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South Brazil pre-colonial sharks: Insights into biodiversity and species distributions

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Abstract

South Brazil's archaeological coastal sites (shellmounds and middens) show a diverse collection of shark faunal remains, some of which belong to species considered rare nowadays for the region. However, shark archaeological remains identification in this region has been historically insufficient and prone to mistakes. This study identified shark fauna and estimated body size (total length) present at two archaeological sites: Rio do Meio (1220-977 Cal B.P.) and Enseada II (4286-3783 Cal B.P.), located in Santa Catarina, South of Brazil. Here, 1600 teeth and 3588 vertebrae were analysed and identified. We showed higher historical shark species richness than previously reported for South Brazil in historical and archaeological studies. In total, we identified at least 15 species of sharks (11 species and four identifications at the genus level). The presence of juvenile shark remains adds to the evidence of pre-colonial fishing impacts in local shark populations. The consistent recovery of adults and juveniles of *Carcharias taurus* points to a possible nursery area on the mouth of Babitonga bay. The high teeth frequency (43%) of *C. taurus* suggests the South Brazil coastline was once home to abundant populations of this critically endangered species. Furthermore, we discuss the presence of rare species nowadays, suggesting a possible historical residency for adult populations of *Carcharodon carcharias* based on the presence of juveniles and young-of-the-year on archaeological sites. The occurrence of *Negaprion brevirostris*, a tropical species, might have been facilitated by ocean current variations.

KEYWORDS
pre-colonial, sharks, species distribution, teeth, vertebrae, zooarchaeology

1 | INTRODUCTION

Zooarchaeological remains have been used to assess the past biodiversity, to understand the ecological changes in a given ecosystem, and have shown that marine fauna species may have been much more abundant and diverse than is currently perceived (Jackson *et al*., 2001; Pinnegar & Engelhard, 2008). The use of zooarchaeological remains has increased in recent years as a source of information about historical biodiversity (*e.g*., Lopes *et al*., 2016; Mendes *et al*., 2018). Despite the limitations of zooarchaeological data (*e.g*., human bias as selective fisheries), studies show it can be used to assess marine Holocene biodiversity, as these are not statistically different from current biodiversity inventories (Mendes *et al*., 2020).

Along the coast of southern Brazil, archaeological sites can be found distributed near coastal lines, mangroves, rivers and lagoons. The hunter-gatherer-fishers are the first known human groups who occupied these areas for at least 7000 years B.P. (before the present), leaving as traces of their occupations artificial structures made of

animal and vegetable remains, mainly bivalve seashells, known as Sambaquis (Fish *et al*., 2013; Gaspar, 1998; Gaspar *et al*., 2011). Around 1400 years B.P., alterations in settlement pattern and materiality have been recorded, such as the introduction of ceramics, known as the Itararé-Taquara (Lessa & Scherer, 2008; Prous, 2019). For these coastal populations, from the middle to late Holocene, aquatic resources were the dominant source of protein (Bastos *et al*., 2014; Colonese *et al*., 2014; Gilson & Lessa, 2021a).

Shark remains such as teeth and vertebrae are ubiquitous in archaeological sites on the south and south-east Brazilian coast. More recent studies identifying the biodiversity of marine fauna present in archaeological sites have been carried out in Brazil's south-eastern region (*e.g*., Lopes *et al*., 2016; Mendes *et al*., 2018). These studies show incredible biodiversity of fish assemblages, evidencing well-developed fisheries and the historical potential for the exploitation and overexploitation of fish populations and possible nurseries areas. For the south region, the work of Fossile *et al*. (2020) is the only one known to date presenting an ecological approach.

As pointed out by Fossile *et al*. (2020), the southern coast of Brazil and the Atlantic Forest are biological hotspots, but few inquiries have been made to explore the zooarchaeological information. In contrast to the high biodiversity of teleost fishes in archaeological sites on the coast of southern Brazil, shark remains are poorly represented in indexed scientific publications. Many of the sites have been studied with an archaeological rather than ecological focus. Historically, studies that set out to identify some of these sharks' remains recorded only four species. These species are *Carcharias taurus* Rafinesque 1810, *Prionace glauca* (Linnaeus 1758), *Carcharodon carcharias* (Linnaeus 1758) and *Galeocerdo cuvier* (Péron & LeSueur 1822) (Beck, 1972; Fossari, 2004; Schmitz, 1992; Schmitz & Bitencourt, 1996; Silva, 1990).

Here, we present a comprehensive assessment of the diversity of sharks uncovered from two archaeological sites in southern Brazil, the second such study in this region after Fossile *et al*. (2020). We provide a detailed synthesis of the biodiversity, rarity and proportions of species found in the past and compare them with present species distributions.

2 | MATERIALS AND METHODS

2.1 | Ethical statement

Ethical concerns do not apply, as this study in no way involved the use or manipulation of live animals, as well as access to legally protected areas.

2.2 | Archaeological sites

The Enseada I archaeological site is a shellmound located at Babitonga bay on the island of São Francisco do Sul, on the north coast of Santa Catarina state, Brazil (Figure 1). This area is characterized by subtropical Atlantic forest and by the largest littoraneous mangrove ecosystem in south Brazil (ICMBio, 2018). The site is located next to the Enseada bay and was heavily disturbed by anthropic actions before its excavation in the year of 1969 to obtain raw material to pave roads and make fertilizer. More than 100 shellmounds have been recorded in Babitonga Bay (Fossile *et al*., 2019, 2020). The deepest layers of the site that correspond to the oldest occupation, with radiocarbon dating of 4286–3783 Cal B.P. (Bueno & Gilson, 2021), are composed mainly of mollusk shells (Beck, 1972). The most recent occupation of

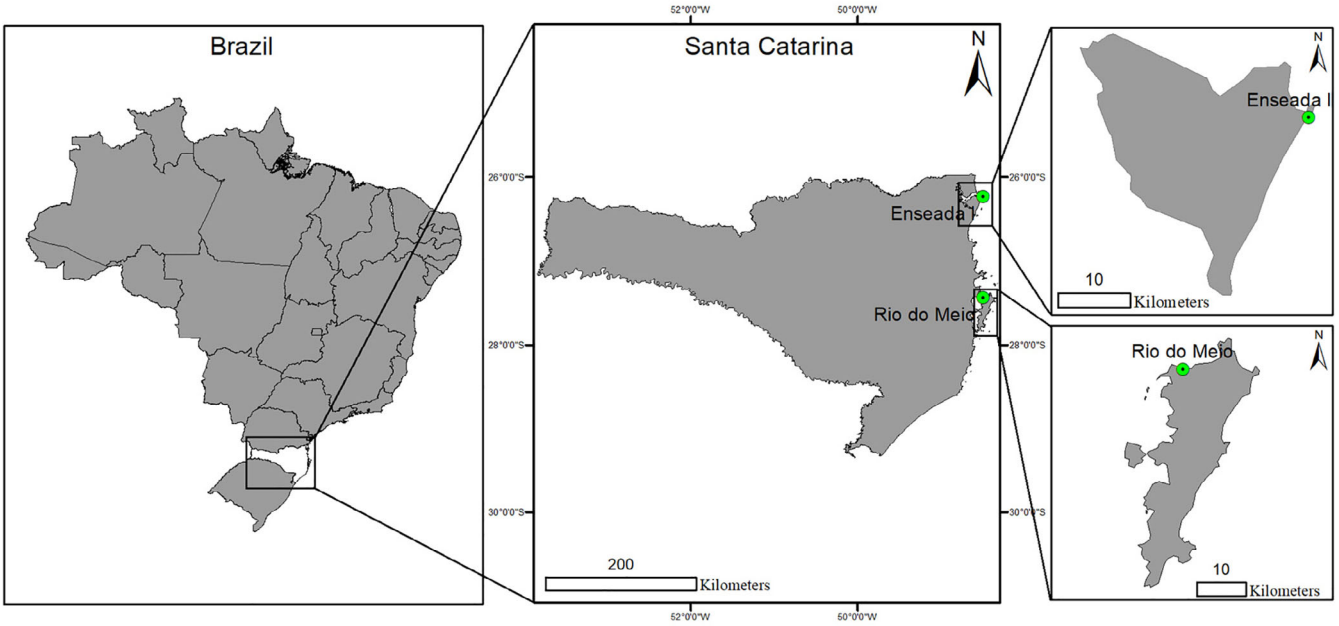

FIGURE 1 Study area along the coast of Santa Catarina, south Brazil, showing the location of both archaeological sites

the shellmound, with a radiocarbon dating of 1220–977 Cal B.P., is situated above this deep layer (Gilson & Lessa, 2020). The archaeological material for the present study was collected from this layer. This layer mainly consisted of fish remains, but it also contained shells of mollusks, in lesser quantity when compared to the oldest occupation (Beck, 1972).

The Rio do Meio shallow site is located at Jurerê beach, north of Santa Catarina Island, Brazil (Figure 1). It was identified in 1987 and excavated in 1996 and 1997. Two main areas were excavated by natural layers: RM I and RM II, with 448 m^2. The site is situated on the waterfront in a dune area with dense vegetation of restinga, which is delimited at the east and west by an elevation of Precambrian rocks, still covered by a Neotropical rainforest, and by a mangrove at the south (Fossari, 2004). The site has been characterized in the Brazilian archaeological context as a shallow site with ceramics ('Sítio Raso com cerâmica'), which differs from 'Sambaquis' or shellmounds, for its physical and morphological characteristics. This term has been chosen as it does not involve any cultural or functional interpretation (Gilson & Lessa, 2021b). This site has two natural stratigraphic layers, historically with three human occupations, the first and the second overlapping, in the same way as the second and third. Four radiocarbon dates (600 ± 30 B.P., 620 ± 30 B.P., 780 ± 60 B.P., 870 ± 30 B.P.) point to occupation and use of the site between 500 and 700 years Cal B.P. (Gilson & Lessa, 2020). Samples in this study came from both stratigraphic layers and all occupations.

Samples from both archaeological sites are listed and stored in the MArquE-UFSC collection, where they were screened and reviewed.

2.3 | Data analysis

To taxonomically identify the faunal remains of sharks, we used comparative anatomy of specimens present in the scientific collection of the Federal University of Santa Catarina (UFSC), identification keys and guides (*e.g.*, Kozuch & Fitzgerald, 1989; Purdy, 2006), illustrations, and recommended websites (Berkovitz & Shellis, 2017), in addition to photo-identification tables for the genus *Carcharhinus* (Voigt & Weber, 2011).

For each shark tooth in the lingual view, we measured crown height (CH, Figure 2) as a parameter to perform comparative size regression to estimate the total shark length (TL) for *C. taurus* and *C. carcharias* (Shimada, 2002, 2004). Shark teeth position in the jaw was estimated based on comparative morphology.

To perform the comparative size regression calculations, the diameter of the vertebrae was used to estimate the individual's total length. We performed size regression analysis for *C. taurus* (Goldman *et al.*, 2006), *C. carcharias* (Natanson & Skomal, 2015), *G. cuvier* (Holmes *et al.*, 2015) and *Negaprion brevirostris* (Poey 1868) (Gruber & Stout, 1983). For the groups identified at the genus level, an averaged regression of multiple species inside the genus was made, using species found in other local archaeological sites and nowadays at the coast of Santa Catarina. These include three species of *Carcharhinus*, *C. plumbeus* (Nardo 1827) (Casey & Natanson, 1992), *C. obscurus* (Lesueur 1818) (Joung *et al.*, 2015) and *C. leucas* (Müller & Henle 1839) (Cruz-Martínez *et al.*, 2005), two species of *Rhizoprionodon*, *R. lalandii* (Müller & Henle 1839) and *R. porosus* (Poey 1861) (Lessa *et al.*, 2009), and two species of *Sphyrna*, *S. zygaena* (Linnaeus 1758) (Coelho *et al.*, 2011) and *S. lewini* (Griffith & Smith 1834) (Kotas *et al.*, 2011).

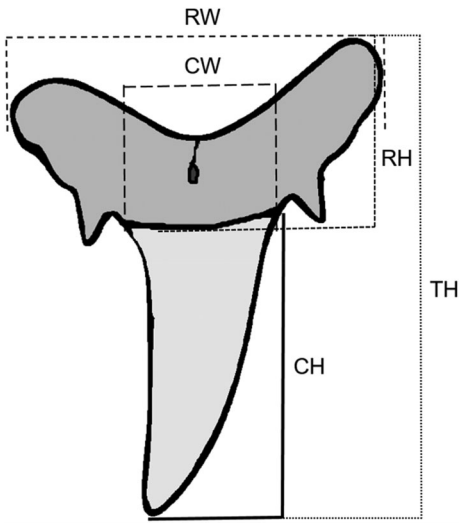

FIGURE 2 Schematics of a shark tooth in lingual view and its measurement codes. CH, crown height; CW, crown width; RH, root height; RW, root width; TL, total length

3 | RESULTS

The total dataset comprises 1647 shark teeth and 4021 shark vertebrae, 1600 teeth and 3588 vertebrae in the Rio do Meio site, and 47 teeth and 443 vertebrae in the Enseada site. We found at least 15 shark species on both archaeological sites (Figures 3 and 4). The most common vertebral remains belonged to the genus *Sphyrna*, *Rhizoprionodon*, *Carcharhinus* and *C. taurus* in the Rio do Meio site, and *Carcharhinus*, *C. taurus* and *Sphyrna* in the Enseada site (Figure 4). Notable findings are remains of *N. brevirostris*, the longfin mako *Isurus paucus* (Guitart 1966) and *C. carcharias*.

Size regression showed that most individuals sampled were fished below their maturation size range. Three of the nine analysed groups had individuals mostly captured at adult size range, *Rhizoprionodon*, *Sphyrna* and *C. taurus* (teeth) (Figure 5).

4 | DISCUSSION

The present study has revealed that previous archaeological studies had underestimated the diversity of sharks represented in shellmounds in southern Brazil. An initial survey of the Rio do Meio (Fossari, 2004) and Enseada (Beck, 1972) sites found three to four species of sharks, while previous archaeological studies on the Santa

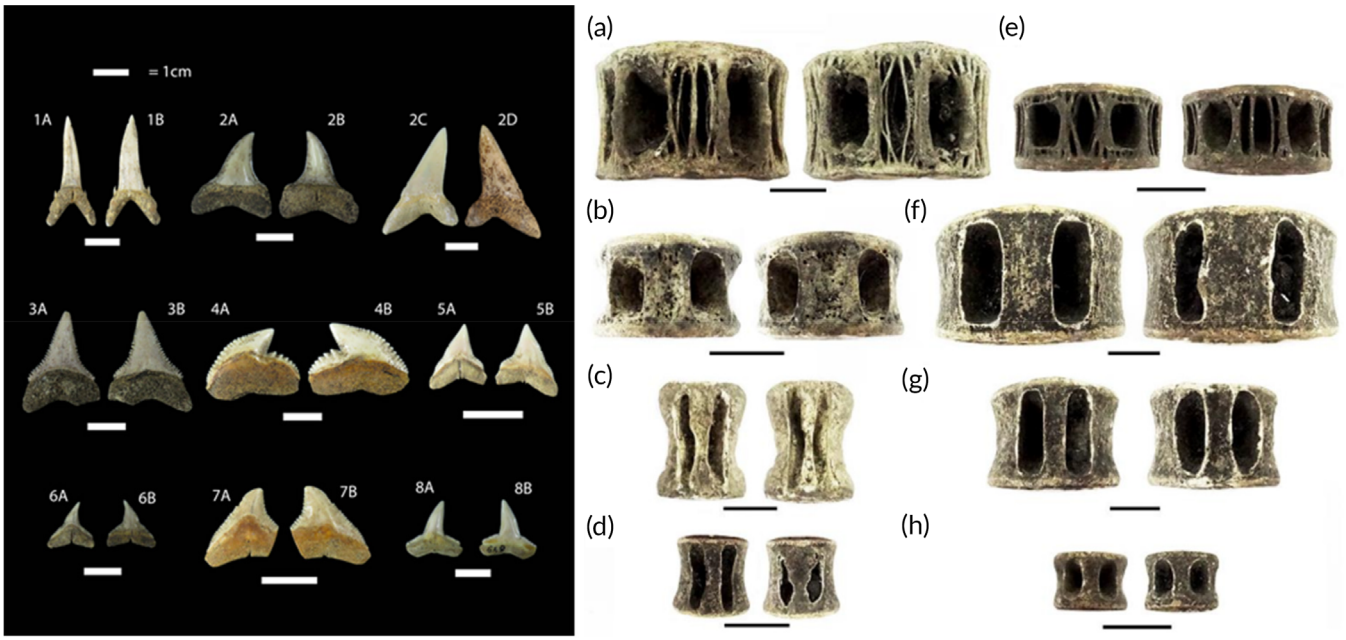

FIGURE 3 Pictures of teeth from the Rio do Meio site (white bar = 1 cm) and central vertebrae from the Enseada site (black bar = 1 cm). 1AB, a) *Carcharias taurus*; 2AB) *Isurus paucus*, lateral tooth; 2 CD) *Isurus paucus*, anterior tooth; 3AB, e) *Carcharodon carcharias*; 4AB, b) *Galeocerdo cuvier*; 5AB) *Carcharhinus plumbeus*; 6AB) *Carcharhinus brachyurus*; 7AB) *Carcharhinus leucas*; 8AB, f) *Negaprion brevirostris*; c) *Sphyrna* sp. d) *Rhizoprionodon* sp. g–h) *Carcharhinus* sp

Catarina coast found a maximum of four sharks species. These sites are Praia da Tapera (Silva, 1990) Armação do Sul (Schmitz, 1992), Rio Lessa e Enseada 1 (Beck, 1972) and Pântano do Sul (Schmitz & Bitencourt, 1996). Furthermore, the taxonomic identification of *Prionace glauca* at the Rio do Meio site in Fossari (2004) were not found in the cited collection during the present study, which indicates that past zooarchaeological identifications might be prone to mistakes (see Gilson & Lessa, 2021c for more details). We suggest that other zooarchaeological collections of southern Brazil should be reviewed.

Size regression shows the exploitation of juvenile sharks of *Carcharhinus*, *Carcharias taurus* and even *Carcharodon carcharias*. On Rio do Meio, 80% of the identified shark centra were of young sharks. The abundant presence of young individuals could indicate past nurseries or pupping areas, but the surrounding marine areas of both archaeological sites were not necessarily considered as a shark nursery, regarding the criteria in Heupel *et al.* (2007). These criteria are (a) young shark abundance in the area is higher related to other areas, (b) they show site fidelity for extended periods (weeks or months) and (c) the area is used by many generations of sharks or used across the years. Another important factor to contribute to a potential nursery area is a protected coastal environment providing food abundance and refuge from predators (Heupel *et al.*, 2007). Within the archaeological context, it is very difficult to identify nursery areas. However, a good indicator would be the recovery of both adults and abundant young sharks in the same area (Heupel *et al.*, 2007), or in the same layers of an excavation (*e.g.*, Herraiz *et al.*, 2020), indicating the return and presence of adult populations into their birth areas. In the present study, the only species with adult specimens consistently recovered along with a high abundance of young is *C. taurus* from Enseada. This site is on the mouth of Babitonga bay, which is, nowadays, a well-known important nursery ground for commercial fisheries and endangered marine species (*e.g.*, groupers and porpoises) and also for the occurrence of large coastal shark species (Gerhardinger *et al.*, 2020). This would point to the mouth of Babitonga bay as a possible nursery area for *C. taurus* in the past.

In addition to the potential existence of nursery areas in the past, another possibility is that precolonial populations exploited juvenile sharks. There is indeed growing evidence from studies of other archaeological sites in Brazil that suggests that sharks might have been historically overexploited (Fossile *et al.*, 2019; Gilson & Lessa, 2021c; Lopes *et al.*, 2016).

The high frequency of *C. taurus* teeth at Rio do Meio (43% of all teeth found), and as the main shark identified at the species level, indicates its greater abundance in the past. Most likely, this species was even more abundant in precolonial times, in line with the perception of fishermen in the region, who claim a declining population of the species in the area over recent decades (Santos *et al.*, 2020). This species is critically endangered worldwide, and in Santa Catarina state the overfishing of great schools of *C. taurus* is recorded by Souza (2000) between 1940 and 1960. For this reason, these populations are collapsing (Chiaramonte *et al.*, 2007; Santos *et al.*, 2020). The last fishing census for Santa Catarina state showed that 5.1 tons of the species were caught in 2012, which would mean an average of 57 individuals. Estimates indicated that 1.2 tons were caught in 2011, 2.3 tons in 2010, 538 kg in 2009, 1.7 tons in 2008, 17 tons in 2007, 49 tons in 2006, 111 tons in 2005, 312 tons in

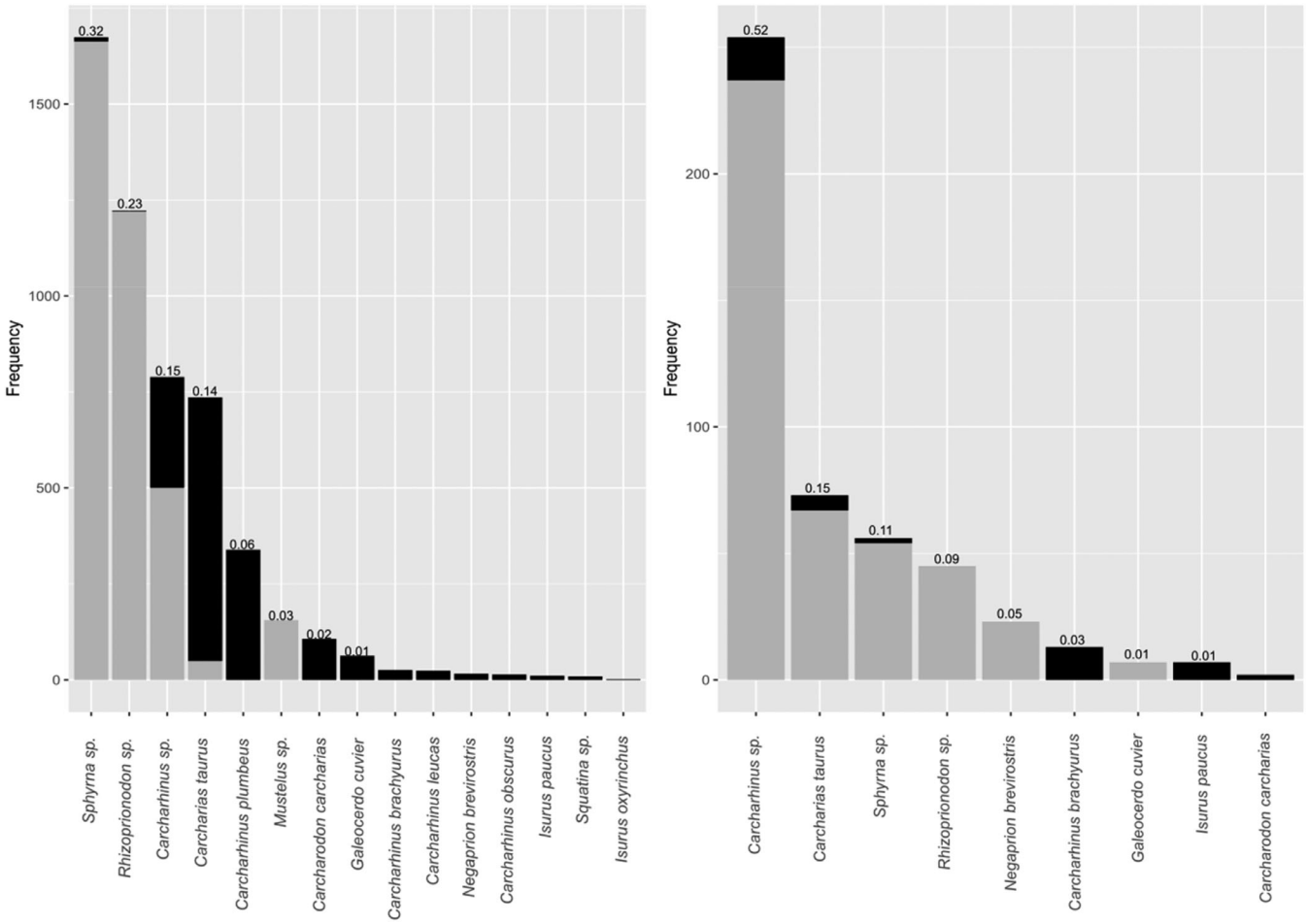

FIGURE 4 Faunal remains frequency by species from the Rio do Meio site (left) and the Enseada site (right). Numbers on top of the charts show the total percentage of the species remains per site. Less than 1% is not labelled. (■) teeth; (■) vertebrae

2004, 187 tons in 2003 and 111 tons in 2002 (Univali/CTTMar, 2003–2013).

Occurrences of *C. carcharias* are considered rare events in Brazil, with only 19 records in Brazilian waters (Soto, 2001). Most of the occurrences were adults (Amorim *et al*., 2018; Gadig & Rosa, 1996), with four of them having been recorded from the south coast of Brazil (Soto, 2001). However, their teeth and vertebrae are common in the south-east Brazil archaeological record (eight out of 13 sites; Lopes *et al*., 2016; Mendes *et al*., 2018). Given the regressed size data for *C. carcharias*, the Enseada site showed evidence of young-of-the-year (YOY, <175 cm), whereas Rio do Meio only showed evidence for juveniles (JWS, >175–300 cm). JWS and YOY individuals of *C. carcharias* are generally restricted to the continental shelf, predating teleost fish, elasmobranchs, birds, dolphins and marine reptiles before a diet shift to marine mammals (Compagno, 2001; Hussey *et al*., 2012), suggesting they were using the area surrounding Rio do Meio and Enseada as a feeding ground.

C. carcharias are typically nomadic predators, staying for short periods at a given site and exploring a broad range of prey (Compagno, 2001; Estrada *et al*., 2006). Holocene environmental conditions around the latitude of Rio do Meio and Enseada encompasses the optimal ecological conditions range for this species and its nursery and pupping grounds (Bruce, 2008; Domeier, 2012). Despite the different chronological and archaeological contexts from Rio do Meio and Enseada, Lopes *et al*. (2016) found evidence of *C. carcharias* YOY further north, at the south-east archaeological sites, suggesting possible nursery areas for this species in the past, as it is known to be a philopatric species (Chapman *et al*., 2015). However, recent acoustic and satellite tag studies have shown that *C. carcharias* YOY migrated 500–720 km from their release location, and up to 1160 km in the north-western Atlantic, varying with seasonality (Curtis *et al*., 2018). Therefore, the distance between potential migration areas of south-eastern and southern archaeological sites overlaps, raising the possibility of different nursery or pupping areas for those locations.

It is possible that adult *C. carcharias* individuals are not abundantly found in our analyses due to potential selective fishing by precolonial populations. However, the co-occurrence in archaeological records of *C. carcharias* and pinnipeds species throughout South America (Cione & Barla, 2008) and the southern coast of Brazil, including the presence of pinnipeds in an archaeological site with similar dating and nearby to Rio do Meio (Castilho & Simões-Lopes, 2001, 2008), corroborates the suggestion for the existence of established

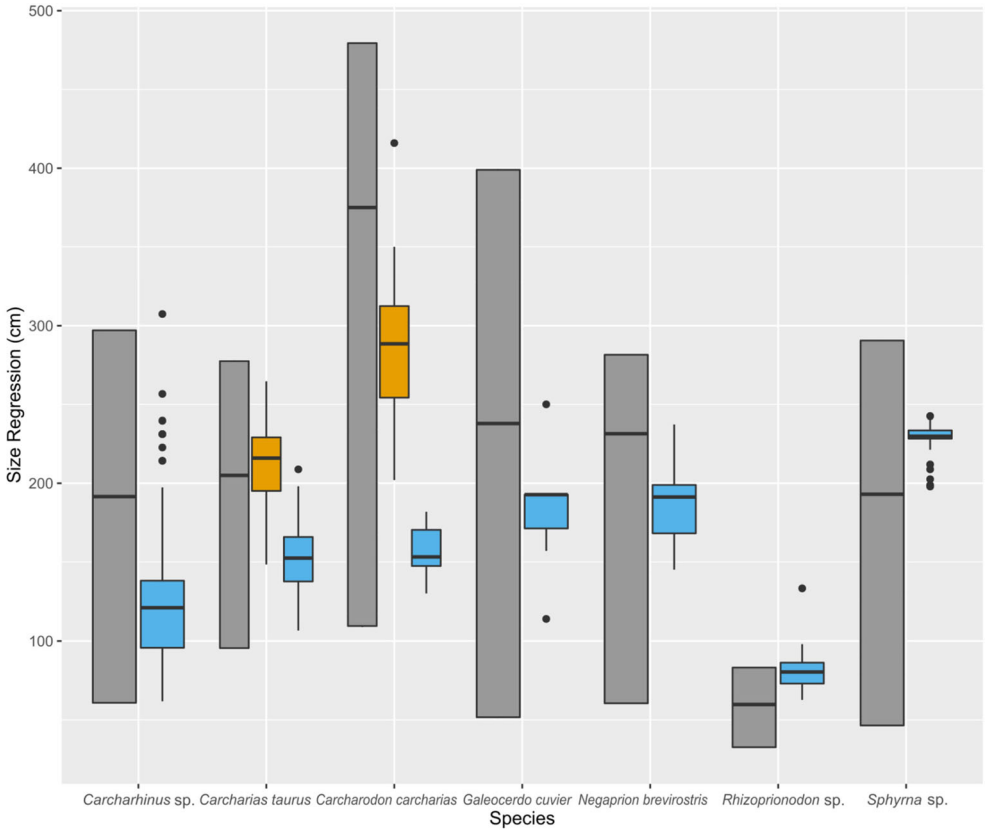

FIGURE 5 Comparative size regression results (total length) of selected shark species individuals of both archaeological sites. Grey bars are present for comparison and show the size at birth (minimum value), the size reached at sexual maturity (black line) and the maximum recorded size (maximum value). Size data were obtained from Compagno (2001). (▬) maturity; (▬) teeth; (▬) vertebrae

adult populations in southern Brazil during the Holocene. Adult individuals of *C. carcharias* are known to aggregate seasonally near pinniped rookeries, which is considered one of their main food items (Brown *et al*., 2010). Archaeological Holocene records from Uruguay, Argentina and southern Brazil suggest pinnipeds were abundant in those areas (Castilho & Simões-Lopes, 2008; Inda *et al*., 2006). Modern colonies are present in Uruguay (Franco-Trecu *et al*., 2019) and were also once extensively abundant in Argentina (Rodriguez & Bastida, 1998). Nowadays adults of *C. carcharias* do not use this area as a residence, and the decline from the south-western Atlantic may be related to historical exploitation of pinniped populations that once supported their adult populations (Cione & Barla, 2008).

The presence of *N. brevirostris* and *I. paucus* at both archaeological sites is intriguing because they are nowadays rarely seen or captured in Brazil (Amorim *et al*., 1998). *N. brevirostris* current range does not include southern Brazil (Soto, 2001) and *I. paucus* is rarely littoraneous (Compagno, 2008). This species was present throughout the Holocene in multiple south-east Brazil archaeological sites (Lopes *et al*., 2016; Mendes *et al*., 2018). This is expected considering that it is a tropical and subtropical species as both juveniles and adults show preference for warmer waters (Morrissey & Gruber, 1993; Tavares *et al*., 2016). Recent records indicate that this species is restricted to northern areas of the Brazilian coast (Soto, 2001). Although the southern Brazilian coast does not represent optimal ecological conditions for *N. brevirostris*, seasonal oscillations in water temperature and higher abundances in the past might have facilitated its range expansion into these higher latitude regions. Furthermore, this species' dispersal might have been facilitated by periodical increases in the strength of the warm Brazil Current (BC) in the past, which correlates with increases in mean sea surface temperature (SST) of ~1.1°C about 1100 years B.P. and lasting hundreds of years (Chiessi *et al*., 2014). This period coincides with the relative dating of Enseada and Rio do Meio. Thus, it is likely that this species had an extended natural distribution to southern Brazil in the late Holocene.

Very little is known about the biology of *I. paucus* (Rigby *et al*., 2019). Many pelagic and oceanic shark species use coastal and continental shelf waters throughout ontogeny to perform many biological functions such as feeding, breeding, giving birth and other activities (Compagno, 2001, 2008). It has been hypothesized that *I. paucus* moves to coastal waters to give birth, as a large proportion of mature, sexually active and pregnant females of *I. oxyrhinchus*, the closest relative to *I. paucus*, were observed in coastal waters of South Africa (Groeneveld *et al*., 2014). *I. paucus* is occasionally captured near the coast in areas of narrow continental shelves, similar to the study sites (Camhi *et al*., 2008; Mahiques *et al*., 2010). These factors suggest that *I. paucus* would have been captured in coastal areas in southern Brazil in the Late Holocene, further reinforcing the possibility of sporadic coastal area use for this rare species.

The present study adds to the body of evidence that anthropogenic fishing activities have probably been altering shark biodiversity and population abundances for hundreds to thousands of years in the Brazilian coastal environment. The presence of species rarely found today in southern Brazil, such as *C. carcharias*, *N. brevirostris* and *I. paucus*, suggests these species potentially occurred in higher

abundances and were widely distributed in the past. These results highlight the negative impacts of overfishing and fishing by pre-colonial populations, often carried out in pupping areas, which possibly were shark nurseries.

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