UNIVERSIDADE FEDERAL DE SANTA MARIA
CENTRO DE CIÊNCIAS NATURAIS E EXATAS
PROGRAMA DE PÓS-GRADUAÇÃO EM BIODIVERSIDADE ANIMAL

Bruna Ceretta Ferreira

PESCANDO FUNÇÕES: ATRIBUTOS FUNCIONAIS EXPLORADOS PELA PESCA ATRAVÉS DO TEMPO

Santa Maria, RS
2022

Bruna Ceretta Ferreira

PESCANDO FUNÇÕES: ATRIBUTOS FUNCIONAIS EXPLORADOS PELA PESCA ATRAVÉS DO TEMPO

Trabalho de Dissertação apresentado ao Programa de Pós-Graduação em Biodiversidade Animal, da Universidade Federal de Santa Maria (UFSM, RS), como requisito parcial para a obtenção do título de Mestre em Ciências Biológicas – Área Biodiversidade Animal.

Orientadora: Profª. Drª. Mariana Bender Gomes

Santa Maria, RS
2022

Declaro, BRUNA CERETTA FERREIRA, para os devidos fins e sob as penas da lei, que a pesquisa constante neste trabalho de conclusão de curso (Dissertação) foi por mim elaborada e que as informações necessárias objeto de consulta em literatura e outras fontes estão devidamente referenciadas. Declaro, ainda, que este trabalho ou parte dele não foi apresentado anteriormente para obtenção de qualquer outro grau acadêmico, estando ciente de que a inveracidade da presente declaração poderá resultar na anulação da titulação pela Universidade, entre outras consequências legais.

Bruna Ceretta Ferreira

PESCANDO FUNÇÕES: ATRIBUTOS FUNCIONAIS EXPLORADOS PELA PESCA ATRAVÉS DO TEMPO

> Trabalho de Dissertação apresentado ao Programa de Pós-Graduação em Biodiversidade Animal, da Universidade Federal de Santa Maria (UFSM, RS), como requisito parcial para a obtenção do título de Mestre em Ciências Biológicas – Área Biodiversidade Animal.

Aprovada em 21 de outubro de 2022.

_____
Mariana Bender Gomes, Drª. (UFSM)
(Orientadora)

_____
Dannieli Firme Herbst, Drª. (UAB Barcelona) – Videoconferência

_____
Marcos Bergmann Carlucci, Dr. (UFPR) - Videoconferência

Santa Maria, RS
2022

AGRADECIMENTOS

Em março de 2020 iniciei meus estudos junto ao PPG de Biodiversidade Animal, uma semana depois tudo parou devido à pandemia. Meses antes, quando descobri que seria aluna de mestrado, nunca imaginei todo o cenário que estaria por vir. Realizei praticamente todo o curso em home office, e assim como muitas pessoas, não foi um período fácil, não só por tudo que estávamos acompanhando no Brasil e no mundo, mas por termos que cuidar de nós mesmos e tentar seguir com nossas atividades habituais e responsabilidades. Desta forma agradeço e dedico este trabalho a todas as pessoas que serão aqui mencionadas. Obrigada por estarem ao meu lado durante esses dois anos e meio e por contribuírem de alguma forma para que tudo se concretizasse.

À professora Mariana Bender, agradeço por todo o apoio, confiança, ensinamentos e conversas. Você é um exemplo de pesquisadora, professora e orientadora.

À CAPES pela concessão da bolsa de mestrado.

Ao Laboratório de Ecologia e Conservação Marinha (Marine Lab) pela amizade, parceria e trocas de conhecimento. Orgulho-me de dizer que somos um grupo composto majoritariamente por mulheres cientistas que amam o mar. Aprendi com vocês que ciência não se faz sozinha e que juntas fazemos muito mais pelo avanço da ciência do que competindo. Quero agradecer principalmente às pessoas que me ajudaram diretamente, seja tirando dúvidas sobre análises e como mexer no R, lendo meu texto e até desabafando sobre a vida de pós-graduação: Hanna, André, Rafaela, Luiza, Malu, Melina e Carine.

Ao professor Dr. Cristian Dambrós e ao Dr. Vinicius Giglio pelo acompanhamento durante os seminários da pós-graduação. Suas contribuições foram fundamentais para a construção do trabalho.

À toda minha família, principalmente meus pais Márcia e Onoir, e meus irmãos Dandara e Igor. Foi graças ao esforço de vocês que consegui chegar até aqui. Obrigada por serem meu suporte e por acreditarem em mim. Também à minha maior apoiadora, a avó Eloísa Ceretta, vou te amar pra sempre, até mesmo quando você começar a esquecer meu nome.

E por fim agradecer a todas as pessoas que compartilham a vida comigo, tornando meus dias mais leves e alegres: Juliana, Alex, Natália, Michele, Rafaela, Fernanda e Taís.

RESUMO

PESCANDO FUNÇÕES: ATRIBUTOS FUNCIONAIS EXPLORADOS PELA PESCA ATRAVÉS DO TEMPO

AUTORA: Bruna Ceretta Ferreira
ORIENTADORA: Mariana Bender Gomes

À medida que as civilizações humanas se desenvolveram e investiram em tecnologia, a pesca tornou-se uma das maiores ameaças aos ecossistemas marinhos, impactando diretamente nas funções ecológicas exercidas pelos seres vivos. No entanto, a exploração de atributos funcionais ao longo do tempo nunca foi avaliada. Aqui investigamos a diversidade funcional de vertebrados marinhos explorados na costa sul-sudeste brasileira em três períodos distintos: Sambaquis (8.720 – 230 anos AP), Colonial (1500 – 1966) e Atual (1967 – 2015). Uma análise de espaços funcionais juntamente com estimativas de densidade de Kernel revelou que todo o espaço de atributos funcionais foi explorado ao longo do tempo. Identificamos 423 táxons pescados, dos quais 56 foram explorados em todos os períodos. Ao longo do tempo, a pesca tem sido funcionalmente seletiva, visando táxons com médio e grande tamanho corporal, especialistas de habitat, invertívoros e macrocarnívoros, hábitos bentopelágicos e pelágicos. Atualmente, a tecnologia de pesca tem impulsionado a captura de novos atributos longe da costa, como táxons de pequeno tamanho corporal, sedentários, bentônicos, solitários e planctívoros. A exploração de todo o espaço funcional mostra que a pesca é uma atividade insustentável ao longo dos séculos, podendo ser inviável no futuro por dois motivos: esgotamento dos estoques e enfraquecimento do funcionamento dos ecossistemas devido à perda de espécies e seus atributos.

Palavras-chave: Abordagem baseada em atributos. Conservação marinha. Diversidade funcional. Ecologia histórica. Exploração a longo prazo. Fauna marinha.

ABSTRACT

FISHING FUNCTIONS: TRAIT EXPLOITATION OVER TIME

AUTHOR: Bruna Ceretta Ferreira
ADVISOR: Mariana Bender Gomes

As human civilizations developed and invested in technology, fishing became one of the greatest threats to marine ecosystems, impacting the ecological functions mediated by trait species. However, the exploitation of functional traits over time have never been assessed. Here we investigated the functional spectrum of marine vertebrate taxa exploited in south-southeast Brazilian coast in three different periods: the Shellmounds (8,720 – 230 years BP), the Colonial (1500 – 1966) and the Current period (1967 – 2015). A functional trait space analysis together with kernel density estimates revealed that the full spectrum of functional traits was fished over time. We identified 423 exploited taxa, of which 56 were exploited in all periods. Over time, fisheries have been functionally selective by targeting habitat specialists, invertivorous and macrocarnivorous taxa, with medium and large body size, benthopelagic and pelagic habits. Currently, fishing technology has boosted the capture of new traits far from the coast, such as planktivorous, sedentary, benthic, solitary, and small-bodied taxa. Fishing the entire functional trait spectrum clearly shows that fishing is an activity unsustainable over the centuries, and may be unfeasible in the future for two reasons: depletion of stocks and ecosystem functioning weakened by the poverty of traits.

Keywords: Functional diversity. Historical ecology. Long-term exploitation. Marine conservation. Marine fauna. Trait-based approach.

SUMÁRIO

INTRODUÇÃO

A defaunação no Antropoceno foi documentada pela primeira vez em florestas tropicais, através de efeitos de cascata trófica devido aos impactos antrópicos em comunidades de mamíferos (DIRZO E MIRANDA, 1991). Este fenômeno foi predominantemente mais documentado em ambientes terrestres e de água doce (YOUNG et al., 2016), mais adiante, estudos foram ampliados para os ecossistemas marinhos (MCCAULEY et al., 2015). A pesca é uma das formas mais antigas de exploração humana dos recursos naturais. A primeira arte de pesca empregada foi encontrada no Congo, há aproximadamente 90.000 anos atrás, feita a partir de ossos de uma espécie extinta de bagre (YELLEN et al., 2005). À medida que as civilizações cresceram e se desenvolveram ao longo do tempo, através do aumento populacional e demanda por recursos, a pesca se expandiu e se tornou mais eficiente (JACKSON et al., 2001), representando hoje a maior causa de defaunação marinha e uma das maiores ameaças aos ecossistemas marinhos (DULVY, SADOVY e REYNOLDS, 2003; MCCAULEY et al., 2015; WORM et al., 2006).

Segundo Jackson et al. (2001), existem três períodos de impactos antrópicos nos ecossistemas marinhos. O período pré-histórico é caracterizado pela pesca oportunista e predominantemente de subsistência, com embarcações simples e limitadas à costa. O período colonial é marcado pela exploração sistemática, esgotamento dos mares costeiros, utilização de embarcações e tecnologias de pesca mais avançadas, além do início da pesca comercial, impulsionada pelo processo de colonização europeu (JACKSON et al., 2001; ERLANDSON e RICK, 2008). O período global é definido pela exploração intensa e em escala global dos recursos marinhos, tecnologia e mecanização da pesca sem precedentes, esgotamento frequente com subsequente substituição dos estoques pesqueiros e exploração de áreas distantes da costa (JACKSON et al., 2001).

A maioria das evidências sobre os impactos da pesca no ambiente marinho concentra-se nos últimos 50 anos (LOTZE & WORM, 2009), com poucas informações sobre a pesca pré-histórica e colonial. No entanto, pesquisas recentes estão começando a revelar impactos antrópicos de longo prazo nos ambientes naturais (BOIVIN e CROWTHER, 2021; EARLY-CAPISTRÁN et al., 2018; MCCLENACHAN et al., 2017), focando principalmente na composição de táxons explorados. Embora os organismos marinhos tenham sido alvo por milênios, com vários registros nos oceanos do mundo (BOURQUE, JOHNSON e STENECK, 2008; PANDOLFI et al., 2003;

RICK e ERLANDSON, 2008), o conhecimento acerca da exploração de atributos das espécies ao longo do tempo ainda é limitado. Por exemplo, registros zooarqueológicos em todo o mundo revelam a pesca precoce da megafauna marinha (mamíferos, elasmobrânquios, peixes ósseos) (RICK e ERLANDSON, 2010; LIMBURG et al., 2008; PESTLE, 2013), alguns sendo pescados até a extinção (GOBALET e JONES, 1995) e outros com suas populações severamente esgotadas e ameaçadas de extinção (LOPES et al., 2016). Também foram observadas mudanças temporais nas características da história de vida, como reduções no tamanho do corpo e declínios no nível trófico em peixes de recife, como garoupas e peixes-papagaio, devido à superexploração deste grupo (WING e WING, 2001).

Apesar de sua distância na 'Árvore da Vida', grupos taxonômicos como peixes ósseos, tubarões, raias e cetáceos compartilham características que têm efeitos diretos e indiretos na estrutura e funcionamento do ecossistema, conhecidos como atributos funcionais (TAVARES et al., 2019), que compreendem dimensões importantes da gama de estratégias e processos desempenhados pelas espécies nos ecossistemas (COOKE et al. 2019; TAVARES et al., 2019; WAECHTER et al., 2021). Atributos como tamanho do corpo e a categoria trófica influenciam no transporte e armazenamento de nutrientes e, portanto, interferem na dinâmica da cadeia alimentar nos ecossistemas marinhos (BELLWOOD et al., 2018; PIMIENTO et al., 2020; TAVARES et al., 2019).

Além disso, atributos funcionais também são indicativos da vulnerabilidade das espécies à extinção (BENDER et al., 2013; CERETTA et al., 2020), uma vez que essas características influenciam na resposta destas frente às ameaças, como por exemplo, espécies que formam agregações reprodutivas são mais vulneráveis à sobrepesca (CHEUNG et al., 2005). Dessa forma, análises de diversidade funcional são fundamentais para avaliar a vulnerabilidade das espécies, bem como para a compreensão da estrutura das comunidades, sendo bons preditores do funcionamento do ecossistema (MASON et al., 2005), como por exemplo índices de riqueza e redundância funcional, amplamente utilizados nas mais diversas áreas (MAURE et al., 2018; TAUPP e WETZEL, 2018; VILLÉGER et al., 2017).

Esforços recentes em pesquisas baseadas em atributos, incluindo diversidade funcional, visam entender os impactos da perda funcional no funcionamento do ecossistema e na manutenção de bens e serviços da natureza derivados (DE BELLO et al., 2021; PIMIENTO et al., 2020). Por exemplo, foi demonstrado que, se os níveis de sobrepesca e outros impactos antrópicos se

mantiverem, a perda de táxons de altos níveis tróficos, como peixes ósseos mesopredadores, tubarões, raias e cetáceos, alterará as cadeias alimentares, a distribuição e a frequência de características em níveis tróficos mais baixos, o que irá afetar diretamente a ciclagem de nutrientes nos recifes do Oceano Atlântico (WAECHTER et al., 2021). Por conseguinte, investigar atributos funcionais no contexto histórico é fundamental para compreender quais os padrões de exploração da diversidade funcional marinha, a partir de referenciais de exploração em cada período da história e suas mudanças ao longo do tempo. Além de trazer informações sobre possíveis preferências de pesca, podemos sugerir quais espécies foram constantemente exploradas, até mesmo quais podem ser consideradas resilientes frente à ameaça persistente ao longo do tempo, ao comparar a exploração pretérita com o status de conservação atual das mesmas. Uma vez que atributos funcionais são proxies para as funções desempenhadas pelas espécies nos ecossistemas, também podemos investigar como as ameaças afetaram ou podem afetar os ecossistemas marinhos.

Aqui avaliamos a diversidade funcional de táxons marinhos – Osteichthyes, Chondrichthyes e Cetacea – explorados pela pesca ao longo do tempo, nas regiões sul-sudeste do Brasil, em três períodos distintos: Sambaquis (8.720 – 230 anos AP), Colonial (1500 – 1966) e Atual (1967 – 2015). Também analisamos o espaço funcional ocupado pelos táxons que persistiram em todos os períodos. Esperávamos identificar um aumento da diversidade funcional explorada ao longo do tempo, devido ao aumento da diversidade taxonômica capturada impulsionada por avanços tecnológicos, como melhorias nas embarcações e aparelhos de pesca (ROUSSEAU et al., 2019), juntamente com a intensificação das atividades pesqueiras (PAULY, 2008) ao longo dos três períodos. Enquanto a maioria das pesquisas sobre pesca se concentra nas mudanças na abundância de espécies e na composição das capturas (FREIRE et al., 2021; JENNINGS et al., 1999), estes estudos negligenciam os potenciais impactos da pesca no espectro de funções fornecidas pelos táxons marinhos (PIMIENTO et al., 2020; WAECHTER et al., 2021). Ao testar essas hipóteses, nosso estudo é o primeiro a avaliar um processo de longo prazo de exploração da diversidade funcional marinha e contribuir para a compreensão do papel da pesca na alteração da biodiversidade marinha ao longo dos séculos.

Estrutura da Dissertação

Esta dissertação está estruturada em formato *Research Article*, conforme as normas da revista *Proceedings of the Royal Society B: Biological Sciences.*

REFERÊNCIAS

BELLWOOD, D.R. *et al.* The meaning of the term 'function'in ecology: A coral reef perspective. **Functional Ecology**, v. 33, n. 6, p. 948-961, 2019.

BENDER, M.G. *et al.* Biological attributes and major threats as predictors of the vulnerability of species: a case study with Brazilian reef fishes. **Oryx**, v. 47, n. 2, p. 259-265, 2013.

BOIVIN, N.; CROWTHER, A. Mobilizing the past to shape a better Anthropocene. **Nature Ecology & Evolution**, v. 5, n. 3, p. 273-284, 2021.

BOURQUE, B.J.; JOHNSON, B.J.; STENECK, R.S. **Possible prehistoric fishing effects on coastal marine food webs in the Gulf of Maine.** Human impacts on ancient marine ecosystems: A global perspective, p. 165-185, 2008.

CERETTA, B.F. *et al.* Testing the accuracy of biological attributes in predicting extinction risk. **Perspectives in Ecology and Conservation**, v. 18, n. 1, p. 12-18, 2020.

CHEUNG, W.W.; PITCHER, T.J.; PAULY, D. A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities of marine fishes to fishing. **Biological conservation**, v. 124, n. 1, p. 97-111, 2005.

COOKE, R.S.C; EIGENBROD, F.; BATES, A.E. Projected losses of global mammal and bird ecological strategies. **Nature Communications**, v. 10, n. 1, p. 1-8, 2019.

DE BELLO, F. *et al.* **Handbook of trait-based ecology: from theory to R tools.** Cambridge University Press, 2021.

DIRZO, R.; MIRANDA, A. Altered patterns of herbivory and diversity in the forest understory: a case study of the possible consequences of contemporary defaunation. Plant-animal interactions: evolutionary ecology in tropical and temperate regions. **Wiley**, New York, p. 273-287, 1991.

DULVY, N.K.; SADOVY, Y.; REYNOLDS, J.D. Extinction vulnerability in marine populations. **Fish and Fisheries**, v. 4, n. 1, p. 25-64, 2003.

EARLY-CAPISTRÁN, M. *et al.* Reconstructing 290 years of a data-poor fishery through ethnographic and archival research: The East Pacific green turtle (Chelonia mydas) in Baja California, Mexico. **Fish and Fisheries**, v. 19, n. 1, p. 57-77, 2018.

ERLANDSON, T.C. Rick J. **Human impacts on ancient marine ecosystems: a global perspective.** Univ of California Press, 2008.

FREIRE, K.M.F. *et al.* Reconstruction of marine commercial landings for the Brazilian industrial and artisanal fisheries from 1950 to 2015. **Frontiers in Marine Science**, v. 8, p. 659110, 2021.

GOBALET, K.W.; JONES, T.L. Prehistoric Native American fisheries of the central California coast. **Transactions of the American Fisheries Society**, v. 124, n. 6, p. 813-823, 1995.

JACKSON, J.B.C *et al.* Historical overfishing and the recent collapse of coastal ecosystems. **Science**, v. 293, n. 5530, p. 629-637, 2001.

JENNINGS, S.; GREENSTREET, S.P.R; REYNOLDS, J.D. Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. **Journal of animal ecology**, v. 68, n. 3, p. 617-627, 1999.

LIMBURG, K.E. *et al.* Prehistoric versus modern Baltic Sea cod fisheries: selectivity across the millennia. **Proceedings of the Royal Society B**, v. 275, n. 1652, p. 2659-2665, 2008.

LOPES, M.S. *et al.* The path towards endangered species: prehistoric fisheries in Southeastern Brazil. **PloS One**, v. 11, n. 6, p. e0154476, 2016.

LOTZE, H.K.; WORM, B. Historical baselines for large marine animals. **Trends in ecology & evolution**, v. 24, n. 5, p. 254-262, 2009.

MASON, N.W.H *et al.* Functional richness, functional evenness and functional divergence: the primary components of functional diversity. **Oikos**, v. 111, n. 1, p. 112-118, 2005.

MAURE, L.A. *et al.* Functional Redundancy in bird community decreases with riparian forest width reduction. **Ecology and Evolution**, v. 8, n. 21, p. 10395-10408, 2018.

MCCAULEY, D.J. *et al.* Marine defaunation: animal loss in the global ocean. **Science**, v. 347, n. 6219, p. 1255641, 2015.

MCCLENACHAN, L. *et al.* Ghost reefs: Nautical charts document large spatial scale of coral reef loss over 240 years. **Science advances**, v. 3, n. 9, p. e1603155, 2017.

PANDOLFI, J.M. *et al.* Global trajectories of the long-term decline of coral reef ecosystems. **Science**, v. 301, n. 5635, p. 955-958, 2003.

PAULY, D. Global fisheries: a brief review. **Journal of Biological Research-Thessaloniki**, v. 9, p. 3-9, 2008.

PESTLE, W.J. Fishing down a prehistoric Caribbean marine food web: Isotopic evidence from Punta Candelero, Puerto Rico. **The Journal of Island and Coastal Archaeology**, v. 8, n. 2, p. 228-254, 2013.

PIMIENTO, C. *et al.* Functional diversity of marine megafauna in the Anthropocene. **Science Advances**, v. 6, n. 16, p. eaay7650, 2020.

RICK, T.C.; ERLANDSON, J.M. Coastal exploitation. **Science**, v. 325, n. 5943, p. 952-953, 2009.

ROUSSEAU, Y. *et al.* Evolution of global marine fishing fleets and the response of fished resources. **PNAS**, v. 116, n. 25, p. 12238-12243, 2019.

TAVARES, D.C. *et al*. Traits shared by marine megafauna and their relationships with ecosystem functions and services. **Frontiers in Marine Science**, v. 6, p. 262, 2019.

TAUPP, T.; WETZEL, M.A. Functionally similar but taxonomically different: Benthic communities in 1889 and 2006 in an industrialized estuary. **Estuarine, Coastal and Shelf Science**, v. 217, p. 292-300, 2019.

VILLÉGER, S. *et al.* Functional ecology of fish: current approaches and future challenges. **Aquatic Sciences**, v. 79, n. 4, p. 783-801, 2017.

WAECHTER, L.S. *et al.* Functional biogeography of marine vertebrates in Atlantic Ocean reefs. **Divers**, v. 28, n. 8, p. 1680-1693, 2022.

WING, S.; WING, E. Prehistoric fisheries in the Caribbean. **Coral Reefs**, v. 20, n. 1, p. 1-8, 2001.

WORM, B. *et al.* Impacts of biodiversity loss on ocean ecosystem services**. Science**, v. 314, n. 5800, p. 787-790, 2006.

YELLEN, J.E. *et al.* A middle stone age worked bone industry from Katanda, Upper Semliki Valley, Zaire**. Science**, v. 268, n. 5210, p. 553-556, 1995.

YOUNG, H.S. et al. Patterns, causes, and consequences of anthropocene defaunation. **Annual review of ecology, evolution, and systematics**, v. 47, n. 1, p. 333-358, 2016.

FISHING FUNCTIONS: TRAIT EXPLOITATION OVER TIME

Bruna Ceretta Ferreira [a b], André Luís Luza [a b c], Mariana Bender Gomes [a b c]

[a] Programa de Pós-Graduação em Biodiversidade Animal, Departamento de Ecologia e Evolução, CCNE, Universidade Federal de Santa Maria, Santa Maria, Rio Grande do Sul, Brazil

[b] Marine Macroecology and Conservation Lab, Departamento de Ecologia Evolução, CCNE, Universidade Federal de Santa Maria, Santa Maria, Rio Grande do Sul, Brazil

[c] Departamento de Ecologia e Evolução, CCNE, Universidade Federal de Santa Maria, Santa Maria, Rio Grande do Sul, Brazil

* Corresponding author: marianabender.bio@gmail.com

Abstract

As human civilizations developed and invested in technology, fishing became one of the greatest threats to marine ecosystems, impacting the ecological functions mediated by trait species. However, the exploitation of functional traits over time have never been assessed. Here we investigated the functional spectrum of marine vertebrate taxa exploited in south-southeast Brazilian coast in three different periods: the Shellmounds (8,720 – 230 years BP), the Colonial (1500 – 1966) and the Current period (1967 – 2015). A functional trait space analysis together with kernel density estimates revealed that the full spectrum of functional traits was fished over time. We identified 423 exploited taxa, of which 56 were exploited in all periods. Over time, fisheries have been functionally selective by targeting habitat specialists, invertivorous and

macrocarnivorous taxa, with medium and large body size, benthopelagic and pelagic habits. Currently, fishing technology has boosted the capture of new traits far from the coast, such as planktivorous, sedentary, benthic, solitary, and small-bodied taxa. Fishing the entire functional trait spectrum clearly shows that fishing is an activity unsustainable over the centuries, and may be unfeasible in the future for two reasons: depletion of stocks and ecosystem functioning weakened by the poverty of traits.

1) **Background**

Fishing is one of the most ancient forms of natural resources' exploitation by humans. The first fishing gear employed by humans was found in Congo, approximately 90.000 years ago, assembled from the remains of an extinct catfish species [1]. As civilizations grew and developed over time, fishing expanded and became more efficient [2], today posing a major threat to marine ecosystems [3,4,5]. The history of marine fisheries and exploitation is organized into three distinct periods [2]. The prehistoric period (hereafter 'Shellmounds') is characterized by opportunistic and predominantly subsistence fisheries, with simple boats and limited near-shore areas. The 'Colonial' period sees the systematic exploration and depletion of coastal seas, along with more advanced technologies and the use of vessels; this period marks the beginning of commercial fishing, during European colonization [2,6]. The global period (hereafter 'Current') is marked by intense and global-scale exploitation, trade and use of marine resources, unprecedented fisheries' technology and mechanization, and frequent depletion with subsequent replacement of fisheries [2].

The majority of evidence on fisheries' impacts on the marine environment is concentrated in the past 50 years [7], with little information of prehistoric and colonial fisheries. Nonetheless, recent research is now revealing the long-term human impacts on natural environments [8,9,10], focusing on the identity of exploited taxa. While marine organisms have been targeted for millennia, with multiple records across the world' oceans [6,11,12], there is limited knowledge on the patterns of trait exploitation over time. For instance, zooarchaeological records across the globe reveal the early fishing of the marine megafauna (mammals, elasmobranchii, bony fishes) [13,14,15], many being fished to extinction [16] and others had their populations severely depleted and were left threatened with extinction [17]. Reef fishes, as groupers and parrotfishes, experienced temporal

changes in life-history traits, such as body size reductions and trophic level declines due to overexploitation [18].

Despite their distance in the 'Tree of Life', taxonomic groups such as bony fish, sharks, rays and cetaceans share traits that have direct and indirect effects on ecosystem structure and functioning [19]. For the marine (mega)fauna, body size and trophic category influence nutrient transport and storage, and therefore the food web dynamics in marine ecosystems [19,20,21]. These traits are also indicative of species' vulnerability to extinction [22,23], and comprise important dimensions of the spectrum of life-history strategies and functions presented by vertebrates [19,24,25]. Furthermore, analyzes of functional diversity are fundamental for understanding the structure of communities, being good predictors of ecosystem functioning [26]. Recent efforts in trait-based research, including functional diversity, aim to understand the impacts of functional loss on ecosystem functioning and the maintenance of derived nature goods and services [21,25,27]. For instance, it has been shown that if the levels of overfishing and other impacts hold, the loss of taxa from high trophic levels, such as mesopredator bony fish, sharks, rays, and cetaceans, will alter food webs, change the distribution and frequency of traits at lower trophic levels, and harm the cycling of nutrients in the Atlantic Ocean reefs [25]. When trait-based approaches are coupled with historical fisheries' data, they can shed light on the impacts of fisheries on ecosystem functioning, and reveal how fisheries and traits relate to each other (e.g., which and when traits were lost or preferentially harvested over time, as well which traits persist to fishing over time).

Here we assessed the functional spectrum of marine taxa harvested over time. We studied multiple marine taxa – Osteichthyes, Chondrichthyes and Cetacea – exploited by fisheries in Southeast Brazil in three different periods: the Shellmounds (8.720 – 230 years BP), the Colonial (1500 – 1966) and the Current period (1967 – 2015). Nonetheless, we also analyzed the functional

spectrum occupied by taxa that persisted across all periods. We expected to identify an expansion of the functional spectrum over time, due to the fishing of more species and a more diversified range of traits (even those taxa occurring far from the coast) boosted by technological advances, such as improvements in the vessels [28], along with the intensification of fishing activities [29] over the three periods. In the 1500s, the Europeans first arrived in Brazil, and marked a new era of resource use and trade, and of unprecedented ecosystem exploitation. Until this time the colonial fisheries in Brazil were essentially small-scale and coastal, with fisheries focused on mangroves, estuaries, lagoons and rivers. Then, with the presence of settlers the fishery activity in the region experienced a marked spatial and taxonomic expansion that lasted until 1960, a decade that anticipates the development of industrial fisheries in the country [30,31].

Taxa can be unevenly distributed across the functional spectrum. Two analytical frameworks useful to better characterize the functional spectrum are provided by Villéger et al. (2008) and Grenié et al., (2017). The first framework consists in evaluating the area occupied by species traits and the regularity in the distribution of species within this area, as measured by the Functional Richness (FRic) and Functional Evenness indices (FEVe) [32]. The second one consists in evaluating how distant is each species from its nearest neighbor, as measured by the Functional Uniqueness index (FUni) [33]. In this way, we regard that expansion of the functional spectrum and the exploited richness over time would cause an increase in FRic. However, with the intensification of fishing, there are two possible scenarios for functional evenness: the decrease in EFve, due to the exploitation of very different functional groups distributed in the functional spectrum; or an increase in FEve, i.e., the uniform exploitation of the entire functional spectrum, due to the harvest of taxa with similar functional traits. Finally, we expect decreases in FUni as fisheries exploit a greater number of species with similar functional traits over time, producing

greater functional redundancy (i.e., more species performing similar functions) [21,25] and therefore lower uniqueness. While most research about fishing focused on changes in species abundance and catch composition [34,35], these studies overlooked the potential impacts of fishing on the spectrum of functions delivered by marine taxa [21,25]. By testing these hypotheses, our research is the first to assess a long-term process of exploitation of the functional spectrum composed of multiple marine taxa, and contribute to understanding the role of fisheries in altering marine biodiversity over centuries.

2) Materials and Methods

2.1) Data collection

We compiled the data about caught taxa using online literature searches for the 'Shellmounds' and 'Current' periods, and using historical documents for the period 'Colonial'. We highlight the importance of assume that when we work with historical material, there are a series of limitations involving disponibility of data, mismatches between informations, among others biases. The literature search for each period was conducted from March 2020 to April 2021, in the following search platforms: Scopus, Web of Science, Scielo, Google Scholar, the Brazilian Catalog of Thesis (CAPES), National Digital Library, among other digital collections. The inspection of historical documents, such as gray literature and naturalist's reports, occurred during the same period. From these sources of information, we gathered and organized data in two databases: (i) taxonomic composition dataset: comprising marine vertebrates – Osteichthyes, Chondrichthyes and Cetacea – caught in three different historical periods (Shellmounds, Colonial, and Current) (Figure. 1; see details in sections 2.2), and (ii) functional traits' dataset: functional traits of taxa regarding their size and behavior (section 2.3).

Irrespective of the analyzed period, taxa were included in our database when cited in literature and historical documents as 'exploited by fisheries', 'used for medical' and 'culinary purposes' in each period. We only considered common names with identification at the genus or species level (hereafter called "taxa"). For example, we didn't include common names that may belong to several species, such as "raias", "cação", "caçonete", "resíduo", "emplastro", "bacalhau", "moreia", "baiacu", "sargo", "pargo". Higher taxonomic levels were not included in our database since trait variation becomes very coarse at higher taxonomic levels. Our study area embraces the south and southeast regions of Brazil, from Rio de Janeiro to Rio Grande do Sul state, which corresponds to the presence of shellmounds in the country [36]. The search protocol for each period is detailed in the next section.
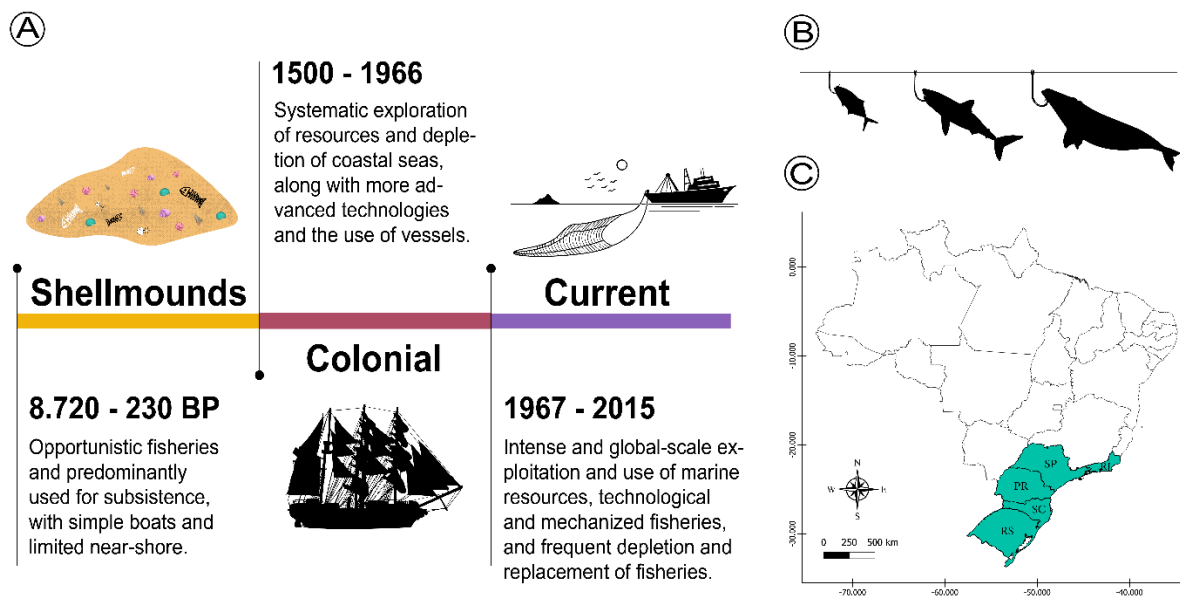

Figure 1. Graphical abstract of the **A)** Temporal scope: time interval of each period and its corresponding definitions according Jackson et al. (2001). **B)** Taxonomic scope of exploited

organisms: Ostheichthyes, Chondrichthyes and Cetacea. **C)** Geographical scope: the southern-southeastern Brazil, from Rio de Janeiro to Rio Grande do Sul states.

2.2) The taxonomic composition dataset

2.2.1) The Shellmounds period

This period comprised from 8.720 to 230 years calibrated before present (cal BP), based on the available zooarchaeological remains from literature review. For this specific period, we did a literature search combining the following keywords with "Brasil/Brazil" (in Portuguese and English): "sambaquis/shellmounds/shell middens", "pescadores-coletores/fisher-gatherers", "ictioarqueologia/ichthyoarchaeology", "paleozoologia/paleozoology", "zooarqueologia/zooarchaeology", and "pescarias pré-históricas/prehistoric fisheries". All marine vertebrate species reported in the literature as present in the shellmounds were considered as captured by 'fisher-gatherers', and were therefore included in our dataset.

2.2.2) The Colonial period

We limited the Colonial period to records from years 1500 to 1966, starting when the Europeans first arrived in Brazil, and ending in 1966 when industrial fishing started to predominate. We know that the brazilian colonial era started in 1500 and finished in 1822, year of the Independence of Brazil, however, to avoid time lacks, we extended the period until 1966, according the beginning of industrial era in Brazil. We compiled historical records from searches in digital collections, such as gray literature, naturalist's reports, logbooks and artwork. The keywords used in the search platforms were, both in Portuguese and English: "pesca colonial/colonial fisheries",

"história da pesca no Brasil/history of fisheries in Brazil", "pesca baleia/whale hunting/whale fisheries", "pesca histórica/historical fisheries", "Brasil colonial/colonial Brazil".

2.2.3) The Current period

This period started in 1967, a year marked by the beginning of intense governmental subsidies for the industrial fishing development in Brazil [31], which finished in 2015 due to the lack of official fishing statistics onwards. The current period dataset was based on data from fisheries statistics reports [37,38,39].

In both Colonial and Current periods, multiple documents contained common names and/or indigenous names (e.g., "Aimoré", "Beijupirá, "Panapaná", etc). To properly identify these species, we searched for popular names in Fishbase, SealifeBase and indexed articles [39,40,41]. For indigenous names from the Colonial period, we used "*Zoonímia tupi nos escritos quinhentistas europeus*" [42], which lists species (and their indigenous names) cited in reports by naturalists and other documents from the 15th and 16th centuries. When documents contained information about common names and its referred species (e.g., "Parati" is the same as *Mugil* sp.), this was applied to identify organisms listed under common names in other documents.

2.3) Functional traits

For each fished taxa cited in the taxonomic composition dataset we compiled the following functional traits: group size, habitat use, maximum body size (cm), mobility, trophic category (diet) and vertical position in the water column (see Table 1 and Trait Guide in supplementary material). We chose these traits due to their link with ecosystem functions. Traits were gathered from several sources [21,23,43,44,45]; when unavailable, the traits were compiled from FishBase [40],

SealifeBase [46], the International Union for Conservation of Nature (IUCN) [47], and from the literature (see supplementary material). Traits were compiled at the species or genus level. For taxa with conflicting or missing information, we chose the most representative category within the taxa, i.e., the most frequent form among the species of a given genus, based on information from the literature. And when trait data were absent, information was extrapolated at the genus level. We confirmed species occurrence in southern Brazil through the Brazilian Biodiversity Information System (SiBBr) [48]. Finally, our trait database was verified by fish, sharks/rays and mammals' specialists.

Before the functional analyses, we standardized the values of species' maximum body size (cm) based on its mean and standard deviation (*scale* function; 'base' R package) [49], and ranked and ordered the vertical position, mobility, group size and habitat use traits (so that species in the surface, pelagic, with high mobility, large aggregations and generalists had higher ranks).

Table 1. List of functional traits and categories used in our study.

Traits	Type	Categories
Group size	nominal	Solitary (SOL); Small aggregations (SMALL); Large aggregations (AGR)
Habitat use	nominal	Specialist (SP); Semi specialist (SS); Semi generalist (SG); Generalist (GE)
Maximum body size	continuous	cm
Mobility	nominal	Sedentary (SED); Roving (ROV); Highly mobile (HMO)
Trophic category	nominal	Planktivores (1 - PLANK); Herbivores and detritivore (2 - HERB); Invertivore (3 - INV); Planktivore-Piscivore (4 – PLANK-PISC); Omnivores (5 - OMNI); Piscivore (6 - PISC); Macrocarnivores (7- MCAR)
Vertical position in water column	nominal	Benthic (BENT); Benthopelagic (BENTP); Pelagic (PEL)

2.4) Data analysis

We used a trait-based approach to link taxonomic and functional trait composition to then build a functional trait spectrum for taxa harvested in Brazilian fisheries over time. The trait-based approach considers the relationship between species and trait composition to produce a

measurement of diversity and a surface (spectrum) of ecological strategies and functions built based on taxon trait values [27,50]. We measured functional diversity and built the functional spectrum separately for the taxa present in the three periods (Shellmounds, Colonial, and Current) and for taxa exploited over the three periods. For each period, we summarized dissimilarity in trait data between taxa using Principal Coordinate Analysis (PCoA) [51] and measured the density of taxa within the functional spectrum built by traits by applying a Kernel Density Estimation (KDE) [52], which revealed areas of high species density (hereafter 'hotspots') [53]. Trait dissimilarity between species considering variation in the six functional traits was calculated using the Gawdis distance to account for different trait scales and avoid the disproportionately high weight that binary and categorical traits have on PCoA. Gawdis is implemented in the 'gawdis' R package [54]. The functional spectrum also served as the basis for calculating functional indices that provide complimentary information about the range and concentration of species in the functional spectrum –Functional Richness (FRic), Functional Evenness (FEve) and Functional Uniqueness (FUni) [21,25,27,32,55]. Finally, we contrasted observed functional indices with null expectations in order to produce estimates independent from species richness.

2.4.1) Kernel density estimation and trait frequency

We performed a Principal Coordinate Analysis (PCoA) to project, in a multidimensional space (hereafter the 'functional spectrum' or 'functional surface'), the matrix of trait dissimilarities between pairs of species, using the *dudi.pco* function ('ade4' R package) [56]. In order to identify shifts in trait space through the fishing periods, and find the traits related to these shifts, we first ran one PCoA analysis and projected the Kernel Density Estimates (KDE) per period to show the probability of a given trait combination within the functional surface (a bimensional trait space

comprising PCoA axes 1 and 2), and then projected the traits in the functional spectrum by calculating the Spearman correlation between trait values and the eigenvectors of the two first PCoA axes. We estimated the KDEs for each period using the *kde* R function ('ks' R package) [52], and produced plots using the 'ggplot2' R package [57]. We used unconstrained bandwidth selectors for building the KDE, once the results depend on the choice of bandwidth used for smoothing kernels [52]. The selected bandwidths were 0.5, 0.9 and 0.99 quantiles, representing the probability of occurrence of taxa in the functional spectrum. We consider as exploited 'hotspots' by fisheries the taxa within 0.5 quantile. By finding the hotspots and the areas of the functional spectrum that considerably shifted in taxa across the periods, and checking which traits were correlated to these shifts, we can assess trait harvesting over time. We complement this analysis with histograms showing the absolute frequency and the density of each trait (% of the species presenting a given trait value) in each period.

2.4.2) Functional diversity indices and null models

To assess trait diversity and fisheries' selectivity, we calculated three functional diversity indices for each period: Functional Richness [32], Functional Evenness [32] and Functional Uniqueness (FUni; or functional originality sensu Mouillot et al., 2013). FRic represents the total volume of the convex hull occupied by taxa in a functional trait space [32,55], FEve indicates the regularity in the distribution of taxa within the trait space [32,55], and FUni quantifies how unique in terms of traits a species is when compared to the other species, therefore representing how isolated a species is in trait space [21,55]. FRic and FEve were calculated using the *dbFD* function, from the 'FD' package (FRic calculated in natural log scale) [58], while FUni was calculated through the *uniqueness* function, in 'funrar' R package [33]. Finally, a null model was applied to

the trait dataset to simulate the functional structure of communities and estimate FRic, FEve and FUni produced by chance [59]. The null model sorted, from the complete dataset of trait values (composed by 422 taxa) the same number of species as found in each period (Shellmounds=216 taxa, Colonial=136, Current=309, all periods=56 taxa), therefore maintaining species richness and frequency while changing species composition in each null model run. We repeated this procedure 1.000 times, resulting in 1.000 values of FRic, FEve and FUni produced by chance. We then compared observed and null index values using violin plots, so that consistent deviations from chance are inferred whether the observed value of an index falls outside the range of random values. All analyses were performed using the R software version 4.1.1 [60].

3) Results and Discussion

Our literature search returned 257 documents with information on exploited taxa in the Shellmounds (n = 45), the Colonial (n = 31) and Current (n = 106) periods, as well as documents containing trait data (n = 75). In total, 423 taxa were included in our taxonomic and functional traits' datasets: 89 genera and 334 species. We found 326 Osteichthyes, 77 Chondrichthyes and 20 Cetacea reported as exploited across the periods. In the earliest period, we identified 216 exploited taxa, contrasting with 136 in the Colonial, 309 in the Current period, and 56 taxa fished in all periods. It is possible that a greater diversity of organisms was exploited in the Colonial period, which could not be recovered due to the limited availability of historical data, especially for fisheries in Colonial Brazil (e.g., non-digitized and illegible documents). When we contrast the Shellmounds and Current periods, 138 novel taxa were exploited (Fig. S1). This might be explained by the increasing anthropogenic impacts associated with human population growth, and the use of more advanced fishing technologies in the latest period [2,29]. Cetaceans were absent in the current

period, since commercial whale fishing was banned in Brazil in 1987 [61]. Further, we found an extinct shark species, *Carcharhinus priscus*, harvested in the Shellmounds period. This species probably had similar traits to other *Carcharhinus* species, yet, since we could not confirm this information, this species was not included in the analyses of functional diversity.

3.1) Fishing functions: the main traits exploited

We expected to identify an expansion of the functional spectrum over time as a result of fishing development. However, we found that fisheries have extensively exploited the same set of traits across periods, as revealed by the 'hotspot' in the center of each functional spectrum (Fig. 2), as well by the peaks in the histograms and density plots (Fig. 3). The first two PCoA axes explained more than half (54%) of total trait variation (Fig. 2). The first axis (PCoA 1) depicts a spectrum of water column use (pelagic to benthic) and mobility (highly mobile to sedentary). The second axis (PCoA 2) depicts a spectrum of maximum body size, trophic categories and habitat use, discriminating generalists, macrocarnivores and large-bodied taxa from specialists, planktivorous and small-bodied species (Fig. 2). Despite this pattern of constant exploitation over time, some traits differed over time (Fig. 3).
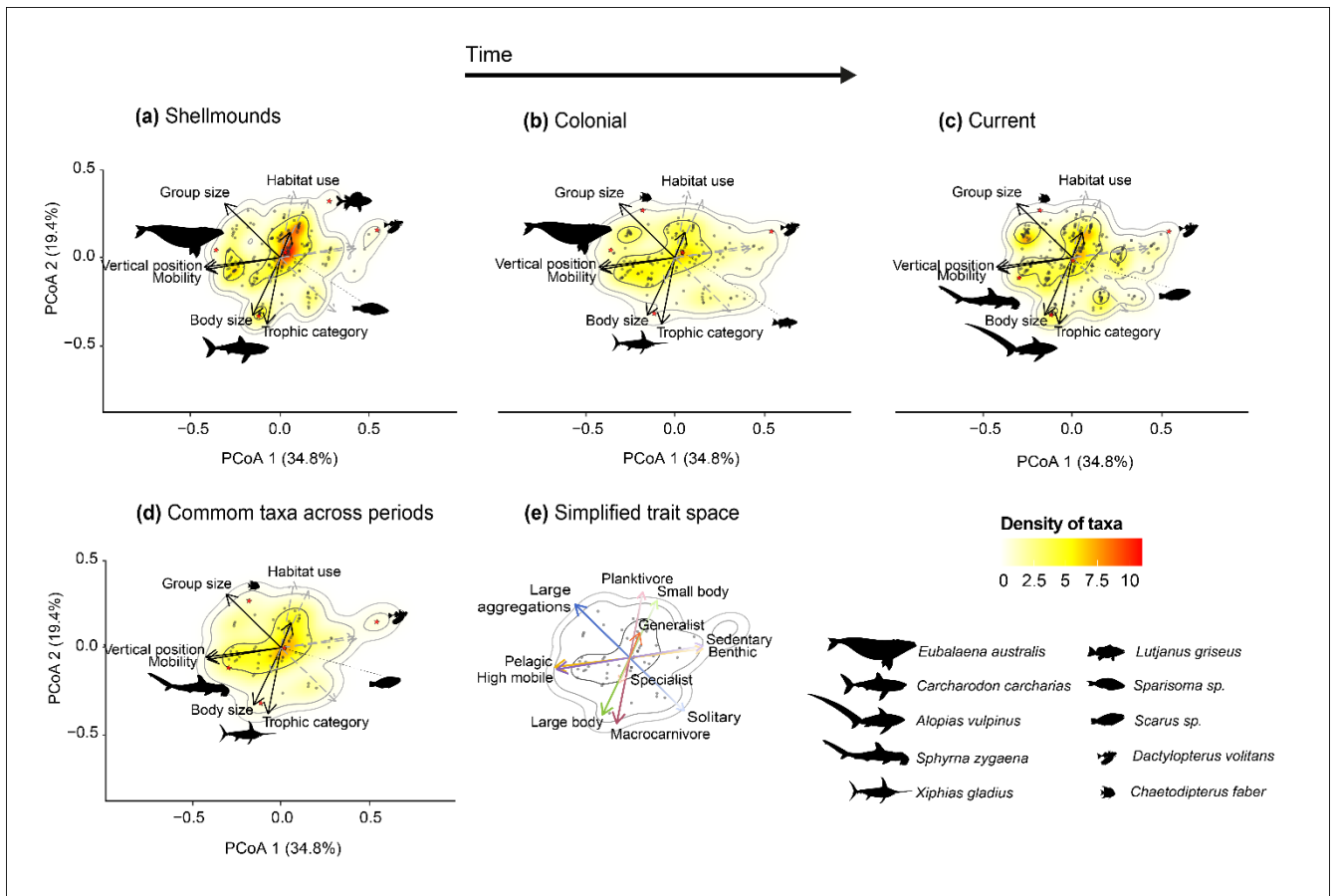
Figure 2. Spectrum of traits exploited by fisheries over time. Projection of captured taxa (dots) on the trait space (PCoA 1, PCoA 2) of each historical period: (a) Shellmounds (n=215), (b) the Colonial (n=136) and (c) the Current (n=309) period; (d) for 56 taxa captured across all periods. The diversity of exploited trait gradients is summarized in (e). Solid arrows indicate the correlation between the traits and the first two PCoA axes. The color gradient represents regions of highest (red) to lowest (white) occurrence probability of taxa in trait space, with contour lines indicating 0.5, 0.95 and 0.99 quantiles. Red and yellow regions within the limit of 0.5 correspond to the functional hotspots exploited by fisheries. Organisms' silhouettes represent taxa in the vertices and in the middle of trait space. Silhouettes were created in Illustrator by the authors.

While the average body size of exploited taxa across periods was 80 cm, it was larger in Shellmounds (92cm) than in the Current period (69cm) (Fig 3a). In the Colonial period, despite the high frequency of small-bodied species, the mean body size reached 91cm, possibly influenced by large cetaceans such as blue whales (*Balaenoptera musculus*) which could measure up to 33m. We perceived a similar exploitation pattern for macrocarnivorous and invertivorous taxa (Fig. 3b). Likewise, there was an increase in the exploitation of planktivores, which, together with the decrease in the size of the explored body, suggests the occurrence of the phenomenon "Fishing down marine food web" in this region, characterized by the gradual transition from the capture of long-lived fish from high trophic levels to lower trophic level short-lived fish [62]. Other precolonial fishing research has revealed the occurrence of both "fishing down" [15,18,63,64], and "fishing up" the food web [65], but our study is the first to suggest the incidence of such processes in such a large time frame. Derived changes in the trophic structure of ecosystems, i.e., the decrease in the trophic level of exploited groups, directly affect ecosystem functioning and food disponibility in trophic chains [4]. In general, exploited taxa were mostly habitat specialists, followed by intermediary categories of habitat use (Fig. 3c). Fishing is also selective towards taxa forming large aggregations (Fig. 3d), which can be explained by the greater ease of capture; that is, high success with low fishing effort. From the past to the current period, we identified an increase in exploitation of solitary (Fig. 3d), sedentary, benthic deep-sea inhabitants' taxa, due to the fishing intensification. The traits mobility and vertical position in the water column show different exploitation patterns: while there were no differences for water column position (Fig 3.f), few sedentary taxa were exploited over time (Fig. 3e). But how do these changes affect ecosystems?
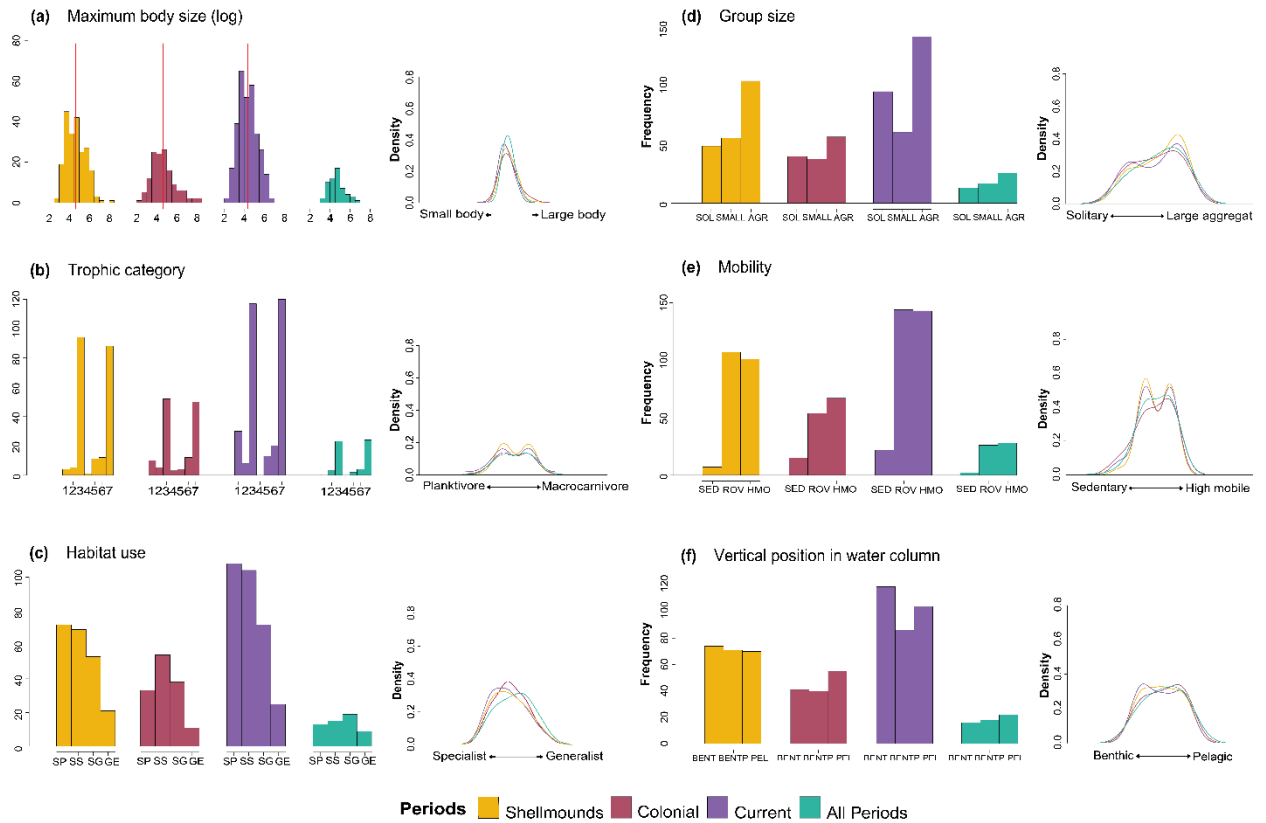
Figure 3. Trait frequency and density (% taxa per trait value) per period in: **(a)** Maximum body size (log); **(b)** Trophic category; **(c)** Habitat use; **(d)** Group size; **(e)** Mobility and **(f)** Vertical position in water column for 1 - Planktivore; 2 - Herbivore; 3 - Invertivore; 4 - Planktivore-piscivore; 5 - Omnivore; 6 - Piscivore and 7 - Macrocarnivore. SP - Specialist; SS - Semi Specialist; SG - Semi Generalist and GE - Generalist; SOL - Solitary; SMALL - Small Aggregations and AGR – Aggregations; SED – Sedentary; ROV – Roving and HMO – Highly Mobile; BENT – Benthic; BENTP – Benthopelagic and PEL – Pelagic. Periods are coded in different colors.

Marine megafauna is characterized by large-bodied, pelagic and highly mobile species that contribute substantially to ecosystem functioning [66]. In consequence of their large body sizes, these organisms consume and excrete large amounts of biomass, impacting trophic dynamics and

the distribution of energy and nutrients across habitats and ecosystems [19,21,66]. Top predators, for example, are essential top-down regulators, controlling food-web dynamics [67], including the abundance, distribution and behavior of their prey [68,69,70]. Large predators such as groupers, sharks and rays are commercially valuable and many species, critical to the functioning of ecosystems, have depleted stocks due to overfishing [71,72]. Medium to small-bodied and pelagic fish are usually of lower trophic categories (invertivores and planktivores), being fundamental pieces in nutrient and energy transfer from lower to higher trophic levels [73]. The loss of such groups could impact the entire ecosystem, reducing the food supply to larger organisms, leading to reductions in their population sizes [74,75]. Although many studies indicate that species with large body sizes are more susceptible to fishing [3,76], small-bodied and lower trophic level species seem just as susceptible as larger ones [74]. Also, the organism's mobility and water column position are related with matter and energy transport, not only altering physically the habitats (bioturbation) [21,25], but also connecting habitats and ecosystems across scales, through the feeding, excretion and transporting of nutrients [19,66]. Despite the capture of several large, pelagic and highly mobile species in the past, current fishing has a much greater impact than in the past, due to the increased demand for food and the development of fishing technologies. It has even been proven that some of these traits are vulnerable to extinction, such as large body size, high mobility, habitat specialty, macrocarnivorous and invertivorous diets [22,23].

Little is known about the functional diversity exploited over time; however, recent studies indicate that fishing significantly impacts the commercial marine fish community, which show less functional regularity in relation to increased fishing pressure [77]. Further, fishing can change the frequency and distribution of ecosystem functions through the removal of specific traits, e.g., multispecies fisheries can create empty niches or new species interactions targeting determined

functional traits [73]. In this way, traits like maximum body size, group size and trophic category should be prioritized for conservation, since they are currently targeted by all fishing modalities [73,78]. However, fisheries have a wide variation in time, space, intensity and fishing gear, which makes it difficult to investigate large-scale impacts in functional diversity. To better illustrate how these traits were exploited over time, we will present a more historical bias, characterizing fishing gears and techniques employed and examples of harvested taxa in each period.

3.2) Trait diversity over time

3.2.1) Shellmounds

In the Shellmounds period, beyond the central hotspot, two other small areas exhibit a high densities of taxa: (i) A gathering of pelagic, highly mobile, medium to large-bodied (>80cm) taxa, forming large schools; represented by jacks (Carangidae), some *Carcharhinus* sharks, as *C. brevipinna* and *C. leucas*, and cetaceans as *Tursiops*, *Stenella*, *Delphinus* and *Pontoporia* dolphins; and (ii) a region assembled by pelagic, highly mobile, solitary or forming small schools, large-bodied and macrocarnivorous taxa as *Orcinus orca*, sharks as *Alopias sp., Carcharodon carcharias, Isurus sp., Prionace glauca*, and other fishes including *Coryphaena hippurus, Xiphias gladius, Sphyraena sp.* (Fig. 2a). The trait frequency histograms (Fig. 3) reflect these patterns of the functional espectrum (Fig. 2a). Such prehistoric fisheries had simple technologies [2], like hook-and-line, traps, spears and nets [13,17, 79,80], including fishing lines made of plant fiber [81].

Following that, we could expect that mostly easy-to-catch organisms, such as coastal, small-bodied, schooling, benthic and sedentary taxa, would be exploited. Certain exploited taxa had traits that would not be considered easy-to-capture, as they appear in small hotspots. For example, catches of large cetaceans such as *Eubalaena australis* and *Balaenoptera sp*. might not

be frequent due to its large body size, yet records revealed the opposite: at least ten different species were consumed by fisher-gatherers, ranging from immature to adult individuals [82]. The two main forms of exploitation would be through the use of scavenged beached whales and the capture of small cetaceans, as dolphins, with fishing nets and harpoons [6,82].

Large Chondrichthyes can also be considered of challenging capture, as *Carcharodon carcharias*, *Alopias sp.*, *Galeocerdo cuvier*, *Sphyrna sp.*, due to their large body size and high mobility [83]. Rays, such as *Dasyatis centroura, Hypanus sp.* and *Gymnura altavela* would also be difficult catches for ancient fishers for their benthic behavior [83]. But then, what possible hypothesis explains the capture of such fauna by ancient fishers? First, it is possible that the majority of the individuals captured were young sharks, which would facilitate fishing [84] and, second, most shellmounds are found in bays, estuaries, lagoons and mangroves [36], coastal regions accessible to ancient fishers and considered as nurseries for several marine species, from fish to sharks [85,86]. This also reveals that coastal ecosystems were already impacted by prehistoric fisheries [17].

Other studies around the globe have also demonstrated similar exploitation patterns, as in southern California, with medium to small (10 to 20 pounds), coastal, pelagic, and shoal-forming species being harvested [81]. Archaeological and isotopic data from a coastal site in Maine demonstrated a decline in top predators, as well as an increase in mesopredators and other pelagic species [12]. Thousands of years ago in Australia, contrary to what was expected of simplicity in fishing, ancient peoples already had the ability to capture large pelagic species, such as tuna, even in the open sea [87]. In addition, along the coast of the state of Rio de Janeiro, within the study region of this work, massive fishing of demersal species and pelagic fish that used coastal regions for feeding and/or reproductive aggregation was reported [17]. In line with these and other studies

[6], our results suggest that fishing has already impacted several functional groups since ancient times.

3.2.2) Colonial

Multiple historical descriptions of settlers and naturalists in those first centuries aimed to describe this new environment and contribute to its colonization, from exploration to domination [80,88,89], offering details on the local flora and fauna, and on the costumes of native people, including food and fishing gear [80,88]. Some of the fishing gear used in this period ranged from conventional and more rudimentary methods, such as hooks and nets, hand fishing, bow and arrow, to elaborate techniques such as the use of 'timbó', an ichthyotoxic substance [80,90]. Other studies of colonial fisheries have demonstrated a similar description of new cultures, as accounts of colonial fisheries in Virginia state that natives already used longlines, and settlers practiced deep-sea fishing with hook and line, even nets [91].

From the 16th to the 18th century, there were many great historical changes around the world. Brazil, a Portuguese colony back then, was therefore directly influenced by the Industrial Revolution occurring in Europe. Together, technological advances, market development and the greater demand for resources with human population growth [92] accelerated human impacts on marine ecosystems [2,93,94]. During the Industrial Revolution, whale oil was used as fuel, fertilizer, animal food among other products [93]. In Brazil, whaling was consolidated as an important economic activity in the second half of the 17th century [95] this is supported by the presence of large cetaceans such as *Balaenoptera musculus* (blue whale)*, Megaptera novaeangliae* (humpback whale) and *Physeter macrocephalus* (sperm whale) among the exploited taxa in the Colonial period.

Also, coastal fish species, such as mullets (*Mugil sp.*), were widely consumed in farms, cities and villages of that period.

Our results show that, in the Colonial period, exploited taxa formed two hotspots (Fig. 2b). A large hotspot in the center of the spectrum, represented by taxa: (I) with intermediate traits, i.e benthopelagic, roving, medium body size (40cm-80cm), and (II) large bodied (>80cm), pelagic and highly mobile taxa, which form small to large schools, such as large cetaceans, and representatives of *Scomberomorus sp.* (mackerels), *Mugil sp.* (mullets), *Thunnus sp.* (tunas) and *Caranx sp.* (jacks), and (III) small bodied (<40cm) taxa, with benthopelagic and roving mobility, low trophic categories, as invertivorous and herbivorous, which form small or large schools, such as *Polydactylus virginicus*, *Conodon nobilis*, and *Archosargus rhomboidalis* and *Acanthurus chirurgus*. The small hotspot is formed by small bodied (<40cm), highly mobile and pelagic planktivores, which form large aggregations, such as *Anchoa tricolor*, *Anchoviella lepidentostole*, *Brevoortia aurea* and *Exocoetus volitans*. Our results (see Fig. 3f) corroborate patterns for North Atlantic, where approximately 40% of captured taxa are pelagic.where three aspects represent the fisheries' expansion in the Colonial period, marked by the lack of energy and food to cope with population growth in coastal regions: the intensification of fishing through more vessels, the preservation of fish and the preference for pelagic species, such as tuna, sardines, anchovies and cod [89].

It is likely that native inhabitants, as well as the first settlers, have maintained their fishing techniques, gear and therefore selectivity since the past, which would explain the similar pattern of pre-colonial exploitation of the functional trait spectrum. Indeed, current artisanal fishing presents similarities to fishing carried out in the past, most notably fishing along coastal regions, in estuaries, lagoons, mangroves and rivers, with part of the fish used for subsistence [30,95], and the fishing

gear employed, such as nets, hook and line and wooden boats [31,95]. Despite imposing lower impacts when compared to large-scale fisheries, small-scale artisanal fisheries still capture multiple functional groups [96], since sedentary and benthic species that form schools with few individuals to highly mobile pelagic species that form large schools [97]. Commercial fishing in Brazil, more specifically in the southeast region, has developed at the beginning of the 20th century, with the arrival of European immigrants and their large boats. In the 1960s, government financial incentives [30,31,98] have largely contributed to a new era of industrial fisheries in Brazil.

3.2.3) Current

Over time, the number of exploited taxa increased and so did the richness of exploited traits (Figure 2c). Similar trait hotspots characterize taxa exploited in the pre-colonial Shellmounds to the Current period (Fig 2a and Fig 2c). In Current fisheries we see the emergence of two novel hotspots. One is formed by sedentary and benthic invertivores, small-bodied specialists and/or semispecialists, such as *Achirus lineatus* and *Symphurus plagusia*, *Amphichthys cryptocentrus* and *Porichthys porosissimus*. The other *hotspot* is composed of solitary, sedentary and benthic taxa, with large body size and high trophic categories, e.g., piscivore and macrocarnivore diets. The latter group is represented by groupers and snappers (*Epinephelus itajara, Hyporthodus sp., Mycteroperca sp., Lopholatilus villarii*), and also Chondrichtyes (*Callorhinchus callorynchus, Squatina sp., Gymnyra sp.,Atlantoraja sp.)*. These reflect changes in capture patterns, in which more benthic, sedentary and solitary have become more frequently exploited traits.

Deep-sea fishing, as trawling, is a major technology that may have caused the exploitation of new taxa and their functions [99,100]. These deep-water fisheries (200m to 1000m) were driven by the depletion of coastal resources [100,101,102], operating effectively in the 2000s through

bottom trawls, bottom gillnets and hook-and-line [103,104]. This has led to the exploitation of new target species (*Hyporthodus niveatus*, *Squatina sp.*, *Atlantoraja sp.*) and a new set of traits. Naturally, several target species of deep-sea fisheries were identified exclusively in the Current period, such as *Galeorhinus galeus, Pseudobatos horkelii, Genypterus brasiliensis, Lophius gastrophysus, Zenopsis conchifer, Paralichthys isosceles, Polymixia lowei*, among others [104]. Thus, fishing expansion into deeper and further waters [29], as well as the development of new fishing technologies and the use of non-selective and destructive fishing gear [105], led to the exploitation of multiple species. In the Current Period, in addition to those trait combinations exploited in the past, two new hotspots in trait space emerged. Today, fishing explores the full trait spectrum. Although this study does not take into account changes in the abundance of exploited taxa, it is necessary to highlight that declines in the abundance of several marine organisms have been documented in recent years, mostly due to overfishing [106,107,108, 109]. On this wise, low functional redundancy, caused by the loss of species abundance, can further compromise the maintenance of ecological functions through local functional extinctions [2,55,110].

3.3) Analyzing the functional spectrum through functional diversity indices and null models

Functional richness has changed over time, following the increase in the richness of harvested taxa. As expected, we observed an increase in the diversity of exploited traits between the Shellmounds (FRic, log scale = 15.56) and Current (FRic = 17.88 log) periods (Fig. 4a). The high taxonomic diversity, reflected by the high functional diversity in Shellmounds, reflects that fisher-gatherers had great navigation and fishing skills, being the coastal fisheries fundamental to the survival of these people [17]. Although, Colonial (FRic = 13.63 log) period didn't present FRic greater than the former one, due to the lack of data for this period as already mentioned. The

Colonial period had the greater FEve (FEve = 0.68), followed by the Current (FEve = 0.57) and Shellmounds periods (FEve = 0.55), this being lower than expected by chance (Fig. 4b). Comparing the FEve index (Fig. 4b) and the funcional spectrum (Fig.2), there were similarities between trait spaces of the Colonial period and that of the 56 taxa caught over time (Fig. 2b and Fig. 2d), and between Shellmounds and Current periods (Fig. 2a and Fig. 2c). These relations can be associated with the second FEve hypothesis: the low values of EFve, as a response to the exploitation of very different functional groups distributed in the functional spectrum. Functional uniqueness also represents functional redundancy within ecosystems, considering the degree of species' isolation in trait space [25,55].

In general, all periods exhibited similar FUni values to each other and within random intervals (Figure 4c). It appears that fisheries have exploited taxa with the same traits, i.e., fisheries harvest high functional redundancy and currently tend to exploit entire functional groups of marine ecosystems. The greatest functional uniqueness was in Colonial period (FUni= 0.0038), demonstrating that this period has more taxa with different functions being exploited, while Shellmounds (FUni = 0.0021) and Current (FUni = 0.0027) had more redundant ecosystem functions exploited. Comparing the former and the last periods, we can infer that there was no change over time in the functional redundancy exploited, nor the harvest of functionally unique taxa, going against our hypothesis. Nonetheless, we highlight that 138 new taxa began to be explored, demonstrating that there was no emergence of new functional groups explored, only an increase in the density of groups that were already explored in the past. Thus, we can imply that the entire functional spectrum was already exploited since the Shellmounds period (Fig. 2a) and over time there was a change in the density of taxa with certain combinations of traits, such as the new exploited hotspots in Current, i.e., more solitary, sedentary and benthic taxa being harvested.
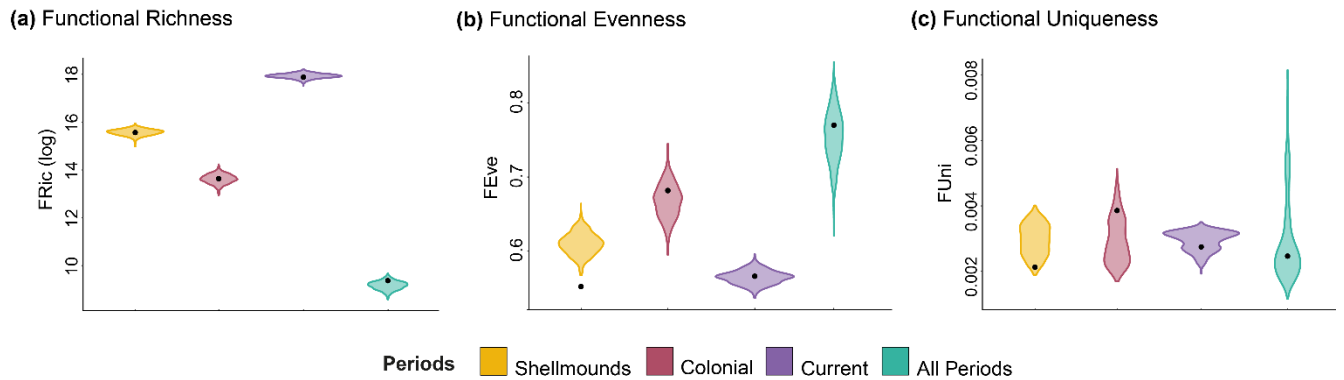
Figure 4. Functional indices of exploited species over time periods. **(a)** Functional Richness (natural log scale); **(b)** Functional Evenness and **(c)** Functional Uniqueness. Observed values are represented by black dots and violin plots represent the distribution of values obtained from null models.

Little is known about the functional diversity exploited over time; however, recent studies indicate that fishing significantly impacts commercial marine fish communities, through the decrease in functional evenness related to the variation in resistance and resilience of fish species to fishing pressure [77]. It should be emphasized that currently fishing tends to remove entire functional groups from coastal marine ecosystems [111], which may affect the heterogeneity and distribution of functional traits, directly affecting the ecosystem functions performed by them [73]. If fisheries exploited fewer functional groups, fewer ecosystem functions would be affected [112], however, what occurs is the exploitation of the entire functional spectrum, jeopardizing the resilience of marine ecosystems.

3.4) Vulnerable or resilient? The 56 taxa exploited over time

Over periods, from the 423 taxa fished, 56 were constantly exploited from the Shellmounds to the Current periods. At the hotspot in the functional spectrum (Fig. 2d) we detected that these taxa have the combination of the most exploited traits in each period. The center of trait space is represented by *Lutjanus griseus* and two genus of Parrotfishes (Scaridae), *Sparisoma sp.* and *Scarus sp.* (Figure 2). Notably, they are reef-associated fish with key functions in the reef such as bioerosion, sediment production and transport, top- down control of algal, among others [113,114]. However, in recent decades, this group has suffered from the effect of fishing, reflected by the decline in the biomass of organisms and in the abundance of populations, which can lead to radical changes in the dynamics and functioning of ecosystems [115,116]. Eight out of 56 taxa are currently threatened with extinction following Brazilian law [47,117], including *Epinephelus itajara, E. marginatus, Genidens barbus, Megalops atlanticus, Pomatomus saltatrix, Scarus sp.* and *Sphyrna zygaena*. Although fishing of *E. itajara* has been banned in 2002, it continues to be recorded in Brazil [35]. Also, among these 56 taxa, some are heavily targeted by current fisheries, such as is the case of *Katsuwonus pelamis*, *Micropogonias furnieri*, *Balistes capriscus*, *Mugil sp.*, *Cynoscion acoupa* and *Cynoscion guatucupa* [35,118]. None of these taxa have shown declines in the catch amount in recent years [35]. More than half (n = 27) are reef-associated, such as *Cephalopholis fulva, Chaetodipterus faber, Dactylopterus volitans,* both *Epinephelus sp.* mentioned before, among others [43]. Thus, the 56 taxa that persisted might be vulnerable to fishing rather than resilient to fishing. But then why does the function (or the portion of the functional spectrum occupied by the species) not disappear? Apparently, this is an effect of species richness. Ecosystem functions performed by these persistent taxa might be well assured due to the high number of taxa with similar trait combinations in the functional spectrum. Avoiding loss of species redundancy

through effective conservation policies and fishing quotas can allow sustainable and lasting fishing of these species that seem to have attributes that allow a rapid replacement of fish stocks (i.e., rapid recovery of population size).

4) Conclusion

Zooarchaeological remains and historical data are vital tools to build long-term knowledge about human impacts on marine ecosystems [119,120]. In spite of the multiple biases and limitations that interfere with the quality of this type of data, such as lack of standardization, reliability of information sources, mistaken or generalized identifications, among others cited by Lopes et al. 2016 [17]. There is a pressing need to validate this type of data as a source of information for the conservation and management of biodiversity through refined curation, translation, digitization and the availability of data. With the advancement of trait-based approaches and the possibility to merge this approach with historical data, we now have the opportunity to learn from the past and improve the future through fisheries management and conservation of ecosystems.

Many studies reveal the existence of different levels of human impact on marine ecosystems in past times [2,14,17,18]. In summary, this research shows that besides targeting certain taxa having functionally redundant traits, fisheries also exploited several traits vulnerable to extinction [23]. We found that (i) fishing is selective, focused on: benthopelagic and pelagic taxa, roving and highly mobile, invertivores and macrocarnivores, forming small to large aggregations, habitat specialists and semi-specialists, with maximum body sizes of ~80cm; (ii) the advancement of fisheries methods possibly led to the exploitation of new traits, from the conquest of new habitats far from the coast, such as planktivores, sedentary, benthic, solitary and small body sized taxa and

(iii) over time, the entire functional spectrum came to be fished. Fisheries tend to remove entire functional groups from coastal marine ecosystems [111], as our analysis demonstrates by the spectrum of functional traits exploited over time.

This study is the first to provide a long-term process of exploitation of the functional spectrum composed of multiple marine taxa, highlighting the potential of zooarchaeological remains, historical data and trait-based approach to predict the possible scenarios of human impacts in the ecosystem functioning. In addition, we supplied a compilation of information regarding long-term fisheries and functional traits that can serve as a basis for several other studies. Conservation plans aimed at maintaining ecosystem functions affect directly the coastal livelihoods and economies and global fisheries [77], therefore the identification of fisheries target traits over time can have significant management implications related to overexploitation of marine ecosystems.

5) Acknowledgements

6) References

1. Yellen JE, Brooks AS, Cornelissen E, Mehlman MJ, Stewart K. 1995 A middle stone age worked bone industry from Katanda, Upper Semliki Valley, Zaire. *Science* **268** (5210). 553-556. (doi:10.1126/science.7725100)

2. Jackson JB *et al*. 2001 Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**. 629-638. (http://www.jstor.org/stable/3084305)

3. Dulvy NK, Sadovy Y, Reynolds JD. 2003 Extinction vulnerability in marine populations. *Fish Fish* **44**, 25-64. (https://doi.org/10.1046/j.1467-2979.2003.00105.x)

4. Worm B et al. 2006 Impacts of Biodiversity loss on ocean ecosystem services. *Science* **314**. 787-790. (https://doi.org/10.1126/science.1132294)

5. McCauley DJ, Pinsky ML, Palumbi SR, Estes JA, Joyce FH, Warner RR. 2015 Marine defaunation: animal loss in the global ocean. *Science* **347**(6219), 1255641. (https://doi.org/10.1126/science.1255641)

6. Rick TC, Erlandson JM. 2008 Human impacts on ancient marine ecosystems - A global perspective. Univ. of California press. (https://www.jstor.org/stable/10.1525/j.ctt1pphh3)

7. Lotze HK, Worm B. 2009 Historical baselines for large marine animals. *Trends Ecol. Evol.* **24**(5). 254-262. (https://doi.org/10.1016/j.tree.2008.12.004)

8. McClenachan L, O'Connor G, Neal BP, Pandolfi JM, Jackson JB. 2017 Ghost reefs: Nautical charts document large spatial scale of coral reef loss over 240 years. *Sci. Adv.* **3**(9). 1-7. (doi:10.1126/sciadv.1603155)

9. Early-Capistrán MM, Sáenz-Arroyo A, Cardoso-Mohedano JG, Garibay-Melo G, Peckham H, Koch V. 2018 Reconstructing 290 years of a data-poor fishery through ethnographic and archival research: The East Pacific green turtle (Chelonia mydas) in Baja California, Mexico. *Fish Fish* **19**. 57-77. (https://doi.org/10.1111/faf.12236)

10. Boivin N, Crowther A. 2021 Mobilizing the past to shape a better Anthropocene. *Nat. Ecol. Evol.* **5**. 273–284. (https://doi.org/10.1038/s41559-020-01361-4)

11. Pandolfi JM et al. 2003 Global trajectories of the long-term decline of coral reef ecosystems. *Science* **301**(5635), 955-958. (https://doi.org/10.1126/science.1085706)

12. Bourque BJ, Johnson BJ, Steneck RS. 2008 Possible prehistoric fishing effects on coastal marine food webs in the Gulf of Maine. Human impacts on ancient marine ecosystems: A global perspective, 165-185. (http://www.jstor.org/stable/10.1525/j.ctt1pphh3.12.)

13. Limburg KE, Walther Y, Hong B, Olson C, Storå J. 2008 Prehistoric versus modern Baltic Sea cod fisheries: selectivity across the millennia. *Proc. R. Soc. B* **275**(1652), 2659-2665. (https://doi.org/10.1098/rspb.2008.0711)

14. Rick TC, Erlandson JM. 2009 Coastal exploitation. *Science*, **325**(5943), 952-953. (https://doi.org/10.1126/science.1178539)

15. Pestle WJ. 2013 Fishing Down a Prehistoric Caribbean Marine Food Web: Isotopic Evidence From Punta Candelero, Puerto Rico. *J. Isl. Coast. Archaeol.* **8:2**, 228-254, (http://dx.doi.org/10.1080/15564894.2013.797943)

16. Gobalet KW, Jones TL. 1995 Prehistoric native american fisheries of the central California coast. *Trans. Am. Fish. Soc.* **124** (6). 813-823. (https://doi.org/10.1577/1548-8659(1995)124%3C0813:PNAFOT%3E2.3.CO;2)

17. Lopes MS *et al.* 2016 The patch towards endangered species: Prehistoric fisheries in Southeastern Brazil. *Plos One* **11**(6), ou 1-36. (https://doi.org/10.1371/journal.pone.0154476)

18. Wing SR, Wing ES. 2001 Prehistoric fisheries in the Caribbean. *Coral Reefs* **20**(1). 1-8. (https://doi.org/10.1007/s003380100142)

19. Tavares DC, Moura JF, Acevedo-Trejos E, Merico A. 2019 Traits shared by marine megafauna and their relationships with ecosystem functions and services. *Front. Mar. Sci.* **6**. 262 (https://doi.org/10.3389/fmars.2019.00262)

20. Bellwood DR, Streit RP, Brandl SJ, Tebbett SB. 2018 The meaning of the term "function" in ecology: A coral reef perspective. *Funct. Ecol.* **33**. 948-961. (https://doi.org/10.1111/1365-2435.13265)

21. Pimiento C, Leprieur F, Silvestro D, Lefcheck JS, Albouy C, Rasher DB, Davis M, Svenning J-C, Griffin JN. 2020 Functional diversity of marine megafauna in the Anthropocene. *Sci. Adv.* **6**(16). 1-12 (https://doi.org/10.1126/sciadv.aay7650)

22. Bender MG, Floeter SR, Mayer FP, Vila-Nova DA, Longo GO, Hanazaki N, Carvalho-Filho A, Ferreira CEL. 2013 Biological attributes and major threats as predictors of the vulnerability of species: a case study with Brazilian reef fishes. *Oryx* **47**(2). 259-265. (https://doi.org/10.1017/S003060531100144X)

23. Ceretta BF, Fogliarini CO, Giglio VJ, Maxwell ML, Waechter LS, Bender MG. 2020 Testing the accuracy of biological attributes in predicting extinction risk. *Perspect. Ecol. Conserv.* **18**. 12-18. (https://doi.org/10.1016/j.pecon.2020.01.003)

24. Cooke RS, Eigenbrod F, Bates AE. 2019 Projected losses of global mammal and bird ecological strategies. *Nat. Commun.* **10**(1), 1-8. (https://doi.org/10.1038/s41467-019-10284-z)

25. Waechter LS, Luiz OJ, Leprieur F, Bender MG. 2021 Functional biogeography of marine vertebrates in Atlantic Ocean reefs. *Divers* **28**(8). 1680-1693. (https://doi.org/10.1111/ddi.13430)

26. Mason NW, Mouillot D, Lee WG, Wilson JB. 2005 Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, **111**(1), 112-118. (https://doi.org/10.1111/j.0030-1299.2005.13886.x)

27. De Bello F, Carmona C, Dias A, Gotzanberger L, Moretti M, Berg M. 2021. Handbook of Trait-Based Ecology: From theory to R Tools. Cambridge University Press. (https://doi.org/10.1017/9781108628426)

28. Rousseau Y, Watson RA, Blanchard JL, Fulton EA. 2019. Evolution of global marine fishing fleets and the response of fished resources. *PNAS* **116**(25), 12238-12243. (https://doi.org/10.1073/pnas.1820344116)

29. Pauly, D. 2008. Global fisheries: a brief review. *J. Biol. Res. (Thessalon*) **9**: 3-9.

30. Diegues AC. 2006 Artisanal Fisheries in Brazil. International Collective in Support of Fishworkers (ICSF). (http://hdl.handle.net/1834/18210)

31. Vasconcellos M, Diegues AC and Kalikoski DC. 2011 Coastal fisheries of Brazil. In Salas S, Chuenpagdee R, Charles A and Seijo JC (eds). Coastal fisheries of Latin America and the Caribbean. FAO Fisheries and Aquaculture Technical Paper. No. 544. Rome, FAO. pp. 73–116.

32. Villéger S, Mason NW, Mouillot D. 2008 New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89**(8), 2290-2301. (https://doi.org/10.1890/07-1206.1)

33. Grenié M, Denelle P, Tucker CM, Munoz F, Violle C. 2017 Funrar: Na R package to characterize functional rarity. *Divers* **23**(12). 1365-1371. (https://doi.org/10.1111/ddi.12629)

34. Jennings S, Greenstreet SP, Reynolds JD. 1999 Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *J. Anim. Ecol.* **68**(3), 617-627. (https://doi.org/10.1046/j.1365-2656.1999.00312.x)

35. Freire KMF *et al*. 2021 Reconstruction of marine commercial landings for the Brazilian industrial and artisanal fisheries from 1950 to 2015. *Front. Mar. Sci*. **8**, 659110. (https://doi.org/10.3389/fmars.2021.659110)

36. Wagner G, Hilbert K, Bandeira D, Tenório MC, Okumura MM. 2011 Sambaquis (Shell mounds) of the Brazilian coast. *Quat. Int.* **239**. 51-60. (https://doi.org/10.1016/j.quaint.2011.03.009)

37. Instituto Chico Mendes de Conservação da Biodiversidade. Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Sudeste e Sul – CEPSUL. Available in: < https://www.icmbio.gov.br/cepsul/>

38. Brazil and Manuel Haimovici. 2007. A Prospecção Pesqueira E Abundância De Estoques Marinhos No Brasil Nas Décadas De 1960 a 1990 : Levantamento De Dados E Avaliação Crítica. Ministério do Meio Ambiente Secretaria de Mudanças Climáticas e Qualidade Ambiental. Brasília.

39. Freire KMF *et al.* 2015 Reconstruction of catch statistics for Brazilian marine waters (1950-2010). *Fish. Cent. Res. Rep.* **23**(4). 3-30.

40. Froese, R. and Pauly D. 1999 FishBase. World Wide Web electronic publication. www.fishbase.org, version (02/2022).

41. Freire KMF, Pauly D. 2005 Richness of common names of brazilian marine fishes and its effect on catch statistics. *J. Ethnobiol.* **25**(2). 279-296. (https://doi.org/10.2993/0278-0771(2005)25[279:ROCNOB]2.0.CO;2)

42. Papavero N, Teixeira DM. 2014 Zoonímia tupi nos escritos quinhentistas europeus. *Núcleo de apoio à pesquisa em etimologia e história da língua portuguesa* **3**. 1-329. (https://doi.org/10.11606/9788575062302)

43. Pinheiro HT. *et al.* 2018 South-western Atlantic reef fishes: Zoogeographical patterns and ecological drivers reveal a secondary biodiversity centre in the Atlantic Ocean. *Divers,* **24**(7), 951-965. (https://doi.org/10.1111/ddi.12729)

44. Parravicini V *et al.* 2020 Delineating reef fish trophic guilds with global gut content data synthesis and phylogeny. *PLoS Biol.* **18**(12). 1-20. (https://doi.org/10.1371/journal.pbio.3000702)

45. Quimbayo JP, Silva FC, Mendes TC, Ferrari DS, Danielski SL, Bender MG, Parravicini V, Kulbicki M, Floeter SR. 2021 Life-history traits, geographical range and conservation aspects of reef fishes from the Atlantic and Eastern Pacific. *Ecology* **102**(5). 1-40. (https://doi.org/10.5281/zenodo.4455016)

46. Palomares MLD, Pauly D. 2022. SeaLifeBase. World Wide Web electronic publication. Available in: <www.sealifebase.org>, version (04/2022).

47. IUCN. 2021. The IUCN Red List of Threatened Species. Version 2021-1. (https://www.iucnredlist.org. Accessed on [26 august 2022])

48. Information System about the Brazilian Biodiversity (SiBBr), 2022. Available in: <https://sibbr.gov.br/>

49. Becker RA, Chambers JM, Wilks AR. 1988 The new S language. Wadsworth & Brooks/Cole. *Computer Science Series*, Pacif Grove, CA.

50. Villéger S, Brosse S, Mouchet M, Mouillot D, Vanni MJ. 2017 Functional ecology of fish: current approaches and future challenges. *Aquat. Sci.* **79**. 783-801. (https://doi.org/10.1007/s00027-017-0546-z)

51. Borcard D, Gillet F, Legendre P. 2018 Unconstrained ordination. In Numerical ecology with R. Use R!. Springer, Cham. 151-201. (https://doi.org/10.1007/978-3-319-71404-2_5)

52. Duong T. 2007 Kernel Density Estimation and Kernel Discriminant Analysis for multivariate data in R. *J. Stat. Softw.* **21**. 1-16. (https://doi.org/10.18637/jss.v021.i07)

53. Díaz S. *et al.* 2016 The global spectrum of plant form and function. *Nature* **529**(7585), 167-171. (https://doi.org/10.1038/nature16489)

54. De Bello F, Botta-Dukát Z, Leps J, Fibich P. 2020 Towards a more balanced combination of multiple traits when computing functional differences between species. *Methods Ecol. Evol.* **12**. 443-448. (https://doi.org/10.1111/2041-210X.13537)

55. Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR. 2013 A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* **28**(3). 167-177. (http://dx.doi.org/10.1016/j.tree.2012.10.004)

56. Dray S, Dufour AB. 2007 The ade4 package: implementing the duality diagram for ecologists. *J. Stat. Softw.* **22**. 1-20 (https://doi.org/10.18637/jss.v022.i04)

57. Wickham H. 2016 gplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. ISBN 978-3-319-24277-4. Available in: <http://ggplot2.org>

58. Laliberté E, Legendre P. 2010 A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91**(1). 299-305. (https://doi.org/10.1890/08-2244.1)

59. Swenson NG. 2014 Functional and phylogenetic ecology in R. Use R!. New York: Springer. **639**. 212. (https://doi.org/10.1007/978-1-4614-9542-0)

60. R Core Team. 2018 R: Language and Environment for Statistical Computing; R Foundation for Statistical Computing, Vienna. (https://www.R-project.org)

61. Lei Federal nº 7.643. Proíbe pesca de cetáceo nas águas jurisdicionais brasileiras, e dá outras providências. Nº (18-12-87) 22079-22079. [Consult. 26 ago. 2022]. Available in: <https://www.legjur.com/legislacao/art/lei_00076431987-0>

62. Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F. 1998 Fishing down marine food webs. *Science* **279**(5352), 860-863. (https://doi.org/10.1126/science.279.5352.860)

63. Hardt MJ. 2009 Lessons from the past: the collapse of Jamaican coral reefs. *Fish Fish*, **10**(2), 143-158. (https://doi.org/10.1111/j.1467-2979.2008.00308.x)

64. Reitz EJ. 2004 "Fishing down the food web": A case study from St. Augustine, Florida, USA. *Am. Antiq.* **69**(1), 63-83. (https://doi.org/10.2307/4128348)

65. Rick TC, Erlandson JM, Braje TJ, Estes JA, Graham MH, Vellanoweth RL. 2008 Historical ecology and human impacts on coastal ecosystems of the Santa Barbara Channel region, California. Human impacts on ancient marine ecosystems: A global perspective, 77-101. (http://www.jstor.org/stable/10.1525/j.ctt1pphh3.8)

66. Estes JA, Heithaus M, McCauley DJ, Rasher DB, Worm B. 2016 Megafaunal impacts on structure and function of ocean ecosystems. *Annu Rev Environ Resour* **41**(1), 83-116. (https://doi.org/10.1146/annurev-environ-110615-085622)

67. Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH. 2007 Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* **315**(5820), 1846-1850. (https://doi.org/10.1126/science.1138657)

68. Lucas Z, Stobo WT. 2000 Shark-inflicted mortality on a population of harbour seals (*Phoca vitulina*) at Sable Island, Nova Scotia. *J. Zool.* **252**(3), 405-414. (https://doi.org/10.1111/j.1469-7998.2000.tb00636.x)

69. Wirsing AJ, Heithaus MR, Dill LM. 2007 Living on the edge: dugongs prefer to forage in microhabitats that allow escape from rather than avoidance of predators. *Anim. Behav.* **74**(1), 93-101. (https://doi.org/10.1016/j.anbehav.2006.11.016)

70. Heithaus MR, Frid A, Wirsing AJ, Worm B. 2008 Predicting ecological consequences of marine top predator declines. *Trends Ecol. Evol.* **23**(4), 202-210. (https://doi.org/10.1016/j.tree.2008.01.003)

71. Sadovy de Mitcheson Y. *et al.* 2013 Fishing groupers towards extinction: a global assessment of threats and extinction risks in a billion dollar fishery. *Fish Fish*, **14**(2), 119-136. (https://doi.org/10.1111/j.1467-2979.2011.00455.x)

72. Dulvy NK. *et al.* 2014 Extinction risk and conservation of the world's sharks and rays. *elife*, **3**, e00590. (https://doi.org/10.7554/eLife.00590)

73. Koutsidi M, Tzanatos E, Machias A, Vassilopoulou V. 2016 Fishing for function: the use of biological traits to evaluate the effects of multispecies fisheries on the functioning of fisheries assemblages. *ICES J. Mar. Sci.* **73**(4), 1091-1103. (https://doi.org/10.1093/icesjms/fsw006)

74. Pinsky ML, Jensen OP, Ricard D, Palumbi SR. 2011 Unexpected patterns of fisheries collapse in the world's oceans. *PNAS* **108**(20), 8317-8322. (https://doi.org/10.1073/pnas.1015313108)

75. Cury PM *et al.* 2011 Global seabird response to forage fish depletion—one-third for the birds. *Science* **334**(6063), 1703-1706. (https://doi.org/10.1126/science.1212928)

76. Jennings S, Reynolds JD, Polunin NV. 1999 Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. *Conserv. Biol* **13**(6), 1466-1475. (https://doi.org/10.1046/j.1523-1739.1999.98324.x)

77. Zhao K, Gaines SD, García Molinos J, Zhang M, Xu J. 2022 Climate change and fishing are pulling the functional diversity of the world's largest marine fisheries to opposite extremes. *Glob. Ecol. Biogeogr* **31**(8), 1616-1629. (https://doi.org/10.1111/geb.13534)

78. Guillemot N, Chabanet P, Kulbicki M, Vigliola L, Léopold M, Jollit I, Le Pape O. 2014 Effects of fishing on fish assemblages in a coral reef ecosystem: from functional response to potential indicators. *Ecol. Indic.* **43**, 227-235. (https://doi.org/10.1016/j.ecolind.2014.02.015)

79. Wing ES, Wing SR. 1995 Prehistoric ceramic age adaptation to varying diversity of animal resources along the west indian archipelago. *J. Ethnobiol.* **15**. 119-148. (https://biostor.org/reference/175199)

80. Pepperell JG. 2018 Fishing for the Past: Casting Nets and Lines into Australia's Early Colonial History. *Rosenberg Publishing Pty Ltd* **1**, 240

81. Salls R. 1989 To catch a fish: some limitations on prehistoric fishing in southern California with special reference to native plant fiber fishing line. *J Ethnobiol.* **9**(2): 173–199. (https://www.jstor.org/stable/40713177)

82. de Castilho PV. 2008 Utilization of cetaceans in shell mounds from the southern coast of Brazil. *ScienceDirect* **108**. 107-114. (https://doi.org/10.1016/j.quaint.2007.09.015)

83. Gonzalez MMB. 2005 Tubarões e raias na pré-história do litoral de São Paulo (Doctoral dissertation, Universidade de São Paulo). DOI. 10.11606/T.71.2005.tde-29092006-114551

84. Gilson SP, Lessa A. 2021 Arqueozoologia do sítio Rio do Meio (SC): discutindo estilo de vida de pescadores-caçadores-coletores através de uma abordagem ecossistêmica. *Revista de Arqueologia,* **34**(1), 217-248. (https://doi.org/10.24885/sab.v34i1.812)

85. Beck MW. 2003 The role of nearshore ecosystems as fish and shellfish nurseries. *Issues Ecol.* **11**, 1-12.

86. Heupel MR, Carlson JK, Simpfendorfer CA. 2007 Shark nursery areas: concepts, definition, characterization and assumptions. *Mar. Ecol. Prog.* **337**, 287-297. (https://doi.org/10.3354/MEPS337287)

87. O'Connor S, Ono R, Clarkson C. 2011 Pelagic fishing at 42,000 years before the present and the maritime skills of modern humans. *Science* **334**(6059), 1117-1121. (https://doi.org/10.1126/science.1207703)

88. da Conceição GC., dos Santos CFM., Oliveros JM, Bracht F. 2013 Da Piracema ao Timbó: A pesca feita pelos colonizadores portugueses na América portuguesa do século XVI. *Conference: VI Congresso Internacional de História.* (http://dx.doi.org/10.4025/6cih.pphuem.86)

89. Bouchard J. 2022 Casting the net: early Atlantic fisheries and colonial expansion, 15-16th centuries. *Tempo* **28**, 160-177. (https://doi.org/10.1590/TEM-1980-542X2022v280109)

90. Del Priore M, Venancio R. 2010 Uma breve história do Brasil. *Editora Planeta do Brasil*.

91. Pearson JC. 1942 The fish and fisheries of colonial Virginia. *The William and Mary Quarterly*, **22**(4), 353-360. (https://doi.org/10.2307/1923334)

92. Lucas RE. 2002 The industrial revolution: Past and future. *Lectures on economic growth*, **109**, 188.

93. Aronson, R. B., Thatje, S., McClintock, J. B., & Hughes, K. A. (2011). Anthropogenic impacts on marine ecosystems in Antarctica. *Ann. N. Y. Acad. Sci.* **1223**(1), 82-107. (https://doi.org/10.1111/j.1749-6632.2010.05926.x)

94. Yao CL, Somero GN. 2014 The impact of ocean warming on marine organisms. *Sci. Bull.* **59**. 468–479. (https://doi.org/10.1007/s11434-014-0113-0)

95. Teh LC, Sumaila UR. 2013 Contribution of marine fisheries to worldwide employment. *Fish Fish* **14**(1), 77-88. (https://doi.org/10.1111/j.1467-2979.2011.00450.x)

96. Mbaru EK, Graham NA, McClanahan TR, Cinner JE. 2020 Functional traits illuminate the selective impacts of different fishing gears on coral reefs. ***J. Appl. Ecol.*** **57**(2), 241-252. (https://doi.org/10.1111/1365-2664.13547)

97. Carvalho F, Castello L, Ferreira B, McDonald G, Power M. 2021 Gear selectivity of functional traits in coral reef fisheries in Brazil. *Coral Reefs* **40**(6), 1915-1929. (https://doi.org/10.1007/s00338-021-02192-w)

98. Giulietti N, Assumpção RD. 1995 Indústria pesqueira no Brasil. *Agricultura em São Paulo,* **42**(2), 95-127.

99. Paiva MP, Rocha CAS, Gomes AMG, Andrade M.F. 1996 Fishing grounds of bottom liners on the continental shelf of south-east Brazil. *Fish. Man. Ecol.* **3**: 25-33. (https://doi.org/10.1111/j.1365-2400.1996.tb00127.x)

100. Palomares MLD, Pauly D. 2019 Coastal fisheries: the past, present, and possible futures. In Coasts and estuaries (pp. 569-576). *Elsevier*. (https://doi.org/10.1016/B978-0-12-814003-1.00032-0)

101. Piñeiro CG, Casas M, Bañón R. 2001. The deepwater fisheries exploited by Spanish fleets in the northeast Atlantic: a review of the current status. *Fish. Res*. **51** (2-3). 311-320. (https://doi.org/10.1016/S0165-7836(01)00254-5)

102. Gordon JDM, Bergstad OA, Figueiredo I, & Menezes G. 2003 Deep-water fisheries of the NortheastAtlantic: I Description and current trends. *J. Northwest Atl. Fish. Sci*. (**1**), 137-150.

103. Perez JAA. 2006 Potenciais de rendimento dos alvos da pesca de arrasto de talude do sudeste e sul do Brasil estimados a partir de parâmetros do ciclo de vida. *Brazilian Journal of Aquatic Science and Technology*, **10**(2), 1-11.

104. Perez A, Angel J, Pezzuto PR, Wahrlich R, Soares ALS. 2009 Deep-water fisheries in Brazil: history, status and perspectives. *Lat. Am. J. Aquat* **37**(3), 513-541. (https://doi.org/10.3856/vol37-issue3-fulltext-18)

105. Selgrath JC, Gergel SE, Vincent AC. 2018 Shifting gears: Diversification, intensification, and effort increases in small-scale fisheries (1950-2010). *PLoS One* **13**(3), e0190232. (https://doi.org/10.1371/journal.pone.0190232)

106. Hutchings JA, Minto C, Ricard D, Baum JK, Jensen OP. 2010 Trends in the abundance of marine fishes. *Can. J. Fish. Aquat. Sci.* **67**(8), 1205-1210. (https://doi.org/10.1139/F10-081)

107. Worm B. and Tittensor DP. 2011 Range contraction in large pelagic predators. *PNAS* **108**(29), 11942-11947. (https://doi.org/10.1073/pnas.1102353108)

108. Burgess MG, Polasky S, Tilman D. 2013 Predicting overfishing and extinction threats in multispecies fisheries. *PNAS* **110**(40), 15943-15948. (https://doi.org/10.1073/pnas.1314472110)

109. Worm B *et al.* 2009 Rebuilding global fisheries. *Science* **325**(5940), 578-585. (https://doi.org/10.1126/science.1173146)

110. Barley SC, Clark TD, Meeuwig JJ. 2020 Ecological redundancy between coral reef sharks and predatory teleosts. *Rev. Fish Biol. Fish.* **30**, 153–172. (https://doi.org/10.1007/s11160-019-09588-6)

111. Micheli F, Halpern BS. 2005 Low functional redundancy in coastal marine assemblages. *Ecol. Lett.* **8**(4), 391-400. (https://doi.org/10.1111/j.1461-0248.2005.00731.x)

112. Murawski SA. 2000 Definitions of overfishing from an ecosystem perspective. *ICES J. Mar. Sci.* **57**(3), 649-658. (https://doi.org/10.1006/jmsc.2000.0738)

113. Bonaldo RM, Hoey AS, Bellwood DR. 2014 The ecosystem roles of parrotfishes on tropical reefs. *Oceanogr. Mar. Biol.* **52**, 81-132. (http://dx.doi.org/10.1201/b17143-3)

114. Longo GO, Ferreira CEL, Floeter SR. 2014 Herbivory drives large-scale spatial variation in reef fish trophic interactions. *Ecol. Evol.* **4**(23), 4553-4566. (https://doi.org/10.1002/ece3.1310)

115. Floeter SR, Halpern BS, Ferreira CEL. 2006 Effects of fishing and protection on Brazilian reef fishes. *Biol. Conserv.* **128**(3), 391-402. (https://doi.org/10.1016/j.biocon.2005.10.005)

116. Bellwood DR, Hoey AS, Hughes TP. 2012 Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. *Proc. R. Soc. B* **279**(1733), 1621-1629. (https://doi.org/10.1098/rspb.2011.1906)

117. Instituto Chico Mendes de Conservação da Biodiversidade. 2018. Livro Vermelho da Fauna Brasileira Ameaçada de Extinção: Volume VI - Peixes. In: Instituto Chico Mendes de Conservação da Biodiversidade (Org.). Livro Vermelho da Fauna Brasileira Ameaçada de Extinção. Brasília: ICMBio. 1232p.

118. Cergole MC, Ávila-da-Silva AO, Rossi-Wongtschowski CLDB. 2005 Análise das principais pescarias comerciais da região Sudeste-Sul do Brasil: dinâmica populacional das espécies em explotação (pp. 101-107). *Instituto Oceanográfico*.

119. Fossile T, Ferreira J, da Rocha Bandeira D, Dias-da-Silva S, Colonese AC. 2020 Integrating zooarchaeology in the conservation of coastal-marine ecosystems in Brazil. *Quat. Int.* **545**, 38-44. (https://doi.org/10.1016/j.quaint.2019.04.022)

120. Gallardo SS, Fossile T, Herbst DF, Begossi A, Silva LG, Colonese AC. 2021 150 years of anthropogenic impact on coastal and ocean ecosystems in Brazil revealed by historical newspapers. *Ocean. Coast. Manag.* **209**. 105662 (https://doi.org/10.1016/j.ocecoaman.2021.105662)

Supplementary material

(a) Richness across periods
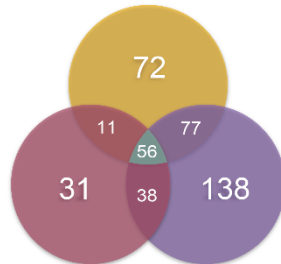
(b) Taxonomic group richness per period

| Periods | ☐ Total | 🟨 Shellmounds | 🟥 Colonial | 🟪 Current | 🟩 All Periods |

Figure S1) A. Richness across periods. Of the 423 taxa exploited over time, 56 were fished in all 3 periods. In the Shellmounds period, a total of 216 taxa were fished, 72 of these being fished exclusively in this period, 11 fished also in the colonial period and 77 fished also in the current period. In the Colonial period, 136 taxa were fished, 31 fished exclusively in this period and 38 fished also in the current one. And in the current period, 138 taxa were fished in this period alone. **B. Taxonomic group richness per period.** Each color represents the total and period richness of each fished taxonomic group. Silhouettes represent the 3 taxonomic groups exploited (Osteichthyes, Chondrichthyes and Cetacea).

Traits Guide

<u>Group size</u>

This trait was divided into three categories: "solitary", "small aggregations" (pairs or schools >20 individuals) and "large aggregations" (more than 20 individuals). For the species for which we did not find information on the detailed number of individuals, only those that formed schools, they were considered as large aggregations. Reproductive aggregations, i.e. spawning, were not considered, only if the species form groups or not in the adult phase.

Habitat use

Habitat use was based on the sum of different habitat types used by the taxa. There are four categories: Specialists (use of 1 or 2 different habitat types); Semi specialists (3 or 4 habitats); Semi generalists (5 or 6) and Generalists (7 or 8). The eight habitat types considered are: biogenic reefs, rocky reefs, rhodolith banks, tide pools, sea grasses, soft bottoms, estuaries/mangroves and open sea (ocean).

Maximum body size

The maximum body size, in centimeters, was defined according to information from Fishbase and SealifeBase. To discuss, we created 3 size classes: small (< 40cm), medium (40 – 80 cm) and large (< 80cm).

Mobility

Represents the organism's ability to move in water, which can be: highly mobile (including vertical, latitudinal and/or coastal–oceanic movements), roving (swimming and foraging slowly, with short movements) and sedentary (little/few displacements, small home range, some are territorial).

Trophic category

The trophic categories were adapted to the following classifications, according to the diet of the groups during the adult phase: planktivore (small organisms in the water column), herbivore/detritivore (turf or filamentous algae and/or undefined organic matter), invertivore (mobile/sessile and macro/micro invertebrates), piscivorous (only fish or fish and cephalopods), omnivore (different groups within the food chain, from plankton, algae and invertebrates to fish), and macrocarnivore (fish, crustaceans and molluscs).

Vertical position

The vertical position in the water column was divided into three categories: pelagic, benthopelagic and benthic. Pelagic taxa forage and live mostly in the water column, benthopelagic individuals

transit between benthic and pelagic zones and benthic taxa are closely associated with bottom, where they can live hidden or foraging close to the bottom.