55 ºC for at least 3 h or overnight.

2. Centrifuge digested tissue for 8 min at 13000 rpm, then transfer the supernatant to a new tube and add 180 µL NaCl (5M). Vortex to homogenize it.

3. Centrifuge sample for 8 min at 13000 rpm, then quickly transfer the supernatant to a new tube e quickly add 840 µL EtOH 99% (ice cold) and manually invert the tube several times.

4. Centrifuge sample for 8 min at 13000 rpm, then discard the supernatant. The DNA pellet will be on the bottom of tube. Add 250 µL 80% EtOH and invert a couple of times.

5. Repeat step 4.

6. Carefully, remove all ethanol and let the pellet air dry for 10-15 min. Leave it open over a sheet paper. Be careful to not let it dehydrate.

7. Rehydrate the DNA adding 90 µL Milli-q water (dH_2O) and store in freezer.

Annex 5. Genetic distances (K2P) of *Harengula* and *O. oglinum* datasets. Values in bold are distances between groups and other values are distances within groups. Clu: *H. clupeola* from Greater Caribbean; Jag: *H. jaguana* from Greater Caribbean; BRA-1: *Harengula* sp. from Brazil region 1; BRA-2: *Harengula* sp. from Brazil region 2; BRA: *O. oglinum* from Brazil; USA-MEX: *O. oglinum* from USA and Mexico, Greater Caribbean; BER: *O. oglinum* from Bermuda, Greater Caribbean

Harengula					***Opisthonema oglinum***			
	Clu	Jag	BRA 1	BRA 2		BRA	USA_MEX	BER
Clu	0.002				BRA	0.005		
Jag	**0.024**	0.007			USA-MEX	**0.005**	0.004	
BRA-1	**0.044**	**0.049**	0.000		BER	**0.008**	**0.005**	0.001
BRA-2	**0.043**	**0.048**	**0.001**	0.001				

4. CONCLUSÃO GERAL

Nesse trabalho, abordarmos aspectos etnoictiológicos da ginga e investigamos os padrões filogeográficos dos dois táxons mais representativos da ginga. No primeiro capítulo, vimos que usar o LEK como uma ferramenta para obter conhecimento taxonômico de peixes comercializados localmente é uma maneira de resolver alguns dos problemas mais básicos associados às estatísticas da pesca: saber realmente o que é capturado pelos pescadores. Além disso, essa fonte de conhecimento é um valioso aliado à conservação. Aqui identificamos que ginga é uma assembleia de juvenis de diferentes espécies (*O. oglinum*, *Harengula* sp., *L. piquitinga* e poucas espécies de Engraulidae), capturados na cidade de Natal, no estado do Rio Grande do Norte. A pressão da pesca sobre os juvenis pode ser uma ameaça para a manutenção dos estoques pesqueiros, que já são considerados como totalmente explotados ou super-explotados, dependendo da quantidade capturada e de algum processo de seleção eventual pela pesca desses juvenis. Por outro lado, a ginga poderia ser considerada uma CIS, dada sua singular importância cultural às comunidades locais, o que poderia facilitar qualquer eventual medida de conservação. Estudos adicionais devem ser feitos para avaliar os impactos da pesca nos juvenis, promovendo o papel da ginga como CIS para garantir a manutenção desses estoques.

No segundo capítulo, com base em análises filogenéticas e filogeográficas e delimitações de linhagens, concluímos que *H. clupeola* e *H. jaguana* são restritas a província Carolinian+Greater Caribbean e uma linhagem distinta de *Harengula* é distribuída pela província Brazilian. Esta linhagem diferente foi isolada das espécies da província Carolinian+Greater Caribbean há 2,4 Myr, esse isolamento provavelmente foi causado pela AOP. No entanto, *O. oglinum* é formado por uma única espécie em toda a sua distribuição no Oceano Atlântico Ocidental. Isso contraria nossa expectativa de que, devido à sua biologia e distribuição geográfica aparentemente semelhantes, essas espécies apresentariam o mesmo padrão filogeográfico. Uma possível razão para isso pode ser que esses peixes não possuem uma biologia tão semelhante à que se pensava anteriormente. Aparentemente, *O. oglinum* pode tolerar todas as alterações ambientais causadas pela AOP, enquanto *Harengula* spp. não, fazendo da AOP uma barreira eficaz para este último. Além disso, a linhagem *Harengula* da província Brazilian mostra duas populações estruturadas e *O. oglinum* mostra três possíveis populações estruturadas, incluindo uma ao sul da AOP. A linhagem distinta de *Harengula* da província Brazilian precisa ser investigada mais a fundo, usando dados morfológicos e outros dados genéticos para avaliar se é um caso de nova espécie ou uma revalidação de espécie.