



Archaeological sharks: changes in the trophic ecology between late Holocene and modern shark communities in South Brazil

Guilherme Burg Mayer^{1,2} · Renato Hajenius Aché de Freitas²

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Abstract

Sharks are essential components of marine communities, and their removal might simplify ecosystems and lead to unpredictable and detrimental effects on the food web. Comparing the isotopic niche of species between archaeological and modern communities can provide information to assess temporal changes in the ecological dynamics of communities. Here, stable isotope analysis was used to compare food web topology metrics between two shark guilds or communities, a late Holocene archaeological community (AC) dating from 700 to 500 years ago and a modern community (MC) trophic web, both from South Brazil. In the same line of comparison, we assess the trophic position of a top predator, *Carcharias taurus*. Results showed topological temporal differences such as higher trophic redundancy and higher patterns of niche overlap in the AC. Higher trophic redundancy could be expected in late Holocene food webs, as similar studies also observed these findings. In contrast, the MC showed less dense packing of species within the isotopic niche space, thus higher niche partitioning and higher trophic diversity, suggesting changing ecological interaction dynamics. We found that *Carcharias taurus* has increased its trophic level, possibly due to a release from the intraspecific competition and a dietary shift towards larger prey items. We suggest that anthropic impacts, such as overfishing, may cause these differences in the trophic position of this species. We also advocate that this study method might help future trophic reconstructions using shark teeth, as information about past marine environments is scarce, and could serve as a baseline for future studies.

Keywords Historical ecology · Isotopic niche · Anthropic impacts · Topology · Trophic level · *Carcharias taurus*

Introduction

Humans are catalysing changes in marine ecosystems through accelerating climate change, pollution, habitat degradation, facilitation of invasive species and causing the collapse of many fisheries, leading to biodiversity loss and impairment of ecosystems structure and functions (Worm et al. 2006; Doney et al. 2012). Some of these impacts started millennia ago, consequently, many ecosystems as

seen today functioned differently in the past (Jackson et al. 2001). As a result, both historically and recently, human impacts caused regime shifts and changed well-established ecosystem dynamics, trophic interactions, and many other ecological aspects in marine ecosystems (Jackson et al. 2001; Erlandson and Rick 2008; Maureaud et al. 2017). In this anthropic context, the original trophic ecology of many species almost certainly was not preserved over the years (e.g. Saporiti et al. 2014; Vales et al. 2017; Bas et al. 2019).

Sharks are a group of highly diverse marine predators inhabiting a wide range of habitats in all oceans (Ebert et al. 2013). It is estimated that more than 1/3 species of Chondrichthyes are threatened according to the IUCN red list (Dulvy et al. 2021). Among these, sharks are of special concern, due to population declines on a global scale over the last century, largely because of overfishing and habitat loss (Ferretti et al. 2010; Worm et al. 2013; Dulvy et al. 2021; Pacoureaux et al. 2021). This general scenario is not different for shark populations in the South Atlantic, and as

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✉ Guilherme Burg Mayer
guilhermelmayer@gmail.com

¹ Programa de Pós-Graduação em Ecologia, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, SC 88040-900, Brazil

² Laboratório de Biologia de Teleósteos e Elasmobrânquios (LABITEL), Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, SC 88040-900, Brasil

off the southern Brazilian coast, shark populations are currently depleted by longline fisheries (Barreto et al. 2016).

Due to their life-history traits, such as late maturity, slow growth and low reproductive rates, shark populations are highly sensitive to changes in survival rates (Ferretti et al. 2010). As such, sharks are not resilient to negative pressures, and therefore, their declines often have consequences in many ecological scales. Broad ecological consequences include trophic cascades, mesopredator release and consequently indirect changes in trophic interactions (Myers et al. 2007; Baum and Worm 2009). While in small scales, removing individual species can lead to changes in relative abundances, life-history parameters, populations size structure, reduced competition and predation intensity for other sharks (Pauly et al. 1998; Ferretti et al. 2010). More simply, sharks removal or declines ultimately simplify oceanic ecosystems (Baum and Worm 2009). Therefore, investigating only the current trophic ecology may not be reliable indicators to the original trophic ecology of sharks in any environment under the influence of heavy anthropic impacts.

To address temporal ecological questions and to reconstruct the trophic ecology of species before modern anthropic impacts, stable isotopes analysis (SIA) of carbon and nitrogen are reliable tools (e.g. Drago et al. 2017; Vales et al. 2017). One of the advantages of SIA is the application in animal remains to assess the isotopic composition in collagen, and consequently further use on museum or prehistoric material, allowing reconstructions of historical food webs. Collagen has shown to be very resistant to diagenetic effects, even in Pleistocene remains (Dobberstein et al. 2009).

The archaeological context from South Brazil provides an opportunity to study trophic ecology of sharks before major anthropic impacts. Archaeological elasmobranch remains, such as teeth and vertebrae, are ubiquitous in archaeological faunal assemblages of southeastern and southern Brazilian coast (Lopes et al. 2016; Mendes et al. 2018; Burg Mayer et al. 2022)—shark teeth and vertebrae stand out due to their highest degree of calcification (Reitz and Wing 2008). SIA in shark teeth provide a singular time integrated dietary isotopic values referent to when teeth begin and end its formation, absorbing into its collagen diet-related stable isotopes from blood amino acids (Zeichner et al. 2017). Therefore, stable isotopes from shark teeth represent an integrated diet signal composition from weeks to months, and not a whole life average.

The archaeological record evidences well-developed prehistoric fisheries targeting sharks and rays (Fossile et al. 2019; Burg Mayer et al. 2022) and shows an exploitation of neonates and juveniles sharks and rays, and suggests an early stage of overexploitation of some medium to large size fish species (Lopes et al. 2016). Records from southeastern and southern Brazil show high shark diversity and the presence

of nowadays rare species at the Brazilian coast (e.g. great white shark, *Carcharodon carcharias*) and species currently with highly reduced populations (e.g. sand tiger shark, *Carcharias taurus*; ICMBio 2018) and many other shark species (Lopes et al. 2016; Mendes et al. 2018; Burg Mayer et al. 2022).

Currently, the subtropical coastal ecosystem off southern Brazil is poorly studied and highly impacted by fishing activities (Kotas 2005; Bornatowski et al. 2018). However, this region shelters a notable community of shark species with high richness (Lucifora et al. 2011; Bornatowski et al. 2014a, b). Some shark species, such as *Carcharhinus obscurus* and *C. taurus*, play important roles as top predators and regulators of lower trophic levels through predation, while other shark species can be considered key elements for their indirect effects in structure of the local and regional food web (Bornatowski et al. 2014a, b). The marine food webs in south Brazil have high structural complexity and are sensitive to reductions in the populations of sharks, which can lead to secondary extinctions through top-down effects (Bornatowski et al. 2014a, b).

In the last decades, major changes in the local and regional marine communities occurred. For example, *C. taurus*, one the most abundant shark remains in Brazilian archaeological shell mounds (e.g. Lopes et al. 2016; Mendes et al. 2018; Burg Mayer et al. 2022), also was historically abundant in the South of Brazil, the species was so abundant that beach trawl fishing caught schools of this shark (Vooren and Klippel 2005). However, as many other shark species of South Brazil, their populations were heavily exploited in the last decades (Kotas 2005; Santos et al. 2020), suggesting currently depleted populations, with unknown consequences to their trophic ecology. Besides, there is no information about the trophic ecology of local sharks before population depletion. Despite several worldwide studies about the ecological consequences of shark population declines, the impacts of these declines remain uncertain (Heithaus et al. 2008; Roff et al. 2016).

Therefore, in this study, we use a historical approach to describe and compare the isotopic niche ecology (isotopic topology and isotopic niche variation) of a modern community (MC) of sharks to an archaeological community (AC) of sharks from the late Holocene. We also assess the trophic position of *C. taurus* in light of this comparison and discuss the potential role of human impacts in changing the trophic ecology of this species.

Materials and methods

Study area and sampling

Archaeological shark teeth were obtained from Rio do Meio site, which is characterised in the Brazilian archaeological context as a shallow site with ceramics ('Sítio Raso com cerâmica'), which differs from 'Sambaquis' or shell mounds, for its physical and morphological characteristics. The site is located in South Brazil (Fig. 1), at the north of the island of Santa Catarina, on Jurere beach, at 27°26'23" S, 48°29'56" W (Fossari 2004). It was identified in 1987 and excavated in 1996 and 1997. Four radiocarbon dates (600 ± 30 B.P., 620 ± 30 B.P., 780 ± 60 B.P., 870 ± 30 B.P.; before present) point to occupation and use of the site between 500 and 700 years cal. (calibrated) B.P. (Gilson and Lessa 2020).

According to Gilson and Lessa (2021), the occupation of Rio do Meio was characterised as a 'functional settlement', centred on capturing and processing marine resources, especially sharks. Archaeozoological results have shown that sharks were an important source of protein for the fisher–hunter–gatherers who occupied the site, with 54.6–75.5% of the fish biomass of the analysed samples

corresponding to sharks. The remains of sharks found at the site include centra and teeth, which provide different insights into hunting and meat processing techniques. The predation of sharks was an intentional activity and an important aspect of the group's subsistence strategy, requiring cooperation and coordination between group members. The cultural choice to hunt and eat sharks may have been influenced by technological, symbolic, and taste-related factors.

Before anthropic interference in area which caused the burial of the site, Rio do Meio site was parallel to Jurere beach coastline, under dunes which were fixated by sand-bank vegetation and near a body of estuarine water (Fossari 2004). This site is surrounded by mangrove to the South and neoproterozoic granite rock mounds to East and West (Fossari 2004).

This study site is at the Southern Brazil shelf (27° S), extending from latitude 34° S to 22° S and characterised as a subtropical temperate environment and by a narrow continental shelf (Mahiques et al. 2010) and conspicuous seasonality effects on sea surface temperature and chlorophyll concentration (Pereira et al. 2009). This section of the shelf is on a transition zone, which lies within the path of the southward flowing Brazil current, dominated by estuarine outflows, and the northward flowing Malvinas current (Piola et al. 2000; Heileman and Gasalla 2009). The primary productivity is highly influenced by terrigenous input, and is affected by cold waters intrusions from the subtropical confluence zone and by the plume carrying sediments originating from La Plata estuary, which might go up to 28° S (Mahiques et al. 2010).

Except for variations in the strength of the Brazil Current (Chiessi et al. 2014) between the latest site datation (724 years cal.B.P.) up to recent times, to our knowledge, there were no major changes in oceanographic conditions in the Southern Brazil Shelf (Mahiques et al. 2009; Nagai et al. 2014).

The archaeological site collection is housed at the Museum of Archeology and Ethnology Oswaldo Rodrigues Cabral (MARquE) at Federal University of Santa Catarina (UFSC) campus in Florianópolis.

To taxonomically identify the faunal remains of sharks, we followed the same criteria as in Burg Mayer et al. (2022): we used comparative anatomy of specimens present in the scientific collection of UFSC, identification keys and guides, illustrations, and recommended websites, in addition to photo-identification tables. To reduce pseudoreplication, we considered teeth to be from different individuals when found in different excavation grids and excavation levels (each level is 10 cm in depth apart from other). By sampling in different parts of the archaeological site, we minimise the risk of sampling the same individuals.

To minimise sampling different class sizes or juveniles for *Carcharhinus* and other considered species, only

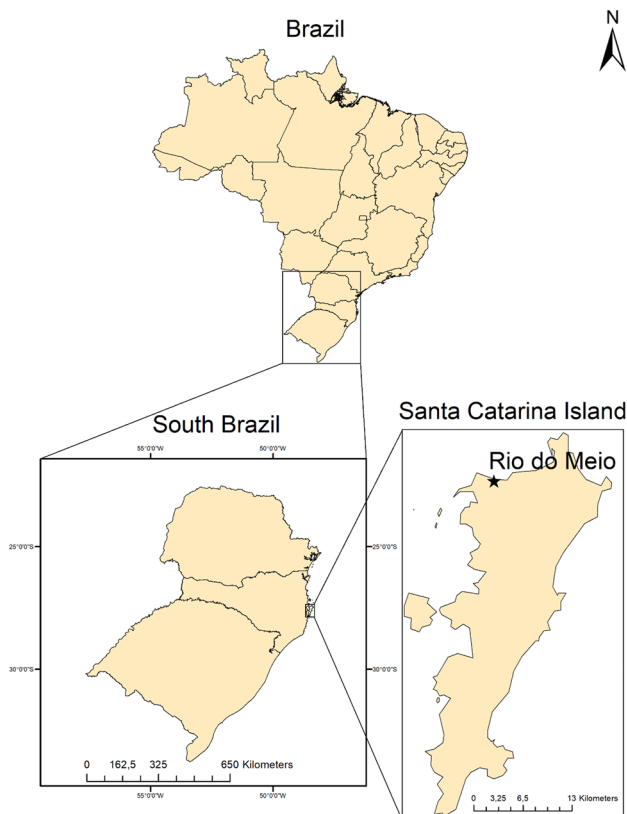


Fig. 1 The location of Rio do Meio archaeological site (star symbol) in South Brazil. The site is at a latitude of 27° S

archaeological teeth with a specific crown height size range were sampled for SIA (Online Resource 1).

Archaeological samples of shark teeth specimens, within the size range specified above, were selected from the site collection housed at MARquE. These include *Carcharhinus plumbeus* ($N=6$), *Carcharhinus brachyurus* ($N=4$), *C. taurus* ($N=14$), *C. carcharias* ($N=7$), *Galeocerdo cuvier* ($N=7$), *Isurus paucus* ($N=4$), *Carcharhinus leucas* ($N=4$) and *Negaprion brevirostris* ($N=4$).

Modern samples of shark teeth specimens, within the size range specified above, were obtained from UNIVALI Oceanographic Museum collection. Specimens from this collection were collected along southern Brazil coast, mainly at the state of Santa Catarina, from 1975 to 2010. These include *C. plumbeus* ($N=6$), *C. brachyurus* ($N=6$), *C. obscurus* ($N=6$), *C. taurus* ($N=10$), *C. carcharias* ($N=1$), *G. cuvier* ($N=1$), *Isurus oxyrinchus* ($N=15$) and *C. leucas* ($N=3$) (Online Resource 2). Both archaeological and modern samples from museums were dry stored for later analysis.

Sample preparation and methodological adaptations

Shark teeth were washed with distilled water and cleaned of external debris with a sandpaper. Samples were then dried at 50 °C for 6 h before powder extraction. The outer layer of the shark teeth is mostly enameloid, a coarsely crystalline matrix which contains relative low organic material (~5%), whereas the inside of teeth is mostly finer grained dentin, containing more organic matrix (15–20%), mainly collagen (LeGeros 1981; Kemp 1984; Enax et al. 2012), that captures the isotopic signal of diet (Vennemann et al. 2001). Therefore, disregarding the enameloid, we extracted dentin to a fine powder using a low-speed cutting drill with bits ranging in size from 800 to 1500 μm .

The choice of using EDTA to decalcify shark teeth powder is explained in Online Resource 1. 1.5 mL of 0.5 M EDTA (pH 8) was added and vortexed to each powdered tooth sample and left to react for 1 week at room temperature. Once samples were visibly demineralised, as evidenced by a translucent powder, they were centrifuged (8 min at 12,000 rpm), the supernatant removed with a pipette. Then samples were vortexed for 30 s embedded in MilliQ deionised water and centrifuged again. This was repeated 11 times, in the 5th and the 10th time the samples were left soaked overnight (adapted from Kim and Koch 2012). Samples were freeze-dried before enclosing approximately 1.5 mg of material into tin cups for isotopic analysis, which is specified in Online Resource 1.

Data analysis

Prior to analysis and when applicable, data were checked for normality using Lilliefors and Shapiro (less than four samples) test, and checked for homogeneity of variance using Levene's test and diagnostic plots in R (R Development Core Team 2018).

A correction factor of 0.022‰ was applied per year (counting from the latest to the most recent year of when shark samples were obtained) to all modern sharks' samples carbon isotope values to account for the Suess effect (Indermühle et al. 1999).

To assess the general preservation state of shark tooth collagen, C:N ratios were considered. Given the inherently different nature of shark skeletons and shark teeth ontogeny from bony fish and mammalian bone, we did not use the classical values of C:N ratios delineated by DeNiro (1985). Shipley et al. (2021) reported $C:N_{\text{atomic}}$ values of 2.9–4.0 for shark tooth collagen, which are the ranges of the samples included in this study (both modern and archaeological) and are within acceptable standards. We converted $C:N_{\text{molar}}$ to $C:N_{\text{atomic}}$ by multiplying the molecular C:N by the ratio between the average atomic mass of C and N (14/12) (Online Resource 3). However, for modern samples, there are concerns with lipid contamination, which we did not extract during lab work. Guiry and Szpak (2020) suggested that modern fish collagen $C:N_{\text{Atomic}}$ ratios should fall between 3.0 and 3.3 to avoid of lipids and other contaminants on the isotopic ratios, especially for $\delta^{13}\text{C}$. To ensure lipids did not impact $\delta^{13}\text{C}$ values for modern samples, we followed Shipley et al. (2021) and Guiry and Szpak (2020). First, there is not a single sample with $C:N_{\text{atomic}} > 3.5$, and therefore, no sample was excluded. Second, we explored the relationship between $\delta^{13}\text{C}$ and $C:N_{\text{atomic}}$ with a linear regression for two species with $N > 10$. We did not find significant relationships for *C. taurus* and for *I. oxyrinchus* (meaning no influence of contaminants in $\delta^{13}\text{C}$ values) and we assume these trends were consistent across species with lower sample sizes.

The package SIBER (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011) was used to calculate and compare for each shark species with a minimum sampling ($N \geq 3$) in both periods, the convex hull or total area (TA), and two estimates for the standard ellipse area: SEAc and SEAb. SEAb is the Bayesian standard ellipse area, and is reported as median values and 95% credible intervals, whereas the SEAc is the small sample corrected ellipse area with no associated errors. SEAc and SEAb are calculated from the variance and covariance of bivariate data and contains approximately 40% of the data, thus they reveal the core niche area and are expected to be insensitive to sample size (Jackson et al. 2011).

SIBER package also was used to compute the Bayesian Layman's metrics for each of the time-separated food web

communities (Layman et al. 2007; Jackson et al. 2011) and further comparison between communities. These isotopic metrics are proxies for the trophic structure of a given community using a dual isotopic approach ($\delta^{13}\text{C}$ – $\delta^{15}\text{N}$), and are calculated based on the distribution and dispersion of species in the δ -space. Five of six of the Layman's metrics were calculated. The $\delta^{15}\text{N}$ range (NR) is a representation of the length of the food web and is the distance between the two species with the most enriched and most depleted $\delta^{15}\text{N}$ values, generally, a larger range in $\delta^{15}\text{N}$ among consumers suggests more trophic levels or a more trophic diversity food web. The $\delta^{13}\text{C}$ range (CR) represents the width of the food web and indicates the various sources of carbon pool driving the food web. The mean distance to centroid (CD) better represents the average degree of trophic diversity within a food web (Layman et al. 2007), as it is unbiased in the case where outliers inflates NR or CR. The CD is measured as the mean Euclidean distance to the centroid estimated from the average Euclidean distance from each species to the centroid of the food web. The mean nearest neighbour distance (NND) represents the trophic redundancy of the food web, as the overall density of species packing within the isotopic niche space. While the standard deviation of nearest neighbour distances (SDNND) represents the overall functional evenness of individual species packing (Layman et al. 2007). Layman's metrics have recently been categorised as 'isotopic functional indices', because they can serve as proxies to the metrics developed by functional ecologists (Belle and Cabana 2020). These isotopic functional indices can be coupled into groups: isotopic functional richness (CR, NR, and TA), isotopic functional divergence (CD) and isotopic functional evenness (NND, SDNND). In this analysis, only same taxa from both communities with the minimum number of samples were used (*C. taurus*, *C. plumbeus*, *C. leucas*, *I. oxyrinchus* and *C. brachyurus*). We then removed each species from the analysis to test their effect on the metrics results. We tested the posterior distributions of the Layman's metrics between communities by pairwise comparison tests (using the approach delineated in SIBER; Jackson et al. 2011). These test the probability that one metric differs from the other (being higher or lower). The results are expressed in confidence probability (e.g. prob = 0.96, a 96% probability).

Shark size was estimated based on teeth regressions equations available for *C. taurus*, giving results in total length (TL, cm; Shimada 2004). Shark teeth position in the jaw was estimated based on compared morphology for *C. taurus*. For modern species with no TL data available, we measured the crown height from second upper tooth directly from their jaws for size regression (Shimada 2004). To proceed with a size-standardised trophic position analysis, we separated data of *C. taurus* in similar size classes among archaeological and modern species. Size regression estimates indicate

that archaeological *C. taurus* ranged from 232 to 274 cm (mean 253.6; $N=9$), modern *C. taurus* ranged from 223 to 273 cm (mean 248.3; $N=7$).

We only used *C. taurus* for the trophic position analysis because size regression equations were only available for this species with minimal sample size in both communities. It is important to standardise size in trophic position analysis, as bigger fish could result in elevated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, due to ontogenetic shifts or feeding niche differences among size classes (e.g. Estrada et al. 2006) and also because trophic level correlates with body size (Jennings 2005).

We calculated the trophic position (TP) for *C. taurus* using the package 'tRophicposition' for R environment, a Bayesian approach that uses Markov Chain Monte Carlo Simulations coupled with stable isotope data and the mean and standard deviation for trophic discrimination factors (TDF; Quezada-Romegialli et al. 2018). Unlike trophic level, TP recognises that species might feed in multiple trophic levels, hence it may become fractional (Vander Zanden and Rasmussen 1996). A prior for the parameter TP was set to a normal distribution of mean of 4.4 (for *C. taurus*) and standard deviation of 0.1, as defined by stomach content analysis (Cortés 1999). TDF values and standard deviations of $\Delta^{13}\text{C}$ ($\Delta^{13}\text{C}_{\text{tilapia}} = 3.1\text{‰} \pm 1\text{‰}$) and $\Delta^{15}\text{N}$ ($\Delta^{15}\text{N}_{\text{tilapia}} = 2.8\text{‰} \pm 0.6\text{‰}$) for shark teeth were obtained from Zeichner et al. (2017) and used to generate a normal distribution ($N=1000$). TP must be calculated relative to a baseline (primary or secondary consumers) of the organism respective food chain (Hussey et al. 2012a). Secondary consumer baselines values for the archaeological species were obtained from premaxilar bone collagen of *Micropogonias furnieri*, from the same archaeological site as this study, and it was considered at a TP of 3 (Milessi et al. 2005). Baselines from MC were obtained from the mussel *Mytilus edulis* (TP = 2; Caut et al. 2009), collected in the years of 1988 and 2014 along the coast of Uruguay and Rio Grande do Sul state, Brazil (Drago et al. 2017). For *C. taurus* in each community, 20,000 iterations were run across Markov Chains to generate TP estimations. The results generated posterior density distribution with associated 95% credible intervals. Similar to the Layman's metrics, we performed pairwise tests in the posterior distributions for differences in the trophic position. The regressed size data were normally distributed.

Table 1 Stable isotopes values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), sample sizes (N) and standard ellipse areas and total areas for both archaeological and modern communities

Species	Period	N	$\delta^{13}\text{C} \pm \text{SD}$	$\delta^{15}\text{N} \pm \text{SD}$	SEAc	SEAb	TA
Sand tiger shark (<i>Carcharias taurus</i>)	700–500 years cal.B.P	14	-10.84 ± 0.53	17.37 ± 1.29	2.35	2.16 [0.92–2.89]	4.57
	Present	10	-11.0 ± 1.20	18.5 ± 0.70	2.8	2.5 [1.07–4.5]	4.19
Sandbar shark (<i>Carcharhinus plumbeus</i>)	700–500 years cal.B.P	6	-11.11 ± 0.96	15.41 ± 1.10	1.67	1.34 [0.94–5.95]	1.74
	Present	6	-12.4 ± 0.82	13.6 ± 2.4	7	5.6 [1.02–6.03]	6.53
Copper shark (<i>Carcharhinus brachyurus</i>)	700–500 years cal.B.P	4	-11.45 ± 0.62	16.52 ± 1.04	2.99	1.99 [0.51–5.66]	1.45
	Present	6	-12.25 ± 0.67	16.00 ± 1.54	3.79	3.03 [0.96–8.38]	3.56
Dusky shark (<i>Carcharhinus obscurus</i>)	Present	6	-11.7 ± 1.35	14.23 ± 1.37	6.55	5.24 [1.87–12.33]	7.36
Mako sharks (<i>Isurus paucus</i> □ and <i>Isurus oxyrinchus</i> ■)	700–500 years cal.B.P.□	4	-12.42 ± 1.73	15.10 ± 1.09	8.53	5.69 [0.86–13.31]	5.41
	Present■	15	-13.16 ± 0.7	14.34 ± 1.4	2.63	2.44 [1.73–5]	5.7
Bull shark (<i>Carcharhinus leucas</i>)	700–500 years cal.B.P	4	-11.57 ± 0.90	15.22 ± 1.05	4.45	2.97 [0.38–8.52]	2.38
	Present	3	-11.73 ± 0.83	13.03 ± 0.85	2.13	1.06 [0.19–3.8]	0.58
Great white shark (<i>Carcharodon carcharias</i>)	700–500 years cal.B.P	7	-11.71 ± 0.73	16.84 ± 0.59	1.19	0.99 [0.44–2.40]	1.54
	Present	1	-12.7	17.74	–	–	–
Tiger shark (<i>Galeocerdo cuvier</i>)	700–500 years cal.B.P	7	-12.96 ± 1.44	14.10 ± 1.44	5.20	4.33 [2.03–10.40]	6.01
	Present	1	-13.50	11.91	–	–	–
Lemon shark (<i>Negaprion brevirostris</i>)	700–500 years cal.B.P	4	-11.67 ± 1.21	15.52 ± 0.28	1.37	0.91 [0.26–2.82]	0.84

SEAc is the ellipse area corrected for small sample sizes; SEAb is the Bayesian estimation of the ellipse area, values in brackets show 95% credible intervals

TA total area of the convex hull, cal.B.P is the calibrated datation before present

Species in the archaeological community: □, species in the modern community: ■

Results

Variation in C:N ratios and $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$

Overall, 50 archaeological shark teeth belonging to 8 species were selected and analysed (Online Resource 3), whereas 48 samples from modern samples were obtained for analysis, belonging mainly to 8 species (Online Resource 2). For the archaeological samples, $\text{C:N}_{\text{atomic}}$ ranged from 3.2 to 4.2, with a mean of 3.44 and a 0.25 SD, whereas for modern

samples, the $\text{C:N}_{\text{atomic}}$ ranged from 3.2 to 3.5, with a mean of 3.29 and a 0.06 SD (Online Resource 3).

Average $\delta^{13}\text{C}$ ranged from -10.9‰ to -12.9‰ for the AC and -11.0‰ to -13.5‰ for MC (Table 1). The most ^{13}C enriched species in both communities were *C. taurus*, whereas the most $\delta^{13}\text{C}$ depleted were *Isurus* and *G. cuvier* (Table 1).

Average $\delta^{15}\text{N}$ values ranged from 14.1 to 17.4‰ for the AC and 13.4 to 18.7‰ for the MC (Table 1). Similar patterns were observed for the most and least ^{15}N -enriched in

both communities. Among the apex predators in both communities, *C. taurus*, *C. brachyurus* and *C. carcharias*, had the most ^{15}N -enriched $\delta^{15}\text{N}$ values, whereas *G. cuvier* was the least ^{15}N -enriched nitrogen isotopic values, also in both communities (Table 1).

Food web topology and isotopic niche variation

I. paucus had the highest variability in SEAb and SEAc in the AC, whereas *C. plumbeus* had the highest variability in SEAb and SEAc in the MC (Table 1). *C. plumbeus* have notably increase their isotopic niche (SEAc) in the present (from 1.67 to 7). An increase was also observed in the SEAc for *C. taurus* (SEAc from 2.35 to 2.8) and *C. brachyurus* (SEAc from 2.99 to 3.79). Other species decreased their SEAc from past to present, such as *I. oxyrinchus* and *C. leucas* (Table 1).

Layman metrics

In the MC, the higher *C. taurus* trophic position, along with lower $\delta^{15}\text{N}$ values for *I. oxyrinchus* and *C. plumbeus* resulted in a significantly larger NR value (prob=0.99) (Fig. 3A). The MC had a significantly higher CD (prob=0.99; Fig. 3A), denoting higher trophic diversity. When comparing to the MC, the AC species were tightly packaged within the isotopic space, suggesting higher trophic redundancy (lower NND, prob=0.97; Fig. 3A).

Trophic position

The trophic position for *C. taurus* was significantly higher in the MC than the archaeological one (prob=0.96; Fig. 4).

Discussion

Our study demonstrated that even in samples dated hundreds of years old, SIA helps evaluate trophic and habitat assessment in multiple shark species using teeth collagen. Our assessment of the historical shark ecology showed three major differences between the archaeological and modern communities. First, the community of sharks off southern Brazil from 700 to 500 years cal.B.P was under a considerable degree of isotopic niche overlap, even when only considering the comparable species with the MC. On the other hand, the MC of sharks exhibited resource partitioning for *C. taurus*, mostly because of its higher trophic position (Fig. 4). Second, the MC had a higher CD, implying a higher trophic diversity whereas the AC was characterised by species being close to each other, or ‘packed’, hence a higher trophic redundancy (e.g. species with similar diets and foraging methods; lower CD and NND, respectively). Third, an

increase in trophic position for *C. taurus* in the MC, could suggest a change in its role in its local ecosystem and could have important implications for other species in the local food web as well as for fisheries management. It is important to note that the isotopic functional evenness (NND and SDNND) and isotopic functional divergence (CD) indices are strongly robust to isotopic baseline shifts, which allows ecological inferences in the comparison of communities with different isotopic baselines (Belle and Cabana 2020).

Patterns of trophic structure

The classical niche theory predicts trophic segregation among coexisting species (Hutchinson 1957; Vandermeer 1972), and dietary niche partitioning in elasmobranch communities are regularly observed in community ecology studies (e.g. White et al. 2004; Kinney et al. 2011). However, we observed considerable isotopic niche overlap/trophic redundancy within the AC (Fig. 2). High niche overlap for a guild of sympatric predators would suggest that prey was not a limiting resource in the past. Other studies have shown high niche overlap and relaxed competition states between top consumers when food items are abundant, leading to stable resource use (e.g. Gallagher et al. 2017). Although pre-colonial environments in southern Brazil were likely to be resource-abundant, more factors would be at play in shaping the patterns of niche overlap observed. High niche overlap could also be the expected outcome of top-down controlled marine systems where predators are near their carrying capacity (Bas et al. 2019). Whereby when under higher states of competition, predators could experience frequent hunger effects, capturing prey according to their encounter rate (Gill 2003). This would lead the predators to share prey items with other competitors, hence sharing niche breadth (Bolnick et al. 2010). However, it is common for great sharks to predate smaller sharks (e.g. Smale 2005; Bornatowski et al. 2014a, b); the sympatry of many apex consumers and the presence of intraguild predation would suggest the presence of a reinforced top-down control, even among the apex predators. Direct and indirect predation effects would also maintain predators and mesopredators populations below the carrying capacity that would be sustained by the abundance of prey resources (Heithaus et al. 2008; Vaudo and Heithaus 2011). If this were the case in the AC, particular trophic levels of shark prey would be under predatory release, which would lead to higher degrees of trophic redundancy and niche overlap in the whole community (Heithaus et al. 2008; Vaudo and Heithaus 2011).

Furthermore, food webs with multiple predators and intraguild predation often result in weakened interactions towards particular prey species (Schmitz 2007), whereas species-diverse food webs may offer prey populations greater resilience due to weaker or diffuse interactions (Montoya

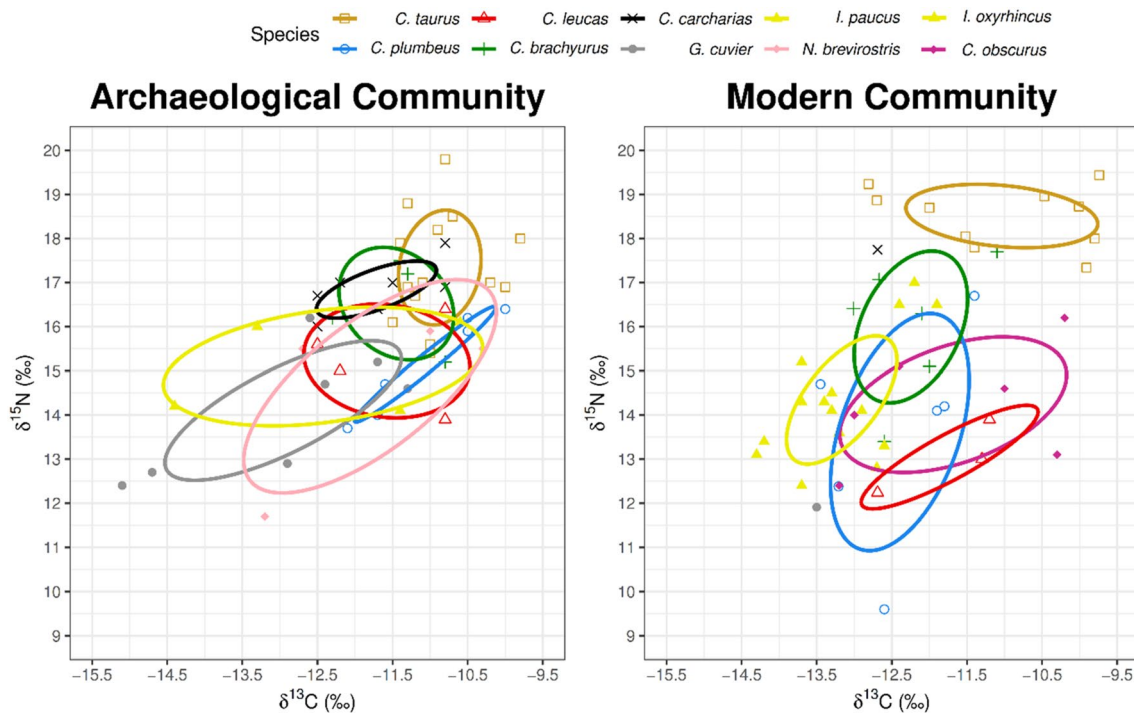


Fig. 2 Isotopic standard ellipses adjusted for small sample sizes (SEAc) representing the isotopic niche or niche width, and their respective niche overlap between ellipses that characterises the degree of shared resource use among species. Samples were not corrected for baseline differences

et al. 2006; Heithaus et al. 2008), trophic redundancy, and populations of predators that are more resilient to decline (lower NND, Fig. 2; Heithaus et al. 2008). The AC higher trophic redundancy would suggest these shark species were co-occurring, leading to a state of ‘stable resource use’. In agreement with a higher degree of niche overlap, NND metric shows that species were more closely distributed in the AC (Fig. 2), suggesting higher trophic redundancy (Layman et al. 2007; Jabot et al. 2017).

Hence, we hypothesise that this multi-predator food web was able to sustain high levels of niche overlap through variable degrees of top-down control and intraguild predation, which would make several prey items under predatory release, leading the community to a state of ‘stable resource use’.

Modern communities might be diversifying their patterns of resource use and decreasing their trophic redundancy, as other studies have also shown higher CD and NND for modern food webs (Saporiti et al. 2014; Bas et al. 2019). The niche hypothesis predicts that a population will exhibit a contracted niche breadth under the influence of strong interspecific competition and an expanded niche breadth when competition is relaxed, by the possibility of adding new resources that otherwise were monopolised by competitors (Bolnick et al. 2010). In previous historical trophic structure comparisons, decreases in niche overlap and trophic redundancy have been linked to competition release for top and

mesopredators (Saporiti et al. 2014). Another explanation for the observed changes in the trophic ecology of the MC comes from the optimal foraging theory, which predicts that when prey becomes less abundant, predators become less selective increasing the consumption of less profitable prey and consequently increasing their trophic niche (Townsend and Winfield 1985; Gill 2003). As humans progress their unsustainable fisheries worldwide, fishing both top predators and their prey and impoverishing the food webs and their ecological relationships (Myers and Worm 2003; Pacoureau et al. 2021) it is plausible to assume that populations of top and mesopredators are progressively diversifying their diets. Both mechanisms cited might explain these observed changes, as in our study, most of comparable species between past and present had an increase in their isotopic niche (Fig. 2; Table 1), reinforcing the idea of a trend in niche and resource diversification.

Regardless, the increase in the trophic niche for these species symbolises the plasticity of sharks to alter their trophic ecology, a feature that must be attributed to their long evolutionary history that has enabled them to adapt to different environmental conditions and prey availability. This plasticity may also have implications for their resilience to human impacts and their role in marine ecosystems.

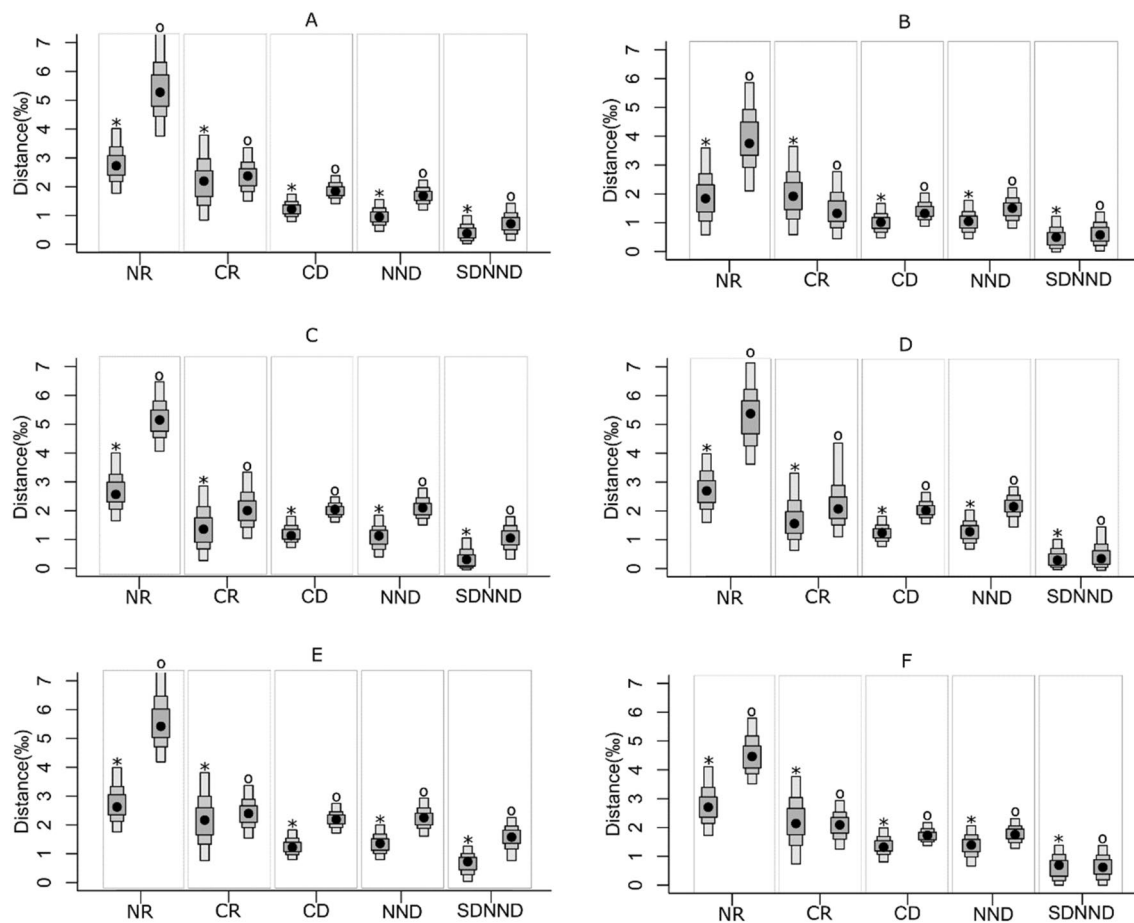


Fig. 3 Community Layman's metrics between Late Holocene archaeological community (*) and modern community (°) from South Brazil. **A** Results using entire community species. **B** Removal of *C. taurus*. **C** Removal of *I. paucus*. **D** Removal of *C. plumbeus*. **E** Removal of *C. brachyurus*. **F** Removal of *C. leucas*. *NR* nitrogen range, *CR*

carbon range, *CD* Centroid distance, *NND* mean nearest neighbour distance, *SDNND* the standard deviation of nearest neighbour distances. The mean is represented by the black circle. The boxes, from lighter to darker grey, represent the 95, 75 and 50% confidence intervals, respectively

The increased trophic position of modern *Carcharias taurus*

Marine food webs often contain four or five trophic levels (Vander-Zanden and Fetzer 2007), and the increase in trophic position generally means that more predation events are taking place. Previous trophic reconstructions studies from archaeological datasets in South America suggested that intensively exploited modern fur seals and sea lions increased their trophic level as a consequence of liberation from intraspecific competition (Drago et al. 2009; Saporiti et al. 2014; Zenteno et al. 2015; Bas et al. 2019). The overall evidence from similar studies suggests that trophic level of predators is density-dependent (Bas et al. 2019). The proposed mechanism behind the increase in trophic level involves a niche shift towards a more selective diet in favour of larger prey as a consequence of intraspecific competition release (Saporiti et al. 2014; Bas et al. 2019),

hence a higher trophic level (Jennings 2005). A similar situation could be playing a role in niche partitioning and the increased trophic position of *C. taurus*, as this species is considered to be overexploited or threatened with overexploitation (ICMBio 2018). The release from intraspecific competition may allow sand tiger sharks to access more abundant and profitable prey resources that were previously defended or exploited by other predators. The principles of optimal foraging theory (MacArthur and Pianka 1966) suggest that predators often select larger prey due to the higher energy return they provide, considering the energy gained from capture and consumption relative to hunting effort. *C. taurus* is mainly a predator of intermediate and higher trophic level elasmobranchs and teleosts (Lucifora et al. 2009; Cortés 1999; Hussey et al. 2015), and competition release may have benefited *C. taurus*, enabling the increase in high trophic level prey in its diet. The intraspecific competition release in question should be even more dramatic for

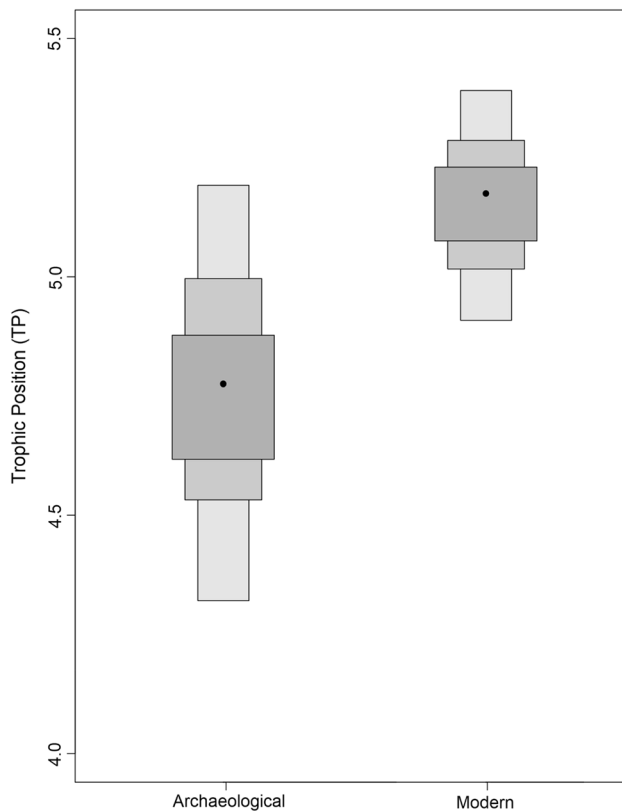


Fig. 4 The posterior estimates of the trophic position for the *C. taurus* in both communities. The mean is represented by the black circle. The boxes, from lighter to darker grey, represent the 95, 75 and 50% confidence intervals, respectively

elasmobranchs, as they have lower population replenishment after severe exploitation, due to their intrinsic life-history traits, such as late maturity, slow growth and low reproductive rates (Ferretti et al. 2010). Furthermore, populations of marine predators under fishing pressure would have constrained growth rates, due to direct and indirect effects of predation (Heithaus et al. 2008). Lower population growth rates would indirectly reduce trophic levels, as it correlates with body size (Jennings 2005), which does not seem to be the case for *C. taurus* in this study.

Modern specimens of *C. taurus* and *Carcharhinus* group have expanded their niche areas in the present (respectively, SEAc from 2.35 to 2.8; and SEAc from 1.6 to 7). As mentioned before, the niche hypothesis might explain this increase in the isotopic niche, suggesting relaxed competition states, thus corroborating the hypothesis that intraspecific competition release is causing the observed increase in trophic level for *C. taurus*, and maybe other *Carcharhinidae*.

In addition, there is mounting evidence that anthropic impacts cause longer food webs (longer NR; Fig. 3) through hunting and fisheries, leading to intraspecific competition

release for some species (Drago et al. 2009; Saporiti et al. 2014; Zenteno et al. 2015; Bas et al. 2019).

The steep increase in $\delta^{15}\text{N}$ values of *C. taurus*, compared to other species in the MC that did not exhibit this pattern, could be a consequence of its predominantly coastal habitat and behaviour. These make the species more vulnerable to human impacts compared to other *Carcharhinidae* sharks such as *C. plumbeus*, *C. brachyurus*, *C. obscurus* and also *I. oxyrinchus*. One such impact, as recently mentioned, is the fishing-induced removal of individuals, which can alter the ecological dynamics of the species. Another noteworthy anthropogenic impact is pollution from wastewater, which may also artificially raise the $\delta^{15}\text{N}$ values within the food webs (e.g. McClelland and Valiela 1998). This could potentially explain some differences observed in the increased values. Nevertheless, even if pollution is playing a role, the relative differences between trophic levels would remain preserved because the calculation of trophic level would account for this shift, as the calculation is based on a baseline source (in this case, a secondary consumer with $\text{TP} = 2$, Fig. 4). In such a scenario, even the baseline source would experience an increase in its $\delta^{15}\text{N}$ values, which would then be reflected in higher level consumers through isotopic fractionation. In addition, we would anticipate observing a similar upward trend in $\delta^{15}\text{N}$ values across the species in the MC.

Caveats and considerations

It may not be surprising that two isotopic snapshots of shark guilds varied over time, reflecting changes in their underlying ecological dynamics. However, in this study, we aimed to describe and report shifts in their trophic structure/topology. It is important to note that these changes in topology are not influenced by isotopic baselines, providing evidence for changes driven by shifts in the species interactions, by anthropic impacts within these systems or the synergy of both. This raises important questions for future research, such as whether similar patterns of variation can be observed in other studies, and what the potential drivers of these changes might be. While we cannot definitively attribute the observed differences in food web topology to anthropogenic impacts, it is likely that human activities have played a role in altering the trophic positions of *C. taurus* and possibly other species. Further investigation using historical data will be necessary to understand the causes and consequences of these changes.

We understand our study is not free of many caveats that comes from using stable isotopes inferences (Hussey et al. 2012b; Shiffman et al. 2012). Turnover rates for teeth only provide inferred average resource use, thus the pattern of niche overlap for AC could be representative of temporal niche partitioning over the same resources. When there are numerous different pathways between baseline primary

producers or secondary consumers and the target organisms under research, the evaluation of niche can become problematic for some highly migratory shark species that feed in multiple habitats (e.g. *C. carcharias*, *C. obscurus*). When dealing with isotopic niche areas, absence of overlap may provide evidence for resource partitioning, however, the presence of overlap may not always mean shared sources use, as different patterns of resource use may lead to similar isotopic values (reviewed in Layman et al. 2012). However, we could assume that species are sympatric and, therefore, did share resources, based in other pre-colonial inhabitants of Brazil, the pre-colonial people mostly likely did not performed extreme far-away fishing trips away from the coast (Gilson and Lessa 2019) even catching typically oceanic species near the coast, as shown for *I. paucus* individuals with enriched carbon values (Fig. 2). Furthermore, high niche overlap among sharks may not be an uncommon occurrence (e.g. Vaudo and Heithaus 2011; Gallagher et al. 2017; Shiffman et al. 2019), although other ecological dynamics may be involved in these examples, this corroborates the plausibility of our findings.

The calculation of a trophic level using a single discrimination factor obscures much of the real complexity behind trophic interactions (Zeichner et al. 2017), whereas scaled discrimination factors may be more accurate (Hussey et al. 2014). It is difficult to speculate on the nature of high rates of niche overlap without further knowledge about past food webs, trophic interactions for rare species, and respective regional past isoscapes. The lack of studies using stable isotopes in sharks in Brazil and available data on regional isoscapes also hampers any comparative studies.

Concluding remarks

Our study adds to the multiple trophic reconstructions of food webs that have found patterns of tightly ‘packed’ communities (NND) in pre-colonial food webs, and patterns of increased trophic diversity (CD) for modern communities and increased trophic position for some species (e.g. Saporiti et al. 2014; Bas et al. 2019; Durante et al. 2022). This suggests a possible pattern for the use of resource in nearly pristine food webs, where trophic redundancy is common. The higher trophic redundancy observed in the archaeological shark community suggests a more redundant and interconnected food web, in such food webs, there is more functional redundancy and therefore increased ecosystem stability and resilience to perturbations. The increase in the trophic position of apex predators and the increase in the diversity of resource use in modern communities need attention, as these suggests a loss of ecological interactions. There is concern that the simplification of ecosystems, due to the loss of species and ecological interactions, leads to diminished

functional redundancy and lower ecosystem resistance and resilience (Worm et al. 2006; Bascompte et al. 2005).

This study shows a possible consequence of anthropic actions that affect trophic interactions and ecology of surviving individuals of populations that would be below carrying capacity, as most sharks populations are sensitive to fishing mortality (Dulvy and Forrest 2010; Ferretti et al. 2010). Until further action is taken to prevent the disappearance of many important species, food webs are becoming gradually poorer than they were before.

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Author contributions GBM: conceived the study and designed the experiments. Material preparation and data collection were performed by all the authors. Data analysis was performed by GBM. The first draft of the manuscript was written by GBM and RHAdF: revised and commented on previous versions of the manuscript. All the authors helped with funding acquisition. All the authors read and approved the final manuscript.

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Availability of data and material The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability Does not apply.

Declarations

Conflict of interest The author informs that no conflict of interest is present.

Ethics approval Ethics approval was not required for this study according to local legislation [11.794 (Arouca Law)/October 8 2008]. Approval to the use of archaeological material in research was obtained through protocol 01500.900346/2017-98 of IPHAN (INSTITUTE OF NATIONAL HISTORIC AND ARTISTIC HERITAGE [‘INSTITUTO DO PATRIMÔNIO HISTÓRICO E ARTÍSTICO NACIONAL’]).

Consent to participate Does not apply.

Consent for publication Does not apply.

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