Coral reef growth pattern in eastern Brazil has not changed since the Holocene

O padrão de crescimento dos recifes de coral no Brasil oriental não foi alterado desde o Holoceno

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Abstract

Lithocronological study of Holocene inshore reef sequences from eastern Brazil, recovered from drill holes and associated with surveys of modern reefs, allows the reconstruction of the growth pattern of reefs since their beginning in the Holocene and its comparison with present-day reefs. The interpretation of the growth pattern of the studied reefs reveals their evolution from a lithofacies of coral-algal bindstone/framestone that was deposited in a low-wave-energy environment to a lithofacies composed of coral rudstone up to a high-energy environment with accumulation of a coral framestone lithofacies. This pattern was mostly influenced by the wave energy regime, regional sea-level history and shallow antecedent reef substrate. Despite the stages of reef evolution not occurring synchronously over time, they did not exhibit any regional variation during their development. The coral fauna that built the reefs did not change much since the beginning of reef growth (approximately 7,000 yr BP), suggesting that the environmental conditions in this region have most likely remained favorable for the development of coral reefs. The coral fauna that built the Brazilian reefs is mostly composed of resistant and well-adapted endemic coral species, which biodiversity has remained constant throughout the development of the reefs.

Key words: Coral lithofacies; Coral biodiversity; Holocene; Abrolhos.

Abstrato

O estudo litocronológico das seqüências dos recifes costeiros do Holoceno do leste do Brasil, recuperado de perfurações e associado a levantamentos de recifes modernos, permitiu a reconstrução do padrão de crescimento dos recifes desde o seu início no Holoceno e sua comparação com os recifes atuais. A interpretação do padrão de crescimento dos recifes estudados revela sua evolução a partir de litofácies coral-algais depositadas em um ambiente de baixa energia de onda a litofácies compostas de rudstone de corais até um ambiente de alta energia com acumulação. de litofácies de framestone de coral. Este padrão foi influenciado principalmente pelo regime de energia das ondas, pela história regional do nível do mar e pelo substrato raso do recife. Apesar dos estágios de evolução dos recifes não ocorrerem de modo sincronico ao longo do tempo, eles não exibiram variação regional durante o seu desenvolvimento. A fauna de corais que construiu os recifes não mudou muito desde o início do crescimento dos recifes (aproximadamente 7.000 anos AP), sugerindo que as condições ambientais nesta região provavelmente permaneceram favoráveis para o desenvolvimento de recifes de coral. A fauna de corais que construiu os recifes brasileiros é composta principalmente por espécies de corais endêmicos resistentes e bem adaptados, cuja biodiversidade permaneceu constante durante o desenvolvimento dos recifes.

Palavras-chave: Litofácies de coral; Biodiversidade de corais; Holoceno; Abrolhos.

1. Introduction

Studies of Holocene inshore reefs along the eastern coast of Brazil (Kikuchi & Leão 1998, Leão & Kikuchi 1999, Leão *et al.* 2003) have revealed reef sequences growing on diverse kinds of substrates of a diverse nature, which are coincident with studies of several Holocene reefs that have been conducted elsewhere in the world (e.g., Shinn *et al.* 1977, Davies & Marshall 1979, Precht 1993, Montaggione & Faure 1997, Camoin *et al.* 1997, Grossman & Fletcher 2004, Engels *et al.* 2004, 2008, Smithers *et al.* 2006, Dechnik *et al.* 2016). Studies of the Brazilian reefs clarified two problems: i) the type of the reef substrate on which the Holocene reef sequences have grown and ii) the rates at which the reefs accumulate calcium carbonate.

The reef growth curves of the studied Holocene reefs from Brazil (Leão *et al.* 2003) defined three distinct periods of reef development: 1. an early period of slow growth, 2. a period of accelerate growth when the reefs established themselves, and 3. a period of decreasing growth after the reefs reached the sea level of that time.

Considering that reef development is, to some extent, an expression of the sampled material, which refers to the coral fauna that built the reefs, in this study, we decided to re-analyze, in detail, lithostratigraphical data from Holocene core sequences and the coral fauna that built old and present-day inshore reefs of the coast of the state of Bahia, based on the hypothesis that changes may have occurred in the last 7,000 years. We worked with two specific objectives: a) to undertake a lithofacies analysis of three core sequences for identifying regional or temporal patterns in reef development through the Holocene and b) to analyze the building coral fauna of Holocene and living reefs to determine whether any change in the composition of their biodiversity occurred.

It is known in the literature that the analysis of composition of the reef structure and its lithochronology will provide information for a better understanding of variabilities in reef development; according to Macintyre *et al.* (1992), these variabilities are most related to the sea-level history, hydrological regime and climate. That this information about paleoenvironmental changes during reef development, as recognized by Pandolfi & Kiersling (2014), will allow us to better identify when changes in the reef building coral fauna are in response to natural or to anthropogenic factors.

2. Material and Methods

The data used in this study were obtained from three reef areas along the coast of the state of Bahia: the Coroa Vermelha reef in the Abrolhos coastal arc, referred to here as the Abrolhos reef, in South Bahia (17°35'S – 18°00'S / 39°00'W – 39°13'W); the Itaparica fringing reef at the entrance of Todos os Santos Bay (12°55'S – 13°10'S – 38°35'W – 38°45'W); and the inshore shallow bank reef from the north coast of the state, the Guarajuba reef (12°38'S – 12°39'S / 38°03'W – 38°10'W) (figure 1). They are distant approximately 600 km from the northmost Guarajuba reef to the Abrolhos reef in the state south coast.

We used subsurface cores and modern coral community surveys. The information from the core sequences was obtained through drill holes previously performed in the studied reef sites using a Winkie Rotary Drill (J.K. Smith and Sons), which recovered 4.5 cm wide cores with sections composed of massive corals and sections that contain coral fragments, and they were all recorded and photographed (Araujo *et al.* 1984, Nolasco & Leão 1986, Leão & Kikuchi 1999). As it is shown in figure 2 the three core sequences have different lengths, being the Abrolhos core the longest one. For the present study, we determined the relative abundance of each recovered coral species using the Abrolhos reef core, where 86 fragments of coral and hydrocoral were identified to the level of species, when possible, and measured through the program Coral Point Count with Excel Extension 3.4 (CPCe 3.4, Kohler & Grill 2006). The relative abundance of the identified coral species was calculated based on their density along the core sequence, and it was considered as representative of the Holocene coral biodiversity.

For determining the relative abundance of the coral fauna from the present-day reefs of Abrolhos reef, we used data obtained during a survey conducted in March 2012, which covered five reefs of the coastal arc of Abrolhos: Pedra Grande (17°45'S / 38°58'W), Ponta Leste (17°44'S / 39°00'W, Ponta Sul (17°46'S / 38°59'W), Pedra Lixa (17°40'S / 39°00'W) and Pedra de Leste(17°46'S / 39°02'W). This survey was performed by applying the methodology proposed in the AGRRA Protocol (Atlantic and Gulf Rapid Reef Assessment, Lang *et al.* 2010), which is based on a visual census. For this study, we calculated the relative abundance of the coral species considering their occurrence within band transects (6 transects – 10 m long x 1 m wide) randomly located at the reefs surface (at depths between 3 m and 8 m). A total of 2,658 coral colonies were measured, and the average density of each species was considered as representative of the coral biodiversity of the living reefs from the coastal arc of Abrolhos. We selected the Abrolhos reefs for representing the living coral fauna because they are the largest and the richest coral reefs of Brazil.

Data about biodiversity of the building coral fauna of Itaparica and Guarajuba reefs (Holocene and present-day reefs) were previously published (Araujo *et al.* 1984, Nolasco & Leão 1986) , and they are used here to perform a comparison with data from the coral biodiversity of Abrolhos reef.

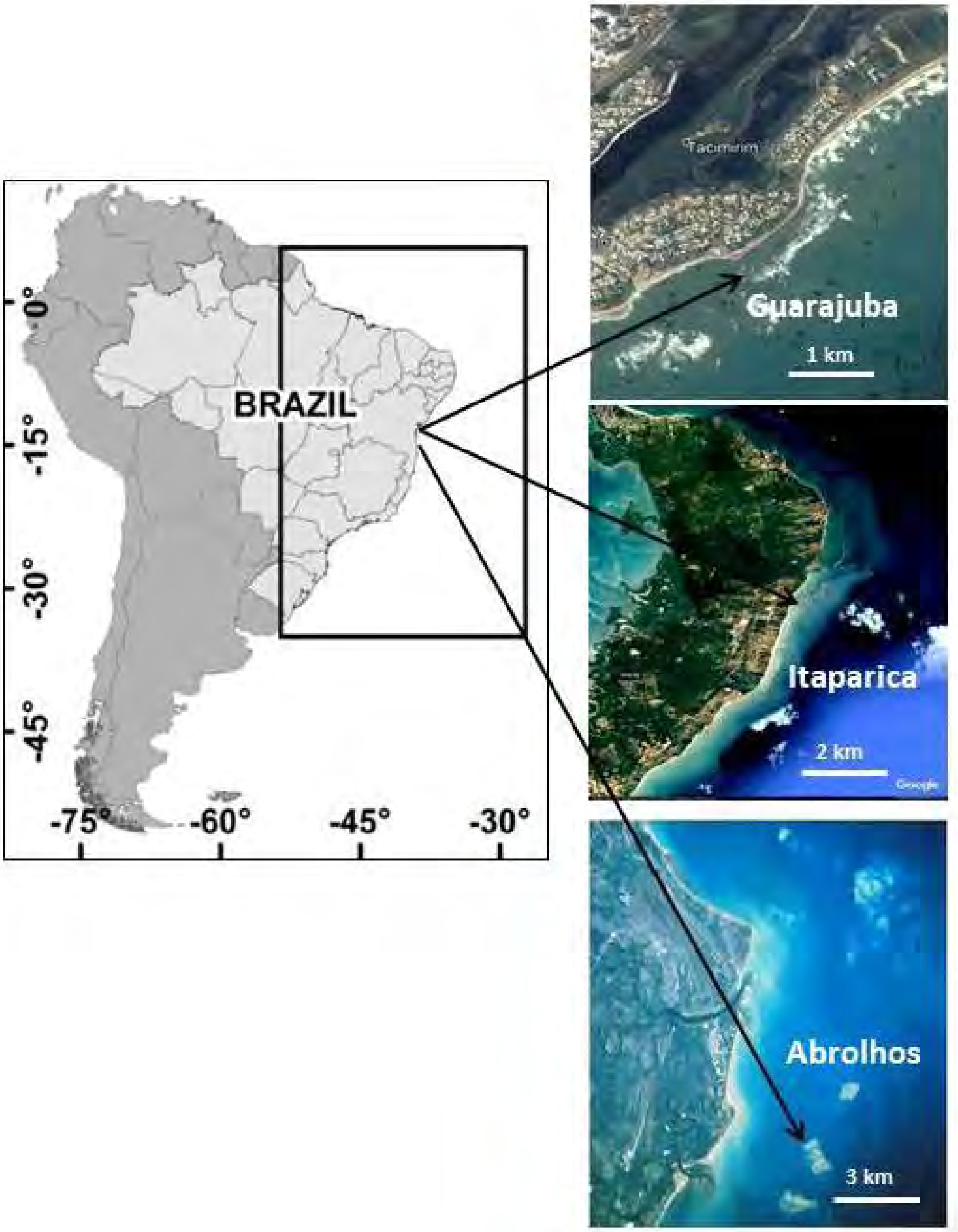

Figure 1: Location of studied reef sites. Images from Google Earth 2018.

3. Results and Discussion

3.1. Coral Lithofacies

The lithochronology analysis of the Holocene sequence of the three studied reef sites, Abrolhos, Itaparica and Guarajuba (figure 2), revealed five lithofacies that best describe the carbonate depositional environment associated with the coral reefs of Bahia: (1) coral-algal bindstone/framestone, (2) mixed skeletal rudstone, (3) branching hydrocoral bindstone/ framestone, (4) massive coral framestone and (5) grainstone. This lithofacies classification is a modified form of the method of Engels *et al.* (2004) that combines bioclast composition and lithology (Longman 1981) in accordance with the Dunham (1962) schema.

(1) Coral-algal bindstone/framestone: the main constituents of this lithofacies is the coral *Mussismilia harttii*, which has a delicate growth form and most likely in growth position incrusted by coralline algae, sometimes with a thin film of incrusting bryozoan, accompanied by fragments of *Agaricia* spp., *Siderastrea* spp. and *Millepora alcicornis*, and occasional coral rudstones, as is illustrated in a section of the core sequence of Abrolhos reef (figure 3 A).

Occurrence: at all three reef sites, this lithofacies occurs in their deepest part of the cores (see figure 2). In Abrolhos reef, it occupies approximately 3.0 m of the lowest part of the Holocene sequence; in Itaparica reef, it is registered in the lowest 2.0 m; and in Guarajuba reef, this lithofacies is seen in the lowest 4.0 m of the core.

Environment: ^{14}C dates from the three core sequences show that the sections of this lithofacies are older than 5,500 cal yr BP in Abrolhos reef, 3,800 cal yr BP in

Itaparica reef, and 6,300 cal yr BP in Guarajuba reef. At this time, the sea-level along the east coast of Brazil was higher than it present position (figure 4). Thus, the initial growth of all reefs occurred at depths approximately between 8 and 10 m, an environment characterized by moderate-to-low wave energy.

(2) Mixed skeletal rudstone: the main components of this lithofacies are a mixture of unsorted, angular or semi-rounded clasts of corals, such as *Agaricia* spp., *Siderastrea* spp., *Favia gravida*, *Mussismilia harttii*, *Porites* spp., *Millepora alcicornis*. This lithofacies is unconsolidated, and most coral pieces lack incrustation. Their sizes are extremely variable, commonly between 2 and 7 cm. figure 3 B illustrates a section of this lithofacies from the Abrolhos reef.

Occurrence: at all three reef sites, this lithofacies occurs at the middle part of the core sequences (see figure 2). In Abrolhos reef, it was identified in two sections: the lowest one is approximately 2.5 m thick, and the upper one has a thickness of approximately 1.5 m. They alternate with a section of lithofacies (3) branching hydrocoral bindstone/framestone. In Itaparica reef, the lithofacies of mixed skeletal rudstone occupies the thickest part of the core sequence, approximately 5.0 m, showing a reef cavity of approximately 1.0 m, between two sections. In Guarajuba reef, this lithofacies has also approximately 5.0 m thickness; it is the thickest section of the entire core sequence.

Environment: in Abrolhos reef, the section of this lithofacies should have been deposited between 5,500 and 4,500 cal yr BP, based on the age of coral fragments from the sections located below and above it. In Itaparica reef, this lithofacies was deposited approximately 6,000 cal yr BP. In both cases the deposition of this lithofacies occurred when sea level was at a depth of approximately 4.0 m (see figure 4). In Guarajuba reef, the section of this lithofacies should have been deposited approximately 3,000 cal yr BP, when sea level was at a depth of approximately 3.0 m. In all cases, this lithofacies should have been deposited in an environment of moderately high energy, with active circulation.

(3) Branching hydrocoral bindstone/framestone: this lithofacies is composed predominantly of the hydrocoral *Millepora alcicornis*, mostly in growth position with branches growing upward. On the surface of the robust branches of *Millepora* skeleton (almost 2 cm thick), there is a layer of incrustation of coralline algae ranging from 2 to 3 mm in thickness. A thin film of incrusting bryozoan covers the internal cavities of the *Millepora* skeleton (figure 3 C).

Occurrence: this lithofacies occurs in the Abrolhos and Guarajuba reefs, and it is absent in the Itaparica core sequence. In Abrolhos reef, a continuous section of almost 1.5 m of thickness is located in the middle part of the core and alternates with the coral rudstone lithofacies. In the Itaparica core, a section of approximately 0.5 m occur in the upper 1.5 m part of the core. Fragments of *Millepora alcicornis* is also registered as coral rubbles in the coral rudstone lithofacies in both the Abrolhos and Itaparica reefs (see figure 2).

Environment: based on the ^{14}C ages of the sections below and above this lithofacies in the Abrolhos core, it was deposited circa 5,000 cal yr BP, when the water column was approximately 3 m deep. And the age of the Itaparica section was between 2,980 and 2,770 cal yr BP, when the sea level was at least 2 m deep (figure 4). These sea level depths indicate an environment of high wave energy.

(4) Massive coral framestone: this lithofacies is composed of the in situ coral *Mussismilia braziliensis* in all three reef sites, Abrolhos, Itaparica and Guarajuba (see figure 2). The coral is mostly in growth position and exhibits few borings, as is illustrated in figure 3 D, from the sequence of Abrolhos reef.

Occurrence: in all three reef sites this lithofacies occurs at the top of the sequences, at depths between 0 and 1.5 m of the core. It has thickness of 1 m in Abrolhos reef, a little more than 1 m in Guarajuba reef and approximately 0.5 m in the Itaparica core sequence (see figure 2).

Environment: the oldest sections are the ones of the Itaparica reef, approximately 5,700 cal yr BP, and the Abrolhos reef, approximately 4,500 cal yr BP. The Guarajuba reef section has an age of approximately 2,770 cal yr BP. Following the sea level curve for the eastern coast of Brazil (figure 4), the sections of this lithofacies, at the top of the reefs, were deposited in depths ranging from 2 to 3 m, indicative of high wave energy environment.

(5) Grainstone: this lithofacies is registered only in the Abrolhos reef sequence (figure 2). It is a moderately-to-well-sorted, medium-to-coarse, rounded carbonate sand, mostly composed of skeletal fragments from organisms living in and around the reefs, such as mollusks, corals, *Millepora,* coralline algae, *Halimeda*, foraminifers, bryozoans, and echinoderms, in addition to worm tubes, crustaceans, and sponge spicules as minor constituents.

Occurrence: sandy sediment occurs in the top of the reef sequence, which is the top of the sandy island where the core was drilled.

Environment: the carbonate sands that form the Coroa Vermelha Island should have been deposited after the reef had stablished, when the sea level attained its present position. It is an environment of high energy characteristic of beaches and/or nearshore environments.

The three cores ranged in penetration depths (measured hole depth), below the sea floor, from 13 m of the Abrolhos reef, 11.5 m of the Guarajuba reef and to 9 m of the Itaparica reef (see figure 2). Comparing the initial growth of the reefs with the sea-level curve for the coast of eastern Brazil (see figure 4), all three Holocene sequences started accumulation in a water column of depth less than 10 m.

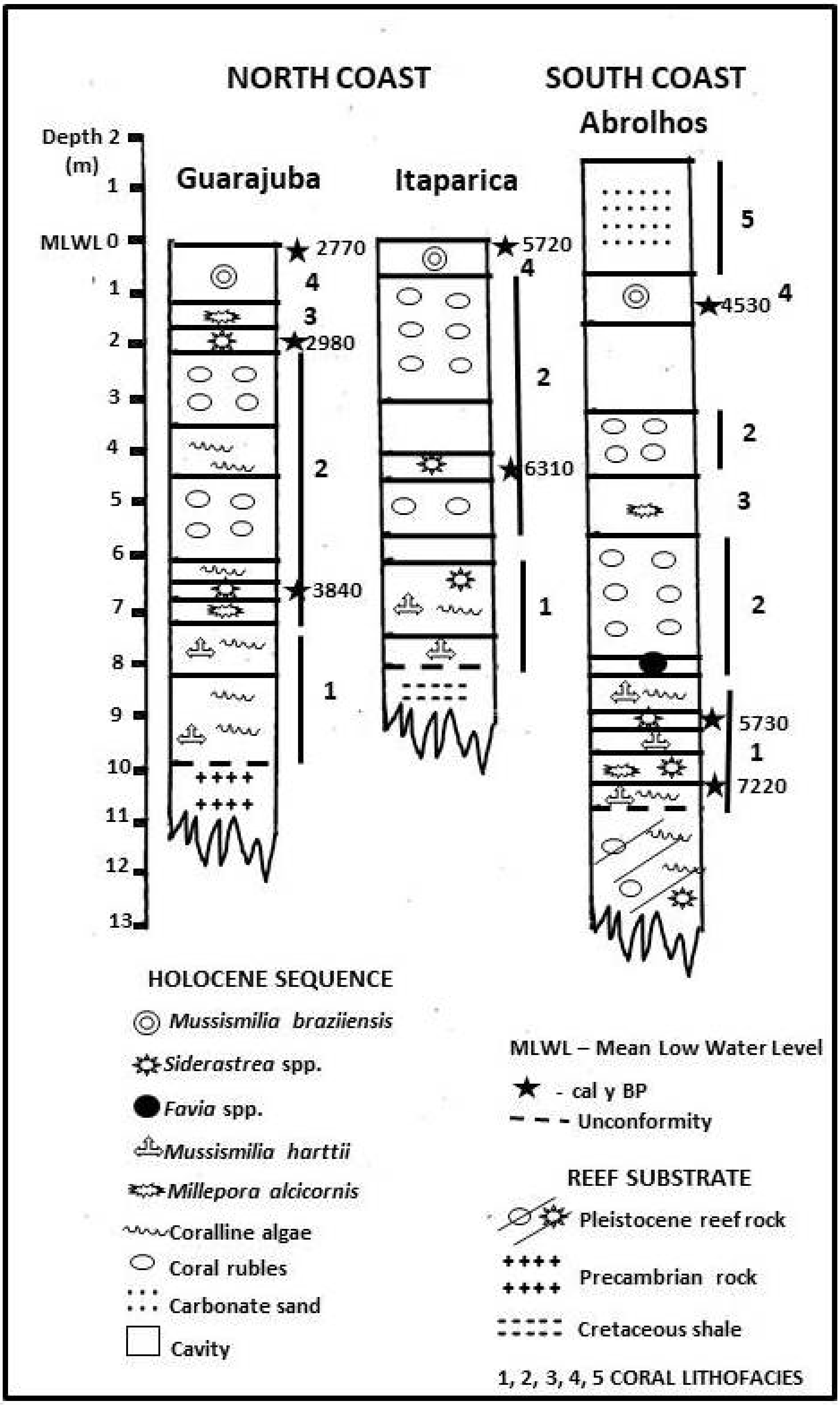

Figure 2: Core logs from the Holocene sequences illustrating the reefs framework (major building corals) and coral lithofacies: 1. Coral-algal bindstone/framestone; 2. Mixed skeletal rudstone; 3. Branching hydrocoral bindstone/framestone; 4. Massive coral framestone; 5. Grainstone. Scale in the left for all three cores.

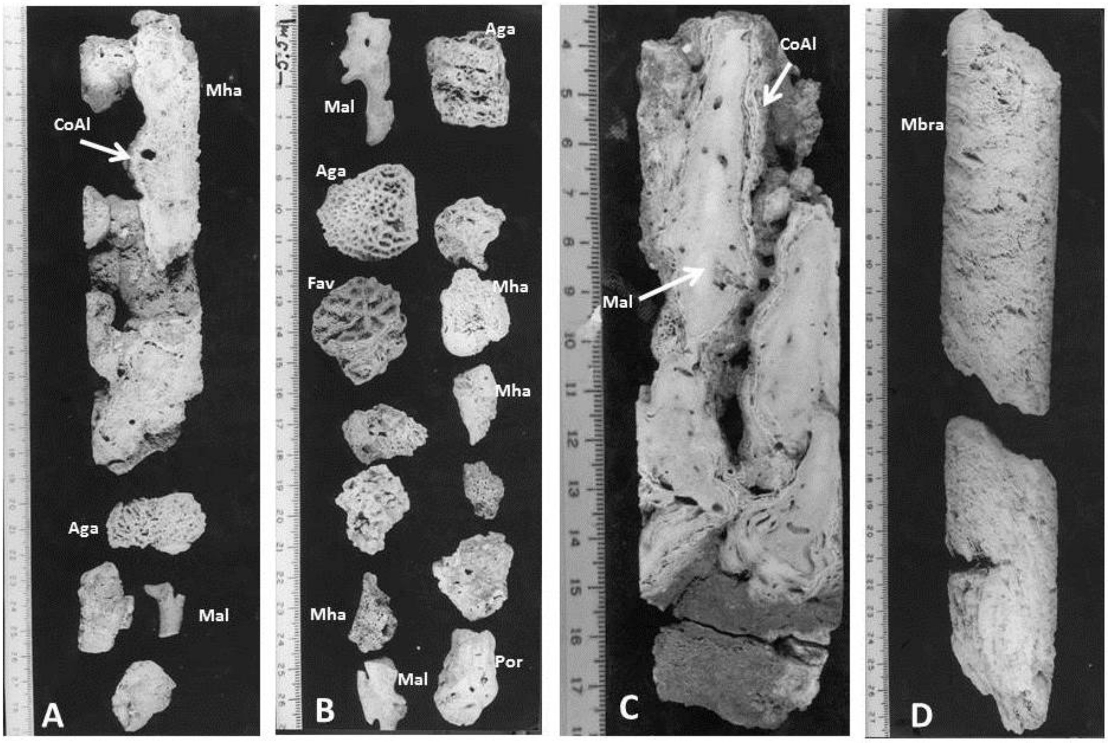

Figure 3: Coral lithofacies common in the Holocene reef of Abrolhos, in order of increasing depositional energy. A – Coral-algal bindstone/framestone; B – Mixed skeletal rudstone; C – Branching hydrocoral bindstone/framestone; D – Massive coral framestone. Mha = *Mussismilia harttii*; CoAl = Coralline algae; Aga = *Agaricia* spp.; Mal = *Millepora alcicornis*; Fav = *Favia gravida*; Por = *Porites* spp.; Mbra = *Mussismilia braziliensis*.

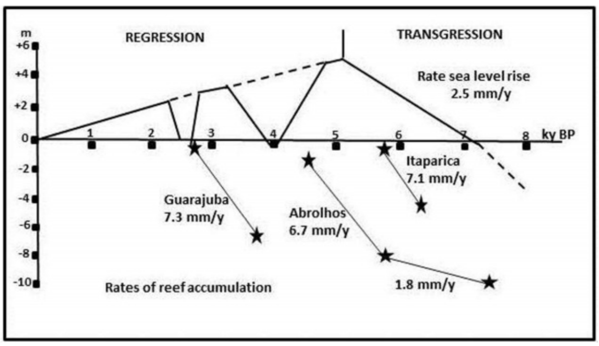

Figure 4: Rate of reef accumulation of Holocene reefs and sea level curve for the coast of the State of Bahia. Stars are ^{14}C dates as in figure 2. Sea level curve modified from Martin *et al.* (1996).

The top of the Abrolhos core was found at approximately 0.5 m below a 2.5 m-thick sandy layer that is the island floor where the core was drilled. At a depth of 11 m, the core exhibits an Holocene unconformity with the antecedent reef substrate; according to Leão & Kikuchi (1999), it is a reef rock of Pleistocene age. The Holocene sequence initiated growth at 7,220 cal yr BP, when the coral-algal framestone/bindstone lithofacies started to be deposited. The Holocene sequence is mainly composed of a framestone of *Mussismilia harttii*, a delicate coral species, which colonies have polyps that grow in a dichotomous form and are incrusted by a layer of coralline algae. The age of 5,730 cal yr BP at the top of this lithofacies indicates that it took more than 1,000 years for the deposition of approximately 2 m of this reef section, a very slow growth rate for reef accretion.

Above it occurs a lithofacies of mixed skeletal rudstone composed of pieces of several coral species, which alternates with the deposition of an expressive growth of the hydrocoral *Millepora alcicornis,* followed by a cavity of approximately 1.5 m, which is a common feature in the reef architecture. This lithofacies is covered by a layer, approximately 1 m thick, of a massive growth of *Mussismilia braziliensis,* the top of which has an age of 4,530 cal yr BP. This lithofacies formed by the endemic coral *Mussismiia braziliensis* crowns the Holocene reef sequences of all studied reef sites. In all of them, this Brazilian fastest growing massive coral (approximately 8 mm annually measured via X-ray, Sugget *et al.* 2012) is mostly responsible for the rapid upward growth of the upper parts of the reefs, which, according to Neumann & Macintyre (1985), characterizes the catch-up mode of reef growth.

The Itaparica core is the shortest one; it reached the reef substrate, a Cretaceous shale that constitutes the island floor, at approximately 8 m deep. The Holocene sequence, which is approximately 8 m thick, is composed of three lithofacies; the oldest one is mainly composed of a framestone of the delicate coral *Mussismilia harttii* incrusted by coralline algae and is accompanied by pieces of the coral *Siderastrea* spp. Above it occurs a lithofacies of mixed skeletal rudstone that constitutes most of this Holocene sequence; it is composed of coral particles of several species. One colony of *Siderastrea* spp., was ^{14}C dated to have an age of 6,310 cal yr BP. Similar to the Abrolhos reef sequence, this lithofacies is crowned by a massive layer of *Mussismilia braziliensis*, the top of which was ^{14}C dated to have an age of 5,720 cal yr BP.

The Guarajuba core is approximately 11 m thick; it reached the reef substrate at a depth of 10 m, an elevation of the Precambrian basement that outcrops along several sections of this coastal region. The Holocene reefal sequence, approximately 10 m in thickness, is the second-longest one from the three studied sites and is composed of four coral lithofacies. At its bottom, similar to the other reef sequences, the coral *Mussismilia harttii* incrusted by coralline algae constitutes the lithofacies coral-algal bindstone/framestone. Above it, the mixed skeletal rudstone lithofacies occupies the largest part of the core, approximately 5.5 m. The ^{14}C dates of colonies of *Siderastrea* spp. from the bottom and the top of this section are 3,840 cal yr BP and 2,980 cal yr BP, respectively, and reveal that this lithofacies took circa 900 years to be deposited. Above it, a half meter of a continuous growth of *Millepora alcicornis* incrusted by coralline algae constitutes the branching hydrocoral bindstone/framestone lithofacies. This lithofacies is capped by an approximately 1.5 m-thick continuous layer of massive growth of *Mussismilia braziliensis*, the top of which has an age of 2,770 cal yr BP.

In all three studied reefs, the Holocene sequences are relatively thin, approximately 11 m thick in the Abrolhos and 10 m in Guarajuba reefs and less than that in Itaparica Island fringing reef. Thicker Holocene sequences are seen occurring in reef sequences described elsewhere in the world (e.g., Shinn *et al.* 1977, Davies & Marshall 1979, Montaggione & Faure 1997, Smithers *et al.* 2006), but core sequences that did not attain thicknesses greater than 10 m are observed in some other reef regions, such as Belize reefs in the North Atlantic Ocean (Pretch 1993), in the Australian Great Barrier Reef (Smithers *et al.* 2006, Rees *et al.* 2006) and reefs from the Hawaiian islands in the Pacific Ocean (Engels *et al.* 2004, Grossmann & Fletcher 2004) (table 1). According to the cited authors, thin Holocene sequences could be the result of a combined influence of the shallow antecedent reef substrate, the regional sea-level history and the wave energy regime.

The shallow depth (approximately 10 m) of the antecedent reef substrate of studied reefs, a Pleistocene reef high in Abrolhos, the rocky island floor in Itaparica reef and outcrop of Precambrian shield in Guarajuba region, creates a narrow space for accommodation of the Holocene reef accumulation and may also have influenced the reefs architecture, as of the isolate bank reefs from the Abrolhos coastal region, the shallow fringing reef bordering the Itaparica Island shore, and the very shallow bank reef attached to the coastline in Guarajuba region. Antecedent reef substrates is a factor that was also considered influencing the Holocene reef development, similar to, for example, reefs in south Hawaii (Grossman *et al.* 2006).

After being stabilized, the reefs started growing when the sea level at the east coast of Brazil was higher than its present position. Their vertical accretion rates varied from an early period with a slow rate, in which suitable substrate existed below the wave base, to a more rapid reef development, a catch-up growth strategy, until they approximately reached sea level.

Table 1: Data regarding Holocene core sequences from various reefs around the world oceans.

Reefs	Thickness of Holocene sequence	Beginning of reef growth ky BP	Type of reef substrate	References
Abrolhos (S Atlantic)	11 m	7,2	Pleistocene reef rock	Leão & Kikuchi 1999
Guarajuba (S Atlantic)	10 m	~4,0	Pre-Cambrian shield	Nolasco & Leão 1986 Kikuchi & Leão 1998
Itaparica (S Atlantic)	8 m	~7,0	Cretaceous shale	Araujo *et al.* 1984
Florida (N Atlantic)	4 m – 14 m	~7,0	Pleistocene carbonate rock	Shinn *et al.* 1977
Belize (N Atlantic)	1.7 m – 2.5 m	~3,5	Pleistocene reef rock	Pretch 1993
Mauritius (Indian)	16 m - 19 m	6,0	Volcanic rock	Montaggioni & Faure 1997
Malokay (Pacific)	0.5 m – 5 m	8,0	Pleistocene reef rock	Engels *et al.* 2004
Oahu (Pacific)	0.25 m – 10 m	7,0	Pleistocene carbonate rock	Grossmann & Fletcher 2004
Australia GBR (Pacific)	5 m – 18 m	7,1	Pleistocene reef rock	Smithers *et al.* 2006
Heron Island –Australia (Pacific)	15.4 m –18.3 m	-	Pleistocene reef rock	Davies & Marshall 1979
One Tree Reef – Australia (Pacific)	19.8 m	-	Pleistocene reef rock	Davies & Marshall 1979
Lizar Island Australia (Pacific)	2.5 – 5.5 m	6,7	Granite basement	Rees *et al.* 2006

The early period of slow growth rate can be attributed to the substrate colonization by the pioneer coral *Mussismilia harttii*, a species with delicate polyps that did not form strong branches or large massive colonies. The depth of approximately 10 m of the available reef substrate surface, where wave energy was moderate, was favorable for the establishment of this particular coral species. This time of slow growth was followed by an intermediate stage of coral rudstone pile-up, in which the water depths and active circulation were sufficient to promote it. And finally this stage gave way to a catch-up framestone accretion, a period of accelerated growth, particularly the one that characterizes the upper section of the reef sequence where *Mussismilia braziliensis* dominates the top of the reefs.

A period of decreasing growth occurred after the reefs had built themselves up to within a few meters of sea level. In such a situation, the erosion in the reef flat would decrease the vertical accretion, coincident with the late Holocene sea-level fall along the east coast of Brazil (see figure 4). Falling sea levels have been considered as a potential factor responsible for erosion of reef flats; some examples are the coral reefs from the Hawaii Islands (Engles *et al.* 2008).

These factors suggest that the development of the reefs during Holocene, in eastern Brazil, was controlled by the regional sea-level variation, the wave energy regime and the shallow antecedent reef substrate. The narrow window for accommodation space for the reefs vertical accretion may have also negatively influenced the lateral expansion of the reef structures, giving the formation of incipient fringing reefs in Itaparica island and isolate shallow bank reefs in Guarajuba and Abrolhos regions.

Despite these stages of reef development not occurring synchronously in time, they did not exhibit any regional variation during their development.

3.2. Coral biodiversity

Holocene sequence

In the longest core, the Abrolhos reef, eighty-six coral fragments were identified, and their densities were calculated; the relative abundance of each species is reported in table 2. Seven species of coral and one of hydrocoral were identified: *Mussismilia harttii, Mussismilia braziliensis, Mussismilia hispida, Agaricia* spp., *Favia gravida*, *Siderastrea* spp., *Porites* spp. and *Millepora alcicornis.*

The coral fragments occupy an area of 898.71 cm^2 along the core, where *Mussismilia harttii* is represented by the greatest number of fragments (25), occupying an area of 336.53 cm^2. It is therefore the species with the highest percent relative abundance (37.45%). *Mussismilia braziliensis* is represented by seven fragments, but they are larger in dimension than those of the other coral species. *Mussismilia braziliensis* ranks second in terms of percent relative abundance (21.69%), occupying an area of 194.92 cm^2. In third position, with a relative abundance of 18.03%, is *Millepora alcicornis*, with 16 fragments occupying an area of 162.00 cm^2. In terms of the number of fragments, *Agaricia* spp. occupies second place (24 pieces), but because the fragments are very small, the area occupied by this species is only 119.40 cm^2, which puts it in fourth place among the other species (13.29%). The coral *Favia gravida* is represented by six fragments, occupying an area of 40.48 cm^2, making this species the fifth in terms of percent relative abundance (4.5%).

The species *Siderastrea* spp., *Mussismilia hispida* and *Porites* spp. all have relative abundances of less than 3% (table 2).

Table 2. Holocene coral biodiversity of Abrolhos reef. Number of coral fragments along the core and the percent relative abundance of coral and hydrocoral species.

Coral species	Number of fragments	Relative abundance (%)
Mussismilia harttii	25	37.45
Mussismilia braziliensis	7	21.69
Millepora alcicornis	16	18.03
Agaricia spp.	24	13.29
Favia gravida	6	4.50
Siderastrea spp.	2	2.94
Mussismilia hispida	2	1.05
Porites spp.	4	1.04
Total	86	100

About the coral biodiversity of the Holocene sequences of Guarajuba and Itaparica reefs, published data refer to the presence of four species in the Guarajuba core and five species in the Itaparica core (table 3). Both cores were most composed with coral rubbles, which pose difficulty for determining the relative abundance of the coral and hydrocoral species. In the Guarajuba core, two species of the genus *Mussismilia* were identified, *M. braziliensis* at the top of the sequence and *M. harttii* at the bottom (see figure 2). Two fragments of *Siderastrea* spp. were ^{14}C dated, and one section of *Millepora alcicornis* was also identified. In the Itaparica core, five species were identified, but as in the Guarajuba sequence, almost the entire core was mostly composed with coral rubbles. Again, *Mussismilia braziliensis* crown the core, and *M. harttii* compose the base of the core. One fragment of *Siderastrea* spp. was ^{14}C dated.

Table 3. Holocene coral biodiversity of Guarajuba and Itaparica reefs. Coral species identified in the core sequences.

Coral species	Guarajuba core*	Itaparica core*
Mussismilia braziliensis	X	X
Mussismilia harttii	X	X
Mussismilia hispida	-	-
Siderastrea spp.	X	X
Favia gravida	-	X
Agaricia spp.	-	-
Porites spp.	-	-
Millepora alcicornis	X	X
Total	**4**	**5**

* Leão *et al.* 1997, Kikuchi & Leão 1998, Leão & Kikuchi 2005.

Present-day reefs

To measure the relative abundance of the corals and hydrocoral from the surface of the coastal reefs of Abrolhos, the densities of 2,658 coral colonies were calculated for five reefs. These colonies have dimensions that vary from 1 to 2 cm in diameter, e.g., the corals *Porites* spp., *Agaricia* spp., *Favia gravida* and *Siderastrea* spp., to the larger colonies equal to or greater than 1 m in diameter, e.g., *Mussismilia braziliensis* and *Mussismilia harttii*, and 3 m wide *Millepora alcicornis* colonies. Eight species of coral – *Mussismilia braziliensis*, *M. hispida*, *M. harttii*, *Montastraea cavernosa*, *Siderastrea* spp., *Favia gravida*, *Agaricia* spp. and *Porites* spp. – and one hydrocoral, *Millepora alcicornis*, constitute the major coral species identified on the surface of the living reefs of Abrolhos (figure 5).

Table 4 lists the relative abundances of the major species of coral and hydrocoral from the present-day reefs of Abrolhos. The four most common species are *Millepora alcicornis* with 44.73% relative abundance, *Mussismilia harttii* with 19.30%, *Montastraea cavernosa* with 16.72%, and *Mussismilia braziliensis* with 12.30%. The other species have relative abundances less than 3%.

Table 4. Coral biodiversity of present-day reefs of Abrolhos. Relative abundance of each species of coral and hydrocoral on the surface of the reefs from the coastal arc of Abrolhos.

Coral species	Pedra Leste %	Pedra Lixa %	Pedra Grande %	Ponta Sul %	Ponta Leste %	Average Costal Arc %
Mussismilia braziliensis	13.36	14.70	12.51	7.62	20.54	12.30
Mussismilia harttii	22.82	18.19	11.61	22.06	17.29	19.30
Mussismiia hispida	3.09	3.87	2.08	1.53	1.85	2.21
Montastraea carvenosa	21.94	18.31	15.35	16.29	13.82	16.72
Siderastrea spp.	5.68	2.04	2.78	0.29	2.73	1.95
Favia gravida	0.77	0.56	1.51	0.42	0.74	0.68
Agaricia spp.	0.33	0.34	0.58	0.21	2.63	0.72
Porites spp.	3.20	2.11	0.93	0.26	2.59	1.39
Millepora alcicornis	28.81	39.88	52.65	51.32	37.81	44.73
Total						100

Published data concerning the relative abundance of the living coral fauna of Guarajuba reef are presented in table 5. Six species are recorded. *Siderastrea* spp. and *Mussismilia hispida* are the most common, with relative abundances of 42% and 31%, respectively. *Agaricia* spp. has 18%, and the species *Montastraea cavernosa*, *Favia gravida* and *Porites* spp. are rarer.

There are not quantified data about the living coral fauna of the Itaparica fringing reef. Araujo *et al.* (1984) refers to the presence of seven coral species on the reef surfaces: *Mussismilia braziliensis*, *Siderastrea* spp., and *Favia gravida* in the intertidal pools at the reef top, *Porites* spp., *Montastraea cavernosa* and *Mussismilia harttii* inside channels that cut the surface of the reef, and the hydrocoral *Millepora alcicornis* that mostly occurs at the borders of the reef.

Table 5. Coral biodiversity of Guarajuba reef. Relative abundance of each species of coral on the living surface of the reef.

Coral species	Relative abundance* %
Mussismilia braziliensis	0
Mussismilia harttii	0
Mussismiia hispida	31
Montastraea carvenosa	5
Siderastrea spp.	42
Favia gravida	3
Agaricia spp.	18
Porites spp.	1
Millepora alcicornis	0
Total	100

* Dutra *et al.* 2000, Leão *et al.* 2008

Figure 5. The major Brazilian coral and hydrocoral species described in the studied reefs: A – *Mussismilia braziliensis*; B – *Mussismilia hispida*; C – *Mussismilia harttii*; D – *Siderastrea* spp.; E – *Agaricia* spp.; F – *Porites* spp.; G – *Montastraea cavernosa*; H – *Favia gravida*; I – *Millepora alcicornis*. Photographs courtesy of C.L. Sampaio.

Overall, the data from the three studied reefs demonstrate that with the exception of the coral *Montastraea cavernosa*, which was not identified in the Holocene sequences, all the other species occur in the studied samples of the Holocene sequence and the present-day reefs (table 6).

Table 6. Coral species identified on the Holocene and Present-day reefs of Abrolhos, Guarajuba and Itaparica.

	HOLOCENE REEFS			PRESENT-DAY REEFS		
Coral species / Reefs	**Abrolhos**	**Guarajuba***	**Itaparica***	**Abrolhos**	**Guarajuba***	**Itaparica***
Mussismilia braziliensis	X	X	X	X		X
Mussismilia harttii	X	X	X	X		X
Mussismiia hispida	X			X	X	
Siderastrea spp.	X	X	X	X	X	X
Favia gravida	X		X	X	X	X
Agaricia spp.	X			X	X	
Porites spp.	X			X	X	X
Montastraea cavernosa				X	X	X
Millepora alcicornis	X	X	X	X		X
Total	8	4	5	9	6	7

*Araujo *et al.* 1984, Leão *et al.* 1997, Kikuchi & Leão 1998, Dutra *et al.* 2000, Leão & Kikuchi 2005.

Few differences are observed in the number of species present in the Holocene cores and the surface of the living reefs. In the Abrolhos reefs, only one more species is observed in the living reefs, *Montastraea cavernosa*, whereas in the Guarajuba and Itaparica reefs, there is an addition of two species in the modern reefs, including *Montastraea cavernosa*.

However, we must take into consideration that throughout the core, it has not been possible to identify various corals to the species level, instead reaching only the level of genus, as for *Agaricia* spp., *Siderastrea* spp. and *Porites* spp. To facilitate the comparison between the two communities (old and living), we added the species identified in the field belonging to the same genus for the present-day reefs. For example, *Agaricia humilis and A. fragilis* were identified as *Agaricia* spp., and *Porites branneri* and *P. astreoides* were identified as *Porites* spp. If we had not combined these two species at the genera level, we would have two more species for the living reefs if only one species of each genus were present in the Holocene sequence.

In the Abrolhos reefs five species have percentages above 10% in the one or two studied coral reef fauna (Holocene and present-day reefs) (*Mussismilia* *braziliensis, Mussismilia harttii, Millepora alcicornis, Montastraea cavernosa* and *Agaricia* spp.), and three of them are common to the Holocene and the modern reefs (*Mussismilia braziliensis, Mussismilia harttii* and *Millepora alcicornis*). There is no great difference in the relative abundance of the other evaluated species: *Agaricia* spp., which has a relative abundance greater than 13% in the Holocene section, did not reach the average of 1% in this living reef. *Montastraea cavernosa*, which reaches a relative abundance greater than 15% in the modern reefs, was not observed in the Holocene sequence.

In the Guarajuba reef, there is a difference in the composition of the coral species. Whereas the two species of the genus *Mussismilia* (*M. braziliensis* and *M. harttii*) occur in the Holocene sequence, they are not observed in the living reef, with *Mussismilia hispida* being the second-most-abundant coral in the modern reef. *Agaricia* spp. is absent in the core sequence, and it occurs with an abundance of 18% in the modern reef.

In the Itaparica reef, the endemic corals *Mussismilia braziliensis*, *Mussismilia harttii* and *Siderastrea* spp. occur in the Holocene and present-day reefs.

In all studied reefs, among the four most-abundant species (relative abundance > 10%) in both old and living reefs, two corals are endemic to Brazil, *Mussismilia harttii* and *Mussismilia braziliensis*, relics forms from the Tertiary Period. They have dominated since the origin of the reefs and persist until today. *Mussismilia harttii* occupies a position closer to the bottom of the cores (approximately 7,000 yr BP), the beginning of reef growth, whereas *Mussismilia braziliensis* occurs at the top of the core sequences (ages ranging from 2,770 cal yr BP to 4,530 cal yr BP to 5,720 cal yr BP) (see figure 2). The location of these two species in the cores can be related to their current reef zonation. In the schematic drawing of figure 6, Laborel (1970) suggests that the species *Mussismilia harttii* prefers greater depths while the species *Mussismilia braziliensis* occupies the upper parts of the reefs. Considering the relationship between the development of the Brazilian reefs and the sea level curve for the east coast of Bahia (see figure 4), the reefs began growing at a depth of approximately 10 m, a favorable environment for the establishment of *Mussismilia harttii*. At the top of the reefs, at shallower depths, *Mussismilia braziliensis* settled and has dominated up to the present.

Montastraea cavernosa was not observed in the studied Holocene sequences; however, it has been recorded in surveyed living reefs off the coast of Bahia (e.g., Kikuchi *et al.* 2003, Leão *et al.* 2003, Kikuchi *et al.* 2010, Leão *et al.* 2010, Francini-Filho *et al.* 2013, Castro *et al.* 2012, Zilberberg *et al.* 2016). Laborel (1970) describes *Montastraea cavernosa* in the large coral pinnacles of Abrolhos (the Brazilian chapeirões) as a species that prefers calm and clear waters at depths between 10 and 20 m, as is illustrated in the coral zonation of figure 6. This water depth is greater than that in which the nearshore reefs off the coast of Bahia developed during the Holocene, which could suggest that this is the reason for the absence of this species in the described Holocene sequences shallower than 10 m. By contrast, recent surveys show that this coral species has been observed in shallower depths in Bahian reefs, for example, in reefs in the interior of Todos os Santos Bay (Cruz *et al.* 2013), in the top of inshore reefs of the Abrolhos region (Castro *et al.* 2012), and in our survey of these living reefs. Thus, the most probable reason for the absence of *Montastraea cavernosa* from the Holocene reefs is a sample issue due to the small number of studied Holocene reef sequences. It is worth of note that, very recently, Bastos *et al.* (2018) drilled three offshore mid-shelf pinnacles in the Abrolhos region and also did not record *Montastraea cavernosa* in the late Holocene cores. This coral species is present in the living walls of these reefs.

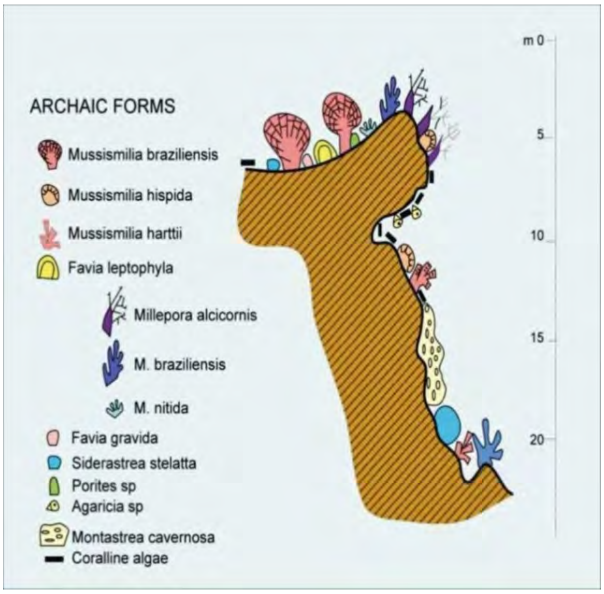

Figure 6. Sketch illustrating the preferred position of coral and hydrocoral species in the present-day coral pinnacle (chapeirão) of Abrolhos, according to Laborel (1970).

Comparing the number of identified coral species present in the Abrolhos core with the number of species recorded in the Holocene sequences of Guarajuba and Itaparica reefs, we observe that the Abrolhos reef sequence exhibits a greater diversity of corals than the other two Holocene sections, twice that of the Guarajuba reef core, which contain only four species and that of the Itaparica reef sequence, with five species (see table 6). These data extend to the Holocene the finding in the literature that the Abrolhos reefs have the highest coral diversity in the whole Southwestern Atlantic Ocean (Laborel 1970, Maida & Ferreira 1997, Castro & Pires 2001, Kikuchi *et al.* 2003, Leão *et al.* 2003).

The characteristic of the composition of the evaluated coral fauna of the reefs from the east coast of Brazil is an indication that their biodiversity did not change much since the beginning of the reef development (approximately 7,000 yr BP), suggesting that the environmental conditions in this region have most likely remained favorable for the development of coral reefs since the beginning of their growth in the Holocene. The coral biodiversity has remained constant throughout the development of the reefs.

We conclude that the growth pattern of the coral reefs from Eastern Brazil has not changed since the Holocene and their building coral fauna are mostly composed of resistant and well-adapted endemic coral species.

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