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ORIGINAL ARTICLE

Damage triggered by bioerosion and surface residence time in Holocene shell beds from Brazil

Daniel Sedorko[1,2] · João Paulo Porto Barros[3] · James H. Nebelsick[2] · Gabriel Eduardo Barea de Barros[4,5] · Juan Bueno Xavier[1] · Patrick Führ Dal' Bó[3] · João Wagner Alencar Castro[1]

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Abstract

Holocene shell beds along the Brazilian coast provide critical records of sea level variations influenced by climatic changes. This study examines the taphonomic implications of bioerosional traces in bioclastic accumulations from coastal sites in Rio de Janeiro State, Brazil. By integrating sedimentological, taphonomic, and taxonomic data, the relationship between bioerosion and shell damage signatures was explored, focusing on three Quaternary localities rich in mollusk shell remains. Detailed analyses using thin sections, X-ray microtomography, and compaction tests identified four distinct bioerosion incipient- traces: *Entobia*, *Caulostrepsis*, *Meandropolydora*, and *Oichnus*. The results show that the one active depositional site has a higher proportion of bioclasts with bioerosion but fewer shells with taphonomic damage compared to two Holocene sites. The higher fragmentation rates at Holocene sites are linked to longer exposure times of bioeroded shells before final burial. These differences suggest that shorter exposure times lead to lower fragmentation rates despite higher bioerosion levels. Mechanical tests confirmed that bioeroded shells are more fragile, breaking into angular fragments, thereby contributing significantly to shell damage. Thus, bioerosion coupled with moderate surface residence times, plays a crucial role in shell fragmentation, with hydrodynamic conditions being a secondary agent of shell damage in high-energy environments.

Keywords Taphonomy · Bioclastic accumulation · Holocene · Mollusca · Neontology · Fragmentation

Introduction

Bioclastic accumulations are formed by hard parts of biogenic origin, regardless of taxonomic composition, state of preservation, or degree of post-mortem modification (Kidwell et al. 1986). These accumulations can be composed of complete shells, fragments, or an admixture of both (e.g. Simões and Kowalewski 1998; Best and Kidwell 2000a, b; Fürsich and Pandey 2003; Schneider-Storz et al. 2008; Neves et al. 2012). The degree of fragmentation within an accumulation can be related to various factors, including physical and biological parameters. Physical factors include water energy and depth of the depositional environment (Speyer and Brett 1986; Kowalewski et al. 1994; Horodyski et al. 2019; Zuschin et al. 2003; Sedorko et al. 2018a, b), while biological parameters include the action of bioeroders on shells, which can dominate over physical parameters as taphonomic agents (Best and Kidwell 2000a; Richiano et al. 2017; Gordillo et al. 2018). In this context, bioerosion can serve as the main factor contributing to shell weakness,

✉ Daniel Sedorko
sedorko@mn.ufrj.br

1 Museu Nacional, Universidade Federal do Rio de Janeiro (UFRJ), Quinta da Boa Vista - São Cristóvão, Rio de Janeiro, RJ, Brazil

2 University of Tübingen, Department of Earth Sciences, Schnarrenbergstrasse 94-96, Tübingen 72076, Germany

3 Departamento de Geologia, Universidade Federal do Rio de Janeiro (UFRJ), Cidade Universitária, Rio de Janeiro, RJ, Brazil

4 Programa de Pós-Graduação em Ecologia e Recursos Naturais, Universidade Federal de São Carlos (UFSCar), São Carlos, SP, Brazil

5 Laboratório de Paleobiologia e Astrobiologia (LPA), Departamento de Biologia (DBio), Universidade Federal de São Carlos (UFSCar), CCHB, Sorocaba, SP 1112, Brazil

which in turn may increase the incidence of fragmentation within bioclastic accumulations affected by high rates of bioerosion (e.g., Oji et al. 2003; Zuschin et al. 2003).

Studying taphonomic processes in bioclastic accumulation has a wide range of implications, not only for recent sedimentary processes but also for the interpretation of fossil shell beds and coquinas, as well as for the fabric analysis of indurated carbonate rocks (e.g., Nebelsick et al. 2011; Rodrigues 2007; Silvestri et al. 2011). An example of the latter is the Cretaceous Morro do Chaves Formation in Brazil, where bioclastic accumulations have been studied within the auspices of hydrocarbon reservoir potentials, such as those present in the pre-salt coquinas of the Campos and Santos Basins (e.g., Thompson et al. 2015; Chinellato 2015; Sauer and Rodrigues 2016; Corbett et al. 2017).

Recent bioclastic accumulations are used here as a case study to analyze the extent to which taphonomic damage can be triggered by bioerosive processes. While bioerosion and hydrodynamic energy are primary factors contributing to shell weakening, other taphonomic processes can also play a significant role in the final degree of fragmentation within the resulting shell bed. Thus, this study aims to test the relationship between bioerosion frequency and fragmentation on shells, applied to the genetic analysis in recent bioclastic accumulations along the Rio de Janeiro coastline, southeastern Brazil.

Study area

The study area is situated between the cities of Cabo Frio and Armação dos Búzios, along the coast of the state of Rio de Janeiro, Brazil (Fig. 1A). The physical geography of this region is dominated by a series of coastal plains ("*restingas*") containing active fluvial settings, supplemented by lagoonal marches and low hills. To the north and west, the area is bordered by a gentle hilly region comprising Precambrian crystalline rocks.

Studies on relative sea level oscillations have identified former positions of coastlines referring to the last Holocene transgression in the coastline of southeastern Brazil. The transgression peak has occurred approximately between 5100 and 4590 cal yrs BP (Cunha et al. 2018; Castro et al. 2018). The paleo sea level is reported to be at least 3 m above of MSL, resulting in a large paleo-lagoon. Barrier-island and beach-ridge systems formed adjacent to the paleo-lagoon on the seaward margin. As the sea level regressed, the lagoonal environment was transformed into an area dominated by marshes (Castro et al. 2021). The occurrence of marine terraces composed of sand and gravel derived from the weathering of headlands is associated with this transformation (Castro et al. 2018).

Bioclastic accumulations are prevalent at various points along the coast, forming significant deposits of Holocene Age (between 5,000 and 7,000 yrs BP) (Martin et al. 1997; Bernardes et al. 2007). The bioclastic deposits in this region are linked to a rise in sea level and subsequent regression of the coastline around 4,900 B.P., resulting in isolated water bodies that became increasingly saline due to continuous and progressive evaporation (Castro et al. 2014). This led to extensive mollusk accumulations stranded along the coast. The focus of this study is on these mollusk accumulations found in the deposits of Marina de Búzios - MB (Ramalho marsh), Reserva Tauá - RT (Malhada marsh), and the mouth of the Una River (UNA) (Fig. 1B-E). Cunha et al. (2018) investigated the UNA site, collecting samples during the dry season, which lasts from May to August, while the here presented data were collected during the storm season, which lasts from September to March, with collection in December (INMET, 2024).

Porto-Barros et al. (2017) dated the base of the shell beds in MB deposit, as 6,290 BP, and RT deposit as 5,790 BP. The surface residence time for the UNA site is inferred to be relatively short, as the bioclastic material collected during the storm season likely reflects reworking and redeposition within a maximum of eight months, based on the seasonal duration of the rainy period (INMET, 2024). In contrast, the MB and RT sites exhibit shells within the same layer spanning age variations exceeding 100 years, suggesting significantly longer surface residence times (Porto-Barros et al., 2017; Cunha et al. 2018).

Methods

Three Holocene bioclastic deposits were selected from the Rio de Janeiro coastline of southeastern Brazil: (1) Marina de Búzios (MB), (2) Reserva Tauá (RT), and (3) Una River (UNA). The MB and RT deposits were formed in restricted lagoons with low hydrodynamic conditions during the Holocene, while UNA represents the mouth of an active river in an area characterized by high wave activity (Porto-Barros et al. 2017).

Sedimentological logs were conducted using the facies analytic method (Walker, 2006) and incorporating taphonomic features (Kidwell et al. 1986; Kidwell and Holland 1991). Approximately 4 dm^3 of samples were collected from each study area for laboratory analysis. Careful washing of the samples was undertaken to prevent additional abrasion and fragmentation of shells. Collection in the modern UNA deposit occurred during summer when storms are more frequent, depositing new shells in the bioclastic accumulation. A 2 mm sieve mesh was employed to remove siliciclastic material of sand size and smaller, leaving bioclastic material

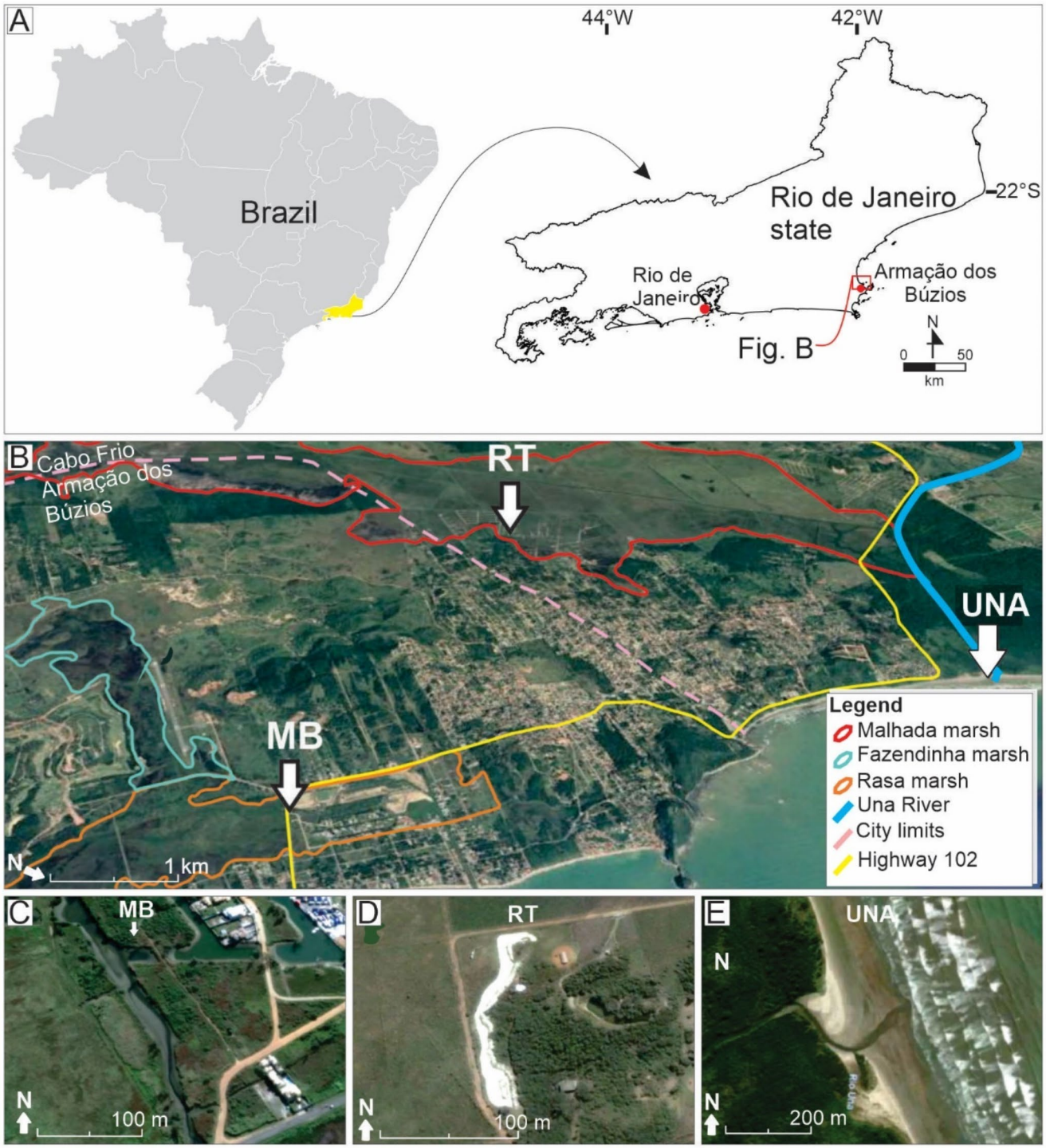

Fig. 1 Location map of studied areas. **A**. Location of Rio de Janeiro state in Brazil. **B**. Location of the studied localities MB = Marina de Búzios (22°45'29" S / 41°57'16" W), RT = Reserva Tauá (22°45'11" S / 41°59'52" W), and UNA = the mouth of the UNA River (22°42'51" S / 41°59'13" W). In yellow, the state of Rio de Janeiro within Brazil. Cabo Rio and Armação dos Búzios are municipalities. **C**-**E**. Close up of the three studied localities.
Modified from Google Earth

in the gravel sized faction. These samples were utilized for taphonomic and ichnotaxonomic analysis using microtomography and mechanical tests. Taphonomic features such as disarticulation, fragmentation, abrasion, dissolution, pigmentation loss, edge rounding, and bioerosion were analyzed (see Table 1). Bioerosion, disarticulation, and fragmentation were categorized as absent or present, while the rest were classified as absent, moderate, or intense (Table 1).

Table 1 Taphonomic signatures and their intensities as used for statistical analysis

Taphonomic signature	Observation	
Bioerosion	Absent	
	Present	
Abrasion	Absent	>90% of the abraded valve area
	Weak	90−50% of the abraded valve area
	Intense	<50% of the abraded valve area
Disarticulation	Absent	
	Present	
Dissolution	Absent	No dissolution
	Weak	<50% of the valve area with dissolution
	Intense	>50% of the valve area with dissolution
Fragmentation	Absent	>90% of the area preserved
	Present	90−0% of the area preserved
Pigmentation	Absent	>90% of the valve area
	Weak	90−50% of the valve area
	Intense	>50% of the valve area
Rounding	Absent	No rounding
	Weak	Edges few rounded
	Intense	All edges rounded

Macroscopic traces of bioerosion on shell surfaces (e.g., perforations, galleries, scrapes, and grooves) were identified based on the classification of Rios (1994) and the WoRMS Editorial Board (2016) online database. Ichnotaxonomic attributions were giveb even though the studied material from MB and RT deposits are subfossil (Holocene), and that the UNA deposit represents an active depositional setting. The traces are considered as "incipient" traces, following the general recommendation against naming modern traces (Bromley and Fürsich 1980). Ten valves were thin sectioned in order to record their shell microstructures, internal taphonomic features and incipient trace fossils. In order to analyze the three-dimensional configuration of the traces, X-ray microtomography was employed using a Skyscan Model 1173 High Energy micro-CT from the Nuclear Instrumentation Laboratory at the Alberto Luiz Coimbra Institute for Graduate Studies and Research in Engineering of the Federal University of Rio de Janeiro.

Mechanical tests were conducted in order to evaluate the effect of bioerosion on shell strength by measuring vertical deformations of valves over time resulting from specific loads. A direct shear test was performed using a press equipped with a densification cell (edometer) measuring 50 mm x 50 mm x 20 mm for sample placement. Each test utilized approximately 30 well-preserved valves larger than 1 cm of the predominant bivalve, *Anomalocardia brasiliana* Gmelin 1791. The material used consisted of valves of comparable size. All valves were placed into the cell in the same orientation with the concave side facing upward). Furthermore, all shells showed a minimal degree of physical alteration. The shells were conducted on two batches of two different groups: one showing no signs of bioerosion, the other showing evident signs of bioerosion by *Entobia*. Valves were cleaned to remove sediment from bioerosive traces if present. The compaction cell was sealed and subjected to pressure by applying normal tension using a rod.

Results were continuously recorded using the Pavitest Shearing 2.1.4.17 software. Loads were applied in four stages, each with progressively higher weights: 5 kg with a normal tension of 0.2 kg/cm², 10 kg with a normal tension of 0.4 kg/cm², 20 kg with a normal tension of 0.8 kg/cm², and 40 kg with a normal tension of 1.6 kg/cm². Each stage lasted a maximum of 15 min, concluding when deformation stabilized.

In order to evaluate the difference in compaction rates between bioeroded vs. non-bioeroded shells in the mechanical tests, we performed two regression models between time vs. cell height, representing the vertical deformation of the cell, divided by the two different groups (bioeroded vs. non-bioeroded). In addition, an Analysis of Covariance (ANCOVA) was employed to evaluate whether or not there is a significant difference between regression models. The Test of Equal or Given Proportions (Z-test for proportions) was used to analyze differences in fragmentation and bioerosion rates between sites. This test compares the proportions across the different groups using a chi-squared distribution in order to assess if observed and expected proportions significantly differ from each other.

All statistical tests and graphical representations were conducted using the R language (v4.4, R Core Team 2024) in the development environment RStudio (v2024.04.1, Posit Team 2024). The packages readxl (Wickham and Bryan 2023) was used for reading sheet files (.xlsx), dplyr (Wickham et al. 2023) for data manipulation, and ggplot2 (Wickham 2016) for the production of graphics. All original data and the R script are included in the Supplementary Information.

Results

Sedimentary and taphonomic analysis

Marina De búzios (MB)

The Marina de Búzios (MB) deposit covers an area of over 6,000 m² and boasts a thickness of approximately 1 m (Fig. 2A–B). Within this deposit, three distinct layers (MB1– MB3) were identified, with only MB1 containing

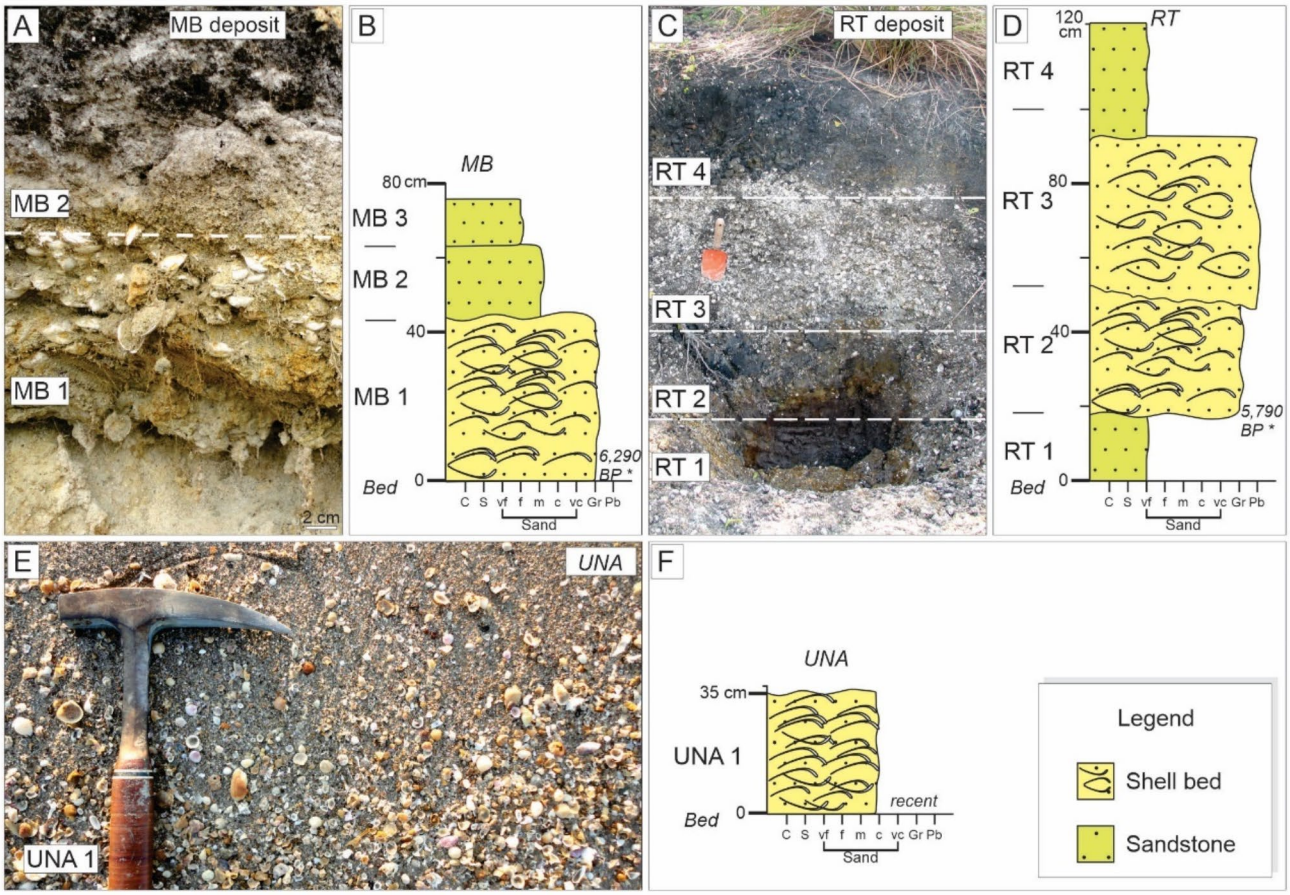

Fig. 2 Sedimentologic features of studied bioclastic. **A**-**B**. Bioclastic beds of the Marina de Búzios deposit (MB) and the sedimentological log (**B**). **C**-**D**. Bioclastic beds of the Reserva Tauá (RT) deposit and the sedimentological log (**D**). **E**-**F**. Shell deposit at the mouth of the Una River (**E**) and the sedimentological log (**F**). Dating based on Porto-Barros et al. (2017)

bioclasts. This layer spans 42 cm in thickness, with a shell proportion ranging between 30–40%.and is dominated by bivalves with a few interspersed gastropods. The bivalve shells predominantly lie parallel to subparallel in relation to the bedding plane, with occasional instances of imbricated orientation. Bivalves within this layer exhibit maximum lengths of 3.2 cm and heights of 4.7 cm. These shells are encased within a matrix of fine, well-sorted sand featuring subangular to subrounded clasts of quartz and biotite, The contact to the upper layer is slightly undulated and abrupt.

The Marina de Búzios (MB) deposit encompasses six bivalve species (Table 2), namely *Anomalocardia brasiliana*, Tellinidae indet., *Lucina pectinata*, *Ostrea* sp., *Trachyardium muricatum* Linnaeus 1758; and *Anadara ovalis* Bruguière 1789, along with three gastropod species: *Thais haemastoma* Linnaeus 1767, *Cerithium atratum* Bruguière 1792, and *Bulla striata* Bruguière 1792. Taphonomic analysis of the 296 bioclasts revealed bioerosion in 100 specimens (33.8%), primarily affecting *Ostrea* sp., *Cerithium atratum*, and *Anomalocardia brasiliana*, while also present in *Anadara ovalis*, Tellinidae indet., and *Lucina pectinata* (Fig. 3). These bioerosive traces are predominantly characterized by *Entobia* and *Caulostrepis*, but also include *Oichnus*. Regarding taphonomic attributes, 34.1% of the bioclasts exhibit abrasion, with the majority of bivalves being disarticulated (98.2%), 28.4% display signs of dissolution, 31.4% show fragmentation, 89.9% show changes in pigmentation, and 1.4% exhibit rounding (Fig. 4).

Reserva tauá (RT)

The Reserva Tauá deposit spans an area of over 8,000 m² with a thickness of approximately 1.5 m (Fig. 2C–D). Four layers were identified (RT1–RT4), two of which contain bioclasts (RT2 and RT3). Layer RT2 measures 30 cm in thickness, with a bioclast proportion ranging between 10 and 20%. The shells predominantly consist of bivalves exhibiting no preferential orientation. Occasional gastropods are also present. All bivalves are disarticulated, with maximum lengths of 2.4 cm and heights of 2 cm and are encased in a dark organic muddy matrix. The transition from Layer RT2 to RT3 is abrupt and slightly undulated. Layer RT3, on the

Table 2 Analysis of bioerosive macrostructures of bioclasts from all deposits

Deposit	"incipient"- ichnogenus	Taxon	Number of bioclasts
MB (N=116)	*Entobia*	*Ostrea* sp.	16
		C. atratum	36
		A. brasiliana	5
		L. pectinata	1
		Tellinidea indet.	1
	Oichnus	*A. brasiliana*	5
		Ostrea sp.	4
	Caulostrepsis	*Ostrea* sp.	35
		C. atratum	8
		A. brasiliana	4
		A. ovalis	1
RT (N=44)	*Oichnus*	*A. brasiliana*	3
	Entobia		20
	Caulostrepsis		21
		Tellinidea indet.	1
UNA (N=153)	*Entobia*	*C. subrostrata*	38
		N. bisulcata	18
		M. cleryana	14
		T. muricatum	11
		B. odites	6
		C. gigas	8
		A. chemnitzi	8
		M. patagonica	5
		O. equestris	3
		A. ovalis	7
		O. puelchana	3
		P. gibbosa	1
		T. mactroides	6
		T. haemastoma	2
		T. viridula	4
		C. macerophylla	1
		C. protea	1
		F. rosea	1
	Meandropolydora	*C. gigas*	1
		B. odites	1
		O. equestris	2
		M. patagonica	1
		P. gibbosa	1
		S. sanguinolenta	1
		S. proficua	1
	Oichnus	*M. cleryana*	1
		C. gigas	2
		O. equestris	3
		Mytilidae indet.	1
		C. rhizophorae	1

other hand, is 45 cm thick, with a shell proportion exceeding 70%. It is also predominantly composed of bivalves with occasional gastropods. Bioclasts can occur concordantly or inclined in relation to the bedding plane. Bivalves range from 0.4 to 3.5 cm in length and 0.3 to 2.9 cm in height.

The RT deposit primarily comprises bivalves, representing three distinct taxa: *Anomalocardia brasiliana*, Tellinidae indet., and *Lucina pectinata* Spengler 1798. Additionally, gastropods from the taxa *Bulla striata*, *Nassarius vibex* Say 1822; and *Neritina virginea* Linnaeus 1758 are also present. Of 150 bioclasts, 42 exhibit bioerosive macrostructures (29.4%). Among these, the majority were found on the bivalve *Anomalocardia brasiliana* with the presence of *Caulostrepsis* and *Entobia* (Fig. 3). Taphonomic analysis revealed that 26.6% of bioclasts display abrasion, 93.7% are disarticulated, 13.3% show signs of dissolution, 29.4% exhibit fragmentation, 70.6% display changes in pigmentation, with no bioclasts exhibiting rounding (Fig. 4).

UNA

The mouth of the river is situated at Rasa Beach, which extends for 8 km. For this study, an area of 10,000 m² was delineated. The deposit comprises a superficial bed, 35 cm thick, consisting of moderately sorted, fine- to coarse-grained sand with subrounded clasts of quartz, muscovite, and bioclasts (Fig. 2E-F), with a shell proportion ranging between 40 and 55%. This deposit exhibits a significantly greater taxonomic diversity compared to other studied localities (Table 2). In total, 27 bivalve species were identified, dominated by *Chione subrostrata* Lamarck 1818, *Mulinia cleryan*a d'Orbigny 1846, *Noetia bisulcata* Lamarck 1819, *Trachycardium muricatum*, and *Anadara chemnitzi* Philippi 1851, alongside four gastropod species: *Tegula viridula* Gmelin 1791, *Bostrycapulus odites* Collin 2005, *Thais haemastoma*, and *Fissurella rosea* Gmelin 1791. These specimens predominantly display a horizontal orientation, with few inclined individuals.

Out of the 206 analyzed bioclasts, macroscopic bioerosion was identified in 154 (74.7%), characterized as *Oichnus* and *Meandropolydora*, but predominantly dominated by *Entobia* (Fig. 3). Among the total, 1.9% of bioclasts exhibit abrasion, 98% of the bivalves are disarticulated, with the few articulated ones found in the "butterfly wing" position. Additionally, 6.3% show signs of dissolution, 15.9% display fragmentation, 51.7% exhibit a change in pigmentation, and 1.9% show rounding (Fig. 4).

A common pattern found in bioclasts from all localities, but especially in the UNA deposit, is the detachment of the shell layers. The bioclasts that exhibited this pattern do not show bioerosion macrostructures on the surface or in thin sections. Degradation of the internal microstructure causing this detachment can be discerned in thin sections (Fig. 5). In contrast to the shell layer detachment, the most recurrent macrobioerosion structure is *Entobia*, which degrades the material by crossing the microstructural layers of the shells.

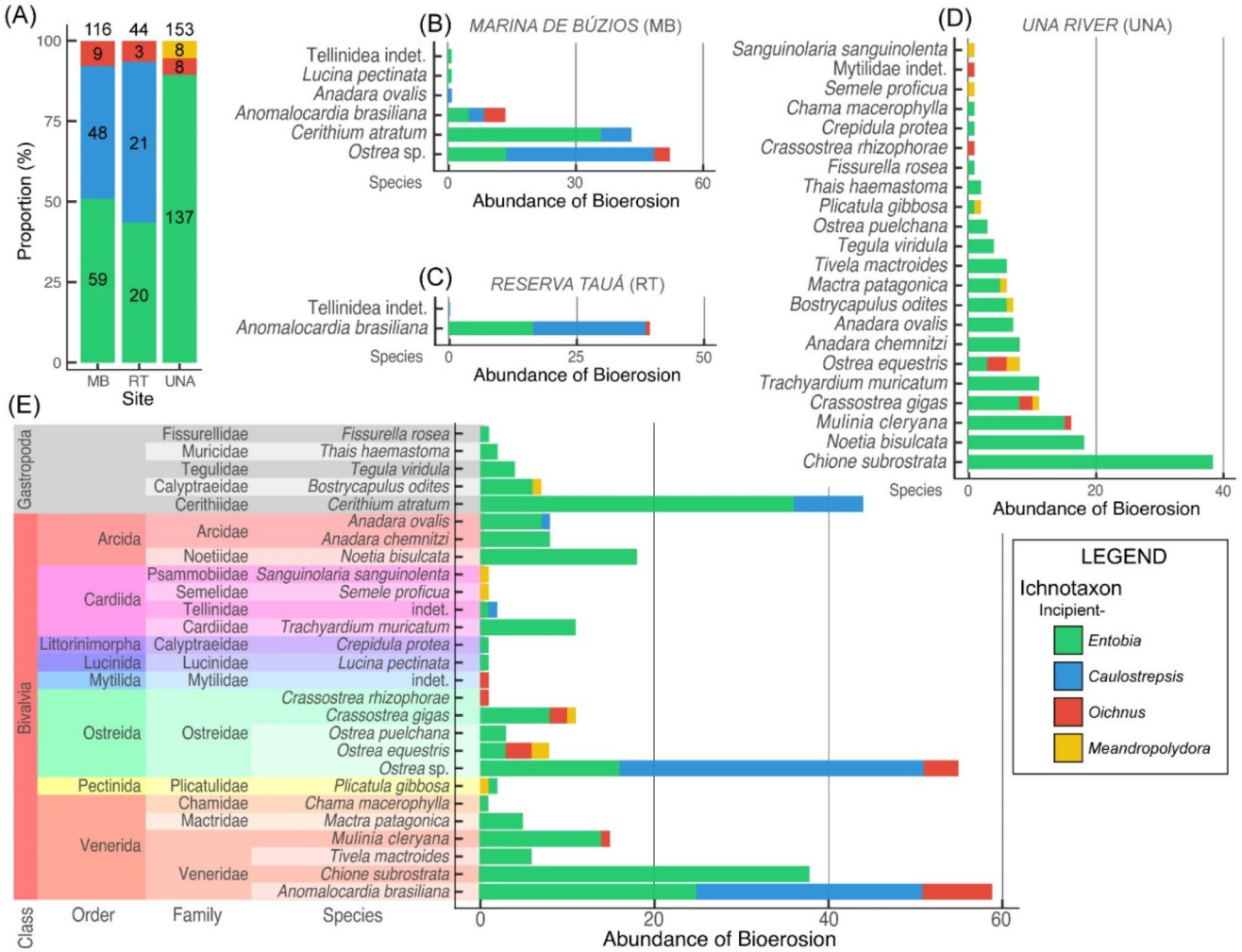

Fig. 3 Proportion of bioerosion present in the bioclasts of the studied deposits. **A**. Proportion of bioerosion among the studied area. **B**-**D**. Abundance of bioerosion on the molluscan taxa from each locality. **E**. Abundance of bioerosion on mollusks from all localities

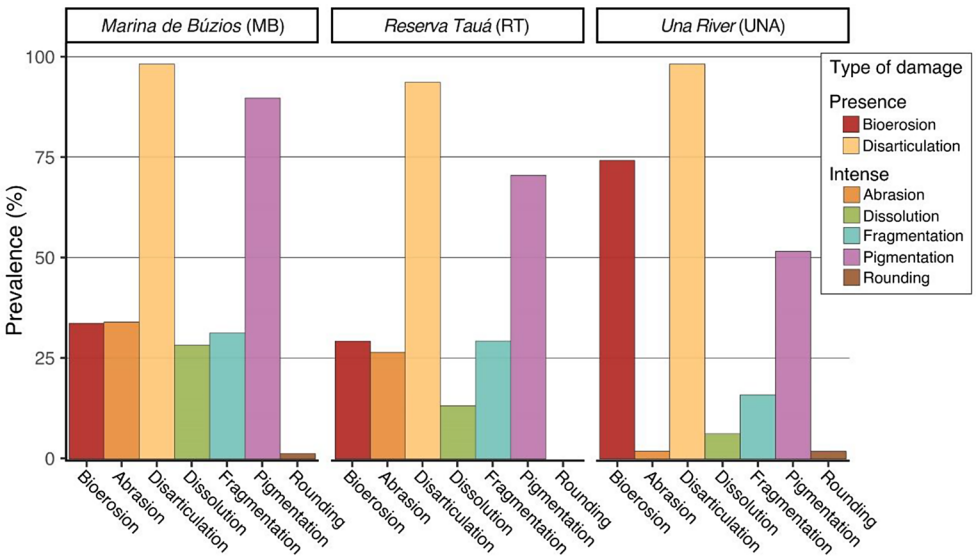

Fig. 4 Proportion of taphonomic damage in studied localities

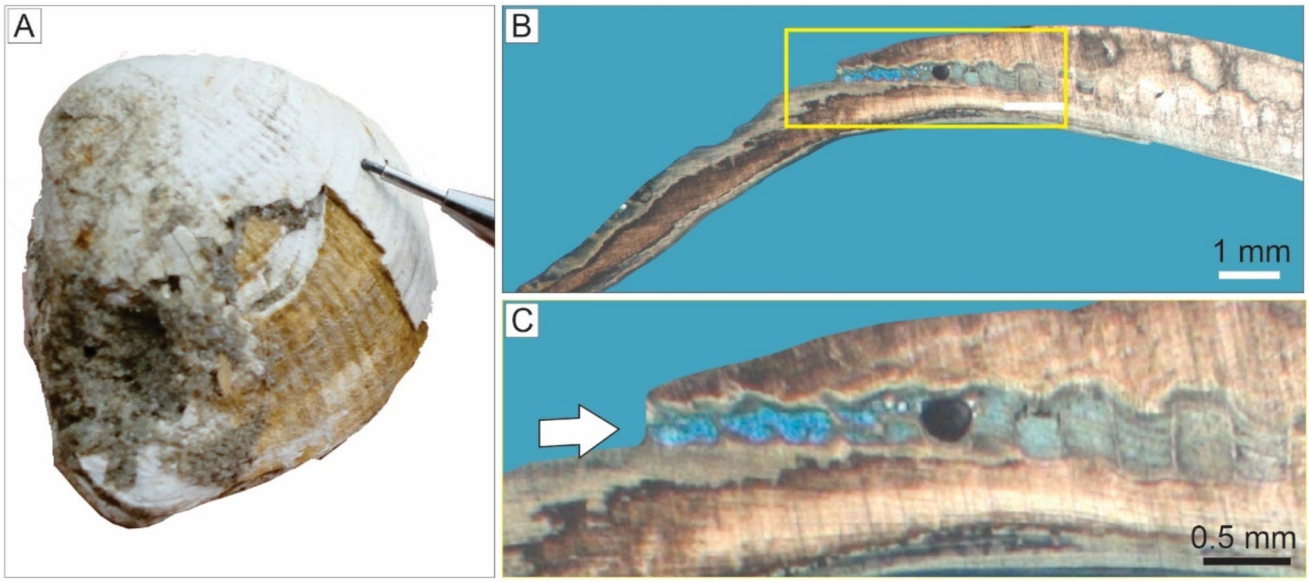

Fig. 5 Example of detachment of layers within bivalves. **A**. Articulated *Anomalocardia brasiliana* showing detachment of layers. **B**. Photomicrograph of *A. brasiliana* valve showing the microstructure of the shell and the location of detachment. **C**. Detail of the detachment structure, showing the rupture planes (arrow) continuous along growth lines

Bioerosion

Four trace morphologies were identified within shells from the studied deposits, in order of dominance: *Entobia* Bronn 1837, produced by boring sponges; *Oichnus* Bromley 1981; mainly produced as a predation scar by carnivorous gastropods boring through the valves, as well as *Caulostrepsis* Clarke 1908; and *Meandropolydora* Voigt 1965; both produced by polychaete worms in bivalves and gastropod shells.

Entobia appears on the surface of the valves as bored apertures (Fig. 6A-H). These apertures may be locally concentrated or widely distributed, both following straight paths, with aperture diameters ranging from 0.1 mm to 1 mm. Microtomographic images reveal the distribution of the connected galleries and also demonstrate that the channels connecting the galleries are less than 0.1 mm in diameter (Fig. 6D). *Oichnus* is manifested as circular penetrative borings through the valves. The holes are beveled, narrowing from the outside to the inside, with diameters ranging from 2 to 3 mm on the external surface and 1–2 mm on the internal surface (Fig. 6I–L). *Caulostrepsis* is present as "U"-shaped, cylindrical galleries typically on the surface of shells., with widths ranging from 1 to 2 mm and lengths ranging from 5 to 20 mm. These traces can also be embedment structures with a single entrance. The limbs of the U-shaped trace are separated by a fragile central wall, which, in some cases, is sinuous and may be enlarged, becoming somewhat distorted (Fig. 7A–C). *Meandropolydora* appears as cylindrical, sinuous, and continuous galleries, lacking branches, and measuring 4 mm long and 1 mm wide. Generally, the gallery is smooth, unbranched, devoid of sculpture and maintains its width along its length. This macrostructure frequently occurs at the border of the valves (Fig. 7D–E).

Comparing the percentage of bioerosion structures in each deposit (with a total of 296 bioclasts) reveals that the MB deposit shows 50.9% *Entobia*, 41.4% *Caulostrepis*, and 7.8% *Oichnus* (Fig. 3A). Conversely, the RT deposit exhibits a 50% incidence of *Caulostrepis*, 43.5% of *Entobia* (Fig. 3A), and 6.5% of *Oichnus*. In contrast, the UNA deposit differs significantly from the previous two, being highly dominated by *Entobia* at 89.5%, followed by *Meandropolydora* at 5.2%, and 5.2% of *Oichnus* (Fig. 3A).

The majority of the bioerosion features are present in three bivalve genera and one gastropod genus with: bivalves of the genus *Anomalocardia* with 59 occurrences of bioerosion traces (in MB and RT deposits), *Chione* with 38 bioerosion traces (in the RU deposit), and the *Ostrea* (including *O. puelchana*, *O. equestris* and *Ostrea* indet.) with 66 bioerosion traces (in the MB and RU deposits), and the gastropd *Cerithium* with 44 bioerosion traces (in the MB deposit). *Ostrea*, *Anomalocardia*, and *Crassotrea* (*C. gigas* and *C. rhizophorae*) are the genera with the presence of more than one ichnospecies: *Crassotrea* with *Oichnus*, *Meandropolydora* and *Entobia*; *Anomalocardia* with *Oichnus*, *Entobia*, and *Caulostrepis*; and *Ostrea* is the only genus with the presence of all ichnotaxa (Fig. 4B–C). Numerous bioerosion traces are found in *Anomalocardia* (20.5% of 258 valves) valves– but *Cerithium* and *Ostrea* present high presence of bioerosions in their shells– *Cerithium* with 44 valves and

84% of bioerosion presence, and *Ostrea* with 68 samples and 76% bearing bioerosion.

Mechanical tests

The four mechanical experiments were conducted on two batches of shells with bioeroded valves and two batches lacking bioerosion. The results, plotted on graphs (Fig. 8), demonstrate a rapid increase in shell density caused by the initial compaction and subsequent breakage. Following this initial phase, there was a very low rate of accommodation until the next stage of compaction occurred. The first stages (ST1) in all compaction tests (bioeroded or non-bioeroded) are characterized by initial compaction of the shells inside the consolidation cell. In the tests with bioeroded shells, this first stage is marked by a higher compaction of shells. During the third stage of the second test (shells lacking bioerosion), the deformation was less than 1 mm.

Deformation rates vary between bioeroded and non-bioeroded shells, as indicated by regression analysis (Fig. 8). Even with a faster compaction rate presented with the non-bioeroded shells, the bioeroeded shells show a higher final compaction (Fig. 8). This difference in compaction rate is attested by the ANCOVA test, confirming a significant difference between the slopes of the linear models ($F=34.17$, $p=3.47e-08$). Bioeroded shells exhibit less intense, but more prolonged vertical displacement, lasting over 60 min compared to ~43 min for non-bioeroded shells (Fig. 8). Bioeroded bioclasts show up to three times higher deformation rates than non-bioeroded ones, particularly evident in the first (ST1) deformation. Although the slope value is higher for non-bioeroded tests (slope = -0.30, $R^2 = 0.90$, $p<2.2e-16$), this can be explained by the shorter duration of the experiment with the regression line indicating continuous and prolonged deformation in the bioeroded tests (slope = -0.21, $R^2 = 0.85$, $p<2.2e-16$). Fragmentation patterns differ significantly between compacted bioeroded and non-bioeroded shells, as showed in Fig. 8 and in the ANCOVA test. Bioeroded shell fragments exhibit angular outlines, and their size distribution is more uniform compared to that of non-bioeroded shells.

Discussion

Taphonomic controls

The influence of bioerosion on shell stability was tested across different depositional environments along the coast of Rio de Janeiro, Brazil. The examined localities, Marina de Búzios (MB), Reserva Tauá (RT), and Una River (UNA), represent distinct settings characterized by varying hydrodynamic conditions and sedimentary regimes. MB and RT deposits were formed in restricted lagoonal environments with low hydrodynamic conditions, exhibiting differing degrees of shell alteration, fragmentation, and bioerosion compared to the UNA deposit, which represents the actual mouth of a river with high wave activity (Martin et al. 1997; Castro et al. 2014; Fig. 9).

The sedimentological and taphonomic analyses reveal notable differences in shell preservation and bioerosion patterns among these localities. The MB deposit presents the highest proportion of fragmentation (31.4% of bioclasts), followed by the RT deposit (29.4% of fragmented bioclasts), and UNA (15.9%). The Z-test showed significant difference between UNA vs. MB ($\chi^2=14.73$, $p=1.24e-4$), and UNA vs. RT ($\chi^2=8.28$, $p=0.004$), but no significant difference between MB vs. RT ($\chi^2=0.10$, $p=0.74$).

Regarding bioerosion, an inverse relation is evident: UNA presents the highest proportion of bioeroded bioclasts (74.7%), followed by the MB deposit (33.8%), and the RT deposit (29.4%) (Fig. 4). The Z-test showed significant difference between UNA vs. MB ($\chi^2=76.87$, $p<2.2e-16$), and UNA vs. RT ($\chi^2=66.21$, $p=4.04e-16$), but no significant difference between MB vs. RT ($\chi^2=0.67$, $p=0.41$).

Bioerosion is a significant taphonomic signature in mollusks, considering that fragmentation can be facilitated by bioerosive structures (Oji et al. 2003). Thus, the longer a bioeroded shell remains available in the taphonomic active zone (TAZ sensu Davies et al. 1989), the more fragmented these shells will be. The observed relationship of more bioerosion and less fragmentation in the UNA death assemblage seems to be related to a shorter exposure time (considering that the deposit is active and damage is still occurring in TAZ).

This relationship between bioerosion and fragmentation incidence aligns with the interpreted depositional settings, suggesting that the MB deposit represents a lagoon, with shell bed deposition in the transgressive phase. MB deposit is slightly older than RT and shows a higher diversity of mollusks (Fig. 9). This diversity is linked to the phase when the lagoon was connected with the sea. The occasional presence of imbricated orientation of some shells indicates the action of tractional flows, likely in more proximal settings in the ancient lagoon (Kidwell et al. 1986; Kidwell and Holland 1991). Additionally, the similar rates of bioerosion (33.8%) and fragmentation (31.4%) suggest a moderate surface residence that allowed fragmentation facilitated by bioerosion structures, and moderate energetic flows for MB deposit.

The RT deposit indicates a protected lagoonal environment with a similar surface residence time that MB deposit but with lower energy tractive flows in the central part of an ancient lagoon. The overall low taxonomical diversity is linked to the development of this lagoon, which gradually

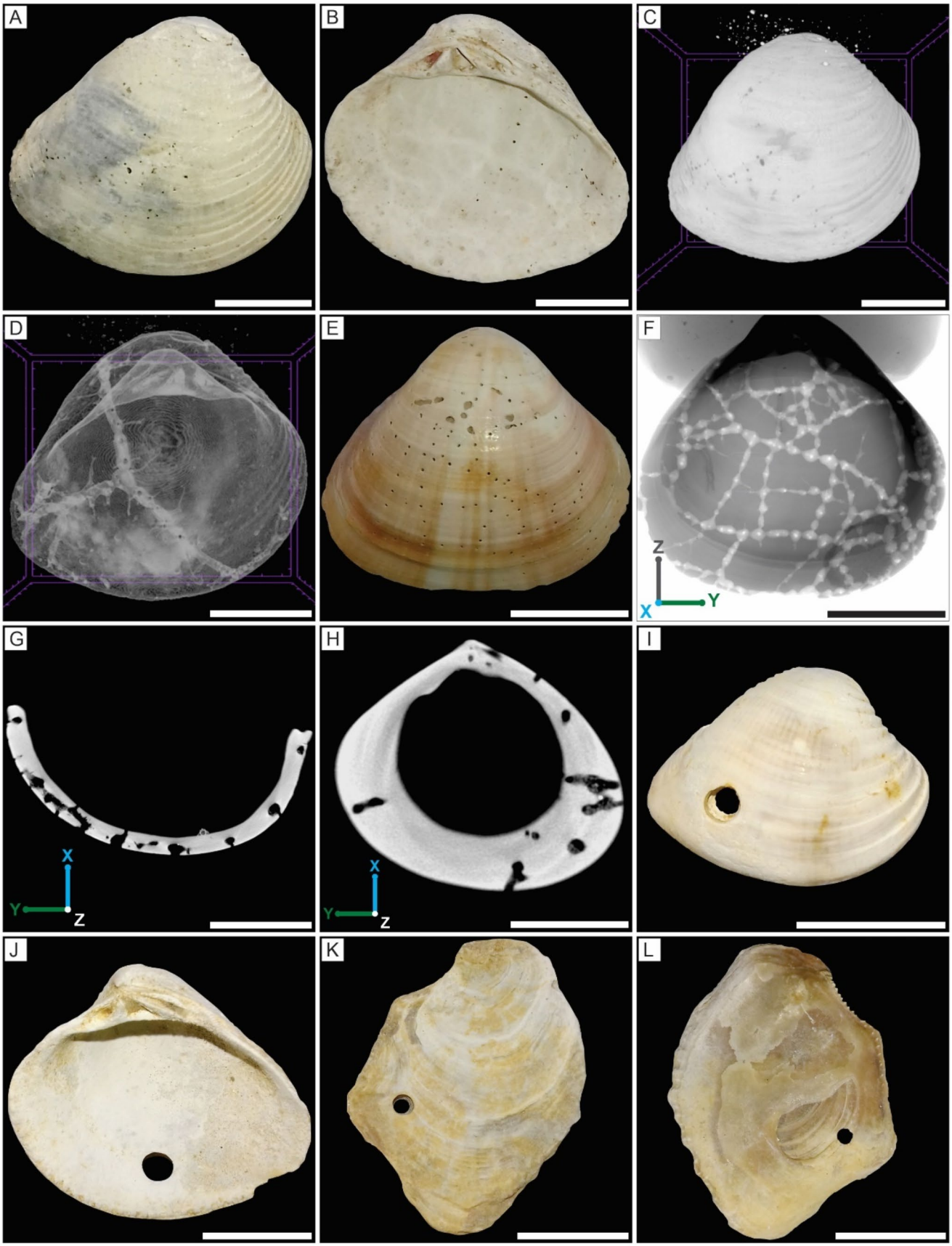
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Fig. 6 Macrobioerosion on studied shells. **A**. Openings of the complex internal net of *Entobia* on external side of a right valve of *Anomalocardia brasiliana*. **B**. Aligned openings on the internal side of *A. brasiliana* (A). **C**-**D**. A 3-D reconstruction of *A. brasiliana* produced by micro-CT scan with surface rendering (**C**) and an interior view of the valve (**D**) showing distribution of galleries, canals and exploratory threads produced by Clionidae sponges. **E**. A valve of *Tivela mactroides* with *Entobia* on the surface. **F**. Galleries and branching of *Entobia* on *T. mactroides* as revealed by micro-Ct analysis. **G**. Cross-sections of *T. mactroides* valve showing the orientation of chambers and connecting passages. **H**. Plan view of *T. mactroides* valve showing the connections of the galleries of *Entobia*. **I**-**J**. *Oichnus* on a *A. brasiliana* valve with external (**I**) and internal (**J**) view. **K**-**L**. *Oichnus* on *Ostrea* sp. valve with external (**K**) and internal (**L**) view. Scale bars = 1 cm

became hypersaline, favoring the dominance of *A. brasiliana* as a result of ongoing regression and consequent isolation from the sea (Fig. 9). The low taxonomic diversity and predominance of *A. brasiliana* (> 80% of individuals) support an inference of high salinity levels in these Holocene lagoons, considering that *A. brasiliana* can survive in the salinity range of 15 to 45 mg L^{-1} (Maia et al. 2017).

Finally, the UNA deposit presents the most bioeroded shells (74.7%) and the most diverse death assemblage compared to the other Holocene localities, reflecting a diverse actual marine community influenced by riverine input and dynamic coastal processes (Castro et al. 2014). Notably, the fragmentation proportion is the lowermost among the three localities (15.9%), which is related to an inferred short exposure time. Collection in this locality occurred during summer, when storms are more frequent and new material was being deposited in the bioclastic accumulation. Thus, although with higher energetic regime, this deposit probably shows less taphonomic damage due to a very short exposure time. A previous analysis in the same locality presented a high degree of fragmented shells, with 78.3% of fragmented bioclasts (Cunha et al. 2018). Bioerosion was very rare and 51% of the bioclastic fragments presented rounded edges in the death assemblage reported by Cunha et al. (2018). The main difference between our results and those from Cunha et al. (2018) is the season of collection, made during the dry season by these authors. It is interesting to observe that the amount of bioerosion during the storm season (74.7%) is very similar to the proportion of fragments observed by Cunha et al. (2018) during the dry season (78.3%). In this sense, in few months, the death assemblage tends to be completely fragmented because the death assemblage is highly bioeroded.

The presence of shells exhibiting detachment of shell layers and degradation of internal microstructure indicates unique taphonomic processes operating within the UNA deposit. Given the depositional setting, the UNA deposit is likely subjected to significant biological activity and abrasion from water movement. Boring organisms, mainly sponges, colonized the shells, weakened their structure, and acting as triggering factor for the detachment of shell layers, without fragmenting them. The detachment of shell layers was facilitated by the dynamic nature of the coastal environment, mainly by physical abrasion from wave action and sediment movement, but bioerosion played a primary role in generating weakness in the shell, as evidenced by the prevalence of macroscopic bioerosion features.

Mechanical tests corroborate the impact of bioerosion on shell strength, revealing differential rates of deformation and fragmentation between bioeroded and non-bioeroded shells from the UNA deposit. Bioeroded shells exhibit higher rates of deformation and more uniform fragmentation, indicative of weakened structural integrity resulting from bioerosion processes. The distinct fragmentation patterns observed in bioeroded material underscore the significance of bioerosion as a key factor influencing shell stability and subsequent preservation (Oji et al. 2003). These findings emphasize the importance of considering bioerosion dynamics in paleoenvironmental reconstructions and taphonomic interpretations, particularly in diverse coastal settings characterized by varying degrees of hydrodynamic energy and sedimentation rates (Wisshak et al. 2015). During the initial phase of each compaction stage, there is a noticeable compaction of the shells within the cell, especially in the bioeroded experiments (Taylor and Layman 1972). Mollusk shells, in general, can be highly resistant to fragmentation, depending on their microstructure (Best and Kidwell 2000a, b). The resistance of transported shells to fragmentation depends on numerous factors, including the structural integrity and microstructure of the shell, the intensity and mode of specific transport mechanisms, as well as the presence of taphonomic features such as bioerosion and encrustation (Fürsich and Pandey 2003; Lazo 2004; Schneider-Storz et al. 2008).

Bioerosion diversity

In the studied deposits, *Entobia* predominates, occurring in high proportion in all three localities but dominating the UNA deposit. *Caulostrepsis* is restricted to RT and MB deposits, while *Meandropolydora* is limited to the UNA deposit. *Oichnus* is present in all three deposits. The UNA deposit, characterized by greater taxonomic diversity, presents a unique pattern of shell detachment attributed to internal microstructural degradation mainly triggered by *Entobia*.

The *Entobia* ichnogenus is a dwelling trace (Wisshak et al. 2019). The borings are produced by sponges from the family Clionidae (Bromley and D'Alessandro 1984). These sponges dwell in carbonate substrates by boring the substrate surface in a complex web of chambers and canals (Bromley and D'Alessandro 1984). The ichnogenus *Oichnus* can be

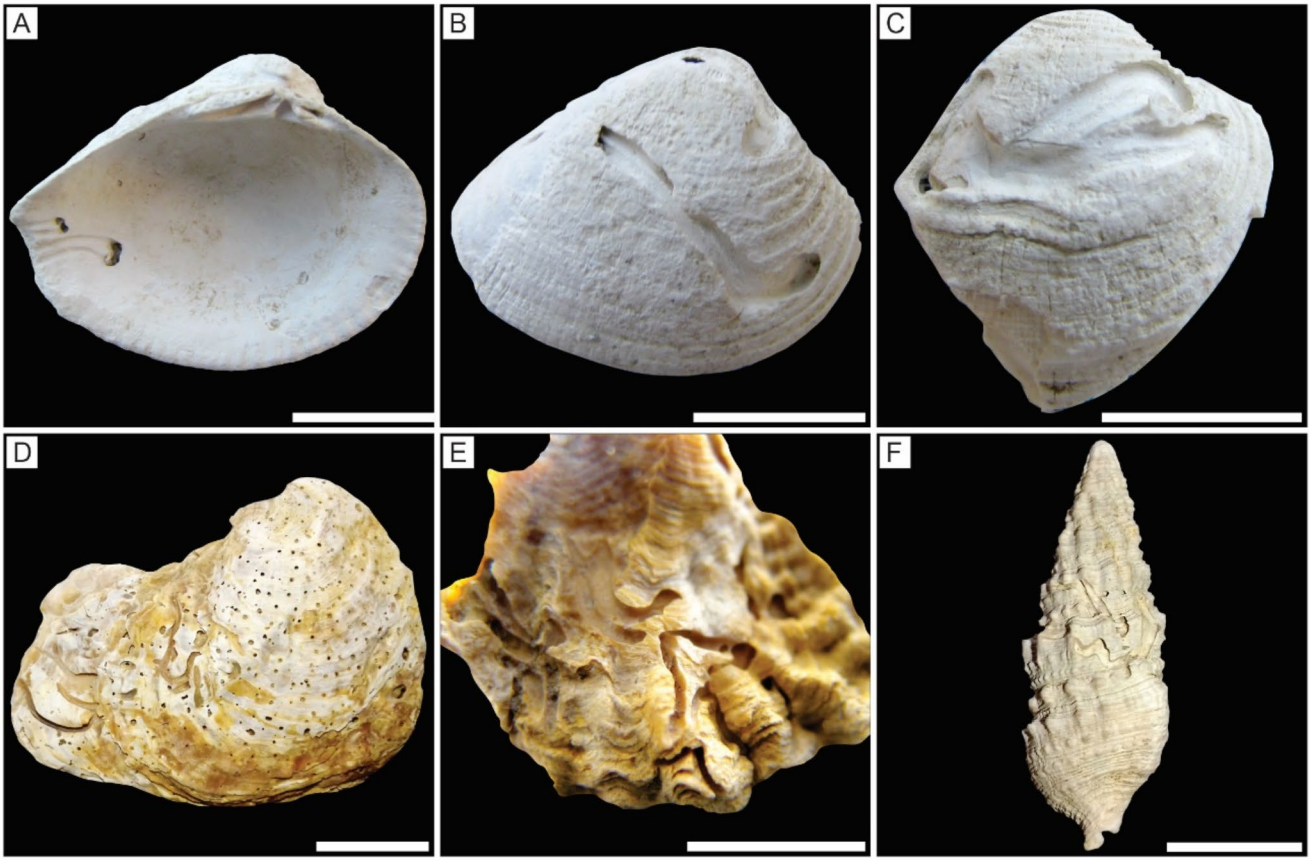

Fig. 7 Macrobioerosion of *Caulostrepsis* and *Meandropolydora*. **A-C**. *Caulostrspsis* on v of the bivalve *Anomalocardia brasiliana*. *Meandropolydora* on the bivalve *Ostrea* sp. F. *Meandropolydora* on the gastropod *Cerithium atratum*. Scale bar = 1 cm

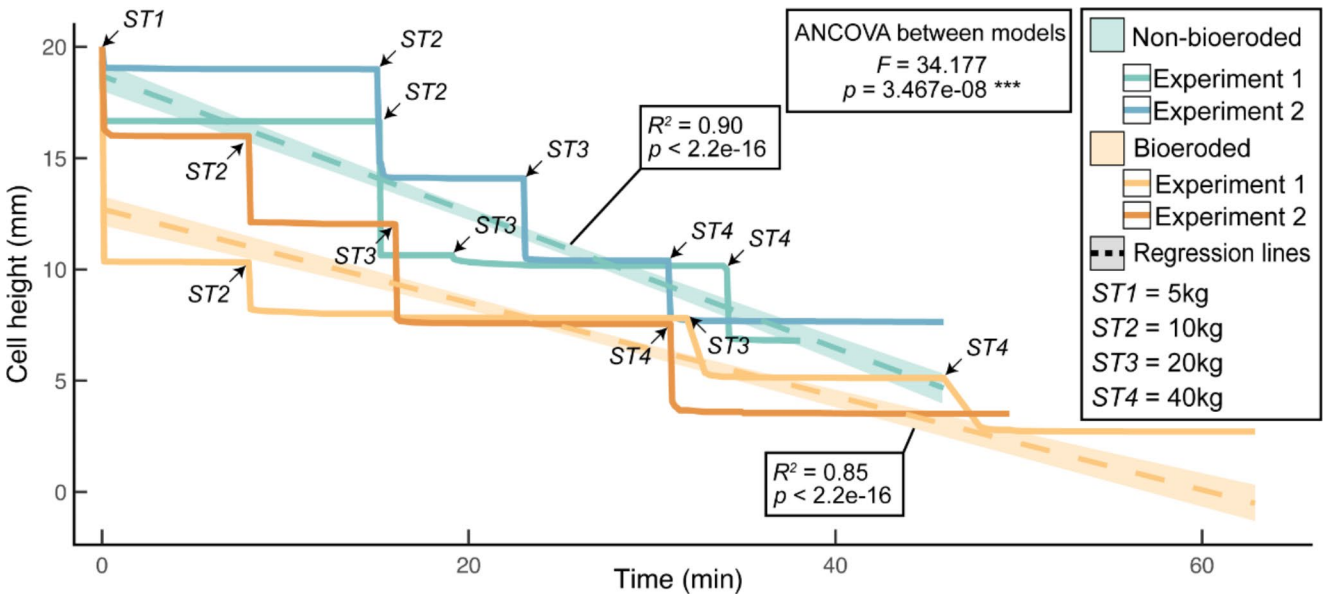

Fig. 8 Results of the mechanical test on non-bioeroded and bioeroded shells. Both tests presenting regression models and also the ANCOVA result between the two linear models. The ANCOVA test show significant difference between regression models. The vertical axis represents the height of the consolidation cell through the different stages (ST-1 to ST-4)

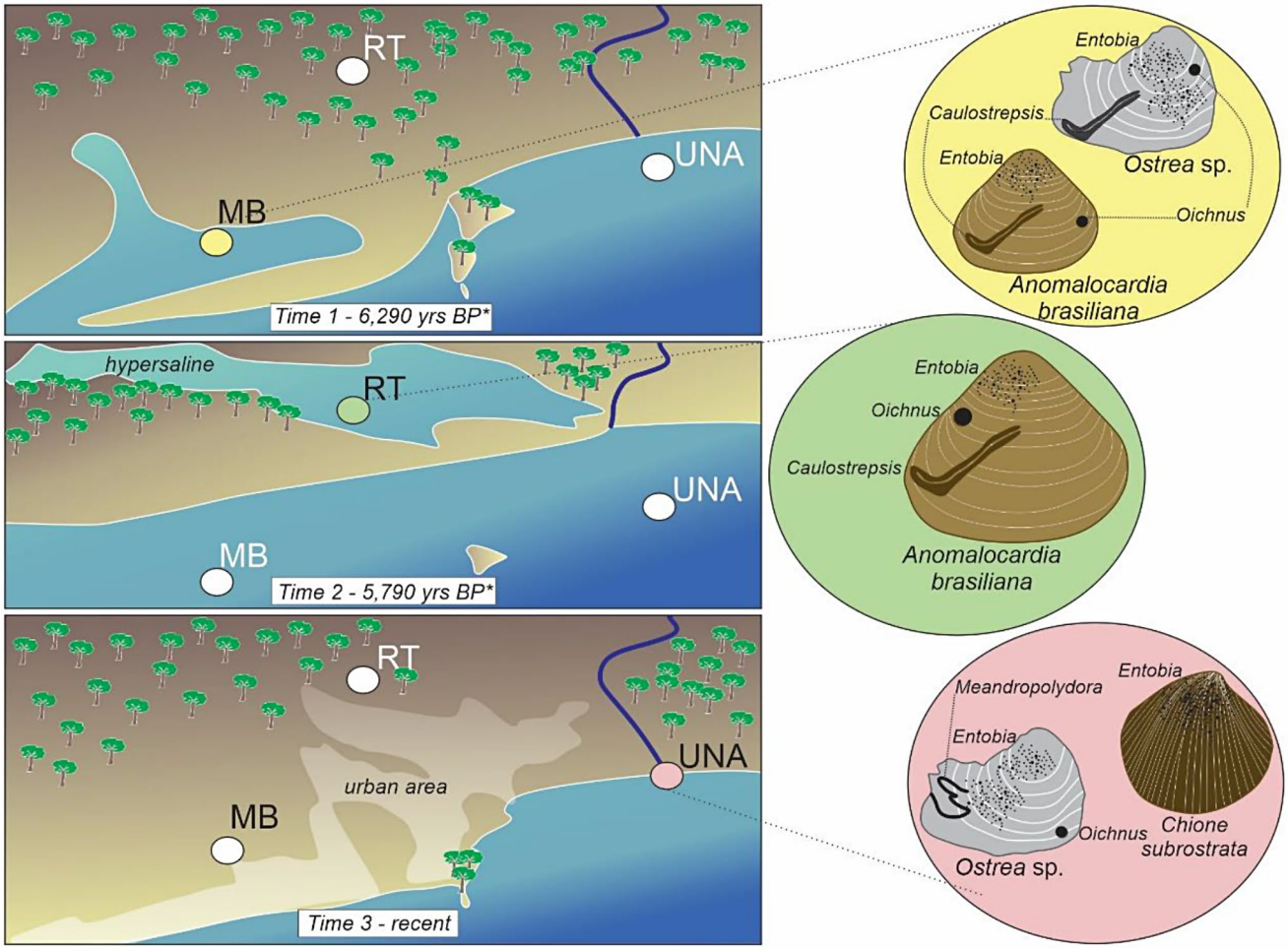

Fig. 9 Inferred depositional setting for the studied localities. Time 1: Deposition of the shell beds from the MB deposits, in a lagoon connected with the sea, common mollusks are bioeroded *Anomalocardia brasiliana* and *Ostrea* sp.; Time 2: Deposition RT deposits in an isolated lagoon, dominated by bioeroded *Anomalocardia brasiliana*; Time 3 (recent– during storm season): Deposition of UNA deposit, a shell bed in a beach influenced by a riverine input (Una River) dominated by a high diverse mollusk fauna, represented by bioeroded *Chione subrostrata* and *Ostrea* sp. Dating based on Porto-Barros et al. (2017)

representing predation or parasitic interactions (Wisshak et al. 2019). Gastropods are most common producers (Klompmaker et al. 2019; Kelley et al. 2003), and the morphology of the trace can indicate the taxonomic group that produced certain drill-holes, such as smooth interiors or beveled edges. The presence of some traces derived from predation interactions can be interpreted as an indicator of an ecologically healthy environment (Wisshak et al. 2015; Kelley et al. 2003; Carriker and Yoshelson 1968).

Both *Caulostrepsis* and *Maeandropolydora* ichnogenera are produced by polychaetes (Bromley and D'Alessandro 1983). These borings are classified as Dominichia traces (Wisshak et al. 2019). Although similar, *Maeandropolydora* has winding borings and *Caulostrepsis* is a U-shaped boring (Buatois et al. 2017). A study by Gravina et al. (2019), in the Underwater Archaeological Park of Baiae (Naples, Italy), found that after one year of exposure, their marble samples presented only *Maeandropolydora* and that *Caulostrepsis* occurred after the second year. The absence of *Caulostrepsis* in UNA deposits corroborates the interpretation of short exposure time for the shell bed, while in the lagoon deposits (RT and MB deposits) only *Caulostrepsis* occurs, suggesting longer surface residence time.

Conclusion

The study encompassed three distinct deposits, each representing varying hydrodynamic conditions: Marina de Búzios (MB) and Reserva Tauá (RT) in lagoonal ancient environments, and Una River (UNA) at the active mouth of a river in the sea. The MB deposit, older than RT, was deposited in the transgressive phase and connected with the sea, while the RT deposit was generated in a protected

lagoonal environment, potentially hypersaline as indicated by dominance of *A. brasiliana*, and deposited in the regressive phase.

The active depositional site (UNA) showed the most bioeroded shells and the lowermost fragmentation proportion, which is related to a short exposure time. Collection in this locality occurred during summer, when storms are more frequent and new material was being deposited in the bioclastic accumulation. When collection was made in dry season, allowing more exposure time, it occurs a high degree of fragmented shells and bioerosion was rare. Thus, in few months, the death assemblage was completely fragmented due to high frequency of bioeroded bioclasts. It was evident that the longer a bioeroded shell remains available in the taphonomic active zone, the more fragmented these shells will be. These findings underscore the role of bioerosion as a significant factor influencing shell stability and subsequent preservation, particularly in dynamic coastal environments.

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