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TUBARÕES ARQUEOLÓGICOS: ECOLOGIA TRÓFICA E USO DE HABITAT DE TUBARÕES NO SUL DO BRASIL, O QUE MUDOU?

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"Tubarões arqueológicos: ecologia trófica e uso de habitat de tubarões no sul do Brasil, o que mudou?"

Por

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“The Holocene has ended. The Garden of Eden is no more. We have changed the world so much that scientists say we are in a new geological age: the Anthropocene, the age of humans” -Sir David Attenborough

RESUMO

As Reconstruções das teias tróficas do Holoceno podem fornecer informações sobre os distúrbios e mudanças em sua estrutura e topologia, e informar sobre padrões alimentares e de uso de habitat (nicho isotópico/ecológico) integrantes. Para tanto, as análises de isótopos estáveis (AIE) de carbono ^{13}C e nitrogênio ^{15}N são eficientes nas reconstruções tróficas de elementos faunísticos datando de centenas de anos atrás. Dentes de tubarões do Holoceno tardio são prevalentes em sítios arqueológicos do litoral sul do Brasil. Portanto, com AIE em colágeno desses dentes, reconstruímos duas teias tróficas sob a ótica de predadores de topo, uma delas é teia trófica do Holoceno (comunidade arqueológica) que data de 724-542 anos atrás, e uma atual (comunidade moderna). Este é o primeiro estudo a utilizar esta abordagem em dentes de tubarão. Entre a comunidade arqueológica e moderna, analisamos majoritariamente um grupo de espécies (do gênero *Carcharhinus*) e outras três espécies. Secundariamente, incluímos espécies consideradas raras atualmente para inferir padrões de uso de habitat. Investigamos especificamente: 1) Diferenças nos valores de $\delta^{13}C$ e $\delta^{15}N$ entre espécies dentro de cada comunidade, indicativos de uso de habitat e posição trófica; 2) padrões de sobreposição de nicho entre as espécies, através da sobreposição da área da elipse isotópica e de comparações com trabalhos de dieta; 3) diferenças topológicas entre comunidades, *e.g.* redundância e diversidade trófica, através de métricas de Layman; 4) análise de posição trófica padronizada por tamanho para uma espécie, e padrões de uso de habitat para espécies consideradas raras. Nossos resultados mostraram um alto grau de sobreposição de nicho entre espécies da comunidade do Holoceno e uma respectiva maior redundância trófica, quando comparado a comunidade moderna. Além disso, encontramos maior posição trófica do tubarão *Carcharias taurus* na comunidade moderna. A diferença na topologia entre comunidades segue um padrão encontrado em estudos similares, e, portanto, sugerem que padrões de alta sobreposição de nicho e/ou redundância trófica poderiam ser comuns antigamente. Sugerimos que diferenças observadas nas comunidades podem ser causadas por impactos antrópicos indicativos de sobrepesca, mas não ocorrem através de simplificação da cadeia trófica, e sim por mudanças na dinâmica populacional para algumas espécies. Além disso, a presença de espécies raras na costa Sul do Brasil pode ter sido facilitada por períodos de mudança climática natural para *Negaprion brevirostris* e pela presença de pinípedes para *Carcharodon carcharias*. Enquanto que para a espécie oceânica plena *Isurus paucus*, encontramos evidência de uso costeiro, indo ao encontro das predições para essa espécie. Futuros estudos podem se beneficiar da metodologia aqui empregada para reconstruções tróficas, uma vez que informações de ambientes marinhos pouco perturbados são escassas, mas podem servir de parâmetros basais para estudos comparativos.

Palavras-chave: isótopos estáveis; tubarões; sobreposição de nicho; Holoceno; redundância trófica; impactos antrópicos

ABSTRACT

Reconstructions of Holocene trophic webs can provide information about their resilience to disturbances and changes in their structure and topology, and information on habitat use patterns (isotopic / ecological niche). For this purpose, stable isotope analyzes (SIA) of ^{13}C carbon and ^{15}N nitrogen are an efficient option for trophic reconstructions in faunal elements dating back hundreds of years. Late Holocene shark teeth are prevalent in archaeological sites on the southern coast of Brazil. Therefore, through EIA in collagen of shark teeth, this study reconstructed two trophic webs from the top predator perspective, a Holocene trophic web (archaeological community) dating from 724-542 years ago, and a current (modern community). This is the first study to use this approach in shark teeth. We analyzed mainly three species and one group of species (from *Carcharhinus* genus) among those communities, and secondarily we included species considered rare today to infer patterns of habitat use. We investigated specifically: 1) Differences in the values of $\delta^{13}C$ and $\delta^{15}N$ between species within each community, indicative of habitat use and trophic position; 2) patterns of niche overlap among species, by analyzing overlaps of area of the standard ellipse area and comparisons with dietary work; 3) topological differences between communities, *e.g.* redundancy and trophic diversity, through Layman metrics; 4) standard size trophic position analysis for one species, and habitat use patterns for species considered rare nowadays. Our results showed a high degree of niche overlap between species of the Holocene community and a corresponding higher trophic redundancy when compared to the modern community. In addition, we found a higher trophic position of *Carcharias taurus* shark in the modern community. Our results show that the difference in the topology between communities follows a pattern found in similar studies, and therefore suggest that patterns of high niche overlap and / or trophic redundancy could be common before. We suggest that observed differences in communities may be caused by anthropic impacts indicative of overfishing, but not by simplification of the food chain, but by changes in population dynamics for some species. In addition, the presence of rare species on the southern coast of Brazil may have been facilitated by periods of natural climate change for *Negaprion brevirostris* and by the abundance of pinnipeds as prey for *Carcharodon carcharias*. While for the full oceanic species *Isurus paucus*, we found evidence of coastal use, corroborating predictions for this species. Future studies may benefit from the methodology used here for trophic reconstructions, since information about past marine environments is scarce, but may serve as baseline parameters for comparative studies.

Keywords: stable isotopes; sharks; niche overlap; Holocene; trophic redundancy; anthropic impacts

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INTRODUÇÃO GERAL

Tubarões e Impactos Antrópicos na Estrutura Trófica

Tubarões compõem um grupo de predadores marinhos altamente diverso que habita uma ampla gama de habitats em todos os oceanos (EBERT *et al*., 2013). Pertencentes à classe dos Chondrichthyes e superordem Selachimorpha, tubarões são importantes componentes de cadeias alimentares marinhas como predadores ou mesopredadores, embora existam diferenças importantes nas dietas entre as espécies (CORTÉS, 1999; BORNATOWSKI *et al*., 2014; YOUNG *et al*., 2014). A grande diversidade de estratégias de alimentação torna a ecologia trófica dos tubarões complexa (CORTÉS, 1999). Os tubarões são tipicamente difíceis de serem estudados em seu ambiente natural, devido as complexidades logísticas de amostragem, já que muitas espécies têm grande porte corporal, hábitos migratórios e oceânicos. O papel trófico de muitas espécies é incerto, fazendo com que mais estudos tróficos sejam essenciais (FERRETTI *et al*., 2013). Entretanto, os impactos antrópicos, especialmente nas últimas décadas, vêm afetando múltiplas interações tróficas, parâmetros populacionais e a estrutura de comunidades e ecossistemas marinhos (STEVENS *et al*., 2000; HEITHAUS *et al*., 2008; FERRETI *et al*., 2010), consequentemente desestabilizando dinâmicas de interações ecológicas bem estabelecidas por tempo evolutivo e biodiversidade ampla.

Estima-se que cerca de ¼ de espécies da classe Chondrichthyes possuam algum grau de ameaça de extinção de acordo com critérios da IUCN (*International Union for Conservation of Nature*), sobretudo devido à sobrepesca (DULVY *et al*., 2014). Dentre os Chondrichthyes, os tubarões enfrentam declínios populacionais em escala global no último século, também pela degradação e perda de habitat (FERRETTI *et al*., 2010; WORM *et al*., 2013; DULVY *et al*., 2014) e mudanças climáticas (YOUNG *et al*., 2015). Atualmente, no Oceano Atlântico Sul, as populações de tubarões afetadas por pesca de espinhéis estão em declínio ou exauridas (BARRETO *et al*., 2016), situação que é agravada pela pesca desregulada podendo acarretar na depleção total das populações de tantas outras espécies nas águas brasileiras (ICMBio, 2016). Para agravar, desde 2012 não há coleta sistemática de dados das frotas que pescam na jurisdição brasileira, juntamente com o cancelamento de programas de observadores a bordo. Tais aspectos mostram um cenário de incertezas quanto ao estado de conservação de espécies de tubarões que habitam a costa brasileira. Essa situação que é agravada pela elevada importação e exportação de carne de tubarões no Brasil (BARRETO *et al.*, 2017). Globalmente, são reconhecidos impactos e até mesmo extinções de estoques pesqueiros que precedem distúrbios antropológicos recentes (JACKSON *et al.*, 2001). Apesar de não possuir a mesma intensidade, a exploração de tubarões como recursos alimentares data de tempos 'pré-históricos' no Brasil, (*e.g.* 8,720 – 985 cal AP (calibrado, antes do presente; LOPES *et al.*, 2016).

Estamos apenas começando a conhecer as consequências ecológicas dos impactos antrópicos nos ambientes marinhos que, infelizmente, são mais notáveis quando ocasionam o colapso de ecossistemas inteiros (ERLANDSON & RICK, 2008). Já sabemos que os impactos da pesca sobre Chondrichthyes podem ocasionar extinções, mudanças na composição e na diversidade de espécies em comunidades, alterar direta ou indiretamente as interações tróficas e mudanças em parâmetros populacionais como de tamanho, idade média e fecundidade (STEVENS *et al.*, 2000).O impacto de qualquer espécie no ecossistema ou na estrutura de comunidades é fortemente influenciado por interações tróficas (MCCANNON *et al.*, 1988), assim como sua função ou papel ecológico (PIMM, 2002; MONTOYA *et al.*, 2006). Historicamente, para que os reais impactos da sobrepesca fossem observados na estrutura de comunidades e ecossistemas, houve uma defasagem de décadas e até mesmo séculos. Isso porque as espécies não pescadas de nível trófico similar assumiam o papel ecológico de espécies sobrepescadas até que elas também eram sobrepescadas ou morriam por efeitos diretos ou indiretos de desbalanços populacionais (JACKSON *et al.*, 2001). Estes desbalanços populacionais são consequências de remoção de espécies ou de níveis tróficos inteiros de um ambiente, e exemplos clássicos são as cascatas tróficas (PAINE, 1980). A eliminação dos predadores desestabiliza os ecossistemas, desencadeando reações em cadeia que, por fim, desmoronam pela escada trófica até o degrau mais baixo (TERBOGH, HOLT & ESTES, 2010). Quando ocorrem, estas reforçam a ideia do papel do controle tipo *top-down* nos ecossistemas (ESTES *et al.*, 2011). Apesar de existirem estudos sobre controle *top-down*, cascatas tróficas e outros impactos ocasionados por declínios populacionais de tubarões e predadores de topo em geral (*e.g.* MYERS *et al.*, 2007; BAUM & WORM, 2009), os impactos desses declínios na estrutura e funções ecossistêmicas ainda permanecem incertos (HEITHAUS *et al.*, 2008; HEUPEL *et al.*, 2014; ROFF *et al.*, 2016).Devido aos impactos antropogênicos atuais, é cada vez mais difícil compreender a ecologia trófica ou alimentar original dos tubarões que habitam o litoral brasileiro, a medida que vamos nos distanciando das condições ecológicas originais das estrutura de população e comunidades das espécies e do ambiente.

Análises de isótopos estáveis para reconstruções de estrutura trófica

Reconstruções tróficas podem trazer informações a respeito da biodiversidade e resiliência ecossistêmica. Entretanto, para muitos ecossistemas marinhos, há ausência de informações de base que antecedem distúrbios antropogênicos (DAYTON et al., 1998; JACKSON et al., 2001). Análises de isótopos estáveis (AIE) de carbono (δ13C) e nitrogênio (δ15N) fornecem uma opção eficiente para averiguar a ecologia trófica e o uso de hábitat por meio da análise de restos faunísticos de organismos que antecedem distúrbios antropogênicos intensos. Com AIE podemos averiguar questões temporais de respostas ecológicas a distúrbios antropogênicos ou mudanças ambientais, e reconstruir os papéis ecológicos originais de espécies (e.g NEWSOME et al., 2007a; ZENTENO et al., 2015; VALES et al., 2017). Essa abordagem em retrospectiva é possível porque espera-se que a proporção de isótopos estáveis de carbono e nitrogênio em um dado consumidor reflitam os valores de suas presas de maneira previsível (DENIRO & EPSTEIN, 1978, 1981; SCHOENINGER & DENIRO 1984). Para os sistemas marinhos, valores de δ15N são adequados para medir a posição ou nível trófico de um dado organismo (MINAGAWA & WADA, 1984; POST, 2002; CAUT et al., 2009). Para tanto, o cálculo de posição trófica deve ser feito relativo a base da cadeia trófica (baseline), ou seja, o valor de δ15N de consumidores primários ou secundários (POST, 2002). É preciso também conhecer o fracionamento isotópico ou trófico, também conhecido como fator de discriminação (Δ) (FRY, 2006). Quando um organismo consome uma presa há um enriquecimento de 15N nos tecidos do consumidor em relação à presa, devido a assimilação preferencial desse isótopo pesado em relação ao seu isótopo mais leve 14N, causando assim bioacumulação (MARTÍNEZ DEL RIO & WOLF, 2005). Portanto, o Δ é simplesmente a diferença isotópica entre o tecido do consumidor e sua presa, mas que envolve muitas complexidades em seu cálculo (e.g. ZEICHNER et al., 2016). Em média, há um enriquecimento entre 2 e 5‰ para o 15N entre diferentes níveis tróficos (POST, 2002), mas estes valores são variáveis de acordo com o grupo taxonômico de estudo, o estado ontogenético do organismo, com o tecido analisado, a dieta de um organismo e seu nível trófico (CAUT et al., 2009). Por exemplo, para peixes marinhos, Caut e colaboradores (2009) encontraram um valor médio de ΔN = 2,5‰ e Hussey e colaboradores (2010) encontraram valores menores para duas espécies de tubarões, Δ15N = 2.29‰ e Δ13C = 0.90‰. O uso de isótopos Δ15N como ferramenta para averiguar a ecologia trófica e níveis tróficos de tubarões está em expansão nas últimas décadas, sobretudo devido às menores restrições metodológicas quando comparado a métodos tradicionais (ROFF et al., 2016). Além de muitos estudos em escala local e global para desvendar a ecologia de tubarões (e.g. POLO-SILVA et al., 2012; ESPINOZA et al., 2015; DICKEN et al., 2016; BIRD et al., 2018) surgem também novas metodologias para calcular posições tróficas (HUSSEY et al., 2015).

A discriminação isotópica também ocorre com isótopos de carbono 13C/12C, havendo um enriquecimento no isótopo pesado em média de 1‰ de um organismo relativo à sua presa (DENIRO & EPSTEIN, 1978; FRY, 2006; MICHENER, 2007). Entretanto, ecólogos dão preferência para o 15N para medições de posição trófica pois o fracionamento isotópico do mesmo responde com maior sensibilidade a esta medida (POST, 2002). A utilidade mais ampla do isótopo de carbono está na sua correlação com proporções isotópicas de fontes de produção primária marinha, dando aos ecólogos o poder de traçar a origem do carbono inserido na alimentação majoritária de um dado organismo. Em sistemas marinhos, o δ13C varia entre zonas bentônicas, pelágicas, costeiras e oceânicas (FRY & SHERR, 1989; HOBSON et al., 1994; FRANCE, 1995, 1997). Assinaturas de δ13C mais enriquecidas em 13C são observadas em áreas com maior concentração de nutrientes e, portanto, maior produtividade primária, como zonas costeiras dominadas por algas e detritos, em contrabalanço às assinaturas empobrecidas em 13C observadas em sistemas oceânicos, dominados por fitoplâncton (FRANCE, 1995, 1997). Além disso, a composição de isótopos de carbono δ13C de um consumidor é muito próxima daquela das suas presas (WADA, 2009). É possível, portanto, diferenciar a contribuição alimentar das assinaturas isotópicas dos consumidores, ou seja, dentre presas bentônicas vs. pelágicas e presas costeiras vs. oceânicas. Alguns estudos já averiguaram a ecologia trófica de tubarões utilizando δ13C com sucesso, inclusive em escala global (e.g. BIRD et al., 2018), revelando variações nos padrões alimentares latitudinais.

O estudo da dieta, posição trófica e uso de hábitat são algumas das informações críticas necessárias para o sucesso de esforços de conservação e manejo (HUSSEY et al., 2012). Tais aspectos biológicos compõem elementos que integram o nicho ecológico das espécies. O conceito clássico de nicho ecológico passou por transformações com as pesquisas de cunho isotópico, já que o nicho ecológico pode ser quantificado usando proporções isotópicas (BEARHOP et al., 2004), denominando-se ‘nicho isotópico’ (NEWSOME et al., 2007b). O nicho ecológico multidimensional de Hutchinson (1957, 1978), pode ser representado como um hipervolume n-dimensional que pode ser particionado em um eixo cenopoiético, representando os componentes ambientais do espaço de nicho, e o eixo bionômico que se refere principalmente aos componentes tróficos do espaço de nicho. A proporção isotópica de carbono pode ser considerada análoga a uma informação de eixo cenopoiético e os valores de 15N pode ser considerada análoga ao eixo bionômico, que em essência, delineiam o nicho isotópico de um dado animal (NEWSOME et al., 2007b; JACKSON et al., 2011). AIE, portanto, são indicadoras viáveis da ecologia trófica, uso de hábitat e nicho ecológico de tubarões (HUSSEY et al., 2011).

Uma das vantagens das AIE é que pode ser realizada em restos faunísticos de acervos de museus, coleções científicas e restos arqueológicos que podem datar de períodos pré-coloniais ou ‘pré-históricos’, representando ambientes marinhos próximos de pristinos. Tal abordagem em restos faunísticos oferece uma oportunidade para revelar perturbações antropogênicas e/ou mudanças ambientais ao longo do tempo e para reconstruir seu papel ecológico original. Nesse contexto, um ponto de referência histórico é essencial não apenas para entender a ecologia trófica de predadores de topo em ambientes pré-históricos, mas também para fornecer metas ou referências para restauração e manejo (JACKSON et al., 2001; TERBOGH & ESTES 2010; BRAJE & RICK, 2011).

O Contexto Histórico e Arqueológico, e a Biodiversidade Marinha

Restos faunísticos de tubarões são comuns em sítios arqueológicos do Sul e Sudeste brasileiro (FOSSARI, 2004; LOPES et al., 2016; MENDES et al., 2018), dentre estes, destacam-se os dentes e as vértebras, pois são as partes que possuem maior grau de calcificação (REITZ & WING, 2008). O valor isotópico de carbono e nitrogênio obtido do colágeno de dentes de tubarões é derivado de isótopos pesados de aminoácidos sanguíneos, e este valor isotópico representa a assinatura isotópica da dieta de um dado organismo (ZEICHNER et al. 2016). Cada dente representará um valor de dieta integrado referente ao seu tempo de formação e erupção, onde estava absorvendo aminoácidos sanguíneos até a formação completa (ZEICHNER et al. 2016). Já que a erupção de dentes em tubarões é constante, o valor isotópico observado dependerá da taxa de formação e substituição de dentes e a posição do dente analisado na mandíbula. Os tubarões têm de cinco a seis séries de dentes em suas bocas, e os dentes migram para a borda da mandíbula em um movimento semelhante a uma correia transportadora (SMITH et al. 2013). Este valor pode variar em uma janela de tempo entre semanas a meses, dependendo das características biológicas e fisiológicas intrínsecas de cada espécie que determinam a taxa de formação e a taxa de rotação. Portanto, os valores de isótopos pesados em dentes de tubarão não representam uma média de valores isotópicos da vida inteira do animal, mas sim um valor isotópico que poderá ser de uma semana a um mês (analisando um dente recém formado) e um valor de no máximo de meses atrás (analisando um dente na última posição da mandíbula).

De acordo com as pesquisas arqueológicas do sudeste brasileiro, o registro faunístico dos sítios arqueológicos é representativo do Holoceno, e indicativas da biodiversidade marinha do passado (MENDES et al., 2018). Estes estudos indicam que a riqueza de espécies e abundância histórica de predadores de topo já foi superior em comparação aos tempos atuais, pela presença de espécies raras que não ocorrem atualmente, e o declínio de parâmetros populacionais que são indicativos de redução populacional (LOPES et al., 2016). Essas afirmações poderiam ser extrapoladas para a fauna encontrada dos sítios arqueológicos do Sul do Brasil (e.g. FOSSARI, 2004), que também mostram ampla biodiversidade de tubarões locais.

Nos sítios arqueológicos tanto do Sudeste como do Sul, destaca-se a presença de espécies cosmopolitas, como o tubarão-tigre, *Galeocerdo cuvier*, e tubarão-branco, *Carcharodon carcharias*, de espécies que possuem atual distribuição fora do observado para o Sul do Brasil, como *Negaprion brevirostris* e de espécies consideradas oceânicas ou plenamente oceânicas, como por exemplo o tubarão-anequim-preto, *Isurus paucus*, e tubarão-galha-branca, *Carcharhinus longimanus*. O tubarão-branco pode ser considerado uma espécie rara atualmente, seu último registro no litoral brasileiro foi na década de 1980 (GADIG & ROSA, 1996). Uma das espécies de tubarão mais abundante nos sítios arqueológicos do Sudeste e do Sul citados é o tubarão-mangona, *Carcharias taurus* (LOPES et al., 2016; MAYER, 2017; MENDES et al., 2018). Porém, atualmente, possui registros esporádicos de avistamento em ambas as regiões da costa brasileira. Dados históricos mostram uma alta abundância dessa espécie no Sul do Brasil algumas décadas atrás, especificamente na ilha de Santa Catarina Souza (2000), e informações de pesca que registravam ocorrências altas de captura na década de 1980 (AGUIAR, 2003; KOTAS, 2005). Porém, atualmente essas populações encontram-se em colapso devido a pesca predatória (AGUIAR, 2003; MMA, 2004; Castro, 2008). Tais registros históricos evidenciam o colapso de populações de tubarões locais e regionais, possivelmente alterando, portanto, as dinâmicas de interações tróficas e impactando diversas funções ecossistêmicas como consequência.

O sítio arqueológico Rio do Meio (FOSSARI, 2004), datado entre 724-542 anos antes do presente, está localizado no norte da ilha de Santa Catarina. Nele foram identificadas 11 espécies de tubarões através de seus dentes (MAYER, 2017). O sítio provê uma oportunidade para que, através de AIE, se averigue a ecologia trófica das espécies que viveram em um período que precede a intensa exploração pesqueira colonial histórica e moderna global (RICK & ERLANDSON, 2008; FERRETTI et al., 2010) e demais impactos antrópicos modernos.

Objetivos e Hipóteses

O objetivo primário desta dissertação é compreender como estavam estruturadas as cadeias tróficas locais em ambiente marinho pouco perturbado, por meio da ecologia trófica de tubarões como predadores de topo e mesopredadores. Busca-se compreender também o uso de hábitat de espécies consideradas raras atualmente, e estabelecer uma linha de base de valores isotópicos de $\delta^{15}N$ para espécies-chave de tubarões no sul do Brasil, que representam a alimentação de predadores de topo em ambientes pouco impactados.

A primeira hipótese testada prediz que os tubarões representativos de ambientes quase pristinos estariam se alimentando em posições tróficas mais elevadas do que observado atualmente, pois impactos antropogênicos estão simplificando os ecossistemas ou encurtando as teias tróficas e levando a um decréscimo no nível trófico para os principais predadores. Isso devido ao colapso de populações de presas de alto nível trófico (e.g. PAULY, 1998), que serviriam como presa potencial para os predadores de topo e mesopredadores. Além disso, esperamos observar deslocamento do nicho isotópico entre mesmas espécies, quando comparadas com as recentes, ou seja, não há uma estrutura constante das teias tróficas. Além disso, não se sabe se espécies de ocorrência rara possuíam residência no Sul do Brasil ou seriam espécies migratórias. Portanto, Nossa segunda hipótese é que as espécies raras teriam tamanho corporal estimado (juvenis para sub adultos) e valores isotópicos indicativos de alimentação em áreas litorâneas costeiras, que juntos possivelmente sugeririam a presença de berçários que sugeririam residência histórica no sul do Brasil.

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

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ABSTRACT

Sharks are important components of marine food webs, but their removal through anthropic impacts might simplify ecosystems and food webs. Here, stable isotope analysis was used to analyze patterns of niche overlap and topological metrics among two communities, a late Holocene (archaeological community) dating from 724-542 years ago, and a modern (modern community) trophic web, both from South Brazil. Secondarily, we included species considered rare today to infer patterns of habitat use in the Holocene. Results showed topological changes such as higher trophic redundancy and patterns of niche overlap in the archaeological community, whereas modern community showed dispersion of species throughout the isotopic space, thus higher niche partitioning and lower trophic redundancy. These findings were also observed in similar studies, suggesting higher trophic redundancy could be common in late Holocene food webs. We suggest that observed differences in South Brazil communities may be caused by anthropic impacts, such as overfishing. However, some observed changes did not simplify modern food web topology, but might have changed population dynamics for some species. In addition, the presence of rare species on the southern coast of Brazil may have been facilitated by periods of natural climate change for *Negaprion brevirostris* and by the presence of pinnipeds prey for *Carcharodon carcharias*. We advocate that this study methods might help future trophic reconstructions using shark teeth, as information about past marine environments is scarce, and serve a baseline for future studies involving the trophic ecology of these high trophic level predators.

Key-words: stable isotopes; sharks; niche overlap; Holocene; trophic redundancy; anthropic impacts

INTRODUCTION

Humans are catalyzing changes in marine ecosystems through accelerating climate change, increasing biodiversity loss, pollution, habitat degradation, facilitation of invasive species and causing the collapse of many fisheries, leading to impairment and loss of ecosystems structure and functions (Worm et al. 2006; Halpern et al. 2008; Doney et al. 2012). Some of these impacts started millennia ago, consequently, some 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 modern anthropic context, the original trophic ecology of many species almost certainly was not preserved over the years (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 about 1/4 species of Chondrichthyes are threatened according to the IUCN red list (Dulvy et al. 2014). 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. 2014). This general scenario is not different for shark populations in the South Atlantic. Off the southern Brazilian coast, shark populations are currently depleted by longline fisheries (Barreto et al. 2016). Worsening this situation, researchers cannot measure population trends due to the suspension of data collection since 2012, causing uncertainty about the conservation status of many species, which in turn is also aggravated by Brazil leading position in importing shark meat worldwide, raising many conservation concerns (Barreto et al. 2017).

Sharks are important components of marine food web as a top or mesopredator (Cortés 1999; Bornatowski et al. 2014b) acting as to regulating prey dynamics through predation or indirectly inducing behavior changes with fear effects (Heithaus et al. 2008). 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; Stevens et al. 2000; Ferretti et al. 2010). More simply, sharks removal or declines ultimately simplify oceanic ecosystems (Baum and Worm 2009). Therefore, modern trophic ecology studies 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 (Schoeninger and Deniro 1984), 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). SIA provides an ecological framework because isotope values of nitrogen $\delta^{15}N$ and carbon $\delta^{13}C$ in the consumer’s tissue is expected to reflect the value of its prey in a predictable way (DeNiro and Epstein 1978, 1981). $\delta^{13}C$ values stay relatively constant from prey to consumers (Wada 2009), while $\delta^{15}N$ increase per trophic step, relative to the species and tissue analyzed, hence being a good indicator of trophic position (Post 2002; Caut et al. 2009). The broader utility of the carbon isotope lies in its correlation with isotopic ratios of primary marine production sources, which allows tracing the carbon origin embedded in most prey of a given organism. In marine systems, $\delta^{13}C$ tends to have more enriched values in benthic, nearshore ecosystems than in typically more depleted values of offshore, pelagic ecosystems (Fry and Sherr 1989; Hobson et al. 1994; France 1995; France and Peters 1997).

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 (Fossari 2004; Lopes et al. 2016; Mendes et al. 2018)—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. 2016). Shark jaws have five to six series of teeth in their mouths, and shark teeth migrate to the edge of the jaw in a conveyor belt–like movement; Smith et al. 2013). Depending on the time length of tooth replacement rates and the teeth position in question, diet signal could come from, for example, anytime between 36 to 180 days for *Carcharhinus plumbeus* (Luer et al. 1990) or 40 to 260 days for *Triakis semifasciata* (Zeichner et al. 2016). Hence, 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 suggests an early stage of overexploitation of medium to large size fishes and the beginning of fish stocks depletion (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;* MMA 2004) and many other shark species (Fossari 2004; Lopes et al. 2016; Mendes et al. 2018;).

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), also was historically abundant in the South of Brazil, as seen in historical underwater fishing (Souza 2000). However, as many other shark species of South Brazil, their populations were heavily exploited in the last decades (Kotas 2005; Castro 2008), suggesting currently depleted populations, with unknown consequences to their trophic ecology. Besides, there is no information about the trophic ecology of these top and mesopredators 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, Heupel et al. 2014, Roff et al. 2016).

Optimal foraging theory predicts that when food get scarce, predators become less selective, capturing prey according to the encounter rate and in turn increasing the consumption of smaller prey and consequently increasing their trophic niche as they add less preferable prey to their diet (Schoener 1971; Werner and Hall 1974; Gill 2003). As humans progress their unsustainable and predatory fisheries worldwide, fishing the higher trophic levels species and decreasing their abundance (Pauly 1998; Myers and Worm 2003) it is plausible to assume that populations of top and mesopredators are progressively feeding more on lower trophic level prey, thus leading to a lower average trophic level.

Therefore, this study uses a historical approach to compare the trophic ecology a modern community of sharks to a community of ten species of sharks from the late Holocene based on SIA of carbon and nitrogen, and discuss the potential role of human impacts in changing their original trophic ecology and habitat changes. Furthermore, we will use $\delta^{13}C$

values to better understand habitat use of rare species in South of Brazil. Would species of rare occurrence nowadays (e.g *N. brevirostris*) be resident in southern Brazil in late Holocene, or would they be migrant species? Our first hypothesis is that ecosystems are being simplified or food webs are being shortened which leads to decreased trophic level for top predators, due to the collapse of many high trophic level fisheries serving as potential prey for top and mesopredators. Additionally, we expect that food web topology will not remain constant over time. Our second hypothesis is that the rare species would have estimated body size (juveniles to sub adults) and isotopic values indicative of nearby nursery areas and feeding in inshore-coastal areas, that together will possibly suggest historical residence in southern Brazil.

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 (Figure 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).

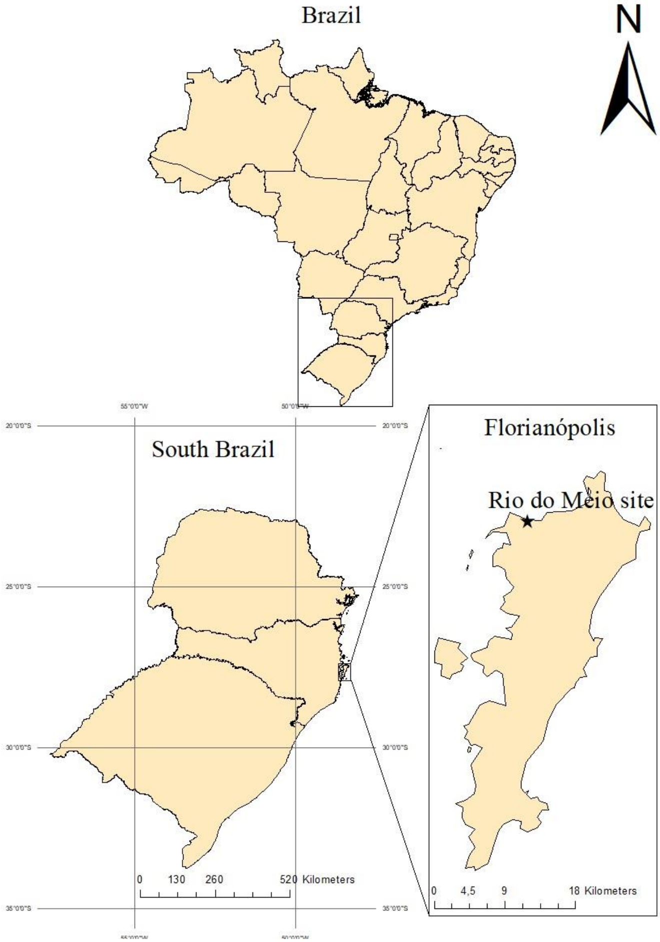


Figure 1. The location of Rio do Meio archaeological site (star symbol) in South Brazil. The site is at a latitude of 27° S.

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 (Tomazzoli and Pellerin 2015).

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; Helleman 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 (Campos et al 1996; 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.

Shark teeth were identified to the lowest taxonomic level possible. Identification were based on compared anatomy/morphology of diagnostic features from different species teeth, using a local scientific reference collection from UFSC, relevant scientific literature for *Carcharhinus* genus (e.g. Voigt and Weber 2011) and shark teeth identification keys (e.g. Purdy 2006). Only well-preserved and robust shark teeth were used (had little taphonomic effects, no noticeable alteration of color or structure damage).

To reduce pseudo replication, we considered teeth to be from different individuals when found in different grids and excavation levels (each level is 10 cm in depth apart from other). To minimize misidentifications and sampling different size class, only superior and anterior teeth for *Carcharhinus* genus were considered, as inferior teeth morphology are mostly homogeneous (see Voigt and Weber 2011). Shark teeth crown height size would theoretically allow a coarse guide to selecting individuals of similar sizes. To minimize sampling different class sizes or juveniles for *Carcharhinus* and other considered species, only teeth with a specific crown height size range were sampled for SIA: *Carcharhinus* group 0.8–1.7 cm (*Carcharhinus obscurus* and *Carcharhinus plumbeus*, N = 6), available total range (ATR): 0.4–1.7 cm; *Carcharhinus leucas* 0.8–1.5 cm (N = 4), ATR: 0.6–1.5 cm; *Carcharhinus brachyurus* 0.8–1.5 cm (N = 4), ATR: 0.4–1.5 cm; *C. taurus* 1.5-2.6 cm (N = 13), ATR: 0.7–2.8 cm; *C. carcharias* 1.2-2.5 cm (N = 7), ATR: 0.6–3 cm; *Galeocerdo cuvier* 1.0-2.5 cm (N = 7) ATR: 0.6–2.5 cm;, *Negaprion brevirostris* 1.1-1.5 cm (N = 4), ATR: 0.5–1.5 cm; *Isurus paucus* 1.55-2.75 cm (N = 4), ATR: 1.55–2.75 cm.

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 *Carcharhinus* group (*C. obscurus*, *C. plumbeus* and *Carcharhinus limbatus*; N = 8), *C. taurus* (N = 9), *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; Supplementary Table 1). 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. Afterwards, samples were dried at 50 ºC 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 mineralized matrix in shark teeth consists of fluoropatite (Ca5(PO4)F) in the outer layer, whereas the inner layer or dentin is mainly made of hydroxyapatite (Ca5(PO4)OH) with some degree of carbonates substitution forming carbonated apatites (LeGeros 1981; Enax et al. 2012; Lubke et al. 2015). The inorganic carbon present in hydroxyapatite of dentin differs in isotopic composition to the organic component (Newsome et al. 2010), therefore the collagen must be isolated prior to SIA. To isolate collagen, it has been suggested the use of ethylenediaminetetraacetic acid (EDTA) in shark vertebrae, likewise made of hydroxyapatite, as an alternative to use hydrochloric acid (HCl) due to the HCL rapid dissolution of both collagen and organic matrix

(Kim and Koch 2012). Furthermore, EDTA is indicated for fossil samples (or presumably samples with diagenetic alterations) because EDTA decalcification is more effective than using HCl, also giving a product free from humic acids (Tuross et al. 1988)

Hence, 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.

Stable Isotope Analysis

Carbon and nitrogen stable isotope ratios were measured using a Costech (4010) elemental analyzer coupled to a Thermo Scientific Delta V isotope ratio mass spectrometer at the University of New Mexico Center for Stable Isotopes (Albuquerque, NM). Stable isotope data are expressed as δ values using the equation $X = [(Rsample – Rstandard)/Rstandard] \times$

1000 (‰), where X is the heavy isotope of interest, Rsample and Rstandard are respectively the ratios of $^{15}N/^{14}N$ and $^{12}C/^{13}C$ for each sample and their standard. Pee Dee Belemnite (V-PDB) limestone and atmospheric N_2 were used as standard reference materials for carbon and nitrogen, respectively. The reported analytical precision was < 0.2‰ for δ15N and < 0.1‰ for $\delta^{13}C$. 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 (Francey et al. 1999; Indermühle et al. 1999).

Data Analysis

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 equal lower ratios of C:N in fresh collected shark tooth (Zeichner et al. 2016), samples found at lower C:N ratios (2:6-2:7) were included in the 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).

In both communities, some species of *Carcharhinus* genus were selected to be grouped in one cluster of isotopic data due to their similar diets and trophic niche: *C. plumbeus*, *C. obscurus* and a *Carcharhinus limbatus* specimen in the modern community (Bornatowski et al. 2014a; Cortés 1999). To make relative inferences about *I. paucus*, we used diet studies for *I. oxyrhincus*, its closest relative, as assume similar trophic ecology in comparing patterns of niche overlap.

To assess the habitat use of species of interest, we considered modern and archaeological *C. taurus* δ^{13}C values to be representative of a coastal and benthic environment, whereas considering modern *Isurus* genus δ^{13}C values to be representative oceanic and pelagic environment. However, archaeological *Isurus* δ^{13}C values were not considered adequate of a solely oceanic-pelagic environment, as the individuals from these species had both enriched and depleted δ^{13}C values. Then, we performed a series of Student t-tests for independent samples for normally distributed data or a Mann-Whitney-Wilcoxon signed rank test for non-normally distributed data or for unequal variances, to compare species habitat use within each community.

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 (Batschelet 1981; Jackson et al. 2011). We used the area of the ellipses to make inferences about the species ecology in each community. Dietary niche overlap was calculated with Stable Isotope Bayesian Ellipses for R (SIBER) using the Stable Isotope Analysis in R (SIAR) package (Parnell and Jackson 2013), by calculating the percentage of ellipse overlap among species. We did not correct for isotopic baselines in this analysis, as the area of the species standard ellipses and food web topology are independent from differences in the isotopic baseline, especially when analyzing each community individually.

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 metrics measure some general food web properties of a given community using a dual isotopic approach ($\delta^{13}C$-$\delta^{15}N$). As with the standard ellipses and TA, no correction for isotopic baselines was necessary because the topology of the food web is independent from baseline influence. Five of six of the Layman’s metrics were calculated. The $\delta^{15}N$ 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 $\delta^{15}N$ values, generally, a larger range in $\delta^{15}N$ among consumers suggests more trophic levels or a more trophic diversity food web. The $\delta^{13}C$ 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, as it is unbiased in the case where outliers inflates NR or CR. It 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. These three metrics are measures of the global structure of the food web, as measures of the total extent of spacing within the $\delta^{13}C$-$\delta^{15}N$ bi-plot space. 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 evenness of individual species packing (Layman et al. 2007). In this analysis, only matching taxa from both communities with the minimum number of samples were used (*C. taurus*, *Carcharhinus*, *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.

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 trophic position analysis, we separated data of *C. taurus* in similar size classes among archaeological (232-274 cm, N

= 9) and modern (223-273 cm, N = 7) species. 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 larger fish could result in elevated $\delta^{13}C$ and $\delta^{15}N$ values, due to ontogenetic shifts or feeding niche differences among size classes (e.g. Estrada et al. 2006) and 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 and standard deviation of 0.1, as defined by stomach content analysis (Cortés 1999). TDF values for shark teeth were obtained from Zeichner et al. (2016). TP must be calculated relative to a baseline (primary or secondary consumers) of the organism respective food-chain (Post 2002). 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 modern community 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). 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.

To test the hypothesis of an overall change in the isotopic niche space between the temporal separated communities, we used the Two-Sample Fisher-Pitman Permutation Test to simultaneously test the SEAb, SEAc and TA of the taxa with the minimum sample comparability required from both communities.

RESULTS

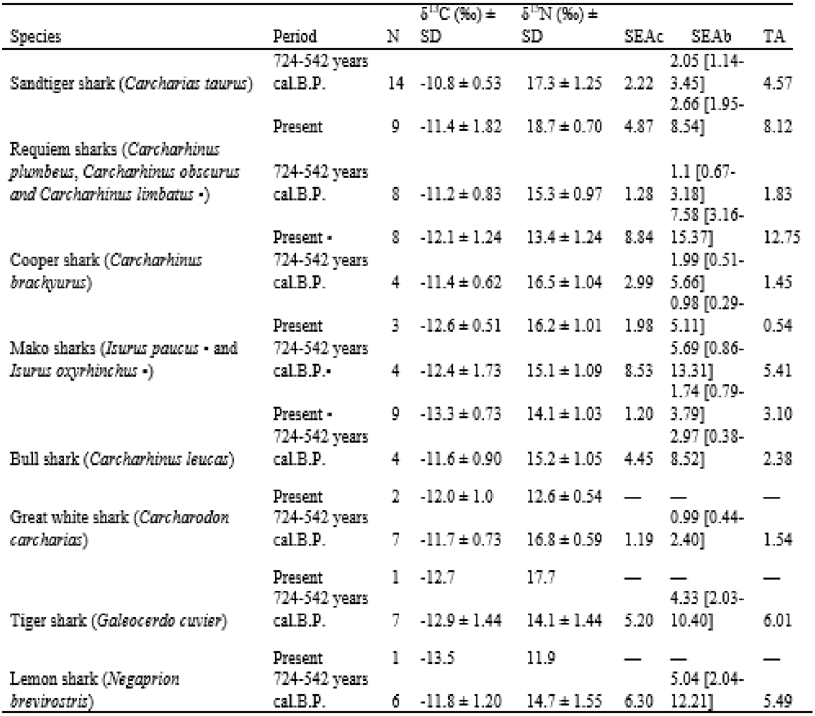
Variation in C:N ratios and $\delta^{13}C$ - $\delta^{15}N$

Overall, 49 archaeological shark teeth belonging to nine species were selected and analyzed (Supplementary Figure 2), whereas 25 samples from modern samples were obtained for analysis, belonging mainly to nine species (Supplementary Table 1). Approximately more than half of archaeological samples C:N ranges lay within the expected value for well-preserved bone collagen ratios (2:9-3:6; DeNiro 1985), and the other half lay within 2.7-2.8 ratios. Four samples of C:N ratio > 3.6 were excluded from the analysis.

Average $\delta^{13}C$ ranged from -10.8‰ to -12.4‰ for archaeological community (arch) and -10.9‰ to -13.5‰ for modern community (mod), suggesting multiple carbon sources for both communities (Table 1). The most ^{13}C enriched species for $\delta^{13}C$ in both communities were *C. taurus*, whereas the least ^{13}C enriched were *Isurus* and *G. cuvier* (Table 1).

Average $\delta^{15}N$ values ranged from 14.1‰ to 17.4‰ for archaeological community and 13.4‰ to 18.7‰ for modern community, suggesting species fed on prey across multiple trophic levels in both communities (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).

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.



Species	Period	N	$\delta^{13}C$ (‰) ± SD	$\delta^{15}N$ (‰) ± SD	SEAc	SEAb	TA
Sandtiger shark (*Carcharias taurus*)	724-542 years cal.B.P.	14	-10.8 ± 0.53	17.3 ± 1.25	2.22	2.05 [1.14-3.45]	4.57
	Present	9	-11.4 ± 1.82	18.7 ± 0.70	4.87	2.66 [1.95-8.54]	8.12
Requiem sharks (*Carcharhinus plumbeus*, *Carcharhinus obscurus and Carcharhinus limbatus* ▪)	724-542 years cal.B.P.	8	-11.2 ± 0.83	15.3 ± 0.97	1.28	1.1 [0.67-3.18]	1.83
	Present ▪	8	-12.1 ± 1.24	13.4 ± 1.24	8.84	7.58 [3.16-15.37]	12.75
Cooper shark (*Carcharhinus brachyurus*)	724-542 years cal.B.P.	4	-11.4 ± 0.62	16.5 ± 1.04	2.99	1.99 [0.51-5.66]	1.45
	Present	3	-12.6 ± 0.51	16.2 ± 1.01	1.98	0.98 [0.29-5.11]	0.54
Mako sharks (*Isurus paucus* ▪ and *Isurus oxyrhinchus* ▪)	724-542 years cal.B.P.▪	4	-12.4 ± 1.73	15.1 ± 1.09	8.53	5.69 [0.86-13.31]	5.41
	Present ▪	9	-13.3 ± 0.73	14.1 ± 1.03	1.20	1.74 [0.79-3.79]	3.10
Bull shark (*Carcharhinus leucas*)	724-542 years cal.B.P.	4	-11.6 ± 0.90	15.2 ± 1.05	4.45	2.97 [0.38-8.52]	2.38
	Present	2	-12.0 ± 1.0	12.6 ± 0.54	—	—	—
Great white shark (*Carcharodon carcharias*)	724-542 years cal.B.P.	7	-11.7 ± 0.73	16.8 ± 0.59	1.19	0.99 [0.44-2.40]	1.54
	Present	1	-12.7	17.7	—	—	—
Tiger shark (*Galeocerdo cuvier*)	724-542 years cal.B.P.	7	-12.9 ± 1.44	14.1 ± 1.44	5.20	4.33 [2.03-10.40]	6.01
	Present	1	-13.5	11.9	—	—	—
Lemon shark (*Negaprion brevirostris*)	724-542 years cal.B.P.	6	-11.8 ± 1.20	14.7 ± 1.55	6.30	5.04 [2.04-12.21]	5.49

When comparing habitat use based on $\delta^{13}C$ values for the archaeological community, *C. taurus* values were significantly higher than *G. cuvier* (t = -3.76, p-value = 0.007), and *C. carcharias* (t = -3.08, p-value = 0.006). For the modern community, among four species, only

C. taurus showed carbon isotopic values significantly higher than *I. oxyrhincus* (t = -3.81, p-value = 0.002)

Food web topology, isotopic niche variation and overlap

Credible intervals for SEAb for most species were variable, with arq. C. taurus and Carcharhinus contained within their modern counterparts, however with an increase in the area for their modern counterparts (Table 1). Isurus had the highest variability in SEAb, however this variability was present in both communities (Table 1). Similarly, the highest SEAc area for the archaeological community belongs to Isurus, and for the modern community, belonging to Carcharhinus (Table 1). Carcharhinus have considerably increase their isotopic niche in the present, compared to the past(Table 1). An increase was also observed in the SEAc for C. taurus (SEAc from 2.35 to 3.10). There were no significant differences between the archaeological and modern species for SEAc (Z = -0.01, p-value = 0.99, SEAb (Z = -0.17, p-value = 0.85) and TA (Z = -0.34, p-value = 0.72).

Individually, extensive dietary overlap among species was detected via SIBER analysis in the whole archaeological community, even when considering only matching species with the modern community (Figure 2; Table 2). The areas with highest niche overlap were among *C. leucas*

(90% of total isotopic area) and *I. paucus* (47% of total isotopic area), followed by *G. cuvier* (61.3% of total isotopic area) and *I. paucus* (37.3% of total isotopic area; Table 2). Individually, *N. brevirostris* isotopic area overlap was the highest (who shared more area with others) followed by *C. leucas*, *C. brachyurus*, *Carcharhinus*, *I. paucus*, *C. carcharias*, *G. cuvier* and *C. taurus*. However, when considering the whole food web, there was a tendency in species individuals sharing more isotopic niche area with *I. paucus*, followed by *C. leucas* and *C. brachyurus*. The single species that shared the most of its own isotopic niche area with other species was the *Carcharhinus* group.

Whereas in the modern community, lower or no overlap values were found (Table 2). Comparing matching species among communities, *C. taurus* was no longer overlapping its isotopic niche with *Carcharhinus*, *C. brachyurus* and *I. oxyrhincus* in the modern community, whereas in the archaeological community, it presented a ‘high’ overlap with *C. brachyrurus* and lower degree of overlap with the others species cited above (Table 2). *Carcharhinus* had a high overlap of 92.8% with *I. paucus* in the archaeological community, while opposite represented only 8.6%.

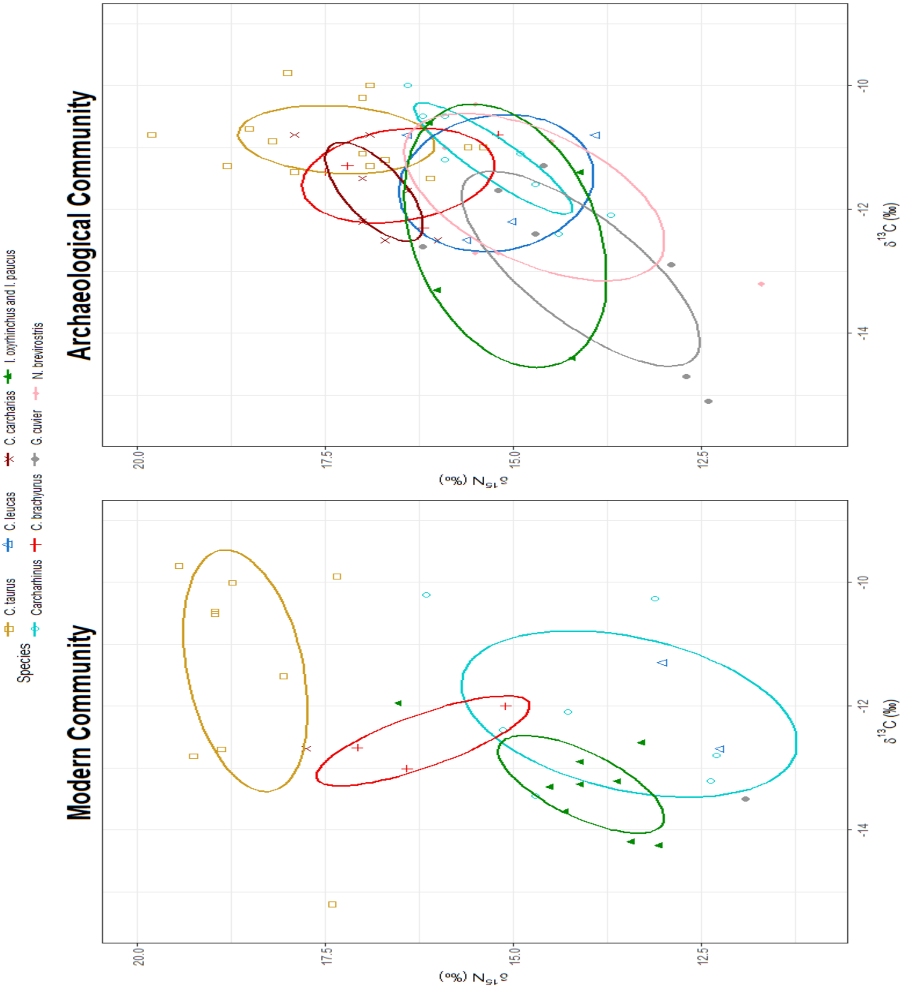


Figure 2. Isotopic Standard Ellipses adjusted for small sample sizes (SEAc) representing the isotopic niche or niche width, and their respective niche overlap between ellipses that characterises the degree of shared resource use by two species. Samples were not corrected for baseline differences.

Table 2. Percentage overlap in standard ellipses (determined using SEAc area) between each pair of shark species. The table is to be read across each row; for example, 2.8% of *C. taurus* ellipse overlaps with *Carcharhinus* group, and 4% of *Carcharhinus* ellipse area overlaps with *C. taurus*.

Species	CT	Car	CB	IP	CL	CC	GC	NB
Carcharias taurus (CT)	–	–	37.2	5.3	3.4	14		
Carcharhinus (Car)	–	–	24.7	92.8	84		28.4	93
Carcharhinus brachyurus (CB)	27.6	10.6	–	43	42.2	33.8	3	17.2
Isurus paucus (IP)	1.4	13.9	15.1	–	47	1.6	37.3	15.8
Carcharhinus leucas (CL)	1.7	24.2	28.4	90	–	2.9	32.1	25
Carcharodon carcharias (CC)	26.1		84	11.7	11	–		
Galeocerdo cuvier (GC)		7	2	61.3	27.5		–	9.5
Negaprion brevirostris (NB)		19	37.5	98.2	80		36.2	–

Modern Species	Car	IO	CB
Carcharhinus (Car)	–	8.6	4.2
Isurus oxyrhincus (IO)	38.2	–	
Carcharhinus brachyurus	18.9		

This latter pattern is somewhat maintained in the present, regarding modern *Isurus*-*Carcharhinus* overlap (14.6%), but has decreased considering the *Carcharhinus*-*Isurus* overlap (26.2%). Despite niche and overlap variation, the overall topology of the food web was relatively constant throughout time, except for *C. taurus* which had an increase in δ^{15}N values in the modern community relative to other species.

Layman Metrics

In the modern community, the higher C. taurus trophic position, along with lower δ15N values for Isurus and Carcharhinus resulted in a significantly larger NR value (p = 0.99) and hence a longer food web (Figure 2). When comparing to the modern community, the archaeological community species were tightly packaged within the isotopic space, suggesting higher trophic redundancy (lower NND, p = 0.97; Figure 3). Furthermore, the archaeological community had an average higher trophic redundancy, as revealed by significantly lower CD (p = 0.99; Figure 2). The SDNND was not significantly different between communities (Figure 2).

Trophic position and size regression

The trophic position for *C. taurus* was significantly higher in the modern community than the archaeological one (p = 0.96), as given by confidence probability in pairwise test of Bayesian posterior distributions at a confidence interval of 95% (Figure 3).

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) and *C. carcharias* ranged from 216-315 (mean 262.9; N = 5).

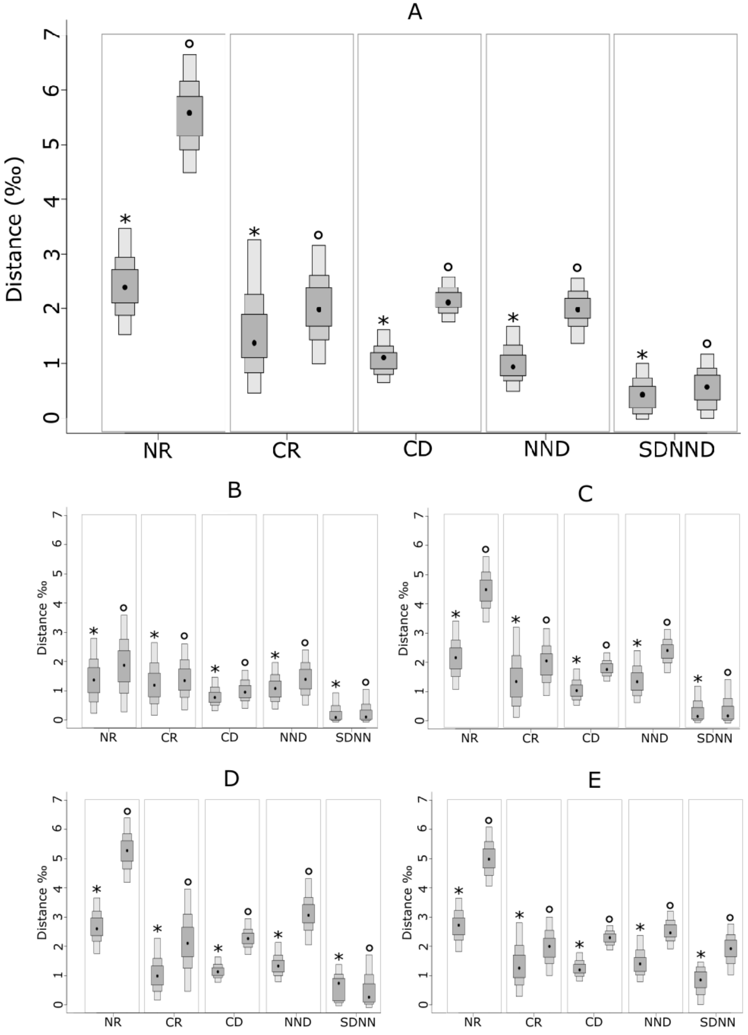


Figure 3. Community Layman’s metrics between Late Holocene archaeological community (*) and modern community (°) from South Brazil. A) Results using entire community species. B) Removal of *C. taurus*. C) Removal of *Carcharhinus* group. D) Removal of *C.*

brachyurus. E) Removal of *I. paucus*. 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.

Figure 4. The posterior estimates of the trophic position for the *C. taurus* in both communities. Mean (solid circle). The boxes represent the 95, 75 and 50% confidence intervals respectively.

DISCUSSION

Our assessment of the historical ecology of sharks by SIA of carbon and nitrogen on shark teeth 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 considerable degree of niche overlap, implying shared resources, even when only considering the four comparable species with the modern community. On the other hand, the modern community of sharks exhibited resource partitioning for *C. taurus*, mostly because of its higher trophic position (Figure 2), and lower isotopic overlap among *Carcharhinus* and *Isurus*. Second, the archaeological community 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, the NR range was higher for the modern community, most likely because of the higher trophic position of *C. taurus* (Figure 2) and its higher $\delta^{15}N$ range, as shown in Figure 2B, where the removal of this species from the analysis, which evened the NR range among communities. This implies in a longer, but not necessarily more trophic diverse, food web. Hence, we reject our first hypothesis that reduces in the abundance of high trophic level prey would lead to reduces in mean trophic level for sharks. But we partially accept our second hypothesis regarding residency of rare species for South Brazil.

Patterns of niche overlap and partitioning and food web topology

Classical niche theory predicts trophic segregation among coexisting species (Hutchinson 1957; Vandermeer 1972), and dietary niche partitioning in elasmobranch communities are regular observed in community ecology studies (e.g. White et al. 2004; Kinney et al. 2011; Flores-Martínez et al. 2017). However, our results show considerable isotopic niche overlap within the archaeological community (Table 2). High niche overlap for a guild of sympatric predators would also suggest that prey were not a limiting resource.Studies have showed higher niche overlap and relaxed competition states between top consumers when food items are abundant, leading to stable resource use (Croxall et al. 1999; Gallagher et al. 2016). Although pre-colonial environments in southern Brazil were likely to be resource abundant, more factors would be at play on shaping the patterns of niche overlap observed. High niche overlap could be the expected outcome on top-down controlled marine systems where predators are near their carrying capacity (Bas et al. 2018). 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 it is common for great sharks to predate smaller sharks (e.g. Smale 2005; Bornatowski et al. 2014a).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. Whereby costly direct and indirect predation effects would maintain predators and mesopredators populations below the carrying capacity that which would be sustained by the abundance of prey resources (Heithaus 2008; Vaudo and Heithaus 2011). If this is the case in the archaeological community, particular trophic levels of shark preys would be under predatory release, which would lead to higher degrees of niche overlap in the whole community (Heithaus 2008; Vaudo and Heithaus 2011). Food webs with the occurrence of multiple predators and intraguild predation often results in decreases of interaction strength towards one particular type of prey species (Schmidtz 2007).

Substantial elasmobranch consumers (particularly other sharks) in the archaeological community are *C. taurus* (Smale 2005; Lucifora et al. 2009), *C. leucas* (Olin et al. 2013; Estupiñán-Montaño et al. 2017), *G. cuvier* (Bornatowski et al. 2014a; Dicken et al. 2017), *I. paucus* (assuming a diet similar to *I. oxyrhinchus*; Groeneveld et al. 2014) and *C. carcharias* (Hussey et al. 2012a). Increased importance of elasmobranch prey (higher index of relative importance, %IRI) with increase body size is observed for *G. cuvier* (Dicken et al. 2017), *C. taurus* (Smale 2005) and for *C. leucas* (Daly et al. 2013). For *I. oxyrhinchus*, a ‘proxy’ for *I. paucus*, teleost fish occurred in 84% (%F in number of stomachs) in offshore captures of *I. oxyrhinchus*, whereas coastal captures showed elasmobranchs occurred in 63.5% (%F), including the consumption of multiple species of *Carcharhinus* (Groeneveld et al. 2014). For *C. carcharias,* elasmobranch prey is particularly important (higher %IRI) for smaller size classes (< 185 cm PCL, pre caudal length) but still predates substantial amounts of sharks and elasmobranchs throughout its ontogeny, although being less important than marine mammals prey for larger individuals (Hussey et al. 2012b). Furthermore, *C. carcharias* and *G. cuvier* are known to predate on individuals of *C. taurus* (Hussey et al. 2012b; Dicken et al. 2017).

Furthermore, species diverse food webs would prevent certain prey populations to be depleted, as they tend to be characterized by weaker or diffuse interactions (Montoya et al. 2006; Heithaus 2008), higher chances of trophic redundancy and populations of predators resilient to decline (lower NND, Figure 2; Heithaus 2008). This community higher trophic redundancy would suggest these shark species are co-occurring, leading to a state of ‘stable resource use’. Hence, we hypothesize that this multi-predator food web would be 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.

Further evidence to corroborate this hypothesis is the presence of isotopic niche overlap between similar trophic position species with similar diet components, such as *Carcharhinus* group, *C. brachyurus* and the generalist *C. leucas* (Car-CB 24.7%; CB-Car 10.6%; CL-Car 24.2%; Car-CL 84%; CL-CB 28.4%; CB-CL 42.2%; Table 2). Although *C. leucas* feeds sometimes at higher trophic levels, they are expected to be consumers of multiple trophic levels (e.g. high amplitude of TP; Hussey et al. 2015). These species would indeed share the majority of their prey base, mainly composed of teleost fish (e.g. Ellis and Musick 2007; Lucifora et al. 2008; Bornatowski et al. 2014a; Estupiñán-Montaño et al. 2017). Likewise, apex predators as *C. taurus* and *C. carcharias* (Cortés 1999; Hussey et al. 2015) showed niche overlap (CT-CC 14%; CC-CT 26.1% Table 2). Besides high consumption of teleost prey, these species are competitors for elasmobranch prey (Smale 2005; Lucifora et al. 2009; Hussey et al. 2012b).

High niche overlap between oceanic and high trophic level species as *I. paucus* and the migratory *G. cuvier* with oceanic habits (Compagno 1988; IP-GC 37.3, GC-IP 61.3; Table 2) are expected for sharing prey from oceanic environments, mainly teleost fish (Groeneveld et al. 2014; Estupiñán-Montaño et al. 2017). However, this overlap could be due to the limited carbon sources in open ocean systems, resulting in homogeneous $\delta^{13}C$ values (Kiszka et al. 2015). Furthermore, *G. cuvier* is a generalist consumer (Bornatowski et al. 2014a; Dicken et al. 2017) thus niche overlap could be expected with several shark species within this study. The lack of niche overlap for *G. cuvier* with apex predators such as *C. taurus* and *C. carcharias* should be due their increasing foraging on prey that have typically lower $\delta^{15}N$ values, such as turtles and some marine mammals, resulting in an average low $\delta^{15}N$ (Dicken et al. 2017), a pattern also found by Shiffman et al. (2019). Therefore, even predating high trophic level prey and sharing resources with other sharks, $\delta^{15}N$ values would be skewed due to generalist habits. This was further corroborated by the sample of modern *G. cuvier* ($\delta^{15}N$ = 11.9‰), with a recorded 345 cm TL (Supplementary Table 1), hence capable of predating high trophic level prey.

The overlap among different TP species, like *C. carcharias* and *C. brachyurus* (Hussey et al. 2015; CC-CB 84%; CB-CC 33.8%; Table 2) would suggest *C. carcharias* individuals were between a specific size range (185-284 cm PCL), where the relative importance of teleost fish is higher (Hussey et al. 2012b), hence sharing prey items with *C. brachyurus*, a ichityofagous species (Lucifora et al. 2009). This is corroborated with our mean size estimates for *C. carcharias* (262.9 cm), and by the single sample of modern *C. carcharias*, which had a estimated size of 300 – 350 cm TL (Supplementary Table 1), showing a higher relative trophic position then archaeological species *C. carcharias*.

Higher isotopic niche overlap among *N. brevirostris* and *I. paucus* (98.2%), *C. leucas* and *I. paucus* (90%), *Carcharhinus* and *I. paucus* (92.8%) in part is probably an artifact due to a combination of small sample size of *I. paucus* (N = 4) with the sporadic nature of *Isurus* genus in the coastal areas (Compagno 1984; Compagno et al. 2008; Table 2). Which consequently favored the broad core isotopic niche area observed, encompassing many species in the bi-plot. However, when using coastal habitats, *I. paucus* (e.g. δ^{13}C -10.8‰, -10.6‰) could be temporarily overlapping its niche with possible more direct competitors for teleost fish and elasmobranch prey (e.g. Groeneveld et al. 2014). Although lower overlaps with typical elasmobranch consumers suggest this species was feeding mainly in teleost prey (IP-CT 1.4%; IP-CC 1.6%; Table 2). This suggests that patterns of resource consumption may differ for species in different areas, and it is further corroborated by Shiffman et al. (2019) who found that patterns of resource use differ for the same shark species even at similar and nearby habitats, denoting trophic plasticity. Further niche overlap is observed with generalists *C. leucas* (IP-CL 47%) and *G. cuvier*, as expected, and other ichthyophagous sharks of the relatively same trophic level (Hussey et al. 2015), e.g. *C. brachyurus* (IP-CB 15.1%; CB-IP 43%) and *Carcharhinus* (IP-Car 13.9%).

In agreement with a higher degree of niche overlap, NND metric shows that species were more closely distributed in the archaeological community (Figure 2), suggesting higher trophic redundancy (Layman et al. 2007; Jabot et al. 2017), due to the presence of diverse predators with similar foraging strategies and per stable resource use. The opposite pattern was therefore observed in the modern community, lower overlap was accompanied of higher dispersal of the species in the isotopic area, as they increased their Euclidian distance to the nearest neighbor and to the food web centroid (higher NND and CD respectively), suggesting this community reduced its trophic redundancy and diversified their trophic niche (Layman et al. 2007; Jabot et al. 2017; Figure 2).

Some of this may be due to the data and different sampling locations. Isotopic niche overlap among modern *I. oxyrhinchus* and *Carcharhinus* stayed relatively similar throughout time (mod IO-Car 38.2%; arch IP-

Car 16.1%; Table 2). This was mainly because modern *I. oxyrhinchus* niche (or SEAc) decreased, as this species were captured offshore, whereas $\delta^{13}C$ values of archaeological *I. paucus* individuals suggests they foraged inshore and offshore (Figure 2), thus favoring a larger core isotopic niche area. This coincided with a concomitantly modern *Carcharhinus* niche increase towards depleted $\delta^{13}C$ environments while and archaeological *Carcharhinus* was mainly restricted to coastal waters, resulting in a larger ellipse. We are unsure as to the commonness of occurrence of *I. paucus* foraging near the coast in pre-colonial food webs.

Mostly of modern *Carcharhinus* species inside this group are *C. obscurus* (N = 4), with one *C. limbatus* and one *C. plumbeus*. *C. obscurus* have a coastal and pelagic distribution, occurring offshore and inshore (Smale 1991) and is capable of substantial movements (Hussey et al. 2009). Besides teleost fish, a substantial prey item for both *I. oxyrhinchus* and *C. obscurus* are cephalopods (e.g. Simpfendorfer et al. 2001; Preti et al. 2012). This suggests these species co-occur and overlap their niches in South Brazil. Individuals of *C. obscurus* presented both enriched (-10.2‰, -10.3‰) and depleted $\delta^{13}C$ values (-12.4‰, -13.2‰) suggesting multiple habitat use. Furthermore, *C. limbatus* and *C. plumbeus* were responsible for two depleted $\delta^{13}C$ values (-12.1‰ and -13.5‰ respectively), increasing the niche overlap towards *I. oxyrhinchus*. *C.*

plumbeus is considered a coastal shark, but may venture further offshore, particularly associated to topographic structures (Grubbs et al. 2007). It may consume considerable amounts of cephalopods, although teleost fish and crustaceans are more important (e.g. McElroy et al. 2006). *C. limbatus* mainly occur in coastal and intertidal areas (Bornatowski 2008; Burgess and Branstetter 2009), and rarely oceanic in winters in Brazil (Gadig 2001) and mainly preying in pelagic and epibenthic teleost fish (Bethea 2004). The *Carcharhinus* deviance from expected enriched $\delta^{13}C$ values for typical coastal species, likewise for some individuals of *C. taurus* (Figure 2), would suggest that the relative importance of oceanic prey for these *Carcharhinus* has increased, resulting in the overlap observed. This is entirely speculative, as lower sample size could be masking general population trends, and baselines for $\delta^{13}C$ may have shifted. However, we suggest that based on mean $\delta^{13}C$ for *C. taurus* in both communities (Table 2), the baseline for coastal areas has remained relatively constant throughout the time of this study.

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. The increase in trophic position of *C. taurus* contradicts the idea that overfishing is simplifying marine food webs by decreasing the average trophic level of consumers and prey populations. Previous trophic reconstructions studies from archaeological datasets in South America suggested that intensively exploited modern fur seals and sea lions increased their own 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. 2018). 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 (MMA 2004). 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), and competition release may have benefited *C. taurus,* enabling the increase in high trophic level prey in its diet. Furthermore, populations of marine predators under predation rates could have constrained growth rates, due to direct and indirect effects of predation (Heithaus 2008). Lower population growth rates would indirectly reduce trophic level, as it increases with body size (Jennings 2005). This could be the case for the archaeological community, whereas in the present, *C. taurus* juveniles and adults may be not under the same amount of predation risk. Interspecific competition release may also be playing a role in the trophic level increase. In the absence of similar trophic position sharks, *C. taurus* could occupy new areas in which it would originally be allopatric, emerging as apex predators (*e. g*. Hammerschlag et al. 2019), hence being able to explore uncontested high trophic level prey.

Although our study has found no support for the evidence of an overall change in the isotopic niche areas for the shark species between communities (SEAc, SEAb and TA), individually, modern *C. taurus* and *Carcharhinus* group have expanded their niche areas in the present (respectively: SEAc from 2.22 to 4.87; and SEAc from 1.28 to 8.84). Niche hypothesis predicts that a population will exhibit a contracted niche breadth under the influence of a 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). Thus, this could corroborate our hypothesis that intraspecific competition release is causing the observed increase in trophic level for *C. taurus*.

At the very least, this study shows a possible consequence of anthropic actions affecting diet and ecology of surviving individuals of populations that would be below carrying capacity, as sharks have low population growth rates that renders them high sensitive to fishing mortality (Dulvy and Forrest 2010; Ferretti et al. 2010). However, there is mounting evidence that anthropic impacts causes longer food webs through hunting and fisheries, leading to intraspecific release for some species which leads to higher NR ranges (Drago et al. 2009; Saporiti et al. 2014; Zenteno et al. 2015; Bas et al. 2018). Furthermore, unrelated or not to anthropic impacts, modern communities might be diversifying their patterns of resource use, as other studies also have shown higher CD and NND for modern food webs (Saporiti et al. 2014; Bas et al. 2019). Modern *Carcharhinus* and *C. taurus* showed a shift tawards 13C-depleted $\delta^{13}C$ values (Figure 2; Table 1), further reinforcing a trend in niche and feeding patterns diversification.

We understand our study is not free of many caveats that comes from using stable isotopes inferences (Hussey et al. 2012a; Shiffman et al. 2012). Turnover rates for teeth only provide inferred average resource use, thus the pattern of niche overlap for archaeological community could be representative of temporal niche partitioning over the same resources. For some highly mobile shark species that forage in multiple habitats (e.g. *C. carcharias*, *C. obscurus*) the evaluation of niche may become complicated when there are multiple contrasting paths between either baseline primary producers or secondary consumers and the target organisms under study. 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 (Simon-Pierre, in press) even catching typically oceanic species near the coast, as shown for *I. paucus* individuals with enriched carbon values (Figure 2). Furthermore, high niche overlap among sharks within modern food webs 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 at play in these examples, this corroborates the plausibility of our findings.

Changes in isotopic baselines may hinder comparisons between time-separated communities, as shifts in trophic niche. Although some inferences might be based on differences among modern and archaeological community, we suggest that baselines for ^{13}C stayed constant throughout time, based on *C. taurus* $\delta^{13}C$ values. Furthermore, food web topology analysis are not dependent on isotopic baselines.

Moreover, the calculation of a trophic level using a single discrimination factor obscures much of the real complexity behind trophic interactions (Zeichner et al. 2016), whereas scaled discrimination factors may be more accurate (Hussey et al. 2014), studies could benefit from species-specific discrimination factors in the future. 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.

Habitat use for rare species

The presence at the archaeological study site of the lemon shark *N. brevirostris* oceanic-pelagic species as the great white shark, *C. carcharias* and the longfin mako *I. paucus* is intriguing, as these species are rarely captured nowadays (Gadig and Rosa 1996; Amorim et al. 1998). *N. brevirostris* current range does not include Southern Brazil (Soto 2001) and *I. paucus* is rarely littoraneous (Compagno 2008). Nevertheless *C. carcharias* teeth and vertebrae are quite frequent in the Southeast Brazil archaeological record (present in eight out of thirteen sites, Lopes et al. 2016). Our results indicate a significant difference between $\delta^{13}C$ values between *C. carcharias* and *C. taurus* and also between *G. cuvier* and *C. taurus* suggesting different feeding areas, as *C. taurus* is a typical littoral species (Compagno 1984). Therefore, *C. carcharias* and *G. cuvier* presented a tendency of feeding in phytoplankton carbon-based offshore environments, as it present typical depleted $\delta^{13}C$ values (Fry and Sherr 1989; Hobson et al. 1994; France 1995; France and Peters 1997). Depleted values of $\delta^{13}C$ in the tissues of cosmopolitan species that undergo large scale oceanic migrations (e.g. Bonfil et al. 2005; Heithaus et al. 2007; Jorgensen et al. 2012; Holmes et al. 2014) are predictable, suggesting feeding in offshore or pelagic oceanic regions.

However, the majority of individuals of *C. carcharias* showed intermediate $\delta^{13}C$ values in comparison to more 13C-depleted $\delta^{13}C$ values of some individuals of *G. cuvier*, *I. paucus* and enriched $\delta^{13}C$ values of *C. taurus* (Figure 2; Table 1). This suggests a more 'deep' offshore foraging for some individuals of *G. cuvier* and *I. paucus*, whereas *C. carcharias* individuals possibly forage in both offshore pelagic and inshore food web, causing a long term representation of variable feeding strategies in $\delta^{13}C$ values (Hussey et al. 2011). Foraging in both inshore-offshore may cause mixed $\delta^{13}C$ values, as marine environments present relative gradients of decreasing influence from macrophytes and other ^{13}C

enriched carbon sources (Hill et al. 2006). *C. carcharias* are typically nomadic predators, staying short periods of time a given site, and explore a broad range prey bases (Compagno 1984; Estrada et al. 2006). Smaller individuals of *C. carcharias* (< 300 cm) are generally restrict to continental seas, predating teleost fish, elasmobranchs, birds, dolphins and marine reptiles, before a diet shift to marine mammals (Compagno 1984; Hussey et al. 2012b). Our results are in agreement with this, given the regressed size data for *C. carcharias* of this study (mean 262.9 cm), individuals might not have undergone extensive oceanic migrations. Hence, their relative more enriched δ^{13}C values in comparison to *G. cuvier* and *I. paucus*, suggest a partial coastal foraging. Further niche overlap with coastal species (e.g. *C. taurus*; Figure 2, Table 2) and one *C. carcharias* individual with an enriched value of δ^{13}C corroborate this (-10.8‰; Figure 3).

Adult individuals of *C. carcharias* are known to aggregate seasonally near pinniped rookeries, and it is considered one their main food items (Long et al. 1996; Brown et al. 2010). Archaeological Holocene records from Uruguay, Argentina and Southern Brazil suggest pinnipeds were abundant in those areas (Inda et al. 2006; Castilho and Simões-Lopes 2008; Bayón and Politis 2014). Currently, modern colonies are present in Uruguay (Franco-Trecu et al. 2019) and were once extensively abundant in Argentina (Rodrigues and Bastida 1998). Modern individuals of pinnipeds still occur at South Brazil, mainly at winter and possibly migrating from larger breeding colonies from Uruguay and Argentina (Silva 2004; Oliveira et al. 2010). Similarly, we suggest pre-colonial pinnipeds could have migrated extensively from breeding colonies to the Brazilian coast, and possibly subsiding small adult populations of *C. carcharias* in Southern Brazil. Alternatively, smaller individuals, as the ones in this study, might have migrated to the area, where pinnipeds colonies were vast. Besides, the co-occurrence in archaeological records of *C. carcharias* and pinnipeds species throughout South America (Cione and Barla 2008) and the southern coast of Brazil, including the presence of pinnipeds in the same archaeological site as this study (Castilho and Simões-Lopes 2001, 2008), corroborates the suggestion of adult populations in Southern Brazil. Furthermore, Lopes et al. (2016) found strong evidence of *C. carcharias* neonates at the Southeast Brazil archaeological sites, suggesting nursery areas at the region for this philopatric species (Chapman et al. 2015). Although, neonates may be related to older archaeological sites then Rio do Meio, therefore different environmental conditions were at play on shaping *C. carcharias* distributions (Bertucci et al. 2018). There was no evidence for neonates at Rio do Meio site, however the Holocene environmental conditions from the sites current datation and the latitude of Rio do Meio site encompasses the optimal niche range for this species and its nursery grounds (Francis 1997; Compagno 1984; Domeier 2012). Thus, the overall evidence suggests that *C. carcharias* were once resident to Southern Brazil, as smaller individuals were inserted into the local food webs (Figure 2), and its relative disappearance from South western Atlantic may be related to historical exploitation of pinnipeds populations that once supported their adult populations (Cione and Barla 2008).

Very little is known about the biology of *I. paucus* (Rigby et al. 2019). Our study showed its δ^{13}C values suggested foraging at both offshore (-14.4‰) and inshore (-10.6‰) environments. In fact, all archaeological species considered oceanic in our study showed typical coastal enriched δ^{13}C values besides δ^{13}C depleted values. Many pelagic and oceanic species use coastal and continental shelf waters throughout ontogeny to perform many biological functions such as feeding, breeding, give birth and other activities (Compagno 1984; Compagno et al. 2008). Groeneveld et al. (2014) observed a large proportion of mature, sexually active and pregnant females of *I. oxyrhinchus,* the closest relative to *I. paucus,* at South Africa coastal waters. The author hypothesizes this species moves to coastal waters to give birth. Furthermore, no δ^{13}C enriched values were found in the teeth of modern *I. oxyrhinchus,* as they were captured at a distance of 185 to 330 km from the coast (this study). *I. paucus* are known to be captured near the coast in areas of narrow continental shelves (Camhi et al. 2008; e.g. Martínez-Ortiz et al. 2015), as the Florianópolis-Mostardas sector (Mahiques et al. 2010). This suggests a coastal capture location for *I. paucus* at this area in Late Holocene, and further reinforces the possibility of sporadic costal area use for a rare species.

N. brevirostris was present throughout the Holocene in multiple southern Brazil archaeological sites (this study; Cardoso 2011). Extending its southernmost distribution in the late Holocene from the State of Rio de Janeiro (Lopes et al. 2016; Mendes et al. 2018) to the state of Santa Catarina. However, it is an unusual distribution, considering the biological traits and modern distribution for this species. *N. brevoristris* is a tropical and subtropical species, inhabitant of coastal and inshore of continental and insular shelfs, and may venture into multiple habitats and ocean waters (Compagno 2001). Currently in western Atlantic, their distribution range between New Jersey (U.S.A; Latitude 39-40° N) to southern Brazil, Rio de Janeiro state (22° S), including the oceanic islands of Atol das Rocas (Freitas et al. 2009) and Fernando de Noronha (Garla et al. 2009; Soto 2001). This species has a marked preference for warmer waters, as periods of parturition for this species are influenced by water temperatures (Tavares et al. 2016) mainly occurring at warmer months of

April and July in the North Western Atlantic (Gruber and Stout 1983) and between January and April at the South Western Atlantic (Freitas et al. 2006; Oliveira et al. 2011). Furthermore, juveniles have shown preference for warmer waters, greater as 30 °C (Morrissey and Gruber 1993). The currently southernmost distribution in the South Atlantic Ocean for nurseries are recognized to be Atol das Rocas and Fernando de Noronha (3.8° to 3° S respectively; Feldheim et al. 2001; Freitas et al. 2009; Garla et al. 2009). This fact along with *N. brevoristris* current distributional range in Brazil would suggest that the establishment of populations as far as to Santa Catarina state (27.5° S) would be unlikely. However, seasonality effects on the Southern Continental Shelf (Pereira et al. 2009) might have historically facilitated periodical migrations of this species towards southern waters

We hypothesize that the presence of *N. brevoristris* in South Brazil Holocene may be due to periods of expansions and contractions in optimal niche ranges due to natural climate change. Periodical increases in the strength of the warm Brazil Current (BC) correlates with increases in mean sea surface temperature (SST) with a periodicity of about 730 years (Chiessi et al. 2014). Core sediments in a latitude of 32° S showed that increases in BC and SST peaked around ~1100 years BP causing an increase around ~1.1 °C in mean SST (Chiessi et al. 2014), this increase stayed relatively constant for a couple of hundred years, which coincides with this study archaeological site datation (724-542 years cal.B.P). This increase in SST might have been higher for a northern latitude such as this study site at 27.5° S. Higher SST could have facilitated the establishment of nursery grounds and (or consequently) the presence of migratory adult individuals at southern latitudes then its preferred habitat.

Thus we suggest that the presence of *N. brevirostris* in late Holocene South Brazil is mainly attributed to migratory and movement patterns, that could be facilitated by increases in BC and SST further south. Furthermore, the niche overlap for this species in the archaeological community was the highest among all the species (Table 2), suggesting *N. brevirostris* could have performed feeding incursions and ‘intruding’ in food webs. The absence of evidence for some degree of niche partitioning in this species may provide clues to the possible sporadic nature of this species in South Brazil.

Concluding remarks

Even in samples dated hundreds of years old, SIA still responded well to a trophic and habitat assessment in multiple shark species using their teeth (e.g. Rowell et al. 2010; Vales et al. 2017). Patterns of $\delta^{13}C$ and $\delta^{15}N$

corresponded well to the expected trophic position (Cortés 1999; Hussey et al. 2015) and habitat use for the species in this study.

Our study adds to the multiple trophic reconstructions of food webs throughout South America 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 higher NR ranges (e.g. Saporiti et al. 2014; Bas et al. 2019). 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 in modern communities needs attention. Populations of sharks and many others taxa are being deeply negatively affected by anthropic impacts (e.g Ferretti et al. 2010; Barreto et al. 2017; Roff et al. 2018). Until no further action is taken to prevent the disappearance of many important species, food webs are becoming gradually poorer as to what they once were.

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CONSIDERAÇÕES FINAIS

Este é primeiro estudo a usar uma abordagem de análises de isótopos estáveis em remanescentes arqueológicos de tubarões, para a reconstrução de teias tróficas e estabelecer inferências ecológicas. Para tanto, teve-se que adaptar metodologias de tratamento e extração de colágeno baseado em outros elementos faunísticos como vértebras. Apesar de desgaste tafonômico nos dentes arqueológicos, AIE demonstrou sucesso em obter valores ‘ecologicamente coerentes’ de nitrogênio e carbono pesado para tubarões, além de taxas de C:N indicativas de colágeno preservado.

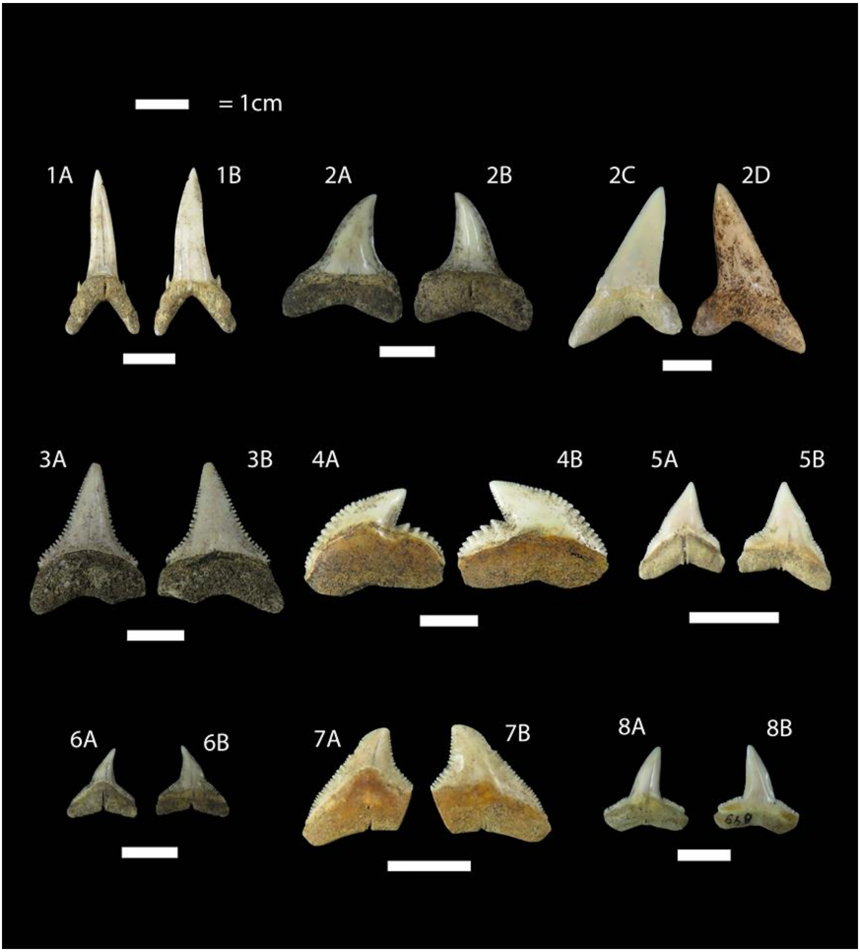
Discutimos padrões de alta sobreposição de nicho presente entre espécies de tubarão de teias tróficas antigas. A partir disso, apresentamos uma hipótese para explicar tal padrão que não é previsto por trabalhos clássicos de nicho e coexistência. Sugerimos que o controle top-down e predação intraguilda podem estar favorecendo o uso estável de recursos alimentares através do mantimento das populações de predadores abaixo de sua capacidade limite, liberando presas de pressões intensas de predação, e possivelmente gerando uma teia trófica com relativa estabilidade. Além disso, sugerimos uma aparente partição de nicho em espécies modernas de *C. taurus* com outras espécies, devido principalmente à elevação de sua posição trófica.

Demonstramos que a natureza das teias tróficas para o Sul do Brasil, sob a ótica de predadores de topo como tubarões, não se mantém constante através do tempo. Indicativos de impactos antrópicos foram observados, como o aumento do nível trófico de *C. taurus*, sugerindo como causa um desequilíbrio populacional ou redução na abundancia de seus competidores diretos, possivelmente devido à sobrepesca. Essa espécie encontra-se criticamente ameaçada no Brasil, mas ainda persiste, indicado por poucos avistamentos e capturas. Outros indicadores de impactos antrópicos são o desmantelamento da observada redundância trófica presente nas teias tróficas antigas, para uma estrutura em teias tróficas atual que sugere uma maior diversificação de estratégias alimentares para espécies remanescentes.

Discutimos a presença de espécies inusitadas ou raras para o Sul do Brasil, como o tropical *N. brevirostris*, o migratório *C. carcharias* e o raro *I. paucus*. Ao que tudo indica, o habitat (clima e presença de presas seletas, inclusive no sítio de estudo) seria favorável para sustentar populações pequenas de *C. carcharias*. Temos evidência de uma informação há muito especulada e prevista, como uso de hábitat costeiro por *I. paucus*, assim como fora observado em seu relativo, *I. oxyrhinchus*.

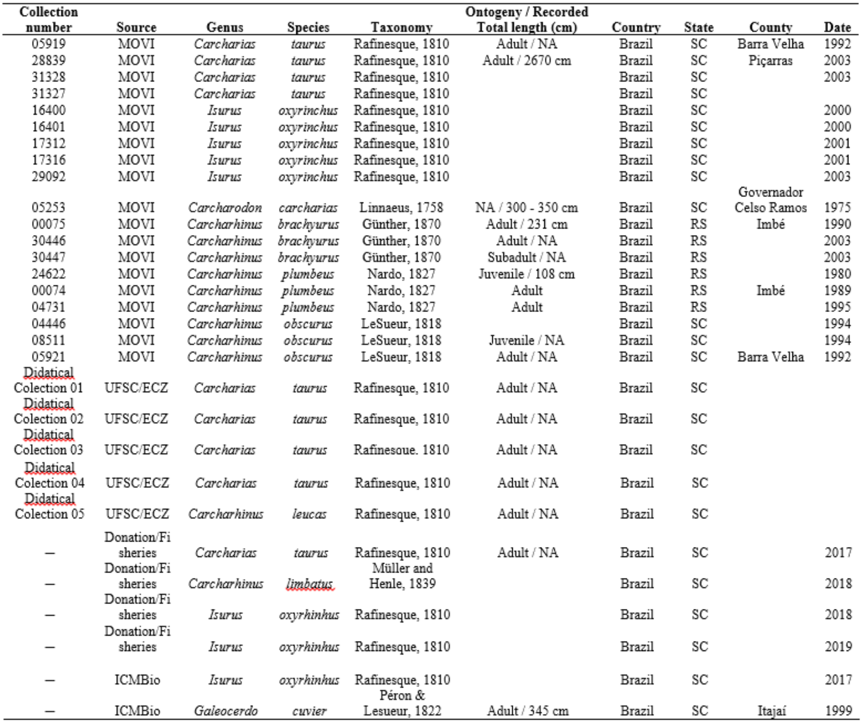
Por fim, sugerimos que a presença de uma espécie tipicamente tropical como o *N. brevirostris* seria facilitada por períodos de mudanças climáticas naturais, devido às alterações na Corrente Brasileira, que traz águas dos trópicos para o subtropical, aumentando a temperatura da superfície marinha. Isso poderia causar uma facilitação de movimentos tipicamente costeiros, em períodos dos quais a espécie estaria se inserindo em teias tróficas locais, resultando em alta sobreposição de nicho.

Futuros estudos poderiam se beneficiar da metodologia aqui empregada para analisar restos faunísticos de tubarões ou fauna marinha, realizando reconstruções tróficas. Informações de base são faltantes em ambientes marinhos. Informações de topologia de rede trófica e de nitrogênio e carbono pesado em um ambiente pouco perturbado podem servir parâmetros basais (baselines) para estudos comparativos. Estamos apenas começando a entender como estavam estruturadas as teias tróficas passadas, através de ‘fotografias’ obtidas através de análises de isótopos estáveis.



Supplementary Figure 1. 1) *Carcharias taurus*; 2AB) *Isurus paucus,* lateral tooth; 2 CD) *Isurus paucus,* anterior tooth; 3) *Carcharodon carcharias*; 4) *Galeocerdo cuvier*; 5)*Carcharhinus plumbeus*; 6)*Carcharhinus brachyurus*; 7) *Carcharhinus leucas*; 8) *Negaprion brevirostris*

Supplementary Table 1. Source, collection number, taxonomy and ontogeny of modern specimens of sharks at South Brazil. Source denotes the obtained location (MOVI – Univali Oceanographic Museum; UFSC/ECZ Federal University of Santa Catarina / Departament of Ecology and Zoology; ICMBio – Chico Mendes Institute for Conservation of Biodiversity). County denotes the general coastal urban area of capture. Date denotes the year of capture from the wild. NA: Not available.



Collection number	Source	Genus	Species	Taxonomy	Ontogeny / Recorded Total length (cm)	Country	State	County	Date
05919	MOVI	*Carcharias*	*taurus*	Rafinesque, 1810	Adult / NA	Brazil	SC	Barra Velha	1992
28839	MOVI	*Carcharias*	*taurus*	Rafinesque, 1810	Adult / 2670 cm	Brazil	SC	Piçarras	2003
31328	MOVI	*Carcharias*	*taurus*	Rafinesque, 1810		Brazil	SC		2003
31327	MOVI	*Carcharias*	*taurus*	Rafinesque, 1810		Brazil	SC		
16400	MOVI	*Isurus*	*oxyrinchus*	Rafinesque, 1810		Brazil	SC		2000
16401	MOVI	*Isurus*	*oxyrinchus*	Rafinesque, 1810		Brazil	SC		2000
17312	MOVI	*Isurus*	*oxyrinchus*	Rafinesque, 1810		Brazil	SC		2001
17316	MOVI	*Isurus*	*oxyrinchus*	Rafinesque, 1810		Brazil	SC		2001
29092	MOVI	*Isurus*	*oxyrinchus*	Rafinesque, 1810		Brazil	SC		2003
05253	MOVI	*Carcharodon*	*carcharias*	Linnaeus, 1758	NA / 300 - 350 cm	Brazil	SC	Governador Celso Ramos	1975
00075	MOVI	*Carcharhinus*	*brachyurus*	Günther, 1870	Adult / 231 cm	Brazil	RS	Imbé	1990
30446	MOVI	*Carcharhinus*	*brachyurus*	Günther, 1870	Adult / NA	Brazil	RS		2003
30447	MOVI	*Carcharhinus*	*brachyurus*	Günther, 1870	Subadult / NA	Brazil	RS		2003
24622	MOVI	*Carcharhinus*	*plumbeus*	Nardo, 1827	Juvenile / 108 cm	Brazil	RS		1980
00074	MOVI	*Carcharhinus*	*plumbeus*	Nardo, 1827	Adult	Brazil	RS	Imbé	1989
04731	MOVI	*Carcharhinus*	*plumbeus*	Nardo, 1827	Adult	Brazil	RS		1995
04446	MOVI	*Carcharhinus*	*obscurus*	LeSueur, 1818		Brazil	SC		1994
08511	MOVI	*Carcharhinus*	*obscurus*	LeSueur, 1818	Juvenile / NA	Brazil	SC		1994
05921	MOVI	*Carcharhinus*	*obscurus*	LeSueur, 1818	Adult / NA	Brazil	SC	Barra Velha	1992
Didatical Colection 01	UFSC/ECZ	*Carcharias*	*taurus*	Rafinesque, 1810	Adult / NA	Brazil	SC		
Didatical Colection 02	UFSC/ECZ	*Carcharias*	*taurus*	Rafinesque, 1810	Adult / NA	Brazil	SC		
Didatical Colection 03	UFSC/ECZ	*Carcharias*	*taurus*	Rafinesque, 1810	Adult / NA	Brazil	SC		
Didatical Colection 04	UFSC/ECZ	*Carcharias*	*taurus*	Rafinesque, 1810	Adult / NA	Brazil	SC		
Didatical Colection 05	UFSC/ECZ	*Carcharhinus*	*leucas*	Rafinesque, 1810	Adult / NA	Brazil	SC		
–	Donation/Fisheries	*Carcharias*	*taurus*	Rafinesque, 1810	Adult / NA	Brazil	SC		2017
–	Donation/Fisheries	*Carcharhinus*	*limbatus*	Müller and Henle, 1839		Brazil	SC		2018
–	Donation/Fisheries	*Isurus*	*oxyrhinhus*	Rafinesque, 1810		Brazil	SC		2018
–	Donation/Fisheries	*Isurus*	*oxyrhinhus*	Rafinesque, 1810		Brazil	SC		2019
–	ICMBio	*Isurus*	*oxyrhinhus*	Rafinesque, 1810		Brazil	SC		2017
–	ICMBio	*Galeocerdo*	*cuvier*	Péron & Lesueur, 1822	Adult / 345 cm	Brazil	SC	Itajaí	1999