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**Mudanças temporais e efeitos ecológicos do octocoral invasor *Latissimia ningalooensis*
em comunidades de recifes rochosos da baía da Ilha Grande, RJ**

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Dissertação apresentada ao Programa de Pós-Graduação em Biodiversidade e Conservação da Natureza, da Universidade Federal de Juiz de Fora como requisito parcial à obtenção do título de Mestre em Biodiversidade e Conservação da Natureza. Área de concentração: Processos Ecológicos e Conservação da Natureza.

Orientadora: Profa. Dra. Simone Jacqueline Cardoso

Coorientador: Prof. Dr. Leonardo Mitrano Neves

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“ O oceano nos deu a vida, está na hora de retornar o favor. ” (Sylvia Earle)

RESUMO

As espécies exóticas invasoras são consideradas uma das principais ameaças à biodiversidade marinha. Usamos um BACI-design para investigar as mudanças nas comunidades bentônicas de recifes rochosos relacionadas à invasão do octocoral *Latissimia ningalooensis* no Atlântico Sudoeste. Mudanças drásticas na estrutura da comunidade bentônica foram restritas ao local invadido e associadas ao crescimento de *L. ningalooensis* sobre algas turf. Por outro lado, o zoantídeo *Palythoa caribaeorum* manteve cobertura estável ao longo dos 9 anos de estudo, indicando maior resistência biótica contra o octocoral. *Latissimia ningalooensis* se espalhou de manchas grandes e bem estabelecidas para novas áreas do recife, aumentando as interações turf-octocoral. Este estudo alerta para o grande potencial invasor do octocoral, devido à sua elevada abundância, capacidade competitiva e de expansão. O declínio na abundância de algas turf após o surgimento de *L. ningalooensis* ameaça a estrutura e o funcionamento dos recifes rochosos dominados por macroalgas.

Palavras-chave: BACI-design, Invasões biológicas, Interações competitivas, *Latissimia ningalooensis*, *Sansibia* sp., Variações espaço-temporais.

ABSTRACT

Invasive alien species are considered one of the main threats to marine biodiversity. We used a BACI design to investigate the changes in rocky reef benthic communities related to the invasion of the octocoral *Latissimia ningalooensis* in the Southwest Atlantic. Drastic changes in benthic community structure were restricted to the invaded site and associated with the growth of *L. ningalooensis* on turf algae. Conversely, the zoanthid *Palythoa caribaeorum* remained stable coverage along the 9-year study period, indicating a greater biotic resistance against the octocoral. *Latissimia ningalooensis* spread from large and well-established patches to new areas of the reef, increasing turf-octocoral interactions. This study warns to the great invasive potential of the octocoral, due to its high abundance, competitive and expansion ability. The decline in abundance of turf-forming algae following the emergence of *L. ningalooensis* threatens the structure and functioning of macroalgal-dominated rocky reefs.

Keywords: BACI-design, Biological invasions, Competitive interactions, *Latissimia ningalooensis*, *Sansibia* sp., Spatial-temporal variations.

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1. INTRODUÇÃO GERAL

A degradação dos ecossistemas marinhos tem sido rápida e aguda, desafiando as iniciativas voltadas ao conhecimento e conservação dos recursos do mar (Norse & Crowder, 2005). Enquanto diversas espécies estão reduzindo devido à poluição, mudanças climáticas e destruição dos habitats (Elahi et al., 2015; Hewitt et al., 2016; Worm et al., 2006), outras invadem novas regiões utilizando vetores antropogênicos (Grosholz & Ruiz, 2003; Rilov & Crooks, 2009; Ruiz et al., 1997). Os ecossistemas costeiros são particularmente vulneráveis a invasões de espécies devido à existência de diversos vetores potenciais de introdução, como a água de lastro, incrustações no casco de navios, aquicultura e o comércio de aquários (Verling et al., 2005; Ruiz et al., 2015). Tais vetores contribuem com a remoção das fronteiras espaciais que separam os ecossistemas, aumentando exponencialmente a disseminação de espécies exóticas marinhas (Canning-Clode, 2015).

Nos últimos anos, estudos relacionados ao impacto de espécies exóticas nas comunidades e ecossistemas nativos são frequentemente encontrados, tornando a biologia da invasão uma temática em desenvolvimento constante com diversas implicações ecológicas e de conservação (Canning-Clode, 2015). Em sistemas marinhos, particularmente, mais de 1500 espécies invadiram locais nos oceanos mundiais, e diversas novas ocorrências são registradas anualmente em escala global (Rabitsch et al. 2012). Estudos recentes demonstraram um grande aumento no registro de invasões biológicas no Atlântico Sudoeste (Schwindt et al., 2020). No litoral brasileiro, o registro de espécies exóticas marinhas tem sido tardio, devido ao aumento no número de espécies estabelecidas (*e.g.* organismos com ciclo de vida completo, com aumento da população e impactos associados) e a diminuição na sua detecção (*e.g.* organismos sem aumento posterior na abundância), o que dificulta o controle do movimento dessas espécies exóticas (Teixeira and Creed, 2020).

A região da baía da Ilha Grande (BIG), no sudeste do Brasil, possui um complexo de ecossistemas marinhos, compreendendo praias arenosas e manguezais, além de recifes rochosos costeiros e insulares. A BIG apresenta um elevado número de espécies marinhas (> 900) e o maior número de unidades de conservação do estado do Rio de Janeiro, sendo classificada como área de extrema importância biológica pelo Ministério do Meio Ambiente (Creed et al., 2007; MMA, 2002). Apesar disso, os ecossistemas da BIG são constantemente ameaçados pela degradação de seus habitats provocada por poluição, assoreamento e industrialização portuária, que causam impactos negativos em sua diversidade e funcionalidade (Alho et al., 2002; Teixeira-Neves et al., 2015). Tais ameaças contribuem para a ampla distribuição de espécies introduzidas, mostrando a alta suscetibilidade desses sistemas a invasões biológicas (Ignacio et al., 2010). O estabelecimento de espécies exóticas como os corais escleractínios *Tubastraea coccinea* e *Tubastraea tagusensis* (Lages et al., 2011; Silva et al., 2014), da alga verde *Caulerpa scalpelliformes* (Falcão & Széchy, 2005) e do molusco *Isognomom bicolor* (Breves-Ramos et al., 2010), vem alterando o funcionamento dos ecossistemas costeiros da região e estão associados a diferentes impactos sobre as comunidades nativas.

A chegada de novos invasores, com potencial para modificar drasticamente a estrutura das comunidades (Carvalho-Junior 2019; Mantelatto et al., 2018), aumenta ainda mais a preocupação sobre os ambientes recifais do sudoeste do Atlântico. Além disso, estudos que busquem avaliar a influência de invasores como a principal causa de mudanças ecológicas na comunidade receptora são fundamentais para a compreensão dos caminhos e impactos de invasões biológicas (Bulleri et al., 2010).

Esta dissertação teve como objetivo investigar as mudanças temporais e efeitos ecológicos do octocoral invasor *Latissimia ningalooensis* sobre as comunidades bentônicas de recifes rochosos da Praia Vermelha, BIG. A dissertação é composta por um capítulo único, o manuscrito intitulado como “*Long-term changes in benthic communities following the invasion*

by an alien octocoral in the Southwest Atlantic, Brazil” que está em avaliação no periódico *Marine Pollution Bulletin*. Neste estudo, utilizando dados anteriores e posteriores à invasão de *L. ningalooensis*, investigamos as mudanças temporais na composição e estrutura das comunidades bentônicas em recifes rochosos invadidos e não invadidos pelo octocoral. Além disso, buscamos identificar as interações biológicas entre o invasor e os organismos nativos através da avaliação de redes de interações de contato. Nós também avaliamos as tendências temporais na cobertura octocoral invasor e dos organismos mais abundantes do recife invadido.

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2. CAPÍTULO ÚNICO: LONG-TERM CHANGES IN BENTHIC COMMUNITIES FOLLOWING THE INVASION BY AN ALIEN OCTOCORAL IN THE SOUTHWEST ATLANTIC, BRAZIL

(Under review in the journal Marine Pollution Bulletin)

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2.1. INTRODUCTION

Biological invasions are an increasing threat to the function and diversity of global ecosystems (Bellard et al., 2016; Catford et al., 2018; Pyšek et al., 2020; Simberloff et al., 2013). The establishment of an alien species (also known as exotic, non-native, or non-indigenous species) in the receiving habitat may cause marked changes in species composition, community structure and ecological processes (Anton et al., 2019; Bradley et al., 2019; Salimi et al., 2021; Simberloff, 2011). Understanding the impacts of invasive alien species on marine communities is critical for identifying the most vulnerable species, predicting future scenarios, and designing effective management measures.

The success of alien species in establishing depends on their biological traits, biotic constraints (Dumont et al., 2011; Kimbro et al., 2013; Vermeij, 1991) and environmental characteristics of the receiving habitat (De Roy et al., 2013; Perkins et al., 2011). Generally, invaders demonstrate typical opportunistic traits such as high genetic variability (Constán-Nava and Bonet, 2012; Giallongo et al. 2021, Sammarco et al. 2017), physiological tolerance (Lagos et al., 2017; Zerebecki and Sorte 2011), and multiple reproductive strategies (Cardeccia et al., 2018; Liu et al. 2017). Likewise, the composition and density of native species regulate competition for resources (Kennedy et al., 2002), and together with abiotic conditions (*e.g.*, temperature, sedimentation, and light) can have positive or negative effects on the invasion progress (Almeida Saá et al., 2020; Kelley, 2014; Thomsen and McGlathery, 2007).

In the marine ecosystems, benthic invaders can spread rapidly and transform communities via bottom-up dynamics and direct habitat modifications (Carter et al. 2019). This is critical for the highly diverse reef environments, where benthic invasive species are affecting biological interactions (Miranda et al., 2016, 2018a), composition and structure of native communities (Faria et al., 2022; Sammarco et al., 2015), functional and trophic diversity (Maggi et al., 2015),

and local primary production (Salvaterra et al., 2013). Most of these studies were related to invasive scleractinian corals and macroalgae, while octocoral invasions remain poorly understood. Currently, the West Atlantic has concentrated several recent octocoral invasions, with records from tropical zones (Altvater and Coutinho, 2015; Menezes et al., 2022; Ruiz-Allais et al., 2014) to the edges of the subtropical border (Carpinelli et al., 2020; Lages et al., 2006; Mantelatto et al., 2018).

In Brazil, seven alien octocorals were recorded invading rocky reef habitats (Altvater and Coutinho, 2015; Carpinelli et al., 2020; Lages et al., 2012; Mantelatto et al., 2018; Menezes et al., 2022; Pires-Teixeira et al., 2021). The two most recent invasion events demand greater attention, because of its rapid spread and local abundance; the xeniids octocorals *Sarcothelia* sp. at Todos os Santos bay, northeastern Brazil (Menezes et al., 2022), and *Latissimia ningalooensis* at Ilha Grande bay (IGB), southeastern Brazil (Mantelatto et al., 2018). These octocorals are typically known as ornamental species and were likely introduced by aquarium release, or an *in-situ* coral cultivation method (Carpinelli et al., 2020; Creed et al., 2020).

Native to the Indo-Pacific region, the encrusting soft octocoral *L. ningalooensis* (Octocorallia, Xeniidae) was found widely distributed along approximately 170 m of the shoreline, at different depths on a single rocky reef of the IGB (Mantelatto et al., 2018). In its first record, the alien octocoral was identified as *Sansibia* sp. (Mantelatto et al., 2018), however, new molecular and morphological analyzes led to the redescription of the taxon to a new genus (*Latissimia*) and species (*Latissimia ningalooensis*) (Benayahu et al., 2022). In the same reef, two other octocoral alien species were found (*Clavularia viridis* and *Erythropodium caribaeorum*) but considered eradicated favored by its low abundance and early detection (Carpinelli et al., 2020; Mantelatto et al., 2018). Conversely, *L. ningalooensis* is highly abundant, and management actions for controlling were tested (ICMBio, 2019) but their effectiveness are still being verified.

The coastal ecosystems of IGB are highly susceptible to biological invasions (Ignacio et al., 2010). The most prominent case of invasive species in the region regards to the sun coral (*Tubastraea coccinea* and *Tubastraea tagusensis*), first detected in the late 1990s (Castro and Pires, 2001; De Paula and Creed, 2004). Currently, sun corals species are widespread distributed along more than 3500 km of the Brazilian southwest Atlantic coastline (de Oliveira Soares et al., 2016) and have been causing serious environmental, social, and economic problems (Lages et al., 2011; Silva et al., 2011, 2014). The arrival of new invaders, with the potential for spreading rapidly throughout the region, calls for an urgent understanding of its impact on reef communities. Therefore, we used a before-after-control-impact (BACI) design to investigate the changes in rocky reef benthic communities associated to the invasion of the octocoral *L. ningalooensis*.

2.2.MATERIAL AND METHODS

2.2.1. Study Area

This study was carried out on coastal rocky reefs adjacent to Vermelha beach, located in Ilha Grande Bay (IGB), southeastern Brazil (23°01'34"S, 44°30'05 "W). The IGB covers an area of approximately 1.000 km², containing around 170 islands surrounded by shallow waters (usually no more than 8 m deep) (Ignacio et al., 2010). The bay has a water surface area of 470 km² and a maximum width of approximately 25 km (Kjerfve et al., 2021). The study area is characterized by narrow rocky shores covered by granite boulders, ending in a sand bottom (interface). In general, the water temperature ranges from 20°C to 31°C (De Oliveira Dias and Bonecker, 2008), with water surface ranging from 15°C to 33°C in some areas of the bay (Barboza and Skinner, 2021). The salinity ranges from 29 to 36 (De Oliveira Dias and Bonecker, 2008), and the local water bodies are influenced by winds and tides with an average amplitude 1.6 m (Nogueira et al., 1991).

2.2.2. Sampling of benthic communities

Our samples were based on an asymmetrical BACI-design, when it is not possible to replicate the impacted site (Underwood, 1992). The invaded site was selected by evaluating the distribution of *L. ningalooensis* of the first record (Mantelatto et al., 2018). For non-invaded sites, in addition to the absence of alien octocoral, rocky reefs were selected close to the invaded site (distance between 200 and 500 meters) and with similar environmental characteristics (*e.g.*, depth, exposure to waves, temperature and salinity) (Fig.1). During our samplings we recorded a new occurrence of *L. ningalooensis* on one of our previously non-invaded sites (C1). We assume that the alien octocoral has not influenced the local benthic communities due to the low coverage registered (< 0.1%). In addition, we removed the alien colony of this site. Therefore, our data were categorized using the following BACI design: (a) an invaded site (Impact - IS) sampled before (2011) and after the invasion (2017 and 2020); (b) a non-invaded site (Control 1 - C1) sampled before (2011) and after the invasion (2020); and (c) a non-invaded site (Control 2 - C2) sampled before (2011) and after the invasion (2020).

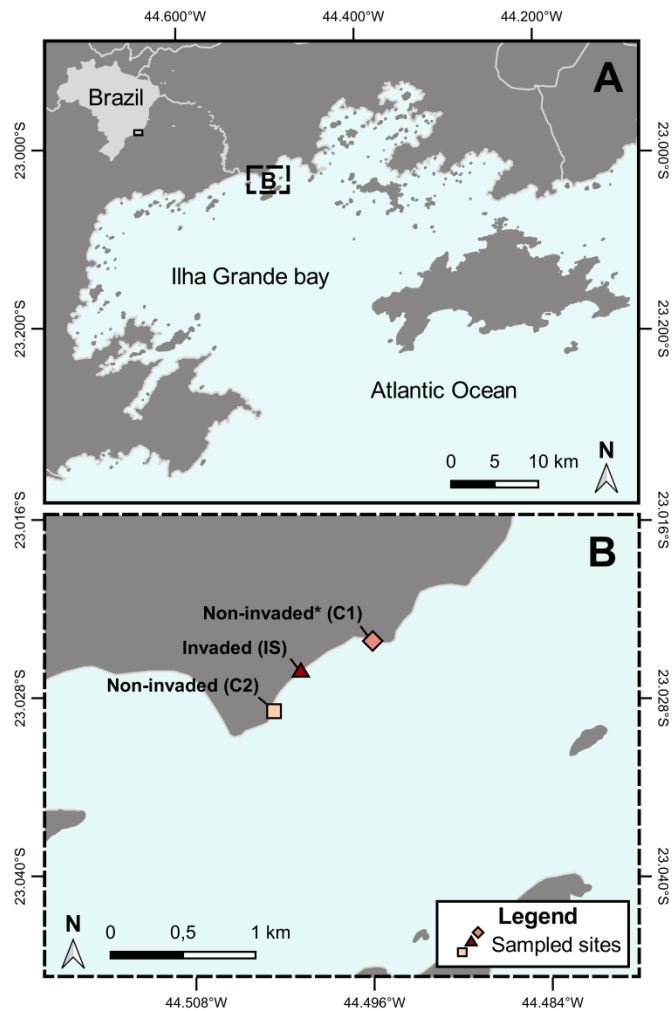


Figure 1 - (A) Map of the study area located in Ilha Grande Bay, Southeastern Brazil. **(B)** Sites sampled, invaded and non-invaded by the invasive octocoral *Latissimia ningalooensis*. The asterisk (*) in C1 represents a new record of *L. ningalooensis*, however the species was managed from the reef.

Benthic communities from all sites and years were sampled using 3.600 cm² (60 cm x 60 cm) PVC photoquadrats along 40 m² (20 m x 2 m) transects to estimate the percentage cover of each organism. For each site, two depth zones were selected: (a) Interface (consolidated substrate, comprising the sand/rock interface – 3.5 m to 7 m deep); and (b) Shallow (upper limit of low tide – 1.5 m to 3.5 m deep). In each zone, we performed three transects by sampling occasion, where 20 photographs were taken per transect. After removing uninterpretable photos, approximately 120 photos per site were selected for each year. A total of 821 photographs were taken at the sampling sites (IS, 3 transects x 2 zones x 3 years; C1 and C2, 3

transects x 2 zones x 2 years). The photographs were taken through SCUBA diving, using a digital camera (Canon Power Shot G9) attached to a waterproof case (WP-DC21) and fixed to the PVC quadrat.

2.2.3. Identification of benthic communities

The software Coral Point with Excel Extensions - CPCe 3.4 (Kohler and Gill, 2006) was used to estimate the percentage of benthic coverage, plotting 40 random points in each photo, and identifying the organisms under each of the points. Benthic organisms were identified at the lowest possible taxonomic level. When identification at a lower level was not possible, taxa corresponding to the genus (e.g., *Sargassum* sp., *Lophocladia* sp., *Diplosoma* sp. and *Mycale* spp.) and morphofunctional groups were assigned (e.g., Turf algae, crustose coralline algae - CCA). We adopted the nomenclature found in the World Register of Marine Species (WoRMS Editorial Board, 2021) and Algae Base (Guiry and Guiry, 2021) for species and genus level. Morphofunctional groups were assigned according to the nomenclature of ecology of coral and rocky reefs studies (Connell et al., 2014; Steneck and Dethier, 1994).

2.2.4. Contact interactions

Physical contact interactions between the alien octocoral and other organisms were estimated through photographs taken at IS, in the years of 2017 and 2020 for each depth zone. Interactions were considered as direct contact between the borders of the octocoral *L. ningalooensis* with other organisms. For each photograph, the contact between *Latissimia* and each native organism was counted once to calculate the frequency of contact occurrence (hereinafter called “interaction frequency” – FI%). Then, an interaction network was created considering the frequency of interactions (> 5%) and the percentage of coverage of organisms

previously identified (adapted from Grillo et al., 2018). Physical contacts was counted by the same researcher (LCJ) to provide a better standardization of the method.

2.2.5. Data analysis

Benthic community data was arcsine-square root transformed to reduce the influence of more abundant and rare organisms. Permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001) was used to test for differences in community structure between years (2011, 2017 and 2020), sites (IS, C1 and C2), and depth zones (Interface and Shallow). Pairwise tests were performed to discriminate differences in benthic communities between years, sites, and zones. The principal coordinate analysis (PCO), combined with vector overlap based on Spearman correlations (correlation > 0.05), was used to visualize the spatiotemporal patterns of species across sites and years. The averages of each transect (six transects per site/year) were used for the PCO analyses. The modified Mann-Kendall test was used to detect significant temporal trends of increase/decrease in the coverage of the most abundant organisms in the invaded site. The modified test is used with variance correction to address possible autocorrelations (Hamed and Ramachandra Rao, 1998).

PERMANOVA pairwise comparisons were performed to assess differences in the most abundant taxa (cover > 1%) between years for each depth zone separately. Bray-Curtis similarity matrices were calculated for multivariate data while Euclidean similarity matrices were calculated for univariate variables. PERMANOVA and PCO analyses were conducted using PRIMER 6.0 + Permanova software (Anderson et al., 2008). Modified Mann-Kendall tests were performed using the ‘modified mk’ package (Patakamuri and O’Brien, 2021) in R-Studio and R version 4.0.4 (R Core Team, 2020).

2.3.RESULTS

2.3.1. Benthic composition

Our study sites were mainly covered by turf algae, the zoanthid *Palythoa caribaeorum*, the fleshy algae *Dichotomaria marginata*, *Lophocladia* sp., *Sargassum* sp. and *Dictyota ciliolata*, and the alien octocoral *L. ningalooensis* in the IS. Turf algae dominated all sites, with greater abundance in IS (percentage cover - 2011 = 68.9%, 2017 = 27%, 2020 = 33.4%) and C1 (2011 = 43.2%, 2020 = 42%), while *P. caribaeorum* was the most abundant taxa in C2 (2011 = 52.4%, 2020 = 48.8%). *Latissimia ningalooensis* was the second most abundant organism in IS at both post-invasion years (2017 = 25.4%, 2020 = 24.6%). Two small patches (< 1 m²) of the alien octocoral were first recorded at site C1 (total coverage < 0.1%; Fig. 2A) in 2020.

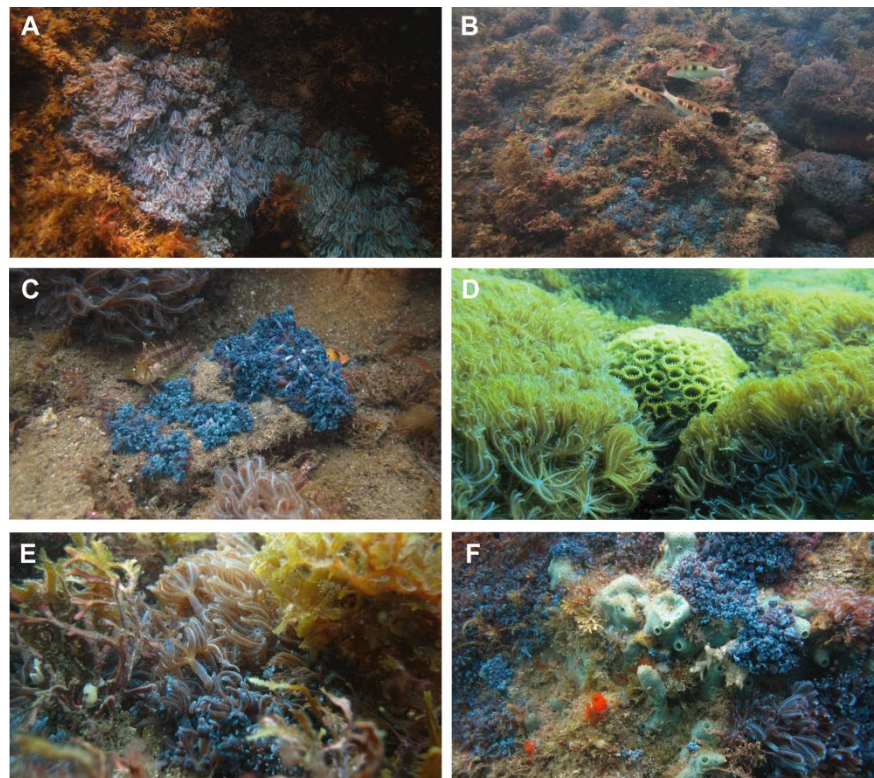


Figure 2 - *Latissimia ningalooensis* in the sampled rocky reefs. (A) New occurrence of the alien octocoral registered in C1. (B) and (C) *Latissimia ningalooensis* occurring at different depth zones on the invaded reef. (D) Solitary colony of *Palythoa caribaeorum* resisting the alien octocoral. (E) and (F) *Latissimia ningalooensis* growing over areas covered by macroalgae and sponges.

In relation to fleshy algae, IS consisted of high cover of *D. marginata* (cover of 5 – 9%), C2 was covered by the highest proportion of *Lophocladia* sp. (2011 = 20.5%; 2020 = 14.7 %), while macroalgae cover in C1 was more evenly distributed between *D. marginata*, *Sargassum* sp. and *D. ciliolata*, mainly in 2020 (cover > 7.5% each). Other invertebrates, such as sponges, hard corals, ascidians, and hydrozoans had low coverage (< 1%) (Fig. 3).

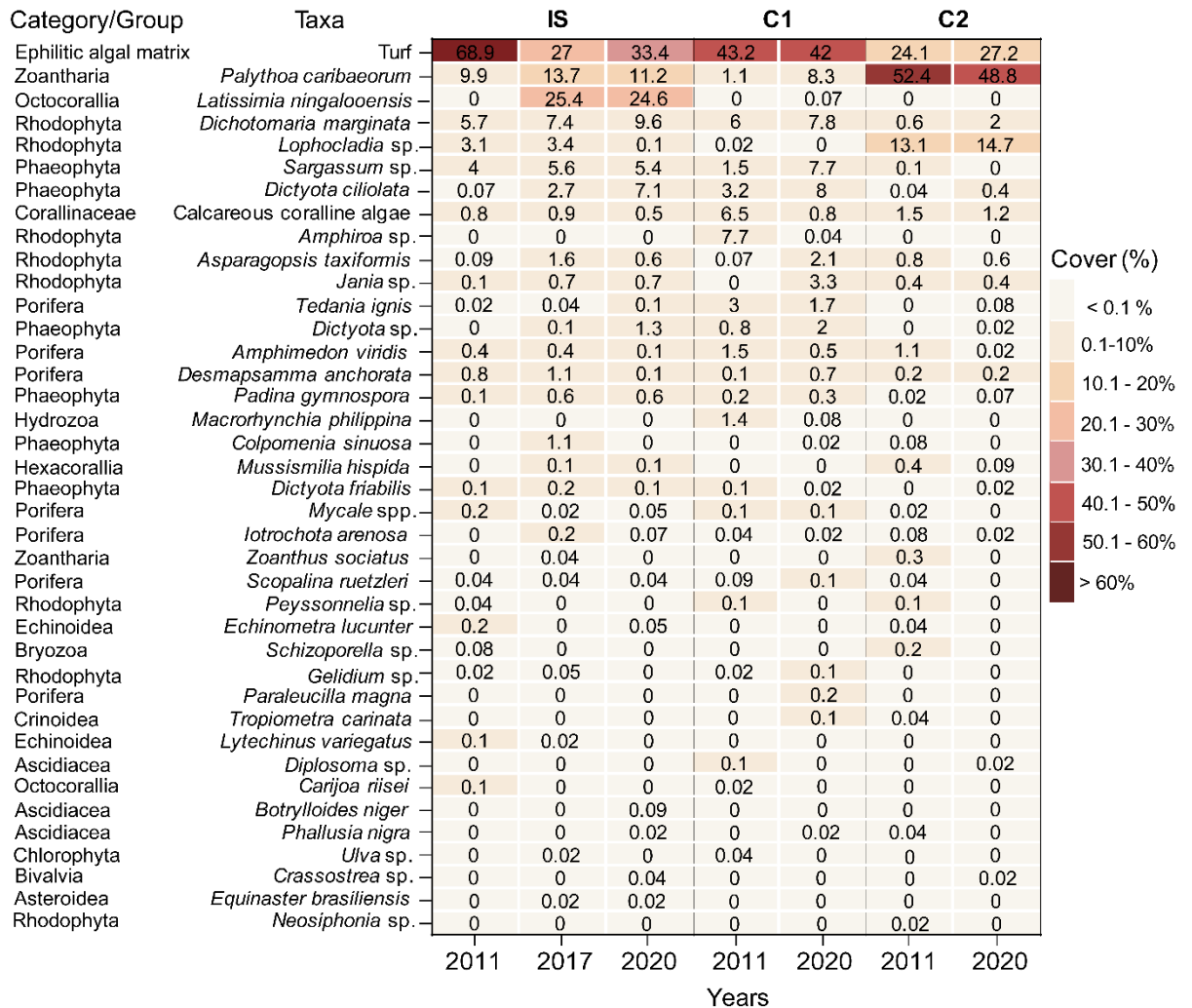


Figure 3 - Heatmap of the abundance of benthic organisms (% cover) between the years and sites sampled.

2.3.2. Spatiotemporal changes in benthic communities

Benthic community structure changed significantly across sites (PERMANOVA, Pseudo- $F = 34.3$, $p = 0.0001$), years (Pseudo- $F = 152.9$, $p = 0.0001$) and zones (Pseudo- $F =$

23.2, $p = 0.0001$), and the interactions between all these factors (Table 1). The PERMANOVA pairwise comparisons confirmed statistical differences in benthic communities between all years for IS and C1 ($p = 0.0001$). In contrast, there were no significant temporal differences in benthic community for site C2 (Table S1).

Table 1 - PERMANOVA test results based on Bray Curtis similarity for differences in benthic community structure across years, sites, and zones.

Source	df	SS	MS	Pseudo- F	P
Year	2	93644	46822	34.38	0.0001
Site	2	4.16580	2.08290	152.98	0.0001
Zone	1	31688	31688	23.27	0.0001
YearxSite	2	77443	38722	28.44	0.0001
YearxZone	2	14421	7210.7	5.29	0.0001
SitexZone	2	28752	14376	10.55	0.0001
YearxSitexZone	2	11609	5804.3	4.26	0.0004
Residuals	807	1.09880	1361.5		

(df = degrees of freedom, SS = sum of squares, MS = mean sum of squares)

The first PCO axis contained 45.1% of the total variation of the benthic cover and was largely associated to the highest *P. caribaeorum* and *Lophocladia* sp. cover in C2 and higher fleshy algae and turf cover in IS and C1 (Fig. 4). The second PCO axis contained 18.8% of the variation and was largely associated with the octocoral *L. ningalooensis* invasion and changes in fleshy algae cover in the IS.

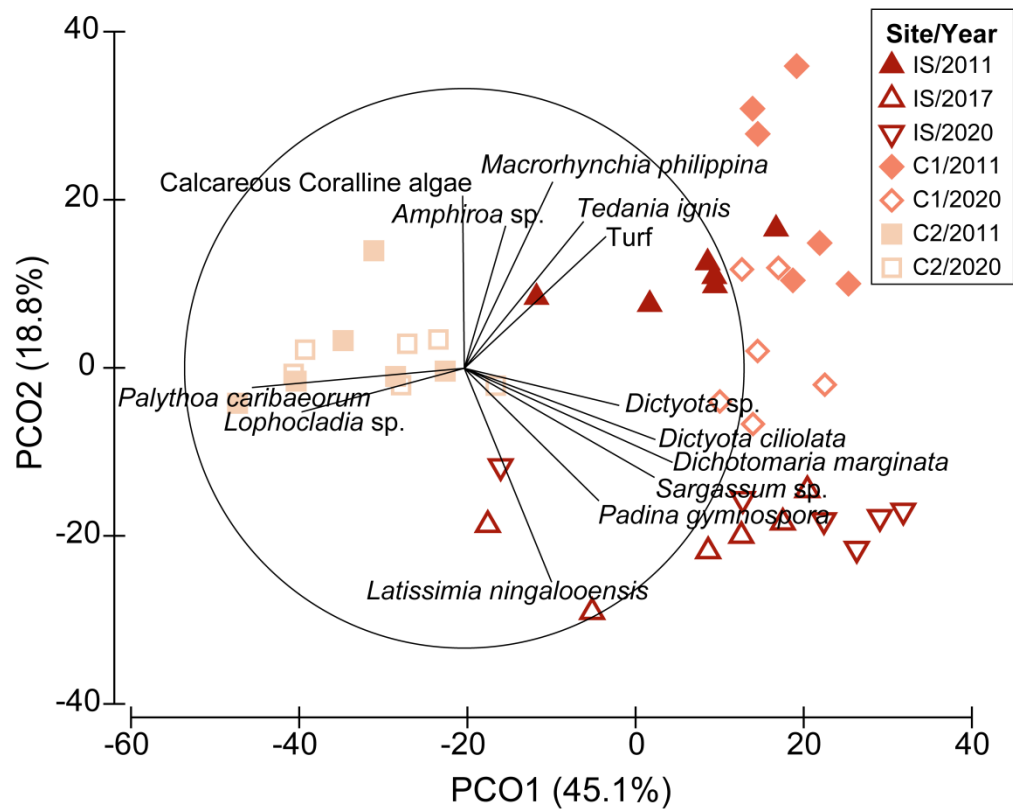


Figure 4 - Principal coordinate analysis (PCO) of the benthic cover between the three sites and years sampled. Benthic organisms that most correlated with the two main axes are superimposed (Pearson correlation index, cut-off point > 0.5).

Turf algae cover decreased in the IS over the years (~40%), varying mainly in the shallowest zone of the rocky reef (Fig. 5). In contrast, turf algae remained stable in the control sites (C1 and C2), except for a small decrease in the interface zone of C1. Similarly, *P. caribaeorum* cover was constant in the shallow areas across all sites. *Latissimia ningalooensis* was similar for 2017 and 2020 in the IS for both interface and shallow zones. In general, the fleshy algae *D. marginata*, *Sargassum* sp. and *D. ciliolata* cover increased from 2011 to 2017/2020 for IS and C1. *Lophocladia* sp. varied mainly between the years of the IS, unlike the CCA which remained similar across the years. *Amphiroa* sp. cover was higher at the shallow zone of C1 in the year of 2011.

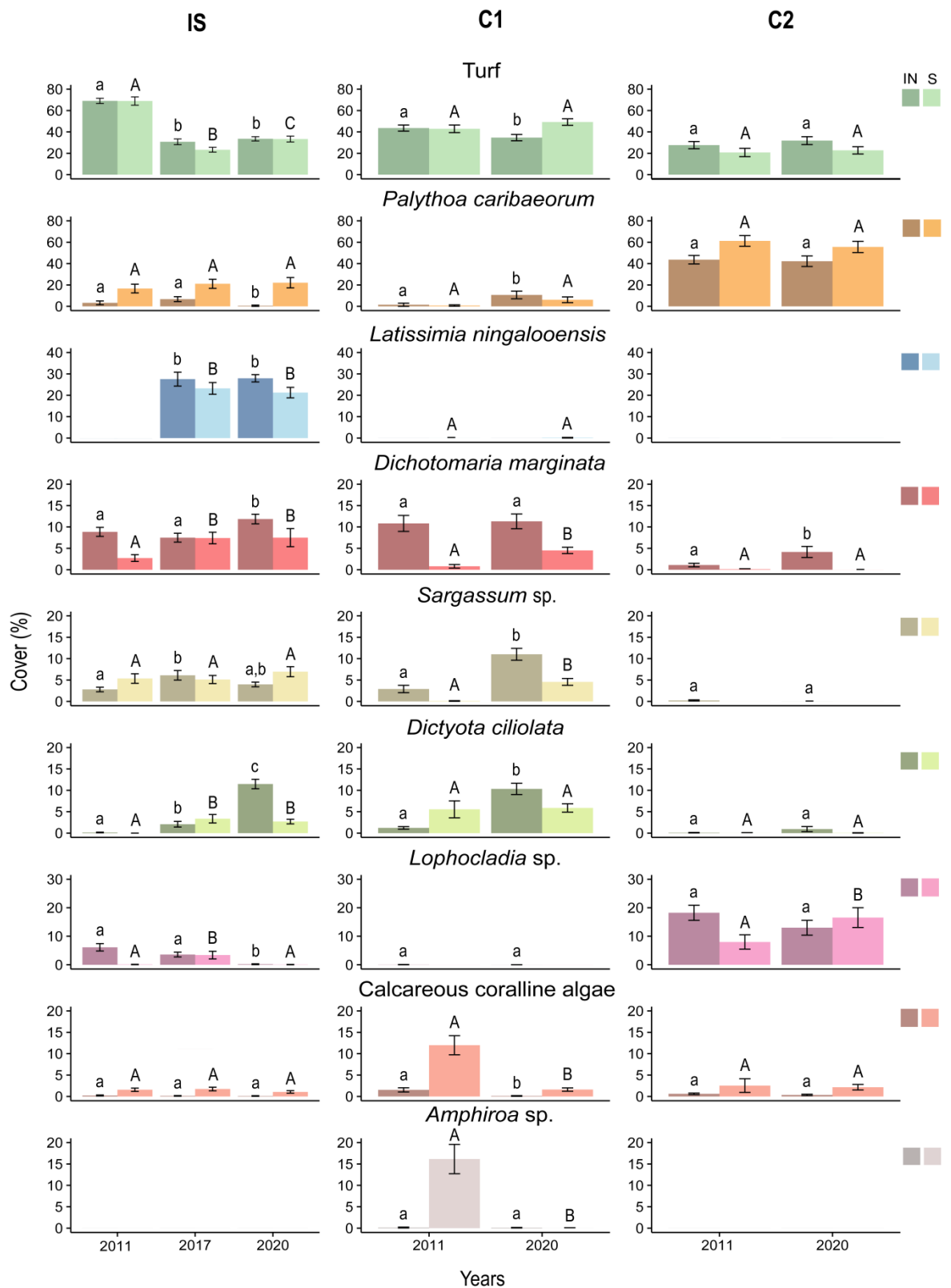


Figure 5 - Bar plots of the benthic cover (mean ± SE) of the most abundant organisms (cover > 1%) for each depth zone of sites invaded and non-invaded by *Latissimia ningalooensis*. Different letters above the bars represent the result of the PERMANOVA pairwise tests for each year's zones. IN = Interface and S = Shallow. Lower case letters for interface and capter letters for shallow.

2.3.3. Post invasions trends

Turf algae abundance decreased markedly after the *L. ningalooensis* invasion for both zones (interface and shallow), but it remains largely distributed in the IS site (FO > 90% for all years). Although *L. ningalooensis* cover remained similar between 2017 and 2020, their frequency of occurrence increased at all depths, mainly for the interface zone (2017 = 79%, 2020 = 100%, Fig. 2B and C). The occurrence of *P. caribaeorum* at the interface varied between years (2011 = 6.6%, 2017 = 20%, and 2020 = 1.6%), with higher frequencies and stability in the shallow zone, where it is more abundant (2011 = 36%, 2017 = 42%, and 2020 = 31%) (Fig. 6).

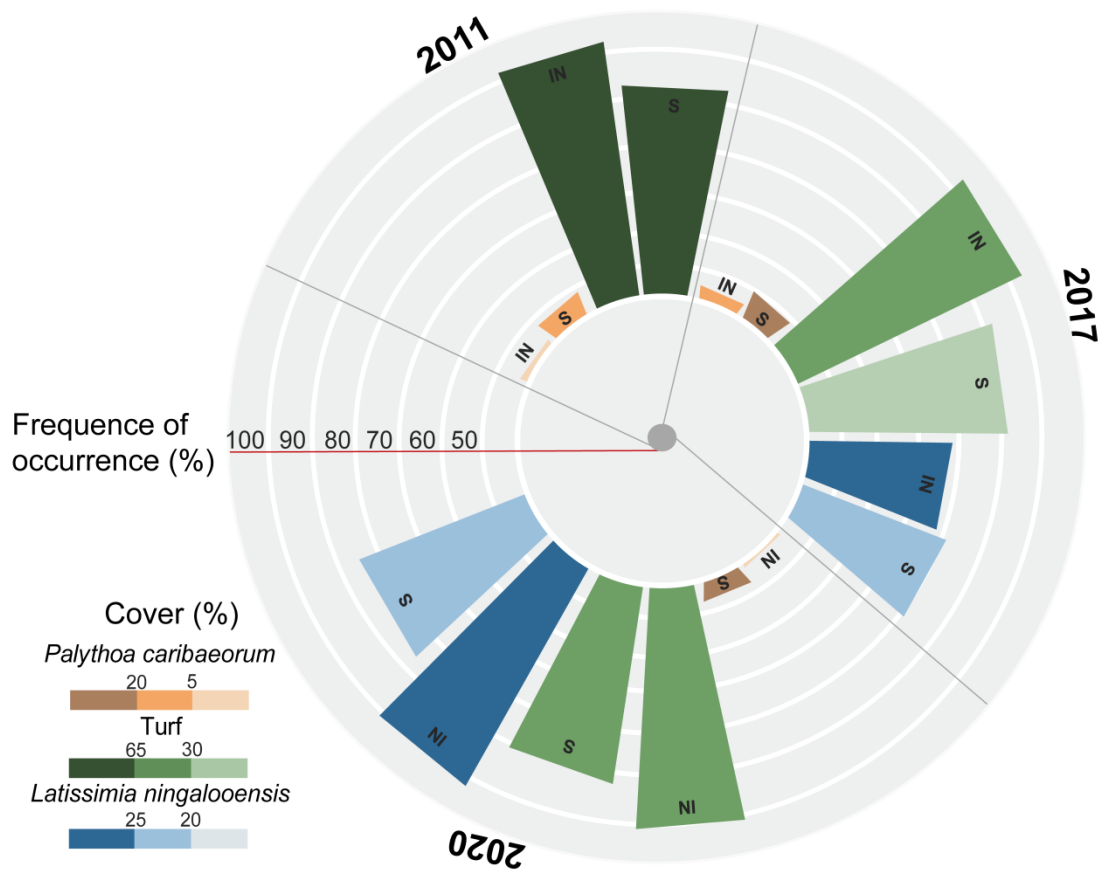


Figure 6 - Circular bar plot of the frequency of occurrence of the three most abundant organisms in the study (turf algae, *Latissimia ningalooensis* and *P. caribaeorum*) for each zone and year of the invaded site. IN = Interface and S = Shallow. The color gradient represents the percentage of coverage for each organism.

After the invasion of *L. ningalooensis*, some trends were observed for turf algae and *P. caribaeorum*. The octocoral showed a significant trend to increase its coverage at the interface (Mann-Kendall test, $p = 0.008$), where it is more abundant and frequent, while no significant trends were identified in the shallow zone (Mann-Kendall test, $p = 0.55$). Differently, turf algae indicated a decreasing trend in their coverage in the two depth zones (Mann-Kendall test, $p < 0.0001$). The zoanthid *P. caribaeorum* showed no significant trend in at the interface (Mann-Kendall test, $p = 0.44$) and in the shallow (Mann-Kendall test, $p = 0.11$) (Fig. S1).

2.3.4. Contact interactions

We observed 796 physical contacts between the alien octocoral and other native benthic organisms. The number of contacts with *L. ningalooensis* increased from 347 to 449 between 2017 and 2020, respectively. Turf algae ($n = 189$), *D. marginata* ($n = 131$), *Sargassum* sp. ($n = 116$), *D. ciliolata* ($n = 97$), and *P. caribaeorum* ($n = 35$) had the highest number of contacts with alien octocoral.

In general, the interaction networks showed that the most abundant organisms were those with greater contact with *L. ningalooensis*. Turf algae and *D. marginata* had the highest frequencies of interactions (FI) with the alien at the interface of 2017 (FI = 72 and 62%, respectively) and in 2020 (FI = 100 and 91%, respectively). In the shallower zone, turf (FI, 2017 = 73%; 2020 = 84%) and *Sargassum* sp. (FI, 2017 = 48%; 2020 = 49%) recorded the largest contacts. Despite the high cover of *P. caribaeorum* in the shallow zone for 2017 and 2020, their interaction with the alien octocoral was lower than that observed for the less abundant fleshy algae (Fig. 7). We identified the alien octocoral overgrowing areas covered by macroalgae and sponges (Fig. 2E and F).

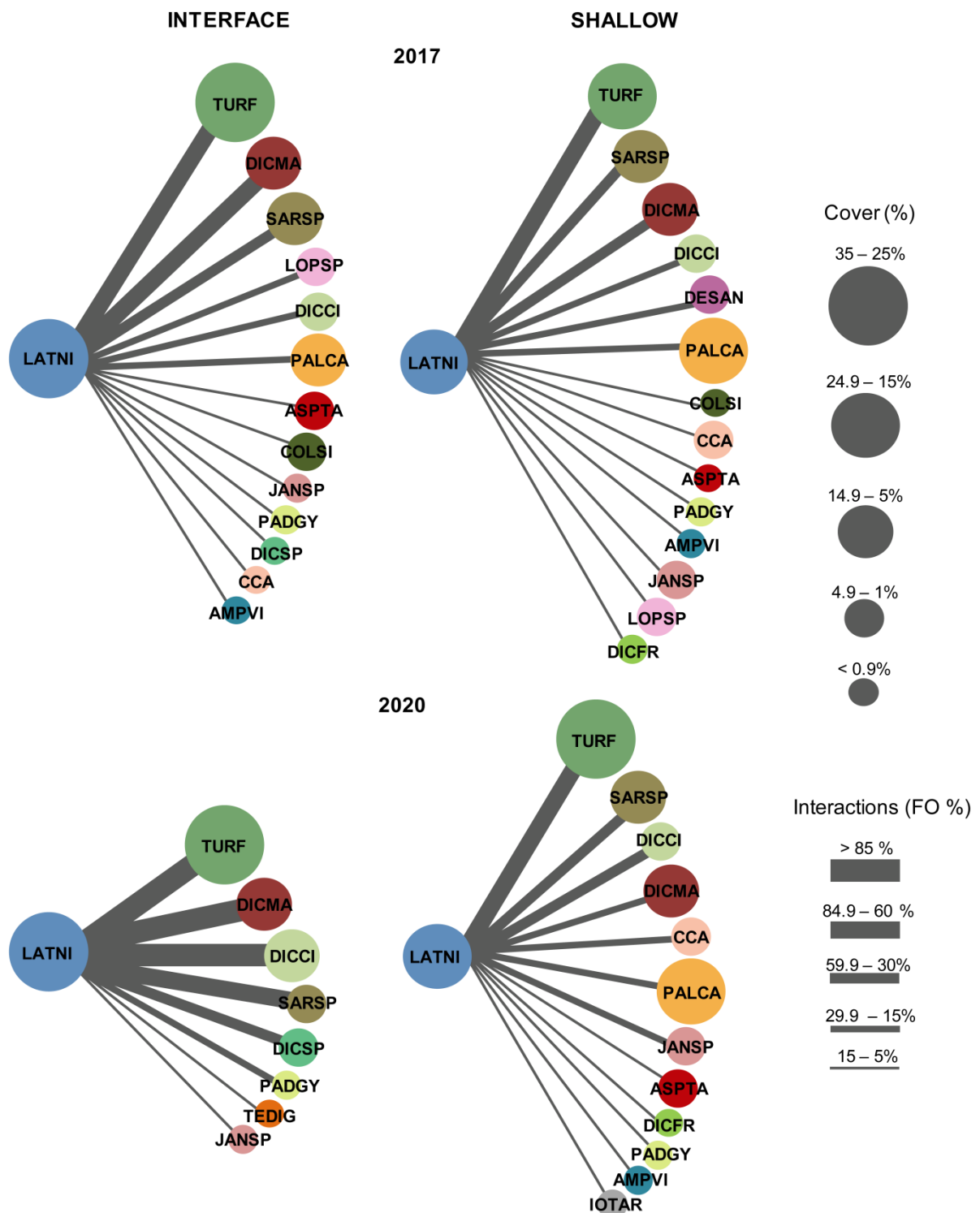


Figure 7 - Networks of interactions with physical contact between the alien octocoral *Latissimia ningalooensis* and other native benthic organisms between the zones and years of the invaded site. The circles represent the percentage of coverage of organisms and the lines represent the frequency of occurrence of interactions (Frequency of interactions > 5%). Species codes: LATNI - *Latissimia ningalooensis*; TURF – turf algae; PALCA – *Palythoa caribaeorum*; DICMA – *Dichotomaria marginata*; SARSP – *Sargassum* sp.; LOPSP – *Lophocladia* sp.; DICCI – *Dictyota ciliolata*; ASPTA – *Asparagopsis taxiformis*; COLSI – *Colpomenia sinuosa*; JANSP – *Jania* sp.; PADGY – *Padina gymnospora*; DICSP – *Dictyota* sp.; CCA – Crustose Coralline algae; AMPVI – *Amphimedon viridis*; DESAN – *Desmapsamma anchorata*; DICFR – *Dictyota friabilis*; TEDIG – *Tedania ignis*; IOTAR – *Iotrochota arenosa*.

2.4.DISCUSSION

The long-term monitoring of benthic communities contributes to understand the impacts of invasive species on the receiving habitat. We show that the alien octocoral *L. ningalooensis* was largely associated with changes in the benthic community structure of the invaded site, related to a 2-fold decrease in turf-forming algae. In contrast, non-invaded sites dominated by zoanthids remained similar over time, with a decrease in calcareous algae cover observed for small patches of the reef. Our results indicate that turf-forming algae are more susceptible to the octocoral invasion, with the zoanthid offering greater biotic resistance.

The influence of the alien octocoral *L. ningalooensis* in the decrease of turf algae cover (~40%) at the invaded site is supported by the relatively stability of algae cover in the non-invaded sites. Turf algae dominates the substrate cover of southwest Atlantic marginal reefs, characterized by high nutrients and/or sedimentation levels (Perry and Larcombe, 2003), and tolerates the increased anthropogenic impacts (Aued et al., 2018). Unlike our results, a 24% increase in turf algae cover was observed for southeastern coast of Brazil between 1967 and 2017, including the IGB region (Gorman et al., 2020).

Octocorals of the Xeniidae family are great colonizers and substrate competitors, due to their ability to overgrow on neighboring organisms and produce toxic or allelopathic secondary metabolites (Benayahu and Loya, 1985, 1981; Coll et al., 1985; Fabricius et al., 2001; Hoang et al. 2016; Sammarco et al., 1983). Encrusting corals compete most successfully against turf algae through abrasion, stinging, allelopathy, or mucus secretion (Swierts and Vermeij, 2016). Conversely, morphological plasticity of stoloniferous turf algae, such as increasing the formation of new ramets, when in contact with corals, may favour their colonisation of coral tissue and resistance against coral invasion (Cetz-Navarro et al., 2015). However, the stability and high abundance of fleshy algae (*D. marginata*, *Sargassum* sp. and *D. ciliolata*) in this study indicated that more developed macroalgal thalluses were not affected by *L. ningalooensis*

invasion. Encrusting octocorals (*Erythropodium hicksoni*) suffocated small macroalgal recruits, but conversely, frondosum macroalgal thallus surrounded and negatively impacted the octocoral (Ling et al., 2020).

Besides areas covered by fleshy algae, zoanthid patches (mainly *Palythoa caribaeorum*) remained stable coverage between pre-and post-invasion data (9-year period), indicating a greater biotic resistance against the octocoral. The ability in reducing the invasive expansion through the reef depends on the depth zone, since *P. caribaeorum* was more abundant in the shallow area and may be more important at sites densely coverage by zoanthids, such as C2. *Palythoa caribaeorum* is an aggressive competitor for space, using different physical strategies (e.g., overgrowth, lateral aggression and point settlement) and chemical defenses associated with the use of palytoxin (Bastidas and Bone, 1996; Silva et al., 2015; Suchanek and Green, 1981). The zoanthid is able to actively compete against invasive corals, through overtopping (Almeida Saá et al., 2020), and passively can hinder the growth of invading corals in the contact zone (Guilhem et al., 2020) (Fig. 2D). In the early stages of the *U. stolonifera* invasion in the Venezuelan reefs, *P. caribaeorum* prevailed over the invader, although eventually, some colonies were completely colonized by the xeniid (Ruiz-Allais et al., 2021).

Asexual reproduction is an important trait of invasive species, mainly in the first stage of invasion (Capel et al., 2017; Liu et al., 2017; Taylor and Hastings, 2005; Wright, 2005), and may be the strategy used to *L. ningalooensis* reaching up to 25% of the benthic cover of the invaded site. Soft corals use a broad array of asexual reproduction, such as simple fission (Benayahu and Loya, 1985), survival and religation of colony fragments (Walker and Bull, 1983) and rapid autotomy of small fragments with root-like processes that enable a rapid attachment onto the substrata (Dahan and Benayahu, 1997). The fragmentation and re-attachment are particularly important for the rapid colonization of the substrate by soft corals (Barneah et al., 2002; Benayahu and Loya, 1985; Fabricius et al., 2001), allowing the spread

from large and well-established patches. The relatively stable cover and the increase to 100% of frequency in 2020 (Fig. 6) suggest that the expansion through small fragments is an important mechanism used by the alien octocoral *L. ningalooensis*. It is also consistent with the increased number of interactions between the alien octocoral and macroalgae, especially turf algae, while contacts with highly defensive zoanthids remained the same. In contrast, turf algae are known to inhibit the settlement of new octocoral recruits (Linares et al., 2012; Wells et al., 2021). Furthermore, many small fragments of *L. ningalooensis* (~2mm) were found near the bottom of the invaded site and overgrowing gastropods and hermit crabs (LCJ and LMN personal observation, Mantellato et al. 2018).

Our results show that the positive trend in octocoral cover expansion corresponded with a decrease in turf algae cover. Furthermore, the high number of turf-octocoral interactions indicates a future reduction in turf cover. Conversely, *P. caribaeorum* cover tends to be stable, as indicated by 9-year study period. Octocorals have increased in abundance in shallow reefs (<30m) in the Caribbean, unlike scleractinians, which have undergone marked declines in abundance (Sánchez et al., 2019). Besides the well-known degraded state of macroalgae dominance in coral reefs (Hughes et al. 2007; McManus and Polsenberg 2004; Mumby 2009), octocorals represent a possible alternate state at reefs previously dominated by scleractinians (Lasker et al. 2020; Sánchez et al. 2019; Tsounis and Edmunds 2017). The dominance of octocorals is related to changes in habitat complexity, functional and trophic structure of the reef communities (Lenz et al., 2015; Norström et al., 2009; Sánchez et al., 2019; Vollstedt et al., 2020). The octocoral *U. stolonifera* expanded their coverage in the Venezuelan reefs to 80% after 8 years of invasion, promoting drastic changes in the coverage of stony corals, hydrocorals and other anthozoans (Ruiz-Allais et al., 2021, 2014). The alien xeniid *Sarcothelia* sp. reached 23.6% of mean coverage in a rocky reef of northeastern Brazil in 2018, also suppressing the previously dominance of turf algae cover (Menezes et al., 2022). In the southwest Atlantic reefs,

the decline in abundance of turf-forming algae following the emergence of invasive octocorals threatens the structure and functioning of the biologically diverse macroalgal-dominated rocky reefs.

We observed *L. ningalooensis* colonies in the intertidal zone and using holdfasts on the sand near the hard substrate. Also, *L. ningalooensis* crossed a shallower sand plain (through Vermelha beach) reaching C1. Although the limitation of hard substrate may hinder the expansion of the octocoral to insular reefs (Mantelatto et al., 2018), invasive xeniids rapidly spread to other sites settled on seagrass fragments and fishing nets (Ruiz-Allais et al., 2021). Currents and winds can spread invasive species attached to floating wood debris and marine litter via rafting, while boats visiting several locations over short period are rapid mechanisms of range expansion and secondary introduction within a region (Kauano et al., 2017; Lewis et al., 2005; Mantelatto et al., 2020). *Latissimia* invasion represents a potential threat to the biodiversity of IGB rocky reefs due to their high local abundance and ability to colonize hard substrates from the intertidal zone to holdfasts over the sand bottom.

The early detection, rapid response and limited invaded area are key aspects related with the success of marine invasive species eradication (Giakoumi et al., 2019; Simberloff, 2021). Subtidal eradications are rare, with few successful cases reported in the literature (Simberloff, 2021). For example, the mussel *Mytilopsis sallei* in Cullen Bay, and the macroalgae *Caulerpa taxifolia* in coastal lagoons of California were successfully eradicated after ~2yrs of invasion through chemical treatment and isolation of invaded areas (Anderson, 2005; Bax et al. 2002). Furthermore, octocoral species were probably eradicated at the invaded site of this study (Carpinelli et al., 2020; Mantelatto et al., 2018), due to their low abundance and early detection. Despite the high abundance of *L. ningalooensis*, its eradication may be possible due to their restricted occurrence at IGB, extending through 170m along a coastal reef. However, it is critical to develop a suitable removal method that minimizes the risk of increasing dispersion.

The eradication of *L. ningalooensis* should be urgently discussed by environmental agencies, managers, and scientists, considering that as an invasive species expands, eradication costs increase and the window of opportunity to perform an eradication program closes (Simberloff, 2003). Eradication and control strategies of alien species require substantial investment and stakeholder engagement (Anderson, 2005; Bax et al. 2002; Marks et al., 2017; Neilson et al., 2018). However, the costs of prevention, control and eradication are substantially lower than the losses of goods and services caused by the impacts of invasive alien species on the environment (Adelino et al., 2021). In Brazil, for example, the large-scale invasion of the scleractinian corals *Tubastraea* spp. affected several marine economic sectors (*e.g.*, fisheries, tourism and oil and gas production) (Braga et al., 2021; Creed et al., 2021), in addition to the well-known ecological impacts on the reef systems (Creed et al., 2017). In relation to *L. ningalooensis*, a rapid response while its occurrence is still restricted makes the control and eradication possible and less expensive when compared to future impacts. The synergism among different actions (*e.g.*, physical and chemical removal methods, impact assessment, environmental rehabilitation, and public awareness programs) is an efficient strategy for managing some alien species (Giakoumi et al., 2019; Ojaveer et al., 2015; Robertson et al., 2020). Therefore, joint efforts between scientists, government agencies, local communities, and potentially impacted industries can contribute to developing a suitable management plan for controlling and eradication of *L. ningalooensis*.

This study is a warning to the invasive potential of *L. ningalooensis*, because of its high abundance, competitive and expansion ability, associated with drastic temporal changes in the benthic community not observed for non-invaded sites. The growth of *L. ningalooensis* on turf algae threatens the southwest Atlantic rocky reefs dominated by macroalgae, and the impacts on function and diversity of reef organisms need further investigation.

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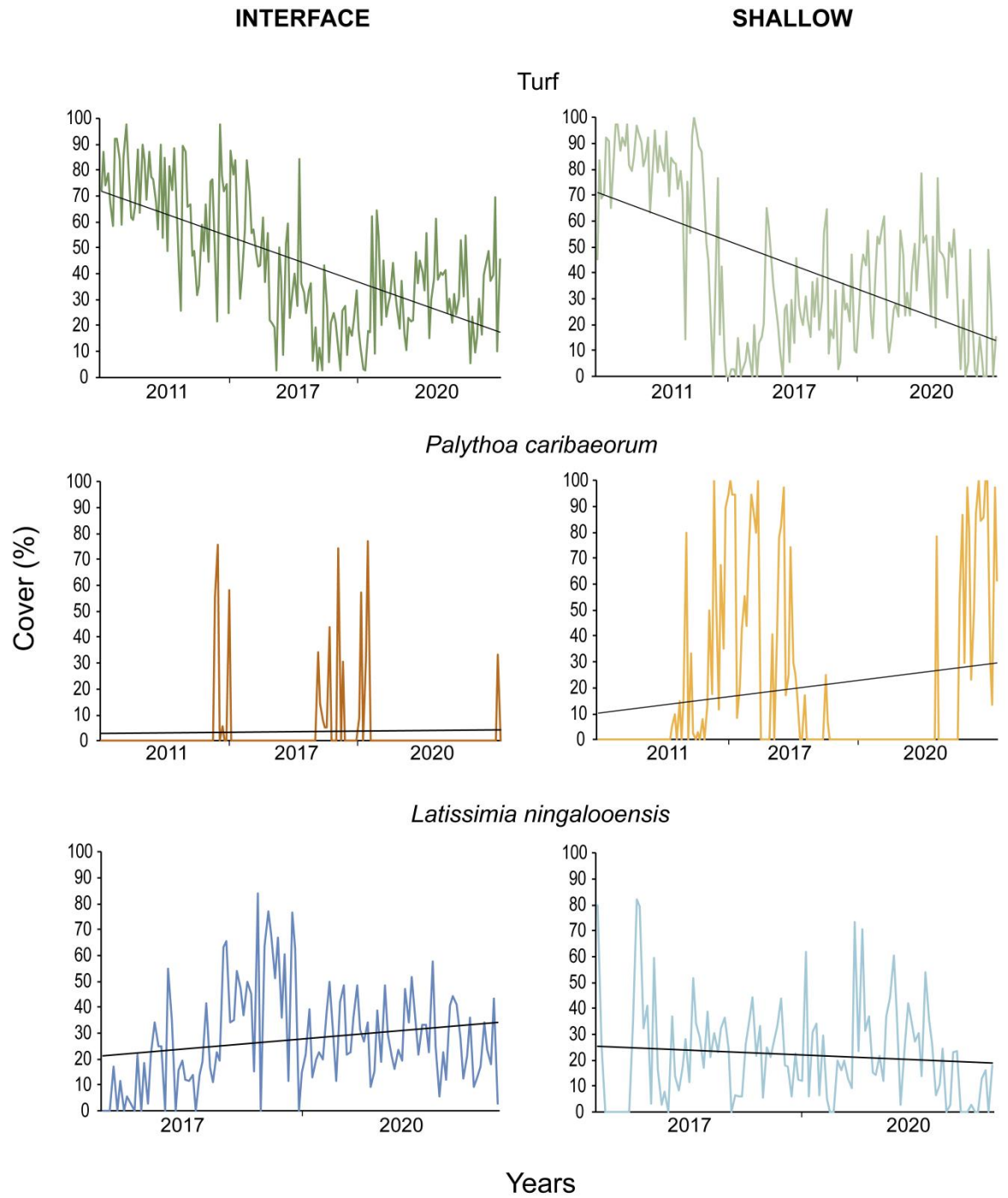
SUPPLEMENTARY MATERIAL

SM1: Table S1: PERMANOVA pairwise test results based on Bray Curtis similarity for differences in benthic community structure across years, sites, and zones.

Pairwise tests		
Source	Levels	<i>P</i>
Year x Site	2011 vs 2017 x IS	0.0001
	2011 vs 2020 x IS	0.0001
	2017 vs 2020 x IS	0.0001
	2011 vs 2020 x C1	0.0001
	2011 vs 2020 x C2	ns
Year x Site x Zone	2011 vs 2017 x IS x Interface	0.0001
	2011 vs 2020 x IS x Interface	0.0001
	2017 vs 2020 x IS x Interface	0.0001
	2011 vs 2017 x IS x Shallow	0.0001
	2011 vs 2020 x IS x Shallow	0.0001
	2017 vs 2020 x IS x Shallow	ns
	2011 vs 2020 x C1 x Interface	0.0001
	2011 vs 2020 x C1 x Shallow	0.0001
	2011 vs 2020 x C2 x Interface	ns
2011 vs 2020 x C2 x Shallow	ns	

(ns = non-significant).

SM2: Fig S1: Line Plot of the temporal trends of the percentage of coverage of turf algae, *Palythoa caribaeorum* and *Latissimia ningalooensis* in different depth zones of the invaded site (IS).



APÊNDICE A – GRAPHICAL ABSTRACT

