Biota Neotropica 18(1): e20170394, 2018
www.scielo.br/bn

biotaneotropica
ISSN 1676-0611 (online edition)
inventory

Biodiversity of Holocene marine fish of the southeast coast of Brazil

***Augusto Barros Mendes*[1], *Michelle Rezende Duarte*[1*] & *Edson Pereira Silva*[1]**

[1]*Universidade Federal Fluminense, Departamento de Biologia Marinha, Niterói, Brazil.*
**Corresponding author: Michelle Rezende Duarte, e-mail: michellerezendeduarte@yahoo.com.br*

MENDES, A. B., DUARTE, M. R., SILVA, E. P. **Biodiversity of Holocene marine fish of the southeast coast of Brazil.** Biota Neotropica. 18(1): e20170394. http://dx.doi.org/10.1590/1676-0611-BN-2017-0394

Abstract: Middens are archaeological sites dating between 8,000 and 1,000 years before present and are commonly found on the Brazilian coast. Data were collected from 68 middens allowing an inventory of 142 fish species, most of them recorded in no more than five sites. Conversely, *Micropogonias furnieri* and *Pogonias cromis* had the highest frequencies of occurrence. The biogeographic, ecological and economic data showed that most of the identified fish are widely distributed in the Western Atlantic (59.72%) and inhabit estuarine environments (53.99%), while most species have a demersal habit (35.92%) and exhibit oceanic migratory behaviour (28.87%). Lastly, the surveyed fish are predominantly carnivorous (72.54%) with some commercial value (96.48%). Chi-squared tests comparing midden inventory and current ichthyofauna checklists failed to show significant differences between them ($p > 0.99$). Thus, the results indicate that zoo-archaeological fish remains are key evidence of Holocene biodiversity and may help the establishment of more complete baselines.

Keywords: *Baselines, Fishermen-Gatherers-Hunters, Ichthyofauna, Middens, Species richness, Zooarchaeology.*

Biodiversidade de peixes marinhos do Holoceno da costa Sudeste brasileira

Resumo: Sambaquis são sítios arqueológicos, datando entre 8,000 e 1,000 anos antes do presente, encontrados na costa brasileira. Neste trabalho, dados ictiológicos referentes a 68 sambaquis da costa Sudeste do Brasil foram compilados e construído um inventário de referência no qual constam 142 espécies, a maioria das quais com registro em não mais que cinco sítios. Por outro lado, as espécies *Micropogonias furnieri* e *Pogonias cromis* apresentaram alta frequência de ocorrência nos sambaquis. Os dados biogeográficos, ecológicos e econômicos mostraram que a maioria das espécies registradas nos sambaquis são de ampla distribuição no Atlântico Ocidental (59.72%), habitam ambientes estuarinos (53.99%), tem um hábito demersal (35.92%) e comportamento oceânico migratório (28.87%). A maioria dos registros diz respeito a peixes carnívoros (72.54%) e com algum valor comercial (96.48%). A comparação da lista de ictiofauna registrada para os sambaquis com uma lista construída com base em inventários atuais de peixes para mesma região não mostrou diferenças significativas (teste de qui-quadrado, $p > 0.99$). Dessa forma, os resultados apresentados indicam que os vestígios de ictiofauna encontrados em sambaquis constituem uma amostra relevante da biodiversidade do Holoceno podendo ser muito úteis na construção de inventários de referências mais completos da fauna ictiológica da costa brasileira.

Palavras-chave: *Ictiofauna, Inventário de referências, Pescadores-Coletores-Caçadores, Riqueza de espécies, Sambaquis, Zooarqueologia*

Introduction

Biodiversity-related research has developed significantly since the 1990s, when ecologists worldwide, concerned with anthropogenic effects on ecosystems, intensified their studies of environmental issues (Amaral & Jablonsky 2005, Lewinsohn & Prado 2005). Biodiversity is defined by the Convention on Biological Diversity as the variability among living beings of all origins, including terrestrial, marine and other aquatic ecosystems, and their associated ecological complexes, including intra- and inter-species as well as ecosystem diversity (Arruda et al. 2000).

Recently, the Census of Marine Life raised the estimated number of known marine species from approximately 230,000 to between 1 and 1.4 million; more than 1,200 new species were identified among specimens collected in known and previously unexplored waters (Costello et al. 2010). Furthermore, in a review of research related to Brazilian biodiversity, Siqueira et al. (2015) found that only 21% of 1,156 references from 2009 to 2014 addressed the richness of aquatic species, indicating that the marine environment remains little studied and is therefore largely unknown. Finally, baselines for long-term studies of marine biodiversity are scarce (Knowlton & Jackson 2008, Pinnegar & Engelhard 2008).

Baselines are reference biodiversity inventories that directly assess the species composition of a specific site for a given spatial extent and time. The data generated by such inventories are one of the most important tools for the conservation and management of natural areas, especially the associated endangered species (Silveira et al. 2010). The establishment of baselines is particularly important for the conservation of marine fish because this group is intensely exploited due to their commercial value and account for a significant share of global fishery production. In Brazil, fisheries have been key to the development of the country, concentrating 70% of the population near the coast, and the sea plays a key role in its history, culture and economy (Rosa & Lima 2008).

To be as accurate as possible, reference inventories of ichthyological fauna should include not only current data but also historic and prehistoric (fossil/sub-fossil) data as well (Furon 1969, Warwick & Light 2002, Willis & Birks 2006, Froyd & Willis 2008, Stahl 2008). However, collecting data on the species compositions of the past is complicated because fossil/sub-fossil records are largely characterised by being incomplete; that is, the biological data (species morphology, richness, diversity and evenness, among others) preserved in those records are influenced by non-linear modifications that occur from the time of death to the final burial of an organism (Ritter & Erthal 2016) and the species preservation potential (Prummel & Heinrich 2005). Therefore, prehistoric records are relatively scarce (Bittencourt et al. 2015).

However, there are some Holocene species composition records from sources including beaches, death assemblages and middens. Beaches and restingas originated in the Holocene, but their characteristics prevent the establishment of a chronology (Lacerda et al. 1984). Conversely, death assemblages allow for accurate chronological estimates and have the great advantage of being natural, thus showing actual tanatocenoses, but these formations are rare along the Brazilian coast (Ritter & Erthal 2016). However, middens, which are archaeological sites dating between 8,000 and 1,000 years before present (BP, according to the convention before 1950), are commonly found on the Brazilian coast and allow a chronology to be established because they show a stratigraphic sequence of different species compositions (Kneip et al. 1988, Gaspar 1998, Scheel-Ybert et al. 2009, Klokler et al. 2010).

Middens were built by groups of prehistoric fishermen-gatherers-hunters, which explains why they are found in estuarine areas at the intersections of rivers and the sea. These sites contain a wealth of resources including sediments, coal, lithic material and, above all, faunal remains. High numbers of molluscs and crustaceans, including sea and sand crabs, as well as echinoderms and fish have been found among the marine zoo-archaeological remains recovered from middens (DeBlasis et al. 2007, Figuti 1993, Lima 2000, Lima et al. 2003).

For fish species, their zoo-archaeological remains indicate their usefulness to midden populations, so most species recorded at these sites have a cultural meaning and show sociocultural and identity relationships and spatiotemporal economic characteristics (Figuti 1998, Barbosa-Guimarães 2013, Wagner & Silva 2014, Lopes et al. 2016). Accordingly, because the ichthyological remains in middens represent the diversity of prehistoric fishes obtained from a selective catch, this data source underestimates the diversity of Holocene fish. That is, the species diversity of the remains found in the middens is lower than that in natural communities (Gonzalez 2005, Costa et al. 2012).

Although midden fish records underestimate natural diversity, they are a key source of information on the ichthyological fauna of the past because prehistoric people could only have caught the fish available in the environments at the time. Furthermore, by-catch occurred; that is, species with no known anthropological relevance were incidentally fished with target species (Reitz & Wing 2008, Villagran & Gianini 2014, Beuclair et al. 2016). Therefore, midden records are a good indicator of Holocene biodiversity, providing data on fish species composition, abundance, distribution and richness as well as cultural information (diet, fishing gear, ritualistic symbols, ornaments and artefacts) (Souza et al. 2010a, Souza et al. 2010b, Faria et al. 2014, Mendes et al. 2014, Rodrigues et al. 2016a, Rodrigues et al. 2016b, Beuclair et al. 2016, Silva et al. 2016).

Thus, although middens are artificial accumulations (that is, built by prehistoric populations) of biological material, the presence or absence of species at these sites provides sufficient data to create a taxonomic list that may be useful for defining a historical record of biological diversity (Stahl 2008), so this study presents an inventory of marine ichthyological biodiversity from southeast Brazilian middens. This list is the first comprehensive inventory of Holocene fish fauna from this region and may help elucidate past natural ocean events, enabling the establishment of more complete baselines to inform conservation and management measures.

Methods

The inventory was constructed from an extensive bibliographical survey of the libraries of universities and institutions with archaeological collections from sites along the southeast coast of Brazil as well as online databases (Web of Knowledge, Scientific Electronic Library Online - SciELO, Google Scholar and the Thesis Database of the Brazilian Federal Agency for the Support and Evaluation of Graduate Education (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – CAPES)). The data sources included scientific articles and books, thesis, dissertations, monographs and technical reports.

The list of species was analysed in terms of absolute and relative species richness and absolute and relative frequencies of occurrence. Absolute species richness is the number of species present at a sampled site, while the relative species richness is the ratio between that number and the total number of species. Similarly, the absolute frequency of occurrence is the number of sites at which a specific species occurs, and the relative frequency is the ratio between that number and the total number of sites.

Furthermore, taxonomic, biogeographic, ecological and economic data on the inventoried species were collected from the FishBase database (Froese & Pauly 2017) and categorised by distribution (range of occurrence), environment (habitat), habit (way of life at specific locations in the water column), behaviour (migratory movements), feeding guild (food requirements) and commercial value (demand for the species in the fish market).

The checklists constructed by Bizerril & Costa (2001) for Rio de Janeiro and Menezes (2011) for São Paulo were compared along with the inventory from the midden zoo-archaeological remains from this study to current ichthyological inventories for the same regions, and the species catalogued in *species*Link, a digital information system that integrates primary data from scientific collections in real time, for Espírito Santo were surveyed. Furthermore, a chi-squared test (χ^2) was performed to assess whether the ratio of commercial and non-commercial species in the midden fish inventory differed significantly from the ratios in current fish checklists.

Results

Data were collected from 68 middens distributed in 19 locations along the coast of three states of the Southeast Region of Brazil: Espírito Santo (ES), Rio de Janeiro (RJ) and São Paulo (SP) (Figure 1). The location with the highest number of middens (12 sites, 17.65%) was Paraty in the state of Rio de Janeiro, which also had the highest number of documented sites (53, 77.95%). Conversely, Espírito Santo had the lowest number of

 http://dx.doi.org/10.1590/1676-0611-BN-2017-0394

middens (2, 2.94%; Table 1). From these total of 68 middens, 49 of them had records of ^{14}C radiocarbonic dates (Figure 2). Occupation time ranged from 8,182 BP (Sambaqui de Camboinhas) to 675 BP (Sítio do Major). However, the majority of them were built and occupied during the period defined by Walker et al. (2012) as Late Holocene.

A total of 142 fish species were inventoried, and most taxa belonged to class Osteichthyes (105, 73.94%). Sciaenidae was the most represented family with 21 species, and *Cynoscion* Gill, 1861 was the genus with the highest number of species, seven in total (Table 2). Of the Chondrichthyes (37, 26.06%), the family with the highest number of species was Carcharhinidae with 17 species, and the most representative genus was *Carcharhinus* Blainville, 1816 with 12 species (Table 3).

The site with the highest species richness was the midden Sambaqui do Algodão in Angra dos Reis with 71 inventoried species and a relative species richness value of 0.5 (Table 1). Most of the inventoried species (63.38%) may be considered rare because they were recorded in no more than five of the 68 study sites. Conversely, *Micropogonias furnieri* (Desmarest, 1823) and *Pogonias cromis* (Linnaeus, 1766) had the highest frequencies of occurrence, being found in 53 (relative frequency = 0.78) and 48 (relative frequency = 0.71) of the sites, respectively.

The biogeographic, ecological and economic data showed that most of the identified fish are widely distributed in the Western Atlantic (59.72%) and inhabit estuarine environments (53.99%), while most species have a demersal habit (35.92%) and exhibit oceanic migratory behaviour (28.87%). Lastly, the surveyed fish are predominantly carnivorous (72.54%) with some commercial value (96.48%; Figure 3).

In comparison to the current fish checklists, the middens contained 17.60% of the species recorded in Rio de Janeiro, 15.57% of the species recorded in São Paulo and 2.13% of the species recorded in Espírito Santo. Overall, 17.57% of the fish recorded in the entire Southeast Region were represented in the middens, but they accounted for 28.07% of the species in the region with some commercial value. Moreover, exclusively historic species were identified including 13 in Rio de Janeiro, 15 in São Paulo, and four in Espírito Santo (Table 4). The results from the χ^2 tests indicated that were no significant differences in the number of commercial species in the historic and current inventories for the states (Rio de Janeiro: $\chi^2 = 4.587 \times 10^{-9}$, degrees of freedom = 3, probability > 0.995; São Paulo: $\chi^2 = 3.549 \times 10^{-12}$, degrees of freedom = 3, probability > 0.995; Espírito Santo: $\chi^2 = 0.106$, degrees of freedom = 3, probability > 0.99) or the entire Southeast Region ($\chi^2 = 6.349 \times 10^{-17}$, degrees of freedom = 3, probability > 0.995).

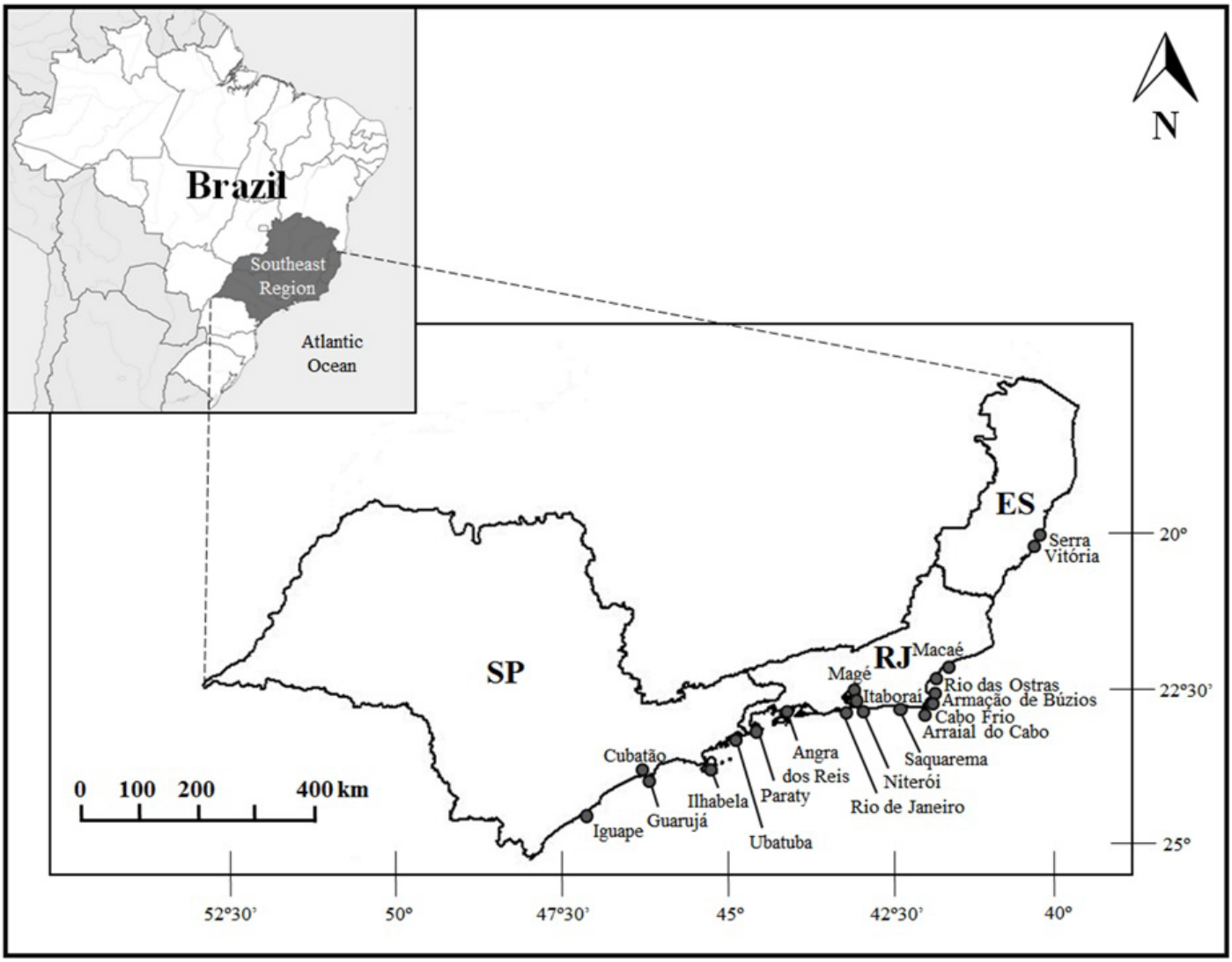

Figure 1. Map of the Southeast Region of Brazil with the locations of the inventoried middens.

Table 1. Middens inventoried in the Southeast Region of Brazil with absolute (Rspp) and relative (relative Rspp) species richness and the associated references from the literature.

Location	Midden	Code	Rspp	Relative Rspp	References
Angra dos Reis	Sambaqui da Caieira	1	27	0.190	Lima 1991, DSc Thesis, FFLCH-USP Lopes et al. 2016, PLoS One 11(6): 1-36
	Sambaqui da Caieira II	2	29	0.204	Lima 1991, DSc Thesis, FFLCH-USP Figuti 1998, Revista Arqueologia 11: 57-70
	Sambaqui do Algodão	3	71	0.500	Lima 1991, DSc Thesis, FFLCH-USP Lopes et al. 2016, PLoS One 11(6): 1-36 Figuti 1998, Revista Arqueologia 11: 57-70
	Sítio do Bigode I	4	38	0.268	Lima 1991, DSc Thesis, FFLCH-USP Lopes et al. 2016, PLoS One 11(6): 1-36 Figuti 1998, Revista Arqueologia 11: 57-70
	Sítio do Major	5	47	0.331	Lima 1991, DSc Thesis, FFLCH-USP Lopes et al. 2016, PLoS One 11(6): 1-36 Figuti 1998, Revista Arqueologia 11: 57-70
	Sítio do Peri	6	39	0.275	Lima 1991, DSc Thesis, FFLCH-USP Lopes et al. 2016, PLoS One 11(6): 1-36 Figuti 1998, Revista Arqueologia 11: 57-70
	Sítio Ilhota do Leste	7	14	0.099	Lima 1991, DSc Thesis, FFLCH-USP Lessa & Carvalho 2015, Bol Mus Para Emílio Goeldi 10: 489-507 Tenório 2003, DSc Thesis, PUC-RS Tenório 2003, Anais XII Congresso da SAB Lessa & Coelho 2010, Rev Mus Arqueol Etnol 20: 77-89
	Sambaqui do Acaiá	8	23	0.162	Lopes et al. 2016, PLoS One 11(6): 1-36
Macaé	Sítio da Ilha de Santana	9	13	0.092	Lima 1991, DSc Thesis, FFLCH-USP
Magé	Sítio Saracuruna	10	5	0.035	Lima 1991, DSc Thesis, FFLCH-USP Mendonça de Souza 1981, Pré-história Fluminense, Instituto Estadual do Patrimônio Cultural, RJ Mello & Mendonça de Souza 1977, Nheengatu 1: 43-58
	Sambaqui Rio das Pedrinhas	11	9	0.063	Mendonça de Souza & Mendonça de Souza 1981-1982, Arquivos do Museu de História Natural-UFMG 6/7: 109-131
	Sambaqui de Sernambetiba	12	2	0.014	Beltão et al. 1981-1982, Arquivos do Museu de História Natural-UFMG 6/7: 145-155 Perez et al. 1995 In: Arqueologia do Estado do Rio de Janeiro, Arquivo Público do Estado do RJ pp. 29-34
	Sambaqui de Amourins	13	1	0.007	Heredia et al. 1981-1982, Arquivos do Museu de História Natural-UFMG 6/7: 175-188
Paraty	Abrigo Ponta do Leste I	14	5	0.035	Mendonça de Souza & Mendonça de Souza 1981-1982, Arquivos do Museu de História Natural-UFMG 6/7: 109-131
	Abrigo Ponta do Leste II	15	5	0.035	Mendonça de Souza 1981, Pré-história Fluminense, Instituto Estadual do Patrimônio Cultural, RJ
	Sambaqui Olho D'Água	16	3	0.021	Mendonça de Souza 1981, Pré-história Fluminense, Instituto Estadual do Patrimônio Cultural, RJ Mendonça de Souza & Mendonça de Souza 1981-1982, Arquivos do Museu de História Natural-UFMG 6/7: 109-131
	Toca do Cassununga	17	5	0.035	Mendonça de Souza 1981, Pré-história Fluminense, Instituto Estadual do Patrimônio Cultural, RJ
	Toca dos Caboclos I	18	5	0.035	Mendonça de Souza & Mendonça de Souza 1981-1982, Arquivos do Museu de História Natural-UFMG 6/7: 109-131
	Abrigo da Ilha Pelada	19	5	0.035	Mendonça de Souza & Mendonça de Souza 1981-1982, Arquivos do Museu de História Natural-UFMG 6/7: 109-131
	Sítio Trindade III	20	6	0.042	Mendonça de Souza 1981, Pré-história Fluminense, Instituto Estadual do Patrimônio Cultural, RJ
	Sambaqui do Forte	21	5	0.035	Mendonça de Souza & Mendonça de Souza 1981-1982, Arquivos do Museu de História Natural-UFMG 6/7: 109-131
	Sambaqui do Perequê-Açu	22	5	0.035	Mendonça de Souza & Mendonça de Souza 1981-1982, Arquivos do Museu de História Natural-UFMG 6/7: 109-131
	Sambaqui da Ilha Comprida	23	5	0.035	Mendonça de Souza & Mendonça de Souza 1981-1982, Arquivos do Museu de História Natural-UFMG 6/7: 109-131
	Sambaqui do Pouso	24	5	0.035	Mendonça de Souza & Mendonça de Souza 1981-1982, Arquivos do Museu de História Natural-UFMG 6/7: 109-131
	Sambaqui de Mamanguá	25	5	0.035	Mendonça de Souza & Mendonça de Souza 1981-1982, Arquivos do Museu de História Natural-UFMG 6/7: 109-131

http://dx.doi.org/10.1590/1676-0611-BN-2017-0394

Table 1. Continued...

Location	Midden	Code	Rspp	Relative Rspp	References
Saquarema	Sambaqui da Beirada	26	21	0.148	Kneip 1994, Documento de Trabalho, Série Arqueologia, Museu Nacional-UFRJ, 2 Magalhães et al. 2001, Documento de Trabalho, Série Arqueologia, Museu Nacional-UFRJ, 5 Barbosa-Guimarães 2013, An Acad Bras Ciênc 85: 415-429 Barbosa-Guimarães 2007, DSc Thesis, MAE-USP Kneip et al. 1988, Revista de Arqueologia 5: 41-54 Kneip et al. 1995 In: Documento de Trabalho, Série Arqueologia, Museu Nacional-UFRJ 3: 3-12 Barbosa-Guimarães 2012, Sci Plena 8: 1-9
	Sambaqui da Madressilva	27	8	0.056	Magalhães et al. 2001, Documento de Trabalho, Série Arqueologia, Museu Nacional-UFRJ, 5 Barbosa-Guimarães 2013, An Acad Bras Ciênc 85: 415-429 Barbosa-Guimarães 2007, DSc Thesis, MAE-USP Kneip 1997, Documento de Trabalho, Série Arqueologia, Museu Nacional-UFRJ, 4
	Sambaqui da Pontinha	28	17	0.120	Kneip 1994, Documento de Trabalho, Série Arqueologia, Museu Nacional-UFRJ, 2 Magalhães et al. 2001, Documento de Trabalho, Série Arqueologia, Museu Nacional-UFRJ, 5 Barbosa-Guimarães 2013, An Acad Bras Ciênc 85: 415-429 Barbosa-Guimarães 2007, DSc Thesis, MAE-USP Kneip et al. 1995 In: Documento de Trabalho, Série Arqueologia, Museu Nacional-UFRJ 3: 3-12
	Sambaqui de Saquarema	29	24	0.169	Lopes et al. 2016, PLoS One 11(6): 1-36 Magalhães et al. 2001, Documento de Trabalho, Série Arqueologia, Museu Nacional-UFRJ, 5 Barbosa-Guimarães 2013, An Acad Bras Ciênc 85: 415-429 Barbosa-Guimarães 2007, DSc Thesis, MAE-USP
	Sambaqui do Moa	30	15	0.106	Kneip 1994, Documento de Trabalho, Série Arqueologia, Museu Nacional-UFRJ, 2 Magalhães et al. 2001, Documento de Trabalho, Série Arqueologia, Museu Nacional-UFRJ, 5 Barbosa-Guimarães 2013, An Acad Bras Ciênc 85: 415-429 Barbosa-Guimarães 2007, DSc Thesis, MAE-USP Machado 2014, MSc Thesis, PPGG-UFPA Silveira 2001, DSc Thesis, FFLCH-USP Costa et al. 2012, Rev Mus Arqueol Etnol 22: 51-65
	Sambaqui do Saco	31	8	0.056	Magalhães et al. 2001, Documento de Trabalho, Série Arqueologia, Museu Nacional-UFRJ, 5 Barbosa-Guimarães 2013, An Acad Bras Ciênc 85: 415-429 Barbosa-Guimarães 2007, DSc Thesis, MAE-USP Kneip 1997, Documento de Trabalho, Série Arqueologia, Museu Nacional-UFRJ, 4
	Sambaqui do Jaconé	32	9	0.063	Barbosa-Guimarães 2013, An Acad Bras Ciênc 85: 415-429 Barbosa-Guimarães 2007, DSc Thesis, MAE-USP
	Sambaqui de Mombaça I	33	3	0.021	Barbosa-Guimarães 2013, An Acad Bras Ciênc 85: 415-429 Barbosa-Guimarães 2007, DSc Thesis, MAE-USP
	Sambaqui de Itaúnas	34	5	0.035	Barbosa-Guimarães 2013, An Acad Bras Ciênc 85: 415-429 Barbosa-Guimarães 2007, DSc Thesis, MAE-USP
	Sambaqui Manitiba I	35	20	0.141	Lopes et al. 2016, PLoS One 11(6): 1-36 Magalhães et al. 2001, Documento de Trabalho, Série Arqueologia, Museu Nacional-UFRJ, 5 Barbosa-Guimarães 2013, An Acad Bras Ciênc 85: 415-429 Barbosa-Guimarães 2007, DSc Thesis, MAE-USP
	Sambaqui da Ponte do Girau	36	3	0.021	Lopes et al. 2016, PLoS One 11(6): 1-36

Table 1. Continued...

Location	Midden	Code	Rspp	Relative Rspp	References
Cabo Frio	Sambaqui do Forte	37	2	0.014	Mendonça de Souza & Mendonça de Souza 1981-1982, Arquivos do Museu de História Natural-UFMG 6/7: 109-131 Costa et al. 2012, Rev Mus Arqueol Etnol 22: 51-65 Kneip 1980, Separata de Pesquisas, Série Antropologia, 31 Kneip et al. 1975, Separata da Revista do Museu Paulista-USP Kneip et al. 1975, An Acad Bras Ciênc 47: 91-97 Gaspar 1991, DSc Thesis, FFLCH-USP Gaspar 2003, Pesquisas, Série Antropologia-IAP 59: 1-163 Souza 2009, Monography, GeoQuater-UFRJ
	Abrigo Arraial do Cabo	38	5	0.035	Mendonça de Souza & Mendonça de Souza 1981-1982, Arquivos do Museu de História Natural-UFMG 6/7: 109-131
	Sambaqui Boca da Barra	39	10	0.070	Gaspar 1991, DSc Thesis, FFLCH-USP Gaspar 2003, Pesquisas, Série Antropologia-IAP 59: 1-163 Barbosa 1999, MSc Thesis, PGCA-UFF
	Sítio do Meio	40	1	0.007	Gaspar 1991, DSc Thesis, FFLCH-USP Gaspar 2003, Pesquisas, Série Antropologia-IAP 59: 1-163 Gaspar & Scaramella 1992, Anais VI Reunião Científica da SAB
	Sambaqui da Salina Peroano	41	2	0.014	Gaspar 1991, DSc Thesis, FFLCH-USP Gaspar 2003, Pesquisas, Série Antropologia-IAP 59: 1-163 Franco & Gaspar 1992, Anais VI Reunião Científica da SAB
	Sítio Ilha de Cabo Frio	42	15	0.106	Lopes et al. 2016, PLoS One 11(6): 1-36
Armação de Búzios	Geribá II	43	1	0.007	Gaspar 1991, DSc Thesis, FFLCH-USP Gaspar 2003, Pesquisas, Série Antropologia-IAP 59: 1-163
Arraial do Cabo	Sítio Colônia de Pesca	44	2	0.014	Gaspar 1991, DSc Thesis, FFLCH-USP Mendonça de Souza et al. 1983-1984, Arquivos do Museu de História Natural-UFMG 8/9: 107-119 Tenório et al. 2010, Rev Mus Arqueol Etnol 20: 127-145 Tenório et al. 2005, Anais XIII Congresso da SAB
	Sítio Ponta da Cabeça	45	9	0.063	Gaspar 1991, DSc Thesis, FFLCH-USP Tenório et al. 2010, Rev Mus Arqueol Etnol 20: 127-145 Tenório et al. 2005, Anais XIII Congresso da SAB
	Sítio do Condomínio do Atalaia	46	1	0.007	Tenório et al. 2005, Anais XIII Congresso da SAB
	Usiminas	47	24	0.169	Lopes et al. 2016, PLoS One 11(6): 1-36
Mangaratiba	Sambaqui do Saí	48	5	0.035	Mendonça de Souza & Mendonça de Souza 1981-1982, Arquivos do Museu de História Natural-UFMG 6/7: 109-131
Rio das Ostras	Sambaqui da Tarioba	49	15	0.106	Tuna 2015, MSc Thesis, PBMAC-UFF
Niterói	Sambaqui de Camboinhas	50	12	0.085	Lopes et al. 2016, PLoS One 11(6): 1-36 Souza Cunha et al. 1981 In: Pesquisas arqueológicas no litoral de Itaipu, Niterói, RJ, Cia de Desenvolvimento Territorial Souza Cunha et al. 1986, Anais XXX Congresso Brasileiro de Geologia Vogel & Veríssimo 1981 In: Pesquisas arqueológicas no litoral de Itaipu, Niterói, RJ, Cia de Desenvolvimento Territoria Kneip & Pallestrini 1984 In: Restigas: origem, estrutura, processo, CEUFF Kneip 1979, Pesquisas de salvamento em Itaipu, Niterói, Rio de Janeiro, Cia de Desenvolvimento Territorial Kneip 1995, Documento de Trabalho, Série Arqueologia, Museu Nacional-UFRJ 2: 83-102
Itaboraí	Sambaqui Sampaio I	51	1	0.007	Pinto 2009, MSc Thesis, PPGArq-UFRJ
Rio de Janeiro	Sambaqui da Embratel	52	2	0.014	Kneip et al. 1984 In: Restigas: origem, estrutura, processo, CEUFF Kneip et al. 1984, Revista de Pré-História 6: 334-360
	Sambaqui do Zé Espinho	53	12	0.085	Kneip et al. 1984 In: Restigas: origem, estrutura, processo, CEUFF Kneip et al. 1984, Revista de Pré-História 6: 334-360 Vogel 1987 In: Coletores e pescadores pré-históricos de Guaratiba, Rio de Janeiro, EDUFF Kneip et al. 1986, Separata da Rev Mus Pau

 http://dx.doi.org/10.1590/1676-0611-BN-2017-0394

Table 1. Continued...

Location	Midden	Code	Rspp	Relative Rspp	References
Cubatão	Sambaqui Piaçaguera	54	63	0.444	Fischer 2012, MSc Thesis, MAE-USP Gonzalez 2005, DSc Thesis, MAE-USP Gonzalez & Amenomori 2003, Rev Mus Arqueol Etnol 13: 25-37 Filippini & Eggers 2005-2006, Rev Mus Arqueol Etnol 5-16: 165-180 Garcia 1972, DSc Thesis, IB-USP Garcia & Uchôa 1980, Revista de Pré-História 2: 5-81 Duarte 1968, O sambaqui visto através de alguns sambaquis, Instituto de Pré-História da USP Borges 2015, DSc Thesis, Muséum National D'Histoire Naturelle de Paris
	COSIPA 1	55	35	0.246	Figuti 1998, Revista Arqueologia 11: 57-70 Gonzalez 2005, DSc Thesis, MAE-USP Figuti 1993, Rev Mus Arqueol Etnol 3: 67-80 Figuti 1994-1995, Revista de Arqueologia 8: 267-283
	COSIPA 2	56	16	0.113	Gonzalez 2005, DSc Thesis, MAE-USP Gonzalez & Amenomori 2003, Rev Mus Arqueol Etnol 13: 25-37 Figuti 1993, Rev Mus Arqueol Etnol 3: 67-80 Figuti 1994-1995, Revista de Arqueologia 8: 267-283
	COSIPA 3	57	9	0.063	Figuti 1987, Institut de Paleontologie Humaine, Paris Figuti 1989, Revista de Pré-História 7: 112-126
	COSIPA 4	58	36	0.254	Figuti 1998, Revista Arqueologia 11: 57-70 Gonzalez 2005, DSc Thesis, MAE-USP Figuti 1993, Rev Mus Arqueol Etnol 3: 67-80 Figuti 1994-1995, Revista de Arqueologia 8: 267-283
Ubatuba	Sítio Tenório	59	38	0.268	Figuti 1998, Revista Arqueologia 11: 57-70 Gonzalez 2005, DSc Thesis, MAE-USP Gonzalez & Amenomori 2003, Rev Mus Arqueol Etnol 13: 25-37 Filippini & Eggers 2005-2006, Rev Mus Arqueol Etnol 5-16: 165-180 Garcia 1972, DSc Thesis, IB-USP Amenomori 1999, MSc Thesis, FFLCH-USP
	Sítio do Mar Virado	60	28	0.197	Gonzalez & Amenomori 2003, Rev Mus Arqueol Etnol 13: 25-37 Amenomori 1999, MSc Thesis, FFLCH-USP Amenomori 2005, DSc Thesis, MAE-USP Uchôa 2009, CLIO-Série Arqueológica 24: 7-40 Nishida 2001, MSc Thesis, MAE-USP
	Sítio Couves 1	61	6	0.042	Amenomori 1999, MSc Thesis, FFLCH-USP
Guarujá	Sambaqui do Buracão	62	54	0.380	Gonzalez & Amenomori 2003, Rev Mus Arqueol Etnol 13: 25-37 Borges 2015, DSc Thesis, Muséum National D'Histoire Naturelle de Paris Duarte 1968, O sambaqui visto através de alguns sambaquis, Instituto de Pré-História da USP Amenomori 2005, DSc Thesis, MAE-USP
	Sambaqui do Mar Casado	63	48	0.338	Gonzalez 2005, DSc Thesis, MAE-USP Gonzalez & Amenomori 2003, Rev Mus Arqueol Etnol 13: 25-37 Borges 2015, DSc Thesis, Muséum National D'Histoire Naturelle de Paris Duarte 1968, O sambaqui visto através de alguns sambaquis, Instituto de Pré-História da USP
	Sambaqui Maratuá	64	24	0.169	Gonzalez 2005, DSc Thesis, MAE-USP
Ilhabela	Sambaqui Abrigo Sul	65	2	0.014	Bendazzoli 2014, DSc Thesis, MAE-USP
Iguape	Abrigo do Pindú	66	2	0.014	Bendazzoli 2014, DSc Thesis, MAE-USP Bonetti 1997, MSc Thesis, FFLCH-USP
Serra	Sambaqui do Péricles II	67	4	0.028	Rhea Estudos e Projetos Ltda 2009, Salvamento e monitoramento arqueológico na área do Alphaville Jacuhy
Vitória	Sítio Campus 2	68	3	0.021	Perota 1972, Revista de Cultura da UFES 3: 39-45

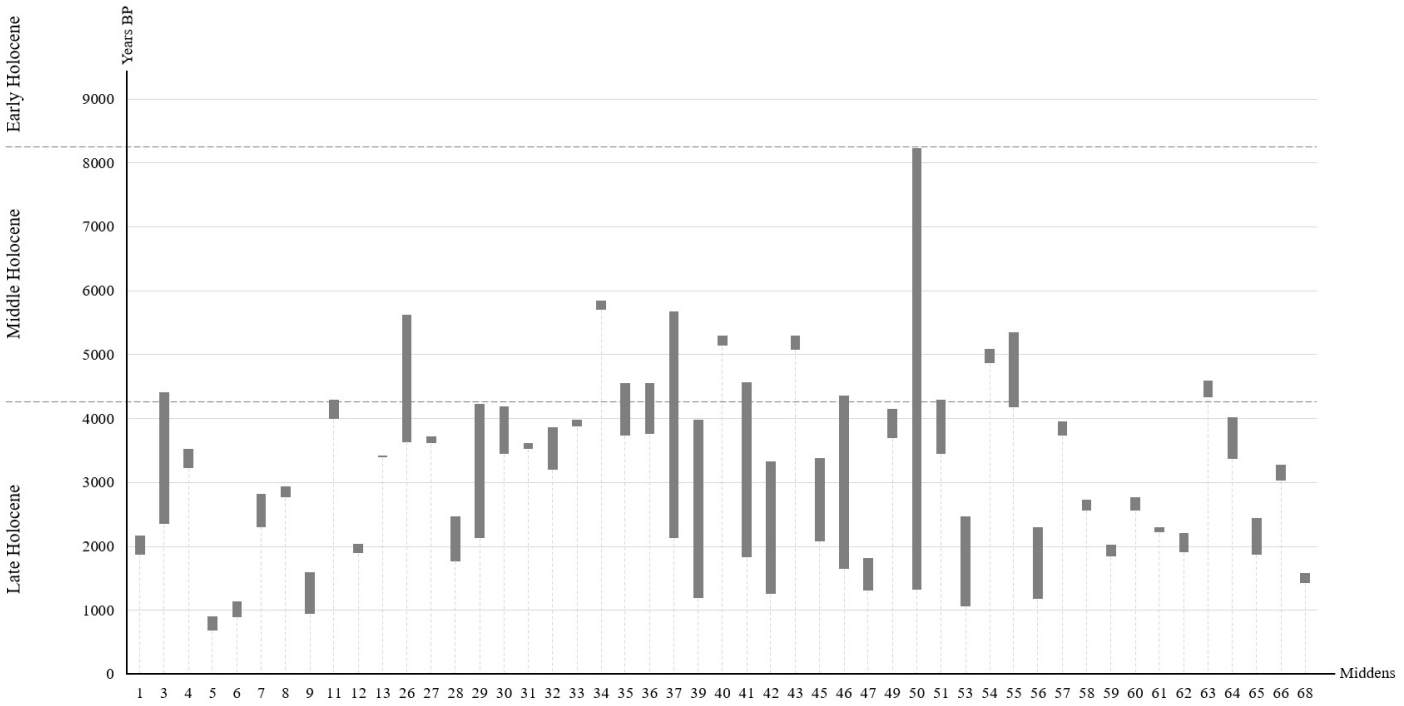

Figure 2. Graphic with the ^{14}C radiocarbonic dates of the 49 inventoried middens of the Southeast Region of Brazil. In the x axis are the middens (codes defined at Table 1) and in the y axis are the ranges of ^{14}C radiocarbonic dating (given in year before present) found in the literature. The different periods of the Holocene were defined based in Walker et al. (2012): Early Holocene (11,700 ~ 8,200 BP), Middle Holocene (8,200 ~ 4,200 BP) and Late Holocene (4,200 BP ~ till today).

Table 2. Marine fish of class Osteichthyes from middens in the Southeast Region of Brazil with their absolute (F) and relative (relative F) frequencies of occurrence as well as the midden(s) in which they were recorded. The codes representing the middens are defined in Table 1.

Family	Species	F	Relative F	Midden(s)
Albulidae	*Albula nemoptera* (Fowler, 1911)	1	0.015	3
Ariidae	*Aspistor luniscutis* (Valenciennes, 1840)	19	0.279	2, 3, 4, 5, 6, 11, 27, 28, 30, 31, 35, 54, 55, 58, 59, 60, 62, 63, 64
	Bagre bagre (Linnaeus, 1766)	23	0.338	1, 2, 3, 4, 5, 6, 9, 10, 11, 20, 21, 22, 23, 24, 25, 48, 50, 54, 55, 58, 59, 62, 63
	Bagre marinus (Mitchill, 1815)	18	0.265	1, 2, 3, 4, 5, 6, 8, 26, 28, 30, 35, 49, 53, 54, 62, 63, 64, 67
	Cathorops spixii (Agassiz, 1829)	18	0.265	2, 3, 4, 5, 6, 26, 28, 29, 30, 35, 54, 55, 57, 58, 59, 62, 63, 64
	Genidens barbus (Lacepède, 1803)	33	0.485	2, 3, 4, 5, 6, 10, 11, 12, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 48, 50, 54, 55, 58, 59, 60, 62, 63
	Genidens genidens (Cuvier, 1829)	19	0.279	2, 3, 4, 5, 6, 8, 26, 28, 29, 35, 49, 50, 54, 55, 58, 59, 62, 63, 64
	Genidens machadoi (Miranda Ribeiro, 1918)	1	0.015	54
	Notarius grandicassis (Valenciennes, 1840)	12	0.176	2, 3, 4, 5, 6, 54, 55, 58, 59, 62, 63, 64
	Potamarius grandoculis (Steindachner, 1877)	2	0.029	54, 63
Balistidae	*Balistes capriscus* Gmelin, 1789	2	0.029	62, 63
	Balistes vetula Linnaeus, 1758	12	0.176	1, 2, 3, 4, 5, 6, 9, 54, 55, 58, 59, 60
Carangidae	*Caranx crysos* (Mitchill, 1815)	4	0.059	29, 54, 62, 63
	Caranx hippos (Linnaeus, 1766)	23	0.338	1, 2, 3, 4, 5, 6, 8, 9, 26, 27, 28, 29, 30, 31, 35, 47, 50, 53, 54, 62, 63, 64, 67
	Caranx ruber (Bloch, 1793)	1	0.015	62
	Chloroscombrus chrysurus (Linnaeus, 1766)	1	0.015	62
	Oligoplites saurus (Bloch & Schneider, 1801)	4	0.059	8, 26, 28, 30
	Selar crumenophthalmus (Bloch, 1793)	1	0.015	8
	Selene vomer (Linnaeus, 1758)	3	0.044	8, 47, 62
	Seriola dumerili (Risso, 1810)	2	0.029	62, 63
	Trachinotus falcatus (Linnaeus, 1758)	1	0.015	65
	Trachurus lathami Nichols, 1920	1	0.015	54
Centropomidae	*Centropomus ensiferus* Poey, 1860	3	0.044	3, 5, 42
	Centropomus parallelus Poey, 1860	6	0.088	35, 47, 54, 62, 63, 64
	Centropomus undecimalis (Bloch, 1792)	16	0.235	3, 11, 26, 27, 28, 29, 30, 32, 35, 54, 57, 62, 63, 64, 67, 69
Coryphaenidae	*Coryphaena hippurus* Linnaeus, 1758	1	0.015	8
Dactylopteridae	*Dactylopterus volitans* (Linnaeus, 1758)	5	0.074	9, 29, 60, 62, 63
Diodontidae	*Chilomycterus spinosus* (Linnaeus, 1758)	12	0.176	1, 2, 3, 4, 5, 6, 47, 49, 54, 55, 58, 59
	Diodon hystrix Linnaeus, 1758	11	0.162	2, 3, 4, 5, 6, 9, 54, 55, 58, 59, 63

Table 2. Continued...

Family	Species	F	Relative F	Midden(s)
Eleotridae	*Dormitator maculatus* (Bloch, 1792)	1	0.015	54
	Eleotris pisonis (Gmelin, 1789)	1	0.015	62
Elopidae	*Elops saurus* Linnaeus, 1766	1	0.015	54
Ephippidae	*Chaetodipterus faber* (Broussonet, 1782)	21	0.309	1, 2, 3, 4, 5, 6, 7, 9, 29, 35, 39, 47, 49, 53, 54, 55, 58, 59, 60, 61, 62
Gerreidae	*Diapterus auratus* Ranzani, 1842	2	0.029	3, 5
	Diapterus rhombeus (Cuvier, 1829)	5	0.074	3, 5, 6, 54, 62
	Eugerres brasilianus (Cuvier, 1830)	2	0.029	54, 62
	Gerres cinereus (Walbaum, 1792)	1	0.015	3
Haemulidae	*Anisotremus surinamensis* (Bloch, 1791)	3	0.044	54, 62, 63
	Anisotremus virginicus (Linnaeus, 1758)	6	0.088	1, 3, 4, 5, 6, 47
	Conodon nobilis (Linnaeus, 1758)	13	0.191	2, 3, 4, 5, 6, 11, 54, 55, 58, 59, 60, 62, 63
	Haemulon aurolineatum Cuvier, 1830	2	0.029	3, 47
	Haemulon plumierii (Lacepède, 1801)	3	0.044	54, 62, 63
	Haemulon sciurus (Shaw, 1803)	1	0.015	3
	Haemulon steindachneri (Jordan & Gilbert, 1882)	3	0.044	1, 3, 47
	Orthopristis ruber (Cuvier, 1830)	10	0.147	1, 2, 3, 4, 5, 6, 54, 55, 58, 59
	Pomadasys crocro (Cuvier, 1830)	1	0.015	63
Hemiramphidae	*Hyporhamphus unifasciatus* (Ranzani, 1841)	2	0.029	1, 3
Holocentridae	*Holocentrus adscensionis* (Osbeck, 1765)	2	0.029	60, 62
Istiophoridae	*Istiophorus albicans* (Latreille, 1804)	1	0.015	47
Kyphosidae	*Kyphosus sectatrix* (Linnaeus, 1758)	3	0.044	9, 49, 60
Labridae	*Bodianus rufus* (Linnaeus, 1758)	4	0.059	3, 8, 42, 47
Lobotidae	*Lobotes surinamensis* (Bloch, 1790)	10	0.147	7, 39, 54, 55, 56, 58, 62, 63, 64, 66
Lutjanidae	*Lutjanus analis* (Cuvier, 1828)	1	0.015	68
	Lutjanus griseus (Linnaeus, 1758)	1	0.015	59
	Lutjanus purpureus (Poey, 1866)	1	0.015	59
	Lutjanus synagris (Linnaeus, 1758)	5	0.074	1, 3, 4, 5, 6
	Ocyurus chrysurus (Bloch, 1791)	1	0.015	47
Malacanthidae	*Caulolatilus chrysops* (Valenciennes, 1833)	1	0.015	53
Megalopidae	*Megalops atlanticus* Valenciennes, 1847	3	0.044	54, 62, 63
Mugilidae	*Mugil liza* Valenciennes, 1836	5	0.074	1, 3, 4, 5, 6
Paralichthyidae	*Paralichthys orbignyanus* (Valenciennes, 1839)	1	0.015	54
Polynemidae	*Polydactylus oligodon* (Günther, 1860)	6	0.088	14, 15, 17, 18, 19, 38
Pomacanthidae	*Pomacanthus paru* (Bloch, 1787)	1	0.015	62
Pomatomidae	*Pomatomus saltatrix* (Linnaeus, 1766)	21	0.309	2, 3, 4, 5, 6, 7, 9, 26, 28, 29, 30, 39, 41, 45, 53, 54, 55, 58, 59, 60, 63
Sciaenidae	*Bairdiella ronchus* (Cuvier, 1830)	13	0.191	1, 2, 3, 4, 5, 6, 32, 49, 54, 55, 57, 58, 59
	Cynoscion acoupa (Lacepède, 1801)	16	0.235	10, 11, 14, 15, 17, 18, 19, 20, 27, 35, 38, 54, 59, 62, 63, 64
	Cynoscion guatucupa (Cuvier, 1830)	1	0.015	64
	Cynoscion jamaicensis (Vaillant & Bocourt, 1883)	12	0.176	1, 2, 3, 4, 5, 6, 8, 32, 34, 49, 55, 58
	Cynoscion leiarchus (Cuvier, 1830)	5	0.074	54, 55, 58, 62, 63
	Cynoscion similis Randall & Cervigón, 1968	6	0.088	1, 3, 4, 5, 6, 36
	Cynoscion striatus (Cuvier, 1829)	3	0.044	28, 29, 35
	Cynoscion virescens (Cuvier, 1830)	19	0.279	11, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 38, 48, 58, 59, 62, 63
	Isopisthus parvipinnis (Cuvier, 1830)	3	0.044	32, 54, 59
	Larimus breviceps Cuvier, 1830	18	0.265	1, 2, 3, 4, 5, 6, 32, 33, 34, 49, 54, 55, 57, 58, 59, 60, 61, 63
	Menticirrhus americanus (Linnaeus, 1758)	2	0.029	49, 59
	Micropogonias furnieri (Desmarest, 1823)	53	0.779	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 38, 39, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64
	Micropogonias undulatus (Linnaeus, 1766)	8	0.118	26, 27, 28, 29, 30, 31, 35, 50
	Ophioscion punctatissimus Meek & Hildebrand, 1925	1	0.015	54
	Pareques acuminatus (Bloch & Schneider, 1801)	1	0.015	35
	Pogonias cromis (Linnaeus, 1766)	48	0.706	2, 3, 4, 5, 6, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 34, 35, 36, 37, 38, 42, 48, 49, 52, 53, 54, 55, 57, 58, 59, 60, 62, 63, 64, 68
	Nebris microps Cuvier, 1830	1	0.015	59
	Stellifer brasiliensis (Schultz, 1945)	1	0.015	54
	Stellifer rastrifer (Jordan, 1889)	2	0.029	32, 54
	Umbrina canosai Berg, 1895	1	0.015	29
	Umbrina coroides Cuvier, 1830	1	0.015	42

Table 2. Continued...

Family	Species	F	Relative F	Midden(s)
Scombridae	*Katsuwonus pelamis* (Linnaeus, 1758)	2	0.029	8, 47
	Scomberomorus cf. *brasiliensis* Collette, Russo & Zavala-Camin, 1978	2	0.029	62, 63
	Thunnus cf. *atlanticus* (Lesson, 1831)	1	0.015	64
Serranidae	*Cephalopholis fulva* (Linnaeus, 1758)	4	0.059	54, 62, 63, 64
	Epinephelus itajara (Lichtenstein, 1822)	4	0.059	54, 62, 63, 64
	Epinephelus morio (Valenciennes, 1828)	6	0.088	3, 47, 54, 62, 63, 64
	Hyporthodus niveatus (Valenciennes, 1828)	2	0.029	26, 29
	Mycteroperca acutirostris (Valenciennes, 1828)	2	0.029	63, 64
Sparidae	*Archosargus probatocephalus* (Walbaum, 1792)	20	0.294	2, 3, 4, 5, 6, 7, 9, 39, 53, 54, 55, 56, 57, 58, 59, 60, 62, 63, 64, 66
	Archosargus rhomboidalis (Linnaeus, 1758)	8	0.118	3, 5, 26, 28, 29, 30, 31, 35
	Calamus pennatula Guichenot, 1868	2	0.029	54, 62
	Diplodus argenteus (Valenciennes, 1830)	2	0.029	9, 60
	Pagrus pagrus (Linnaeus, 1758)	8	0.118	26, 28, 29, 30, 35, 47, 49, 53
Sphyraenidae	*Sphyraena barracuda* (Edwards, 1771)	1	0.015	5
	Sphyraena guachancho Cuvier, 1829	1	0.015	3
Tetraodontidae	*Lagocephalus laevigatus* (Linnaeus, 1766)	24	0.353	2, 3, 4, 5, 6, 7, 8, 9, 26, 28, 35, 39, 42, 49, 54, 55, 56, 58, 59, 60, 61, 62, 63, 67
	Sphoeroides spengleri (Bloch, 1785)	5	0.074	2, 3, 4, 5, 6
	Sphoeroides testudineus (Linnaeus, 1758)	5	0.074	2, 3, 4, 5, 6
Trichiuridae	*Trichiurus lepturus* Linnaeus, 1758	17	0.250	2, 3, 4, 5, 6, 8, 42, 47, 53, 54, 55, 58, 59, 60, 62, 63, 65
Triglidae	*Prionotus punctatus* (Bloch, 1793)	1	0.015	1

Table 3. Marine fish of class Chondrichthyes from middens in the Southeast Region of Brazil with their absolute (F) and relative (relative F) frequencies of occurrence as well as the midden(s) in which they were recorded. The codes representing the middens are defined in Table 1.

Family	Species	F	Relative F	Midden(s)
Alopiidae	*Alopias superciliosus* Lowe, 1841	2	0.029	3, 50
	Alopias vulpinus (Bonnaterre, 1788)	6	0.088	3, 53, 55, 56, 58, 60
Carcharhinidae	*Carcharhinus acronotus* (Poey, 1860)	8	0.118	1, 3, 5, 42, 54, 62, 63, 64
	Carcharhinus altimus (Springer, 1950)	2	0.029	3, 9
	Carcharhinus brachyurus (Günther, 1870)	2	0.029	3, 5
	Carcharhinus brevipinna (Müller & Henle, 1839)	8	0.118	3, 8, 26, 29, 42, 47, 49, 50
	Carcharhinus falciformis (Müller & Henle, 1839)	1	0.015	3
	Carcharhinus leucas (Müller & Henle, 1839)	10	0.147	3, 45, 54, 55, 56, 58, 59, 60, 62, 63
	Carcharhinus limbatus (Müller & Henle, 1839)	11	0.162	1, 3, 4, 5, 6, 8, 45, 54, 62, 63, 64
	Carcharhinus longimanus (Poey, 1861)	2	0.029	3, 45
	Carcharhinus obscurus (Lesueur, 1818)	10	0.147	3, 8, 26, 29, 54, 55, 56, 58, 62
	Carcharhinus perezii (Poey, 1876)	1	0.015	3
	Carcharhinus plumbeus (Nardo, 1827)	10	0.147	1, 3, 5, 6, 26, 45, 47, 55, 56, 58
	Carcharhinus porosus (Ranzani, 1839)	5	0.074	1, 3, 4, 5, 6
	Negaprion brevirostris (Poey, 1868)	9	0.132	1, 2, 3, 4, 5, 6, 8, 29, 42
	Prionace glauca (Linnaeus, 1758)	9	0.132	44, 54, 55, 56, 57, 58, 59, 60, 62
	Rhizoprionodon lalandii (Müller & Henle, 1839)	4	0.059	3, 4, 5, 6
	Rhizoprionodon porosus (Poey, 1861)	3	0.044	3, 4, 5
	Galeocerdo cuvier (Péron & Lesueur, 1822)	23	0.338	1, 2, 3, 4, 5, 6, 7, 8, 30, 42, 44, 45, 46, 47, 54, 55, 56, 58, 59, 60, 62, 63, 64
Dasyatidae	*Bathytoshia centroura* (Mitchill, 1815)	6	0.088	3, 7, 26, 29, 39, 50
	Hypanus americanus (Hildebrand & Schroeder, 1928)	2	0.029	54, 63
	Hypanus guttatus (Bloch & Schneider, 1801)	1	0.015	3
Ginglymostomatidae	*Ginglymostoma cirratum* (Bonnaterre, 1788)	3	0.044	54, 62, 63
Gymnuridae	*Gymnura altavela* (Linnaeus, 1758)	1	0.015	7
Lamnidae	*Lamna nasus* (Bonnaterre, 1788)	7	0.103	1, 3, 4, 5, 6, 42, 47
	Carcharodon carcharias (Linnaeus, 1758)	23	0.338	1, 2, 3, 4, 5, 6, 7, 8, 26, 29, 42, 45, 47, 50, 54, 55, 56, 58, 59, 60, 62, 63, 64
	Isurus oxyrinchus Rafinesque, 1810	15	0.221	3, 7, 8, 37, 39, 42, 45, 47, 54, 55, 56, 58, 60, 62, 63
	Isurus paucus Guitart, 1966	1	0.015	7
Myliobatidae	*Aetobatus narinari* (Euphrasen, 1790)	24	0.353	3, 8, 9, 26, 28, 29, 30, 31, 35, 39, 42, 47, 49, 50, 54, 55, 56, 58, 59, 60, 61, 62, 63, 64
	Myliobatis goodei Garman, 1885	5	0.074	54, 55, 56, 58, 59
	Rhinoptera bonasus (Mitchill, 1815)	10	0.147	7, 39, 54, 55, 56, 58, 59, 60, 62, 63
	Rhinoptera brasiliensis Müller, 1836	5	0.074	54, 59, 60, 61, 62
Odontaspididae	*Carcharias taurus* Rafinesque, 1810	26	0.382	1, 2, 3, 4, 5, 6, 7, 8, 35, 40, 41, 42, 43, 45, 47, 50, 53, 54, 55, 56, 57, 58, 59, 60, 62, 63
Sphyrnidae	*Sphyrna lewini* (Griffith & Smith, 1834)	2	0.029	3, 60
	Sphyrna mokarran (Rüppell, 1837)	2	0.029	3, 29
	Sphyrna tiburo (Linnaeus, 1758)	2	0.029	54, 59
	Sphyrna zygaena (Linnaeus, 1758)	4	0.059	3, 5, 47, 59

 http://dx.doi.org/10.1590/1676-0611-BN-2017-0394

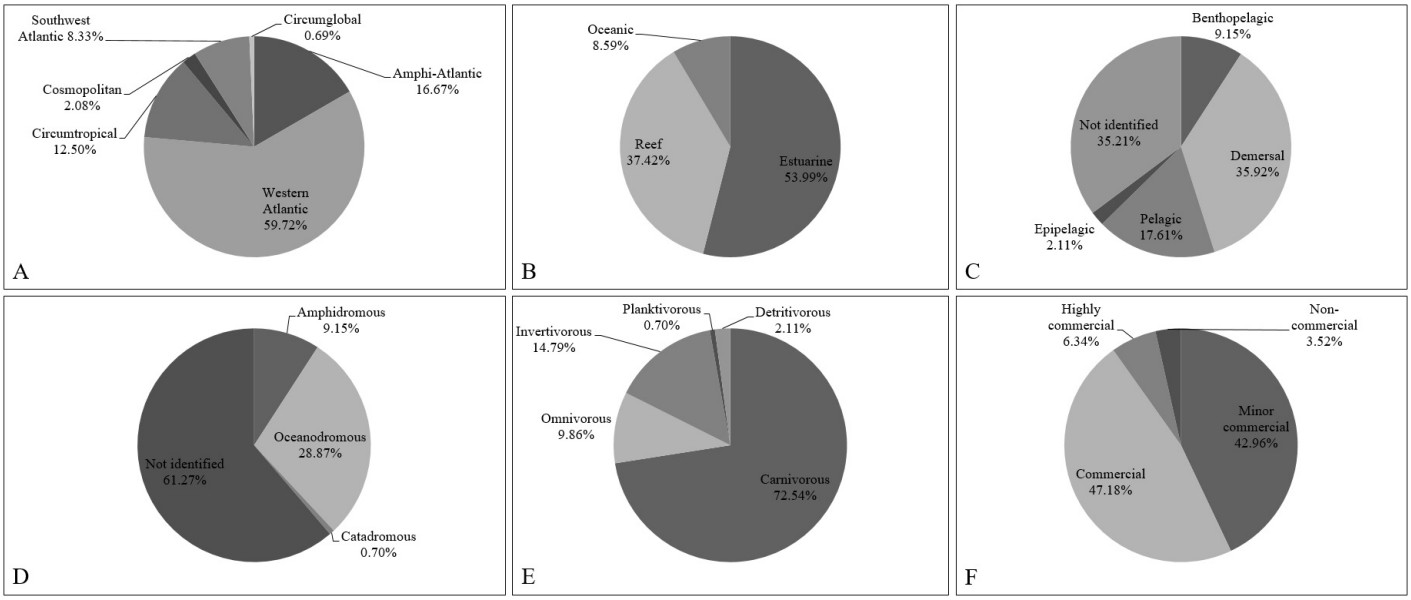

Figure 3. Biogeographical, ecological and economic data for the inventoried fish. A = Distribution; B = Environment; C = Habit; D = Behaviour; E = Feeding guild; F = Commercial value.

Table 4. Number of species from current fish inventories and middens from Rio de Janeiro (RJ), São Paulo (SP), Espírito Santo (ES) and the entire Southeast Region.

n spp.	RJ	SP	ES	Southeast Region
Overall Past	104	90	6	142
Overall Present	591	578	282	808
Commercial Past	101	87	6	137
Commercial Present	412	340	196	488
Past Exclusive	13	15	4	5

Discussion

Middens are artificial accumulations of wildlife and cultural remains that were built by groups of pre-colonial humans during the Holocene (Lima et al. 2003, Mendes et al. 2014). Therefore, the species compositions of the organisms found in middens are presumably non-random and biased samples of natural biological communities at those sites because they were influenced or determined by various cultural factors, including food preference, the technological level of the fishing gear, harvesting and hunting artefacts, food taboos, funerary or ritualistic practices and how the materials were discarded and/or used. Therefore, some researchers believe that the faunal data from middens have selectivity biases that complicate any related inferences about ecosystems and their biodiversity (Baisre 2010, Rodrigues et al. 2016a). However, the comparison between the inventory of the marine fish identified in middens and those from general surveys of ichthyological fauna showed no significant differences in the number of species either with or without commercial value, indicating that middens contain data that are not solely applicable to prehistoric fisheries. Such wildlife remains apparently represent the fauna existing at the time that the archaeological sites were created but are also repositories of broader biodiversity data, despite any bias associated with the composition of zoo-archaeological remains (Lindbladh et al. 2007, Froyd & Willis 2008).

In a recent study using taxonomic tests, Faria et al. (2014) showed that the malacological taxonomic diversity in the Tarioba midden (Rio de Janeiro, Brazil) was not significantly different from that of a comprehensive list of the mollusc species from the entire coast of the state of Rio de Janeiro. Those findings and the results of the present study suggest that middens may contain key indicators of past biodiversity, despite their limitations, and furthermore, some studies of middens have shown detectable changes in species composition over time (Dalzell 1998, Lotze & Milewski 2004, Rosenberg et al. 2005, Maschner et al. 2008, Souza et al. 2016).

Studies focused on inventorying the fish species in middens have usually involved a limited number of sites (sampling areas). For example, Kloker et al. (2010) recorded 17 fish species from two sites on the south coast of Brazil (Santa Catarina state). In contrast, as part of a greater sampling effort, Lopes et al. (2016) recorded 97 fish species in 13 sites located on the coast of Rio de Janeiro, and in this study, the study area corresponded to 68 middens distributed over 1,000 km of the southeast coast of Brazil.

In using even greater effort than that undertaken by Lopes et al. (2016), this study used data which came from different kinds of publications (scientific articles, books, thesis, dissertations, monographs, technical reports etc) encompassing 48 years (1968-2016) of studies in the field. Therefore, the data compiled here came from a myriad of objectives and methodologies, for example, primary data which came from excavations were originated since superficial sampling till total material recovery. Following excavation the material recovered were dry sieved or under current water using different mesh sizes (2 to 10mm). Identification of the zoo-archaeological vestiges was done by handling different manuals and reference collections. Due to that the list recovered was carefully scrutinized. Criteria such as using only the more inclusive taxa and species with biogeographic range defined were used. Furthermore, the Linean definition of the species was fully checked for ambiguities and classification changes. In using these criteria any inconvenience related to the heterogeneity of sources were

surpassed and the methodological choice gave an extensive baseline of fishes biodiversity during the Holocene in the Brazilian Coast.

The species richness from the midden fish inventory in this study was lower than that of current fish checklists (Bizerril & Costa 2001, Menezes 2011, *species*Link), which likely resulted from the selected sampling methods. All current checklists were developed from extensive bibliographical surveys that included studies that employed diverse methods (fishing records, scientific collections, the testimony of scientific experts, museum collection documents and environmental monitoring) as well as data accumulated from several years of academic research. In contrast, the midden records were fundamentally related to prehistoric fisheries or related cultural activities (fishing gear, ritualistic symbols, ornaments and artefacts) as well as by-catch. In all cases, the midden fish records were always informed by an understanding of prehistoric culture; that is, the midden fish inventory was constructed with data from archaeological studies of fishing cultures and thus focused on a limited number of target species.

Regarding the target species, the occurrence frequencies of *M. furnieri* and *P. cromis* in middens indicate that they were preferentially fished species. Barbosa-Guimarães (2013) observed that *M. furnieri* was the main fish species in Saquarema middens (Rio de Janeiro, Brazil) and thus inferred that it was the primary food of the midden peoples of that region. In turn, Souza Cunha et al. (1981) notes the presence of *Pogonias* sp. in the midden Sambaqui de Camboinhas (Niterói, state of Rio de Janeiro, Brazil), and the remains of that genus are commonly found in coastal middens (Kneip et al. 1975). Lopes et al. (2016) recorded *M. furnieri* and *P. cromis* as two of the three most common species in their study of Rio de Janeiro middens, and these two species are currently considered key fishery resources in the Southeast Region of Brazil (Mulato et al. 2015, Santos et al. 2016). Furthermore, estuarine, demersal and carnivorous species typically have significant commercial value, thus composing key fishing stocks (Tacon 1994, Santos & Câmara 2002, Haimovici et al. 2014), and it can be deduced that such species were critical fishing resources for midden peoples in the past.

On the one hand, the presence of species such as *M. furnieri* and *P. cromis*, which occur at high relative frequencies in middens, indicates that midden fish inventories contain prehistoric fishery data, but the numbers of fish with and without commercial value in middens are not significantly different from those in checklists of ichthyological fauna for the same sites. Moreover, the high number of exclusive species with low frequencies of occurrence in middens corroborates the hypothesis that midden fish records contain key data on Holocene ichthyological fauna and that such species are most likely by-catch. Additionally, the occurrence frequencies show that it is unlikely that midden peoples from neighbouring regions consumed different or unique species. Thus, the results from this study indicate that middens contain data on midden fishing and culture as well as past biodiversity.

Biodiversity inventories are essential for establishing baselines that inform species management and conservation measures (Gordillo et al. 2014), especially those related to endangered species, including fish. Currently, the effects of overfishing, pollution, invasive species and other ecological impacts have reduced marine ichthyological diversity (Povey & Keough 1991, Brosnan & Crumrine 1994, Polunin & Roberts 1996, Costello et al. 2010). Therefore, the study of ichthyological midden remains is a key tool for understanding prehistoric biodiversity, enabling the establishment of a historical perspective and thus more complete baselines to inform more effective management measures and reduce the threat of extinction currently faced by marine fishes.

In summary, the midden inventory of the Holocene marine fish of the southeast coast of Brazil contains data on prehistoric fisheries, which is supported by the high number of species with low frequencies of occurrence (or unique species) as well as by chi-squared tests that failed to show significant differences between the midden fish inventory and current ichthyofauna checklists. Thus, the results from this study clearly indicate that zoo-archaeological fish remains are key evidence of Holocene biodiversity.

Acknowledgments

The authors would like to thank CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) for financial support and Pos-doc Scholarship for MRD (Programa Nacional de Pós-Doutorado-PNPD) and Masters Scholarship for ABM.

Author Contributions

Augusto Barros Mendes: Contribution to data collection, contribution to data analysis and interpretation, contribution to manuscript preparation and contribution to critical revision, adding intelectual content.

Michelle Rezende Duarte: Contribution to data analysis and interpretation, contribution to manuscript preparation and contribution to critical revision, adding intelectual content

Edson Pereira da Silva: Substantial contribution in the concept and design of the study, contribution to data collection, contribution to data analysis and interpretation, contribution to manuscript preparation and contribution to critical revision, adding intelectual content

Conflicts of interest

The authors declare that there is no conflict of interest related to the publication of the data in this article.

References

AMARAL, A.Z.C. & JABLONSKY S. 2005. Conservation of marine and coastal biodiversity in Brazil. Conserv. Biol. 19:625-631.

ARRUDA, R.S.V., SILVA, V.C.F., FIGOLS, F.A.B. & ANDRADE, D. 2000. Os saberes tradicionais e a biodiversidade no Brasil. In: Biodiversidade e comunidades tradicionais no Brasil (A.C. Diegues, ed). Núcleo de Pesquisas Sobre Populações Humanas e Áreas Úmidas Brasileiras, Ministério do Meio Ambiente, Conselho Nacional de Pesquisa, São Paulo.

BAISRE, J. 2010. Setting a baseline for Caribbean fisheries. J. Isl. Coast. Archaeol 5:120-147.

BARBOSA-GUIMARÃES, M. 2013. Fishing strategies among prehistoric populations at Saquarema Lagoonal Complex, Rio de Janeiro, Brazil. An. Acad. Bras. Cienc. 85:415-429.

BEAUCLAIR, M., DUARTE, M.R. & SILVA, E.P. 2016. Sambaquis (shell mounds) and mollusk diversity in the past history of Araruama Lagoon, Rio de Janeiro, Brazil. Pan-Am. J. Aquat. Sci. 11:47-59.

BITTENCOURT, J.S., KUCHENBECKER, M., VASCONCELOS, A.G. & MEYER, K.E.B. 2015. O registro fóssil das coberturas sedimentares do Cráton do São Francisco em Minas Gerais. Geonomos 23:39-62.

BIZERRIL, C.R.F.S. & COSTA, P.A.S. 2001. Peixes marinhos do estado do Rio de Janeiro. FEMAR-SEMADS, Rio de Janeiro.

BROSNAN, D.M. & CRUMRINE, L.L. 1994. Effects of human trampling on marine rocky shore communities. J. Exp. Mar. Biol. Ecol. 177:79-97.

COSTA, S.A.R.F., LUZ, Z.A.S., SILVEIRA, M.I. & MORAES-SANTOS, H.M. 2012. Contribuição à zooarqueologia do Sambaqui do Moa: novos vestígios ictiológicos. Rev. Mus. Arqueol. Etnol. 22:51-65.

COSTELLO, M.J., COLL, M., DANOVARO, R., HALPIN, P., OJAVEER, H. & MILOSLAVICH, P. 2010. A census of marine biodiversity knowledge, resources, and future challenges. PLoS One 5(8): e12110. https://doi.org/10.1371/journal.pone.0012110 (last access on 15/06/2017)

DALZELL, P. 1998. The role of archaeological and cultural-historical records in long-range coastal fisheries resources management strategies and policies in the Pacific Island. Ocean Coast. Manage. 40:237-252.

DEBLASIS, P.A.D., KNEIP, A., GIANINNI, P.C., GASPAR, M.D. & SCHEEL-YBERT, R. 2007. Sambaquis e paisagem: dinâmica natural e arqueologia regional no litoral do sul do Brasil. Arqueologia Suramericana 3:29-61.

FARIA, R.G.S., SILVA, E.P. & SOUZA, R.C.C.L. 2014. Biodiversity of marine molluscs from Sambaqui da Tarioba, Rio das Ostras, Rio de Janeiro (Brazil). Revista Chilena de Antropologia 29:49-54.

FIGUTI, L. 1993. O homem pré-histórico, o molusco e o sambaqui: considerações sobre a subsistência dos povos sambaquieiros. Rev. Mus. Arqueol. Etnol. 3:67-80.

FIGUTI, L. 1998. Estórias de arqueo-pescador: considerações sobre a pesca nos sítios de grupos pescadores-coletores do litoral. Revista de Arqueologia 11:57-70.

FROESE, R. & PAULY, D. (eds) 2017. FishBase. World Wide Web electronic publication. Available from: http://fishbase.org, version 10/2017.

FROYD, C.A. & WILLIS, K.J. 2008. Emerging issues in biodiversity & conservation management: The need for a palaeoecological perspective. Quaternary Sci. Rev. 27:1723-1732.

FURON, R. 1969. La distribución de los seres. Editorial Labor, Barcelona.

GASPAR, M.D. 1998. Considerations about the sambaquis of the Brazilian coast. Antiquity 72:592-615.

GONZALEZ, M.M.B. 2005. Use of *Pristis* spp. (Elasmobranchii: Pristidae) by hunter-gatherers on the Coast of São Paulo, Brazil. Neotrop. Ichthyol 3:421-426.

GORDILLO, S., BAYER, S.B, BORETTO, B. & CHARÓ, M. 2014. Mollusk shells as bio-geo-archives: evaluating environmental changes during the Quaternary. Springer, Berlin/Heidelberg.

HAIMOVICI, M., FILHO, J.M.A. & SUNYE, P.S. (eds) 2014. A pesca marinha e estuarina no Brasil: estudos de caso multidisciplinares. Editora da FURG, Rio Grande.

KLOKLER, D., VILLAGRÁN, X.S., GIANNINI, P.C.F., PEIXOTO, S. & DEBLASIS, P. 2010. Juntos na costa: zooarqueologia e geoarqueologia de sambaquis do litoral sul catarinense. Rev. Mus. Arqueol. Etnol. 20:53-75.

KNEIP, L.M., CRANCIO, F. & FRANCISCO, B.H.R. 1988. O Sambaqui da Beirada (Saquarema, RJ): aspectos culturais e paleoambientais. Revista de Arqueologia 5:41-54.

KNEIP, L.M., CUNHA, F.L.S., COELHO, A.C.S. & MELLO B.E.M. 1975. O "Sambaqui do Forte": correlações arqueológicas, geológicas e faunísticas (Cabo Frio, RJ-Brasil). An. Acad. Bras. Cienc. 47:91-97.

KNOWLTON, N. & JACKSON, J.B.C. 2008. Shifting baselines, local impacts, and global change on coral reefs. PLoS Biol. 6(2):e54. https://doi: 10.1371/journal.pbio.0060054 (last access on 15/06/2017)

LACERDA, L.D., ARAUJO, D.S.D., CERQUEIRA, R. & TURCQ, B. (eds) 1984. Restingas: origem, estrutura, processos. CEUFF, Niterói.

LEWINSOHN, T.M. & PRADO, P.I. 2005. Quantas espécies há no Brasil? Megadiversidade 1:36-42.

LIMA, T.A. 2000. Em busca dos frutos do mar: os pescadores-coletores do litoral centro-sul do Brasil. Rev. USP 44:270-327.

LIMA, T.A., MACARIO, K.D., ANJOS, R.M., GOMES, P.R.S., COIMBRA, R.S. & ELAMORE, E. 2003. AMS dating of early shellmounds of the southeastern Brazilian coast. Braz. J. Phys. 33:276-279.

LINDBLADH, M., BRUNET, J., HANNON, G., NIKLASSON, M., ELIASSON, P., ERIKSSON, G. & EKSTRAND, A. 2007. Forest history as a basis for ecosystem restoration: a multidisciplinary case study in a south Swedish temperate landscape. Restor. Ecol. 15:284-295.

LOPES, M.S., BERTUCCI, T.C.P., RAPAGNÃ, L., TUBINO, R.A., MONTEIRO-NETO, C., TOMAS, A.R.G., TENÓRIO, M.C., LIMA, T.A., SOUZA, R.C.C.L., CARRILLO-BRICEÑO, J.D., HAIMOVICI, M., MACARIO, K.D., CARVALHO, C. & SOCORRO, A.O. 2016. The path towards endangered species: prehistoric fisheries in Southeastern Brazil. PLoS One 11(6):e0154476. https://doi: 10.1371/journal.pone.0154476 (last access on 15/06/2017)

LOTZE, H.K. & MILEWSKI, I. 2004. Two centuries of multiple human impacts and successive changes in a North Atlantic food web. Ecol. Appl. 14:1428-1447.

MASCHNER, H.D.G., BETTS, M.W., REEDY-MASCHNER, K.L. & TRITES, A.W. 2008. A 4500-year time series of Pacific cod (*Gadus macrocephals*) size and abundance: archaeology, oceanic regime shifts, and sustainable fisheries. Fish. Bull. 104:386-394.

MENDES, A.B., SILVA, E.P. & SOUZA, R.C.C.L. 2014. Biodiversity of marine fishes from Shellmounds of Ilha Grande Bay, Rio de Janeiro, Brazil. Revista Chilena de Antropologia 29:55-59.

MENEZES, N.A. 2011. Checklist dos peixes marinhos do Estado de São Paulo, Brasil. Biota Neotrop. 11:33-46.

MULATO, I. P., CORRÊA, B., & VIANNA, M. 2015. Distribuição espaço-temporal de *Micropogonias furnieri* (Perciformes, Sciaenidae) em um estuário tropical no Sudeste do Brasil. Bol. Inst. Pesca 41, 1-18.

PINNEGAR, J.K. & ENGELHARD, G.H. 2008. The "shifting baseline" phenomenon: a global perspective. Rev. Fish Biol. Fisher. 18:1-16.

POLUNIN, N.V.C. & ROBERTS, C.M. (eds) 1996. Reef fisheries. Chapman & Hall, London.

POVEY, A. & KEOUGH, M.J. 1991. Effects of trampling on plant and animal populations on rocky shores. Oikos 61:355-368.

PRUMMEL, W., & HEINRICH, D. 2005. Archaeological evidence of former occurrence and changes in fishes, amphibians, birds, mammals and molluscs in the Wadden Sea area. Helgoland Mar. Res. 49:55-70.

REITZ, E.J. & WING, E.S. 2008. Zooarchaeology. Cambridge University Press, New York.

RITTER, M.N. & ERTHAL, F. 2016. Time-averaging e suas implicações para o registro fóssil marinho. Terrae Didatica 12:81-103.

RODRIGUES, F.B., DUARTE, M.R., SOUZA, R.C.C.L., SOARES-GOMES, A. & SILVA, E.P. 2016a. Holocene crustaceans from the Tarioba shell mound, Rio das Ostras, Rio de Janeiro, Brazil. Check List 12:1-5.

RODRIGUES, F.B., GAROFALO, R., SOUZA, R.C.C.L., TAVARES, M.D.S. & SILVA, E.P. 2016b. Coleção de subfósseis de sambaquis do Laboratório de Genética Marinha e Evolução-UFF. Scientia Plena 12:1-14.

ROSA, R.S. & LIMA, F.C.T. 2008. Os peixes brasileiros ameaçados de extinção. In: Livro vermelho da fauna brasileira ameaçada de extinção: Peixes (A.B.M. Machado, G.M. Drummond & A.P. Paglia, eds). Ministério do Meio Ambiente, Brasília.

ROSENBERG, A.A., BOLSTER, W.J., ALEXANDER, K.E., LEAVENWORTH, W.B., COOPER, A.B. & MCKENZIE, M.G. 2005. The history of ocean resources: modeling cod biomass using historical records. Front. Ecol. Environ. 3:84-90.

SANTOS, P.R.S., EINHARDT, A.C.M.C. & VELASCO, G. 2016. A pesca artesanal da miragaia (*Pogonias cromis*, Sciaenidae) no estuário da Lagoa dos Patos, Brasil. Bol. Inst. Pesca 42:89-101.

SANTOS, T.C.C. & CÂMARA, J.B.D. (eds) 2002. GEO Brasil 2002: perspectivas do meio ambiente no Brasil. Edições IBAMA, Brasília.

SCHEEL-YBERT, R., BIANCHINI, G.F. & DEBLASIS, P. 2009. Registro de mangue em um sambaqui de pequeno porte do litoral sul de Santa Catarina, Brasil, a cerca de 4900 anos cal BP, e considerações sobre o processo de ocupação do sítio Encantada III. Rev. Mus. Arqueol. Etnol. 19:103-118.

SILVA, E.P., SOUZA, R.C.C.L., ARRUDA, T.A. & DUARTE, M.R. 2016. Sambaquis: mostra da biodiversidade pré-histórica. Ciência Hoje 57:30-33.

SILVEIRA, L.B., BEISIEGEL, B.M., CURCIO, F.F., VALDUJO, P.H., DIXO, M., VERDADE, V.K., MATTOX, G.M.T. & CUNNINGHAM, P.T.M. 2010. Para que servem os inventários de fauna? Cad. Est. Av. 24:173-207.

SIQUEIRA, T., BINI, L.M., THOMAZ, S.M. & FONTANETO, D. 2015. Biodiversity analyses: are aquatic ecologists doing any better and differently than terrestrial ecologists? Hydrobiologia 750: 5-12.

SOUZA CUNHA, F.L., VOGEL, M.A.C., VERÍSSIMO, S.G. & MAGALHÃES, R.M.M. 1981. Restos de vertebrados do Sambaqui de Camboinhas. In: Pesquisas arqueológicas no litoral de Itaipu, Niterói, RJ (L.M. Kneip, L. Pallestrini & F.L. Souza Cunha, eds). Cia de Desenvolvimento Territorial, Rio de Janeiro.

SOUZA, R.C C L., LIMA, T A. & SILVA, E.P. 2010a. Holocene molluscs from Rio de Janeiro state coast, Brazil. Check List 6:301-308.

SOUZA, R.C.C.L., LIMA, T.A., DUARTE, M.R. & SILVA, E.P. 2016. Changes in patterns of biodiversity of marine mollusks along the Brazilian coast during the late Holocene inferred from shell-mound (sambaquis) data. Holocene 26:1802-1809.

SOUZA, R.C.C.L., TRINDADE, D.C., DECCO, J., LIMA, T.A. & SILVA, E.P. 2010b. Archaeozoology of marine mollusks from Sambaqui da Tarioba, Rio das Ostras, Rio de Janeiro, Brazil. Zoologia 27:363-371.

STAHL, P.W. 2008. The contributions of zooarchaeology to historical ecology in the neotropics. Quatern. Int. 180:5-16.

TACON, A.G.J. 1994. Feed ingredients for carnivorous fish species: alternatives to fish meal and other fisheries resources. In: FAO Fisheries Circular, 881. FAO, Roma.

VILLAGRAN, X.S. & GIANNINI, P.C.F. 2014. Shell mounds as environmental proxies on the southern coast of Brazil. Holocene 24:1-8.

WAGNER, G.P. & SILVA, L.A. 2014. Prehistoric maritime domain and Brazilian shellmounds. Archaeological Discovery 2:1-5. http://dx.doi.org/10.4236/pst.2014.21001 (last access on 15/06/2017)

WALKER, M.J.C., BERKELHAMMER, M., BJÖRCK, S., CWYNAR, L.C., FISHER, D.A., LONG, A.J., LOWE, J.J., NEWNHAM, R.M., RASMUSSEN, S.O. & WEISS, H. 2012. Formal subdivision of the Holocene Series/Epoch: A discussion paper by a Working Group of INTIMATE (Integration of ice-core, marine and terrestrial records) and the Subcommission on Quaternary Stratigraphy (International Commission on Stratigraphy). J. Quat. Sci. 27(7):649-659.

WARWICK, R.M. & LIGHT, J. 2002. Death assemblages of molluscs on St Martin's Flats, Isles of Scilly: a surrogate for regional biodiversity? Biodivers. Conserv. 11:99-112.

WILLIS, K.J. & BIRKS, H.J.B. 2006. What is natural? The need for a long-term perspective in biodiversity and conservation. Science 314:1261-1265.

Received: 15/06/2017
Revised: 16/12/2017
Accepted: 17/12/2017
Published online: 15/01/2018