



**UNIVERSIDADE FEDERAL DO RIO GRANDE DO NORTE**

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Influência de um vale na plataforma continental sobre as  
comunidades de recifes biogênicos no litoral do Rio  
Grande do Norte

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Natal (RN)

Janeiro – 2019

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## Resumo

Comunidades naturais são estruturadas por fatores físicos e biológicos que determinam as dinâmicas locais de coexistência entre espécies. Em ambientes recifais, condições como dinâmica de correntes, ondas, temperatura, profundidade e disponibilidade de nutrientes tem um papel importante na estruturação das comunidades. Uma limitação frequente em ambientes marinhos é a disponibilidade de nutrientes. O efeito de massa em ilhas onde o aporte temporário de nutrientes alóctones mantém a diversidade em torno de ilhas oceânicas, bem como a transformação de carbono orgânico dissolvido em particulado por esponjas (*sponge-loop*) tem papel importante na manutenção de ecossistemas diversos em condições oligotróficas. A maioria dos recifes brasileiros são de formação rochosa ou arenítica e recebem grande influência de sedimentos e matéria orgânica continental, sendo dominados por macroalgas e com baixa cobertura de corais. Recifes biogênicos ocorrem por exemplo no banco dos Abrolhos e no sul da Bahia onde há alta cobertura de corais. Recentemente foram descritos, sob o ponto de vista geológico, recifes de formação biogênica e alta cobertura de corais na região setentrional do Brasil. Neste trabalho descrevemos a comunidade de bentos e peixes desses recifes utilizando fotoquadrados do substrato bentônico e censos visuais da comunidade de peixes. Três áreas recifais foram escolhidas ao redor de um vale inciso no leito submarino, potencialmente uma fonte importante de nutrientes para os recifes, onde exploramos a variabilidade a leste, oeste e ao centro do canal. Encontramos maior cobertura de corais e menor cobertura de macroalgas nos recifes localizados no centro do vale inciso. A biomassa total de peixes foi similar entre as áreas, porém a distribuição entre grupos funcionais variou. A biomassa de peixes invertívoros e piscívoros foi maior ao centro do vale, potencialmente devido à maior disponibilidade de alimentos. Nossos resultados revelam que o vale pode estruturar comunidades recifais de forma similar ao que ocorre através do efeito de massa em ilhas. O trabalho contribui para a descrição das comunidades biológicas que formam estes recifes biogênicos recém descobertos, bem como para avaliar o efeito do vale inciso sobre estes recifes, preenchendo lacunas no conhecimento à respeito deste tipo de formação recifal no Brasil e gerando informações preliminares que futuramente possam ser utilizadas para guiar o manejo e conservação desses ecossistemas únicos.

## **Abstract**

Natural communities are structured by physical and biological factors that drive the local dynamics of species coexistence. On reef habitats, conditions such as currents, waves, temperature, depth and nutrient availability play important roles on structuring communities. Nutrient availability is a frequent limitation in marine environments. The island mass effect, for instance, when the allochthonous nutrient supply supports a diverse ecosystem, and the transformation of dissolved organic carbon into particulate matter by sponges (sponge-loop) have an important role on maintaining ecosystems on oligotrophic conditions. Most Brazilian reefs are rocky or sandstone formations with a great influence of continental run-off, being mostly dominated by macroalgae and presenting low coral cover. Biogenic reefs in Brazil occur in the Abrolhos bank and southern Bahia state, presenting high coral cover. Recently, biogenic reefs with high coral cover were geologically described on northern Brazilian coast. We described benthic and fish communities in these reefs using photoquadrats of benthic substrates and visual census of fish community. Three reef areas were chosen around a valley, a potential pathway for nutrient input to the reefs, exploring variations among reefs at east, west and at the center of the valley. We found higher coral cover and lower macroalgal cover on reefs located within the valley. Fish biomass was similar among areas, but biomass distribution differed among functional groups. Invertivores and piscivores biomass was greater on reefs within the valley, potentially resulting from higher food availability resulting from increasing nutrient input. Our results reveal that the valleys may structure reef communities similarly to what happen with the island mass effect. This work contributes to description of biological communities composing these outer shelf biogenic reefs, elucidates the potential effects of the valley on these reefs, and fills a gap on the knowledge on these kind of reef formation in Brazil, generating information that can be further used for guiding management and conservation of those unique ecosystems.

## LISTA DE FIGURAS

1	Local de estudo.....	16
2	Cobertura bentônica e análise de coordenada principal dos grupos bentônicos.....	20
3	Biomassa de grupos funcionais de peixes e análise de coordenada principal dos grupos funcionais de peixes.....	22
4	Análise de redundância entre grupos bentônicos e de peixes.....	23
5	Cobertura dos grupos bentônicos por área.....	37
6	Biomassa dos grupos funcionais de peixes por área.....	38

## LISTA DE TABELAS

1	Grupos bentônicos.....	34
2	Grupos de peixes.....	35
3	Granulometria e composição dos sedimentos.....	37

# CONTEÚDO

<b>INTRODUÇÃO GERAL</b>	<b>8</b>
<b>CAPÍTULO ÚNICO</b>	<b>11</b>
<b>1 Introduction</b>	<b>13</b>
<b>2 Material and Methods</b>	
2.1. Study site.....	15
2.2. Field Procedures.....	16
2.3. Sediment analysis.....	17
2.4. Data analysis.....	17
<b>3 Results</b>	
3.1. Abiotic and sediment data.....	18
3.2. Benthic community.....	19
3.3. Fish community.....	21
<b>4 Discussion</b>	<b>23</b>
<b>5 Conclusions</b>	<b>28</b>
<b>Acknowledgements</b>	<b>28</b>
<b>References</b>	<b>29</b>
<b>Supplementary information</b>	<b>34</b>
<b>CONCLUSÃO GERAL</b>	<b>39</b>
<b>ANEXO</b>	<b>40</b>



## INTRODUÇÃO GERAL

Nos ambientes marinhos, condições como disponibilidade de alimento, ação das ondas, temperatura, profundidade e correntes de maré estão entre os principais atributos estruturadores das comunidades (Dollar, 1982; Littler and Littler, 1985; Kraines et al., 2001; Kleypas et al., 1999; Gove et al., 2015; Pinheiro et al., 2018). A disponibilidade de alimento é um fator chave para determinar como dinâmicas de controle base-topo (“bottom-up control”) em produtores primários estruturam toda a comunidade através de diferentes níveis tróficos, de organismos bentônicos a peixes. (Stuhldreier et al., 2015; Gove et al., 2015; Morais et al., 2017; Quimbayo et al., 2018). Sendo assim, entender como a disponibilidade de alimento afeta as comunidades marinhas é de grande importância para compreender as dinâmicas que sustentam tais comunidades (Burkepile et al., 2006).

Uma das principais questões a respeito de ambientes recifais é sobre como estes ecossistemas altamente diversos ocorrem em águas extremamente pobres em nutrientes (Rougerie et al., 1992; De Goeij et al., 2013). Um fenômeno que explica este paradoxo dos nutrientes nos ambientes recifais é o efeito de massa em ilhas (“*island mass effect*” ou IME), onde uma elevada biomassa fitoplanctônica concentra-se ao redor de ilhas oceânicas, sustentando sistemas de alta produtividade ao transformar matéria orgânica dissolvida em matéria orgânica particulada, consumível pela fauna (Gove et al., 2016). De forma similar, o efeito “*sponge loop*” também exerce um papel importante nos ambientes recifais ao disponibilizar matéria orgânica dissolvida para a fauna e também por manter a matéria orgânica dentro do ecossistema (De Goeij et al., 2013). Compreender os mecanismos que sustentam uma produtividade primária que leva a

alta biodiversidade em ambientes recifais é de grande importância para o conhecimento ecológico destes ambientes.

Na costa brasileira, o grande aporte continental de água doce e sedimento no oceano resultam em águas frequentemente turvas e impõe um regime de grande aporte de nutrientes nos recifes costeiros, o que favorece o crescimento de macroalgas e prejudica a saúde dos corais. Sendo assim, a maioria dos recifes brasileiros são dominados por macroalgas, possuem baixa cobertura de corais (Aued et al., 2018) e são formados por rochas areníticas (Leão et al., 2016). Porém, recifes afastados da costa ocorrem em águas mais oligotróficas e podem depender do IME ou do *sponge loop*, induzidos pela circulação submarina e características geomorfológicas da plataforma, para manter suas produtividades primárias. Algumas formações recifais biogênicas com alta cobertura de corais (>15%) podem ser encontradas no banco dos Abrolhos e no sul da Bahia (Teixeira et al., 2013; Leão et al., 2016; Mazzei et al., 2016; Bastos et al., 2018). Além dessas formações mais conhecidas, uma extensa formação recifal biogênica foi descrita recentemente na região setentrional do estado do Rio Grande do Norte, conhecidos como Recifes do Açú (*Açú reefs*; Gomes et al., 2016; Nascimento Silva et al., 2018). Estes recifes recém descritos estão localizados próximos a uma depressão (até 20 metros) em forma de vale na plataforma continental, que pode desempenhar um papel importante na estruturação das comunidades bentônicas e nectônicas por agir como uma rota de transporte de nutriente provenientes de águas mais profundas até raso. O aporte de nutrientes tem origem em um canyon submarino conectado diretamente ao vale (Almeida et al., 2015; Gomes et al., 2016) e este aporte pode potencialmente estar estruturando as comunidades recifais sob sua influência.

Estudamos as comunidades de peixes e bentos dos recifes do Açú e avaliamos os potenciais fatores estruturantes das comunidades. Nosso objetivo foi compreender a influência do vale nas comunidades de peixes e de bentos. Esperávamos encontrar comunidades bentônica e de peixes enriquecidas nos recifes localizados ao centro do vale, de forma similar ao que ocorre em ilhas oceânicas onde águas ricas em nutriente induzidas por correntes de ressurgência geram aumento na abundância de organismos bentônicos bioconstrutores, como corais e algas calcárias; além de um aumento na biomassa de peixes invertívoros, piscívoros e onívoros, devido ao aumento na produção primária e oferta de alimento. Nossos resultados suportam a hipótese de que o aporte de nutrientes do vale podem estar estruturando ambas comunidades, bentônica e de peixes, em recifes sob influência do vale. As características das comunidades destes recifes apresentam padrões semelhantes aos que resultam do IME (ex. maior cobertura de corais e biomassa de peixes invertívoros e piscívoros).

## **CAPÍTULO ÚNICO**

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# **Underwater valley at the continental shelf structures benthic and fish assemblages of biogenic reefs**

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## **Abstract**

Underwater relief and topography may influence currents, waves, temperature, depth and nutrient availability, factors that play important roles on structuring reef communities. The formation of valleys at the continental shelf, for instance, may result in unique geomorphologies that influences environmental factors on a local scale. Therefore, reefs within the valley and on its adjacencies are likely to experience different conditions despite the geographical proximity. An extensive biogenic reef formation at the Brazilian Equatorial shelf occurring within and around a valley was recently described from the geological perspective. Given the relative paucity of biogenic reefs along the Brazilian coast, understanding these biological communities is critical. We assessed benthic and fish communities in these reefs using photoquadrats and visual census, respectively. We studied reefs within the valley, on the West and East of the depression, to evaluate if the stronger tidal currents within the valley and its connection to a submarine canyon would differentially affect benthic and fish communities among these areas. We found higher coral cover and lower macroalgal cover on reefs located within the valley. Fish biomass was similar among areas, but biomass distribution differed among functional groups. Invertivores and piscivores biomass was greater on reefs within the valley, potentially resulting from higher food availability and nutrient input. This work provides information on biological communities in these outer shelf biogenic reefs around valleys, a novel approach to this formation, showing that environmental factors associated to underwater valleys may structure reef communities even within small spatial scales. This effect may be due to local topography and current condition, to the nutrient-rich currents from the submarine canyon reaching the reefs through the valley and aiding primary productivity, or by a combination of these factors.

**Keywords:** reef fish; corals; incised valley; community structure

**Regional terms:** Brazil; Rio Grande do Norte; Açu Reefs

## 1. Introduction

In marine ecosystems, conditions such as wave exposure, temperature, depth and tidal currents are among the most important drivers of community structure (Dollar, 1982; Littler and Littler, 1985; Kraines et al., 2001; Kleypas et al., 1999; Gove et al., 2015; Pinheiro et al., 2018). Nutrient availability may also be a key factor for determining how bottom-up control on primary producers structures the entire community across different trophic levels, from benthic organisms (Stuhldreier et al., 2015; Gove et al., 2015) to fish assemblages (Morais et al., 2017; Quimbayo et al., 2018).

The submarine relief and reef topography influence many of these drivers, determining depth and hydrodynamic conditions such as local currents and water circulation, which may affect critical ecological processes of reef communities including nutrient uptake (Lowe & Falter, 2015; Wolanski, 2018). At the Great Barrier Reef, for instance, reef topography combined with tidal action, local winds and currents, determine water circulation and, consequently, larval dispersal, and transportation of sediments and nutrients among reefs (Lambrechts et al., 2008). Therefore, to elucidate the dynamics of reef communities it is important to assess the influence of environmental factors that result from the submarine relief.

At the continental shelf, the formation of valleys due to a combination of estuarine or riverine erosion with tidal currents influenced by sea level fluctuation may result in unique geomorphologies (Clark 2009). At the Brazilian Equatorial shelf, for instance, a valley depression (up to 24 m of relief) that extends 40 km from the present

day shoreline to the outer shelf was recently described and comprise an extensive biogenic reef formation within and around the valley (Açu Reefs; Gomes et al. 2016; Nascimento Silva et al., 2018). The valley significantly affect local tidal currents, which can be three fold higher within the valley in comparison to adjacent areas (Gomes et al. 2015). The influence of coastal sediments and nutrient input on the valley and its adjacencies is limited due to a discontinuity of the valley closer to the shore, that resulted from sea level variation, and because the current riverine outflow is not strong enough to reach the valley 30-40 km from the coast (Gomes et al. 2016). However, the valley is connected to a submarine canyon at the shelf break that may be an important pathway for nutrient-rich deep water to reach shallower areas and potentially affect biological dynamics (Almeida et al., 2015; Gomes et al., 2015, 2016). Therefore, reefs within the valley and adjacent to it experience different conditions of tidal currents and nutrient inputs, which may be reflected in the structure of benthic and fish communities.

Brazilian reefs are generally dominated by macroalgae and algal turf, with low coral cover, as a combined result of biogeographical processes, narrow continental shelf and sediment-rich waters (Aued et al., 2018). As a result, biogenic reefs in Brazil are mostly concentrated in the Eastern area of Abrolhos and South of Bahia state, where the continental shelf is larger (Leão et al. 2016). These areas also comprise most Brazilian reefs with coral cover higher than 15% (Teixeira et al., 2013; Leão et al., 2016; Mazzei et al., 2016; Aued et al., 2018; Bastos et al., 2018). Therefore, the recent discover and geomorphological description of the biogenic Açu reefs at the Equatorial coast of Brazil prompted the need to understand these biological communities and underlying processes in these reefs within and adjacent to the underwater valley.



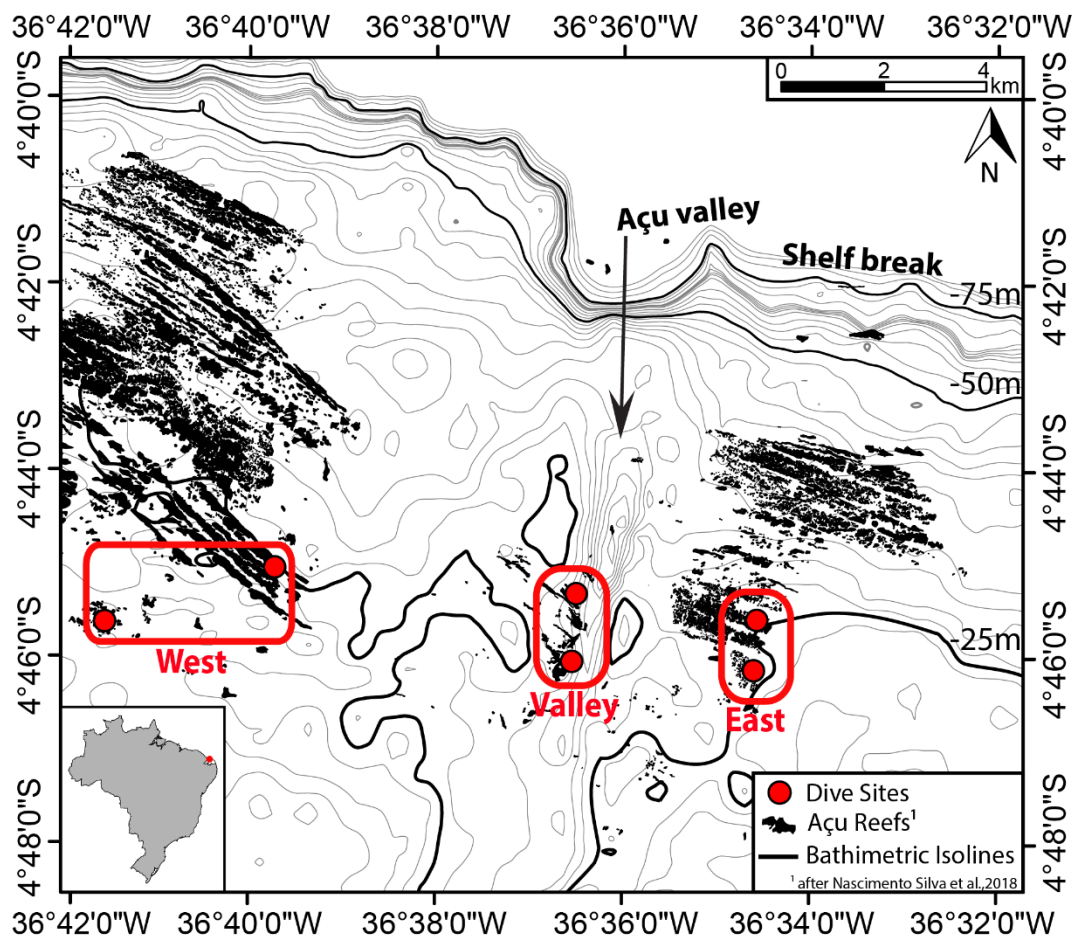
We assessed benthic and fish communities in the newly discovered Açú reefs and evaluated potential differences among reefs within and adjacent to the valley. Our goal was to compare both benthic and fish communities among these reefs and to evaluate the relationship between benthic and fish assemblages. We expected to find a higher richness of benthic organisms and higher fish biomass at the center of the valley, because the disturbance caused by tidal currents would promote a more heterogeneous benthic community and/or because these communities could be potentially benefitting from nutrient-rich waters coming up from the valley, increasing local primary production and alimentary resources. We showed that reef community within the valley is different from adjacent areas, even in a small spatial scale, indicating that environmental factors associated to the presence of the valley structure benthic and fish assemblages.

## **2. Material and Methods**

### **2.1. Study site**

This study was conducted at the northern continental coast of Brazil, in the state of Rio Grande do Norte (Fig. 1; 4°45'17.35"S; 36°40'1.10"O) where reef formations were recently mapped and described by geologists (Gomes et al., 2015; Gomes et al., 2016; Nascimento Silva et al., 2018). These reefs are 30 kilometers offshore, and consist of large boomies that have a patchy distribution and are between the middle and the end of the continental shelf, with depths varying from 20 to 40 meters (Gomes et al., 2015). Reefs occur inside and around the Açú valley that crosses the continental shelf northward from near shore to the shelf end (Gomes et al., 2016), where it connects to a submarine canyon that extends to the deep ocean (Almeida et al., 2015). This valley is

lined approximately N-S, has width of 1 kilometer, with negative relief of up to 24 meters in relation to the margins and steep walls with slopes of up to 1:20 (5%). The currents have an average of 22 cm/s and a maximum of 51 cm/s within the valley with approximately N-S direction affected mainly by the influence of the tide, which channelize the currents. Outside the valley, the average current is 30 cm/s predominantly oriented parallel to the edge of the platform (approximately E-W). The valley has a key role on sediment and nutrient transportation across the continental shelf and from deep up to the shallow continental shelf (Almeida et al., 2015; Gomes et al., 2016).



**Fig. 1:** Study area with samples sites indicated by red circles. Consolidated reef formation are represented by black marks. Bathimetric isolines represented by black and grey lines. Açú valley depression indicated by black arrow.

## 2.2. Field Procedures

Fieldwork was conducted between September and October 2017 in reefs distributed across three areas at the valley formation (East and West valley, and Valley), with depths between 17 and 29 meters (Fig. 1). Diving in the area is restricted to the months of June to October, when wave conditions are mild and water visibility increases (up to 20m) allowing diving activity. Water temperature along the water column was obtained *in situ* through a CTD device (Castaway CTD). Sediment samples from the reef and the adjacent sand bottom were collected, frozen and used for composition, granulometry, carbonate and organic content analyses. Reef morphology is similar among these areas, despite being inside the valley or adjacent to it, and consist of large boomies with sizes varying from 120 m<sup>2</sup> to 500 m<sup>2</sup>, approximately. Transects were deployed on top of these boomies and replicated to cover most of it without overlap. We assessed reef fish assemblages using underwater visual censuses (40m<sup>2</sup> belt transects; *sensu* Floeter et al. 2007) where a diver swam unrolling a 20m measure tape counted, identified and estimated the size of every fish observed within one meter of each side of the tape (20m x 2m transect). Fishes were assigned to functional groups based on literature (diurnal planktivores, mobile invertebrate feeders, macrocarnivores, nocturnal planktivores, omnivores, piscivores, scrapers, sessile invertebrate feeders, spongivores and territorial herbivores; Ferreira et al., 2004; Longo et al., 2014). Estimates of fish biomass were obtained based in length-weight relationships obtained in the literature (Froese & Pauly 2017). A second diver swam along the same transect and took standardized 25x25cm photoquadrats of the benthic substrate every meter (20 pictures per transect). All photos were analyzed using PhotoQuad 1.4 software to distribute 30 points on each image (stratified random mode; Trygonis & Sini, 2012).

Organisms under each point were identified to the lowest taxonomic resolution possible, and grouped in functional categories (corals, coralline algae, filamentous algae, foliose algae, sponges and turf; Littler & Littler, 1984; Foster et al., 1991; Steneck & Dethier, 1994; Bell & Barnes, 2001; Aued et al. 2018).

### 2.3. Sediment analysis

Sediment samples were soaked on fresh water and decanted for three days, when the above water was removed and the process repeated three times to remove salt. Samples were then placed to dry on incubator, homogenized and analyzed for granulometry, carbonate and organic content (based on Vital et al. 2008).

### 2.4. Data analysis

To evaluate differences on fish biomass and benthic cover among and within areas, we used permutation-based analysis of variance. Differences on benthic composition (square-root transformed benthic cover data) and fish assemblages (log-transformed functional groups biomass data) between the three areas (Valley, East and West; grouping variables) were assessed using principal coordinate analysis (PCoA). In addition, a permutation multivariate analysis of variance (PERMANOVA) was used to evaluate differences among areas. To assess how benthic composition influences fish assemblages, we used redundancy analysis (RDA) based on fish biomass data since it embeds information on both abundance and size-class distribution. Variables with variance inflation factor (VIF) higher than three were removed to avoid high collinearity (Zuur et al., 2010). Differences in the organic matter and carbonate content percentages on sediment composition among areas were accessed using permutation-based analysis of variance (Wheeler 2016). All analysis were performed on R software (R Core Team,

2017) using the packages “ape” (PCoA; Paradis & Schliep, 2018), “car” (VIF; Fox & Weisberg, 2017), “lmPerm” (permutation-based ANOVA; Wheeler & Torchiano, 2016) and “vegan” (ANOVA, PERMANOVA, RDA; Oksanen et al., 2017), and the boxplots were plotted using the “yarr” package (Phillips 2017).

### 3. Results

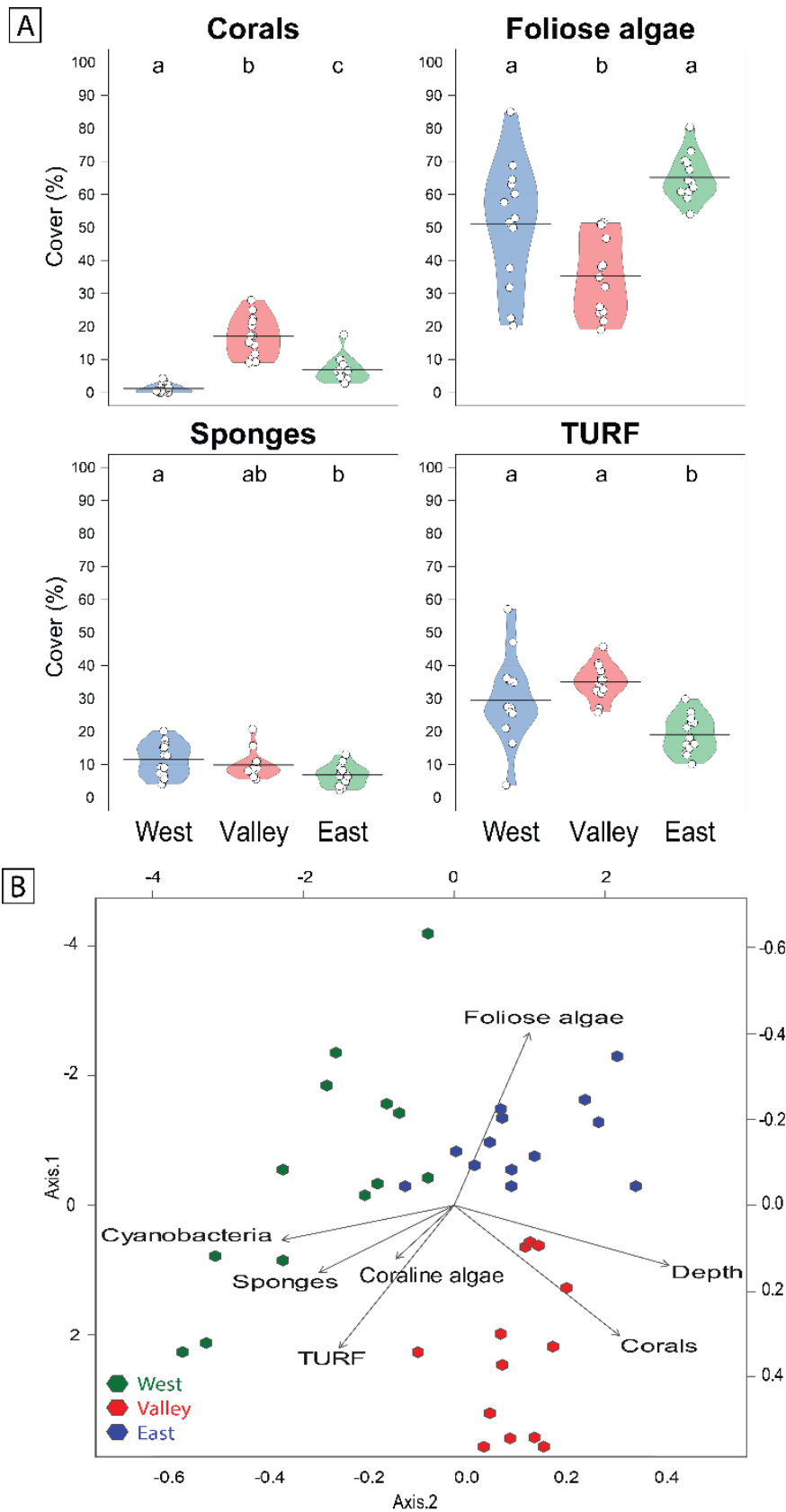
#### 3.1. Abiotic and sediment data

Mean water temperature was similar among the areas ( $26.4 \pm 0.5$  °C). Sediment within reefs and borders was composed by bioclastic sand with grain size increasing from East to West. The sediment was mostly thin with very fine sand in the East side, it varied from the thinnest category to very thick sand within the valley, and was thicker, varying from sand with granules to sand with nodules and shells, in the West side. Sediments from West reefs also presented a higher content of organic matter in comparison to the other areas (DF = 2, Sum of Squares = 11.11,  $p < 0.01$ ) and greater carbonate content in comparison to the East area (DF = 2, Sum of Squares = 249.19,  $p < 0.05$ ; Table S2).

#### 3.2. Benthic community

We recorded 25 benthic components (species and functional groups), among them six scleractinian corals species (*Agaricia agaricites*, *Agaricia fragilis*, *Madracis decactis*, *Montastraea cavernosa*, *Mussismilia hispida*, *Siderastrea sp.*) and one hydrocoral (*Millepora brasiliensis*); fifteen sponges (four of which were not identified to the species level) and a high prevalence of foliose algae within the genera *Canistrocarpus* and

*Dictyota* (Table S1). Reefs of the three sites were dominated by foliose algae and epilithical algal matrix dominated by non-calcified species (algal turf, *sensu* Connell et al., 2014), summing up to 70% of the cover, followed by sponges ( $9.4 \pm 2.3\%$ ). Coral cover differed among the three reef areas, where reefs within the valley had greater coral cover ( $17.04 \pm 1.7\%$ ; DF = 2, Sum of Squares = 0.52,  $p < 0.01$ ) followed by eastern ( $6.9 \pm 1.09\%$ ) and western reefs ( $1.17 \pm 0.36\%$ ). The dominant coral was *Siderastrea sp.* followed by *Montastraea cavernosa* (up to 86% and 44% of the total coral cover in some sites, respectively). Overall benthic community composition differed among the three reef areas (Fig. 2, Fig S1; PERMANOVA df=2, Pseudo-F=18.56,  $R^2=0.51$ ,  $p < 0.01$ ). West reefs presented the lowest coral cover, high foliose algal cover, similar to the east, and the highest sponge cover; reefs within the valley had the highest coral cover and the lowest foliose algae cover; and east reefs presented the highest foliose algae cover with the lowest turf and sponges mean. Coralline algae, cyanobacteria, filamentous algae, hydrozoans and zoanthids were present but were less than 5% of the cover in the studied reefs, reason why these groups were not included in the tests.

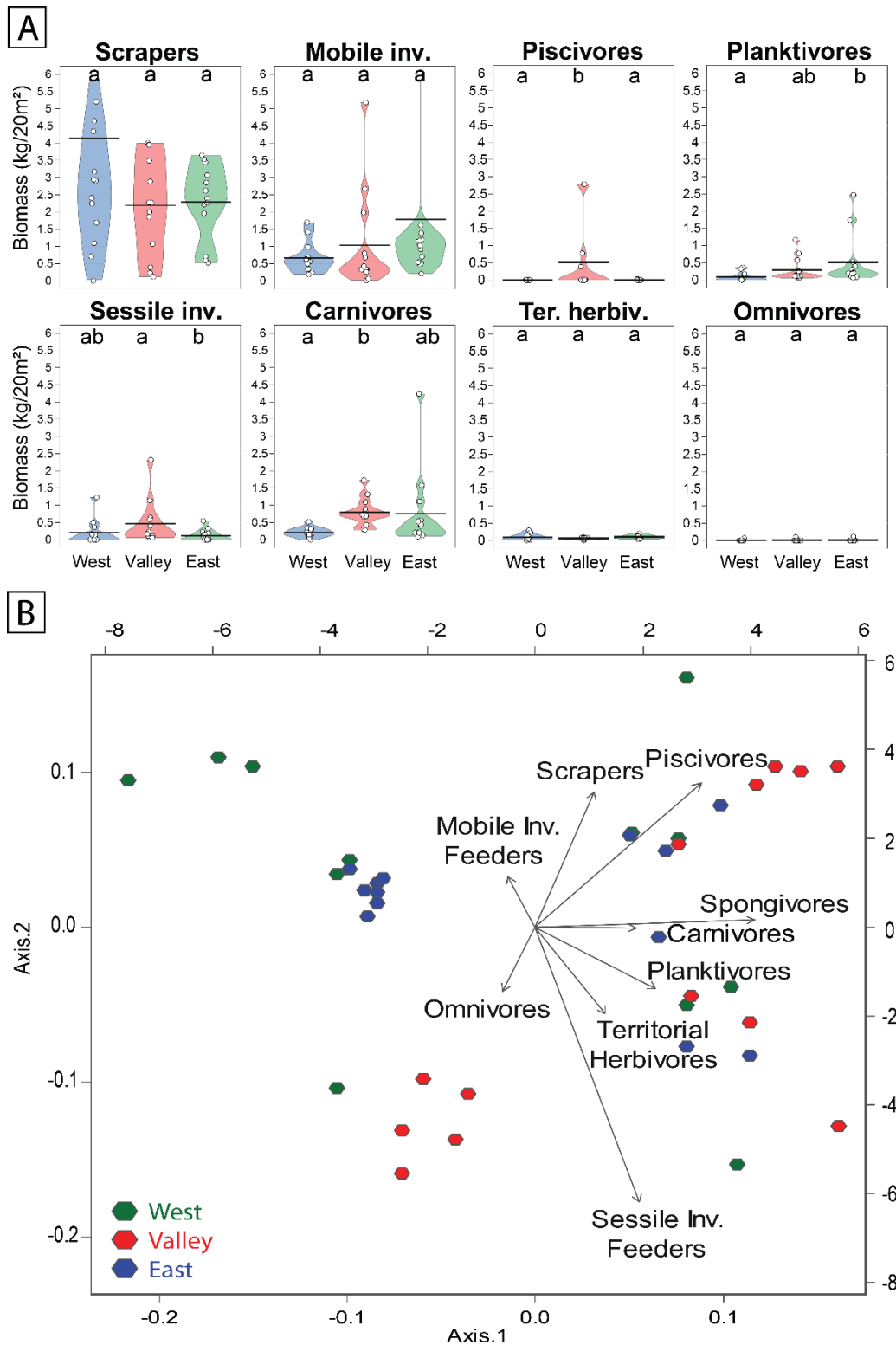


**Fig. 2** Percent cover of benthic groups by area. Differences of groups among areas represented by letters above each group result from permutation-based analysis of variance. Black lines in the plots indicate the central tendency; points represent each sample unity and the width of colored polygons represent the density of data points (A). Principal coordinate analysis (PCoA) of benthic cover among the three reefs areas. Vectors represent benthic categories and depth, and dots represent the scores for each transect (B). PCoA scores are presented in Table S3.

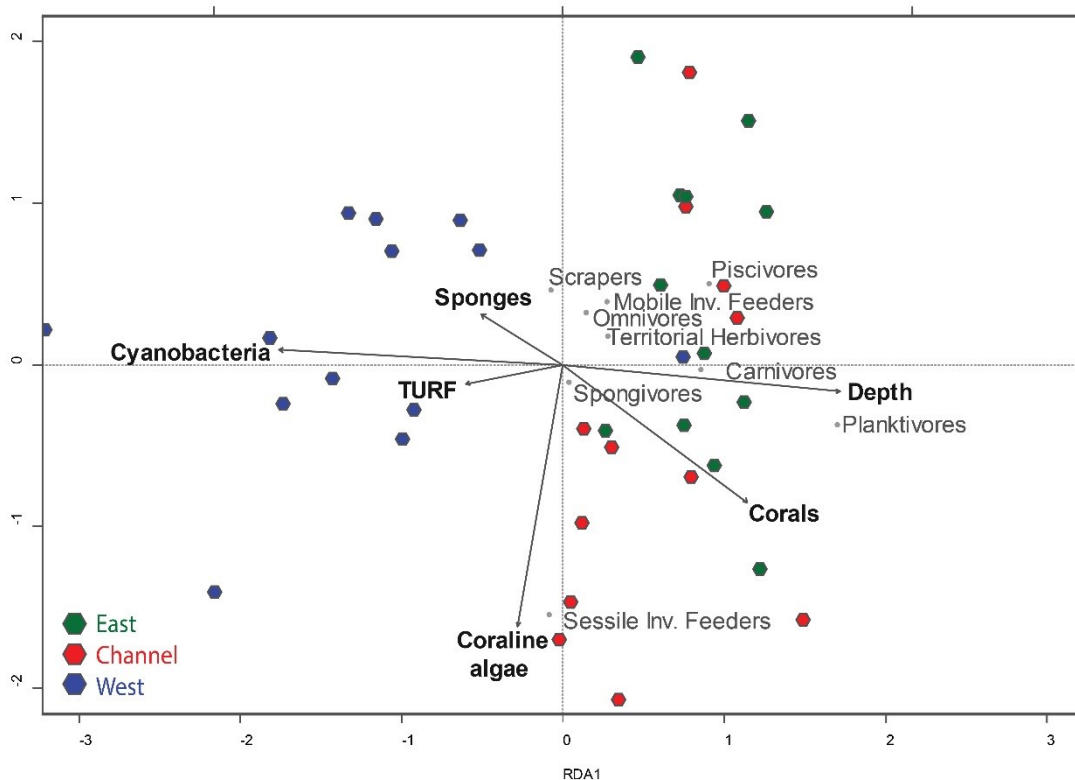
### 3.3. Fish community

A total of 49 reef fish species within 20 families and 8 functional groups were recorded and additional 7 species were seen during the sampling effort but were not recorded within the transects (see Table S4). Overall fish biomass did not differ among reefs sites ( $7.25 \pm 1.14$  kg/40m<sup>2</sup>,  $8.71 \pm 1.7$  kg/40m<sup>2</sup> and  $7.83 \pm 2.43$  kg/40m<sup>2</sup> at east, valley and west areas respectively; DF = 2, Sum of Squares = 0.0707,  $p = 0.599$ ) but the biomass of some functional groups varied within and among areas (Fig. 3, Fig. S2). On the three areas scrapers' biomass were greater than all other groups (West: DF = 7, Sum of Squares = 5.70,  $p > 0.01$ ; Valley: DF = 7, Sum of Squares = 3.37,  $p > 0.01$ ; East: DF = 7, Sum of Squares = 4.83,  $p > 0.01$ ), followed by mobile invertebrate feeders. In the reefs within the Valley, fish biomass was better distributed among all functional groups and it differs from both others areas (Fig. 3; PERMANOVA df=2, Pseudo-F=4.287,  $R^2=0.19$ ,  $p<0.01$ ). West reefs presented low biomass on groups other than scrapers that comprised most of fish biomass in this area (76%); reefs within the valley presented higher biomass of piscivores and sessile invertebrate feeders; and east reefs presented high mobile invertebrate feeders, carnivores and planktivores biomass. Benthic composition exerts influences on reefs fishes' assemblage distribution, where most fishes functional group are related to for high coral cover areas, avoiding most other benthic groups, with exception of sessile invertebrate feeders, that was related to coralline algae (Fig. 4; RDA; ANOVA on RDA:  $p < 0.05$ , adjusted  $R^2 = 0.09$ ). Foliose algae was removed from the redundancy analysis to avoid collinearity, since the variance inflation factor (VIF) of this variable was higher than three (Zuur et al., 2010).





**Fig. 3:** Biomass of reef fish functional groups (kg/40m<sup>2</sup>) by area. Differences of groups among areas represented by letters above each group result from permutation-based analysis of variance. Black lines in the plots indicate the central tendency; points represent each sample unity and the width of colored polygons represent the density of data points (A). Principal coordinate analysis (PCOA) of fish biomass at the three reef sites. Vectors represent benthic categories and depth, and dots represent the scores for each transect (B). PCOA scores are presented in Table S5.



**Fig. 4:** Redundancy analysis on the composition of reef fish assemblages (biomass), benthic cover and depth.

#### 4. Discussion

The Açú reefs were dominated by algae and sponges, containing high biomass of scrapers (mainly Labridae: Scarini but also Acanthuridae) and mobile invertebrate feeders, but low biomass of commercially important carnivorous fishes. Corals were more abundant in the reefs within the valley, where the foliose algal cover was lower. When compared to reefs on the West and East, reefs within the valley experience different conditions, as they are slightly deeper than the surrounding reefs and subject to daily stream currents induced by tide movements (Fig. 1; Gomes et al., 2016). These conditions may limit algal growth in the reefs within the valley allowing higher coral cover, more diverse and complex communities. Alternatively, the connection of the

valley with an underwater canyon at the shelf break and the daily tidal currents in the N-S direction (see Gomes et al., 2015, 2016) may facilitate the emergence of nutrient-rich water from deeper areas through the valley in small upwelling events, which could be affecting the structure of benthic and fish communities. Whether this localized potential upwelling event occurs daily with the tidal currents or is a seasonal event is still unclear, but sediment analysis supports its existence (see Gomes et al., 2015, 2016). Differences in the physical conditions, even within the same geomorphological formation and in areas relatively close to each other, may cause variability in the structure of both benthic and reef fish assemblages at more local scales (Gove et al., 2015; Longo et al., 2015; Pinheiro et al., 2013, 2018).

Brazilian reefs are mostly dominated by algae and coral cover is generally low (~5%), rarely reaching more than 10% (Aued et al., 2018). In comparison to other Brazilian reefs, the reefs we studied within the valley area had a high coral cover (~17% on average), while the adjacent east and west reefs had higher macroalgal cover, following the pattern already observed for most Brazilian reefs. These differences likely result from the strong and frequent stream current that reaches the reefs within the valley, where current speed may be three-fold higher than in the adjacent areas (Gomes et al., 2016). Strong currents can reduce macroalgal abundance and biomass by directly removing it from the substrate and hindering fixation, particularly when the disturbance is intense and frequent (Steneck & Dethier, 1994; Page-Albins et al., 2012). These phenomena would allow high coral cover and contribute to the establishment of more diverse benthic communities and consequently fish assemblages.

The alternative hypothesis would be that corals are benefiting from currents that bring nutrient-rich waters from the deep submarine canyon connected to the Açu valley (Gomes et al., 2016), which may enhance planktonic primary production (Gove et al., 2016; Wedding et al., 2018). An interesting parallel to this hypothesis comes from oceanic islands and the 'Island mass effect' (IME), in which the naturally enhanced phytoplanktonic biomass around oceanic islands benefits reef building organisms such as hard corals and crustose coralline algae, as well as planktivores and piscivores fishes (Gove et al., 2016). Sponges can also be an important pathway to transform dissolved organic matter (DOM) into particulate matter that can be used by benthic organisms higher on food web (De Goeij et al., 2013). Therefore, by allowing the entry of allochthonous nutrients that are rapidly assimilated by phytoplankton and sponges, than made available for reef organisms, the valley could be facilitating the occurrence of a similar process.

Sediment granulometry can also be an important factor for determining abundance, distribution and habitat preference of benthic organisms (Jayaraj et al., 2008; Bell et al., 2015). High deposition of fine sediment may negatively affect the distribution of filter feeders that prefer coarser sediment, while fine sediment is preferred by deposit feeders (Jayaraj et al., 2008). Sponges, for instance, were more common in the West and reefs within the valley where sediments were coarser in comparison to the East reefs. Sediment may affect sponges in many ways, jeopardizing feeding, respiration, reproduction, survival and growth (Bannister et al., 2012; Powell et al., 2014; Bell et al., 2015). Carbonate sediments and organic matter, that were more common in the Western reefs, are likely carried from the Eastern and Valley reefs by the predominant E-W current outside the Valley (Almeida et al., 2015). If this is a valid

assumption, then the N-S tidal currents within the Valley (Gomes et al., 2016) can also play an important role in bringing organic matter and carbonate sediment through the valley, which are carried and accumulate in the Western reefs. This variability on conditions among reefs structure benthic communities and scale up to determine fish assemblages (Essmer et al., 2011; Gove et al., 2016; Pinheiro et al., 2018; Quimbayo et al., 2018)

Overall fish biomass in these areas were comparable to the average biomass along Brazilian coast, and the dominance of scrapers and mobile invertebrate feeders was already documented in areas close to this region (see RNN site in Morais et al., 2017). The relatively homogeneous distribution of fish functional groups among the reef areas indicate that the differential conditions provided by the valley are more likely to affect fish assemblages by modifying resource availability in the benthic community. Because alimentary resource availability play an important role determining the abundance patterns and distribution of mobile organisms such as reef fishes (Floeter et al., 2007; Pinheiro et al., 2013, 2018), changes in benthic communities among reef areas may be reflect on the structure of fish communities.

The studied reefs are located at an important area within the Brazilian biogeographic province (Floeter et al. 2007; Pinheiro et al. 2018), occurring close to equatorial line (5°S) right after the division of the North Brazil Current. Despite the relatively high coral cover observed in the reefs within the valley and the large extension of biogenic reefs in this region (see Gomes et al. 2016), it was incredibly notable that only few to none top-predators fishes were seen during the surveys (no sharks and few groupers) and any endangered fish species was recorded (IUCN 2018; Table S4). The Açú

Reefs could be a close-to-pristine reef and a refuge for endangered species because of its distance from coast (~30km) and rough oceanographic conditions, but the paucity of endangered species and top predators, reinforces the idea that they were depleted due to human activities. There were clear evidences of strong fishing pressure, such as ghost nets and fishing gears, in these reefs indicating that despite being newly discovered by scientists it was probably known long ago by local fisherman.

## **5. Conclusions**

This study demonstrate that physical and abiotic factors associated to underwater valleys structure reef communities even within small spatial scales. This can occur due to differences in local conditions such as topography and currents, through nutrient-rich currents reaching the reefs through the valley and aiding primary productivity, or by a combination among these factors.

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## Supplementary information

**Table S1.** Benthic groups recorded in the photoquadrats from Açú reefs, Brazil. Benthic groups and used names: Porifera: Sponges; Cnidaria: Corals; Algal turfs: Turf; Cyanobacteria; Crustose algae: CCA; Filamentous algae; Foliose macroalgae: Foliose algae.

Benthic groups	Areas		
	West	Valley	East
<b>Phylum Porifera</b>			
Encrusting form	X	X	X
Massive form	X	X	X
Tubular form	X	X	X
<b>Phylum Cnidaria</b>			
Class Hydrozoa			
<i>Millepora brasiliensis</i>			X
Unknown hydrozoan	X		
Order Zoanthidea			
<i>Zoanthus sociatus</i>	X		
Order Scleractinia			
<i>Agaricia agaricites</i>		X	
<i>Agaricia fragilis</i>	X	X	
<i>Madracis decactis</i>		X	X
<i>Montastraea cavernosa</i>	X	X	X
<i>Mussismilia hispida</i>			X
<i>Siderastrea sp.</i>	X	X	X
<b>Algal turfs</b>			
Non-calcified turf	X	X	X
<b>Cyanobacteria (microfilm)</b>	X	X	X
<b>Crustose algae</b>			
Crustose coralline algae	X	X	X
Rhodolith	X		
<b>Filamentous algae</b>			
Unknown Filamentous algae	X		X
<b>Foliose macroalgae</b>			
<i>Canistrocarpus sp.</i>	X	X	X
<i>Dictyota sp.</i>	X	X	X
Unknown Foliose algae	X		
<b>Sand and sediment</b>	X		X

**Table S2.** Sediment granulometry by site and area. Index ranging from finest to thicker grain size category

Area	Granunometric classification	Index	Organic Matter	Carbonate
East	Thin to very fine bioclastic sand	1	5.11 ± 0.13%	85.03 ± 2.81%
	Thin to very fine bioclastic sand	1		
	Thin to very fine bioclastic sand	1		
	Bioclastic sand with granules	2		
Valley	Thin to very fine bioclastic sand	1	5.6 ± 0.13%	90.72 ± 2.42%
	Bioclastic sand with granules	2		
	Average bioclastic sand	3		
	Thick to very thick bioclastic sand	4		
West	Bioclastic sand with granules	2	7.37 ± 0.44%	96.2 ± 0.94%
	Thick to very thick bioclastic sand	4		
	Bioclastic sand with granules	2		
	Bioclastic sand with nodules or shells	5		

**Table S3.** Scores of the principal coordinate analysis (PCOa) on benthic cover.

Benthic group	Dimension 1	Dimension 2
Corals	2.98	3.25
Coraline algae	0.14	-0.13
Cyanobacteria	0.43	-1.84
Foliose algae	-9.02	3.39
Sponges	0.89	-1.53
TURF	4.59	-3.15
Depth	0.74	2.27

**Table S4.** Mean abundance  $\pm$  standard error and mean biomass  $\pm$  standard error (kg/40m<sup>2</sup>) of reef fish species (Grouped by families) recorded among the three reefs areas of Açu reefs. Functional groups abbreviations: dpla = diurnal planktivores, minv = mobile invertebrate feeders, mcar = macrocarnivores, npla = nocturnal planktivores, omni = omnivores, pisc = piscivores, scrp = scrapers, sinv = sessile invertebrate feeders, spon = spongivores, ther = territorial herbivores. IUCN categories: DD = Data deficient, LC = Least Concern, NE = Not Evaluated, NT = Near Threatened. \* Species seen during sampling effort but not recorded in the transects.

Family / Species	Functional group	Mean abundance $\pm$ Standard error			Mean biomass $\pm$ Standard error			IUCN category
		West	Center	East	West	Center	East	
<b>Acanthuridae</b>								
<i>Acanthurus chirurgus</i>	turf	3.67 $\pm$ 0.65	3.5 $\pm$ 0.93	3.8 $\pm$ 1.07	0.49 $\pm$ 0.11	0.35 $\pm$ 0.11	0.28 $\pm$ 0.09	LC
<i>Acanthurus coeruleus</i>	sinv	0.11 $\pm$ 0.11	0 $\pm$ 0	0 $\pm$ 0	0.01 $\pm$ 0.01	0 $\pm$ 0	0 $\pm$ 0	LC
<b>Chaetodontidae</b>								
<i>Chaetodon ocellatus</i>	sinv	0.67 $\pm$ 0.33	1 $\pm$ 0.38	0.1 $\pm$ 0.1	0.04 $\pm$ 0.02	0.05 $\pm$ 0.02	0 $\pm$ 0	LC
<i>Chaetodon striatus</i>	sinv	0 $\pm$ 0	0.38 $\pm$ 0.38	0.2 $\pm$ 0.2	0 $\pm$ 0	0.01 $\pm$ 0.01	0.02 $\pm$ 0.02	LC
<b>Cirrhitidae</b>								
<i>Amblycirrhitus pinos</i>	minv	0.11 $\pm$ 0.11	0.13 $\pm$ 0.13	0.2 $\pm$ 0.13	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	LC
<b>Dasyatidae</b>								
<i>Dasyatis americana</i>	minv	0 $\pm$ 0	0 $\pm$ 0	0.1 $\pm$ 0.1	0 $\pm$ 0	0 $\pm$ 0	1.13 $\pm$ 1.13	NE
<b>Epinephelidae</b>								
<i>Cephalopholis fulva</i>	mcar	4 $\pm$ 0.73	7.38 $\pm$ 1.87	5.7 $\pm$ 1.34	0.31 $\pm$ 0.06	1 $\pm$ 0.24	0.28 $\pm$ 0.05	LC
<i>Epinephelus adscensionis</i>	mcar	0 $\pm$ 0	0 $\pm$ 0	0.1 $\pm$ 0.1	0 $\pm$ 0	0 $\pm$ 0	0.06 $\pm$ 0.06	LC
<i>Mycteroperca bonaci</i>	pisc	0 $\pm$ 0	0.5 $\pm$ 0.19	0 $\pm$ 0	0 $\pm$ 0	0.84 $\pm$ 0.44	0 $\pm$ 0	NT
<i>Paranthias furcifer</i>	dpla	0 $\pm$ 0	0 $\pm$ 0	0.1 $\pm$ 0.1	0 $\pm$ 0	0 $\pm$ 0	0.01 $\pm$ 0.01	LC
<b>Grammatidae</b>								
<i>Gramma brasiliensis</i> *	minv							NE
<b>Gobiidae</b>								
<i>Coryphopterus glaucofrenum</i> *	omni							LC
<i>Elacatinus figaro</i>	minv	0.11 $\pm$ 0.11	2 $\pm$ 0.78	0.1 $\pm$ 0.1	0 $\pm$ 0	0.01 $\pm$ 0	0 $\pm$ 0	NE

<b>Haemulidae</b>								
<i>Anisotremus surinamensis</i>	minv	0 ± 0	0.13 ± 0.13	0 ± 0	0 ± 0	0.08 ± 0.08	0 ± 0	DD
<i>Anisotremus virginicus</i>	minv	0.22 ± 0.15	0.25 ± 0.16	0.2 ± 0.13	0.04 ± 0.03	0.1 ± 0.09	0.02 ± 0.02	LC
			12.25 ±	15.3 ±				
<i>Haemulon aurolineatum</i>	minv	4 ± 2.52	7.97	4.18	0.17 ± 0.1	0.93 ± 0.61	0.56 ± 0.14	LC
<i>Haemulon plumierii</i>	minv	0.33 ± 0.17	0.38 ± 0.18	0.1 ± 0.1	0.02 ± 0.01	0.05 ± 0.03	0.01 ± 0.01	LC
<i>Haemulon squamipinna</i>	minv	0 ± 0	0 ± 0	2 ± 2	0 ± 0	0 ± 0	0.04 ± 0.04	NE
<b>Holocentridae</b>								
<i>Holocentrus adscensionis</i>	minv	0.56 ± 0.24	0.63 ± 0.26	0.4 ± 0.22	0.06 ± 0.03	0.05 ± 0.02	0.05 ± 0.03	LC
<i>Myripristis jacobus</i>	npla	0.56 ± 0.24	0.13 ± 0.13	1 ± 0.3	0.02 ± 0.01	0.01 ± 0.01	0.04 ± 0.01	LC
<b>Labridae</b>								
<i>Bodianus rufus</i>	minv	4.11 ± 0.93	7 ± 1.39	6.5 ± 0.87	0.61 ± 0.2	0.44 ± 0.09	0.45 ± 0.09	LC
<i>Clepticus brasiliensis</i>	dpla	0 ± 0	0.5 ± 0.5	4.4 ± 2.27	0 ± 0	0.11 ± 0.11	0.39 ± 0.23	LC
<i>Halichoeres brasiliensis</i>	minv	0.11 ± 0.11	0 ± 0	0.1 ± 0.1	0 ± 0	0 ± 0	0.01 ± 0.01	DD
<i>Halichoeres dimidiatus</i>	minv	0.33 ± 0.17	0.25 ± 0.16	0.1 ± 0.1	0.01 ± 0.01	0.02 ± 0.01	0 ± 0	LC
<i>Halichoeres maculipinna</i>	minv	0 ± 0	0 ± 0	0.1 ± 0.1	0 ± 0	0 ± 0	0 ± 0	LC
<i>Halichoeres poeyi</i>	minv	1.22 ± 0.36	0 ± 0	0.3 ± 0.15	0.03 ± 0.01	0 ± 0	0 ± 0	LC
<i>Scarus zelindae</i>	scrp	3.67 ± 1.12	4.5 ± 1.57	2.5 ± 0.85	0.79 ± 0.25	0.9 ± 0.29	0.55 ± 0.25	DD
<i>Sparisoma amplum</i>	scrp	3.22 ± 1.24	3.75 ± 1.19	2.4 ± 0.4	3.02 ± 1.82	1.91 ± 0.45	1.78 ± 0.34	LC
<i>Sparisoma axillare</i>	scrp	0.22 ± 0.15	0 ± 0	0.1 ± 0.1	0.02 ± 0.02	0 ± 0	0.02 ± 0.02	DD
<i>Sparisoma frondosum</i>	scrp	4.67 ± 0.91	2.63 ± 0.82	1.2 ± 0.53	1.65 ± 0.42	0.4 ± 0.16	0.35 ± 0.21	DD
		13.78 ±		15.2 ±				
<i>Thalassoma noronhanum</i>	dpla	4.67	24 ± 7.72	3.98	0.11 ± 0.04	0.16 ± 0.05	0.11 ± 0.03	LC
<b>Lutjanidae</b>								
<i>Lutjanus analis</i>	mcar	0 ± 0	0.25 ± 0.16	0.2 ± 0.13	0 ± 0	0.1 ± 0.07	0.51 ± 0.39	NT
<i>Lutjanus jocu</i>	mcar	0 ± 0	0.25 ± 0.25	0 ± 0	0 ± 0	0.03 ± 0.03	0 ± 0	DD
<i>Ocyurus chrysurus</i>	mcar	0 ± 0	1.5 ± 1.22	1.1 ± 0.57	0 ± 0	0.16 ± 0.1	0.13 ± 0.05	DD

<b>Malacanthidae</b>								
<i>Malacanthus plumieri</i> *	mcar							LC
<b>Monacanthidae</b>								
<i>Cantherhines pullus</i>	omni	0.11 ± 0.11	0.25 ± 0.25	0.1 ± 0.1	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	LC
<b>Mullidae</b>								
<i>Pseudupeneus maculatus</i>	sand	0.78 ± 0.52	0 ± 0	0.5 ± 0.5	0.03 ± 0.02	0 ± 0	0.03 ± 0.03	LC
<b>Muraenidae</b>								
<i>Gymnothorax miliaris</i>	mcar	0 ± 0	0 ± 0	0.1 ± 0.1	0 ± 0	0 ± 0	0 ± 0	LC
<b>Myliobatidae</b>								
<i>Aetobatus narinari</i> *	mcar							NT
<b>Opistognathidae</b>								
<i>Opistognathus sp.</i> *	dpla							NE
<b>Ostraciidae</b>								
<i>Acanthostracion polygonia</i>	sinv	0 ± 0	0 ± 0	0.1 ± 0.1	0 ± 0	0 ± 0	0.02 ± 0.02	LC
<b>Pomacanthidae</b>								
<i>Holacanthus ciliaris</i>	spon	0.22 ± 0.15	0.63 ± 0.42	0 ± 0	0.13 ± 0.11	0.22 ± 0.15	0 ± 0	LC
<i>Holacanthus tricolor</i>	spon	0.89 ± 0.35	1 ± 0.33	0.6 ± 0.16	0.12 ± 0.05	0.18 ± 0.06	0.1 ± 0.03	LC
<i>Pomacanthus paru</i>	spon	0 ± 0	0.25 ± 0.25	0.1 ± 0.1	0 ± 0	0.28 ± 0.28	0.01 ± 0.01	LC
<b>Pomacentridae</b>								
<i>Chromis multilineata</i>	dpla	0.56 ± 0.44	5 ± 2.28	8.6 ± 3.85	0 ± 0	0.06 ± 0.03	0.09 ± 0.03	LC
<i>Chromis scotti</i>	dpla	0 ± 0	10.5 ± 5.1	4.4 ± 1.26	0 ± 0	0.13 ± 0.06	0.04 ± 0.01	LC
<i>Microspathodon chrysurus</i>	ther	0.22 ± 0.15	0 ± 0	0 ± 0	0.02 ± 0.01	0 ± 0	0 ± 0	LC
<i>Stegastes fuscus</i>	ther	0.56 ± 0.44	0 ± 0	0.1 ± 0.1	0.01 ± 0.01	0 ± 0	0 ± 0	LC
<i>Stegastes pictus</i>	ther	18.89 ± 4.96	14 ± 3.57	18.6 ± 2.59	0.11 ± 0.04	0.1 ± 0.02	0.13 ± 0.02	NE
<b>Serranidae</b>								
<i>Serranus baldwini</i>	minv	0.11 ± 0.11	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	LC



**Sphyraenidae**

<i>Sphyraena barracuda</i> *	pisc								LC
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**Synodontidae**

<i>Alphestes afer</i> *	mcar								LC
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<i>Synodus synodus</i>	pisc	0 ± 0	0 ± 0	0.1 ± 0.1	0 ± 0	0 ± 0	0 ± 0		LC
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**Tetraodontidae**

<i>Canthigaster figueiredoi</i>	sinv	0.44 ± 0.29	0.75 ± 0.31	0.3 ± 0.21	0 ± 0	0.01 ± 0.01	0 ± 0		LC
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<i>Sphoeroides spengleri</i>	minv	0 ± 0	0 ± 0	0.1 ± 0.1	0 ± 0	0 ± 0	0 ± 0		LC
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**Table S5.** Scores of the principal coordinate analysis (PCOa) on the biomass of fish functional groups.

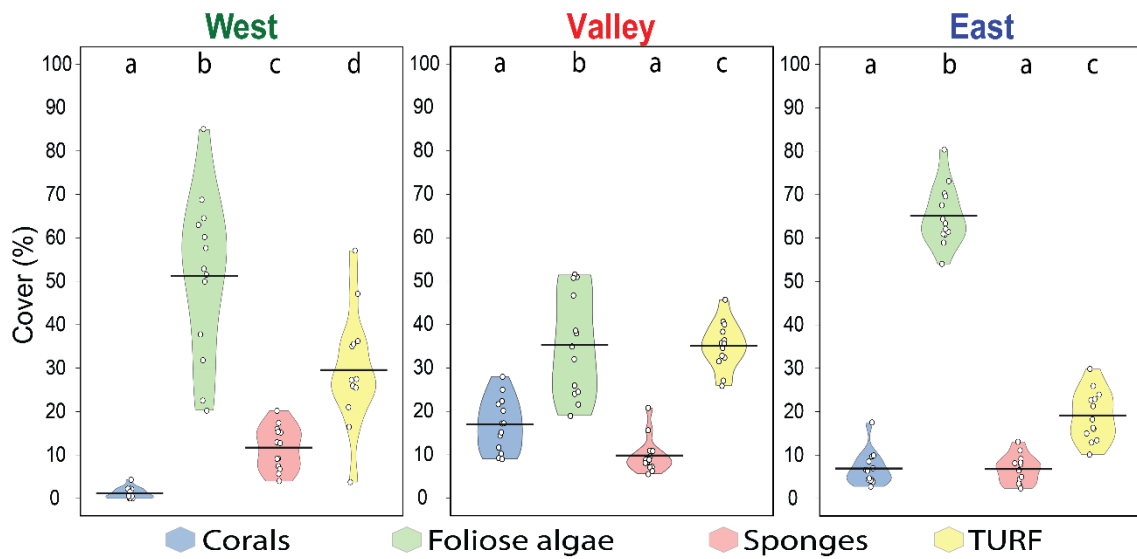
<b>Fishes group</b>	<b>Dimension 1</b>	<b>Dimension 2</b>
Carnivores	0.04	0.14
Mobile Invertebrate Feeders	-0.15	0.16
Omnivores	0	0
Piscivores	0.05	0.04
Scrapers	0.13	-0.86
Sessile Invertebrate Feeders	0.12	-0.02
Territorial.Herbivores	-0.01	-0.01
Planktivores	-0.05	0.1

**Table S6.** Redundancy analysis scores.

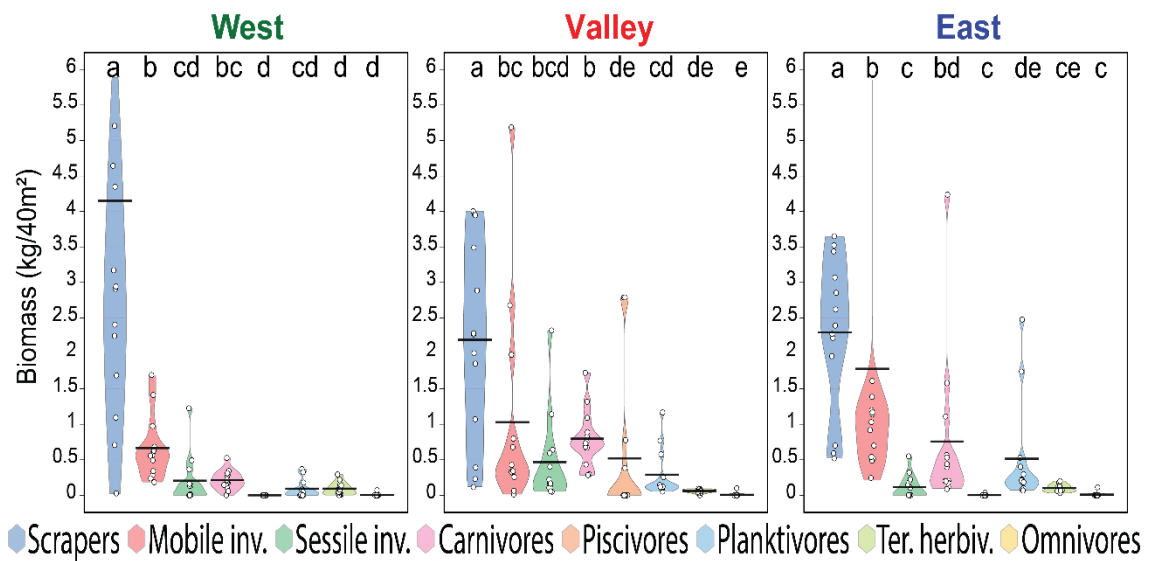
	RDA1	RDA2	RDA3	RDA4	RDA5	RDA6
Carnivores	0.96	-0.43	-0.30	0.33	-0.24	0.14
Mobile Invertebrate Feeders	0.18	0.71	-0.01	0.08	0.08	-0.02
Omnivores	0.13	0.07	-0.35	0.21	0.08	0.037
Piscivores	0.91	0.012	-0.85	-0.07	0.04	-0.17
Scrapers	-0.13	0.22	-0.54	-0.29	0.19	0.20
Sessile Invertebrate Feeders	0.33	-1.71	0.14	-0.08	0.16	-0.01
Territorial Herbivores	0.26	0.19	0.19	0.54	0.25	0.01
Planktivores	1.77	0.45	0.53	-0.25	0.04	0.03

**Table S7.** Redundancy analysis biplot scores for constraining variables.

	RDA1	RDA2	RDA3	RDA4	RDA5	RDA6
Corals	0.62	-0.62	-0.11	-0.25	-0.23	0.32
Coraline.algae	-0.05	-0.36	0.64	0.22	-0.34	-0.54
Cyanobacteria	-0.79	-0.29	0.08	0.48	-0.17	0.17
Sponges	-0.18	-0.51	-0.20	0.63	0.45	-0.26
Depth	0.81	-0.09	-0.09	-0.04	-0.37	0.43
TURF	-0.22	-0.46	-0.47	0.16	-0.54	-0.44



**Fig. S1.** Percent cover of benthic groups within areas. Differences among groups within each area represented by letters above each group result from permutation-based analysis of variance. Black lines in the plots indicate the central tendency; points represent each sample unity and the width of colored polygons represent the density of data points.



**Fig. S2.** Biomass of reef fish functional groups (kg/40m<sup>2</sup>) within each area. Differences among groups within each area represented by letters above each group result from permutation-based analysis of variance. Black lines in the plots indicate the central tendency; points represent each sample unity and the width of colored polygons represent the density of data points.

## **CONCLUSÃO GERAL**

Este trabalho elucidou um padrão que pode estruturar comunidades recifais em zonas de ressurgência ao longo da quebra da plataforma continental, por sustentar suas produtividades primárias de forma similar ao que ocorre em ilhas oceânicas, onde as circulações das correntes submarinas induzidas por características geomorfológicas da plataforma transportam nutrientes de águas mais profundas até recifes em águas mais rasas e oligotróficas. Estes resultados podem contribuir com informações iniciais para futuros estudos a respeito destes padrões observados, assim como para uma melhor compreensão dos ambientes recifais que ocorrem próximos as bordas da plataforma continental.

## ANEXO

**Capítulo aceito para publicação no livro:** Seafloor Geomorphology as Benthic Habitat: GeoHab Atlas of seafloor geomorphic features and benthic habitats -2nd Edition.

### **Nature and conditions of outer shelf habitats on the drowned Açú Reef, NE Brazil**

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**Running title:** Outer shelf habitats on the drowned Açú Reef.

#### **Abstract**

This study presents the environmental boundaries and quality of the outer shelf Açú Reefs in northeastern Brazil by integrating multiple approaches including satellite images, bathymetry and backscatter imagery, surficial sediments, benthic foraminifera and underwater surveys. The outer shelf is narrow, shallow and steep (~6km wide; 25-80m deep), with sand bodies, valleys (~500m wide and 15m of relief), reef knolls and ridges (~4 m height). Hard coral cover can reach ~17% (6 species; genus *Montastraea*, *Siderastrea*, *Mussismilia*, *Madracis*) and sponge cover was ~10% (16 species). Endemic Brazilian parrotfish were common (e.g., *Scarus zelindae*, *Sparisoma amplum*), but top predators were absent. Soft sediment habitats are well correlated with 65 foraminiferal species, which have a Caribbean-type reef community, including *Buccella peruviana* evidencing upwelling and nutrient enrichment. Although the benthic habitat is good, exhibiting suitable conditions for developing reef communities, reef fish assemblages indicate a declining trend based on a high confidence quantitative data and current threats.

**Keywords:** foraminifera, mixed sedimentation, hard coral, reef fish, valley, shelf edge, ecotone.