



PPG Ecologia & Conservação  
  
Universidade Estadual de Santa Cruz

**UNIVERSIDADE ESTADUAL DE SANTA CRUZ**  
**PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E**  
**CONSERVAÇÃO DA BIODIVERSIDADE**

**DOUGLAS MORAES**

**MPA EFFECTS ON HERBIVOROUS FISHES AT THE LARGEST REEF BANK**  
**IN THE SOUTHERN ATLANTIC**

**ILHÉUS – BAHIA – BRASIL**

**Fevereiro de 2023**

**DOUGLAS MORAES**

**MPA EFFECTS ON HERBIVOROUS FISHES AT THE LARGEST REEF BANK  
IN THE SOUTHERN ATLANTIC**

Dissertação apresentada à Universidade Estadual de Santa Cruz, como parte das exigências para obtenção do título de Mestre em Ecologia e Conservação da Biodiversidade

Área de concentração: Ecologia e Conservação da Biodiversidade

Orientador: Carlos Werner Hackradt.

Co-orientadores: Fabiana César Félix-Hackradt e João Lucas Leão Feitosa.

**ILHÉUS – BAHIA – BRASIL**

**Fevereiro de 2023**

M828

Moraes, Douglas.

MPA effects on herbivorous fishes at the largest reef bank in the Southern Atlantic / Douglas Moraes.  
– Ilhéus, BA: UESC, 2023.  
41f. : il.

Orientador: Carlos Werner Hackradt  
Dissertação (Mestrado) – Universidade Estadual de Santa Cruz. Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade – PPGECB

Inclui referências e apêndice.

1. Parques e reservas marinhos. 2. Peixes. 3. Herbívoro. 4. Assembleia. 5. Grupos funcionais. 6. Abrolhos, Arquipélago dos (BA). I. Título.

CDD 333.72

**DOUGLAS MORAES**

**MPA EFFECTS ON HERBIVOROUS FISHES AT THE LARGEST REEF BANK  
IN THE SOUTHERN ATLANTIC**

Dissertação apresentada à Universidade  
Estadual de Santa Cruz, como parte das  
exigências para obtenção do título de  
Mestre em Ecologia e Conservação da  
Biodiversidade

Ilhéus, 27 de janeiro de 2023.

---

Prof. Dr. Carlos W. Hackradt  
UFSB/ CFCAm  
(orientador)

---

Prof. Dr. Mirco Solé Kienle  
UESC/ DCB

---

Dra. Natália Carvalho Roos  
UFSB/ CFCAm

## **AGRADECIMENTOS**

À Universidade Estadual de Santa Cruz, por conceder a infraestrutura para o desenvolvimento da pesquisa.

Ao Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade pela oportunidade de cursar o mestrado.

Ao Laboratório de Ecologia e Conservação Marinha (LECOMAR) pelo apoio e infraestrutura concedida para a elaboração da pesquisa.

À Fundação de Amparo a Pesquisa do Estado da Bahia (FAPESB) pela concessão da bolsa de estudos.

Ao Prof. Carlos Werner Hackradt pela orientação, pela amizade e pelo apoio.

Aos professores João Lucas Leão Feitosa e Fabiana César Félix-Hackradt pela coorientação e pelo apoio.

Aos colegas de laboratório pelo apoio, ensinamentos, pelo convívio, pela amizade e colaboração.

À Mariana Riecken pelo imenso apoio, colaboração, dedicação, amor e carinho.

O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Código de Financiamento 001.

## RESUMO

Os recifes de corais são constantemente explorados para aquisição de recursos apesar da importância desses locais para a vida marinha. Por isso, acredita-se que a criação de áreas marinhas protegidas (AMPs) pode garantir a integridade dos processos ecológicos essenciais, por exemplo, herbivoria. Nesse contexto, o presente trabalho avaliou a influência da AMP localizada no maior banco de recifes do Atlântico Sul (onde está localizado o Parque Nacional Marinho dos Abrolhos), usando a estrutura da assembleia de peixes herbívoros como uma ferramenta de investigação. Foram realizados censos visuais subaquáticos e foto-quadrados para avaliar a assembleia dos peixes herbívoros, a estrutura do habitat e a comunidade bentônica. Foram encontradas 17 espécies pertencentes a 5 famílias. As espécies foram classificadas de acordo com a sua função como herbívoras, na qual o grupo funcional mais abundante encontrado foram os raspadores, seguidos pelos herbívoros territoriais, consumidores de macroalgas, consumidores de matrizes de algas epilíticas e os escavadores. As espécies também foram agrupadas em quatro classes de tamanho buscando entender o efeito das AMPs sobre o crescimento desses peixes. A análise de componentes principais (PCA) foi utilizada para identificar possíveis diferenças estruturais entre os diferentes locais, e o resultado da análise indicou que a inclinação dos recifes é a variável que mais se destaca. Os resultados da PERMANOVA apontaram diferenças significativas entre as áreas estudadas, dentre as quais Abrolhos possui o maior número de indivíduos e a maior biomassa, indicando um efeito positivo da AMP. Por fim, a análise de correspondência canônica (CCA) demonstrou quais organismos bentônicos e/ou dados ambientais abióticos mais influenciaram a presença das espécies de peixes herbívoros. Os resultados apresentados mostram a contribuição da AMP sobre a assembleia de peixes herbívoros; portanto, corroborando com a importância da criação de novas AMPs, especialmente nas áreas onde os recifes biológicos estão presentes.

Palavras-chave: áreas marinhas protegidas; peixes herbívoros; estrutura da assembleia; grupo funcional

## **ABSTRACT**

Coral reefs are constantly exploited for resource acquisition despite their importance to marine life. For this reason, it is thought that the creation of marine protected areas (MPAs) can guarantee the integrity of essential ecological processes (e.g., herbivory). In this context, the presented research evaluates the influence of the MPA located in the largest reef bank of South-western Atlantic (which contains Abrolhos Marine National Park), using the assemblage structure of herbivorous fishes as a tool of investigation. We used underwater visual census (UVC) and underwater photo-quadrats to assess the herbivorous fishes' assemblage, the habitat structure and benthic community. We found 17 fish species belonging to 5 families. We classified the species according to their role as herbivore, in which the most abundant functional group found was the scrapers, followed by territorial herbivores, macroalgae consumers, epilithic algal matrix consumers and excavators. The species were clustered into four size classes to understand the effect of the MPA over fish growth. A principal component analysis was used to identify the structural differences in habitat considering zones, and the analysis indicates 'inclination' as the most prominent variable. The PERMANOVA results pointed significant differences among the studied areas, in which Abrolhos hold a higher number of individuals and biomass, indicating a positive effect of the MPAs. Finally, a canonical correspondence analysis demonstrated which benthic organism and/or environmental abiotic data most influence the presence of the herbivorous fish species. The results presented here show the benefits of the MPA over the herbivorous fishes' assemblage, thus corroborating with the importance of the creation of new MPAs, especially in areas where biological reefs are in place.

**Key-words:** marine protected areas; herbivorous fishes; assemblage structure; functional group.

# Sumário

INTRODUÇÃO GERAL .....	8
1. INTRODUCTION.....	13
2. METHODS .....	15
2.1. Study Area.....	15
2.2. Sampling Design .....	16
2.3. Data Analysis .....	18
3. RESULTS .....	19
3.1. Herbivorous fishes assemblage structure .....	19
3.2. MPA effect on herbivorous fish assemblage.....	23
3.3. Habitat structure and benthic community .....	30
4. DISCUSSION .....	32
5. CONCLUSION .....	34
6. REFERENCES.....	35
APPENDIX .....	39



## INTRODUÇÃO GERAL

Diversos estudos mostram que a proliferação excessiva das algas pode reduzir a colonização, a sobrevivência de recrutas e o crescimento de corais por meio da competição por espaço (Bruno et al., 2019). Essa mudança de dominância de corais para dominância de algas é chamada de “mudança de fase” ou phase-shift (Hughes, 1994). Apesar de serem processos naturais em alguns recifes, estudos mostram que, em sua maioria, esse aumento exacerbado de macroalgas é resultado de ações antrópicas danosas, como a sobrepesca, a poluição e as mudanças climáticas (Hughes, 1994; Bellwood et al. 2004; Jackson et al. 2014).

A sobrepesca de peixes herbívoros pode alterar a estruturação dos recifes, favorecendo a cobertura de macroalgas e prejudicando o recrutamento de organismos bioconstrutores, por exemplo os corais escleractíneos (Bruno et al., 2019; Estes et al., 2011; Jackson et al., 2014).

Além disso, a mortalidade de corais, causada pelo aquecimento excessivo das águas do oceano como efeito da mudança climática, e perturbações localizadas ou eventos súbitos de perturbação (como ciclones ou surtos de doença), agridem os recifes disponibilizando espaços para a proliferação de organismos com crescimento acelerado como as algas (Bruno et al., 2019; Puk et al., 2015).

Neste contexto, o bom desempenho da atividade dos peixes herbívoros seria capaz de reverter a dominância de macroalgas, ampliando a capacidade dos recifes de resistir a essas perturbações e às ações humanas destrutivas. Isso porque, herbívoros são capazes de manter as algas sob controle ou mesmo impedir a alternância de fases indesejadas por meio de sua atividade de forrageio sobre os recifes de corais, servindo as algas de alimento para essas espécies (Hughes et al., 2007a; Dell et al., 2020).

Os recifes dominados por macroalgas também parecem ter uma complexidade estrutural diferente dos recifes dominados por corais, já que, com a diminuição de cobertura de corais, a complexidade estrutural decresce (Graham & Nash, 2013). Esta perda de complexidade, por sua vez, evoca a diminuição da biomassa e diversidade dos peixes dos recifes de coral, corroborando para um círculo vicioso (Puk et al., 2015).

Portanto, à medida que aumenta a degradação dos recifes de coral, a relevância da herbivoria se torna ainda maior, o que amplia a importância da existência de áreas de proteção que reduzam a pesca desses animais de forma a garantir atividades de forrageio (Puk et al., 2015). A proteção, nesse sentido, é essencial para a resiliência dos recifes de corais e para a manutenção dos processos ecológicos e funcionalidade das teias tróficas (Sale et al., 2005; Hughes et al., 2007b).

As áreas marinhas protegidas (AMPs) são zonas geograficamente delimitadas, criadas por meio de instrumentos legais, que se destinam à gestão e conservação da biodiversidade e dos ecossistemas marinhos (Gaines et al., 2010). Normalmente, essas áreas são livres de pesca, e por isso chamadas de áreas no-take.

Diversos estudos mostram que a exclusão de pesca nessas áreas é responsável pelo aumento da biodiversidade local, e, por conseguinte, corrobora para a eficiência dos processos ecológicos nos recifes (Topor et al., 2019; Rasher et al., 2013). Por exemplo, em ambientes recifais no oceano Pacífico foi visto que a cobertura de corais dentro das AMPs varia de 38 a 56%, enquanto nas áreas não protegidas ficam apenas entre 4 a 16%. Já a cobertura de algas apresenta resultados opostos, cerca 1 a 2% dentro das áreas protegidas e 49 a 91% fora delas. Ademais, biomassa de herbívoros encontrada também difere entre regiões protegidas e não protegida, nas AMPs elas são 660 a 1615% maior do que em zonas de pesca (Hughes et al., 2007b)

Esses resultados demonstram que a pesca contínua em áreas não protegidas reduz a quantidade de herbívoros abaixo do nível que seria necessário para manter uma cobertura saudável do coral (que é consequência indireta de seu processo de alimentação), o que causa alterações em toda comunidade daquele ecossistema (Puk et al., 2015). Por isso, alguns autores sugerem inclusive que os efeitos das AMPs se estendem para além dos recifes protegidos, beneficiando todo o sistema em que área está inserida (Sale et al., 2005; Hughes et al., 2007b).

A importância da implementação de parques marinhos protegidos, portanto, se dá porque estes ambientes são capazes de aumentar a atividade de forrageio, promovendo a remoção da macroalga em excesso, o que também corrobora para prevenir regimes de alternância da dominação de algas. Ademais, o gerenciamento da riqueza de herbívoros por meio da criação de AMPs também tem o potencial de auxiliar a proteção de outras espécies relevantes nesses locais, indiretamente promovendo a biodiversidade da ictiofauna na região (Topor et al., 2019; Bonaldo et al., 2017).

A atividade de forrageio de peixes nos recifes de corais é um processo multifacetado, geralmente subdividido em diversas categorias (Bruno et al., 2009; Topor et al., 2019). Os peixes herbívoros possuem diferentes papéis nesse processo e são classificados em grupos funcionais de acordo com a atividade de forrageio que cada um realiza, isto é, seu comportamento alimentar (Puk et al., 2015).

Como as espécies de herbívoros têm diferentes morfologias do trato digestório, diferentes alvos nutricionais e tolerâncias variáveis para os diferentes tipos de defesas químicas e estruturais das macroalgas, a diversidade de grupos funcionais desses peixes favorece o consumo das diversas variedades de algas, tornando a atividade de forrageio mais efetiva em determinada localidade (Rasher et al., 2013; Clements et al., 2017; Topor et al., 2019). Assim, os efeitos da herbivoria nos recifes de corais não dependem somente da biomassa elevada, mas, sim, da alta diversidade dentro das áreas protegidas.

A composição da comunidade de herbívoros também afeta a atividade de forrageio por meio da densidade desses animais. Peixes maiores retiram um volume maior de alga a cada mordida do que as espécies menores, de forma que a amplitude de consumo está diretamente associada ao tamanho das “bocas que se alimentam” naquela localidade. Essas espécies de grande porte são de alto interesse comercial, tornando-as vulneráveis à exploração, sendo as primeiras que desaparecem em consequência da pesca (Bejarano et al., 2013; Taylor et al., 2014; Topor et al., 2019).

Como a presença excessiva de macroalgas nos corais afeta diretamente a saúde dos recifes, a remoção delas é considerada essencial para a saúde e conservação de ecossistemas marinhos. Embora outras espécies contribuam para a remoção dessas algas, os peixes herbívoros têm papel dominante nesse contexto; ou seja, os processos ecológicos nos recifes de corais dependem diretamente da riqueza desses herbívoros no local. O desaparecimento de espécies-chave de peixes é inclusive uma das métricas da perda de resiliência dos recifes de coral (Bruno et al., 2009; Topor et al., 2019).

Assim, conclui-se que a implementação e a gestão efetiva das áreas de proteção são capazes de trazer benefícios diretos para os ambientes recifais, por meio do aumento da atividade de forrageio que previnem o domínio de algas, e, indiretamente auxiliam a manutenção da saúde do ecossistema marinho (Hughes et al., 2007b).

## REFERÊNCIAS

- Bellwood, D. R.; Hughes, T. P.; Folke, C.; Nyström, M. **Confronting Coral Reef Crisis**. *Nature*. 2004. 429: 827-833.
- Bejarano, S.; Golbuu, Y.; Sapolu, T.; Mumby, P. J. **Ecological Risk and the Exploitation of Herbivorous Reef Fish Across Micronesia**. *Marine Ecology Progress Series*. 2013. 482: 197-215.
- Bonaldo, R. M.; Pires, M. M.; Guimarães Junior, P. R.; Hoey, A. S.; Hay, M. E. **Small Marine Protected Areas in Fiji Provide Refuge for Reef Fish Assemblages, Feeding Groups, and Corals**. *Plos One*. 2017. 12(1): 1-26.
- Bruno, J. F.; Sweatman, H.; Precht, W. F.; Selig, E. R.; Schutte, V. G. W. **Assessing Evidence of Phase Shifts from Coral to Macroalgal Dominance on Coral Reefs**. *Ecology*. 2009.. 90(6): 1478-1484.
- Bruno, J. F.; Côté, I. M.; Toth, L. T. **Climate Change, Coral Loss, and the Curious Case of the Parrotfish Paradigm: Why Don't Marine Protected Areas Improve Reef Resilience?** *Annual Review of Marine Science*. 2019. 11: 307-334.
- Clements, K. D., German, D. P., Piché, J., Tribollet, A., & Choat, J. H. **Integrating ecological roles and trophic diversification on coral reefs: multiple lines of evidence identify parrotfishes as microphages**. *Biological Journal of the Linnean Society*. 2017. 120(4), 729-751.
- Dell, C. L., Longo, G. O., Burkepile, D. E., & Manfrino, C. **Few herbivore species consume dominant macroalgae on a Caribbean coral reef**. *Frontiers in Marine Science*. 2020. 7, 676.
- Floeter, S. R.; Krohling, W.; Gasparini, J. L.; Ferreira, C. E. L.; Zalmon I. R. **Reef fish community structure on coastal islands of the southeastern Brazil: the influence of exposure and benthic cover**. *Environmental Biology of Fishes*. 2007. 78: 147-160.
- Friedlander, A. M; DeMartini, E. E. **Contrasts in Density, Size, and Biomass of Reef Fishes Between the Northwestern and the Main Hawaiian Islands: The Effects of Fishing Down Apex Predators**. *Marine Ecology Progress*. 2002. 230: 253-264.
- Gaines, S. D., White, C., Carr, M. H., & Palumbi, S. R. **Designing marine reserve networks for both conservation and fisheries management**. *Proceedings of the National Academy of Sciences*. 2010. 107(43), 18286-18293.
- Hughes, T. P. **Catastrophes, Phase-shifts, and Large-Scale Degradation of a Caribbean Coral Reef**. *Science*. 1994. 265: 1547-1551.
- Hughes, T. P. et al. **Phase Shifts, Herbivory, and the Resilience of Coral Reefs to Climate Change**. *Current Biology*. 2007a. 17: 360-365.

- Hughes, T. P. et al. **No-take areas, herbivory and coral reef resilience.** Trends in ecology & evolution. 2007b. 22(1), 1-3.
- Jackson, J., Donovan, M., Cramer, K., & Lam, V. **Status and trends of Caribbean coral reefs: 1970-2012.** Gland, Switzerland: Global Coral Reef Monitoring Network; International Union for the Conservation of Nature (IUCN). 2014.
- Kuffner, I. B.; Paul, V. J. **Effects of the Benthic Cyanobacterium *Lyngbya majuscula* on larval recruitment of the Reef Corals *Acropora surculosa* and *Pocillopora damicornis*.** Coral Reefs. 2004. 23: 455-458.
- Lewis, S. M.; Wainwright, P. C. **Herbivore Abundance and Grazing Intensity on a Caribbean Coral Reef.** Journal of Experimental Marine Biology and Ecology. 1985. 87: 215-228.
- MacNeil, M. A.; Graham, N. A. J.; Cinner, J. E.; Wilson, S. K.; Williams, I. D.; Maina, J.; Newman, S.; Friedlander, A. M.; Jupiter, S.; Polunin, N. V. C.; McClanahan, T. R. **Recovery Potential of the World's Coral Reef Fishes.** Nature. 2015. 520: 341-344.
- Meekan, M. G.; Choat, J. H. **Latitudinal variation in abundance of herbivorous fishes: a comparison of temperate and tropical reefs.** Marine Biology. 1997. 128: 373-383.
- Mumby, P. J.; Steneck, R. S. **Coral Reef Management and Conservation in Light of Rapidly Evolving Ecological Paradigms.** Trends in Ecology and Evolution. 2008. 23(10): 555-563.
- Nash, K. L.; Abesamis, R. A.; Graham, N. A. J.; McClure, E. C.; Moland, E. **Drivers of Herbivory on Coral Reefs: Species, Habitat and Management Effects.** Marine Ecology Progress Series. 2016. 554: 129-140.
- Rasher, D. B.; Hoey, A. S.; Hay, M. E. **Consumer Diversity Interacts with Prey Defenses to Drive Ecosystem Function.** Ecology. 2013. 94(6): 1347-1358.
- Sale, P. F.; Cowen, R. K.; Danilowicz, B. S.; Jones, G. P.; Kritzer, J. P.; Lindeman, K. C.; Planes, S.; Polunin, N. V. C.; Russ, G. R.; Sadovy, Y. J.; Steneck, R. S. **Critical Science Gaps Impede Use of No-take Fishery Reserves.** Trends in Ecology and Evolution. 2005. 20(2): 74-80.
- Topor, Z. M.; Rasher, D. B.; Duffy, J. E.; Brandl, S. J. **Marine Protected Areas Enhance Coral Reef Functioning by Promoting Fish Biodiversity.** Conservation Letters. 2019. e12638. 1-9.

# **MPA EFFECTS ON HERBIVOROUS FISHES AT THE LARGEST REEF BANK IN THE SOUTHERN ATLANTIC**

**Moraes, Douglas<sup>1,2</sup>, Félix-Hackradt, Fabiana C.<sup>2</sup>, Feitosa, João L. L.<sup>3</sup>, Hackradt, Carlos W.**

1. Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz;
2. Marine Ecology and Conservation Lab. Centre for Environmental Science. Universidade Federal do Sul da Bahia;
3. Laboratório de Pesquisa Ictiológica e Ecologia Recifal. Universidade Federal de Pernambuco.

## **1. INTRODUCTION**

Coral reefs are among the most biodiverse and structurally complex ecosystems on Earth. They are known for harboring 25% of all marine life (Nash et al., 2016) and for providing goods and services to coastal countries, including seafood production, shoreline protection and tourism-recreation (Moberg & Folke, 1999). Despite their significance, coral reefs have been threatened by human activities such as overexploitation, inappropriate waste discharge, and climate change (Jackson et al., 2001; Bellwood et al., 2004; Hughes et al., 2017).

Excessive and continuous fishing has decreased the trophic level of targeted fishes from large piscivorous towards smaller planktivorous and herbivorous fishes, consequently reducing the abundance of herbivores below the ideal level to control algal growing and thus leading to an unbalanced competition between algae (fast-growing organisms) and corals (slow-growing organisms) (Pauly et al., 1998; Jackson et al., 2001; Freire & Pauly, 2010; Bejarano et al., 2013). In situations in which herbivory is reduced, exacerbated algal growth covers the substrate, hindering new coral recruits and decreasing the potential of coral to thrive into the adult life stage, interfering directly on reef structural complexity and, consequently, on the fauna associated to these

environments (Hughes et al., 2007a; Topor et al., 2019). Structural complexity, found in coral reefs, has the potential to raise fish density and biomass, whilst it is also linked to coral cover improvement and algal blooming reduction (Hackradt et al., 2011; Graham & Nash, 2014). In addition, the herbivory processes may prevent the transition between coral dominance to algae dominance, so called phase-shift (Done, 1992; Hughes et al., 2007a; Bruno et al., 2019).

Herbivorous foraging activities in coral reefs is a multifaceted process in which fishes are classified into different functional groups (FGs) according to their foraging behavior (Bonaldo et al., 2014; Puk et al., 2015; Topor et al., 2019). Since herbivorous species have different morphology of the pharyngeal jaw apparatus, different nutritional targets and variable tolerance to different macroalgal chemical and structural defenses, FG diversity in herbivorous fishes gives an advantage in the use of resources; therefore, herbivory positive effects in coral reefs depends not only on high abundance, but also on a high diversity of herbivorous fishes (Burkepile & Hay, 2008; Bruno et al., 2009; Rasher et al., 2013; Duffy et al., 2016; Topor et al., 2019). The presence of distinct functional groups on coral reefs may reflect over the functioning of the entire ecosystem. Understanding the population structure of herbivorous fishes can predict future trends about the conservation status in these changing habitats (Schowalter, 2022).

The creation of Marine Protected Areas (MPAs) represents a valuable strategy to support fisheries stocks and habitat conservation so marine species can flourish and perform the most important ecosystem processes that maintains reef systems, which is the case of the herbivorous species (Bonaldo et al., 2017; Topor et al., 2019).

It is estimated that coral cover found inside MPAs reaches more than 35% when compared to those in unprotected areas, while algal cover follows the opposite trend (Hughes et al., 2007b). Moreover, herbivores biomass is also distinct between protected and non-protected areas, studies rated this variable between 660% and 1615% higher in MPAs than in regular fishing areas (Hughes et al., 2007b). Thus, the implementation and effective management of MPAs seem essential to generate benefits to coral reef environments, raising herbivores foraging activity which supports improvements in the organisms present in these ecosystems (Hughes et al., 2007b).

Regarding the given information, the hypothesis formulated was that the assemblage structure of herbivorous fishes differs between MPAs and unprotected areas.

This is the expected outcome due to the overfishing of large herbivores in reef areas with no protection regulation (Floeter et al., 2006). Consequently, abundance and biomass would be lower out of MPAs delimitation (Hawkins & Roberts, 2004). Thus, to test the influence of MPAs over the abundance, biomass and assemblage structure of herbivorous fishes in the Abrolhos Bank, a study was conducted in three distinct coral reef areas during a period of three years (Abrolhos parcel as the MPA, Paredes parcel and Cassurubá reef as the unprotected sites). In the study, six sectors were sampled on each location employing the UVC technique to identify fish species and estimate their abundance, size and biomass. To compare the differences among variables, we analyzed fish population data using Permutational Analysis of Variance (PERMANOVA) and data from environment (e.g., structural complexity and heterogeneity) and benthic species were analyzed using Principal Component Analysis.

## **2. METHODS**

### **2.1. Study Area**

The study was conducted in three distinct coral reef areas using unbalanced design, Abrolhos parcel as the MPA, Paredes parcel and Cassurubá reefs as the unprotected sites.

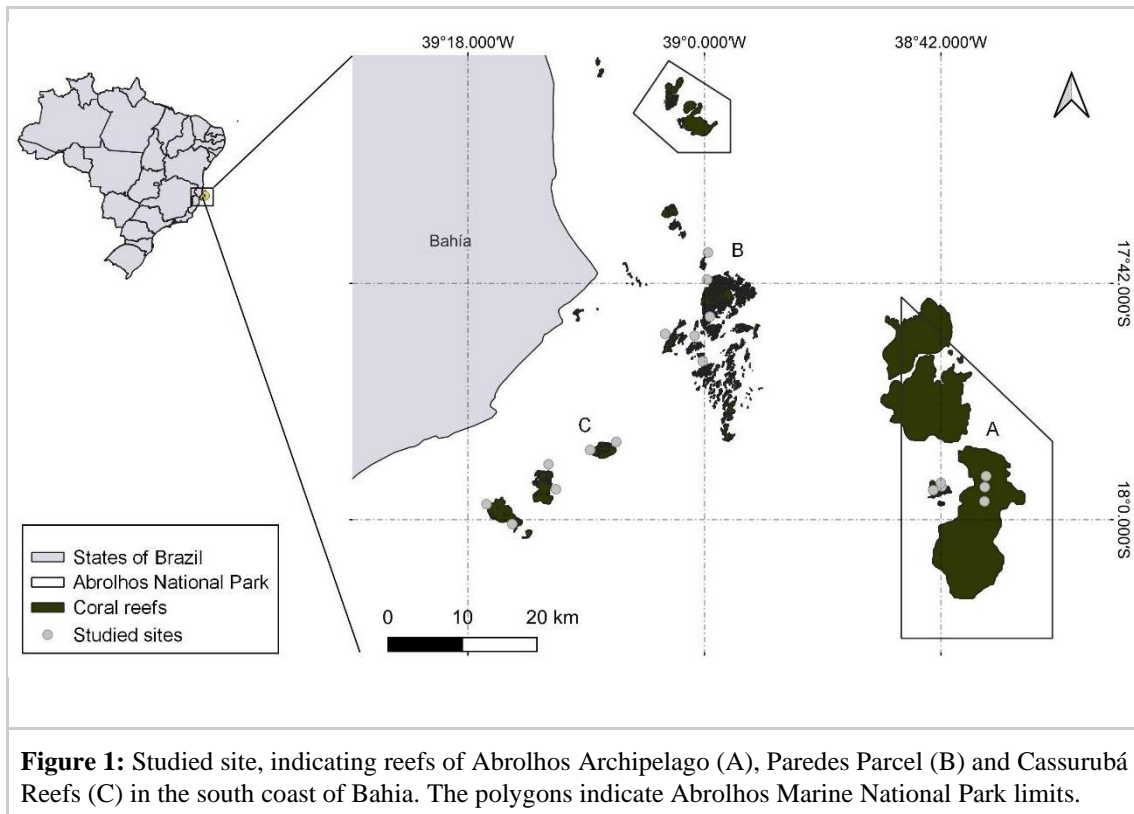
Abrolhos Bank is an enlargement of the eastern Brazilian continental shelf, which holds the largest coral reef formation in the country (Leão et al., 2001). The reef presents a high coral cover and high endemism index, comprising approximately 25% of Brazilian marine fish species and about 33% of scleractinian corals (Moura, 2002; Leão et al., 2003; Francini-Filho et al., 2013). Furthermore, it encompasses the highest biological diversity in the South Atlantic (Moura, 2002; Leão et al., 2003; Francini-Filho et al., 2013).

The Abrolhos Bank encompasses many shallow reef formations. The Cassuruba reef complex is positioned in a coastal arch formation, surrounding 6 nautical miles (nm) from the coast where lies Sebastião Gomes, Coroa Vermelha and Viçosa reefs (**Figure 1**). Positioned further to north, at 11 nm from the coast, is the Paredes reef. Lastly, 35 nm far from the coast, is located the Abrolhos National Marine Park.

The park is composed of two discontinuous areas. The smaller is called Timbebas reef and was not assessed in this study. The larger one contains two coral reef formations, mostly fringing reefs, surrounding the islands that compose the Abrolhos Archipelago



(17°96'S, 38°70'W) comprehending the following islands: Santa Barbara, Redonda, Siriba, Guarita and Sueste. In this region it is located a typical coral reef pinnacle structure formation, called Abrolhos archipelago, which was chosen as the MPA area for the current study.



## 2.2. Sampling Design

To test the influence of MPAs over the abundance and biomass of herbivorous fish populations, we evaluated the herbivorous fish assemblage spatial distribution in different locations by applying an unbalanced sampling design based on Beyond-BACI (Underwood, 1994; Glasby, 1996).

The sampling design for this study is as follows: we defined protection (P) as the fixed factor with 2 levels to compare protected and unprotected reefs. Three zones (Z) were chosen as the random factor, which consequently has three levels (Cassuruba, Paredes and Abrolhos), nested in protection. As mentioned in the previous section, Paredes and Cassuruba reefs were assessed as unprotected reef environments and Abrolhos Parcel as

the protected one. In each location, six sectors (S) were sampled with six random point count Underwater Visual Census (UVC) each, which were nested in location (L).

The UVC data was collected according to Minte-Vera et al. (2008) stationary method, where fish identification and counting occurred in a cylinder within a 4- and 2-meters radius, during a period of five minutes each. Fishes smaller than 20 cm were counted within the smaller radius, while fish 20 cm or more in total length were counted within the largest radius. Abundance and biomass data were standardized to square meter (m<sup>2</sup>). In total 425 UVCs were performed in this study.

All herbivorous fishes were identified by the lowest possible taxonomic level, and their size was estimated in 2 cm size classes. Further, we divided each species into size classes considering their minimum and maximum size found in literature, with sizes proportionally distributed among four classes, in a way all species were analyzed with the same size classes amount. Fish abundance was recorded in classes following a geometric scale (cf. Harmelin 1987, García-Charton & Pérez-Ruzafa 2001, Hackradt et al. 2011).

Further, we clustered fishes into functional groups (FGs) according to their foraging routine as specified in Halpern & Floeter (2008) and the following FGs were found: scrapers (SCRP), macroalgae consumer (MALG), excavator (EXCV), territorial herbivores (THER), epilithic algal matrix consumer (TURF). This approach is important to evaluate possible differences in the functional structure of the herbivorous fishes' assemblage in protected and unprotected areas. Finally, biomass was calculated based on length-weight parameters ( $W = a \times L^b$ ) for each species using from the literature (Hackradt et al. 2011; Froese & Pauly, 2022).

Additionally to fish surveys, we collected environmental data that might have repercussions on the fish assemblage features, which are (i) depth, (ii) heterogeneity estimates of habitat (percentage of consolidated reef coverage, sand, gravel and seagrass/macroalgae), (iii) rugosity (estimated on a scale of 1 to 5, being scale 1 the flattest surfaces and 5 where reef ripples are greater than the observer), and finally (iv) reef inclination (categorized between 0°-30°, 30°-60°, 60°-90°, Félix-Hackradt et al. 2014; Garcia-Charton 2004). For the estimation of these environmental variables, the 8m-circumference of the stationary visual census was evaluated by the same researcher that assessed the fishes. Complementarily, we characterized the benthic cover using the photo-quadrats method (Francini-Filho et al., 2008), being the 8m-circumference divided into

four equal parts, and two opposing sides were assessed by photo-quadrats (e.g., southwestern and northeastern sides) in each of the stationary point surveys. Each photo-quadrats apparatus has an area of approximately 0.5 m<sup>2</sup> (70 × 80 cm), and they are composed of 15 high-quality photos measuring 22 × 15 cm each (cf. Francini-Filho et al. 2013). We identified benthic organisms in higher hierarchical groups (e.g., epilithic algal matrix, hard coral, zoanths, sponges, etc) using 450 random points per photo-quadrats (i.e., 30 points per photograph) with Coral Point Count with Excel extensions software (CPCe) (Kohler & Gill, 2006).

### **2.3. Data Analysis**

We tested the variables looking for significant differences using Permutational Analysis of Variance (PERMANOVA) in PRIMER 6 software with PERMANOVA+ Extension, comparing species abundance, functional groups abundance, size classes abundance and biomass of herbivorous fishes among the distinct zones. Data was log-transformed prior to the analysis. This multivariate model was chosen as a path to assess the influence of protection on herbivorous fishes' species, as well as their assemblage structure.

In addition, habitat structure collected from coral reefs abiotic data and from the results obtained in CPCe from photo-quadrat images were analyzed using the software PRIMER to run a Principal Component Analysis (PCA), searching for structural differences in habitat in the distinct locations and determining the main strengths which play an important role in habitat structuration. We applied the Kaiser criterion (Yeomans & Golder, 1982), which suggests using the principal components (PCs) with eigenvalues >1. Prior to PCA, we transformed data values to enable the analysis of many distinct values characteristics. For habitat complexity, data (represented by scales) was log-transformed, the same was done with benthic cover data (abundance category). Since heterogeneity has values represented by a percentage, data was fourth square root transformed (Clarke & Ainsworth, 1993).

Finally, a Canonical Correspondence Analysis (CCA) was run to estimate which environmental drivers and benthic organisms have the most influence on the assemblage of herbivorous fishes. This analysis was made on PAST statistical software.

### 3. RESULTS

#### 3.1. Herbivorous fishes assemblage structure

Visual censuses counted more than 7127 individuals of the herbivorous fish in reef fish assemblage, belonging to 17 species from 5 families along a period of three-year observation. Fishes were classified into functional groups (FGs) to assess the group's abundance and their relative frequency (%RF). **Table 1** presents all sampled herbivorous fishes' species clustered by FG.

**Table 1:** Fishes classified into functional groups (FGs)

Scrapers	Territorial herbivores	Macroalgae browsers	Epilithal algal matrix consumer	Excavator
<i>Acanthurus bahianus</i>	<i>Ophioblennius trinitatis</i>	<i>Kyphosus sp.</i>	<i>Acanthurus coeruleus</i>	<i>Scarus trispinosus</i>
<i>Acanthurus chirurgus</i>	<i>Microspathodon chrysurus</i>	<i>Sparisoma radians</i>		
<i>Scartela cristata</i>	<i>Stegastes fuscus</i>			
<i>Cryptotomus roseus</i>	<i>Stegastes pictus</i>			
<i>Scarus zelindae</i>	<i>Stegastes variabilis</i>			
<i>Sparisoma axillare</i>				
<i>Sparisoma amplum</i>				
<i>Sparisoma frondosum</i>				

The five most abundant species in the three studied zones correspond to almost 80% of all observed herbivorous fishes in this research were *Acanthurus bahianus* (RF= 19.43%), *Stegastes fuscus* (RF= 18.19%), *Scarus trispinosus* (RF= 16.23%), *Sparisoma axillare* (RF= 14.85%) and *Acanthurus chirurgus* (RF= 9.82%) (**Table 2**).

Scrapers (SCRP) were the most abundant FG (N = 3541), followed by territorial herbivores (THER; N = 1697); excavators (EXCV; N = 1181); epilithal algal matrix consumers (TURF; N = 677); and, finally, the macroalgae browsers (MALG; N = 65; **Table 2**).

In terms of relative frequency, the most representative FG, SCRP totalizes RF=47.05% of censused species, followed by 29.40% of THER. MALG presents a RF of 11.75%,

while TURF and EXCV represents RF=5.90% each. Considering the mean size among FGs, species belonging to the SCRП group keep the smallest ( $5 \pm 1$  cm) and the highest ( $35.14 \pm 14.27$  cm) species mean size. In terms of abundance in the distinct FGs, the SCRП group also holds the most elevated number, and the second most abundant is THER, followed by EXCV, TURF and MALG (**Table 2**).

**Table 2:** Mean abundance ( $\pm$ SD), mean biomass ( $\pm$ SD), the relative frequency (RF%) (%), mean size  $\pm$ SD and functional guild of herbivorous reef fishes. Species identified only at the genus level were not considered here. The acronyms CARE, PARP and AMNP stand for Cassurubá Reefs, Paredes Parcel (Unprotected Zones) and Abrolhos National Marine Park, respectively and indicate the sampling zone.

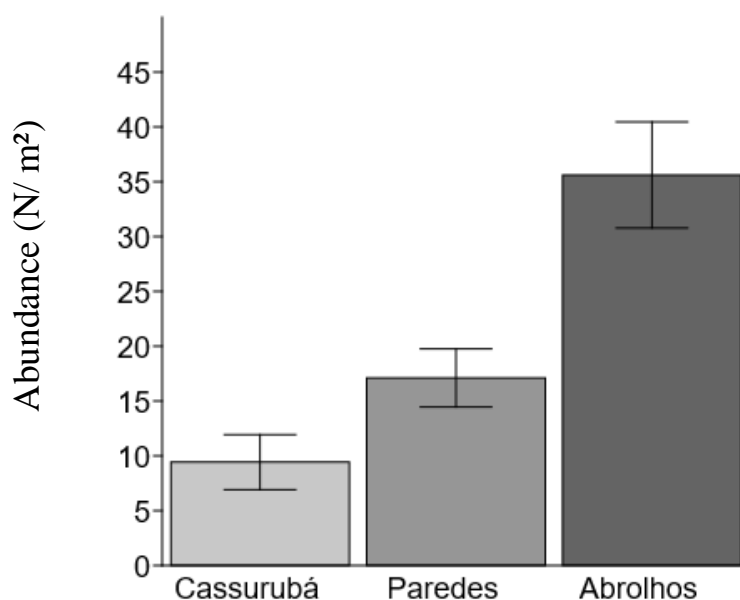
FAMILY/ SPECIES	Abundance			Biomass			RF%	MEAN SIZE ( $\pm$ SD)	FUNCTIONAL GROUPS
	CARE	PARP	AMNP	CARE	PARP	AMNP			
<b>Acanthuridae</b>									
<i>Acanthurus bahianus</i>	234 (1.69 $\pm$ 3.51)	544 (3.80 $\pm$ 4.03)	607 (4.21 $\pm$ 5.88)	42.8 $\pm$ 8.17	87.70 $\pm$ 10.87	279.15 $\pm$ 57.73	19.43	10.48 $\pm$ 5.91	SCRP
<i>Acanthurus chirurgus</i>	101 (0.73 $\pm$ 1.15)	216 (1.51 $\pm$ 2.16)	383 (2.66 $\pm$ 7.53)	69.18 $\pm$ 13.63	83.20 $\pm$ 14.83	647.97 $\pm$ 201.39	9.82	17.46 $\pm$ 7.88	SCRP
<i>Acanthurus coeruleus</i>	23 (0.16 $\pm$ 0.54)	207 (1.44 $\pm$ 3.51)	447 (3.10 $\pm$ 4.43)	38.05 $\pm$ 19.48	195.37 $\pm$ 75.40	980.13 $\pm$ 313.55	9.49	16.4 $\pm$ 8.72	TURF
<b>Blenniidae</b>									
<i>Ophioblennius trinitatis</i>	2 (0.01 $\pm$ 0.12)	0	0	0.03 $\pm$ 0.02	—	—	0.028	6 ( $\pm$ 0)	THER
<i>Scartela cristata</i>	0	0	2 (0.01 $\pm$ 0.11)	—	—	0.04 $\pm$ 0.03	0.028	7 $\pm$ 1.41	SCRP
<b>Kyphosidae</b>									
<i>Kyphosus sp.</i>	0	0	59 (0.41 $\pm$ 3.60)	—	—	198.46 $\pm$ 180.43	0.82	16.56 $\pm$ 16.39	MALG
<b>Labridae (Scarinae)</b>									
<i>Cryptotomus roseus</i>	1 (0.07 $\pm$ 0.08)	0	2 (0.01 $\pm$ 0.11)	0.01 $\pm$ 0.01	—	0.02 $\pm$ 0.019	0.042	5 $\pm$ 1	SCRP
<i>Scarus trispinosus</i>	80 (0.58 $\pm$ 2.65)	354 (2.47 $\pm$ 3.36)	723 (5.02 $\pm$ 12.33)	0.01 $\pm$ 0.01	—	0.02 $\pm$ 0.019	16.23	26.57 $\pm$ 17.54	EXCV
<i>Scarus zelindae</i>	0	48 (0.33 $\pm$ 1.04)	193 (1.34 $\pm$ 2.45)	—	45.10 $\pm$ 20.73	557.84 $\pm$ 101.42	3.38	22.76 $\pm$ 10.65	SCRP
<i>Sparisoma amplum</i>	0	5 (0.03 $\pm$ 0.27)	24 (0.16 $\pm$ 0.56)	—	41.03 $\pm$ 37.69	330.92 $\pm$ 128.02	0.40	35.14 $\pm$ 14.27	SCRP
<i>Sparisoma axillare</i>	406 (2.94 $\pm$ 5.99)	298 (2.08 $\pm$ 2.89)	355 (2.46 $\pm$ 5.77)	377.28 $\pm$ 95.03	94.10 $\pm$ 26.57	447.09 $\pm$ 118.94	14.85	13.98 $\pm$ 8.61	SCRP
<i>Sparisoma frondosum</i>	2 (0.01 $\pm$ 0.17)	12 (0.08 $\pm$ 0.29)	98 (0.68 $\pm$ 1.49)	1.08 $\pm$ 1.08	13.02 $\pm$ 4.81	422.59 $\pm$ 92.30	1.57	23.54 $\pm$ 12.79	SCRP

<i>Sparisoma radians</i>	6 (0.04±0.36)	0	0	1.22±1.08	—	0.084	9 ±5.33	MALG	
<b>Pomacentridae</b>									
<i>Microspathodon chrysurus</i>	0	3 (0.02±0.25)	1 (0.006±0.08)	—	2.46±2.46	0.54±0.54	0.056	15.5 ±1	THER
<i>Stegastes fuscus</i>	268 (1.94±2.26)	218 (1.52±2.12)	811 (5.63±4.65)	22.02±3.00	29.00±4.56	53.85±4.86	18.19	8.05 ±2.28	THER
<i>Stegastes pictus</i>	0	3 (0.02±0.14)	191 (1.32±2.45)	—	0.99±0.69	6.59±1.06	2.72	6.06 ±2.17	THER
<i>Stegastes variabilis</i>	28 (0.20±0.47)	39 (0.27±0.64)	133 (0.92±2.40)	2.14±0.56	3.23±	9.73±3.86	2.80	7.03 ±2.92	THER
<b>TOTAL Mean</b>	23.369 (+38.314)	32.62 (±31.92)	56.388(±55.288)						
<b>TOTAL ABUNDANCE</b>	1151	1947	4029	100.891	85.66	507.665			

### 3.2. MPA effect on herbivorous fish assemblage

To assess the MPA effect on the herbivorous fish assemblage we compared the differences among the studied sites considering the following variables: abundance and biomass, which were analyzed separately.

Abundance analysis showed that most individuals are located inside the MPA, where we found 56.53% of the total fish abundance (N= 4029), while in Paredes we found 1947 individuals (27.31%) and in Cassurubá 1151 individuals (16.15%) (Figure 2).



**Figure 2.** Mean abundance of herbivorous fishes in each zone of the studied area.

Next, searching for significant differences in the assemblage structure of herbivorous fishes between protected and unprotected areas we used Permutational Analysis of Variance (PERMANOVA) to the level of random points of UVCs (in each sector) for the variables general species abundance, functional groups abundance and size classes abundance.

The results for species abundance demonstrate significant differences between Abrolhos, Paredes and Cassurubá ( $p < 0.001$ ; represented by the factor Zone [Zo] in **Table 3**. However, regarding the Protection factor [Pr], results presented no statistically significant differences. Sectors [Se], which are randomly selected along areas, also presented significant differences

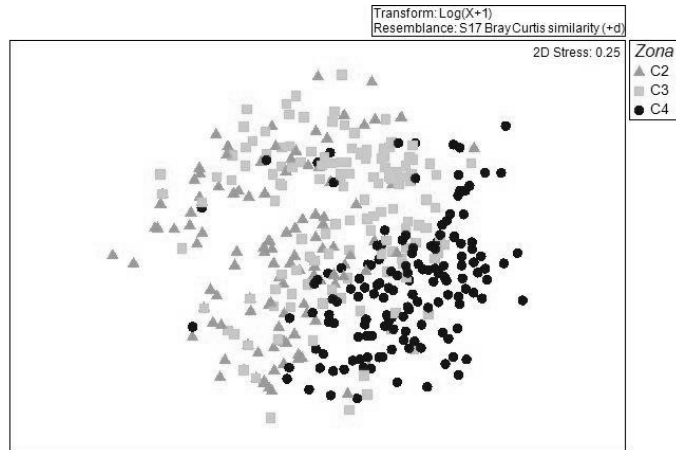


( $p < 0.001$ ). Abundance is higher in Abrolhos parcel (MPA), where reefs are fully protected from anthropogenic activities. Additionally, we analyzed the environmental data and benthic cover data as covariates in PERMANOVA. The variables with significant differences were: (the presence of) sponges ( $F=2.39$ ,  $p=0.039$ ), epilithic algal matrix ( $F=3.16$ ,  $p=0.009$ ), hard corals ( $F=3.14$ ,  $p=0.009$ ) and zoanthids ( $F=2.83$ ,  $p=0.017$ ); and also, the percentage of reef found on the sea bottom, the rugosity ( $F=3.83$ ,  $p=0.002$ ) of the reef and the depth ( $F=3.95$ ,  $p=0.002$ ) in which UVCs were done. The analysis of the covariates guided us to understand the influences of the habitat structure and the benthic community over the herbivorous fishes.

A Multidimensional scaling (MDS) analysis results present differences pointed out by PERMANOVA are. **Figure 3** indicates the Abrolhos parcel, represented by black circles, almost isolated from the two unprotected zones. Yet the analysis stress was quite high, the 3D model showed the same pattern seen here.

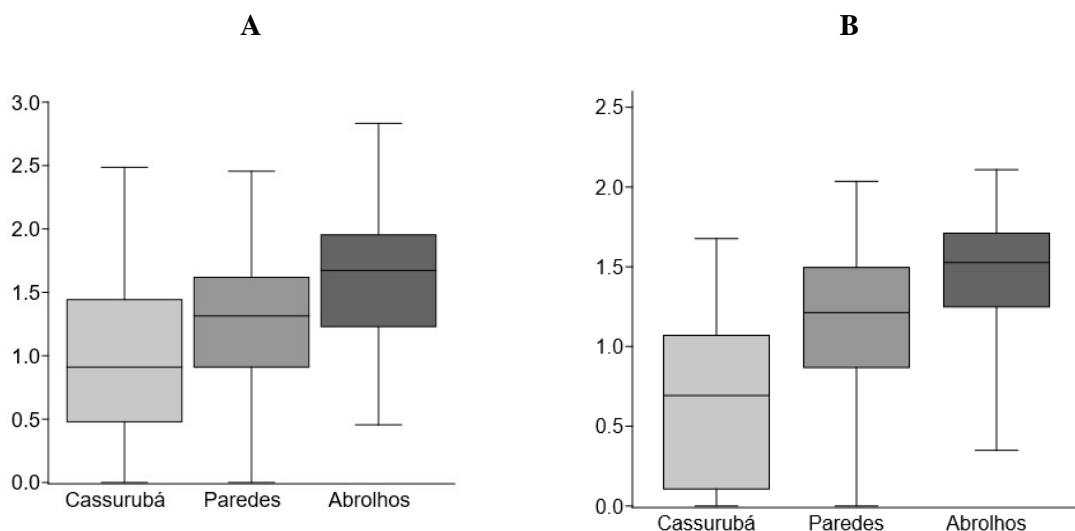
**Table 3.** Permutational Analysis of Variance performed over herbivorous reef fish abundance. Pr= Protection; Zo= Zone; Se= sector; df= Degrees of freedom; SS: Square Sum and MS: Mean Square.

ABUNDANCE							
Source	df	SS	MS	Pseudo-F	P (perm)	Unique perms	P (MC)
Pr	1	68060	68060	1.6621	0.6712	3	0.2942
Zo (Pr)	1	40228	40228	7.9583	<b>0.0001</b>	9918	0.0001
Se (Zo(Pr))	15	76448	5096.5	4.5133	<b>0.0001</b>	9827	0.0001
Res	407	4.596e <sup>5</sup>	1129.2				
Total	424	6.4254e <sup>5</sup>					



**Figure 3.** MDS of the herbivorous fishes' abundance resemblance matrix. Abrolhos is represented by the black circle.

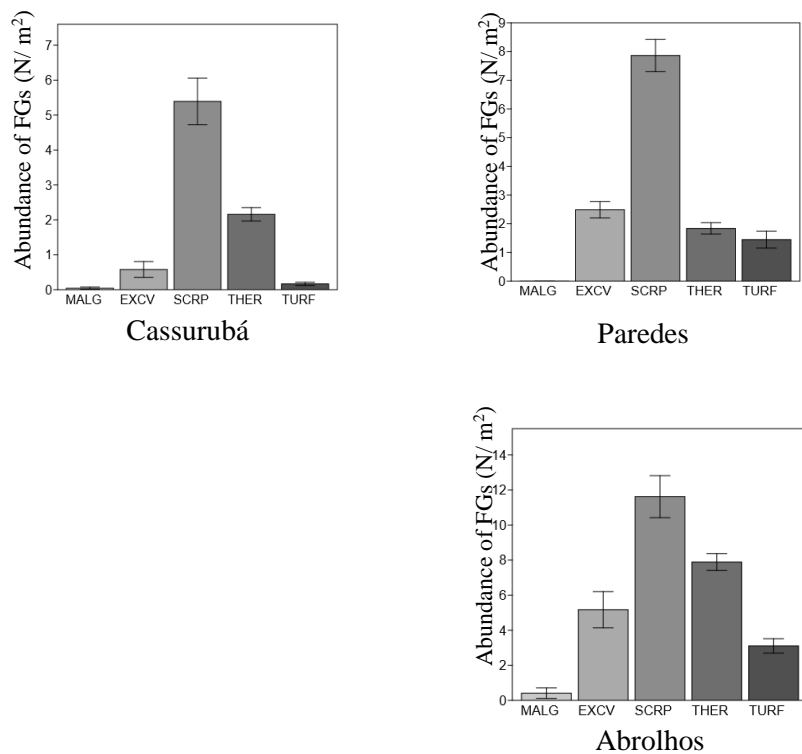
Abrolhos also has the highest species richness (**Figure 4**), and it is the only location where all fish families found, Kyphosidae was not censused on the unprotected areas (**Table 1**). Moreover, Shannon diversity index indicates that Abrolhos hold the most diverse ecosystem in terms of herbivorous fishes (mean  $1.44 \pm 0.04SE$ ), while Paredes had a mean  $1.14 (\pm 0.03SE)$  and Cassurubá  $0.68 (\pm 0.04SE)$ . Yet, the PERMANOVA results showed no significant differences among the sites when the Shannon index was tested (**Table 4**).



**Figure 4.** A) Margalef index showing species richness in each area. B) shows Shannon diversity index in the three studied sites.

**Table 4.** Permutational Analysis of Variance performed over the Shannon biodiversity index. Pr= Protection; Zo= Zone; Se= sector; df= Degrees of freedom; SS: Square Sum and MS: Mean Square.

SHANNON BIODIVERSITY INDEX							
Source	df	SS	MS	Pseudo-F	P (perm)	Unique perms	P (MC)
<b>Zo</b>	5	16.517	3.3035	0.95165	0.5013	9935	0.5009
<b>Se (Zo)</b>	30	104.14	3.4713	1.2159	0.1123	9834	0.1172
<b>Res</b>	108	308.34	2.855				
<b>Total</b>	143	429					



**Figure 5:** Abundance of the distinct functional groups of herbivorous fish in the studied sites. EXCV Excavators; MALG Macroalgal feeder.; SCRIP; THER; and TURF

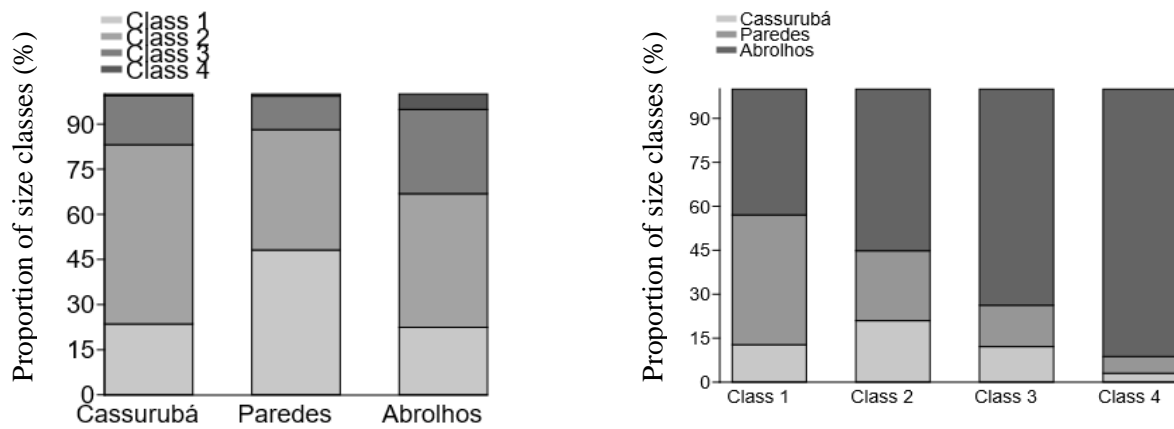
Functional groups (FGs) are more abundant in Abrolhos, where all FGs were represented by fishes' assemblage. Although Paredes is the second most abundant in terms of FGs, MALG was not found in this unprotected zone. Cassurubá was the least abundant in all FGs (**Figure 5**)

The PERMANOVA of the abundance from the distinct functional groups resulted in significant differences in the factors Zone ( $p < 0.001$ ), in a large spatial variability context and the same results applied for Sector ( $p < 0.001$ ), in a small spatial variability (**Table 5**).

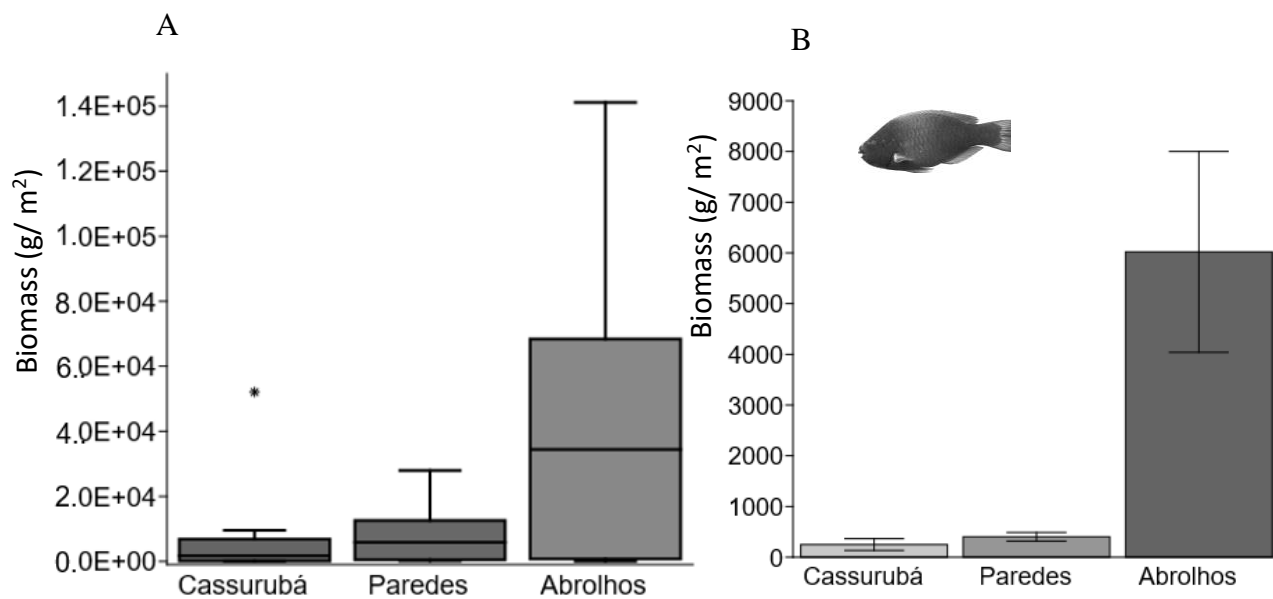
**Table 5.** Permutational Analysis of Variance performed over herbivorous reef fish functional groups abundance. Pr= Protection; Zo= Zone; Se= sector; df= Degrees of freedom; SS: Square Sum and MS: Mean Square,

FUNCTIONAL GROUPS							
Source	df	SS	MS	Pseudo-F	P (perm)	Unique perms	P (MC)
Pr	1	50490	50490	1.6545	0.6679	3	0.307
Zo (Pr)	1	29978	29978	10.228	<b>0.0006</b>	9946	0.0002
Se (Zo(Pr))	15	44336	2955.8	5.0371	<b>0.0001</b>	9886	0.0001
Res	407	2.3883e <sup>5</sup>	586.8				
Total	424	3.6276e <sup>5</sup>					

Lastly, in the matter of abundance, we plot the data in proportion of size classes of the fish assemblage in the distinct zones. We found 2120 individuals belonging to **Class 1**, 3270 to **Class 2**, 1542 to **Class 3** and 229 to **Class 4**. The percentage of size classes in each area is illustrated in **Figure 6**. In Abrolhos we found the highest number of individuals in all classes of size, except Class 1 which was higher in Paredes. The MPA holds 42.92% of the individuals in Class 1, 55.17% of individuals in Class 2, 73.74% in Class 3 and 91.2% in Class 4. On the other hand, Cassurubá has the lowest number in all classes, represented by 12.78% in Class 1, 20.98% in Class 2, 12.12% in Class 3 and 3.1%. Paredes differs significantly from Cassurubá only in Class 1; this class is represented by 44.30% of individuals in Paredes, even higher than Abrolhos, whilst Class 2 has 23.85% of the total, Class 3 14.14% and Class 4 5.7%. In the results of PERMANOVA, all factors showed significant differences. Protection [Pr] resulted in  $p < 0.001$ , the studied sites [Zo] and the sectors inside location [Se] also showed significant differences,  $p = 0.002$  and  $p = 0.01$ , respectively.



**Figure 6:** Relative representativeness of fish size classes in each of the sampled zones, first by location and then from the size classes perspective.



**Figure 7:** Biomass (g) of all herbivorous fishes, except *Scarus trispinosus*, in the studied areas (A). Biomass (g) of *Scarus trispinosus* alone in the three locations (B).

The biomass analysis followed a similar pattern and resulted in a higher fish mass value inside the Abrolhos parcel, followed by Cassurubá and Paredes (**Table 7**). In terms of kilograms per area, the variance between the non-protected areas and the MPA reflects the contrasting size classes among the sites (see size classes analysis below). We found a mean value of 0.507 kg

(73.2%) in Abrolhos, while in Cassurubá and Paredes the mean values were 0.100 kg (14.5%) and 0.085 kg (12.3%), respectively.

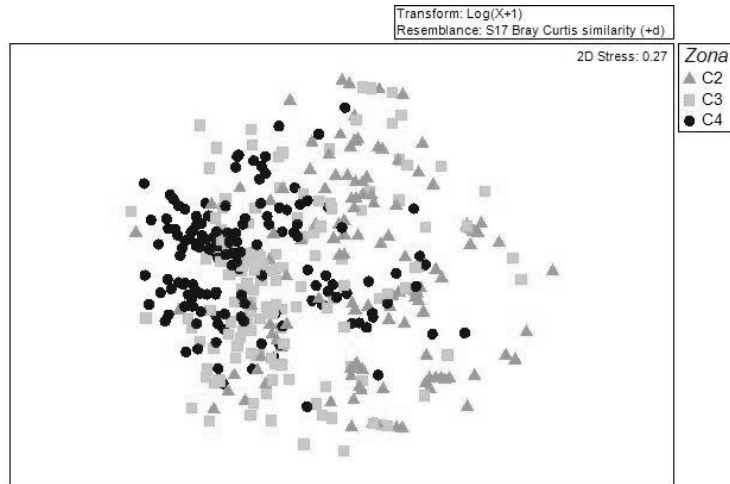
**Table 7.** Permutational Analysis of Variance performed over herbivorous reef fish biomass. Pr= Protection; Zo= Zone; Se= sector; df= Degrees of freedom; SS: Square Sum and MS: Mean Square,

BIOMASS							
Source	df	SS	MS	Pseudo-F	P (perm)	Unique perms	P (MC)
Pr	1	74181	74181	1.3498	0.6637	3	0.3774
Zo (Pr)	1	53997	53997	9.1315	<b>0.0001</b>	9950	0.0001
Se (Zo(Pr))	15	89392	5959.4	3.7932	<b>0.0001</b>	9846	0.0001
Res	407	6.3944e <sup>5</sup>	1571.1				
Total	424	8.5437e <sup>5</sup>					

**Figure 7** shows the biomass of the herbivorous fish species in the distinct location. *Scarus trispinosus* was not considered to avoid distortion in the data presented because of their discrepant body size, the biomass data of this species is presented separately (see figure 7b). The boxplot reinforces that the biomass in Abrolhos is greater than the non-protected areas, in which Abrolhos distinguishes in terms of its interquartile range, third quartile and extreme value.

We also searched for significant differences among sites regarding the biomass of the herbivorous fishes. We used PERMANOVA to obtain our results. Following the same patterns of the abundance analysis, biomass also resulted in significant differences between zones when considering *S. trispinosus* in the analysis (see Zo in **Table 7**). Sectors [Se] also presented significant differences.

A MDS was used as a tool to identify where differences shown in PERMANOVA test are located. However, the analysis did not show a clear pattern of distribution, presenting samples aggregated mostly in the same direction. Analysis of the 3D model shows Cassurubá as the most disperse zone in the graph. However, the stress of the analysis was high and the ordination may be arbitrary (**Figure 8**).

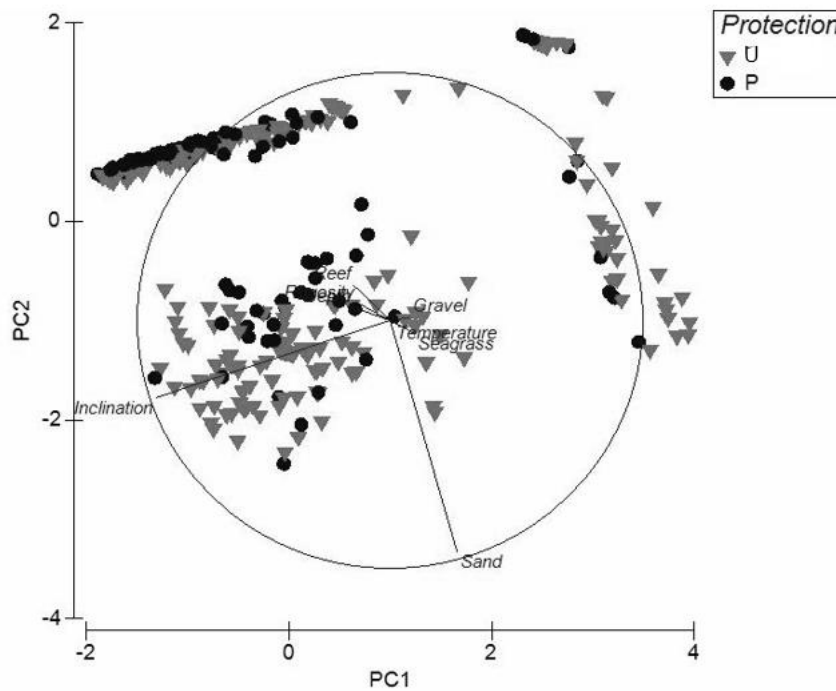


**Figure 8.** MDS of the herbivorous fishes' biomass resemblance matrix

### 3.3. Habitat structure and benthic community

The Principal Component Analysis (PCA) was used to investigate structural differences in habitat in the distinct zones to determine the main strengths which play an important role in habitat structuration. This is important to characterize what environmental variables are the most related to the presence of the herbivorous assemblage in the studied areas. Following the Kaiser criterion, we selected here the principal components (PCs) 1 and 2. In **Figure 9**, the PC1 axis (related to the principal component 1) has the variable inclination as the one which most influences the PC, and it is influencing both protected and unprotected areas' structure. For the axis PC2 (related to the principal component 2) sand is the variable which most influences the group of PCs, and it is present mostly in the unprotected area, but a small number of sites. Both PC1 and PC2 are responsible for 78.5% of variable aggregation.

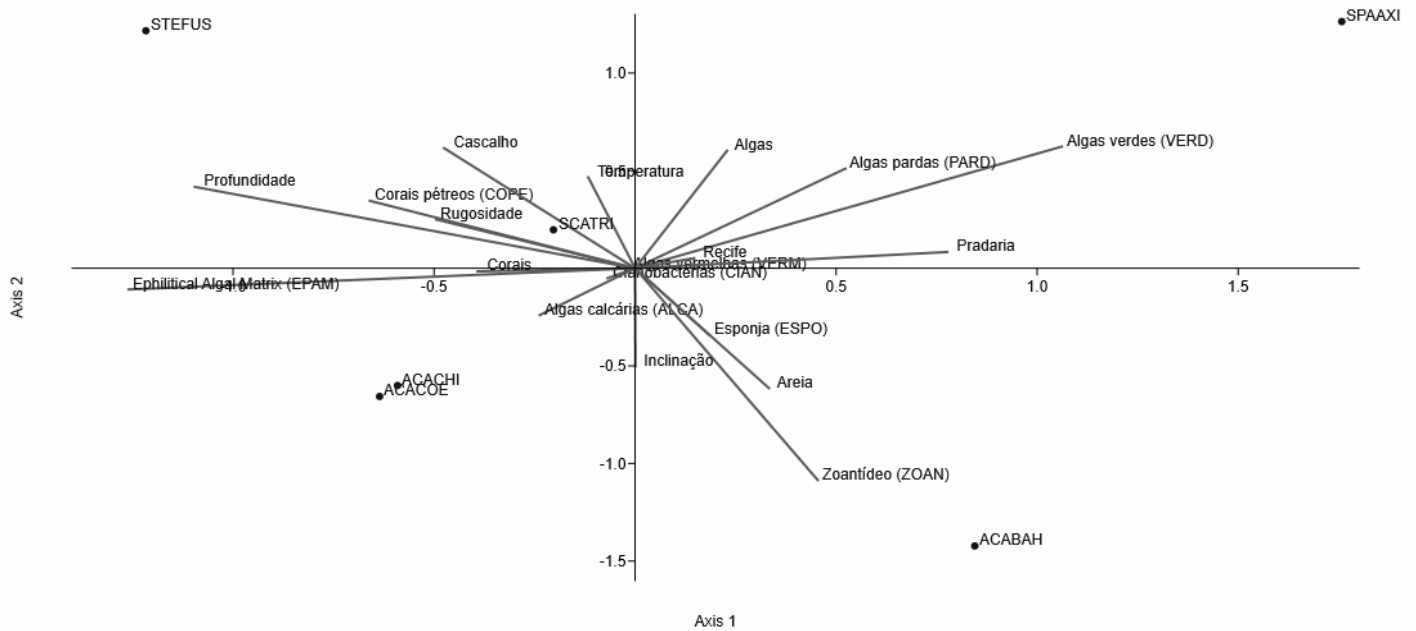
Inclination could be similarly compared to the reef height, and a higher number of this variable indicates that the reef reaches between 60° to 90° angle. When the variable inclination comes to this level, it represents a well-structured reef, which progressed throughout the time, whereas, sand is a poor-structured environment, where its unconsolidated bottom turn coral settlement difficult.



**Figure 9** Principal Component Analysis of the environmental data (heterogeneity and complexity) of the distinct studied areas. U= unprotected and P= protected areas.

Lastly, we used Canonical Correspondence Analysis (CCA) to estimate which environment forces and benthic organisms have the most influence in determining the assemblage of herbivorous fishes' assemblages. We selected the most abundant species which represent all functional groups (FGs) found here, consequently, obtaining results which can be replicated to the herbivorous fish assemblages. *Sparisoma axillare* (SPAAXI) seems to be influenced by the presence of different types of algae (e.g, green algae and brown algae) which are present in places where seagrass is predominant, and for seagrasses and general algae in terms of bottom composition. On the other hand, *Acanthurus chirurgus* and *Acanthurus coeruleus* avoid flesh algae and are more associated with calcareous algae and are influenced somehow by turf (EPAM). *Acanthurus bahianus* (ACABAH) showed a strong linkage with the benthos zoanths and sand on the seafloor. *Scarus trispinosus* (SCATRI) showed a relationship with hard corals and rugosity, as well as gravel appear as a structural influence over *S. trispinosus* population; moreover, this species seems to be related to the depth range.





**Figure 10:** A Canonical Correspondence Analysis of the most abundant fish species and the habitat structure data and benthic cover data collected. The species which represent the herbivorous fish assemblage in the analysis are (by their acronym): ACABAH, STEFUS, SCATRI, SPAAXI, ACACHI, ACACOE.

#### 4. DISCUSSION

The study was conducted in the largest reef bank of the South-western Atlantic, where distinct coral reef structures are located (Leão & Dominguez, 2000, Leão & Kikuchi, 2001). However, fish species richness is lower than regions in the subtropical (Floeter, et al. 2001). Despite that, fish assemblages suffer due to overfishing in the region (Freire & Pauly, 2010). Here we evaluated the effectiveness of marine protected areas over the herbivorous fishes' assemblage, to reach this goal we analyzed abundance and biomass of this trophic group in and out the MPA.

Our PERMANOVA results revealed a clear pattern between protected and unprotected areas. Whereas the protection factor almost did not present significant differences between MPAs and unprotected areas, factor zone, which is in a larger spatial variability context, resulted in significant differences. The same occurred to sector, which is in a smaller spatial variability context, and also presented significant differences in results. This pattern suggests that the

expressive variance influences the analysis, because the high dispersion prevents the identification of contrasts among variables in the protection factor level.

The greater results in terms of abundance and biomass in the protected area are consistent with studies that indicate how marine areas can enhance fisheries assemblage (Claudet et al., 2006). Therefore, our data indicate that the Abrolhos Marine National Park is effective in protecting herbivorous fishes' assemblages. The area under protection presented variables consistency higher in this study. The high abundance and biomass of these herbivores demonstrate the potential of the area to maintain a coral dominance state, consequently, avoiding a phase-shift. This phenomenon is well reported in areas where species of macroalgae consumers were lost (Roberts, 1995; Bellwood et al., 2004; Hughes et al., 2010; Brandl et al., 2019).

Clustering herbivorous fishes into functional groups is a method to quantify resilience of a certain marine ecosystem (Heenan & Williams, 2013). Our study found that functional guild structure is more evident in Abrolhos, since the FGs are more representative in this site, emphasizing a possible link between a well-structured fish assemblage and marine protected areas.

Regarding the size classes of the herbivorous fishes, Abrolhos also holds the highest number of individuals in the classes which comprises the bigger sizes. This reflects especially the prohibition of fishing inside the MPA, assuring fishes successfully reach adult life stages and reach their maximum size (Pauly et al., 1998; Freire & Pauly, 2010; Froese et al., 2016). Graham et al. 2005 says that size spectra - which is the relationship between the size and the abundance of fishes - is related to fisheries exploitation, if the size spectra reach a lower level, the abundance will do so. Our results demonstrate that size classes are significantly different among areas and higher in Abrolhos in terms of the larger sizes (class 3 and 4), thus we have evidence here that Abrolhos MPA is more prone to keep the integrity of the herbivorous assemblage than the unprotected areas.

Following the CCA results, it demonstrates that *S. axillare* is influenced by different types of macroalgae, especially green algae, but also brown algae. Following an opposite pattern, although *S. axillare* population is abundant in all assessed areas, the species is more abundant in Cassurubá instead of Abrolhos. This suggests that unprotected areas influence the presence of certain species, thus, the impact is not limited to abundance reduction but also in changing of fishes' assemblage structure and, consequently, may cause loss of ecosystem functionality. Another possibility driving the abundance of *S. axillare* in Cassurubá is the representativity of

seagrass, the variable most aligned with the axis which the herbivore is associated, and mostly found in Cassurubá than in the other zones.

On the other hand, *S. fuscus* is associated with hard corals and boulders, this pattern may indicate their territorial behavior. The species is usually observed overseeing their territory by swimming around a small area and then hiding in a hole or underneath a reef formation. Depth is the variable which most influences the axis in the direction of *S. fuscus*, Chaves et al. (2021) found that depth is a significant variable for *Stegastes* genus, especially in the tropical region.

*Scarus trispinosus* did not demonstrate a strong relationship with any variable, yet the presence of hard corals and boulder, the reef rugosity and temperature are the variables which most explain the species presence. *Acanthurus bahianus* and *Acanthurus chirurgus* take nearly the same place, and the variable which most explained the presence of both was calcareous algae. Lastly, *Acanthurus bahianus* appeared to be influenced mainly by zoanthids and sponges of benthic community, followed by sand and inclination as the abiotic variables. Inclination and sand which appeared as a predictor in PCA only influenced *A. bahianus* in this analysis, hence barely affect the herbivorous fish assemblage of the Abrolhos reef bank.

## 5. CONCLUSION

This study aimed to understand if MPA is an effective tool in marine coastal management, considering biomass and abundance of a group of herbivorous fishes as the main variables. In view of the results presented found, protection is related to positive outcomes in the fish assemblage, since Abrolhos showed higher abundance and biomass of the sampled herbivorous fish groups, being the variance between the protected and the unprotected areas highly significant. This result is consistent with the initial hypothesis that the assemblage structure of herbivorous fishes differs between MPAs and unprotected areas, corroborating the benefits of the MPA over the herbivorous fishes' assemblage, thus corroborating with the importance of the creation of new MPAs, especially in areas where biological reefs are in place.

In this perspective, the results are an important tool to develop strategic policies in relation to the MPA efficiency and fisheries management in the surrounding unprotected areas. A more comprehensive study, like a more robust FG analysis, could provide more understanding on how MPAs, by enhancing herbivorous fishes assemblage, can strengthen coral reefs resilience through the protection of key functional roles.

## 6. REFERENCES

- Bellwood, D. R.; Hughes, T. P.; Folke, C.; Nyström, M. **Confronting the Coral Reef Crisis**. *Nature*. 2004. 429: 827-833.
- Bonaldo, R.; Hoey, A. S.; Bellwood, D. R. **The Ecosystem Roles of Parrotfishes on Tropical Reefs**. *Oceanography and Marine Biology*. 2014. 52: 81-132.
- Brandl, S. J. **Coral Reef Ecosystem Functioning: Eight Core Processes and the Role of Biodiversity**. *Frontiers in Ecology and the Environment*. 2019. 17(8): 445-454.
- Bruno, J. F.; Côté, I. M.; Toth, L. T. **Climate Change, Coral Loss, and the Curious Case of the Parrotfish Paradigm: Why Don't Marine Protected Areas Improve Reef Resilience?** *Annual Review of Marine Science*. 2019. 11: 307-334.
- Bruno, J. F. et al. **Assessing Evidence of Phase Shifts from Coral to Macroalgal Dominance on Coral Reefs**. *Ecology*. 2009. 90(6): 1478-1484.
- Burkepile, D. E. & Hay, M. E. **Herbivore Species Richness and Feeding Complementarity Affect Community Structure and Function on a Coral Reef**. *National Academy of Science*. 2016. 105(42): 16201-16206.
- Castaña, D.; Morales-de-Anda, D.; Prato, J.; Cupul-Magaña, A. L.; Echeverry, J. P.; Santos-Martinez, A. **Reef Structural Complexity Influences Fish Community Metrics on a Remote Oceanic Island: Serranilla Island, Seaflower Biosphere Reserve, Colombia**. In: *Oceans. Multidisciplinary Digital Publishing Institute*. 2021. p. 611-623.
- Chabanet, P. et al. **Relationships Between Coral Reef Substrata and Fish**. *Coral Reefs*. 1997. 16: 93-102.
- Chaves, L. C. T. et al. **Drivers of Damselfishes Distribution Patterns in the Southwestern Atlantic: Tropical and Subtropical Reefs Compared**. *Neotropical Ichthyology*. 2021. 19(4): e210010.
- Clarke, K. R. & Ainsworth, M. **A Method of Linking Multivariate Community Structure to Environmental Variables**. *Marine Ecology Progress Series*. 1993. 92: 205-219.
- Claudet, J., Pelletier, D.; Jouvenel, J. Y. ; Bachet F.; Galzin, R. **Assessing the effects of marine protected area (MPA) on a reef fish assemblage in a northwestern Mediterranean marine reserve: Identifying community-based indicators**. *Biological Conservation*. 2006. 130(3) 349-369.
- Done, T. J. **Phase Shift in Coral Reef Communities and Their Ecological Significance**. *Hydrobiologia*. 1992. 247: 121-132
- Duffy, J. E.; Lefcheck, J. S.; Stuart-Smith, R. D.; Navarrete, S. A.; Edgar, G. J. **Biodiversity Enhances Reef Fish Biomass and Resistance to Climate Change**. *Proceedings of the National Academy of Sciences*. 2016. 113 (22): 6230-6235.
- Félix-Hackradt, F. C.; Hackradt, C. W.; Treviño-Otón, J.; Pérez-Ruzafa; García-Charton. **Habitat Use and Ontogenetic Shifts of Fish Life Stages at Rocky Reefs in South-Western Mediterranean Sea**. 2014. 88: 67-77.

- Floeter, S. R.; Halpern, B. S.; Ferreira, C. E. L. **Effects of Fishing and Protection on Brazilian Reef Fishes**. *Biological Conservation*. 2006. 128: 391-402.
- Francini-Filho, R. B. et al. **Dynamics of coral reef benthic assemblages of the Abrolhos Bank, eastern Brazil: inferences on natural and anthropogenic drivers**. *PloS one*. 2013. 8(1), e54260.
- Freire, K. M., & Pauly, D. **Fishing down Brazilian marine food webs, with emphasis on the east Brazil large marine ecosystem**. *Fisheries Research*. 2010. 105(1), 57-62.
- Froese, R.; et al. **Minimizing the Impact of Fishing**. *Fish and Fisheries*. 2016. 17(3): 785-802.
- Garcia-Charton, J. A. & Pérez-Ruzafa, Á. **Spatial Pattern and the Habitat Structure of a Mediterranean Rocky Reef Fish Local Assemblage**. 2001. 138: 917-934.
- Glasby, T. M. **Analysing Data from Post-impact Studies Using Asymmetrical Analyses of Variance: A Case Study of Epibiota on Marinas**. *Australian Journal of Ecology*. 1997. 22: 448-459.
- Graham, N. A. J. & Nash, K. L. **The Importance of Structural Complexity in Coral Reef Ecosystems**. *Coral Reefs*. 2013. 32: 315-326.
- Halpern, B. S., Floeter, S. R. **Functional diversity responses to changing species richness in reef fish communities**. *Marine Ecology Progress Series*. 2018. 364: 147-156.
- Hawkins, J. P., Roberts, C. M. **Effects of Artisanal Fishing on Caribbean Coral Reefs**. *Conservation Biology*. 2004. 18: 215-226.
- Heenan, A., & Williams, I. D. **Monitoring herbivorous fishes as indicators of coral reef resilience in American Samoa**. *PloS One*. 2013. 8 (11), e79604.
- Hughes, T. P. et al. **Phase Shifts, Herbivory, and the Resilience of Coral Reefs to Climate Change**. *Current Biology*. 2007a. 17: 360-365.
- Hughes, T. P. et al. **No-take areas, herbivory and coral reef resilience**. *Trends in ecology & evolution*. 2007b. 22(1), 1-3.
- Hughes, T. P.; et al. **Rising to the Challenge of Sustaining Coral Reef Resilience**. *Trends in Ecology and Evolution*. 2010. 25(11): 633-642.
- ICMBIO [online]. Disponível em: <<https://www.icmbio.gov.br/parnaabrolhos/guia-do-visitante.html>> , Acesso em 20 de outubro de 2021.
- Jackson, J. B. C. et al. **Historical Overfishing and the Recent Collapse of Coastal Ecosystems**. *Science*. 2001. 293: 629-638.
- Kohler, K. E., Gill, S. M. **Coral Point Count With Excel Extensions (CPCe): a Visual Basic Program for the Determination of Coral and Substrate Coverage Using Random Point Count Methodology**. *Computer and Geoscience*. 2006. 32: 1259-1269.
- Leão, Z. M. A. N., Kikuchi, R. K. P. **The Abrolhos Reefs of Brazil**. In: *Coastal Marine Ecosystems of Latin America*. Springer, Berlin, Heidelberg. 2001. p. 83-96.
- Leão, Z. M. A. N.; Kikuchi, R.K.P.; TESTA, V. **Corais e Recifes de Coral do Brasil**. Em: *Recifes de Coral da América Latina*. Elsevier Science. 2003. p. 9-52.

- Luckhurst, B. E. & Luckhurst, K. **Analysis of the Influence of Substrate Variables on Coral Reef Fish Communities**. Marine Biology. 1978. 49: 317-323.
- Minte-Vera, C. V.; Moura, R. L.; Francini-Filho, R. B. **Nested Sampling: An Improved Visual-Census Technique for Studying Reef Fish Assemblages**. Marine Ecology Progress Series. 2008. 367: 283-293.
- Mora, C. (Ed.). **Ecology of Fishes on Coral Reefs**. Cambridge: Cambridge University Press. 2015. doi:10.1017/CBO9781316105412
- Moura, R. L. **Brazilian Reefs as Priority Areas for Biodiversity Conservation in the Atlantic Ocean**. In: Proceeding of the 9<sup>th</sup> international Coral Reef Symposium, Bali, Indonesia. 2002. p. 917-920.
- Nash, K. L. et al. **Drivers of Herbivory on Coral Reefs: Species, Habitat and Management Effects**. Marine Ecology Progress Series. 2016. 554: 129-140.
- Oakley-Cogan, A.; Tebbett, S. B.; Bellwood, D. R. **Habitat Zonation on Coral Reefs: Structural Complexity, Nutritional Resources and Herbivorous Fish Distributions**. PlosOne. 2020. 15(6).
- Pauly, D.; Christensen, V.; Dalsgaard, J.; Froese, R.; Torres Jr, F. **Fishing Down Marine Food Webs**. Science. 1998. 279: 860-863.
- Puk, L. D.; Ferse, S. C. A.; Wild, C. **Patterns and Trends in Coral Reef Macroalgae Browsing: a Review of Browsing Herbivorous Fishes of the Indo-Pacific**. Reviews in Fish Biology and Fisheries. 2015. 26: 53-70.
- R Core Team. **R: A Language and Environment for Statistical Computing**. Vienna: R Foundation for Statistical Computing. 2021. Available online at <https://www.R-project.org/>
- Rasher, D. B.; Hoey, A. S.; Hay, M. E. **Consumer Diversity Interacts with Prey Defenses to Drive Ecosystem Function**. Ecology. 2013. 94(6): 1347-1358.
- Roberts, C. M. **Effects of Fishing on the Ecosystem Structure of Coral Reefs**. Conservation Biology. 1995. 9(5): 988-995.
- Rogers, A; Blanchard J. L.; Mumby, P. J. **Vulnerability of Coral Reef Fisheries to a Loss of Structural Complexity**. Current Biology. 2014. 24: 1000-1005
- Schowalter, T. D. Population Ecology. In: **Insect Ecology: An Ecosystem Approach**. 2022. 5<sup>th</sup> Ed: 207-208.
- Topor, Z. M. et al. **Marine Protected Areas Enhance Coral Reef Functioning by Promoting Fish Biodiversity**. Conservation Letters. 2019. e12638.
- Torres, F. M. M. S. G; Feitosa, J. L. L., Vêras, L. V. M. V. Q. **Efeitos da Abundância de Peixes Sobre a Alimentação do Bobó (*Sparisoma axillare*) nos Recifes da APA Costa dos Corais**. Trabalho de Conclusão de Curso. Ciências Biológicas. 2021. Recife. 55p.
- Underwood, A. J. **Beyond BACI: Experimental Designs for Detecting Human Environmental Impacts on Temporal Variations in Natural Populations**. Australian Journal of Marine and Freshwater Research. 1991. 42: 569-87.

Underwood, A. J. **Beyond BACI: The Detection of Environmental Impacts on Populations in the Real, But Variable, World.** *Journal of Experimental Marine Biology and Ecology.* 1992. 161: 145-178.

Underwood, A. J. **Detection, Interpretation, Prediction and Management of Environmental Disturbances: Some Roles for Experimental Marine Ecology.** *Journal of Experimental Marine Biology and Ecology.* 1996. 200: 1-27

Yeomans, K. A. & Golder, P. A. **The Guttman-Kaiser Criterion as a Predictor of the Number of Common Factors.** *Journal of the Royal Statistics Society.* 1982. 31(3): 221-229.

## APPENDIX

**Anexo 1.** Method used to cluster species into sizes classes. Each species were divided in four classes according to their minimum and maximum size found during underwater visual census.

<u>ACABAH</u> <b>Classe 1</b> < 7 <b>Classe 2</b> 7 a 14 <b>Classe 3</b> 15 a 22 <b>Classe 4</b> 23 a 28	<u>ACACHI</u> <b>Classe 1</b> < 9 <b>Classe 2</b> 9 a 18 <b>Classe 3</b> 19 a 28 <b>Classe 4</b> 29 a 36	<u>ACACOE</u> <b>Classe 1</b> < 11 <b>Classe 2</b> 11 a 20 <b>Classe 3</b> 21 a 30 <b>Classe 4</b> 31 a 38	<u>CRYSOS</u> <b>Classe 1</b> < 5 <b>Classe 2</b> 5 a 8 <b>Classe 3</b> 9 a 12 <b>Classe 4</b> 13 a 16
<u>KYPSP</u> <b>Classe 1</b> < 15 <b>Classe 2</b> 15 a 28 <b>Classe 3</b> 29 a 42 <b>Classe 4</b> 43 a 58	<u>MICCHR</u> <b>Classe 1</b> < 7 <b>Classe 2</b> 7 a 12 <b>Classe 3</b> 13 a 18 <b>Classe 4</b> 19 a 22	<u>OPHTRI</u> <b>Classe 1</b> ≤ 1 <b>Classe 2</b> 1,1 a 2,5 <b>Classe 3</b> 2,6 a 4,5 <b>Classe 4</b> 4,6 a 5,5	<u>SCACRI</u> <b>Classe 1</b> < 3 <b>Classe 2</b> 3 a 6 <b>Classe 3</b> 7 a 10 <b>Classe 4</b> 11 a 14
<u>SCATRI</u> <b>Classe 1</b> < 19 <b>Classe 2</b> 19 a 36 <b>Classe 3</b> 37 a 54 <b>Classe 4</b> 55 a 70	<u>SCAZEL</u> <b>Classe 1</b> < 13 <b>Classe 2</b> 13 a 24 <b>Classe 3</b> 25 a 38 <b>Classe 4</b> 39 a 50	<u>SPAAMP</u> <b>Classe 1</b> < 15 <b>Classe 2</b> 16 a 28 <b>Classe 3</b> 29 a 42 <b>Classe 4</b> 43 a 54	<u>SPAAXI</u> <b>Classe 1</b> 2 a 10 <b>Classe 2</b> 12 a 20 <b>Classe 3</b> 22 a 30 <b>Classe 4</b> 32 a 40
<u>SPAFRO</u> <b>Classe 1</b> 2 a 10 <b>Classe 2</b> 12 a 22 <b>Classe 3</b> 24 a 34 <b>Classe 4</b> 36 a 44	<u>SPARAD</u> <b>Classe 1</b> < 5 <b>Classe 2</b> 6 a 10 <b>Classe 3</b> 11 a 16 <b>Classe 4</b> 17 a 20	<u>STEFUS</u> <b>Classe 1</b> < 5 <b>Classe 2</b> 6 a 10 <b>Classe 3</b> 11 a 16 <b>Classe 4</b> 17 a 20	<u>STEPIC</u> <b>Classe 1</b> < 5 <b>Classe 2</b> 6 e 8 <b>Classe 3</b> 9 e 12 <b>Classe 4</b> 13 e 16
<u>STEVAR</u> <b>Classe 1</b> < 5 <b>Classe 2</b> 6 a 8 <b>Classe 3</b> 9 a 12 <b>Classe 4</b> 13			