



UNIVERSIDADE FEDERAL DA BAHIA - UFBA

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Mestrado em Ecologia: Teoria, Aplicação e Valores

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**Efeito das relações competitivas interespecíficas envolvendo
Tubastraea spp. (Scleractinia, Dendrophyllidae) e *Palythoa*
caribaeorum (Zoantharia, Sphenopidae)**

Salvador, dezembro de 2022

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Àwà ní ìbí tí àwà lònì, nítòrípè à dúrò léjìkà, awò n' tí wòn wa síwàjú wà.
Estamos aonde estamos hoje porque estamos sobre os ombros daqueles que vieram antes de nós. (Provérbio Iorubá)

Dedico a minha vó Detinha (*in memorian*) e a meu avô Nelson (*in memorian*)!

A Nanã, Oxum e Yemanjá! Àse!

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Texto de divulgação

EFEITO DAS RELAÇÕES COMPETITIVAS INTERESPECÍFICAS ENVOLVENDO ESPÉCIES DO CORAL-SOL INVASOR (*Tubastraea* spp.) E O CORAL NATIVO BABA-DE-BOI (*Palythoa caribaeorum*)

Nelma dos Santos Freitas

Em um ecossistema, as interações competitivas são importantes para a estruturação da comunidade, pois, pode interferir na sobrevivência, crescimento e reprodução dos competidores envolvidos, e assim afetar a biodiversidade nos habitats. Entretanto, com o aumento, ao longo das últimas décadas, da ocorrência de espécies invasoras associadas às atividades humanas e seus vetores, estas interações tornam-se ainda mais prejudiciais para alguns organismos, já que espécies invasoras podem competir por recursos e reduzir a abundância de espécies nativas e alterar a estrutura de comunidades biológicas nativas.

Neste contexto, destaca-se a bioinvasão do coral-sol, *Tubastraea* spp., oriundo do oceano Pacífico. A ocorrência deste gênero na costa brasileira foi registrada pela primeira vez no final da década de 80 em plataformas de petróleo e gás no litoral do Rio de Janeiro. Atualmente, colônias de coral-sol encontram-se integradas, principalmente, às comunidades bioincrustantes de substratos artificiais, como marinas, píeres, cascos de navios, plataformas, e comunidades bentônicas de costões e afloramentos rochosos, e no litoral da Bahia, em regiões estuarinas e recifes de corais, áreas que se destacam como ecossistemas marinhos de alta biodiversidade.

Os corais do gênero *Tubastraea* são competidores habilidosos, apresentando várias estratégias que facilitam suas chances de sobrevivência no ambiente marinho, tais como alta fecundidade, rápido crescimento e dispersão, defesas químicas potentes e agressividade competitiva provocando danos e até a morte de espécies nativas, além de alterar a estrutura de comunidades bentônicas locais. Apresentando também estratégias elaboradas de competição, o coral nativo *Palythoa caribaeorum*, chamado popularmente de “baba-de-boi”, possui altas taxas de crescimento e formam tapetes espessos no substrato, e aliado a esta característica, a espécie produz uma forte biotoxina, a paliotoxina, dominando assim o espaço e restringindo o crescimento de

seus concorrentes. Nos ambientes recifais, zoantídeos coloniais como *P. caribaeorum* são importantes, pois contribuem com a produção primária e servem como recurso alimentar para diversas espécies. Esse encontro de titãs foi avistado em regiões de costão rochoso nos estados do Rio de Janeiro e São Paulo, onde registrou-se o coral nativo *P. caribaeorum* coexistindo com *T. tagusensis* e também com *T. coccinea*.

Assim, objetivando ampliar a compreensão sobre as habilidades competitivas entre as espécies de *Tubastraea*, i.e., *T. tagusensis* e *T. coccinea*, e destas com *P. caribaeorum*, foi elaborado um experimento manipulativo, reproduzindo situações de competição a partir do contato direto entre as espécies do coral-sol e destas com o zoantídeo. A partir desse estudo observou-se que nenhum dano tecidual foi detectado em nenhuma amostra de *Tubastraea* durante o experimento intragenérico. Enquanto *P. caribaeorum* sofreu retração, deposição de muco e sobrecrecimento, sendo identificada redução da área ocupada pelo zoantídeo apenas durante a interação com *T. tagusensis*. Constatou-se também que *T. tagusensis* exibe habilidades competitivas superiores em relação a espécie nativa *P. caribaeorum*, entretanto não foram encontrados valores significativos para a interação desta com *T. coccinea*. Apesar de ser um imponente adversário da guerra química na disputa por espaço, *P. caribaeorum* teve suas habilidades competitivas superadas por *T. tagusensis* sugerindo que além do arsenal químico, esta espécie de coral invasor possa ter sua morfologia como mais um ponto a seu favor.

Diante disso, investigar as interações competitivas entre organismos introduzidos e espécies nativas contribui para o entendimento da relação entre as populações, dos mecanismos envolvidos e como a diversidade local será afetada, sendo também uma preocupação prioritária para o desenvolvimento de políticas de manejo e mitigação de impactos associados à bioinvasão.

Resumo

O espaço é um recurso limitado para o estabelecimento de espécies bentônicas em substratos consolidados. Considerando a introdução de espécies invasoras, os efeitos da interação competitiva interespecífica devem ser avaliados, uma vez que a prevalência desses organismos sobre as espécies nativas depende de um repertório de estratégias não totalmente compreendido. Os corais *Tubastraea* se espalharam ao longo do Oceano Atlântico, sendo observados principalmente em substratos artificiais. Em contraste com a Grande Barreira de Corais no Oceano Pacífico, onde mais de 300 espécies foram identificadas, a diversidade de escleractíneos de águas rasas no Brasil é reduzida (21 espécies) com as principais espécies construtoras de recifes representadas pelo gênero *Mussimilia*. *Palythoa caribaeorum* é um zoantídeo nativo com altas taxas de crescimento, e colônias com pólipos curtos embebidos no *coenenchyma*. A espécie forma tapetes espessos em substratos duros, produzindo também uma forte biotoxina: a palitoxina. Para estudar a interação entre *Tubastraea* spp. e *P. caribaeorum*, um experimento manipulativo foi desenvolvido *in situ* na Baía de Todos-os-Santos (12°S, Bahia). Duas espécies (e respectivos morfotipos), *Tubastraea tagusensis* (dendróide) e *Tubastraea coccinea* (plocóide), foram testadas. Nenhum dano tecidual foi detectado em nenhuma amostra de *Tubastraea* durante o experimento interespecífico. *P. caribaeorum* sofreu retração, deposição de muco e sobrecrescimento, sendo identificada redução da área ocupada pelo zoantídeo apenas durante a interação com *T. tagusensis*. Além de uma guerra química entre dois organismos aleopáticos fortes, a prevalência do morfotipo dendróide sobre *Palythoa caribaeorum* traz a preocupação de que a resposta do zoantídeo também possa ser influenciada pela morfologia de *Tubastraea*.

Palavras-chave: competição interespecífica, zoantídeo, coral-sol, bioinvasão, Atlântico Sudoeste

Abstract

The space is a limited resource for the establishment of benthic species on consolidated substrates. Considering the introduction of invasive species, the effects of the interspecific competitive interaction must be evaluated, once the prevalence of these organisms over native species depends upon a repertory of strategies not fully understanding. *Tubastraea* corals became overspread along the Atlantic Ocean, being majorly observed on artificial substrates. In contrast with the Great Barrier Reef in the Pacific Ocean, where more than 300 species have been identified, the diversity of shallow water scleractinians in Brazil is reduced (21 species) with major reef building species represented by the genus *Mussimilia*. *Palythoa caribaeorum* is a native zoanthid with high growth rates, and colonies with short polyps embedded in the coenenchyma. The species forms thick mats on hard substrates, also producing a strong biotoxin: the palytoxin. To study the interaction between *Tubastraea* spp. and *P. caribaeorum*, a manipulative experiment was developed *in situ* in the Todos-os-Santos Bay (12°S, Bahia State). Two species (and respective morphotypes), *Tubastraea tagusensis* (dendroid) and *Tubastraea coccinea* (plocoid), were tested. No tissue damage was detected in any *Tubastraea* sample during the interspecific experiment. *P. caribaeorum* underwent retraction, mucus deposition and overgrowth, being a reduction of the area occupied by the zoanthid identified only during the interaction with *T. tagusensis*. Beyond a chemical warfare between two strong alleopathic organisms, the prevalence of the dendroid morphotype over *Palythoa caribaeorum* brings into concern that the zoanthid response may be also influenced by *Tubastraea* morphology.

Keywords: interspecific competition; zoanthid; sun coral; bioinvasion; Southwestern Atlantic

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Effect of interspecific competitive relationships involving *Tubastraea* spp. (Scleractinia, Dendrophyllidae) and *Palythoa caribaeorum* (Zoantharia, Sphenopidae)

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Abstract

The space is a limited resource for the establishment of benthic species on consolidated substrates. Considering the introduction of invasive species, the effects of the interspecific competitive interaction must be evaluated, once the prevalence of these organisms over native species depends upon a repertory of strategies not fully understanding. *Tubastraea* corals became overspread along the Atlantic Ocean, being majorly observed on artificial substrates. In contrast with the Great Barrier Reef in the Pacific Ocean, where more than 300 species have been identified, the diversity of shallow water scleractinians in Brazil is reduced (21 species) with major reefbuilding species represented by the genus *Mussimilia*. *Palythoa caribaeorum* is a native zoanthid with high growth rates, and colonies with short polyps embbeded in the coenenchyma. The species forms thick mats on hard substrates, also producing a strong biotoxin: the palytoxin. To study the interaction between *Tubastraea* spp. and *P. caribaeorum*, a manipulative experiment was developed *in situ* in the Todos-os-Santos Bay (12°S, Bahia State). Two species (and respective morphotypes), *Tubastraea tagusensis* (dendroid) and *Tubastraea coccinea* (plocoid), were tested. No tissue damage was detected in any *Tubastraea* sample during the interspecific experiment. *P. caribaeorum* underwent retraction, mucus deposition and overgrowth, being a reduction of the area occupied by the zoanthid identified only during the interaction with *T. tagusensis*. Beyond a chemical warfare between two strong alleopathic organisms, the prevalence of the dendroid morphotype over *Palythoa caribaeorum* brings into concern that the zoanthid response may be also influenced by *Tubastraea* morphology.

Keyword: interspecific competition; zoanthid; sun coral; bioinvasion; Southwestern Atlantic

INTRODUCTION

In the marine environment, consolidated substrate is a limiting ecological resource for a great variety of organisms, being the larvae settlement and the space dominance generally defined by complex competitive interactions (Jackson 1977, Connell 1978). During the establishment and maintenance of the surrounding substrate, sessile cnidarians naturally display an aggressive behavior, being solitary and colonial scleractinians ‘armed’ creatures and very creative competitors. (Lang 1973, Thomason & Brown 1986). In addition to a set of specialized stinging cell structures (the nematocysts), these calcifying organisms have adapted other mechanisms for feeding, removing or preventing the establishment of potential competitors as, for instance, by extruding the mesenterial filaments (Lang 1973); using sweeper tentacles (Hidaka & Yamazato 1984) and the elongated sweeper polyps (Peach & Hoegh-Guldberg 1999), and by secreting a thick mucous layer laden with nematocysts (Chadwick 1988). Moreover, corals also produce powerful biotoxins, which has been considered a strong component of the marine chemical warfare (Koh & Sweatman 2000). Indeed, competition for space mediated by chemical substances may involve specific, and very complex behavioral strategies (Jackson & Buss 1975). And successful bioinvaders are known to use a repertory of substances for defense, expansion and colonization of new areas (Pereira 2004, Parker & Hay 2005, Lages *et al.* 2006).

In the last decades, the record of the occurrence of bioinvasion associated with human activities has increased significantly (Carlton 2001, Junqueira *et al.* 2009, Sammarco *et al.* 2014, Creed *et al.* 2016), worrying researchers and environmental managers worldwide due to the magnitude of the threat to marine biodiversity (Ruiz & Carlton 2003, Molnar *et al.* 2008, Seebens *et al.* 2013). Brazilian scleractinian fauna has been characterized by a low diversity of zooxanthellate corals, being the *Mussismilia* (together with coralline algae and milleporids) the main builder genus of coastal reefs (Neves *et al.* 2006, Leão *et al.* 2016). Indeed, the report of invasive scleractinians is uncommon in the Atlantic Ocean, but *Tubastraea* corals started being introduced in the Caribbean by the early 1940s. Studies have suggested that *Tubastraea coccinea* probably reached the Americas through the Panama Canal (Fenner 2001, Fenner & Banks 2004), dispersing and occupying artificial substrates in the northern Mexico Gulf (Sammarco *et al.* 2012), then extending its distribution range to Brazil (De Paula & Creed 2004). *Tubastrea tagusensis* was originally described to the Pacific Ocean, but has been defined as cryptogenic, and invasive in the Southwestern Atlantic – together with the congener *Tubastraea micranthus* (from Indian and Pacific Ocean), *T. tagusensis* has been also reported to the Gulf of Mexico (De Paula & Creed 2004, Mantelatto *et al.* 2011, Creed *et al.* 2016, Figueroa *et al.* 2019).

Popularly known as ‘sun corals’, these azooxanthellate scleractinians dispersed along the Brazilian coast after being first reported to Northern Rio de Janeiro State (22°S) in the late

1980s, being suggested that colonies were accidentally transported by oil platforms (Castro & Pires 2001). In 2008 *Tubastraea* was observed northwards on a shipwreck in warmer waters in the Todos-os-Santos Bay (12°S, Bahia State), a protected area with pristine ecosystems, including coral reefs, mangroves and estuaries (Sampaio *et al.* 2012). In this particular coastal section, the sun corals have established on artificial and natural substrates, becoming integrated to the benthic and biofouling communities, expanding on shipwrecks, navigation buoys, decks, piers, as well as, on rocky outcrops and coral reefs (Sampaio *et al.* 2012, Miranda *et al.* 2016 a, b). Specific defense mechanisms (physical and chemical) may promote *Tubastraea* local settlement and ecological interactions (Lages *et al.* 2012, Miranda *et al.* 2016b). Moreover, these corals have particular biological properties that apparently increase dispersion to new environments and high population densities, including sexual and asexual reproduction, early maturity, multiple brooding cycles, large number of propagule production, larvae with high swimming capacity and varied competency period, and fusion among larvae and juveniles during early development (Ayre & Resing 1986, Paz-Garcia *et al.* 2007, Glynn *et al.* 2008, Capel *et al.* 2014, Mizrahi *et al.* 2014, Luz *et al.* 2020).

The expansion of *Tubastrea* spp. along the Brazilian coast have been attributed to multiple invasions, and secondary introduction events (Sampaio *et al.* 2012, Capel *et al.* 2019). However, local interactions, and the effects of sun corals on natural communities remain poorly understood. Based on manipulative experiments, it has been observed aggressive behavior of *Tubastraea* when colonies were put into contact with two highly distributed reef-building species, *Mussismilia hispida* and *Siderastrea stellata* (Creed 2006, Santos *et al.* 2013, Miranda *et al.* 2016b), suggesting an unfavorable competitive scenario for native corals (Santos *et al.* 2013, Miranda *et al.* 2016a). Regarding the presence of *Tubastraea* in the benthic communities on consolidated substrates, other ecological interactions are expected to occur. In the Tropical Northeast Coast, coral communities are usually characterized by an extensive cover of the colonial zoanthid *Palythoa caribaeorum*, which plays an important role in the habitat structure and composition (Silva *et al.* 2015, Durante *et al.* 2018). Beyond contributing to primary production, it shelters and provides food for a myriad of organisms, being also susceptible to bleaching during seawater warming events – although not calcified as scleractinians, these are also zooxanthellate cnidarians (Suchanek & Green 1981, Sebens 1982, Williams & Bunkley-Williams 1988, Stampar *et al.* 2007, Francini-Filho & Moura 2010, Longo *et al.* 2012). Zoanthids are capable to exclude a variety of reef organisms (e.g., scleractinians, octocorals, other zoanthids, hydrocorals, sponges, algae (Suchanek & Green 1981, Acosta 2001, Pérez *et al.* 2005), being the competitive abilities often associated to an aggressive behavior (Suchanek & Green 1981, Mendonça-Neto & Gama 2009), an accelerated growth capacity (Suchanek & Green 1981, Rabelo *et al.* 2013), as well as, to the production of the palytoxin, a very poisonous

organic compound (Moore & Scheuer 1971, Suchanek & Green 1981, Gleibs *et al.* 1995, Amir *et al.* 1997).

In Brazil, *P. caribaeorum* was recorded coexisting with *T. tagusensis* and *T. coccinea* in colder waters and rocky shores in the Southeastern coast (Arraial do Cabo and Ilha Grande – 22°S, Rio de Janeiro State) (Okada *et al.* 2012). Luz & Kitahara (2017) observed a negative effect of the *Tubastraea* on *Palythoa* in Búzios Island (23°S, São Paulo State), describing retraction and necrosis of the zoanthid marginal tissues when it was into contact with sun coral colonies. Recently, Saá *et al.* (2020) registered the interaction between *T. coccinea* and *P. caribaeorum* in the Marine Biological Reserve of Arvoredo (27°S, Santa Catarina State), describing two zoanthid responses: ‘overtopping’ and ‘avoidance’. Contrasting with the Southeastern, the Northeastern coast is under influence of the Brazilian Current, with warmer waters and true coral reef formations. Data approaching the impact of *Tubastraea* on *Palythoa* in distinct conditions have not been evaluated yet. Therefore, comparing with previous studies and based on manipulative experiments developed in a warmer natural environment, we aimed to investigate the competitive interaction between *Tubastraea* and *P. caribaeorum* from the Todos-os-Santos Bay (12°S, Bahia State). Results may contribute to predict, and understand possible changes in the structure of benthic communities under influence of *Tubastraea* and variable environmental scenarios.

MATERIALS AND METHODS

Study area

Tubastraea sampling and the experimental protocol were developed at the Marina de Itaparica (MI) (12°53'21.28"S, 38°41'3.44"W, Itaparica Island), located in Todos-os-Santos Bay (TSB), eastern Brazilian coast (Figure 1). In the area, colonies of *Tubastraea* settled on submerged floats, piers, pillars and branches of vegetation, presenting a low cover average ($1,0 \pm 1,25\%$) (Miranda *et al.* 2012, Guimarães 2016). The TSB is the second largest bay in the country, being the most biodiverse environment of the South Atlantic (Leão & Kikuchi 2005, Lessa *et al.* 2009). Artificial substrates provided by seawall, nautical signs, piers, decks and shipwrecks, as well as oil platforms are available in the bay, attracting the establishment of fouling invasive species (Mangelli & Creed 2012, Miranda *et al.* 2016a). Nevertheless, the TSB comprises pristine ecosystems of great diversity, including coral reefs and mangroves, being considered a priority area for conservation (Leão *et al.* 2003, Barros *et al.* 2012). Although the coexistence of *P. caribaeorum* with *Tubastraea* has not been locally registered, other zoanthid species (e. g., *Zoanthus sociatus*) have a syntopic occurrence in the study area, being observed vertically with other sessile organisms on the MI structure, including other coral species (*Phylangia americana*, *Astrangia brasiliensis*, *Mussismilia hispida*, *Montastraea cavernosa*, *Favia gravida*, *Siderastrea stellata*) (authors obs. pess.).

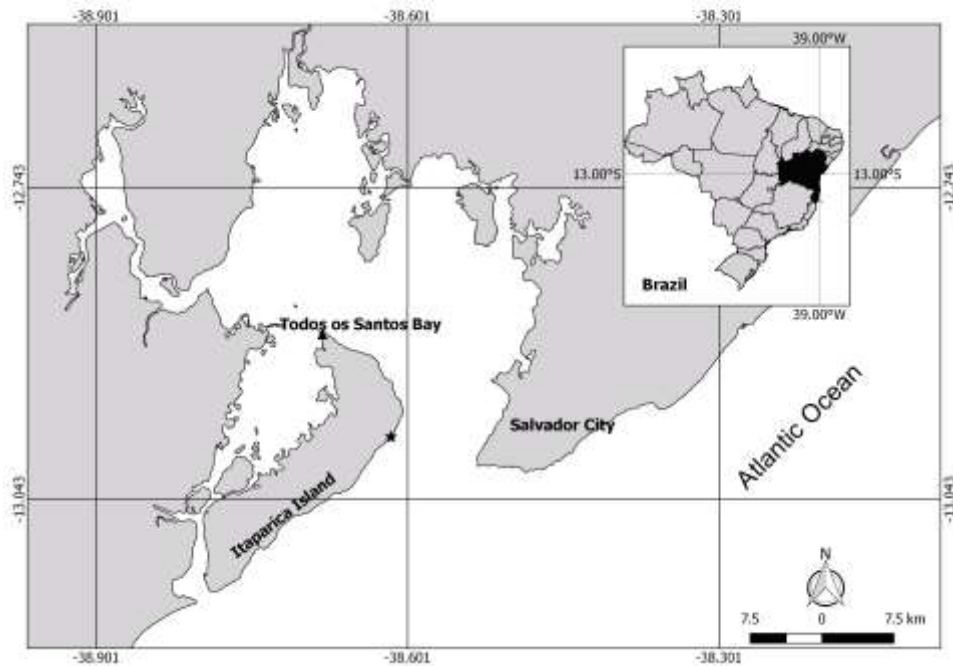


Fig. 1. Study area of the manipulative experiment, and sampling sites.

Experimental design

Considering the complex coral morphology, the analysis of the competitive interactions *Tubastraea* vs. *Palythoa* took into account two major *Tubastraea* morphotypes: dendroid (colonies with the corallites projecting higher over the colony surface) and plocoid (corallites shorter). To maintain the conditions of the natural environment for the species, the manipulative experiments were realized *in situ*, between June and December/2017. Sun corals were collected by scuba diving between 4.0 to 6.0 m depth, being the colonies removed from the MI columns with a spatula, avoiding fragmentation, and then enclosed in individual plastic bags. Samples were transferred to containers with local sea water, and kept under constant aeration. Samples of *P. caribaeorum* were collected in the tidal pools of the Pinaunas Reef (12°58'14.7"S 38°36'29.1"W), Itaparica Island (Figure 1), during low tide, following the same protocol described to *Tubastraea*.

For the experiments, a total of 24 *Tubastraea* colonies with 8.0 to 12.0 cm in diameter, and 18 colonies of *P. caribaeorum* varying between 5.0 to 10.0 cm long, and 4.0 to 5.0 cm wide in diameter were selected. Samples of *Tubastraea* were separated in two sets: 12 plocoid (*T. coccinea*) and 12 dendroid (*T. tagusensis*). The species were transplanted and fixed with non-toxic epoxy (*Tubolit MEM*®) in polyethylene plates, where four treatments were placed: (i) *P. caribaeorum* isolated (control) (Pc); ii) *P. caribaeorum* vs. *T. tagusensis* (Pc vs. Tt); iii) *P. caribaeorum* vs. *T. coccinea* (Pc vs. Tc); iv) *T. coccinea* vs. *T. tagusensis* (Tc vs. Tt). Each

treatment was replicated six times, using 24 plates (20.0 x 20.0 cm), being each plate corresponding to an experimental unit.

The plates were drilled on the sides, numbered and tied with a galvanized wire in six columns of the MI structure, at 2.0 to 4.0 m depth. Arranged randomly, four plates were fixed to each column, one from each treatment, at 15 m of distance from each other. In the experimental units, the pairs of the colonies were positioned at a very small distance, allowing the contact between the tissues, particularly during the expansion of the tentacles.

The experiment remained *in situ* for a continuous period of 190 days, being monitored in the 7th d, 21st d, 45th d, 120th d, 160th d and 190th d. During scuba diving, photographic records were made using a camera support (25 cm away from the plates) to standardize the focal distance. The images were analyzed using the software *Image J*® to measure the colonial area (cm²) of *P. caribaeorum*. To verify the competitive behavior between species, and whereas corals could be more active at night than during the day, two-night dives were also made on the 40th and 70th days.

Two replicates of *P. caribaeorum* vs. *T. coccinea* became strongly unhealthy on the 21st d, causing almost total colony mortality. Without an accurate diagnosis, the colonies were removed to avoid possible contamination of the experiment. After the 120th d, organisms from the neighboring community settled on the plate of the two replicates of the treatment *P. caribaeorum* vs. *T. tagusensis*. To avoid skewed data, these were discarded from the analysis. And, to keep the balance among the treatments, two replicates were removed at random from the control.

Statistical analyses

The evaluation of the existence of significant differences between the growth data of *P. caribaeorum* in the experimental treatments was performed using one-way ANOVA for repeated measures (Gotelli & Ellison 2011), considering the period between the 7th and 120th days. Data homocedasticity and normality were tested using Levene and Shapiro-Wilk tests, respectively (Zar 2010, Gotelli & Ellison 2011). When significant differences were found, the post-hoc Tukey test was applied (Gotelli & Ellison 2011). The analyses were carried out using R software environment for statistical computing (R Core Team 2015).

RESULTS

All contact pair between the *Tubastraea* congeners, or *Tubastraea* spp. vs. *P. caribaeorum*, did not result in colony damage to any sun coral sample. *Tubastraea* tissues remained healthy, being not observed retraction and/or avoidance response.

Similarly, the control treatment of *P. caribaeorum* remained healthy, and mucus deposition did not occur. However, in the presence of *Tubastraea* spp., 62.5% of the zoanthid

colonies deposited a mucus layer, principally over the contact zone, being the reaction observed from 7th d of the experiment (Figure 2 A-B).

During night time, *T. coccinea* and *T. tagusensis* showed elongated polyps, and tentacular contact with the mucus deposition area of *P. caribaeorum* (Figure 2 C). The projection of mesenterial filaments and/or the action of sweeper tentacles were not recorded during the experiment.

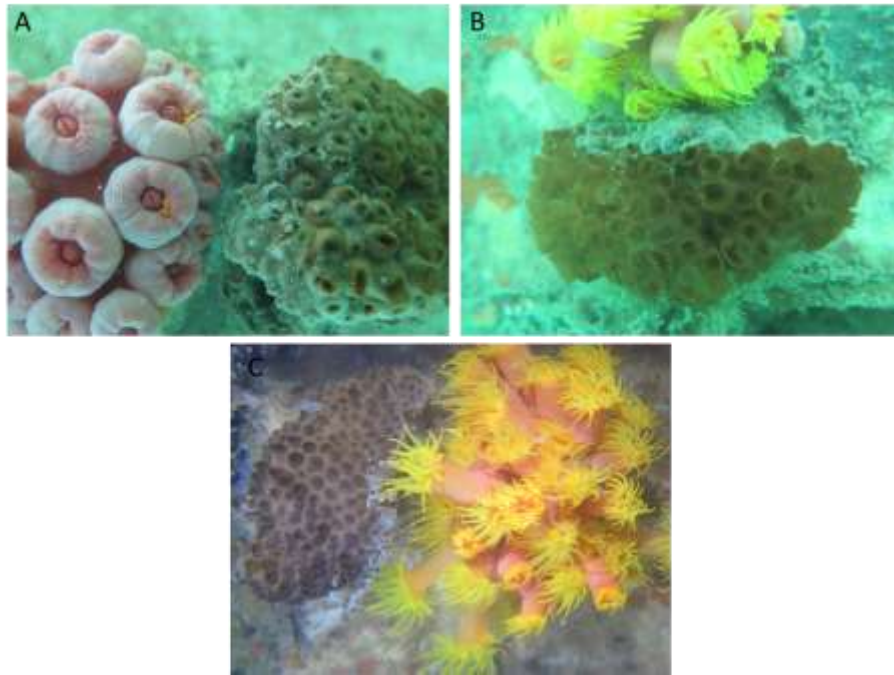


Fig. 2. Interactions between species after 7th day. (A) Mucus deposition in *Palythoa caribaeorum* Duchassaing & Michelotti, 1860 vs. *Tubastraea coccinea* Lesson, 1830. (B). *P. caribaeorum* Duchassaing & Michelotti, 1860 vs. *T. tagusensis* Wells, 1982. (C). *Tubastraea* elongated polyps in contact with *P. caribaeorum*.

Initially, *P. caribaeorum* showed a ‘shrinkage’ of the colony area when into contact with *Tubastraea* spp. By the 21st day of the experiment, 37.5% of the *Palythoa* underwent overgrowth *Tubastraea* (Figure 3 A-B). The overgrowth response reduced by the end of the experiment (120th d), when 50% of the *Palythoa* replicates demonstrated retraction of the tissue margins (Figure 3 C-D). In contrast, *Tubastraea* polyps remained intact.

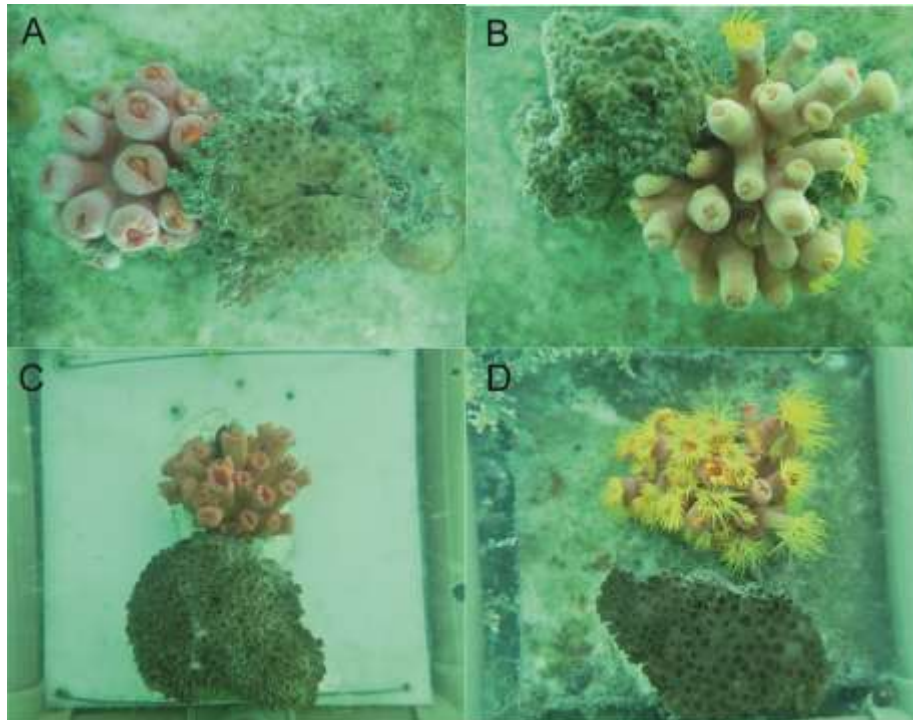


Fig. 3. (A-B) Overgrowth of *Palythoa caribaeorum* (Duchassaing & Michelotti, 1860) on plocoid and dendroid *Tubastraea*, respectively. (C-D) Avoiding behavior observed in *P. caribaeorum* in contact with *Tubastraea tagusensis* (Wells, 1982) between the 7th and 120th days of the experiment, respectively.

Tubastraea larvae were unexpectedly identified near the interspecific contact zone. Indeed, after 120 days of experiment, founding polyps of *T. tagusensis* were developing on the edge of a *Palythoa* colony (Figure 4).



Fig. 4. Recruit of *Tubastraea* on the colony base of *Palythoa caribaeorum* (Duchassaing & Michelotti, 1860) after 120th days of the experiment.

Considering the comparative analysis, statistical differences were revealed among the treatments. Tukey test identified significant difference between the treatment Tt vs. Pc with the *Palythoa* control (Table 1, Figure 5). The area of *Palythoa* showed an average reduction of 21.33 cm² in Tt vs. Pc treatment when compared to *Palythoa* control. On the other hand, there was no significant difference in the treatments Tc vs. Pc when compared to *Palythoa* control (Table 1, Figure 5). At the end of the experiment, the colonies of *Palythoa* (control) increased in average of 23.36%, representing a growth rate of 1.63 cm² per month.

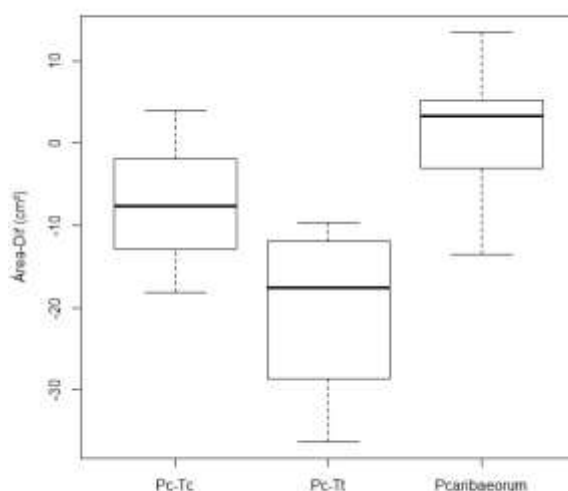


Fig. 5. Boxplot of the interquartile difference between *Palythoa caribaeorum* (Pcaribaeorum) and the treatments *P. caribaeorum* vs. *Tubastraea coccinea* (Pc-Tc) and *P. caribaeorum* vs. *Tubastraea tagusensis* (Pc-Tt). Plots show the median (middle line), 25th and 75th quartiles (box edges) e full range of the data (whiskers).

Table 1. Results of the comparative analysis (ANOVA): *Palythoa caribaeorum* (control); *P. caribaeorum* vs. *Tubastraea tagusensis*; *P. caribaeorum* vs. *T. coccinea*.

		GL	SQ	F	p	Reduction area Pc (%)
Treatments (Species)		2	923.7	4.324	0.0497*	
Residual		10	1122.8			
Post-hoc Tukey test	Dif					
Pc-Tc/Pcaribaeorum	-8.343				0.5634	27,44
Pc-Tt/Pcaribaeorum	-21.335				0.0399*	42,94
Pc-Tt/Pc-Tc	-12.991				0.3063	

*p < 0.05

DISCUSSION

Despite almost 40 years since the introduction of the sun corals in Brazil (Castro & Pires 2001), studies on competition are majorly restricted to the interaction between *Tubastraea* and sponges (Silva *et al.* 2017), and the secondary effects on the associated fauna (Nogueira *et al.* 2021). Actually, during the monitoring of a decommissioned oil-platform in the TSB, Neves (*pers. obs.*) reported a process of intrageneric interaction involving two different morphotypes of *Tubastraea* - although resulting in some degree of overgrowth, with incrusting plocoid colonies prevailing over the dendroid ones, the contact was not related to any apparent tissue damage. Indeed, dendroid bright yellow polyps were healthy and even taller than expected, supporting a scenario of intrageneric competitive tolerance (Neves *op. cit.*). Intrageneric interaction was also experimentally studied by Hennessey & Sammarco (2014). The authors selected two distinct species, the branching *Tubastraea micranthus* (dendroid), and the incrusting *T. coccinea*, and similarly did not observe overgrowth. Instead, the authors described a kind of ‘avoidance response’, with *T. coccinea* retracting to the contact of the congener tentacles. In contrast, in this study, *T. coccinea* polyps stretched towards *T. tagusensis* (Figure 3B), suggesting a similar trend observed by Neves (*op. cit.*). Nevertheless, considering the species behavior may vary regionally, and accordingly to the opponent strategies (and morphologies), the idea that congeners may overgrow each other, needs to be better evaluated.

Certainty, the synergy between ecological factors (e.g, physicochemical, biotic) vs. anthropocentric activities are influencing the distribution and space occupation of *Tubastraea* in the TSB, but the processes that define each variable involved remain poorly understood, being probably a key question to explain patterns of competitive interactions, and local population abundancies as well. For instance, on rocky shores in colder environments in southeastern Brazilian coast, *T. coccinea* is, apparently more abundant in artificial substrates than natural ones, while *T. tagusensis* may be abundant in both types of substrates (Mangelli & Creed 2012). In northeastern coast section, *Tubastraea* has been majorly found on artificial substrates (Sampaio *et al.* 2012). Among coral species, larval substrate selection has been characterized as a critical factor that may determine post-settlement survival, being the selective behavior probably mediate by chemical cues, that promote conspecific recognition, and the appropriate habitat for settlement (Ritson-William *et al.* 2010) Other studies support that the densities of *T. tagusensis* may overcome the congener *T. coccinea* (Creed & De Paula 2007), and native coral population at the TSB as well (Miranda *et al.* 2016b). But in the TSB, *Tubastraea* remain preferably established on artificial structures, settled on cirripeds and oysters (authors *pers. obs.*) Thus, long-term studies are crucial to evaluate the patterns involved in the establishment of exotic species, as a tool to elucidate how intrageneric/interspecific interactions may influence competition during larvae settlement, and early development.

Although dendrophylliid corals are expected to show aggressive behavior during competitive interactions (Creed 2006, Santos *et al.* 2013, Sammarco *et al.* 2015, Miranda *et al.* 2016b), the extrusion of the mesenterial filaments, or the action of sweeper tentacles were not observed in *Tubastraea* – even after 40 days of experiment, when (according to the literature) they could be expected to be observed (Sebens & Miles 1988, Goldenberg *etwh al.* 1990, Lapid *et al.* 2004). Sweeper tentacles of some species usually retreat after attacking the opponent's tissues, a behavior that may be attributed to feeding, and/or to the high energy cost in maintaining these structures (Wellington 1980, Chornesky 1983, Lapid *et al.* 2004).

Elongated polyps of *T. tagusensis* were observed facing the mucus deposition zone of the *Palythoa* pair. Similarly, Miranda *et al.* (2016 b) describe polyps of *T. tagusensis* extended over dead and living zones of *Siderastrea stellata* colonies. *Palythoa* is known to produce a thick mucus layer with nematocysts which, besides protecting the colony against desiccation, could prevent *Tubastraea* attack and overgrowth. Originally described as a carbohydrate complex (plus lipid and protein), coral mucus may also trap organic matter (enriched with nitrogen and phosphorous), becoming to corals and other organisms a valuable food source (Krupp 1982, Kropp 1986, Huettel *et al.* 2006). Paradoxically, the toxicity of *Palythoa* may be 'not inherent' to the species, instead it is likely to be regulated by the environmental conditions and associated organisms (Melo *et al.* 2012). Thus, assuming that palytoxin toxicity/concentration may be highly unstable, it would be interesting to test whether the zoanthid mucus (or any other cnidarian mucus) may 'attract' in some way the sun corals as an alternative food source. Nevertheless, the mucus film formed on the colony of *P. caribaeorum* during the experiments has never been cited in the literature, being clearly a protective mechanism to avoid tissue damage in the contact zone due to aggressive behavior of *Tubastraea*. Futhermore, the avoidance response of *P. caribaeorum* during contact with *T. tagusensis* also configure a reaction against an efficient competition repertory, e.g., projection of mesenterial filaments; sweeper tentacles; elongated sweeper polyps, and allelopatic secondary metabolites (Sorokin 1995, Koh & Sweatman 2000, Connel *et al.* 2004, Lages *et al.* 2012, Santos *et al.* 2013, Hennessey & Sammarco 2014, Miranda *et al.* 2016b). In colder environment, Luz & Kitahara (2017), described the same retreat behavior in *P. caribaeorum* – the species was observed delimiting space, and avoiding contact with *T. tagusensis*. Indeed, considering that *T. coccinea* has massive or incrusting colonies while the dendroid congener has a colony base substantially reduced, space competition may be target by very distinct demands for the two species. And to the zoanthid, the avoidance response could in fact be an efficient strategy to inhibit sun coral growth by surrounding it and delimiting a 'safe area'.

Palythoa caribaeorum has a notable growth rate, ranging between 0.015 cm.day⁻¹ to 0.4 cm.day⁻¹ (Suchanek & Green 1981, Mendonça-Neto & Gama 2009, Costa *et al.* 2011, Silva *et al.* 2015). The overgrowth strategy is probably one of the major mechanisms adopted by the

species to defeat competitors (Suchanek & Green 1981, Bastida & Bone 1996). The overgrowth behavior has been mentioned in encounters between the zoanthid and sponges, gorgonians, hydrocorals, bivalves and other zoanthids as well (Suchanek & Green 1981, Bastida & Bone 1996). However, in this study, *Palythoa* overgrowth occurred temporally. And, after the zoanthid retreat, *Tubastraea* tissues (which was partially covered) were unharmed. The sponge *Desmapsamma anchorata* may grow over *Tubastarea* colonies, being able to cause tissue losses in the sun corals (De Paula 2007, Meurer *et al.* 2010). To avoiding the sponge overgrowth, it has been suggested that *T. coccinea* could defend itself by using the mesenterial filaments and/or allelochemical substances (De Paula 2007). In Guilhem *et al.* (2020), *T. coccinea* had a significant negative impact on the growth of *P. caribaeorum*, while *T. tagusensis* had no effect. The authors considered that the zoanthid presented biotic resistance to invasive species, particularly against *T. tagusensis*, due to competition mediated by physical and/or chemical mechanisms. Here, *Tubastraea tagusensis* was assumed to be competitively more efficient than *P. caribaeorum*, but the impact on the zoanthid apparently remained restricted to the reduction of the occupied area – probably the first stage of the delimitation of a ‘safe area’. Controversially, this ‘safe area’ was selected by sun coral larvae for settlement, representing a favorable reinforcement to the action of the parental colonies. Clearly the defense mechanisms adopted by the zoanthid were unable to prevent the establishment of *Tubastraea* recruits in the surroundings of the area previously occupied, highlighting the superior competitive ability of these dendrophyllids.

Therefore, the study of competition between native species and introduced organisms is fundamental to comprehend how local diversity will be affected, being also a priority concern for the development of management policies and impact mitigation.

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APÊNDICE

Journal of the Marine Biological Association of the United Kingdom

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Keywords. Please provide up to ten key words.

Headings. Follow the style and hierarchy for each section as shown below (but see later for taxonomy):

INTRODUCTION (1st heading, upper case, left justified).

MATERIALS AND METHODS (1st heading, upper case, left justified).

RESULTS (1st heading, upper case, left justified) then:

The sampled population (2nd heading, bold, left justified)

DENSITY AND BIOMASS (3rd heading, small caps, left justified)
Reproduction and development (4th heading, lower case italics, left justified)

DISCUSSION (1st heading, upper case, left justified). Subheadings, if used, should follow the instructions under RESULTS.

ACKNOWLEDGMENTS (1st heading, upper case, left justified). You may acknowledge individuals or organizations that provided advice, support (non-financial). Formal financial support and funding should be listed in the following section.

FINANCIAL SUPPORT. Please provide details of the sources of financial support of all authors, including grant numbers. For example, 'This work was supported by the Medical Research Council (grant number XXXXXXXX)'. Multiple grant numbers should be separated by a comma and space,

and where research was funded by more than one agency, the different agencies should be separated by a semi-colon, with 'and' before the final funder. Grants held by different authors should be identified as belonging to individual authors by the authors' initials. For example, 'This work was supported by the Wellcome Trust (A.B., grant numbers XXXX, yyyy), (C.D., grant number ZZZZ); the Natural Environment Research Council (E.F., grant number FFFF); and the National Institutes of Health (A.B., grant number GGGG), (E.F., grant number HHHH)'. Where no specific funding has been provided for research, please provide the following statement: 'This research received no specific grant from any funding agency, commercial or not-for-profit sectors'.

Taxonomy should be presented as follows:

SYSTEMATICS (1st heading, upper case, centre justified)

Order AMPHIPODA Latreille, 1816

Suborder GAMMARIDEA Latreille, 1803

Family UROTHOIDEA Bousfield, 1978

Genus *Carangolia* Barnard, 1961

Carangolia barnardi sp. nov.

(Figures 1–6)

Carangolia spp.: Elizalde et al., 1993; Sorbe & Weber, 1995; Dauvin & Sorbe, 1995. (left justified)

TYPE MATERIAL (taxon omic subheadings, small caps, left justified)

Holotype: adult female (oostegites developed) 2.69 mm, completely dissected and mounted on 12 slides. (OXYBENT VIII, TS05-R, N4; coordinates: 43°49.34'N 02°02.74'W; water depth: 550 m) (MNH Am5129); coll. J.-C. Sorbe, 19 April 1999.

Paratype: adult male (penile papillae developed) 3.88 mm partially dissected, with both first antennae, maxillipeds, epimeral plates, pleopods, and second antenna and second gnathopod mounted on three slides; rest as five pieces preserved in 70% ethanol. (ECOMARGE 93, TS08-A,

Ni; 44°34.57'N 02°12.60'W; water depth: 740–746 m) (MNHN-Am5130); coll. J.-C. Sorbe, 23 June 1993. Twenty-one additional specimens in J.-C. Sorbe Collection.

COMPARATIVE MATERIAL
EXAMINED

Carangolia cornuta Bellan-Santini & Ledoyer, 1986. Holotype: female completely dissected on single slide (Museo Civico di Storia Naturale di Verona, slide no. 3276); RV 'Marion Dufresne' Cruise MD08 to Marion and Prince Edward Islands, Station 17BB97 (Marion Island: 46°52.5'S 37°53.5'E); collected on 25 March 1976 with Okean grab on muddy sand, 110 m depth.

DIAGNOSIS

Carangolia with well developed pointed process on posterolateral corner of head. Coxal plate 1 with anterior and posterior margins subparallel, distal margin straight. Coxal plate 7 pointed. Basis of pereopod 6 slender, not oblong. Dactylus of pereopod 5 elongate (more than 12 times longer than wide). Telson devoid of spines.

KEY FOR THE GENERA OF THE
ALVINOCARIDIDAE (small caps, left justified)

1. Posterior telson margin armed only with spines, without plumose seta.....2
Posterior telson margin armed with plumose.....3
(Insert a line space between each point)
2. Rostrum long, depressed laterally; pterygostomal spine present; lash on first maxilliped rudimentary.....*Alvinocaris*
Rostrum short, compressed dorsoventrally, without teeth; pterygostomal spine absent; lash on first maxilliped well developed.....*Iorania*
3. Short rostrum present; exposed eyes separated from each other; distolateral spine present on scaphocerite.....*Chorocaris*

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Fig. 1. *Ceratothoa collaris* Schioedte & Meinert, 1883, adult female: (A) pereopod 1; (B) pereopod 7; (C–G) pleopods 1–5 ventral view; (H) uropods. Scale bars: A–G, 2 mm; H, 3 mm.

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Table 1. Tenacity of *Elminius modestus* and *Balanus perforatus* cypris larvae to natural biofilms developed at high (83 s^{-1}) and low (15 s^{-1}) shear rates. Forces of temporary adhesion are given as 10^4 Nm^{-2} .

Surface	<i>Elminius modestus</i>			<i>Balanus perforatus</i>	
	N	Mean	±SE	N	Mean
No biofilm	30	8.19	0.258	30	6.75
Low shear	30	7.59	0.274	30	4.94
High Shear	30	9.20	0.219	30	6.50
	Bartlett's statistic = 1.44 <i>P</i> =0.486			Bartlett's statistic <i>P</i> =0.248	

N, number; SE, standard error.

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The online platform gives authors the opportunity to include data that would be impossible or impractical to include in the printed version. These data might substantially enhance the importance of the research and might also be of benefit to readers. Authors may include tables and figures as well as data such as videos, 3-D structures/images, extensive datasets and any other supplementary material not suitable for print duplication. All supplementary material must be submitted with the original manuscript. Supplementary data should be referred to in the text with the prefix "S" (e.g. Supplementary Table S1, Supplementary Figure S1). Supplementary files will not be copy-edited, and will be published as supplied.

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Dashes. Hyphen between connecting words; en-dash between ranges e.g. 3–10, B–G, and between opposite words e.g. male–female pairs, size–frequency, etc.

REFERENCES (1st heading, upper case, left justified)

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Marshall SM, Nicholls AG and Orr AP (1939) On the growth and feeding of young herring in the Clyde. *Journal of the Marine Biological Association of the United Kingdom* 23, 427–455.

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El Haj AJ, Whiteley NM and Harrison P (1992) Molecular regulation of muscle growth over the crustacean moult cycle. In El Haj A.J. (ed.) *Molecular biology of muscle*. Cambridge: Cambridge University Press, pp. 151–165. [SEB Seminar Series, no. 46.]

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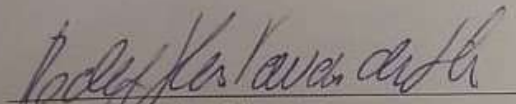
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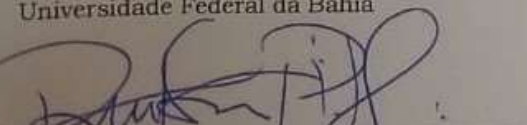
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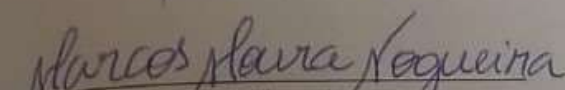
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