

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. *Palythoa caribaeorum* is a native zoanthid with high growth rates, and colonies with short polyps embedded in the coenenchyma. 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, but no statistical difference was recorded. The study of competition between native species and introduced organisms is fundamental to comprehend how local diversity will be affected.

Key words: interspecific competition; zoanthid; sun coral; bioinvasion; Southwestern Atlantic.

Efeito das relações competitivas interespecíficas envolvendo *Tubastraea* spp. (Scleractinia, Dendrophyllidae) e Palythoa caribaeorum (Zoantharia, Sphenopidae. Resumo: O espaço é um recurso limitado para o estabelecimento de espécies bentônicas em substratos consolidados. Considerando a introdução de espécies exóticas, os efeitos da competição interespecífica devem ser avaliados, uma vez que a prevalência destes organismos sobre espécies nativas depende de um repertório de estratégias não totalmente compreendidas. Corais Tubastraea se tornaram amplamente distribuídos ao longo do Oceano Atlântico, sendo principalmente observados em substratos artificiais. Palythoa caribaeorum é um zoantídeo nativo que possui altas taxas de crescimento e colônias com pólipos curtos inseridos no cenêmquima. Para estudar as interações entre Tubastraea spp. e P. caribaeorum, um estudo manipulativo foi desenvolvido in situ na Baía de Todos-os-Santos (12°S, Estado da Bahia). Duas espécies (e respectivos morfotipos), Tubastraea taqusensis (dendróide) e Tubastraea coccinea (plocóide), foram testadas. Não foi detectado dano ao tecido em nenhuma amostra de Tubastraea durante o experimento interespecífico. P. caribaeorum sofreu retração, deposição de muco e crescimento excessivo, mas não foi identificada diferença significativa entre os tratamentos. O estudo da competição entre espécies nativas e organismos introduzidos é fundamental para compreender como a diversidade local será afetada.

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

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). 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 mucus 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, Lages et al. 2006).

In the last decades, the record of the occurrence of bioinvasion associated with human activities has increased significantly (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 et al. 1997, 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). *Tubastraea 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 & Hicks 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 accidentally suggested that colonies were 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 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 (Paz-Garcia et al. 2007, Glynn et al. 2008, Capel et al. 2014, Mizrahi et al. 2014, Luz et al. 2020).

The expansion of *Tubastraea* 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 reef-building distributed 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 scleractinians, calcified as these are also zooxanthellate cnidarians (Suchanek & Green 1981, Sebens 1982, Williams & Bunklev-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. taqusensis 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 Т. 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

Tubastraea Study area: 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**), eastearn Brazilian coast (Fig. 1). In the area, colonies of Tubastraea settled on submerged floats, piers, pillars and branches of vegetation, presenting a low cover average (1,0±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 (Phylanaia americana, Astranaia Mussismilia hispida, Montastraea brasiliensis, cavernosa, Favia gravida, Siderastrea stellata) (authors pers. Obs.).

Experimental design: Considering the complex coral morphology, the analysis of the competitive interactions *Tubastraea vs. Palythoa* considered two majors *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



Figure 1. Study area of the manipulative experiments and sampling in the Todos-os-Santos Bay. **Triangle:** Marina de Itaparica. **Star:** Pinaunas reef.

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 Pinaúnas Reef (12°58'14.7"S 38°36'29.1"W), Itaparica Island (Fig. 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. 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, and 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 three replicates of the treatment *P. caribaeorum vs. T. tagusensis.* To avoid skewed data, these (160th d and 190th d) were deleted from the analysis. And, to keep the balance among the treatments, three replicates were removed at random from the control.

Statistical analyses: Data homoscedasticity and normality were tested using Levene and Shapiro-Wilk tests, respectively (Zar 2010, Gotelli & Ellison 2011). As the data do not fit in assumptions for parametric analysis, we performed The Friedman Two-Way Analysis of Variance by Ranks to evaluate the existence of significant differences between the

growth data of *P. caribaeorum* in the experimental treatments, considering the period between the 7th and 120th days. 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 (Fig. 2 A-B).

During nighttime, *T. coccinea* and *T. tagusensis* showed elongated polyps, and tentacular contact with the mucus deposition area of *P*.

caribaeorum (Fig. 2 C-D). The projection of mesenterial filaments and/or the action of sweeper tentacles were not recorded during the experiment.

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* (Fig. 3A-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 (Figs. 3c–3d). In contrast, *Tubastraea* polyps remained intact.

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, 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. (Figure 4). Considering the comparative analysis, no statistical differences were recorded (p= 0.223).



Figure 1. Interactions between species after the 7th day. A: Mucus deposition in *Palythoa caribaeorum* vs. *Tubastraea coccinea*. B-C: *Palythoa caribaeorum* vs. *Tubastraea tagusens*is. D: *Tubastraea* elongated polyps in contact with *Palythoa caribaeorum*.



Figure 2. A-B: Overgrowth of *Palythoa caribaeorum* on plocoid and dendroid *Tubastraea*, respectively. C- D: Avoiding behavior observed in *Palythoa caribaeorum* in contact with *Tubastraea tagusensis* between the 7th and 120th day of the experiment, respectively.



Figure 3. Recruit of *Tubastraea* sp. on the colony base of *Palythoa caribaeorum* in the 120th day of the experiment.

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). 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 plocoid *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 physicochemical, biotic) factors (e.g., vs. are influencing anthropocentric activities the distribution and space occupation of Tubastraea int 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 & In northeastern coast section, Creed 2012). 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*. taqusensis 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, Goldberg *et 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 (Lapid *et al.* 2004).

Elongated polyps of *T. taqusensis* were observed facing the mucus deposition zone of the Palythoa pair. Similarly, Miranda et al. (2016b) 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 *Palvthoa* 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*. Furthermore, the avoidance response of P. caribaeorum during contact with T. taqusensis also configure a reaction against an efficient competition repertory, e.g., projection of mesenterial filaments; sweeper tentacles; elongated sweeper polyps, and allelopathic secondary metabolites (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 colony base substantially reduced, а 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 study, Palythoa overgrowth this occurred temporally. And, after the zoanthid retreat, Tubastraea tissues (which was partially covered) were not injured. 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 allelochemical mesenterial filaments and/or substances (De Paula 2007). In Guilhem et al. (2020), T. coccinea had a significant negative impact on the growth of *P. caribaeorum*, while *T.* taqusensis had no effect. The authors considered that the zoanthid presented biotic resistance to invasive species, particularly against *T. taqusensis*, 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 dendrophylliids.

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.

Acknowledgements

We would like to thank the 'Programa de Pós-Graduação em Ecologia e Biomonitoramento', Biology Institute/UFBA for supporting N. Freitas with grant and scholarship.

References

- Acosta, A, Sammarco, P. W. & Duarte, L. F. 2001. Asexual reproduction in a zoanthid by fragmentation: the role of exogenous factors. *Bulletin of Marine Science*, 68: 363–381.
- Amir I, Harris J. B. & Zar, M. A. 1997. The effect of palytoxin on neuromuscular junctions in the anococcygeus muscle of the rat. *Journal of Neurocytology*, 26: 367–376.
- Barros, F, Costa, P. C., Cruz I., Mariano, D. L. S. & Miranda, R. J. 2012. Habitats Bentônicos na Baía de Todos os Santos. *Revista Virtual Química*, 4 (5): 551–565.
- Capel, K. C. C., Migotto, A. E., Zilberberg, C. & Kitahara, M. V. 2014. Another tool towards invasion? Polyp "bail-out" in *Tubastraea coccinea*. *Coral Reefs*, 33: 1165.
- Castro, C. B. & Pires, D. O. 2001. Brazilian Coral Reefs: What we Already Know and What is Still Missing. *Bulletin of Marine Science*, 69: 357–371.
- Chadwick, N. E. 1988. Competition and locomotion in freeliving fungiid coral. *Journal of Experimental Marine Biology and Ecology*, 123: 189–200.
- Creed, J. C. 2006. Two invasive alien azooxanthellate corals, *Tubastraea coccinea* and *Tubastraea tagusensis*, dominate the native zooxanthellate *Mussismilia hispida* in Brazil. *Coral Reefs*, 25: 350–350.
- Creed, J. C. & De Paula, A. F. 2007. Substratum preference during recruitment of two invasive alien corals onto shallow-subtidal tropical rocky shores. *Marine Ecological Progress Series*, 330: 101–111.
- Creed, J. C., Fenner, D., Sammarco, P., Cairns, S., Capel, K., Junqueira, A. O. R., Cruz, I., Miranda, R. J., Carlos-Junior, L., Mantelatto, M. C. & Oigman-Pszczol, S. 2016. The invasion of the azooxanthellate coral *Tubastraea* (Scleractinia: Dendrophylliidae) throughout the world: history, pathways and vectors. **Biological Invasions**, 19: 283–305.
- Costa, D. L., Gomes, P. B., Santos, A. M., Valença, N. S., Vieira, N. A. & Pérez, C. D. 2011. Morphological plasticity in the reefzoanthid

Palythoa caribaeorum as an adaptive strategy. *Annales Zoologici Fennici*, 48: 349– 358.

- De Paula, A. F. & Creed, J. C. 2004. Two species of the coral *Tubastraea* (Cnidaria, Scleractinia) in Brazil: a case of accidental introduction. *Bulletin of Marine Science*, 74: 175–183.
- De Paula, A. F. 2007. Biologia reprodutiva, crescimento e competição dos corais invasores Tubastraea coccinea e Tubastraea tagusensis (Scleractinia: Dendrophylliidae) com espécies nativas. PhD. Thesis. Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro.
- Durante, L. M., Cruz, I. C. S. & Lotufo, T. M. C. 2018. The effect of climate change on the distribution of a tropical zoanthid (*Palythoa caribaeorum*) and its ecological implications. *PeerJ*, 6: e4777. Published online: 17 may 2017.
- Francini-Filho, R. B. & Moura, R. L. 2010. Predation on the toxic zoanthid *Palythoa Caribaeorum* by reef fishes in the Abrolhos Bank, eastern Brazil. *Brazilian Journal of Oceanography*, 58 (1): 77–79.
- Fenner, D. 2001. Biogeography of three Caribbean corals (Scleractinia) and the invasion of *Tubastraea coccinea* into the Gulf of Mexico. *Bulletin of Marine Science*, 69: 1175–1189.
- Fenner, D. & Banks, K. 2004. Orange Cup Coral *Tubastraea coccinea* invades Florida and the Flower Garden Banks, Northwestern Gulf of Mexico. *Coral Reefs*, 505–507.
- Figueroa, J. & Hicks, D. W. 2019. Hiding in plain sight: invasive coral *Tubastraea tagusensis* (Scleractinia: Hexacorallia) in the Gulf of Mexico. *Coral Reefs*, 38: 395-403.
- Gleibs, S., Mebs, D. & Werding, B. 1995. Studies on the origin and distribution of palytoxin in a Caribbean coral reef. *Toxicon*, 33: 1531– 1537.
- Glynn, P. W., Colley, S. B., Maté, J. L., Cortés, J.,
 Guzman, H. M., Bailey, R. L., Feingold, J. S.
 & Enochs, I. C. 2008. Reproductive ecology of the azooxanthellate coral *Tubastraea coccinea* in the Equatorial Eastern Pacific: Part V. Dendrophylliidae. *Marine Biology*, 153: 529–544.
- Goldberg, W. M., Grang, K. R., Taylor, G. T. & Zuniga, A. L. 1990. The structure of sweeper tentacles in the black coral *Antipathes fiordensis*. *Biological Bulletin* (Woods Hole), 179: 96–104.

- Gotelli, N. J. & Ellison, A. M. 2011. **Princípio de estatística em ecologia**. Porto Alegre: Artmed.
- Guilhem, I. F., Mais, B. P. & Creed, J. C. 2020. Impact of invasive *Tubastraea* spp. (Cnidaria: Anthozoa) on the growth of the space dominating tropical rocky shore zoantharian *Palythoa caribaeorum* (Duchassaing and Michelotti, 1860). *Aquatic Invasions*, 15 (1): 98–113.
- Guimarães, D. S. D. 2016. Malacofauna associada ao coral bioinvasor Tubastraea tagusensis Wells, 1982 (Scleractnia: Dendrophyliidae) na Baía de Todos-os-Santos, Bahia. Master's degree Dissertation. Universidade Federal da Bahia, Bahia, Brazil.
- Hennessey, S. M., & Sammarco, P. W. 2014.Competition for space in two invasive Indo-Pacific corals — *Tubastraea micranthus* and *Tubastraea coccinea*: Laboratory experimentation. *Journal of Experimental Marine Biology and Ecology*, 459: 144–150.
- Hidaka, M. & Yamazato, K. 1984. Interspecific interactions in a scleractinian coral *Galaxea fasicularis*: induced formation of sweeper tentacles. *Coral Reefs*, 3:77–85.
- Huettel, M., Wild, C. & Gonelli, S. 2006. Mucus trap in coral reefs: Formation and temporal evolution of particle aggregates caused by coral mucus. *Marine Ecology Progress Serie*, 307: 69–84.
- Jackson, J. B. C. 1977. Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. *The American Naturalist*, 111: 743–767.
- Jackson, J. B. C. & Buss, L. 1975. Allelopathy and spatial competition among coral reef invertebrates. *Proceedings of the National Academy of Sciences of the United States of America*, 72: 5160–5163.
- Koh, E. G. L. & Sweatman, H. 2000. Chemical warfare among scleractinians: bioactive natural products from *Tubastraea faulkneri*, Wells kill larvae of potential competitors. *Journal of Experimental Marine Biology and Ecology*, 251: 141–160.
- Kropp, R. K. 1986. Feeding biology and mouthpart morphology of three species of Coral Gall Crabs (Decapoda: Cryptochiridae). *Journal of Crustacean Biology*. 6(3): 377–384.
- Krupp, D. A. 1982. The composition of the mucus from the mushroom coral, *Fungia scutaria*. *Proceedings of the Fourth International*

Coral Reef Symposium, Manila, 1982, pp. 69–73 (2).

- Lages, B. G., Fleury, B. G., Ferreira, C. E. L. & Pereira, R. C. 2006. Chemical defense of an exotic coral as invasion strategy. *Journal of Experimental Marine Biology and Ecology*, 328: 127–135.
- Lages, B. G., Fleury, B. G., Hovell, A. M. C., Rezende, C. M., Pinto, A. C. & Creed, J. C. 2012. Proximity to competitors change secondary metabolites of nonindigenous cup corals, *Tubastraea* spp., in the southwest Atlantic. *Marine Biology*, 159: 1551–1559.
- Lang, J. 1973. Interspecific aggression by scleractinian corals. 2: Why the race is not always to the swift. *Bulletin of Marine Science*, 23: 260–279.
- Lapid, E. D., Wielgus, J., Chadwick-Furman, N. E. & Gan, R. 2004. Sweeper tentacles of the brain coral *Platygyra daedalea*: induced development and effects on competitors. *Marine Ecology Progress Series*, 282: 161– 171.
- Leão, Z. M. A. N., Kikuchi, R. K. P. & Testa, V. 2003. Corals and Coral Reefs of Brazil. In: Cortés J. (ed) *Latin American Coral Reefs*, *April 2003. Elsevier Science*, pp. 9–52.
- Leão, Z. M. A. N. & Kikuchi, R. K. P. 2005. A Relic Coral Fauna Threatened by Global Changes and Human Activities, Eastern Brazil. *Marine Pollution Bulletin*, 51: 599–611.
- Leão, Z. M. A. N., Kikuchi, R. K. P., Ferreira, B. P., Neves, E. G., Sovierzoski, H. H., Oliveira, M. D. M., Maida, M., Correia, M. D. & Johnsson, R. 2016. Brazilian coral reefs in a period of global change: A synthesis. *Brazilian Journal* of *Oceanography*, 64 (sp2): 97–116.
- Lessa, G. C., Cirano, M., Tanajura, C. A. S. & Silva, R. R. 2009. Oceanografia Física. In: Vanessa Hatje e Jailson B. de Andrade. (Org). *Baía de Todos os Santos: Aspectos Oceanográficos*. Salvador: EDUFBA, pp. 69–119 [vol 1].
- Longo, G. O., Krajewski, J. P., Segal, B. & Floeter, S. R. 2012. First record of predation on reproductive *Palythoa caribaeorum* (Anthozoa: *Sphenopidae*): insights on the trade-off between chemical defenses and nutritional value. *Marine Biodiversity*, 5: 1–3.
- Luz, B. L. P. & Kitahara, M. V. 2017. Could the invasive scleractinians *Tubastraea coccinea* and *T. tagusensis* replace the dominant zoantharian *Palythoa caribaeorum* in the Brazilian subtidal? *Coral Reefs*, 36: 875.

- Luz, B. L. P., Di Domenico, M., Migotto, A. E. & Kitahara, M. V. 2020. Life-history traits of *Tubastraea coccinea*: Reproduction, development, and larval competence. *Ecology and Evolution*, 10(13): 6223-6238.
- Mangelli, T. S. & Creed, J. C. 2012. Análise comparativa da abundância do coral invasor *Tubastraea* spp. (Cnidaria, Anthozoa) em substratos naturais e artificiais na Ilha Grande, Rio de Janeiro, Brasil. *Iheringia*, 102 (2): 122–130.
- Mantelatto, M., Creed, J., Mourão, G., Migotto, A. & Lindner, A. 2011. Range expansion of the invasive corals *Tubastraea coccinea* and *Tubastraea tagusensis* in the Southwest Atlantic. *Coral Reefs*, 30: 397.
- Melo, L. F. A., Camara, C. A. G., Oliveira, L. L. D. S. S., Modesto, J. C. A. & Pérez, C. D. 2012. Toxicity against *Artemia salina* of the zoanthid *Palythoa caribaeorum* (Cnidaria: Anthozoa) used in folk medicine on the coast of Pernambuco, Brazil. *Biotemas*, 25 (3): 145–151.
- Mendonça-Neto, J. P. & Gama, B. A. P. 2009. The native *Palythoa caribaeorum* overgrows on invasive species in the intertidal zone. *Coral Reefs*, 28: 497.
- Meurer, B. C., Lages, N. S., Pereira, O. A., Palhano, S. & Magalhães, G. M. 2010. First record of native species of sponge overgrowing invasive corals *Tubastraea* coccinea and *Tubastraea tagusensis* in Brazil. *Marine Biodiversity Records*, 3: 1–3.
- Miranda, R. J., Porto, L., Cruz, I. C. S.& Barros, F. 2012. Coral invasor *Tubastraea* spp. em recifes de corais e substratos artificiais na Baía de Todos os Santos (Ba). In *Livro de resumos Congresso Brasileiro de Oceanografia*. *Rio de Janeiro*, 13-16 *november 2012*. Associação Brasileira de Oceanografia, pp. 1527–1532.
- Miranda, R. J., Costa, Y., Lorders, F. L., Nunes, J. A.
 C. & Barros, F. 2016a. New records of the alien cup-corals (*Tubastraea* spp.) within estuarine and reef systems in Todos os Santos Bay, Southwestern Atlantic. *Marine Biodiversity Records*, 9: 35.
- Miranda, R. J., Cruz, I. C. & Barros, F. 2016b. Effects of the alien coral *Tubastraea tagusensis* on native coral assemblages in a southwestern Atlantic coral reef. *Marine Biology*, 163: 1–12.

- Mizrahi, D., Navarrete, A. S. & Flores, A. A. V. 2014. Uneven abundance of the invasive sun coral over habitat patches of different orientation: an outcome of larval or later benthic processes? *Journal of Experimental Marine Biology and Ecology*, 452: 22–30.
- Molnar, J. L., Gamboa, R. L., Revenga, C. & Spalding, M. D. 2008. Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment*, 6: 485–492.
- Moore, R. E. & Scheuer, P. J. 1971. Palytoxin: A new marine toxin from a coelenterate. *Science*, 172: 495–496.
- Neves, E. G., Johnsson, R., Sampaio, C. & Pichon, M. 2006. The occurrence of *Scolymia cubensis* in Brazil: revising the problem of the Caribbean solitary mussids. *Zootaxa*, 1366: 45–54.
- Nogueira, M. M., Alves, J., Neves, E. & Johnsson, R. 2021. The competition of native sponges and the sun coral *Tubastraea* spp. does not influence the morphological pattern of a new *Photis* (Photidae: Senticaudata). *Journal of Natural History*, 55 (33,34): 2065–2081.
- Okada, N., Vaccani, A., Behrends, E., Santos, R., Costa, H., Moura, F. & Freret-Meurer, N. 2012. Comunicação de alarme em duas espécies de cnidário, *Tubastraea* sp. e *Palythoa caribaeorum* (Cnidaria: Anthozoa). *Revista Brasileira de Zoociências*, 14 (1,2,3): 155–165.
- Paz-García, D. A., Reyes-Bonilla, H., González-Peralta, A. & Sánchez-Alcántara, I. 2007. Larval release from *Tubastraea coccinea* in the Gulf of California, Mexico. *Coral Reefs*, 26: 433.
- Peach, M. & Guldberg, O. H. 1999. Sweeper polyps of the coral *Goniopora tenuidens* (Scleractinia: Poritidae). *Invertebrate Biology*, 118: 1–7.
- Pereira, R. C. 2004. A química defensiva como potencial invasor de espécies marinhas. In: Silva J.S.V and Souza, R. C. C. L. (eds) Água de lastro e bioinvasão. Rio de Janeiro, BR: Interciência, pp. 173–189.
- Pérez, C. D., Vila-Nova, D. A. & Santos, A. M. 2005. Associated community with the zoanthid *Palythoa caribaeorum* (Duchassaing & Michelotti, 1860) (Cnidaria, Anthozoa) from littoral of Pernambuco, Brazil. *Hydrobiologia*, 548: 207–215.

- Rabelo, E. F., Soares, M. O. & Matthews-Cascon, H. Competitive 2013. interactions among Zoanthidae) zoanthids (Cnidaria: in an northeastern intertidal zone of Brazil. Brazilian Journal of Oceanography, 61: 35-42.
- Ritson-William, R., Arnold, S. N., Fogarty, N. D., Steneck, R. S., Vermeij, M. J. A. & Paul, V. J. 2010. New Perspectives on Ecological Mechanisms Affecting Coral Recruitment on Reefs. *Smithsonian Contributions to the Marine Sciences*, 38: 437–457.
- Ruiz, G. M., Carlton, J. T., Grosholz, E. & Hines, A.
 H. 1997. Global Invasions of Marine and Estuarine Habitats by Non-Indigenous Species: Mechanisms, Extent, and Consequences. *American Zoologist*, 37: 621– 632.
- Saá, A. C. A., Crivellaro, M. & Winter, B. B. 2020. Unraveling interactions: do temperature and competition with native species affect the performance of the non-indigenous sun coral *Tubastraea coccinea*? *Coral Reefs*, 39: 99– 117.
- Sammarco, P. W., Atchison, A. M., Boland, G. S., Sinclair, J. & Lirette, A. 2012. Geographic expansion of hermatypic and ahermatypic corals in the Gulf of Mexico, and implications for dispersal and recruitment. *Journal of Experimental Marine Biology and Ecology*, 436-437: 36–39.
- Sammarco, P. W., Porter, S. A., Sinclairm, J. & Genazzio, M. 2014. Population expansion of a new invasive coral species – *Tubastraea micranthus* – in the northern Gulf of Mexico. *Marine Ecology Progress Series*, 495: 161– 173.
- Sammarco, P. W., Porter, S. A., Genazzio, M. & Sinclair, M. 2015. Success in Competition for Space in Two Invasive Coral Species in the western Atlantic *Tubastraea micranthus* and *T. coccinea. Plos One* 10 (12), e0144581.
- Sampaio, C. L. S., Miranda, R. J., Maia-Nogueira, R. and Nunes JACC (2012) New occurrences of the nonindigenous orange cup corals *Tubastraea coccinea* and *T. tagusensis* (Scleractinia: Dendrophylliidae) in Southwestern Atlantic. *Check List*, 3: 528– 530.
- Santos, L. A. H., Ribeiro, F. V. & Creed, J. C. 2013. Antagonism between invasive pest corals *Tubastraea* spp. and the native reef-builder *Mussismilia hispida* in the southwest Atlantic.

Journal of Experimental Marine Biology and Ecology, 449: 69–76.

- Sebens, K. P. 1982. Intertidal distribution of zoanthids on the Caribbean coast of Panama: effects of predation and desiccation. *Bulletin* of Marine Sciences, 32: 316–335.
- Sebens, K. P. & Miles, J. S. 1988. Sweeper tentacles in a gorgonian octocoral: morphological modifications for interference competition. *Biological Bulletin (Woods Hole)*, 175: 378– 387.
- Seebens, H., Gastner, M. T. & Blasius, B. 2013. The risk of marine bioinvasion caused by global shipping. *Ecology Letters*, 16: 782–90.
- Silva, J. F., Gomes, P. B., Santana, E. C., Silva, J. M., Lima, E. P., Santos, A. M. M. & Pérez, C. D. 2015. Growth of the tropical zoanthid *Palythoa caribaeorum* (Cnidaria- Anthozoa) on reefs in northeastern Brazil. *Anais da Academia Brasileira de Ciências*, 87 (2): 985–996.
- Silva, A. G., Fortunato, H. F. M., Lôbo-Hajdu, G. & Fleury, B. G. 2017. Response of native marine

sponges to invasive *Tubastraea* corals: a case study. *Marine Biology*, 164: 78.

- Stampar, S. N., Silva, P. & Luiz-Jr, O. J. 2007. Predation on the Zoanthid Palythoa caribaeorum (Anthozoa, Cnidaria) by a Hawksbill Turtle (*Eretmochelys imbricata*) in Southeastern Brazil. Symposium on Sea Turtle Biology and Conservation, 117 3.
- Suchanek, T. H. & Green, D. J. 1981. Interspecific competition between *Palythoa caribaeorum* and other sessile invertebrates on St. Croix reefs, U.S. Virgin Islands. **Proceeding of the** Fourth International Coral Reef Symposium, Manila, 2: 679–684.
- Thomason, J. C. & Brown, B. E. 1986. The nidom: an index of aggressive proficiency in scleractinian corals. *Coral Reefs*, 5, 93–101.
- Williams, E. H. & Bunkley-Williams, L. 1988. Bleaching of Caribbean coral reef symbionts. Proceedings of the Sixth International Coral Reef Symposium, Austrália, 3: 313– 318.
- Zar, J. H. 2010. *Biostatistical Analysis*, 5th. edition. Upper Saddle River: Pearson Hall.

Received: October 2022 Accepted: March 2023 Published: September 2023