Archaeological sharks: Late Holocene changes in trophic ecology and habitat use of sharks in South Brazil

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Abstract

Sharks are essential components of marine food webs, but their removal might simplify ecosystems and food webs. 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 724 – 542 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 dispersion of species throughout the isotopic 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.

Introduction

Humans are catalyzing 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 Chondrichthyces 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; Pacoureau et al. 2021). This general scenario is not different for shark populations in the South Atlantic, as 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 1988; 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 bone to assess the isotopic composition in collagen, and consequently further use on museum or prehistoric material, allowing reconstructions of historical food webs. Bone collagen have shown to be very resistant to diagenetic effects, even in Pleistocene bone 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 aminoacids (Zeichner et al. 2017). Therefore, stable isotopes from shark teeth represents an integrated diet signal composition from weeks to months, and not a whole life average.

The archaeological record evidence well-developed prehistoric fisheries targeting sharks and rays 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).

As such, major changes in the local and regional marine communities occurred. C. taurus, one the most abundant shark remains in Brazilian archaeological shellmounds (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 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, isotopic niche variation, and overlap) 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, a shallow site (a shellmound variation) in South Brazil (Fig. 1), located at the north of the island of Santa Catarina, on Jurere beach, at 27°26'23"S, 48°29'56"W (Fossari 2004). The site dates around 724 – 542 years cal.B.P. (calibrated, before present; Fossari 2004).

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 sandbank 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 34ºS to 22ºS and characterized 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 Maldivas 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, 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, and to reduce pseudo replication and misidentifications, we followed the same criteria as in Burg Mayer et al. (2022).

To minimize sampling different class sizes or juveniles for *Carcharhinus* and other considered species, only archaeological teeth with a specific crown height size range were sampled for SIA (Online Resource 1).

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 1980 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), *I. oxyrhinchus* (N = 9), *C. brachyurus* (N = 3), *C. leucas* (N = 2) and *G. cuvier* (N = 1; Online Resource 2). Both archaeological and modern samples from museums were dry stored for later analysis.

To assess the habitat use and validate δ¹³C values for some species of interest, we considered the classification provided by Fishbase (Froese and Pauly 2018) regarding the species habitat use. Following this classification we attributed modern and archaeological *C. taurus* δ¹³C values to be representative of a reef-associated environment.

**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 hours 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 mm.

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 one week at room temperature. Once samples were visibly demineralized, as evidenced by a translucent powder, they were centrifuged (8 minutes at 12,000 rpm), the supernatant removed with a pipette. Then samples were vortexed for 30 seconds embedded in MilliQ deionized 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).
C:N ratios were considered to assess the general preservation state of bone collagen, usually, C:N ratios between 2:9 – 3:6 are indicative of well-preserved bone collagen ratios or collagen without contaminants (DeNiro 1985). Nevertheless, these ratios are mostly used to check bone collagen integrity for mammals and bony fish (see Szpak 2011). Given the inherently different nature of shark teeth ontogeny from bony fish and mammalian bone, and the lower ratios of C:N in fresh collected shark tooth (Zeichner et al. 2017), samples found at lower C:N ratios (2:6 – 2:7) were included in the analysis.

We performed Student t-tests for independent samples for normally distributed data to compare habitat use for *C. taurus* between communities.

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 ≥ 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 (δ¹³C-δ¹⁵N), 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 δ¹⁵N 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 δ¹⁵N values, generally, a larger range in δ¹⁵N among consumers suggests more trophic levels or a more trophic diversity food web. The δ¹³C 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 neighbor 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 neighbor distances (SDNND) represents the overall functional evenness of individual species packing (Layman et al. 2007). Layman’s metrics have been recently being categorized 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, Isurus oxyrinchus* and *Carcharhinus 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* and *C. carcharias*, giving results in total length (TL, cm; Shimada 2003, 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 2003, 2004). To proceed with a padronized by size trophic position analysis, we separated data of *C. taurus* in similar size classes among archaeological and modern species. Size regression estimates indicates that archaeological *C. taurus* ranged from 232 to 274 cm (mean 253.6; N = 9), modern *C. taurus* ranged from 223–273 cm (mean 248.3; N = 7). To make inferences about the trophic ecology of *C. carcharias*, we also calculated its estimated TL, which ranged from 216–315 (mean 262.9; N = 5).

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 standardize size in trophic position analysis, as bigger fish could result in elevated δ¹³C and δ¹⁵N 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 recognizes that species might feed in multiple trophic levels, hence it may become fractional (Zander 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 Δ¹³C and Δ¹⁵N 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 (Milesi 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, 20000 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.

**Results**
Variation in C:N ratios and $\delta^{13}C - \delta^{15}N$

Overall, 50 archaeological shark teeth belonging to nine species were selected and analyzed (Online Resource 3), whereas 47 samples from modern samples were obtained for analysis, belonging mainly to nine species (Online Resource 2). For the archaeological samples, 29 out of 50 samples C:N ranges lay within the expected value for well-preserved bone collagen ratios (2:9 – 3:6), and the other 21 samples lay within 2.7–2.8 ratios. Samples of C:N ratio > 3.6 were excluded from the analysis.

Average $\delta^{13}C$ 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 for $\delta^{13}C$ in both communities were *C. taurus*, whereas the least $\delta^{13}C$ enriched were *Isurus* and *G. cuvier* (Table 1).
Table 1

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

<table>
<thead>
<tr>
<th>Species</th>
<th>Period</th>
<th>N</th>
<th>$\delta^{13}$C ± SD</th>
<th>$\delta^{15}$N ± SD</th>
<th>SEAc</th>
<th>SEAb</th>
<th>TA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sandtiger shark (Carcharias taurus)</td>
<td>724 – 542 years cal.B.P.</td>
<td>14</td>
<td>-10.84 ± 0.53</td>
<td>17.37 ± 1.29</td>
<td>2.35</td>
<td>2.16 [0.92–2.89]</td>
<td>4.57</td>
</tr>
<tr>
<td>Present</td>
<td>10</td>
<td></td>
<td>-11.0 ± 1.20</td>
<td>18.5 ± 0.70</td>
<td>2.8</td>
<td>2.5 [1.07–4.5]</td>
<td>4.19</td>
</tr>
<tr>
<td>Requiem shark (Carcharhinus plumbeus)</td>
<td>724 – 542 years cal.B.P.</td>
<td>6</td>
<td>-11.11 ± 0.96</td>
<td>15.41 ± 1.10</td>
<td>1.67</td>
<td>1.34 [0.94–5.95]</td>
<td>1.74</td>
</tr>
<tr>
<td>Present</td>
<td>6</td>
<td></td>
<td>-12.4 ± 0.82</td>
<td>13.6 ± 2.4</td>
<td>7</td>
<td>5.6 [1.02–6.03]</td>
<td>6.53</td>
</tr>
<tr>
<td>Cooper shark (Carcharhinus brachyurus)</td>
<td>724 – 542 years cal.B.P.</td>
<td>4</td>
<td>-11.45 ± 0.62</td>
<td>16.52 ± 1.04</td>
<td>2.99</td>
<td>1.99 [0.51–5.66]</td>
<td>1.45</td>
</tr>
<tr>
<td>Present</td>
<td>6</td>
<td></td>
<td>-12.25 ± 0.67</td>
<td>16.00 ± 1.54</td>
<td>3.79</td>
<td>3.03 [0.96–8.38]</td>
<td>3.56</td>
</tr>
<tr>
<td>Dusky shark (Carcharhinus obscurus)</td>
<td>Present</td>
<td>6</td>
<td>-11.7 ± 1.35</td>
<td>14.23 ± 1.37</td>
<td>6.55</td>
<td>5.24 [1.87–12.33]</td>
<td>7.36</td>
</tr>
<tr>
<td>Mako sharks (Isurus paucus and Isurus oxyrinchus)</td>
<td>724 – 542 years cal.B.P.</td>
<td>4</td>
<td>-12.42 ± 1.73</td>
<td>15.10 ± 1.09</td>
<td>8.53</td>
<td>5.69 [0.86–13.31]</td>
<td>5.41</td>
</tr>
<tr>
<td>Present</td>
<td>15</td>
<td></td>
<td>-13.16 ± 0.7</td>
<td>14.34 ± 1.4</td>
<td>2.63</td>
<td>2.44 [1.73–5]</td>
<td>5.7</td>
</tr>
<tr>
<td>Bull shark (Carcharhinus leucas)</td>
<td>724 – 542 years cal.B.P.</td>
<td>4</td>
<td>-11.57 ± 0.90</td>
<td>15.22 ± 1.05</td>
<td>4.45</td>
<td>2.97 [0.38–8.52]</td>
<td>2.38</td>
</tr>
<tr>
<td></td>
<td>Present</td>
<td>3</td>
<td>-11.73</td>
<td>13.03</td>
<td>2.13</td>
<td>1.06</td>
<td>0.58</td>
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<td></td>
<td></td>
<td></td>
<td>± 0.83</td>
<td>± 0.85</td>
<td>± 0.85</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Great white shark</td>
<td>724 - 542 years cal.B.P.</td>
<td>7</td>
<td>-11.71</td>
<td>16.84</td>
<td>1.19</td>
<td>0.99</td>
<td>1.54</td>
</tr>
<tr>
<td>(Carcharodon carcharias)</td>
<td></td>
<td></td>
<td>± 0.73</td>
<td>± 0.59</td>
<td></td>
<td>[0.44 - 2.40]</td>
<td></td>
</tr>
<tr>
<td>Tiger shark (Galeocerdo cuvier)</td>
<td>724 - 542 years cal.B.P.</td>
<td>7</td>
<td>-12.96</td>
<td>14.10</td>
<td>5.20</td>
<td>4.33</td>
<td>6.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>± 1.44</td>
<td>± 1.44</td>
<td></td>
<td>[2.03 - 10.40]</td>
<td></td>
</tr>
<tr>
<td>Lemon shark (Negaprion brevirostris)</td>
<td>724 - 542 years cal.B.P.</td>
<td>4</td>
<td>-11.67</td>
<td>15.52</td>
<td>1.37</td>
<td>0.91</td>
<td>0.84</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>± 1.21</td>
<td>± 0.28</td>
<td></td>
<td>[0.26 - 2.82]</td>
<td></td>
</tr>
</tbody>
</table>

Average $\delta^{15}$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 $\delta^{15}$N values, whereas $G$. cuvier was the least $^{15}$N-enriched nitrogen isotopic values, also in both communities (Table 1).

$C$. taurus $\delta^{13}$C values among temporal communities did not significantly differ $t = -0.25, p = 0.8$.

**Food web topology, isotopic niche variation and overlap**

*Isurus* had the highest variability in SEAb the AC, whereas *C. plumbeus* had the highest variability in SEAb in the MC (Table 1). The highest SEAc area for the AC belongs to *Isurus*, and for the MC, belonging to *C. plumbeus* (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 *Isurus* and *C. leucas* (Table 1).

**Layman Metrics**

In the MC, the higher *C. taurus* trophic position, along with lower $\delta^{15}$N values for *Isurus* 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. 3).

**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 724 – 542 years cal.B.P were 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 in a higher trophic diversity whereas the AC was characterized 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. 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. 2016). 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, co-occurring archaeological shark species were not likely near carrying capacity, as these sharks too were under predation pressure from subsistence catches of pre-colonial natives (e.g. Fossile et al. 2019; Burg Mayer et al. 2022), and it is common for great sharks to predate smaller sharks (e.g. Smale 2005; Bornatowski et al. 2014). 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 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 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 et al. 2006; 
Heithaus 2008), trophic redundancy, and populations of predators that are more resilient to decline (lower 
NND, Fig. 2; Heithaus 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 hypothesize 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 also have 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 monopolized 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 marine 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, all comparable species 
between past and present showed a shift towards depleted δ13C values and most of them had an 
increase in their isotopic niche (Fig. 2; Table 1), reinforcing the idea of a trend in niche and resource 
diversification. For example, the C. plumbeus deviance from expected enriched δ13C values for typical 
coastal species, likewise for some individuals of C. taurus (Fig. 2), would suggest that the relative 
importance of pelagic prey has increased. Changes in isotopic baselines may hinder isotopic 
comparisons between time-separated communities, but we suggest that based on C. taurus δ13C values
among temporal communities that did not significantly differ, the baseline for coastal areas has remained relatively similar.

Regardless, the increase in the trophic niche for these species symbolizes 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.

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). 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 proposed mechanism behind the increase in trophic level involves a niche shift towards a more selective diet on bigger prey as a consequence of intraspecific competition release (Saporiti et al. 2014; Bas et al. 2019), hence a higher trophic level (Jennings 2005). *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 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 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).

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. 2016; 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 isoescapes. The lack of studies using stable isotopes in sharks in Brazil and available data on regional isoescapes 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 would suggest a possible pattern for the use of resource in nearly pristine food webs, where trophic redundancy is common. The increase in the trophic position of apex
predators and the increase in the diversity of resource use in modern communities needs attention. 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.

Declarations

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Conflicts of interest/Competing interests (include appropriate disclosures)

The author informs that no conflict of interest is present.

Ethics approval (include appropriate approvals or waivers)

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 (include appropriate statements)

Does not apply

Consent for publication (include appropriate statements)

Does not apply

Availability of data and material (data transparency)

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

Code availability (software application or custom code)

Does not apply

Authors' contributions

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

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Figures
Figure 1

The location of Rio do Meio archaeological site (star symbol) in South Brazil. The site is at a latitude of 27° S.
Figure 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 by two species. Samples were not corrected for baseline differences.
Figure 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. brachyrurus. F) Removal of C. leucas. Mean (solid circles) and 50%, 75% and 95% credible. NR: nitrogen range; CR: carbon range; CD: Centroid distance; NND: mean nearest neighbor distance; SDNND: the standard deviation of nearest neighbor distances. The mean is represented by the black circle. The boxes, from darker to lighter grey, represent the 95, 75 and 50% confidence intervals respectively.
Figure 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 darker to lighter grey, represent the 95, 75 and 50% confidence intervals respectively.

Supplementary Files
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