



Sambaquis (shell mounds) and mollusk diversity in the past history of Araruama Lagoon, Rio de Janeiro, Brazil

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Abstract. The Araruama Lagoon is hypersaline and due to this presents low diversity. The aim of this work was to use data from shell mounds to make inferences regarding the mollusk diversity and environmental conditions in the past of the Lagoon. Species registered for the shell mounds were analyzed by relative occurrence and richness among sites, categorization per habitat, feeding guilds and anthropological use. The results suggest that diversity in the Araruama Lagoon was higher in the past than today, and that it was reduced as a consequence of changes in the lagoon geomorphology and hydrology. The results also suggest that the development of the shell mound builders culture may be associated with the evolution of the Lagoon, which was probably their main source of mollusks.

Key Words: Biodiversity, hypersalinity, bivalves, gastropods, zooarchaeology

Resumo: Sambaquis e diversidade de moluscos do passado da Lagoa de Araruama, Rio de Janeiro, Brazil. A Lagoa de Araruama é uma laguna que apresenta baixa diversidade devido a suas condições de hipersalinidade. No presente trabalho, tanatocenoses de moluscos de sambaquis são utilizadas para inferir as condições ambientais do passado da Lagoa. São apresentados dados de ocorrência relativa das espécies registradas nos sambaquis e a riqueza específica dos catorze sítios arqueológicos estudados. Além disso, para todas as espécies são descritos habitat, modo de alimentação e uso antropológico. Os resultados sugerem que a diversidade na Lagoa de Araruama foi maior no passado, sofrendo redução em tempos mais recentes devido a mudanças na sua geomorfologia e hidrologia. Do mesmo modo, aspectos da cultura sambaqueira podem estar relacionados com as mudanças sofridas pela lagoa que, provavelmente, foi a principal fonte de moluscos para as populações humanas no Holoceno Recente.

Palavras-chave: Biodiversidade, hipersalinidade, bivalves, gastrópodes, zooarqueologia

Introduction

The Araruama Lagoon is located in Southeastern Brazil (22° 49' - 22° 47' S and 42° - 42° 23' W). It is in a region of semi-arid climate, with a reduced drainage basin and a limited connection with the Atlantic Ocean, which results in increasing salinity towards the inner lagoon (André *et al.*, 1981; Kjerfve *et al.*, 1996). Due mainly to its hypersalinity, the Araruama Lagoon presents quite peculiar ecological characteristics (Reis &

Yoneshigue-Valentin, 1996), such as the existence of a strong environmental gradient which facilitates the identification of patterns of species distribution. For example, a decrease in diversity occurs towards the inner lagoon – where the salinity normally varies between 40 and 65 ‰ (Kjerfve *et al.*, 1996; Souza *et al.*, 2003; Silva *et al.*, 2005) – for encrusting communities (Bezerra, 1987; Correia, 1987), diatoms (Sylvestre *et al.*, 2001), macroalgae (Reis & Yoneshigue - Valentin, 1996) and macrobenthos

(Araújo, 1998; Martins, 2000; Silva *et al.*, 2005).

The origin of the lagoon goes as far as 7000 BP when it started to go through a progressive process of sectioning due to the formation of sand barriers and later isolation from the sea (Turcq *et al.*, 1999). It is supposed that around 5000 BP the salinity was lower than today. In a subsequent period (4900/4500 BP) salinity probably increased due to a drier period which also coincides with its final enclosure. A humid period occurred around 2300/2000 BP and decrease the Lagoon's salinity. However, since 2200 BP drier conditions would have predominated (Scheel-Ybert, 2000; Sylvestre *et al.*, 2005). These variations in the salinity of the lagoon were estimated according to changes in mangrove vegetation (Scheel-Ybert, 2000) and diatom species diversity (Sylvestre *et al.*, 2005). However, the evolution of benthic macrofauna diversity in this highly dynamic environment in the last 7000 years was not explored so far.

The first evidences of human occupation in Southeastern Brazil littoral are archaeological sites known as *sambaquis* (shell mounds). These cultural deposits of varying size and defined stratigraphy have seashells as their major constituent, and can encompass a wide range of functions and origins (Gaspar *et al.*, 2008). The shell mound builders are believed to have been specialized in the exploitation of the coastal environment, especially bays and lagoons (Lima, 1987; Perota *et al.*, 1987; Gaspar, 2003; Gaspar *et al.*, 2008). In fact, the lagoon may have been the main circulation space of the shell mound builders from the region (Kneip, 2004).

The most ancient shell mounds in Southeastern Brazil date back about 7000 BP (e.g. Sambaqui de Cambainhas, 7958 ± 224 BP, Kneip & Pallestrini, 1984; and Sambaqui do Algodão, 7860 ± 80 BP, Lima *et al.*, 2004). In the surroundings of Araruama Lagoon, the most ancient datings were obtained in Sambaqui do Forte (5520 ± 120 BP, Kneip & Pallestrini, 1984) and Sambaqui do Meio (5180 ± 80 BP, Scheel-Ybert, 2000). One of the most recent datings was found in the Sambaqui Salinas Peroano, 1830 ± 45 BP (Scheel-Ybert, 2000).

The aim of this work was to use data from shell mounds to make inferences regarding the past mollusk diversity and environmental conditions of the Lagoon. The shell mound builders may have selected mollusks and seashells in a wide range of ways for a multitude of reasons, but they could only have picked up what was available in the environment. Based on this assumption, it is possible

to use data from shell mounds to elucidate some issues about the evolution of the malacofauna diversity in this highly dynamic environment in the last 7000 BP and, as the gathering of mollusks by shell mound builders was not at random, it is also interesting to study the relationship among people, mollusks and the lagoon.

Material and Methods

Mollusk lists for Araruama Lagoon were obtained from the works of Kneip (1977), Gaspar (1991), Mello (1998; 1999) and Souza *et al.* (2010; 2011; 2012). It was chosen to work with mollusks from non-consolidate substrata, since this substratum prevails in the lagoon (Primo & Bizerril, 2002). The archaeological sites were chosen based on Gaspar (1991). This author, deducing that shell mound builders gathered their resources in the closest places they could find them, defined exploitation territories for some pre-historic populations of Rio de Janeiro State (Southeast Brazil). All the three exploitation territories that include the Araruama Lagoon comprise a part or the totality of the three lagoon areas defined by the Instituto Nacional de Pesquisas Hidrológicas (INPH) (Primo & Bizerril, 2002), based on sediment and hydrochemical characteristics (Figure 1). This coincidence made it possible to correlate data from shell mounds in the exploitation territories (from now on called Territories 1, 2 and 3) with those sediment and hydrochemical defined areas (From now on called Areas 1, 2 and 3).

It is worth of note that the shell mounds are being destroyed since the XVI century (Leonardos, 1938; Gaspar *et al.*, 2008). Many, or maybe most of them, did not last enough to be registered. And among the sites that were registered, mollusks were not properly studied in most of them. The mollusk species list used in this work is the result of an exhaustive survey of all the literature about the shell mounds present in the three territories mentioned above (Kneip, 1977; Gaspar, 1991; Mello, 1998; 1999; Souza *et al.*, 2010; 2011; 2012). Another survey about the ecology and anthropological use of these mollusks was performed. For comparison, censuses of living fauna were consulted (Silva, 1988; Araújo, 1998; Ribeiro, 1999; Martins, 2000; Grillo, 2001). Species habitats (Table I and Table II) and feeding guilds (Table II) were defined based on information from the literature (García-Cubas, 1981; Antolí & García-Cubas, 1985; Rios, 1994; Arruda *et al.*, 2003; Souza *et al.*, 2011). Each species was defined just for one of the categories established.

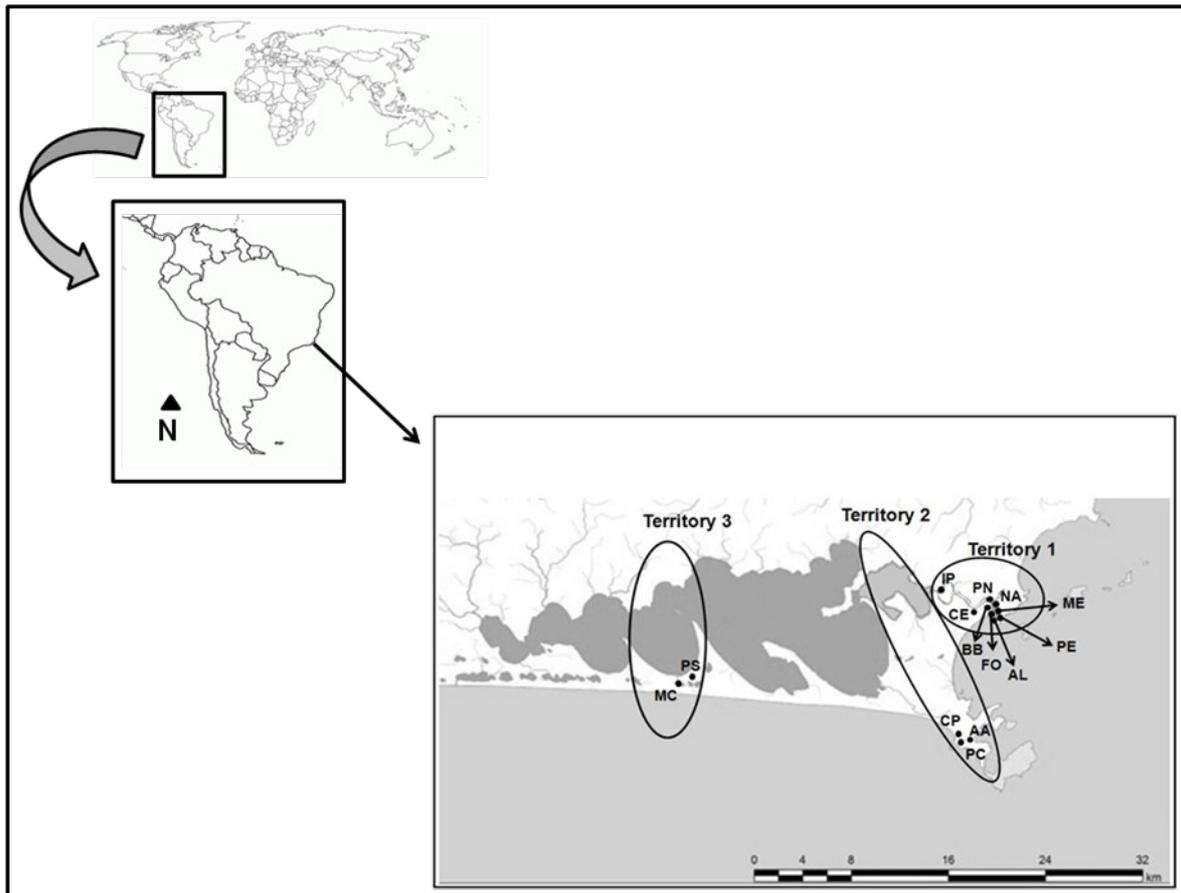


Figure 1. Araruama Lagoon localization and demarcation of its exploration territories and areas (Ovoid shapes delimit exploration territories and lagoon areas are differentiated by grey shades following the territories numeration). Black circles represent archaeological sites, identified by abbreviatures (FO – Forte; BB – Boca da Barra; NA – Nacil; AI – Arco-íris; PE – Peró; PN – Salinas Peroano; ME – Meio; CE – Cemitério; IP – Ilha Palmer; AA – Abrigo Praia dos Anjos; PC – Ponta da cabeça; CP – Colônia de Pescadores; MC – Morro da Concha; PS – Praia Seca).

Table I. Habitat categories description.

Category	Abbreviation	Description
Coastal, low-hydrodinamism environments	CL	Species that occur in coves, bays and coastal lagoons and are probably stenohaline (There was no reference to their survival in hypersaline or brackish water in the literature).
Coastal, low-hydrodinamism, hypersaline environments	CL(h)	Species that occur in coves, bays and coastal lagoons and are probably eurihaline (There were references to their survival in hypersaline water and frequently also in brackish water).
Coastal high hydrodinamism environments	CH	Species that occur in exposed, high energy beaches. References register their occurrence in sea water salinity only.
Sublittoral Zone of Continental Platform	PL	Species commonly found in the Sublittoral Zone of the Continental Platform and are probably stenohaline.

Two geographical scales were used for the analysis (Birks, 1987). Firstly, archaeological sites were treated as independent units. After that, all archaeological sites within each territory were pooled as a new unit. An integrated approach was used to study the mollusks biodiversity which include data on number of species (species richness), the presence and absence of species (relative

occurrence), the percentage of species per habitat and feeding guilds, and anthropological use of the species (species which could be used in some way by the shell mound builders).

The relative occurrence was calculated by the formula: $F = pa/P \times 100$, where: pa = is the number of sites where the species “a” occurred and P is the total number of sites. For Area 1, which

Table II. List of mollusk species registered for the shell mounds, sites in which they were found, feeding guilds and habitat categories (description in Table I). Area 1: FO – Forte, BB – Boca da Barra, NA – Nacil, AI – Arco-íris, PE – Però, PN – Salinas Peroano, ME – Meio; CE – Cemitério, IP – Ilha Palmer; Area 2: AA – Abrigo Praia dos Anjos, PC – Ponta da cabeça, CP – Colônia de Pescadores; Area 3: MC – Morro da Concha, PS – Praia Seca. CL, CL (h), PL and CH are defined in Table I.

Taxa	Shell mounds	Feeding guilds	Habitat Category
<i>Anadara notabilis</i>	PE, IP, BB, PN, FO, CE, ME	Suspensivorous	CL
<i>Anomalocardia brasiliiana</i>	PE, IP, BB, PN, FO, CE, ME, NA, PC, PS	Suspensivorous	CL (h)
<i>Chione cancellata</i>	IP, BB, PN, PC	Suspensivorous	CL (h)
<i>Chione cancellata</i>	IP, BB, PN, PC	Suspensivorous	CL (h)
<i>Lirophora paphia</i>	ME	Suspensivorous	PL
<i>Codakia costata</i>	BB	Suspensivorous	PL
<i>Codakia orbicularis</i>	PE, BB, ME	Suspensivorous	CL
<i>Donax hanleyanus</i>	BB	Suspensivorous	CL
<i>Dosinia concêntrica</i>	ME	Suspensivorous	PL
<i>Phacoides pectinatus</i>	PE, IP, BB, PN, FO, CE, ME, PC, AA, PS	Suspensivorous	CL (h)
<i>Megapitaria maculata</i>	PE, BB, PN, CE	Suspensivorous	CL
<i>Maetra fragilis</i>	IP, CP, AA	Saprophogous	CL (h)
<i>Pitar fulminatus</i>	BB	Suspensivorous	CL
<i>Tivela mactroides</i>	BB, ME	Suspensivorous	CL
<i>Trachycardium muricatum</i>	PE, BB, PN, ME	Suspensivorous	CL (h)
<i>Globivenus rigida</i>	BB, ME, PC	Suspensivorous	CL
<i>Bulla striata</i>	PE, BB, PN, ME	Carnivore	CL (h)
<i>Calliostoma adpersum</i>	PC	X	CL
<i>Cerithium atratum</i>	PE, BB, PN, FO, CE, ME, PC	Herbivore	CL
<i>Siuratus senegalensis</i>	PE, IP, BB, FO, CE, ME, AA	Carnivore	CL
<i>Cymatium parthenopeum</i>	PE, BB, FO, ME	Carnivore	CH
<i>Modulus modulus</i>	BB	X	CL
<i>Natica canrena</i>	BB, ME	Carnivore	CL
<i>Neritina virgínea</i>	BB, PN	Herbivore	CL (h)
<i>Oliva circinata</i>	BB	Carnivore	CL
<i>Oliva reticularis</i>	ME	X	CL
<i>Olivancillaria vesica auricularia</i>	BB, PN, FO, CE, ME	Carnivore	CL
<i>Olivancillaria vesica vesica</i>	BB, PN, CP, PC	Carnivore	CL
<i>Polinices hepaticus</i>	ME	Carnivore	CL
<i>Polinices lacteus</i>	BB, FO	X	CL
<i>Pugilina morio</i>	BB	Carnivore	CL
<i>Lobatus costatus</i>	BB, PN, FO, AI, CE	Herbivore	CL
<i>Strombus pugilis</i>	PE, BB, PN, ME, PC	Herbivore	CL

showed the highest species richness but also the biggest number of sambaquis sampled, it was done a Kruskal-Wallis test of species richness calculated for all possible combinations of 2 and 3 shell mounds

from this area against all the possible combinations of 2 and 3 shell mounds from areas 2 and 3. Cluster analysis was done for both geographical scales used for analysis, using the unweighted pair wise group

method (UPGMA) with the Bray-Curtis similarity coefficient. These analyses (Kruskal-Wallis test and Cluster) were performed using the software *Past 2.08* (Hammer *et al.*, 2001).

Results

Thirty two mollusk species are registered for the shell mounds (Table II), fifteen bivalve and seventeen gastropod species (Figure 2). Most of these species are not currently found in the Araruama Lagoon. From the thirty two species registered, only eight - *Anomalocardia brasiliiana*, *Bulla striata*, *Cerithium atratum*, *Codakia costata*, *Cymatium parthenopeum*, *Lirophora paphia*, *Phacoides pectinatus* and *Neritina virginea* – were found in a recent sampling of the Araruama Lagoon bottom and only two genera – *Donax* and *Olivancillaria* – were collected in the oceanic beach that occupies most of the region, Massambaba Beach (Veloso *et al.*, 2003).

The richest archaeological site (14 gastropod and 12 bivalve species) was Sambaqui Boca da Barra, next to the entrance of the Itajuru Channel and the poorest (one species) were Nacil and Arco-Íris, next to the Channel entrance, and Morro da Concha, at Massambaba Shoal. Only sites next to the Channel entrance have more than ten species registered. It is remarkable that all species registered for shell mounds from Araruama Lagoon are represented in very few sites located between the channel entrance and the Japonês Island, and that 22 species found in these shell mounds cannot be found in any other sambaqui alongside the Lagoon. All possible combinations of 2 shell mounds from Area 1 showed species richness which are higher than

those from Area 3 in 80.6% of the random combinations. If the procedure is repeated using all possible combinations of 3 shell mounds, the result is even higher, 93.1% of the random combinations are higher than those for sambaquis from Area 2. Furthermore, a Kruskal-Wallis test (Table III) showed that these random combinations of 2 and 3 sambaquis from Area 1 shows species richness which are significantly higher than random combinations of 2 and 3 sambaquis from Areas 2 and 3.

The percentage of species per habitat may indicate where these species were most probably gathered (Figure 3). In Area 1 most of the species are stenohaline from low hydrodynamic coastal environments. In Area 3 the only two species registered are from hypersaline low hydrodynamic coastal environments (*Anomalocardia brasiliiana* and *Phacoides pectinatus*). The other species found in the Area 3, *Phacoides pectinatus*, was recently found alive only in Areas 1 and 2, but not in Area 3.

Figure 4 shows the proportion of feeding guilds found for the three lagoon areas. The suspension-feeders are the most important group representing 50% of the organisms found in Area 1, 40% in Area 2 and 100% in Area 3.

From the total of registered species, 65.63% can present some anthropological use (Table IV) that would justify their presence in the sambaquis. Relative occurrence frequency values can be found in Table IV. The most frequent species were *Anomalocardia brasiliiana* (0.79), *Phacoides pectinatus* (0.71), *Anadara notabilis*, *Cerithium atratum* and *Siratus senegalensis* (0.50) (Figure 5).

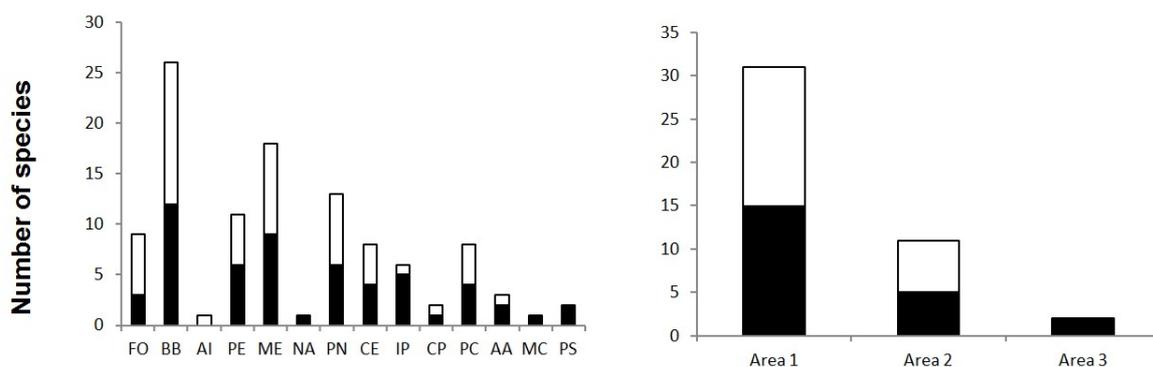


Figure 2. Number of species (species richness) in archaeological sites and in exploitation territories/lagoon areas (white bars are gastropod and black bars are bivalve). Area 1: FO – Forte, BB – Boca da Barra, NA – Nacil, AI – Arco-íris, PE – Perú, PN – Salinas Peroano, ME – Meio; CE – Cemitério, IP – Ilha Palmer; Area 2: AA – Abrigo Praia dos Anjos, PC – Ponta da cabeça, CP – Colônia de Pescadores; Area 3: MC – Morro da Concha, PS – Praia Seca.

Table III. Results for Kruskal-Wallis test comparing species richness from random combination of 2 and 3 sambaquis from Area 1 versus species richness from random combinations of 2 and 3 sambaquis from Areas 2 and 3 taken together.

Number of sambaquis	Number of random combinations		P
	Area 1	Area 2 + Area 3	
2	36	10	0.000057
3	29	4	0.000550

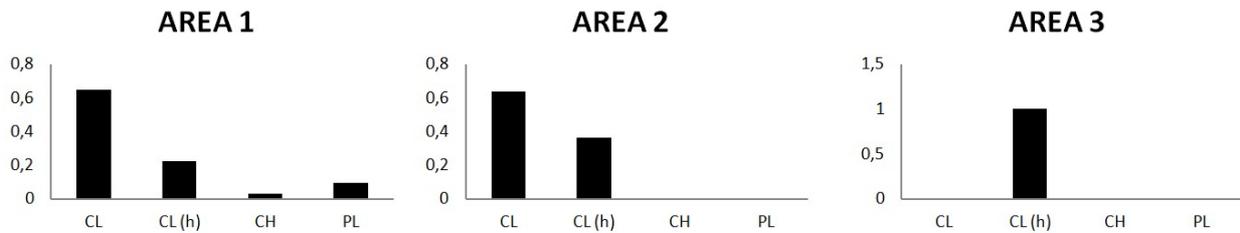


Figure 3. Species percentage per habitat (CL – coastal, low hydrodynamism environments; CL(h) – Hypersaline, coastal, low hydrodynamism environments; CH – coastal, high hydrodynamism environments and PL – sublittoral platform).

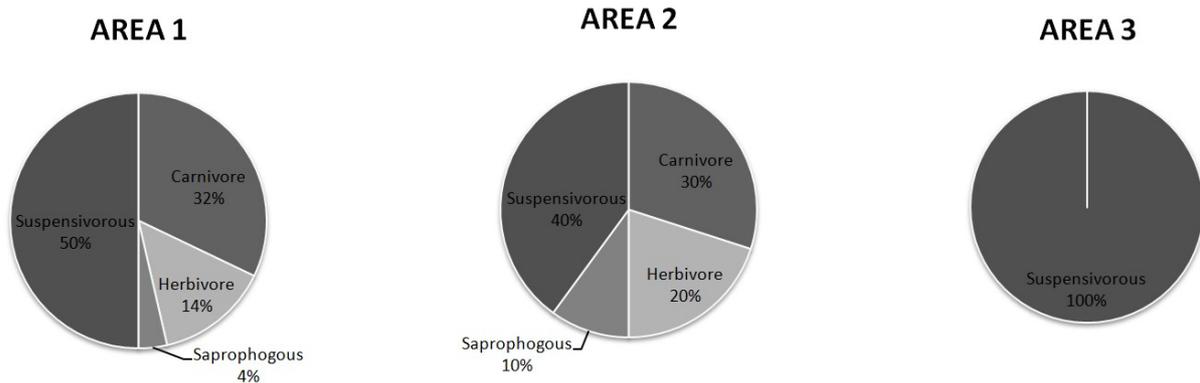


Figure 4. Species percentage per feeding guilds.

Except for *Cerithium atratum* and *Siratus senegalensis* all these species are edible. Seventy percent of the species were found in the shell mounds of Area 1. Two euryhaline species were found in all areas: *Anomalocardia brasiliiana* and *Phacoides pectinatus*.

The cluster analysis using archaeological sites as units distinguished two groups and two isolated sites (Figure 6). However, if the cluster analysis is done pooling archaeological sites within each territory, the results show that Area 2 is more similar to Area 1 than to Area 3 (Figure 7), grouping always with high statistical support estimated by bootstrap.

Discussion and Conclusions

Compared with the surveys of the lagoon

living fauna (Silva, 1988; Araújo, 1998; Ribeiro, 1999; Martins, 2000; Grillo, 2001; Silva *et al.*, 2005), shell mounds show a relatively high number of species from Area 1. This result is probably explained by the many environments explored by shell mound builders (Carvalho, 1984; Gaspar, 1991). However, if populations of all sites had comparable access to the oceanic beaches, it is possible that species richness was really higher in this area. Silva *et al.* (2005) defined this area as the one with the present greatest diversity of species and it is possible that this was also true in the past. According to Pérez-Ruzafa & Diego (1993), most studies on coastal lagoons reveals that greater productivity and diversity are found in areas of stronger estuary-ocean contact. This result was also

found by Gordon (2000) in Muni Lagoon, Ghana, García-Cubas (1981) in Laguna de Términos, México, and Parker (1959) in Laguna Madre, Texas (the former and latter are also hypersaline lagoons). Therefore, it is possible that Area 1 presented a great diversity and abundance in the past.

Most of the species registered in Area 1 are from low hydrodynamic coastal environments (with salinity similar to the sea) or from the sublittoral zone. Considering that neither the current lagoon conditions (high salinity) nor the nearby oceanic beaches (high hydrodynamics) support this kind of fauna and, moreover, that the pre-historic populations of all areas had equal access to the sublittoral zone, it can be concluded that Area 1 probably presented somewhat different hydrological conditions in the past. Lessa (1990)'s study about the past conditions of the Itajuru Channel (the channel that connects the Lagoon to the Ocean) suggests that this channel probably consisted of a succession of interconnected small lagoons that presented greater depth than nowadays. A wider and deeper channel would present greater oceanic influence and stability, creating conditions that would make possible colonization by many species poorly

tolerant to environmental variation and change, like those from low hydrodynamic beaches and from the sublittoral zone. Organisms from the low hydrodynamic and sublittoral zones are commonly found in lagoon regions with strong oceanic influence (Parker, 1959; García-Cubas, 1981; Pérez-Ruzafa & Diego, 1993). Lessa (1990)'s hypothesis also is corroborated by the result found for Area 3, since greater oceanic influence in the Itajuru Channel would affect the inner areas of the lagoon which would be consequently less subject to an extreme salinity gradient.

The present work is based on data from death assemblages and not communities. Species probably arrived or come from distinct environments and were gathered in a selective way. However, if we consider that sorting was practiced similarly by shell mound builders from the three areas/territories, it is possible to accept that the trophic diversity found among areas reflects in some way the past environment from the Lagoon. The highest trophic diversity was found in Area 1, what is an indication that this fauna is little affected by physical factors such as salinity (Grillo, 2001). This result agrees with the previous discussion on richness and habitat.



Figure 5. The most frequent species found in the shell mounds: *Anomalocardia brasiliiana* (A), *Phacoides pectinatus* (B), *Anadara notabilis* (C), *Cerithium atratum* (D) and *Siratus senegalensis* (E). Photos: Raquel Garofalo Faria.

Table IV. Definition of species registered in shell mounds which can be useful (1) for human populations or which doesn't have a known utility (0) and relative occurrence of species per archaeological site and exploitation territory.

Taxa	Utilization*	Sites	Territories
<i>Anadara notabilis</i>	1	0.50	0.33
<i>Anomalocardia brasiliiana</i>	1	0.79	1.00
<i>Chione cancellata</i>	1	0.29	0.67
<i>Lirophora paphia</i>	1	0.07	0.33
<i>Codakia costata</i>	0	0.07	0.33
<i>Codakia orbicularis</i>	1	0.21	0.33
<i>Donax hanleyanus</i>	1	0.07	0.33
<i>Dosinia concêntrica</i>	1	0.07	0.33
<i>Phacoides pectinatus</i>	1	0.71	1.00
<i>Megapitaria maculata</i>	1	0.29	0.33
<i>Mactra fragilis</i>	1	0.21	0.67
<i>Pitar fulminatus</i>	1	0.07	0.33
<i>Tivela mactroides</i>	1	0.14	0.33
<i>Trachycardium muricatum</i>	1	0.29	0.33
<i>Globivenus rígida</i>	1	0.21	0.67
<i>Bulla striata</i>	0	0.29	0.33
<i>Calliostoma adpersum</i>	0	0.07	0.33
<i>Cerithium atratum</i>	0	0.50	0.67
<i>Siratus senegalensis</i>	0	0.50	0.67
<i>Cymatium parthenopeum</i>	1	0.29	0.33
<i>Modulus modulus</i>	0	0.07	0.33
<i>Natica canrena</i>	0	0.14	0.33
<i>Neritina virgínea</i>	1	0.14	0.33
<i>Oliva circinata</i>	0	0.07	0.33
<i>Oliva reticularis</i>	0	0.07	0.33
<i>Olivancillaria vesica auricularia</i>	1	0.36	0.33
<i>Olivancillaria vesica vesica</i>	1	0.29	0.67
<i>Polinices hepaticus</i>	0	0.07	0.33
<i>Polinices lacteus</i>	0	0.14	0.33
<i>Pugilina morio</i>	1	0.07	0.33
<i>Lobatus costatus</i>	1	0.36	0.33
<i>Strombus pugilis</i>	1	0.36	0.67
Total	21	X	X
Percentage of species that can be useful	65.63%	X	X

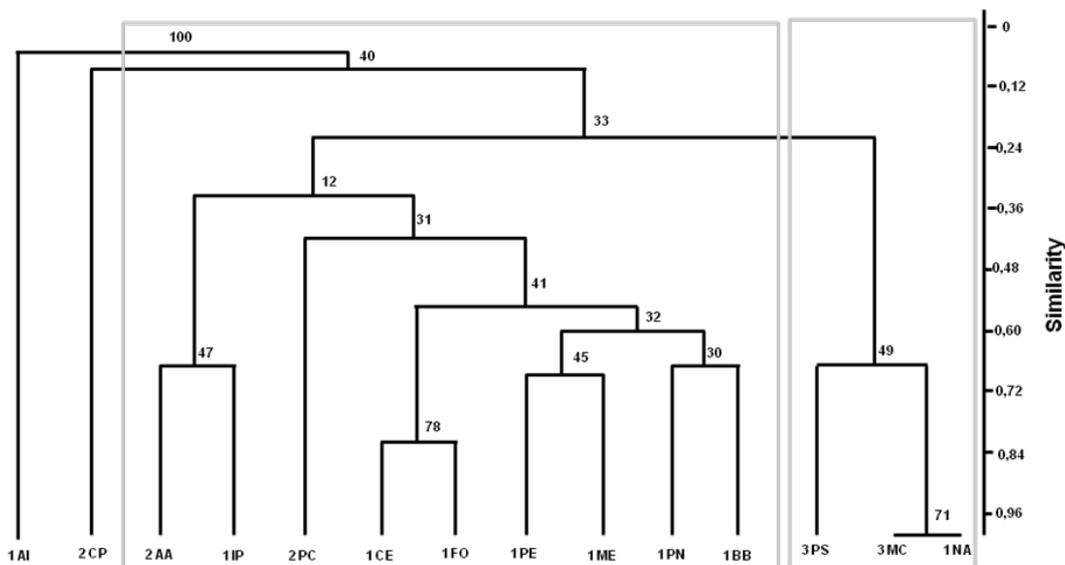


Figure 6. Archaeological sites cluster analysis.

The high proportion of carnivores found in Areas 1 and 2 may represent an evidence of human selection. Carnivores may possibly have been attractive to gatherers to different reasons such as palatability, size, nutritional value etc. Studies correlating mollusk characteristics with pre-historic people interests and their presence in sambaquis are desirable and would help to elucidate this question.

The number of species recovered from shell mounds of the Araruama Lagoon showed that diversity was higher in the past than in recent times. Such results support the idea that mollusk diversity in Araruama Lagoon has been decreasing in the last 7000 years and that the diversity reduction is towards the survival of those species which are euryhaline. Furthermore, shell mounds showed a biodiversity that decreases from Area 1 to 3, what agree with the salinity gradient present in the lagoon nowadays.

These data indicate that probably a salinity gradient was all the time present in the lagoon although less pronounced than today. Additionally to all that, the results obtained for Area 3 (a low number of species, all of them euryhaline), also suggest that the lagoon probably showed already a higher salinity than the ocean during the times of sambaquis' people. However, the salinity difference was probably less pronounced, since nowadays only few, small individuals of *Anomalocardia brasiliiana* are able to live in this area of the Lagoon.

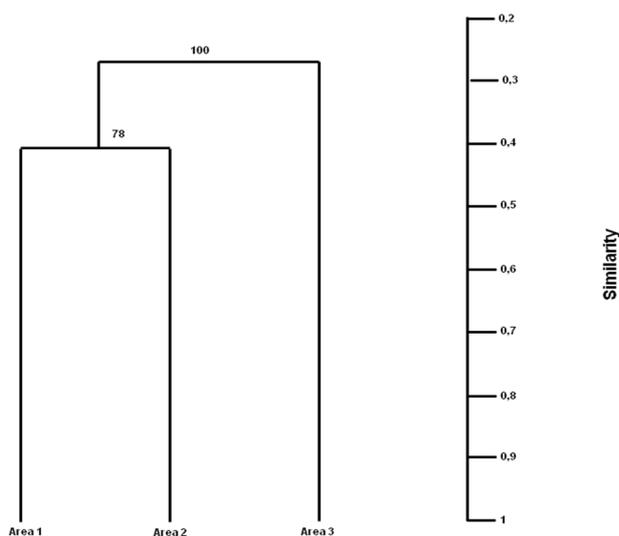


Figure 7. Exploitation territories/lagoon areas cluster analysis.

An alternative explanation for these data would be that the number of shell mounds which present data on mollusks for Area 1 (9) is greater

than for the other two areas (3 at Area 2 and 2 at Area 3). However, all possible combinations of 2 shell mounds from Area 1 showed species richness which is still higher. If the procedure is repeated now using all possible combinations of 3 shell mounds the result is even higher, and in both cases the differences are statistically significant. Therefore, it seems that the gradient of reducing mollusks biodiversity towards the inner lagoon is not an artifact. As productivity and diversity in lagoons are frequently related to oceanic influence (Pérez-Ruzafa & Diego, 1993), it is very probable that species richness was greater in the past, when the lagoon was still in a process of progressive isolation from the sea until to its definitive enclosure (Turcq *et al.*, 1999). Moreover, shell mounds which surround Area 1 are composed mostly by species known to be not tolerant to variations in salinity. The censuses of Silva *et al.* (2005), however, have shown that nowadays euryhaline species predominate in this Area. Therefore, the presence of stenohaline species in the shell mounds from Area 1 is evidence that the lagoon presented a malacofauna less limited by hypersalinity than today. Also, the presence of species from the sublittoral zone and high hydrodynamic beaches suggest that oceanic influence was greater than today. Yet, the presence of *Phacoides pectinatus* in shell mounds associated to area 3 suggests less severe conditions in the past. *P. pectinatus*, a species frequently found in mangroves and to some degree tolerant to hypersalinity (Cruz-Ábrego, 1994), cannot be found nowadays farther than area 2. Additionally, data on feeding guilds inferred from death assemblages show higher trophic complexity for Area 1, decreasing towards Area 3 where only suspensivorous were found. All these inferences point to claim that the salinity gradient was already present in the past.

The shell mounds encompass thousands of years, and consequently a great number of cohorts of mollusks. This process of time-averaging lead to inflate diversity, as does the practice of gathering mollusks in different environments. On the other hand, selection by shell mound builders, taphonomic processes, and selection made by researchers (whose studies were interested in cultural aspects of shell mounds vestiges rather than their information about biological diversity) tend to reduce species richness (Kidwell & Bosence, 1991; Kidwell, 2002; Prummel & Heinrich, 2005). Therefore, species richness alone can become complex and ambiguous as an indicator

of diversity in the past (Kidwell, 2002). These factors probably are on the basis of the ambiguous results obtained for Area 2, which presented a lower diversity than shown by nowadays censuses for living fauna.

The greater oceanic influence in the past (Turcq *et al.*, 1999) conferred more stability to the Araruama Lagoon, restricting the salinity gradient and, therefore making possible its continuous exploitation by human populations. The establishment of the shell mound builders approximately at the same time that these lagoons were forming was probably not a coincidence. However, there are not clear evidences nor enough knowledge about this culture to understand to such an extent the evolution of the lagoons favored the colonization of these areas by the shell mound builders. The results obtained here, in special the percentage of species per habitat, suggest that the Araruama lagoon was the main source of mollusks to these populations. Frequency and percentage of species of potential anthropological use also suggest that the mollusks (or their shells) were not gathered at random, but attended some purposes such as food, ornament, confection of artifacts, symbolic meaning, pigments, and fish bates (Mendonça-de-Souza & Mendonça-de-Souza, 1983; Carvalho, 1984; Kneip, 1994; Mello, 1998; 1999). The fact that not all species have an inferred utility is probably related with our incomplete knowledge regarding the mollusk utilization by pre-historic populations. They can be also "accidental" species. Gaspar (1991) suggests that the presence of small gastropods of unknown utility in some shell mounds is due to some kind of trawl-net which would accidentally catch these organisms. A poor selectivity in the use of seashells by the gatherers during the process of shell mound building should also be considered (Afonso & DeBlasis, 1994). Although the mollusk shells could also have been used as building material, this function was probably not the only purpose of mollusk gathering. The high frequency of species of anthropological use in the shell mounds probably means that they were widely used by the pre-historic human populations and were commonly present in the environment. The high proportion of species of low occurrence can be attributed to selective gathering, scarcity in the environment or accidental capture, but we have not elements to choose one or another factor.

Kneip (2001) noted that composition of mollusk fauna among archaeological sites which are close to each other varies. She attributed this

variation to cultural differences between human populations which build the sambaquis up. In a similar way, Tenório (1995) explained these differences as a result of some role of mollusk in the social identification of different sambaquis cultures. Therefore, it is possible that some species present in only one archaeological site had a peculiar significance for the population of a sambaqui or group of sambaquis.

In summary, the hypersaline condition of the Araruama Lagoon seems to have been present at least since its enclosure, around 5000 BP, as well as a gradient of decreasing diversity towards the inner lagoon caused by an increasing gradient of salinity. But due to greater oceanic conditions in the past, it probably presented greater stability and less limiting conditions favoring higher species richness and productivity which would have favored the development of the shell mound builders society in its region.

Acknowledgment

The authors would like to thank Chris Day for her help in improving the English in this article.

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Received: December 2015

Accepted: March 2016

Published: April 2016