



# The historical ecology of subsistence and early commercial fisheries in mangrove systems in Brazil

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## ABSTRACT

Human population growth and the technological advancements of the 20th and 21st centuries have significantly altered human-environment interactions and led to unprecedented anthropogenic footprints on coastal and ocean systems. Despite thousands of years of exploitation for subsistence and, later, commercial purposes, the ecology of mangrove fisheries along the Brazilian coast and the consequences of these activities remain poorly understood. This is largely due to a pervasive lack of historical baselines, and highlights the conservation crises affecting some of the world's biodiversity hotspots. In this study, we used otolith metrics and stable isotope analysis to investigate changes in the body length and trophic ecology of several demersal species recovered from pre-colonial (4500 cal BP to 1500 AD) and historical (late 19th and early 20th centuries AD) archaeological sites in Babitonga Bay, the largest mangrove system in southern Brazil. Our results revealed that pre-colonial and historical fisheries exploited a wide range of mangrove habitats, encompassing brackish to marine systems. Pre-colonial subsistence fisheries, however, targeted predominantly small and juvenile individuals in nursery areas, while early commercial fisheries targeted larger adult specimens, likely due to their higher commercial value. Our study shows that some drivers of stock overexploitation, such as the preferential capture of large and adult individuals, were found to be occurring more than 150 years ago along the southern Brazilian coast. Given the deep roots of human footprints in Brazil, our findings underscore the significance of incorporating historical data into the formulation of fisheries management strategies in subtropical and tropical regions.

## 1. Introduction

Brazil encompasses some of the most diverse biomes on earth, such as the Amazon and the Atlantic Forest, and one of the world's most

extensive mangrove systems (de Lacerda et al., 2022; Ottoni et al., 2021). Mangroves offer numerous ecosystem services (from food provisioning to carbon storage (Ottoni et al., 2021)), and provide for diverse coastal populations, including traditional communities (Indigenous,

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Caboclos, small-scale fisheries) who secure their food and livelihoods from resources therein. It has recently been estimated that ~53% of small-scale fishers in Brazil engage in either part-time or full-time fishing activities in or around mangrove systems, amounting to nearly 300,000 people (zu Ermgassen et al., 2020). Conservation and management of mangrove systems in Brazil, therefore, are of high priority and have been addressed through distinct mechanisms, including the establishment of Marine Protected Areas with varying levels of access and use (Maretti et al., 2019). Despite these efforts, mangrove conservation is the subject of continuous debate, with effective protection jeopardised by political and economic disputes (Bernardino et al., 2021; Ottoni et al., 2021). Moreover, fisheries monitoring programs remain scarce, with irregular and geographically scattered statistics spanning just a few decades (Freire et al., 2021; PMAP-SC, 2016). The ecological and conservation status of several species remains uncertain (ICMBio, 2018), and significant gaps persist regarding the origin and changing nature of past anthropogenic footprints on mangrove habitats.

Several species historically exploited in mangrove systems continue to be pursued today for both commercial and household consumption. Among these, whitemouth croaker (*Micropogonias furnieri*) and white sea catfish (*Genidens barbus*) have been subject to exploitation since pre-colonial times (Fossile et al., 2020, 2023a), with catches declining in response to overfishing over the past few decades (Haimovici and Cardoso, 2016; Mendonça et al., 2020). By contrast, there remains a significant knowledge gap concerning various species of lesser commercial value that are vital for household consumption and local poverty alleviation, such as barred grunt (*Conodon nobilis*) (Lima et al., 2019; Passarone et al., 2019; Silva-Júnior et al., 2019; Vianna et al., 2004). Information on the ecology and biology of barred grunt is limited, particularly in southern Brazil (Cardoso de Melo et al., 2020; Da Silva et al., 2019; Ferreira et al., 2019; Lira et al., 2019). Due to low population numbers and substantial fishing pressure from various fisheries (shrimp, artisanal, recreational), barred grunt has been identified as highly susceptible to stock collapse and overexploitation (Freire et al., 2016; Passarone et al., 2019; Pinsky et al., 2011; Verba et al., 2020). Moreover, recreational fishing has grown significantly in Brazil since the second half of the 20th century, potentially intensifying pressure on numerous species, including barred grunt and fat snook (*Centropomus parallelus*) which are commonly caught by this sector (Chaves, 2021; Freire et al., 2020; Motta et al., 2016). Information on the size and the trophic ecology of these species, however, remains scarce in the region.

Whitemouth croaker are commonly found in estuaries, coastal lagoons, and shallow coastal waters, where they tend to form schools and exhibit bottom-feeding behaviour, consuming a variety of prey (Haimovici et al., 2016; Pizzochero et al., 2017). White sea catfish are often found in estuaries, mangroves, and freshwater environments. They are nocturnal feeders, primarily feeding on smaller fish and invertebrates (Avigliano et al., 2017, 2022). Barred grunt also inhabit coastal waters, estuaries, and mangroves, feeding on smaller fish and invertebrates, and often forming schools (Da Silva et al., 2019). Similarly, fat snook are typically found in estuarine and coastal areas, including mangroves. They are carnivorous, and prey on fish and crustaceans (Costa-e-Silva et al., 2021; Daros et al., 2016; Feltrin Contente et al., 2009).

For at least 7000 years, mangrove systems have supported numerous Indigenous populations along the southern Atlantic Forest coast of Brazil. Large shell mounds, locally known as *sambaquis* (De Blasis et al., 1998), and other shallow coastal sites produced by later groups using Taquara-Itaré ceramics (Rohr, 1984), offer glimpses of past human perception and cultural value of mangrove habitats. Faunal remains from these sites hold clues to Indigenous ecological knowledge related to species diversity, distribution and habitat, as well as their provisioning (food) and cultural services (symbolic, ritualistic, etc.) (Fossile et al., 2023a; Gilson et al., 2023; Klokler, 2016; Lopes et al., 2016). It has been estimated that annual captures of demersal fish by pre-colonial Indigenous groups were comparable to or higher than historical subsistence fisheries in these regions (Fossile et al., 2019, 2023a). Their per capita

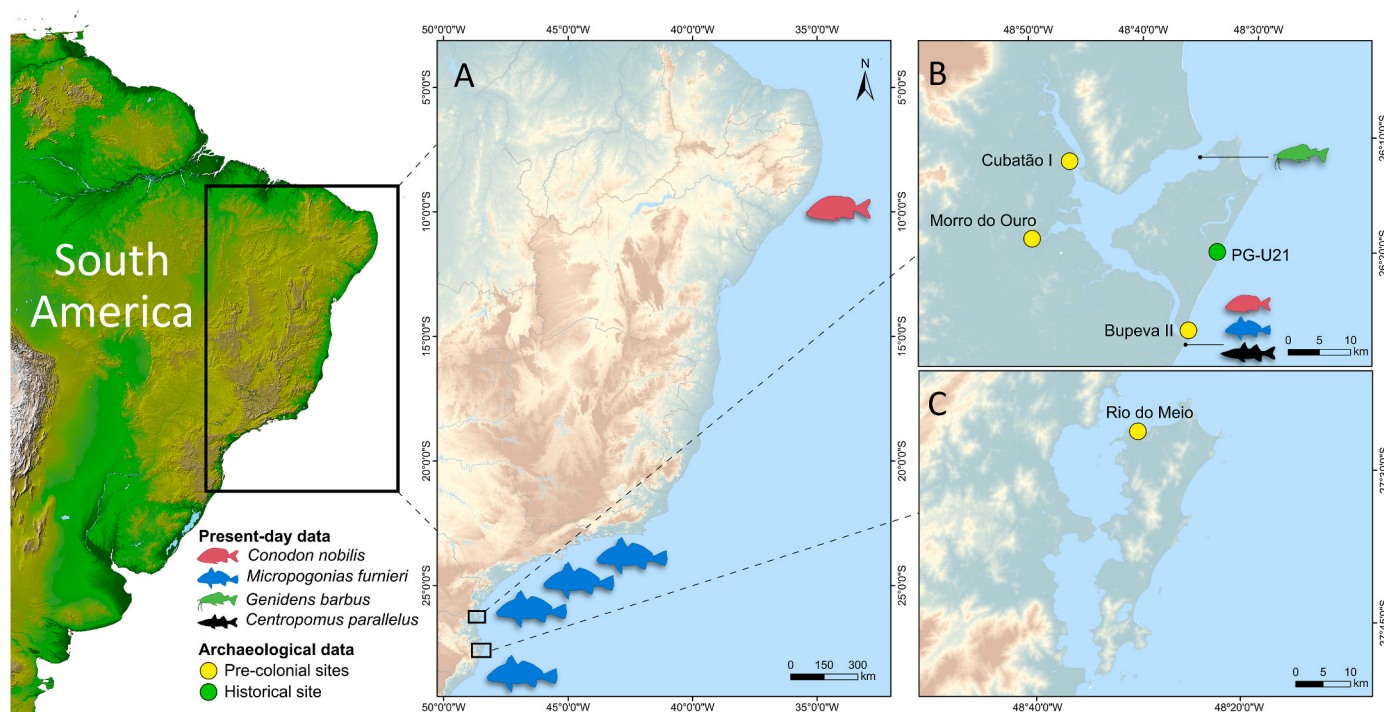
intake of marine proteins remains unequalled among modern small-scale coastal fisheries (Colonese et al., 2014; Toso et al., 2021), even among those that retain some ecological knowledge rooted in Indigenous traditions (Nardoto et al., 2011, 2020). Many questions remain, such as which fishing grounds were preferentially used by pre-colonial Indigenous populations, whether specific species or size classes were targeted or more general fish communities, and whether species-specific strategies were implemented (Fossile et al., 2019; Gilson and Lessa, 2021a; Lopes et al., 2016). Little is known about the potential adverse effects of thousands of years of fishing, and whether these resources were somehow managed to ensure sustainable levels of exploitation.

European colonisation from the 16th century onward brought unprecedented changes to Brazilian coastal environments. Notably, it led to the replacement of Indigenous populations, the marginalisation of their ecological knowledge, and the commoditization of natural resources, which has fundamentally reshaped human-environment interactions in the region (Dean, 1997). Historical documents from the last 150 years attest to an intensification of anthropogenic pressures on Brazilian mangrove ecosystems due to evolving political agendas related to industrialization, agricultural practices, commercial fishing, and urbanisation (Herbst et al., 2023; Sandoval Gallardo et al., 2021). Fishing restrictions and sanctions documented since at least the late 19th century (e.g. 1880–1890) indicate that some local stocks were already experiencing the effects of overfishing, with the impacts exacerbated by profit- and efficiency-seeking fisheries policies introduced throughout the 20th century (Abdallah and Sumaila, 2007; Herbst et al., 2023; Pincinato and Gasalla, 2010; Sandoval Gallardo et al., 2021). While historical sources offer valuable insights into exploited species and the drivers of exploitation, they often lack details regarding size and feeding behaviour of targeted species (Herbst et al., 2023), which are crucial for stock assessments (Casini et al., 2009; Shin et al., 2005).

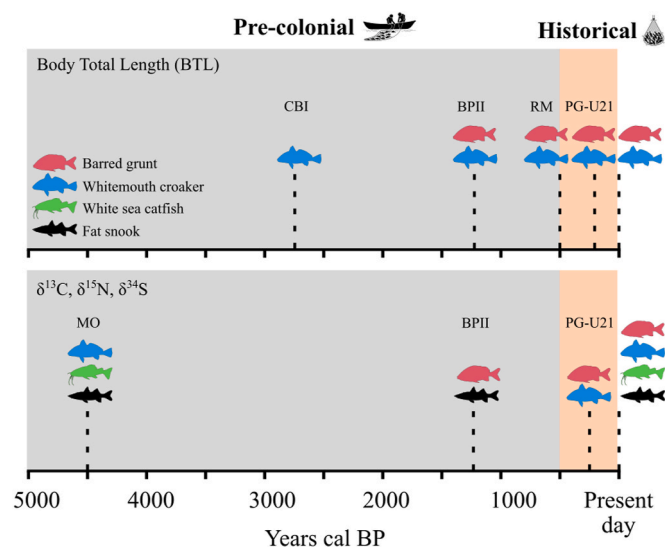
In order to address some of the gaps, here we analysed the body total length and trophic ecology of various demersal fish species, including barred grunt, whitemouth croaker, white sea catfish and fat snook, retrieved from pre-colonial (prior to 1500 AD, SI1) and historical (late 19th and early 20th centuries AD, SI1) archaeological sites in Babitonga Bay, Santa Catarina state (Fig. 1). This region is home to the largest mangrove ecosystem in southern Brazil, which hosts a large number of pre-colonial and historical archaeological sites with evidence of subsistence and commercial fishing (Brito et al., 2017; Fossile et al., 2019, 2020; Saint-Hilaire, 1936). Body total length of archaeological specimens captured for subsistence and commercial purposes was estimated, and the stable carbon, nitrogen, and sulphur isotopic composition of bone collagen was analysed from various species to investigate the ecology of pre-colonial and historical catches (Fig. 2). Our objective was to explore differences in species size and fishing ground preferences between pre-colonial and historical fisheries, and to provide for the first time in the region glimpses of ecological baselines predating the onset of intensive commercial fisheries from the mid 20th century.

## 2. Analytical background

Stable isotope analyses have been extensively employed to reconstruct the trophic ecology and behavioural patterns of marine species. Stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope analysis of marine vertebrates, for example, is a well-established approach for studying animal physiology, niche differentiation and trophic connections within food webs (Braje et al., 2017; Newsome et al., 2010; Peterson et al., 1986). Bulk tissue  $\delta^{13}\text{C}$  values trace the energy flow from distinct photosynthetic pathways at the base of the food web, including sources like terrestrial, freshwater and marine primary producers (Peterson and Fry, 1987; Sholto-Douglas et al., 1991). Bone collagen is typically  $^{13}\text{C}$ -enriched by ~3.5 per mil (‰) compared to assimilated food items, thus it can complement trophic information often obtained from a consumer's nitrogen isotopic composition (Matsubayashi et al., 2018;



**Fig. 1.** Overview of the study area showing (A) the geographic position of measured body size in present-day populations of barred grunt and whitemouth croaker (Da Silva et al., 2019; Haimovici et al., 2016); (B) the location of pre-colonial (Morro do Ouro, Bupeva II, Cubatão I) and historical (Praia Grande Unidade 21) archaeological sites analysed, including the catch location of present-day species used for stable isotope analysis; and (C) the location of the pre-colonial site of Rio do Meio. Maps were generated using ArcGIS 10.8 (<https://www.arcgis.com>) and Inkscape 1.3 (<https://inkscape.org/>) on data publicly available from NASA/JPL-Caltech (adapted from <https://www.jpl.nasa.gov/images/pia03388-south-america-shaded-relief-and-colored-height>), Brazilian Agricultural Research Corporation - EMBRAPA (Embrapa and de, 2021), Natural Earth (<https://www.naturalearthdata.com/>), Brazilian Institute of Geography and Statistics - IBGE (<https://www.ibge.gov.br/geociencias/todos-os-produtos-geociencias.html>), National Institute for Space Research - INPE (Assis et al., 2019) and Phylopic 2.0 (<https://www.phylopic.org/>).



**Fig. 2.** Timeline illustrating the dates of the archaeological sites from which samples were analysed for body total length (BTL) and stable isotopes (Morro do Ouro - MO, Cubatão I - CBI, Bupeva II - BPII, Rio do Meio - RM, Praia Grande Unidade 21 - PG-U21), along with the present-day species analysed. Figure generated with Inkscape 1.3 (<https://inkscape.org/>) using publicly available silhouettes from Phylopic 2.0 (<https://www.phylopic.org/>).

Sholto-Douglas et al., 1991). Nitrogen isotopes reflect the protein fraction in diet, and studies have shown that bone collagen  $\delta^{15}\text{N}$  values in marine fish tend to increase by  $\sim 1\text{‰}$ – $2.5\text{‰}$  with each successive trophic

level (Matsubayashi et al., 2018; Sholto-Douglas et al., 1991). Stable sulphur isotopes ( $\delta^{34}\text{S}$ ) provide additional information on energy and nutrient flow, particularly between benthic and pelagic ecosystems (Connolly et al., 2004; Peterson et al., 1986; Szpak and Buckley, 2020). Sulphur in bone collagen is found in the essential amino acid methionine, and is transferred through the food web with relatively minor, but variable, isotopic fractionation (Guiry et al., 2021; McCutchan et al., 2003; Nehlich, 2015; Szpak and Buckley, 2020). In marine environments, planktonic algae and seaweed uptake and assimilate marine sulphates ( $\sim +21\text{‰}$ ) producing little isotope fractionation (Fry, 2007; Peterson et al., 1986). By contrast, dissimilatory sulphate reduction by anaerobic bacteria/archaea causes high isotope fractionation of marine sulphates in nearshore environments (e.g. estuaries), producing  $^{34}\text{S}$ -depleted sulphides ( $\sim -26\text{‰}$ ) or other oxidation products that are used by plants such as mangroves and seagrasses rooted in anoxic sediments (Connolly et al., 2004; Fry, 2007; Fry et al., 1982; Goldhaber, 2003; Okada and Sasaki, 1997; Peterson et al., 1986). This results in  $^{34}\text{S}$ -depleted organic matter at the base of the food web compared to marine algae and seaweed. Nearshore habitats are also exposed to continental waters with extremely variable  $\delta^{34}\text{S}$  values ( $-40\text{‰}$  to  $+20\text{‰}$ , (Nehlich, 2015) compared to marine sulphates (Peterson et al., 1986), but their isotopic effect on food webs will be perceptible only in very low saline habitats (Fry and Chumchal, 2011). Stable isotope analysis of archaeological faunal remains has been increasingly used to uncover the ecology of past fisheries (Braje et al., 2017; Elliott Smith et al., 2023; Guiry et al., 2022), and more recently, this approach has been extended to archaeological fish records from Brazil (Burg Mayer and de Freitas, 2023; Toso et al., 2021). However, these applications are limited to stable carbon and nitrogen isotopes, while sulphur isotopes have remained unexplored to date in the region. Furthermore, the limited isotope record for fish prevents our understanding of the



evolution of food webs and coastal habitats used by past human groups in the southwestern Atlantic Ocean, as well as the extent of recent anthropogenic impacts on coastal systems.

Otolith analyses are commonly applied to estimate fish body length, age and growth rate, which are particularly important for fisheries management purposes (Oliveira et al., 2019; Santos et al., 2017). Decreasing fish body length is considered an indicator of intensive fishing in stock assessments (Gulland and Rosenberg, 1992; Lorenzen et al., 2016; Shin et al., 2005). Variations in species' size can change the length at which the first maturity occurs, potentially rendering conservation measures ineffective (Santos et al., 2015). Fish body length and age at first sexual maturity, in fact, are frequently used to determine the smallest size at which a species can be sustainably caught (Minimum Landing Size - MLS) (Alonso-Fernández et al., 2021; Myers and Mertz, 1998). Additionally, metric studies employing otoliths and fish vertebrae have been used to track the impact of early fisheries in other regions (Ainis et al., 2021; Andrews et al., 2023; Barrett, 2019; Braje et al., 2017; Guiry et al., 2021). In Brazil, however, otoliths from archaeological sites have only received cursory attention for past fisheries reconstructions (Fossile et al., 2019; Garcia, 1970; Gilson and Lessa, 2021a; Lopes et al., 2016).

### 3. Material and methods

#### 3.1. Sample selection for stable isotope analysis

Species commonly exploited in southern Brazil since pre-colonial times were selected for stable carbon ( $\delta^{13}\text{C}$ ), nitrogen ( $\delta^{15}\text{N}$ ) and sulphur ( $\delta^{34}\text{S}$ ) isotope analyses. Specifically, bones of barred grunt (*Conodon nobilis*), whitemouth croaker (*Micropogonias furnieri*), white sea catfish (*Genidens barbatus*) and fat snook (*Centropomus parallelus*) were recovered from pre-colonial and historical archaeological sites in Babitonga Bay. Pre-colonial sites included the shellmound Morro do Ouro (MO), in Joinville, and the shellmound Bupeva II (BP II), in São Francisco do Sul. MO and BP II show evidence of fishing and shellfish harvesting. MO, in addition, contains several human burials and was therefore used as a cemetery by pre-colonial groups (Figuti, 2009; Fossile et al., 2019; Goulart, 1980). BP II shows a reoccupation by ceramic producing groups (Taquara-Itararé tradition) in the most recent phase of the site (Bandeira, 2004). Bones of white sea catfish ( $n = 100$ ) and fat snook ( $n = 23$ ) from MO were recovered from deposits radiocarbon dated between 4800–4550 and 4500–4100 cal BP (Pezo-Lanfranco et al., 2018). Bones of barred grunt ( $n = 20$ ) and fat snook ( $n = 20$ ) from BP II were retrieved from deposits radiocarbon dated to 1000–750 and 650–500 cal BP (95.4% confidence interval [CI], SI1).

Bones were also sampled from the historical site Praia Grande Unidade 21 (PG-U21), a rural settlement in São Francisco do Sul (Alves and Oliveira, 2002). There, samples of barred grunt ( $n = 20$ ) and whitemouth croaker ( $n = 20$ ) were selected from deposits radiocarbon dated to 1690–1950 and 1510–1800 AD (68.4% CI) (Fossile et al., 2023b). The material culture at this site (coins and ceramic artefacts), however, constrains the chronology of the archaeological deposits to the late 19th to early 20th centuries AD (Alves and Oliveira, 2002). Whenever possible, specimens were selected to represent individual animals by sampling the same anatomical element (dentary, premaxilla, articular, hyomandibular, pharyngeal teeth). The permits for stable isotope analysis of archaeological samples were obtained from the *Instituto do Patrimônio Histórico e Artístico Nacional* (IPHAN, protocol n.º 01510.000196/2019–63 and 01510.000823/2021–81).

For comparative purposes, bones of modern (present-day) adult individuals of barred grunt ( $n = 25$ ), whitemouth croaker ( $n = 11$ ), white sea catfish ( $n = 20$ ) and fat snook ( $n = 18$ ) were also sampled for stable isotopic analysis. Modern samples caught in Babitonga Bay and adjacent coastal waters were commercially acquired in Joinville between 2018 and 2019 and registered in the *Sistema Nacional de Gestão do Patrimônio Genético e do Conhecimento Tradicional Associado* (SisGen, n.º RF54A7C

and R22244B) following article 22 of Decree 8.772, of May 11, 2016. Furthermore, pre-colonial whitemouth croaker ( $n = 8$ ) from MO previously analysed for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (Toso et al., 2021) were also included in this study.

Due to the absence of formal statistical relations for estimating the body length of the studied species based on distinct bones, we were unable to confidently assign an age to the analysed specimens. Nevertheless, with the exception of barred grunt, visual comparison suggests that pre-colonial specimens were smaller than their modern counterparts (fat snook, whitemouth croaker, white sea catfish). Historical specimens (barred grunt, whitemouth croaker) were instead similar to or larger than modern counterparts.

#### 3.2. Collagen extraction

The bone collagen of archaeological ( $n = 203$ ) and modern ( $n = 74$ ) samples was extracted at the stable isotope facilities of the Institute of Environmental Science and Technology (ICTA-UAB). Archaeological bones (50–630 mg) were physically cleaned and immersed in 0.6M hydrochloric acid (HCl) at 4 °C for several days. Bones were then rinsed with ultrapure water and immersed in 0.05M sodium hydroxide (NaOH) for 20 min at room temperature. NaOH wash cycles were repeated as needed, typically 1 or 2 times, until no further colour change occurred in the solution. Samples were rinsed three times with ultrapure water for 10 min each to ensure the complete removal of NaOH (Ambrose, 1990; Szpak et al., 2017). Samples were gelatinized in 0.001M HCl (pH3) at 80 °C for 48 h. The supernatant containing collagen was then filtered using Polyethylene Eze filters (9 mL, pore size 60–90 µm, Elkay Laboratories Ltd.), then frozen for at least 48h at –20 °C and lyophilised. Bones from MO were relatively small in size (50% of the samples  $\leq 300$  mg), thus a decision was made to not treat them with NaOH in order to prevent sample loss (Chisholm et al., 1983; Rudakova and Zaikov, 1987). A paired analysis on both treated and untreated NaOH samples from the site revealed no significant differences in both atomic and isotopic values (SI2). The same collagen extraction protocol was applied to the modern bone samples (22–340 mg), with the exception that lipids were first removed by sonicating samples 3 times for 15 min in a dichloromethane:methanol solution (2:1) prior to collagen extraction. The NaOH wash was applied to modern samples to aid in the removal of non-collagen proteins (Guiry and Szpak, 2020). While archaeological bones may contain variable trace amounts of lipids (Colonese et al., 2015), there is no apparent effect on the atomic and stable isotope composition of archaeological bone remains in the region (Toso et al., 2021). As a consequence, lipids were not extracted from archaeological bones.

#### 3.3. Stable isotope analysis

Stable isotope analysis of successfully extracted samples was performed at SUERC, East Kilbride (UK). One hundred and fourteen samples were analysed using a Delta V Advantage continuous-flow isotope ratio mass spectrometer coupled via a ConFloIV to an IsoLink elemental analyser (Thermo Scientific, Bremen, Germany) as described in Sayle et al. (2019). Bone collagen (~0.7 mg) was combusted in the presence of oxygen in a single reactor containing tungstic oxide and copper wires at 1020 °C to produce  $\text{N}_2$ ,  $\text{CO}_2$  and  $\text{SO}_2$ . A magnesium perchlorate trap was used to eliminate water produced during the combustion process, and the gases were separated in a GC column heated between 70 °C and 240 °C. Helium was used as a carrier gas throughout the procedure.  $\text{N}_2$ ,  $\text{CO}_2$ , and  $\text{SO}_2$  entered the mass spectrometer via an open split arrangement within the ConFloIV and were analysed against their corresponding reference gases. The International Atomic Energy Agency (IAEA) reference materials USGS40 (L-glutamic acid,  $\delta^{13}\text{C}$  (V-PDB) =  $-26.39 \pm 0.04\text{‰}$ ,  $\delta^{15}\text{N}$  (AIR) =  $-4.52 \pm 0.06\text{‰}$ ) and USGS41a (L-glutamic acid,  $\delta^{13}\text{C}$  (V-PDB) =  $36.55 \pm 0.08\text{‰}$ ,  $\delta^{15}\text{N}$  (AIR) =  $47.55 \pm 0.15\text{‰}$ ) were used to normalise  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values. Two in-house standards (GS2,

$\delta^{34}\text{S}$  (V-CDT) =  $-10.28 \pm 0.18\text{‰}$  and GAS2,  $\delta^{34}\text{S}$  (V-CDT) =  $18.56 \pm 0.10\text{‰}$ ) that are calibrated to the International Atomic Energy Agency (IAEA) reference materials IAEA-S-2 (silver sulfide,  $\delta^{34}\text{S}$  (V-CDT) =  $22.62 \pm 0.08\text{‰}$ ) and IAEA-S-3 (silver sulfide,  $\delta^{34}\text{S}$  (V-CDT) =  $-32.49 \pm 0.08\text{‰}$ ) were used to normalise  $\delta^{34}\text{S}$  values. Normalisation was checked using the well characterised Elemental Microanalysis IRMS fish gelatin standard B2215 ( $\delta^{13}\text{C}$  (V-PDB) =  $-22.92 \pm 0.10\text{‰}$ ,  $\delta^{15}\text{N}$  (AIR) =  $4.26 \pm 0.12\text{‰}$ ,  $\delta^{34}\text{S}$  (V-CDT) =  $1.21 \pm 0.24\text{‰}$ ) and/or USGS88 (marine collagen,  $\delta^{13}\text{C}$  (V-PDB) =  $-16.06 \pm 0.07\text{‰}$ ,  $\delta^{15}\text{N}$  (AIR) =  $14.96 \pm 0.14\text{‰}$ ,  $\delta^{34}\text{S}$  (V-CDT) =  $17.10 \pm 0.44\text{‰}$ ). Precision is determined to be  $\pm 0.2\text{‰}$  for  $\delta^{15}\text{N}$ ,  $\pm 0.1\text{‰}$  for  $\delta^{13}\text{C}$  and  $\pm 0.4\text{‰}$  for  $\delta^{34}\text{S}$  and is based on repeated measurements of Elemental Microanalysis IRMS fish gelatin standard B2215. 19% of samples were analysed in duplicate.

Samples with insufficient aliquots for sulphur isotope analysis ( $n = 26$ , 10%) had their stable carbon and nitrogen isotope values determined in the Stable Isotope Analysis Laboratory in ICTA-UAB. Duplicate collagen samples (0.5 mg) were analysed using an elemental analyser (EA) Flash (ThermoScientific, Bremen, Germany) coupled to a Thermo Delta V Advantage isotope ratio mass spectrometer (IRMS) with a ConFlo IV interface (ThermoScientific, Bremen, Germany). The IAEA reference material (IAEA 600, caffeine,  $\delta^{13}\text{C}$  (V-PDB) =  $-27.77 \pm 0.04\text{‰}$ ,  $\delta^{15}\text{N}$  (AIR) =  $1.0 \pm 0.2\text{‰}$ , IAEA, Vienna, Austria) and the United States Geological Service (USGS) reference material (USGS 62, caffeine,  $\delta^{13}\text{C}$  (V-PDB) =  $-14.79 \pm 0.04\text{‰}$ ,  $\delta^{15}\text{N}$  (AIR) =  $20.17 \pm 0.06\text{‰}$ , USGS, Reston, VA) were used to normalise  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values. The analytical error (standard deviation) was determined to be  $0.04\text{‰}$  for  $\delta^{13}\text{C}$  and  $0.07\text{‰}$  for  $\delta^{15}\text{N}$ . Results are reported as per mil (‰) relative to the internationally accepted standards V-PDB, AIR and V-CDT. Present-day collagen  $\delta^{13}\text{C}$  values were corrected for the Suess effect using a  $\delta^{13}\text{C}$  correction factor of  $+1.8\text{‰}$  observed in the South Atlantic (Eide et al., 2017).

We employed standard ellipses to delineate present-day and historical ecological niches based on modern and archaeological bone collagen  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and  $\delta^{34}\text{S}$  values. Ecological niches were built using SIBER 2.1.8 (Stable Isotope Bayesian Ellipses in R (Jackson et al., 2011), ) in RStudio (RStudio Team, 2020). Comprehensive information on the model parameters and assumptions can be found in Jackson et al. (2011). In brief, Bayesian methods were applied to generate standard ellipses that elucidate the isotopic and ecological niches of taxonomic species within a given community. These ellipses were individually constrained using the average isotopes values from each species, encompassing 95% of the data ( $p = 0.95$ ). Subsequently, the Standard Ellipse Area correction (SEAc) was used to calculate the degree of overlap among these species' niches.

### 3.3.1. Otolith samples and estimated body total length

Otoliths of barred grunt and whitemouth croaker were sampled from pre-colonial (BPII) and historical (PG-U21) sites for estimating the body total length (BTL). These species were selected due to their relative abundance and the ease of taxonomic identification based on their otolith morphometric traits. Otoliths of barred grunt ( $n = 11$ ) from BPII were retrieved from bulk archaeological deposits sieved with 5 mm mesh size. Otoliths of barred grunt ( $n = 177$ ) and whitemouth croaker ( $n = 129$ ) from PG-U21 were sieved from bulk archaeological deposits using a 2.5 mm mesh size. Otoliths were identified through side-by-side comparison with reference collections at the *Museu Arqueológico de Sambaqui de Joinville (MASJ)* and the *Laboratório de Arqueologia e Patrimônio Arqueológico (LAPARq)* of the *Universidade da Região de Joinville (Univille)*. Some species were also identified by comparison with the digital Collection of Otoliths of Teleost Fishes from the Southeast-South Region of Brazil (COSS-Brasil) of the Oceanographic Institute of the University of São Paulo (Rossi-Wongtschowski et al., 2016). Otoliths were first sorted by laterality and then the length (OL) measured using a Digimess 150 mm digital calliper. OL was used to estimate body total length (BTL) according to equations for present-day populations of barred grunt (Oliveira et al., 2021) and whitemouth croaker (Haimovici

et al., 2023) in the Southwestern Atlantic Ocean:

$$\text{Barred grunt, BTL} = 1.3292 * \text{OL}^{1.1623} \quad (r = 0.98, n = 76). \quad \text{Eq. 1}$$

$$\text{Whitemouth croaker, BTL} = 24.34 + 22.57 * \text{OL} \quad (r = 0.99, n = 93). \quad \text{Eq. 2}$$

We extended our analysis to previously published OL data for barred grunt and whitemouth croaker from other pre-colonial archaeological sites in southern Brazil (Fig. 1B and C). These included otoliths from Cubatão I (CBI,  $n = 37$  whitemouth croaker) dated between 3550–3100 and 2350–2000 cal BP (Fossile et al., 2019) and from Rio do Meio (RM,  $n = 911$  whitemouth croaker;  $n = 37$  barred grunt) dated between 650–500 and 550–250 cal BP (Gilson and Lessa, 2020, 2021a). Cubatão I is a shellmound located in Babitonga Bay, containing evidence of human burials and intense fishing and shellfish exploitation (Fossile et al., 2019). Rio do Meio (RM), situated on Florianópolis Island, is a shallow site with the presence of ceramic artefacts attributed to Taquara-Itararé tradition (Fossari, 2004; Gilson and Lessa, 2021b). Faunal remains from these sites were recovered from bulk deposits sieved with 5 and 2 mm mesh sizes. Otoliths from CBI and RM were measured using a Zeiss Stemi 200 magnifier with a Dino-Eye coupled camera (DinoCapture software) and Digimess 150 mm digital calliper. OL is presented with one decimal place for comparison with data previously published for Rio do Meio (Gilson and Lessa, 2021a). OL comparisons between sites were performed using statistical tests in Past 4.10 (Hammer et al., 2001) and RStudio Software (RStudio Team, 2020). Since the normal distribution of OL could be rejected (Shapiro-Wilk W), the Kruskal Wallis non-parametric test followed by the Wilcoxon rank sum test (Bonferroni method) was used for OL comparisons (see SI6).

### 3.3.2. Measured BTL in present-day populations

The estimated BTL of archaeological individuals was compared to measured values in modern specimens collected from the Southwestern Atlantic Ocean as part of biological studies (Da Silva et al., 2019; Haimovici et al., 2016) (Fig. 1A). Ideally, BTL data should originate from populations in similar environmental conditions to those found in archaeological contexts. In the case of whitemouth croaker ( $n = 357$ ), this was achieved by using BTL data from southern Brazil, caught using bottom trawling at depths below 50 m, between latitudes  $22^\circ\text{S}$  and  $29^\circ\text{S}$  and recorded in 1989 and 1990. The fishing area corresponds to the FAO Fishing Area 41.2.1 (Santos (FAO, 2023)). This includes the coastal and offshore zones of the states of Santa Catarina, Paraná, São Paulo, and Rio de Janeiro (Haimovici et al., 2016), which are in close proximity to the archaeological specimens.

Conversely, the lack of studies and methodological limitations related to BTL of modern barred grunts from southern and southeastern Brazil introduced uncertainties in data comparison. For example, BTL data collected by Pina and Chaves (2009) were obtained from accidentally captured specimens (bycatch) and may not represent the entire population. In the case of Pombo et al. (2014), the BTL data derived from specimens captured in shallow coastal waters (less than 4 m deep) and therefore may be biased toward juvenile individuals. To address these limitations, we have used barred grunt BTL data from specimens ( $n = 410$ ) collected from FAO Fishing Area 41.1.2 (Natal (FAO, 2023)), specifically at latitude  $09^\circ\text{S}$  in the state of Alagoas, between 2009 and 2012 (Da Silva et al., 2019). These data include specimens captured using various methods, such as beach seines, gillnets, and trawls (Da Silva et al., 2019).

It is important to emphasise that the BTL of modern studies should represent the size distribution of the underlying populations, while archaeological specimens are fisheries resources, as such their BTL are largely influenced by fishing goals, gear type and market forces, among others (Cooke et al., 2021; Haimovici et al., 2016; Sjöberg, 2015; Wolff et al., 2015), as well as recovery techniques and taphonomic processes (Campbell, 2005; Grayson, 2014; Reitz and Wing, 1999). Comparisons between BTL of archaeological catches and modern populations for stock size assessment, therefore, is not straightforward (Plank et al.,

2018).

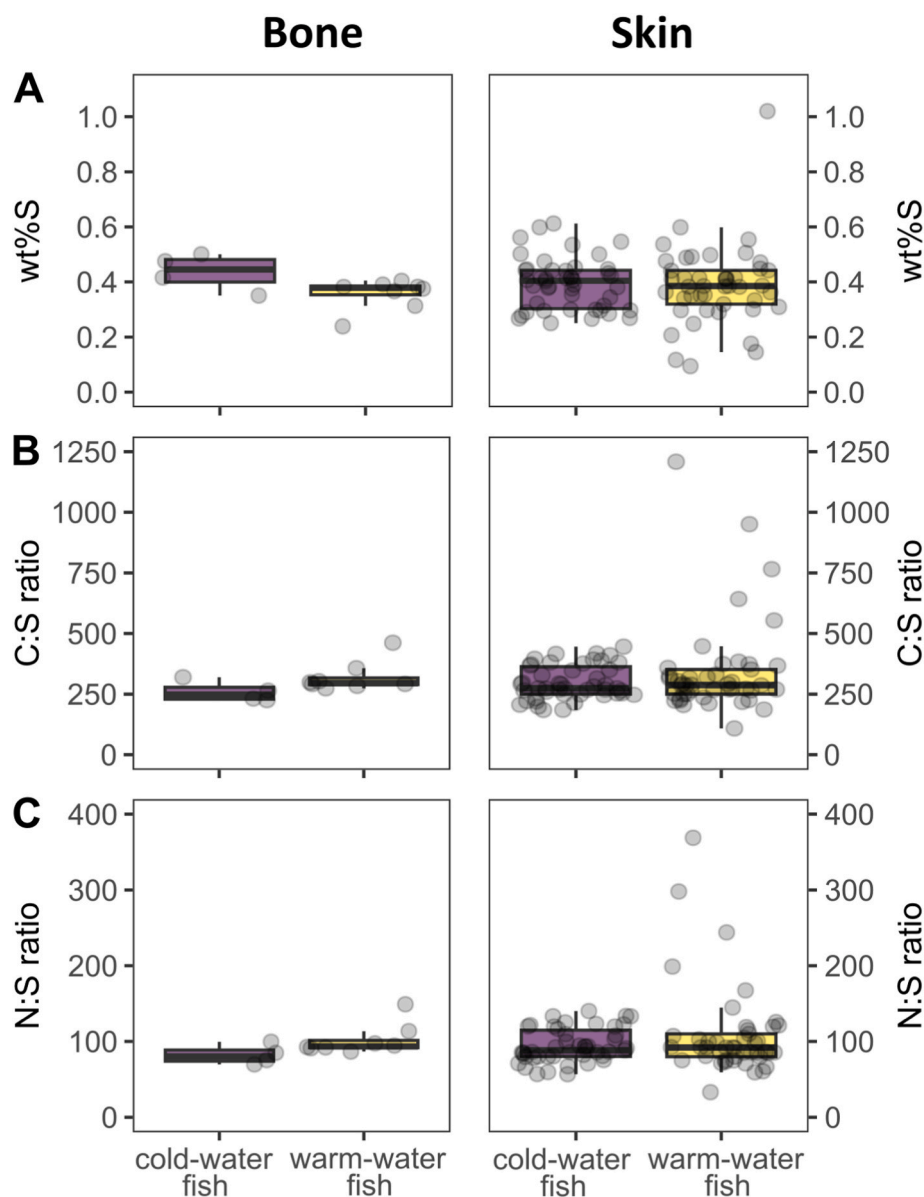
## 4. Results

### 4.1. Collagen composition in modern fish

Collagen extracted from all modern bones ( $n = 74$ ) presented wt%C (39.22%–45.49%), wt%N (13.87%–16.38%), and C:N molar ratios (3.10–3.57) consistent with well-preserved bone collagen (Ambrose, 1990; Guiry and Szpak, 2021; van Klinken, 1999) (SI2, SI3). For eight samples (11%), the C:N was higher ( $>3.30$ ) than reported for modern bony fish (3.00–3.30) (Guiry and Szpak, 2021). Elevated C:N in modern samples may be produced by the presence of lipids and non-collagen proteins present in the extracts (Guiry and Hunt, 2020; Guiry and Szpak, 2020, 2021), but these are expected to have been adequately removed by the defatting and NaOH wash processes employed. At least in the case of lipids, the lack of a negative correlation between the  $\delta^{13}\text{C}$

values and the C:N molar ratios ( $r = -0.17$ ,  $p = 0.16$ , Pearson correlation, SI4) (Guiry and Szpak, 2021) assures that modern collagen samples retained their genuine  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values.

The wt%S ranged from 0.34% to 0.62% (median 0.44%), with average C:S and N:S molar ratios of  $263.06 \pm 30.8$  (182.10–341.15) and  $81.44 \pm 10.4$  (54.60–105.45), respectively. Some samples ( $n = 13$ ) had lower wt%S than the acceptable ranges for intact archaeological (0.40–0.85%) and modern (0.52–0.83%) fish bone collagen, established primarily from cold-water species like *Gadus morhua* (Nehlich and Richards, 2009). Our average C:S and N:S molar ratios exceeded those of Nehlich and Richards (2009) (C:S =  $175 \pm 50$ ; N:S =  $60 \pm 20$ ), and instead, aligned with wt%S reported in modern bone collagen from marine (0.24–0.49%) (Kittiphattanabawon et al., 2005; Privat et al., 2007), and freshwater species (0.31–0.38%) (Muyonga et al., 2004), from tropical and subtropical regions. Comparable C:S (209–461) and N:S (67–149) molar ratios were reported in additional studies by (Kittiphattanabawon et al., 2005; Privat et al., 2007). Notably, various studies



**Fig. 3.** Collagen wt%S, C:S and N:S molar ratios for cold-water and warm-water bony fish species observed in bone and skin from amino acid compositions (Szpak, 2011). While the differences in wt%S ( $p = 0.67$ ), C:S ( $p = 0.73$ ), and N:S ( $p = 0.77$ ) between cold-water and warm-water fish (considering only skin) were not statistically significant (Kruskal-Wallis test after rejecting normal distribution with Shapiro-Wilk normality test,  $p < 0.05$ ), it is still evident that several warm-water fish tend to exhibit lower wt%S values when compared to cold-water species.



highlight differences in C:N ratios between cold- and warm-water bony fish species (Guiry and Szpak, 2020; Gustavson, 1955; Rigby and Spikes, 1960); however, a closer look at the available data also points to differences in wt%S, and C:S and N:S ratios. For example, Szpak's collated data (Szpak, 2011) for modern skin ( $n = 91$ ) and bone ( $n = 12$ ) across marine and freshwater species from subtropical and tropical regions (warm-water fish) show a wider range of methionine and thus wt%S values (0.09–1.02%) compared to those from polar and temperate zones (0.25–0.61%, cold-water fish) (Fig. 3). Even though the observed differences were not statistically significant (Kruskal-Wallis test,  $p < 0.05$ , for skin only), this also leads to higher average C:S ( $343 \pm 198$ ) and N:S ( $109 \pm 61$ ) ratios in warm-water fish than in cold-water species (CS =  $297 \pm 69$ , NS =  $95 \pm 22$ ), which are consistent with our results. Elemental composition of modern fish bone collagen presented here suggests that the existing sulphur quality benchmarks (Nehlich and Richards, 2009) do not encompass the full spectrum of wt%S found in modern fish collagen, especially those originating from warmer habitats, thus inviting further investigation.

#### 4.2. Stable isotope values in modern fish

Median  $\delta^{13}\text{C}$  values ranged from  $-10.98\text{‰}$  (barred grunt) to  $-9.72\text{‰}$  (white sea catfish), reflecting assimilated carbon from benthic microalgae and marine phytoplankton (Garcia et al., 2007). Fat snook exhibited a wider range of  $\delta^{13}\text{C}$  values ( $-15.49\text{‰}$  to  $-8.99\text{‰}$ ), indicating that individuals with  $^{13}\text{C}$ -depleted collagen assimilated organic matter in habitats with a higher input of continental waters (Daros et al., 2016; Garcia et al., 2007). Median  $\delta^{15}\text{N}$  values of modern individuals ranged from  $+13.08\text{‰}$  (whitemouth croaker) to  $+16.04\text{‰}$  (white sea catfish), and distinguished piscivore (white sea catfish (Beneditto et al., 2018)) from invertivorous (fat snook (Feltrin Contento et al., 2009)), and omnivorous (barred grunt and whitemouth croaker) species feeding primarily on invertebrates and sporadically on fish (Pizzochero et al., 2017). Niche partitioning among species is evident through two CN ellipses groups: one featuring white sea catfish at a higher trophic level, with a slight overlap with fat snook, and the other encompassing barred grunt, whitemouth croaker, and fat snook, sharing food resources and habitats at a lower trophic position (Fig. 4A). Median  $\delta^{34}\text{S}$  values ranged from  $+12.03\text{‰}$  (white sea catfish) to  $+17.69\text{‰}$  (barred grunt), and further separated species based in distinct feeding grounds (Connolly et al., 2004; Fry, 2007; Goldhaber, 2003; Okada and Sasaki, 1997; Peterson et al., 1986), as expressed by the CS ellipses (Fig. 4B). Specifically, higher  $\delta^{34}\text{S}$  values in barred grunt suggest the species feed predominantly on  $^{34}\text{S}$ -enriched food webs located nearshore or in areas exposed to the open sea with a stronger influence of marine sulphates. In comparison, lower  $\delta^{34}\text{S}$  values in white sea catfish, fat snook and whitemouth croaker are indicative of  $^{34}\text{S}$ -depleted food webs in shallow and inner-estuarine waters (Pizzochero et al., 2017). The  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and  $\delta^{34}\text{S}$  values were not significantly correlated with the measured BTL, which might be due to the fact that modern specimens were mostly large adult individuals (SI4). The only exception was a moderate negative correlation between  $\delta^{13}\text{C}$  and BTL in white sea catfish ( $r = -0.46$ ,  $p = 0.039$ , SI4), which could potentially be explained by the wide range of environments occupied by this species, forming brackish (spawning in estuarine waters and migrating to freshwater, marine waters or both) and freshwater residents (Avigliano et al., 2017, 2022).

#### 4.3. Collagen stable isotopes of archaeological fish remains

Collagen was successfully extracted from 140 out of 203 archaeological fish samples. Of these, 122 samples had C:N molar ratios (3.09–3.60) typical of well-preserved archaeological bone collagen (Ambrose, 1990; DeNiro, 1985; van Klinken, 1999). 107 samples had enough collagen for  $\delta^{34}\text{S}$  analyses, exhibiting wt%S ranging from 0.24% to 0.59%. Of these, 72 samples had wt%S values consistent with values observed in modern individuals (0.34%–0.59%). 35 samples had lower

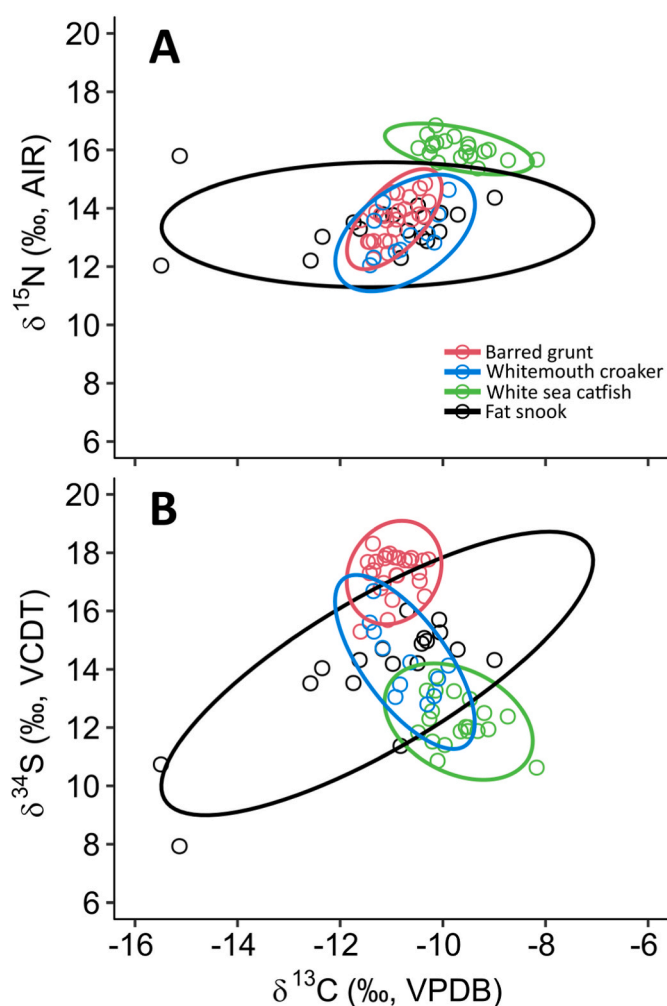
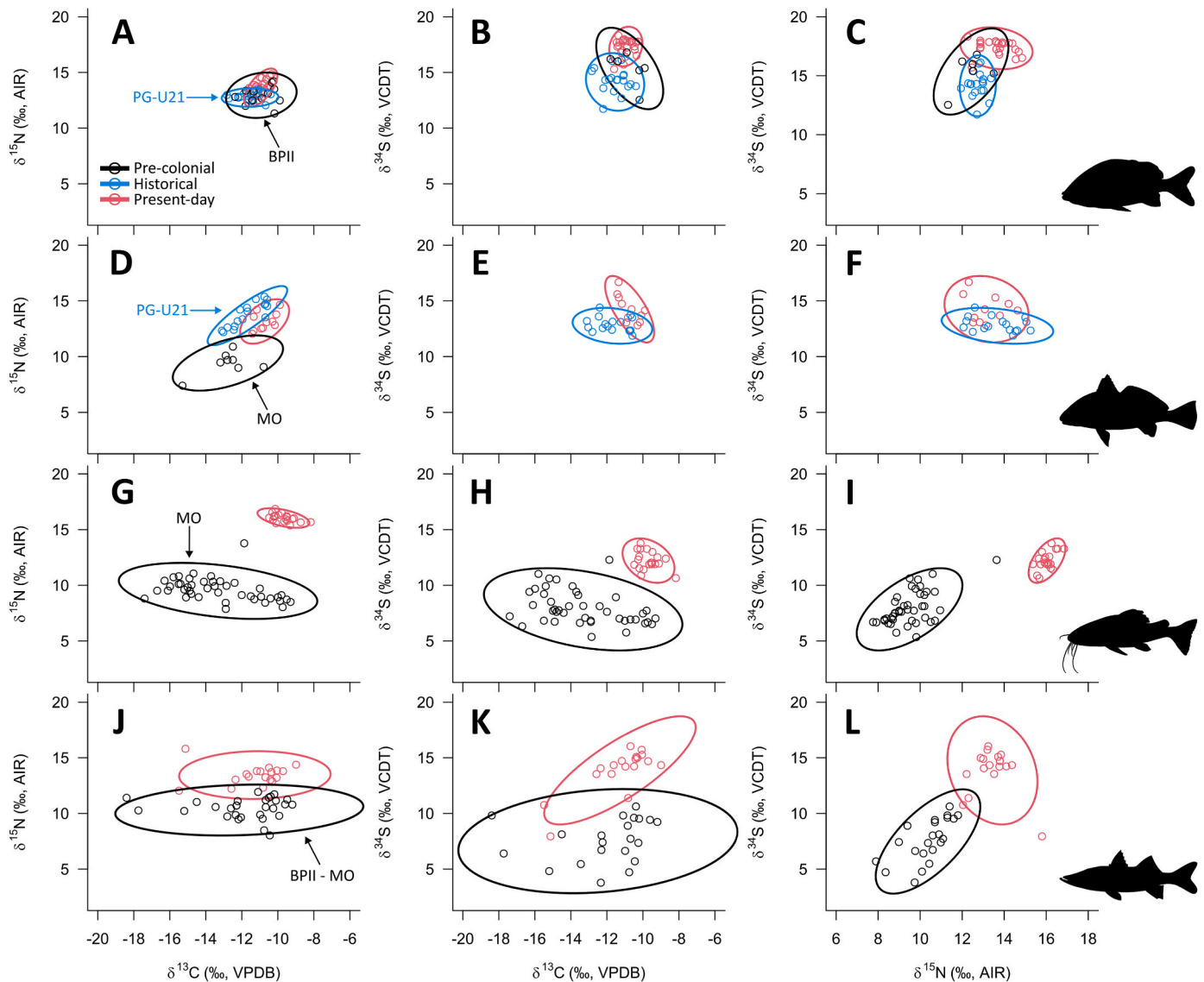


Fig. 4. Ellipse-derived isotopic niches according to (A) carbon and nitrogen and (B) carbon and sulphur isotope compositions.

wt%S values than modern counterparts (0.24%–0.33%) but yielded comparable  $\delta^{34}\text{S}$  results to those within acceptable wt%S values, thus their  $\delta^{34}\text{S}$  values were deemed reliable (Fig. 4A and B).

Median  $\delta^{13}\text{C}$  values ranged from  $-13.60\text{‰}$  (white sea catfish) to  $-11.04\text{‰}$  (fat snook), with the wider range of values observed in pre-colonial fat snook ( $-21.40\text{‰}$  to  $-9.20\text{‰}$ ) from MO and BP11, and white sea catfish ( $-17.40\text{‰}$  to  $-9.30\text{‰}$ ) from MO. We found no significant correlation between  $\delta^{13}\text{C}$  values and C:N ratios ( $r = -0.12$ ;  $p = 0.15$ ) indicating that carbon stable isotope values were not affected by lipids or humic acids. Median  $\delta^{15}\text{N}$  values ranged from  $+9.40\text{‰}$  (white sea catfish) to  $+13.93\text{‰}$  (whitemouth croaker), whereas the median  $\delta^{34}\text{S}$  values ranged from  $+7.45\text{‰}$  (fat snook) to  $+14.27\text{‰}$  (barred grunt) (Fig. 5). Pre-colonial white sea catfish from MO had  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and  $\delta^{34}\text{S}$  values significantly lower than their modern counterparts, which is evident by the lack of overlap in the CN, CS and NS ellipses (SI4). Fat snook from MO and BP11 exhibited  $\delta^{15}\text{N}$  and  $\delta^{34}\text{S}$  values significantly lower than modern specimens, but indistinguishable  $\delta^{13}\text{C}$  values, with some overlap in the CN, CS and NS ellipses. Similarly, the  $\delta^{13}\text{C}$  values of pre-colonial whitemouth croaker from MO were indistinguishable from modern specimens, with significant differences only between  $\delta^{15}\text{N}$  values. By contrast, barred grunt from BP11 show comparable  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values with modern specimens, with the exception of  $\delta^{34}\text{S}$  values. Finally, barred grunt and whitemouth croaker from PG-U21 had  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and  $\delta^{34}\text{S}$  values significantly lower than modern specimens, with the exception of the comparable  $\delta^{15}\text{N}$  values between modern and historical whitemouth croaker.



**Fig. 5.** Stable isotope values for (A–C) barred grunt, (D–F) whitemouth croaker, (G–I) white sea catfish, (J–L) fat snook. Pre-colonial whitemouth croaker ( $n = 8$ ) individuals from Morro do Ouro (MO) previously analysed for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (Toso et al., 2021) were also included in our study.

#### 4.4. Estimated body size

Archaeological barred grunt had median BTL of 21.58 cm (10.67–28.56 cm,  $n = 11$ , BP11), 22.88 cm (4.80–30.89 cm,  $n = 177$ , PG-U21) and 23.64 cm (17.97–28.80 cm,  $n = 37$ , RM) (SI5), and were statistically indistinguishable between sites (SI6). By contrast, modern specimens had a median BTL of 22.00 cm (2.8–35.4 cm,  $n = 410$ ), which was significantly smaller than specimens captured in RM at 650–500 and 550–250 cal BP and in PG-U21 in the late 19th–early 20th centuries AD (Fig. 6A). As barred grunt reach sexual maturity at a BTL of  $\sim 14$  cm (Da Silva et al., 2019; Lira et al., 2019), the majority of the archaeological specimens, regardless of their chronology, can be largely assigned to adult and sexually mature individuals. However, it is worth noting that sexual maturity may differ according to seawater temperatures (Donelson et al., 2014; Tobin and Wright, 2011). The reference used herein is from warmer waters of northern Brazil, which may differ from the colder waters of southern Brazil.

The estimated BTL of archaeological whitemouth croaker exhibited medians of 30.92 cm (16.36–49.24 cm,  $n = 37$ , CBI), 35.39 cm (15.98–62.70 cm, RM) and 43.80 cm (21.08–74.36 cm,  $n = 129$ , PG-U21) (Fig. 6B). The results revealed a significantly higher BTL in

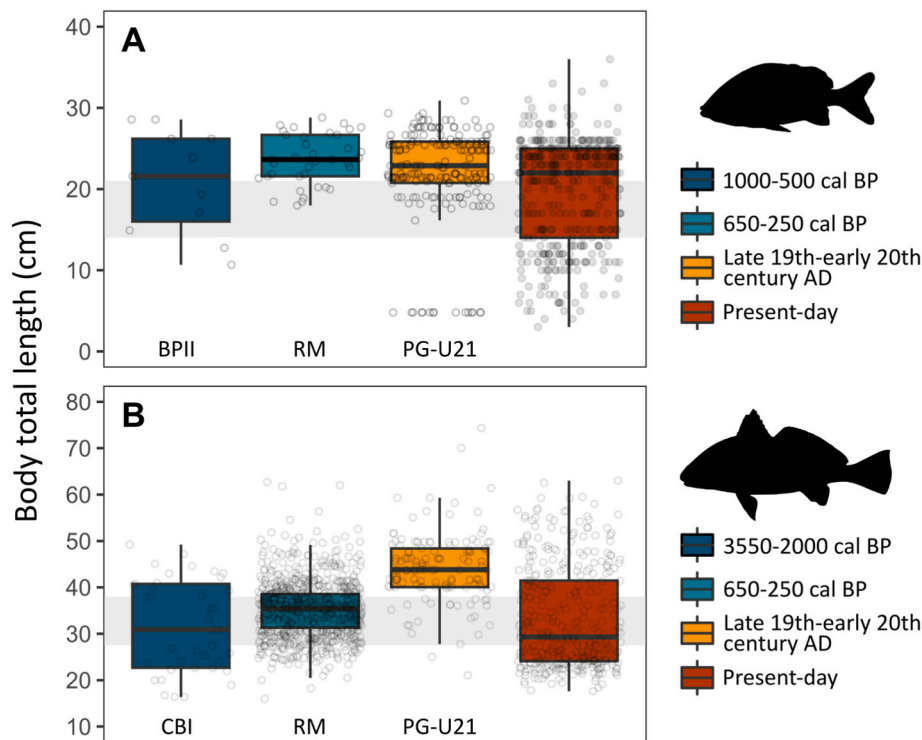
historical (PG-U21) compared to pre-colonial (CBI, RM) specimens (SI6). Moreover, the median BTL of pre-colonial (CBI, RM) and historical (PG-U21) specimens were also significantly higher than modern counterparts, which had a median value of 29.00 cm (17.60–63.00 cm,  $n = 357$ , SI6). A few individuals from the late 19th–early 20th centuries AD also exceeded the maximum BTL of modern specimens in the region and elsewhere (Froese and Pauly, 2020). In southeastern Brazil, whitemouth croakers typically attain sexual maturity at a BTL of approximately 27 cm (Haimovici et al., 2016, 2021; Vazzoler, 1991), therefore the archaeological specimens from pre-colonial and historical periods can be predominantly assigned to sexually mature, adult individuals.

## 5. Discussion

### 5.1. Pre-colonial fisheries

Stable isotope analyses have been extensively employed to uncover feeding, residential and mobility patterns among marine organisms, and also to reconstruct the ecology of past fishing practices (Barrett et al., 2011; Braje et al., 2017; Fry and Chumchal, 2011; Guiry et al., 2022; Newsome et al., 2010). In this study, we have expanded this approach to





**Fig. 6.** Body total length of (A) barred grunt and (B) whitemouth croaker across time periods. The size interval of first sexual maturity is represented by the grey bar for each species (barred grunt, (Da Silva et al., 2019; Lira et al., 2019), whitemouth croaker (Haimovici et al., 2016, 2021)). The horizontal lines correspond to the medians and the hinges to the 25th (Q1) and 75th (Q3) percentiles. The whiskers extend from the hinge to the smallest or largest observation greater than or equal to  $-1.5 \times \text{IQR}$  (interquartile range) or less than or equal to  $+1.5 \times \text{IQR}$ , respectively. The individual observations are represented by circles.

investigate pre-colonial and historical fisheries operating in Babitonga Bay for at least 4500 years. Overall, the results suggest that pre-colonial groups exploited a range of mangrove habitats. Specifically, groups residing at MO (4800–4550 and 4500–4100 cal BP) and CBI (3550–3100 and 2350–2000 cal BP), located in the inner sector of the bay, primarily targeted white sea catfish, fat snook, and whitemouth croaker within a gradient of freshwater-brackishwater to full marine habitats. The wide range of  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  values observed in these species reflect dietary heterogeneity, thus suggesting the capture of transient animals. Pre-colonial groups inhabiting BPII (1000–750 and 650–500 cal BP), an open coastal site, exploited fat snook with a broader range of  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  values, indicating a wider home range. However, they also targeted barred grunt from less diverse isotopic niches, which we attribute to stocks residing mostly in open coastal areas (Da Silva et al., 2019; Pombo et al., 2014).

Inter-specific isotopic variability in pre-colonial times was much higher than seen today. The wider range of  $\delta^{13}\text{C}$  values in pre-colonial white sea catfish and fat snook, and their significantly lower  $\delta^{15}\text{N}$  and  $\delta^{34}\text{S}$  values compared to modern counterparts, suggest that small and juvenile individuals were the primary targets of pre-colonial groups in Babitonga Bay. The lower  $\delta^{15}\text{N}$  and  $\delta^{34}\text{S}$  values of pre-colonial specimens also indicate diets based on benthic foods under a higher influence of sedimentary sulphides (Fry and Chumchal, 2011), again suggesting these were juvenile populations residing predominantly inside the bay. Direct comparison between archaeological and modern specimens, however, is hampered by the influence of anthropogenic activities on the  $\delta^{15}\text{N}$  and  $\delta^{34}\text{S}$  of modern aquatic food webs (Diebel and Vander Zanden, 2009; Wayland and Hobson, 2011; Zhao et al., 2003). The high  $\delta^{15}\text{N}$  values of the modern specimens may reflect inputs from untreated sewage, agricultural fertilisers, and industrial products, which have significantly increased in Babitonga Bay in recent decades (Barros et al., 2010). The presence of smelting, galvanic, and textile industries in the region since the late 19th century (Kalb and Carelli, 2020; Lima and

Sanson, 2008) may also account for the substantial shifts in fish  $\delta^{34}\text{S}$  values over time (Wayland and Hobson, 2011), however the isotopic directions derived from these processes are unknown in the area.

Nevertheless, the BTL data from whitemouth croaker from CBI support the view that small individuals were commonly exploited in pre-colonial times. Instead, for barred grunt, large adults and sexually mature individuals were consistently exploited, as shown by derived BTLs from BPII, but also from RM (650–500 and 550–250 cal BP). Even though BTL data from otoliths are susceptible to issues of preservation and recovery techniques (Grayson, 2014; Reitz and Wing, 1999), these factors are unlikely to have significantly affected our size reconstructions. First, the mesh size used at RM (2 mm) is regarded as suitable for retrieving small archaeological fish remains (Zohar and Belmaker, 2005). Second, some of the smaller individuals, including both barred grunt and whitemouth croaker, were recovered from pre-colonial sites using larger mesh sizes (BPII and CBI). Finally, Fossile et al. have recently assessed the impact of recovery techniques on archaeological fish remains in southern Brazil and found no direct correlations between mesh size and species richness (Fossile et al., 2023a). Together, these lines of evidence suggest that archaeological otoliths accurately reflect the original catch composition processed at the sites.

We found no evidence that pre-colonial Indigenous groups over-exploited mangrove fish species in Babitonga Bay, even though our results suggest their preference for juvenile individuals, as demonstrated in other regions (Lopes et al., 2016). Regrettably, the temporal resolution of our study is low and the number of sites is limited for conclusive interpretations to be drawn. The isotope values of juvenile whitemouth croaker, fat snook, and white sea catfish possibly indicate that these species were pursued in shallow, protected coastal habitats using a wider array of mass harvesting fishing devices, including nets, traps and weirs, which are documented in the Brazilian archaeological record (Colonese et al., 2023; Fossile et al., 2023c; Melo Júnior et al., 2016). Adult barred grunt could have been caught in deeper waters off the

continental shelf using selective fishing gear such as baited fishing hooks (Fossile et al., 2023c; Toso et al., 2021). Interestingly, groups occupying MO ~4500 years ago would have been exposed to more marine conditions due to the higher sea level (+2.6m) compared to present day (Angulo et al., 2006). However, the  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  values of fat snook, whitemouth croaker, and white sea catfish from this site reveal the capture of estuarine populations. Thus, despite coastal environmental changes linked to sea level fluctuations over the last 4500 years, our stable isotope and BTL results indicate a preference for shallow and sheltered estuarine waters by Mid to Late Holocene pre-colonial fisheries, where people of varying ages, strengths, and skills could have contributed to the collective nature of Indigenous fisheries.

## 5.2. Historical fisheries

Caches of whitemouth croaker and barred grunt in the late 19th and early 20th centuries AD were likely driven by both subsistence and the development of commercial fisheries to meet increased demands from local and regional markets (Fossile et al., 2023b; Herbst et al., 2023). Following the industrialization trends observed in European and North American countries (Lam and Pitcher, 2012; Pitcher and Lam, 2015; Roberts, 2010), and spurred by political agendas aimed at enhancing state control over economic activities, the period between the late 19th and early 20th centuries marked the beginning of national-level fisheries incentives in Brazil. Between the 1850s and 1930s, a series of policies were designed to bolster the country's commercial and industrial sectors. They entailed fiscal incentives for private investors (concession for catching, salting and drying fish in 1859), the establishment of official regulatory bodies (e.g., *Inspetoria da Pesca* in 1912), the creation of landing and seafood markets (*Entrepósitos de pesca* in 1933), and the establishment of schools dedicated to training local fishing communities in 'modern' fishing techniques (Abdallah and Sumaila, 2007; Diegues, 1983; Haimovici, 1998; Herbst et al., 2023; Neto et al., 2021).

Within this context, BTL data from barred grunt and whitemouth croaker indicate that most of the specimens in PG-U21 were adults and even larger than modern individuals from Babitonga Bay and southern Brazil. Given the historic and current economic importance of whitemouth croaker (Haimovici et al., 2021; Vieira et al., 1945), the high frequency of larger individuals could be the outcome of some early market forces, such as the effect of higher unit prices for larger individuals (Maynou, 2022; Sjöberg, 2015). Nowadays, barred grunt has limited market demand and is mainly pursued for household consumption (Lima et al., 2019; Passarone et al., 2019; Pina and Chaves, 2009), but large individuals may have had a higher market value in the past. The presence of a few juvenile individuals may be linked to bycatch (taxa accidentally caught), which has been documented in the region since at least the early 20th century (Sandoval Gallardo et al., 2021).

Significantly, the observation that some archaeological specimens of whitemouth croaker were larger than those reported for modern populations suggests past stocks were less affected by overfishing compared to modern populations. It is possible that the life history traits of these species, such as the high fecundity and multiple spawning events of whitemouth croaker, likely contributed to their resilience in the context of low-impact fishing communities. Nevertheless, long-term removal of large individuals is known to produce deleterious effects on fish populations, notably through the decline of offspring and spatial disruption in recruitments (Gwinn et al., 2015). For example, fecundity and reproduction is higher in some species at a more advanced age and larger size, while the time and location of reproduction may also change depending on these same factors (Arlinghaus et al., 2010). Studies have also shown that egg quality and larval performance traits are influenced by the size of female phenotypes, and that recruitment can be affected by size-dependent maternal effects on early survival, and their capacity to recover from overexploitation (Arlinghaus et al., 2010; Venturelli et al., 2009; Walters et al., 2008). While further studies are needed, our results suggest that some key demersal stocks have experienced size truncation

for at least 150 years. It is worth noting that local restrictions, sanctions, and reports of bycatch have been documented in southern Brazil since at least the late 19th century, and increased throughout the 20th century (Herbst et al., 2023; Sandoval Gallardo et al., 2021). This implies that the anthropogenic impacts documented from the mid-20th century (Abdallah and Sumaila, 2007; Pincinato and Gasalla, 2010) actually affected stocks that had already undergone decades or even centuries of selective fishing practices.

The overlap of CN ellipses between historical and modern barred grunt and whitemouth croaker confirms that specimens in PG-U21 were primarily targeted in fully marine habitats, which concentrate large and adult individuals (Pizzochero et al., 2017). These were possibly caught using handlines and gillnets, which are attested by the presence of fish hooks and sinkers in historical sites in the region (Alves and Oliveira, 2002; Bandeira et al., 2001). In particular, gillnets have been documented in Santa Catarina since the 1870's (Herbst et al., 2023) and are currently some of the most commonly used fishing gear for demersal species in southern Brazil (Mendonça and Pereira, 2014). Subtle differences in the median  $\delta^{15}\text{N}$  values, however, highlight the complexity of the nitrogen cycle in regional marine food webs. For example, while archaeological barred grunt had a lower median  $\delta^{15}\text{N}$  value (−0.90‰) compared to modern specimens, the opposite offset was observed for whitemouth croaker (+0.85‰). For barred grunt the offset could be linked to ontogenetic differences in feeding behaviour, as suggested by the observed positive correlation between  $\delta^{15}\text{N}$  and  $\delta^{34}\text{S}$  values. Conversely, differences in whitemouth croaker are not easily explained in terms of size-related habitat segregation, even though the BTL of these individuals could not be estimated. These could instead be attributed to temporal differences (e.g. seasonal, inter-annual) in feeding ecology (Pizzochero et al., 2017) that cannot be addressed with bulk collagen isotope data.

## 5.3. Archaeology's contribution to conservation debates in Brazil

Our study advocates for the integration of long-term data into fisheries assessment and management practices to establish more informed reference baselines in Brazilian mangrove systems. In contrast to other aquatic organisms, like whales and manatees whose overexploitation has been relatively well-documented since colonial times (Brito, 2012; Domning, 1982; Ellis, 1969; Vieira and Brito, 2017), historical anthropogenic impacts on fish stocks before major public policies of the 20th century remain overlooked among environmental historians and fisheries scientists in Brazil (Abdallah and Sumaila, 2007; Freire et al., 2021; Pincinato and Gasalla, 2010; Reis-Filho, 2020). This oversight can be attributed to a general assumption that, until the second half of the 20th century, Brazilian fisheries were primarily for local subsistence or incipient local markets (Mussolini, 1953), and thus had minimal impact on marine stocks.

Archaeological and historical studies in the North Atlantic, however, provide compelling evidence that even relatively modest levels of commercial exploitation can lead to overfishing (Barrett et al., 2004a, 2004b, 2011; Holm et al., 2022; Lotze and Milewski, 2004; Roberts, 2010; Schijns et al., 2021). While historical drivers of marine over-exploitation, such as human population growth, religious requirements, technological advancements, urbanisation, mercantilism, and market economy (Lam and Pitcher, 2012; Pitcher and Lam, 2015; Roberts, 2010), were also present in colonial Brazil, their effects on riverine and coastal fisheries have yet to be comprehensively assessed. This gap in our knowledge risks fostering misconceptions about the conservation status of organisms and ecosystems, also known as "shifting baseline syndrome" (Fulton et al., 2022; Pauly, 1995). Archaeology emerges as one of the few sources of information capable of addressing historical amnesia on Brazilian coastal environments, while offering valuable insights into the evolving nature of fisheries in the South Atlantic.

## 6. Conclusion

Mangrove systems in Brazil have supported human societies since prehistoric times, but the benefits they provide have become increasingly threatened by overexploitation, habitat degradation, pollution, and climate change in recent times. Understanding the origin and evolving nature of these anthropogenic stressors can help identify historical turning points and anticipate future drivers of change. Fish stable isotopes and body size analyses suggest that Indigenous and late colonial groups had minimal detrimental impacts on mangrove fish stocks in Babitonga Bay, southern Brazil. The preference for targeting large and adult individuals by subsistence-commercial fisheries 150 years ago, however, indicate that some drivers of fish decline and contemporary market forces shaping the fishing industry, such as fish species price and size considerations, have a long history in the region. Here we show that stable isotopes and metric analysis of archaeological fish remains can provide insights into past stocks and fishing practices before the intensive fishing of the 20th and 21st centuries.

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## Data and materials availability

All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials.

## CRediT authorship contribution statement

**Thiago Fossile:** Conceptualization, Investigation, Methodology, Resources, Visualization, Writing – original draft, Writing – review & editing. **Krista McGrath:** Writing – review & editing, Writing – original draft, Resources, Methodology, Conceptualization, Investigation. **Pau Comes:** Writing – review & editing, Methodology. **Joan Villanueva:** Writing – review & editing. **Kerry Louise Sayle:** Writing – review & editing, Methodology. **Simon-Pierre Gilson:** Writing – review & editing. **Manuel Haimovici:** Writing – original draft, Methodology, Conceptualization, Writing – review & editing. **Maria Cristina Alves:** Writing – review & editing. **Magda Carrion Bartz:** Writing – review & editing. **Dione da Rocha Bandeira:** Writing – review & editing. **Fernanda Mara Borba:** Writing – review & editing. **Jessica Ferreira:** Writing – review & editing. **André Carlo Colonese:** Writing – review & editing, Writing – original draft, Visualization, Resources, Project administration, Methodology, Investigation, Conceptualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jas.2024.105986>.

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