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Research Article

Resistance to desiccation and healing regeneration in the sun coral

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Abstract

Sun corals, *Tubastraea* spp., are native to the Indo-Pacific Ocean, but have established populations in different areas of the Atlantic Ocean. *Tubastraea* spp. are considered invasive in Brazil, being targets of a National Plan for Prevention, Control and Monitoring. One of the objectives of this plan is to develop scientific research and technology, focused on subsidies for the prevention and management of sun coral dissemination. Through manipulative experiments under controlled laboratory conditions, we analyzed the effects of exposure to air in sun coral colonies during different time intervals, to provide general biosecurity subsidies for possible management operations using desiccation. In addition, we recorded the coral ability to regenerate soft tissues damaged after trauma due to desiccation. We observed that *Tubastraea* sp. resists up to four hours out of seawater without permanent damage, despite being a typical subtidal organism. The number and severity of wounds and loss of soft tissues increased with exposure time to air, which affected the recovery capacity of this coral. Full mortality of the colonies (all polyps dead) was achieved only after four days of exposure to air. In addition, the healing regeneration process was recorded here for the first time in sun corals. The proportion of polyps partially retaining soft tissues involved in feeding is determining for the recovery of the entire colony, which can occur in just two weeks. Such data offer relevant biosecurity subsidies for possible management operations using desiccation.

Key words: *Tubastraea,* invasive corals, invasive species, biological invasion, environmental management, marine ecosystems

Introduction

Tubastraea spp. (Dendrophylliidae, Scleractinia), popularly known as sun coral, are native to the Indo-Pacific Ocean but have established populations in natural and artificial areas of North and South Atlantic Oceans (Boschma 1923; Vaughan and Wells 1943; Fenner 2001; Castro and Pires 2001; Cairns 2000; Fenner and Banks 2004; De Paula and Creed 2004; Brito et al. 2017; Silva et al. 2019). These corals were registered for the first time in Brazil by Castro and Pires (2001) in Rio de Janeiro State; the genus has spread along the Brazilian coast since then, and now is found discontinuously between Ceará and Santa Catarina states (Creed et al. 2017a).

Tubastraea spp. are considered invasive in Brazil, being targets of a National Plan for Prevention, Control and Monitoring (Brasil 2018). The 9th objective of this plan aims to develop scientific research and technology, preferably focused on subsidies for the prevention and management of sun coral dispersion. Since 2006, initiatives to control *Tubastraea* spp. based on manual removal have been locally implemented in natural habitats, mainly in three marine protected areas, by environmental government agencies, non-governmental organizations, researchers, and volunteers in Brazil (Creed et al. 2017b). Recent studies indicate that is virtually impossible to reduce and subsequently maintain at low densities *Tubastraea* spp. populations through a single management procedure; repetitive interventions are needed at each locality, ideally with a 2–3-month interval between removal events (Savio et al. 2021). De Paula et al. (2017) and Crivellaro et al. (2021) suggested that after the first control effort, follow-up within 6 to 12 months may be sufficient. Creed et al. (2021) also believe that repeated removal is the best option for controlling sun coral populations but contend that a single removal may be sufficient at low densities (cover < 10%). The question is how feasible it is to scale up the repeated manual removal procedure in natural habitats with an extensive and heavily dense *Tubastraea* coverage. It is important to highlight that undertaking large-scale removals requires the availability of continuous human and financial resources (Savio et al. 2021). However, at the southern limit of distribution of *Tubastraea* in Brazil, the early detection and rapid response were insufficient for achieving eradication of a small, isolated population in an important Marine Reserve (Crivelllaro et al. 2020). These authors mentioned the presence of sun corals in crevices inaccessible to manual removal, fact also pointed out by Savio et al (2021). Colonies located at greater depths (> 30 m) also represent a limitation regarding manual management (Savio et al. 2021).

In addition to manual removal in natural areas, some recent studies have been developed to test experimental methods for sun coral control. The methods applied in most studies performed so far require alteration of environmental conditions and release of toxic substances into the seawater, limiting their use under conditions in which the target structure must be isolated from the environment (e.g., by encapsulation or other type of containment). Experiments with low salinity treatments achieved 100% mortality of colonies exposed for 2 hours in fresh water (Moreira et al. 2014). The “wrapping” technique was tested to kill isolated colonies with plastic and raffia sheets. In this case, at least seven days of treatment were necessary to achieve the conditions of starvation, anoxia, or physical attrition (with the wraps) to kill completely all colonies (Mantelatto et al. 2015). Sodium hypochlorite (NaClO) was tested at different concentrations under laboratory conditions to evaluate its effect on sun coral mortality. Concentrations higher than 20 ppm were lethal after sixty hours of exposure, however, 150 ppm was the lowest NaClO concentration that caused the death of 100% of the colonies within few hours (≤ 5 hours). Solutions in seawater containing more than 150 ppm of this salt are the best option to be employed in the management and control of the sun coral in restricted areas (Altvater et al. 2017). This method has been also applied to control biofouling caused by mussels (Rajagopal et al. 2002). Acetic acid, a chemical agent considered somewhat less harmful to the environment, was applied in full and half concentration to eliminate sun corals by two methods, complete immersion, and multiple injections, obtaining uneven results. The immersion method was effective, but the corals died completely just one month after applying the treatment. Through multiple injection applications, it was not possible to kill all the polyps in the colonies, which after a while recovered (Creed et al. 2019).

As other modular organisms (e.g., ascidians and bryozoans), corals are made up of repeating units (polyps) that transfer energy to each other, exploiting resources and competing for space more efficiently than solitary invertebrates (Bak and Luckhurst 1980; Ryland and Warner 1986). In addition, they are capable of survive despite the death of some of their components, which is known as partial mortality (Hughes and Jackson 1985). This leads to colony fragmentation, affecting its dispersal potential and population dynamics (Hughes et al. 1992). This characteristic, combined with regeneration abilities (damage recovery and tissue reorganization) allow corals to survive after traumas of different nature and intensity. However, regeneration processes can be affected by factors such as environmental conditions, colony morphology, size and shape of the lesion, periodicity of trauma, and are species-specific (Holstein et al. 2003). Some evidence of regeneration has been reported for sun coral fragments, based on records of tissue retraction and reorganization that trigger the generation of new polyps (Luz et al. 2018), but no healing processes has been detected so far. Also, *Tubastraea* shows a broad tolerance to temperature and desiccation, as indicated by its abundance in very shallow waters occasionally exposed to air (0.1–0.5 m) (De Paula and Creed 2005). Based on such information, we investigate here some characteristics related to the resistance and resilience of sun coral to desiccation.

Desiccation is a technique where the vessel or structure is removed from the water and left on a hard stand until all biofouling has died. This procedure is commonly used to treat biofouling on aquaculture and fishing equipment and has been proposed as a mitigation tool to manage vessel biofouling risks (Inglis et al. 2012; Hopkins et al. 2015). The method is not a feasible option for large commercial vessels over 30 m, as the cost for prolonged dry-dock operation would be prohibitive (Inglis et al. 2012). Other logistical challenges for using desiccation in biofouling control on large vessels are the limited number of dry docks, and the availability and cost of heavy lift vessels (Hilliard et al. 2006; Hopkins and Forrest 2010; Hopkins et al. 2015). Nevertheless, desiccation may be promising in situations where surfaces to be treated—vessels, buoys, floats etc.—are not too large and can be lifted or transported ashore without major logistic or budget constraints.

Tubastraea spp. live in the infralittoral zone, but populations established in shallow waters are potentially exposed to desiccation during extreme low tides. Here we conducted manipulative experiments, under controlled laboratory conditions, subjecting adult colonies of this coral to different periods of exposure to air. We expected that the longer corals remained under desiccation, the higher the mortality or the lower the potential for recovery, because a greater amount of tissue to be repaired implies an increasing energy expenditure and deviation from primary metabolic pathways. We performed the experiments by observing *Tubastraea* healing regeneration capacity while recording soft tissue recovery. We aimed to quantify the gradual increase in tissue damage, with progressive loss of regenerative capacity as the corals are exposed to longer periods of desiccation. This allowed us to estimate the minimum exposure time to desiccation to achieve 100% mortality in sun coral colonies, a relevant biosecurity information for possible use of desiccation as a mitigation tool to manage vessel biofouling risks.

Materials and methods

Coral collection and preparation for the experiment

Two species of *Tubastraea* were previously described for the Brazilian coast (*T. coccinea* and *T. tagusensis*). Colonies collected for this work were preliminarily identified as *T. tagusensis;* however, Bastos et al. (2022) identified three morphotypes from Brazil which were genetically delimited into two species: *T. coccinea* (Morphotypes I and II) and *Tubastraea* sp. (Morphotype III). Morphotype I has morphological patterns of *T. aurea,* but there was no molecular divergence to support the species differentiation and it continues to be recognized as a morphological variant of *T. coccinea*. The third morphotype is both morphologically and genetically distinct from *T. coccinea* and is not representative of *T. tagusensis* despite earlier records of this species in Brazil. For this reason, we adopted the denomination sun coral or *Tubastraea* sp. referring to the dendroid morphotype previously identified as *T. tagusensis*.

Sun coral colonies were collected in April 2018 from rocky shores of Búzios Island, São Paulo, Brazil (23°48′11″S; 45°08′21″W), a small island (755 ha in area), 25 km from mainland, which is inhabited by a small fishing community made up of about 70 families (Begossi 1996). The prevailing climate is wet tropical with warm summers, frequent tropical storms, and dry winters with sudden drops in temperature due to cold fronts from the southeast. Field work was carried out at two sampling sites, separated by approximately 3 km, known locally as "Pedra Lisa" and "Ponta Leste". At these sites the benthic communities are dominated by

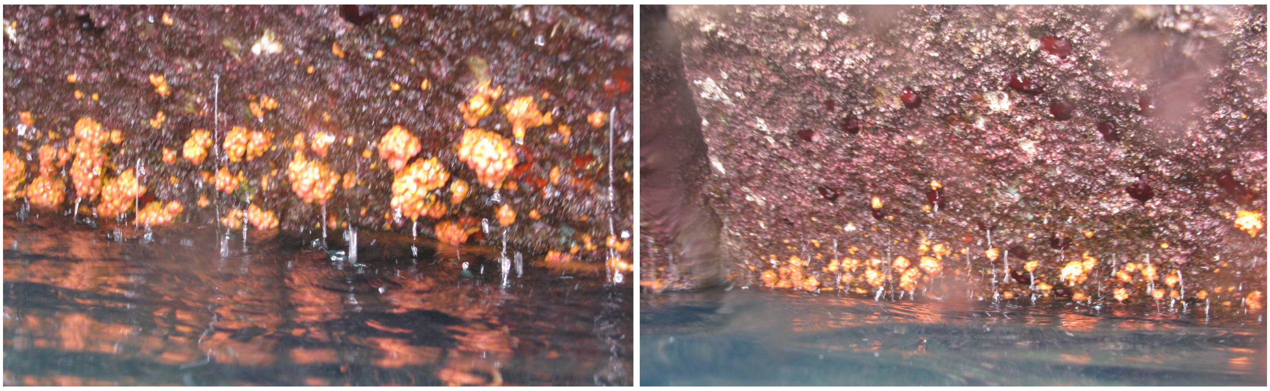

Figure 1. *Tubastraea* sp. colonies exposed to air at low tide. Búzios Island, southeastern Brazil. Photographs by Damián Mizrahi.

different species, depending on the substrate orientation: filamentous algae, *Sargassum* spp. and zooxanthellate corals (*Mussismilia hispida* and *Madracis decactis*) dominated on upward-facing surfaces, while on vertical walls and downward-facing areas suspension-feeders invertebrates prevail, such as bryozoans, encrusting sponges, colonial ascidians, and the cnidarians *Parazooanthus* spp. and *Carijoa riisei* (Mizrahi et al. 2014; Mizrahi et al. 2017; Vinagre et al. 2018). For these sites, we have recorded numerous colonies of sun corals attached to exposed vertical walls, out of the seawater at low tides (Figure 1).

A total of 200 colonies were mechanically removed by scuba diving from the natural substrate with a hammer and chisel, avoiding coral fragmentation. Specimens of *Tubastraea* sp. were collected over a 200 m extension area for each sampling site, at a depth of 2 to 8 m, maintaining a minimum distance of 3 meters between the collecting points to obtain independent samples. Once detached from rocky substrate, each colony was immediately packaged underwater in a ziplock bag filled with seawater for transport. At the laboratory, the corals were transferred to 500 L tanks and kept in an open seawater circulation system, with a retention mesh (150 µm) at the outflow, to prevent the escape of larvae and other biogenic materials. Every 3 to 4 days, live zooplankton collected with a 200 µm mesh net was offered as food supply to the corals. After one month of acclimatization to laboratory conditions, sun coral colonies with a similar volume and number of polyps, exhibiting reddish orange coenosarc, free of epibionts or wounds (indicating good physiological condition), were chosen for the experiments (n = 60). The volumetric size of each colony was estimated by measuring the liquid contained in a beaker, displaced after introducing each colony (mean ± se = 73.31 ± 2.48 g dm^{-3}). The number of polyps per colony was counted with the naked eye; considering polyps with diameter between 0.5 and 1 cm (mean ± se = 64.63 ± 1.57) and was not different between groups of replicates (ANOVA: $F_{6,50} = 0.6193$, $p < 0.7748$).

Experimental procedure: exposure of sun coral to desiccation

For each replicate, a colony was placed into a 1.9 L jar containing filtered seawater (< 5 µm mesh size) supplied through a continuous open flow system.

Laboratory conditions were kept controlled with constant temperature (25 °C) and natural photoperiod, under dim light conditions. After 24 hours of acclimation, colonies were removed from jars and exposed to air, inside the laboratory. Relative humidity, monitored every hour by a Campbell Scientific™ hygrograph (sensor mod: CS2215, data logger mod: CR10X), remained stable within 68.8–78.0%. The experiment was carried out considering nine treatments (n = 6 each) relating to different desiccation durations: $t_1 = 2$ h, $t_2 = 4$ h, $t_3 = 8$ h, $t_4 = 12$ h, $t_5 = 20$ h, $t_6 = 38$ h, $t_7 = 52$ h, $t_8 = 72$ h, $t_9 = 96$ h and a control trial, t_{ctr} (without removing the colonies from seawater). After exposure to air, each colony was returned to the jar linked to the culture system for a period of three days, for the observation of partial mortality and coenosarc loss. Seawater flow contributed to the spontaneous removal of necrotic tissues from affected polyps, preventing the proliferation of decomposing organisms such as bacteria and fungi. Then, corals were transferred to 500 L tanks with an open seawater flow system, under natural conditions of light and temperature. Each colony was marked for identification, periodically fed, and monitored every 3–4 days to record the number of polyps affected by desiccation. The entire experiment lasted for 96 days.

Data were grouped into four categories corresponding to different degrees of polyp damage: X_1) dead polyps, without any living tissue; X_2) polyps with more than 50% of coenosarc loss (no remains in the mouth area); X_3) polyps with up to 50% of coenosarc loss (partially preserved in mouth and gastrovascular cavity); and X_4) healthy and intact polyps (Figure 2). The initial number of polyps assigned to each category of health condition was recorded at t_0 (when corals were returned to seawater after desiccation), to measure deleterious effects. Replicates of each treatment were monitored until there was no change in the number of damaged polyps for at least four inspections (approximately 10 days with no changes). The number of polyps for each category of health condition (X_1 to X_4) were compared between the onset (t_0) and the end of the experiment (96 days, t_f), to detect possible differences in the soft tissue regeneration of the corals subjected to the different treatments. Data for variables (X_1 to X_4) were grouped in different ways for statistical analysis. A one-way ANOVA and a *Tukey* test were used to compare (i) the percentage of affected polyps by desiccation ($X_1 + X_2 + X_3$) at t_0; (ii) the regeneration rate, as estimated by the percentage of polyps damaged by desiccation at t_0 that recover to fully healthy polyps at t_f (calculated here as X_4t_{f} - X_4t_0); and (iii) the ratio of partially damaged polyps in each colony due to desiccation, calculated as the quotient between X_3/X_2 for data collected at t_0. Comparisons of these data between treatments were related to evidence of desiccation stress and effects on coral resilience. Data used to compare (ii) treatments did not meet the assumption of homoscedasticity, even after applying transformations. However, since it is an experiment with balanced replicates (n = 6) between treatments, an ANOVA test was applied, according to Underwood (1997).

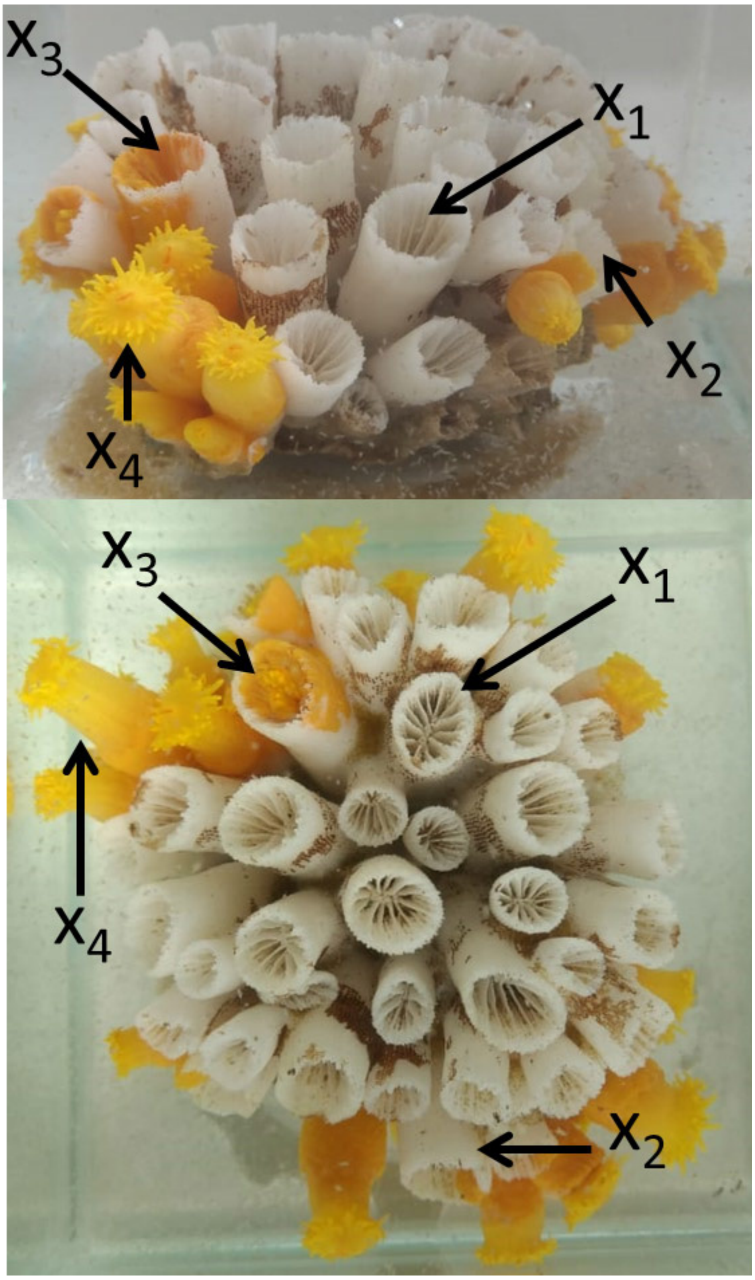

Figure 2. Top and side view of a sun coral colony that has been exposed to desiccation. The polyps that retain soft tissues extend its tentacles to feed on plankton. According to the degree of damage suffered, the polyps were classified as: X_1: dead polyp (calcareous skeleton fully exposed), X_2: polyps that lost more than 50% of soft tissues (no remains in mouth), X_3: polyps that lost up to 50% of soft tissues (partially or completely preserved in mouth and gastrovascular cavity) and X_4: completely healthy polyps. Photographs by Milena C. Silva and Damián Mizrahi.

For (iii) it was necessary to perform a data transformation to $y = \sqrt{(x + 1)}$ to meet homoscedasticity (*Levene* test: $F = 2.14$, $p = 0.105$). The software *Statistica* v.10.1 was used to undertake all statistics.

Results

Desiccation effects

As expected for an organism inhabiting the infralittoral, the percentage of damaged polyps at t_0 (X_1, X_2 and X_3 grouped together for this first analysis)

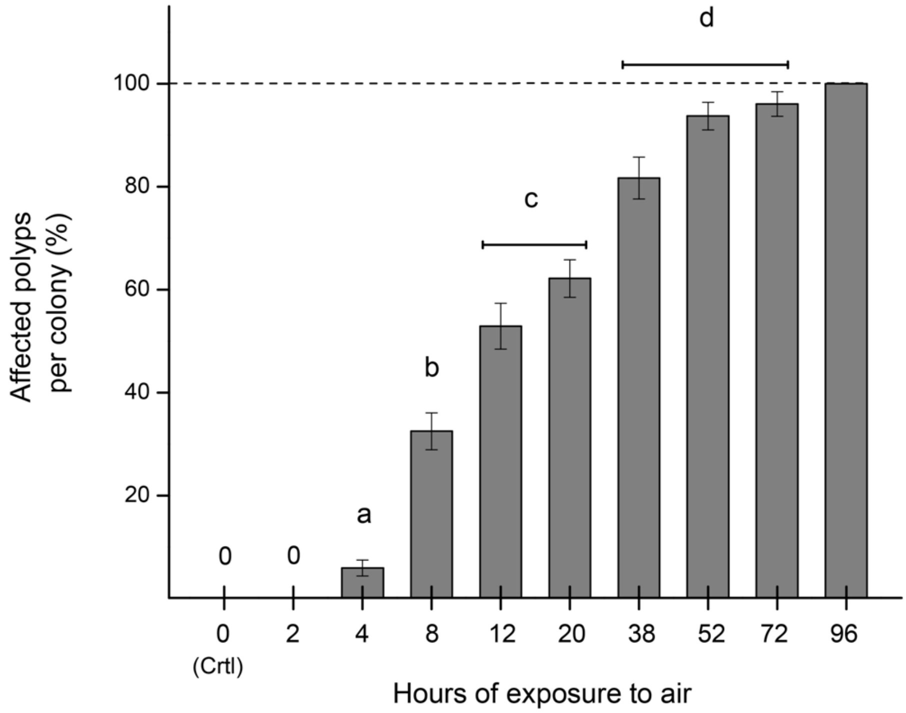

Figure 3. Percentage (mean ± ES) of polyps that lost soft tissues, $X_1+X_2+X_3$, in corals subjected to different periods of desiccation. The control treatment, indicated as "0 h (crtl)", estimates the potential effects due to manipulation. Different letters above the bars indicate significant differences ($p < 0.05$) between treatments with intermediate effects ($n = 6$).

was higher in colonies exposed to air for a longer time. The corals exposed during 2 h of desiccation (Supplementary material Figure S1) remained unchanged and with signs of good health (coenosarc without wounds, strong orange coloration and functional mouth and polyps) throughout the experiment. Similar results were obtained for the control treatment, meaning that no significant manipulation effects occurred. For treatments resulting in intermediate damages to corals (0 < % of affected polyps < 100) the effect of exposure to air differed strongly with time (ANOVA: $F_{6,35} = 100.2$, $p < 0.0001$). *Ad hoc* tests showed four response groups (*Tukey* test: $p < 0.005$, Figure 3): a) colonies subjected to 4 h of desiccation had just over 5% of affected polyps, X_3, with minimal soft tissue damage (Figure S2), b) corals exposed 8 h to air suffered damages of varying severity in 32.45% of their polyps, with individuals being assigned mainly to the X_3 group and some to X_1 and X_2 (Figure S3), c) for the 12 h and 20 h treatments the amount of affected polyps was statistically similar (about 50% per colony) but with a trend of a slightly greater effect in corals exposed for 20 h (Figures S4 and S5), and d) specimens exposed to air for 38 h, 52 h and 72 h suffered effects in more than 80% of polyps, and again an increasing trend in soft tissue damage was noticed with longer exposures. For the first case (Figure S6) some polyps slightly affected by desiccation (X_3) were still detected, which were practically absent in the two treatments that lasted longer (Figures S7 and S8). After 96 h of exposure to air, all polyps completely lost their soft tissues, i.e., all colonies died, and no recovery occurred (Figure S9).

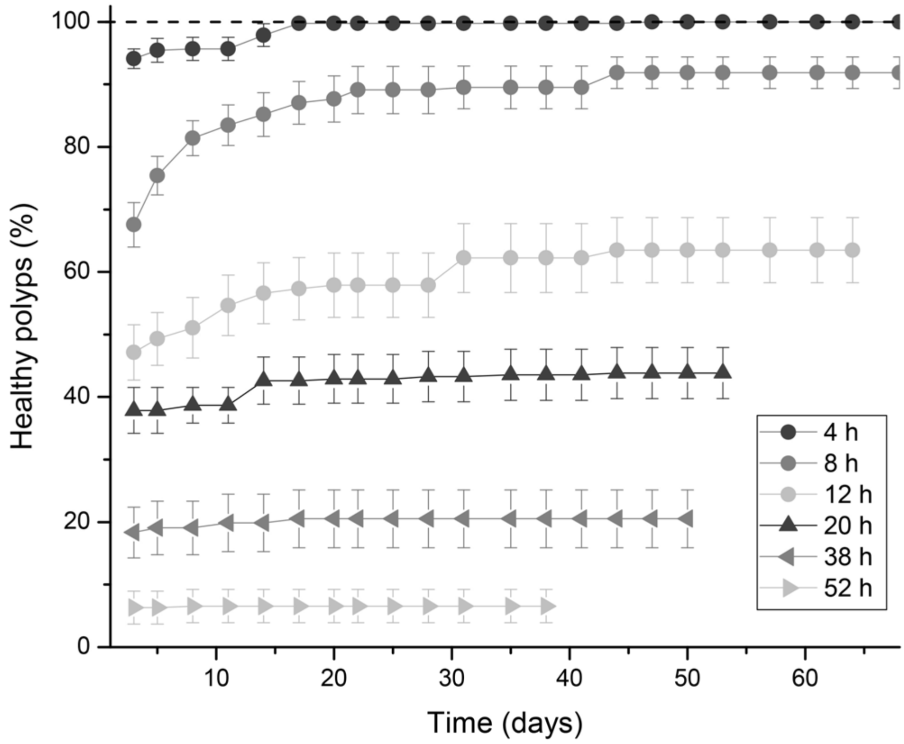

Figure 4. Health of sun coral colonies (in percentage of polyps, X_4) over time after having suffered desiccation trauma during different time intervals, indicated in hours (mean ± SE) and represented with different geometric symbols and shades of gray, as indicated in the graph.

Therefore, four days was the minimum time interval required to achieve complete desiccation and death of colonies by the method described here.

Healing regeneration

Coral colonies more intensely damaged by desiccation recovered at a lower extent, and the regeneration process occurred mainly during the first two weeks after reintroduction to seawater, for most treatments (Figure 4). While the colonies exposed to desiccation for 4 hours fully recovered, tissue regeneration was reduced to 92% of polyps for corals exposed to air for 8 h and barely exceeded 63% for those treated for 12 h. Only 43.8% of the polyps regenerated tissues when the treatment lasted 20 h, and those colonies exposed to air for 38 and 52 h recovered their soft tissue in only a few polyps (less than 3%). None of the polyps healed after 72 h of desiccation, although some of them survived until the end of the experiment (96 days). Soft tissues were completely lost in colonies exposed for 96 h, with no signs of healing. For both the shorter exposure to air (2 h) and the "control" treatment, sun coral colonies were unaffected and consequently no regenerative process occurred.

Regardless of treatment and replicates, tissue regeneration was not homogeneous for polyps within the same colony, which is explained by the initial uneven tissue damage (see example in Figure 5). In addition, the number of healthy polyps never decreased once recovered, which suggests optimal maintenance conditions during the experiment.

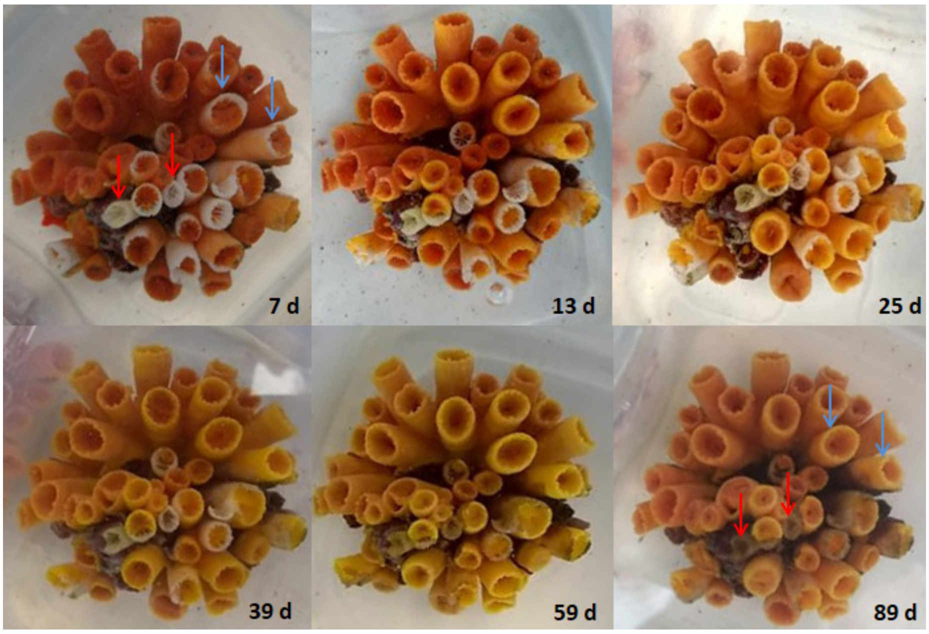

Figure 5. Progression in time of a sun coral exposed to desiccation for 8 hours. The two blue arrows indicate polyps slightly affected by desiccation (X_3), with soft tissues in the mouth and gastrovascular cavity partially preserved, which fully recovery. On the contrary, the red arrows indicate two polyps with more severe initial damage (X_2) that were not able to regenerate tissues and finally died and were colonized by biofilm. Photographs by Milena C. Silva and Damián Mizrahi.

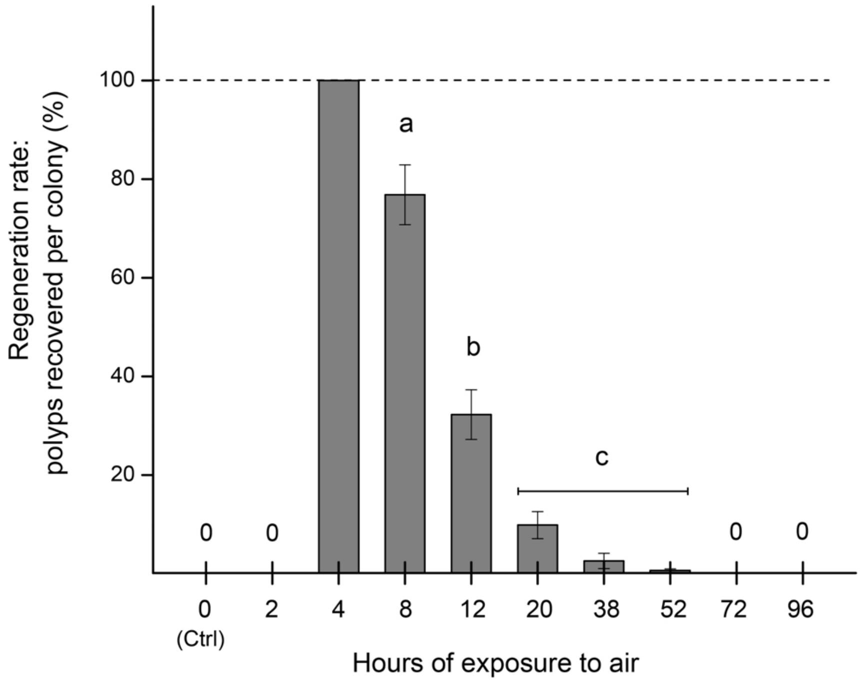

Figure 6. Regeneration rates (mean ± SE) in sun coral colonies subjected to different desiccation treatments (specified in number of hours of exposure to air, on the x-axis). Different letters above the bars indicate significant differences between treatments for recovery of polyps to fully health condition (X_4).

Comparisons between treatments for healing regeneration rates showed significant differences (ANOVA: $F_{1,25}$ = 70.4, p < 0.0001) which were discriminated by *a posteriori Tukey's* contrast (p < 0.005) and indicated with letters in Figure 6. Colonies exposed 8 h to air recovered in a higher

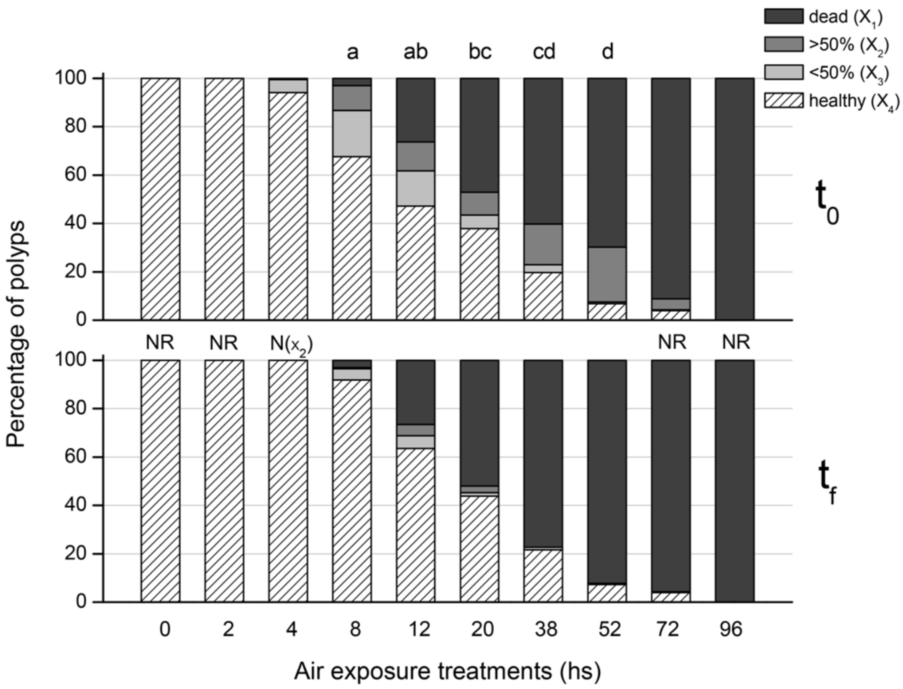

Figure 7. Comparisons of percentages of polyps with different conditions (X_1 to X_4) in sun coral colonies after exposure to desiccation for different periods of time (indicated in hours on the "x" axis), at the start (t_0, upper graph) and at the end of the experiment (t_f, lower graph). Different letters on the bars indicate similarities and differences between treatments from the *post hoc* contrasts for the X_3/X_2 ratio at t_0 – data transformed to $\sqrt{(x_3/x_2)}$+1-. The acronym "NR" indicates no regeneration and "N(X2)" means no records of polyps X_2.

percentage (more than double in number of polyps) than those exposed for 12 h, showing a differential response threshold of the coral between these exposure times. Corals treated for 20 h or longer recovered from damages in up to 10% of polyps, which means an additional significant decrease in healing. Since regeneration was null for the 72 h and 96 h treatments (no recovered polyps), and the 2 h and controls treatments had no affected polyps, these cases were not included in the comparisons of regeneration rates. The results for the 4h treatment were not considered either, since at t_0 polyps were not affected in more than 50% of their soft tissues (NX_2). Data for treatments without tissue regeneration (NR) were excluded from this analysis.

The comparison between treatments for the proportions of polyps partially affected by desiccation (X_3/X_2 at t_0) shows significant differences (ANOVA: $F_{1,25} = 17.74$, $p < 0.0001$), and the *post hoc* contrasts (*Tukey's* test: $p < 0.005$) confirmed a decreasing value of this ratio as exposure time to desiccation increased (discriminated by letters in Figure 7). The recovering from X_2 and X_3 conditions at t_0, to fully healthy polyps X_4 at t_f was uneven between different desiccation treatments. The longer the exposure time to desiccation, the more intense the damage inflicted on the colonies, thus decreasing the percentage of lightly damaged polyps and the regenerative potential of the corals. Furthermore, no dead polyps (X_1) exhibited any kind of tissue recovery, even when surrounded by healthy polyps, so we rule out the possibility of any "inter-polyp" regenerative contribution in such cases (see example in Figure 5).

Discussion

Here we report, for the first time, data on gradual variation in soft tissue damage in sun corals exposed to air for different time intervals. In addition, we identified the minimum period necessary to completely kill this coral by desiccation, offering biosecurity subsidies for possible management operations. Most descriptions of natural areas colonized by *Tubastraea* sp. report that its distribution is concentrated in shallow waters, from the intertidal zone to a few meters deep (*e.g.,* Mizrahi 2008; De Paula 2007; De Paula et al. 2014; Sampaio et al. 2012; Mizrahi et al. 2014; Brito et al. 2017). These colonization patterns, as well as records of sun corals outside the water column during extreme low tide events (M&M section, Figure 1), together with the results presented here, are evidence of partial resistance to desiccation in this coral, despite being a typical subtidal benthic organism. Although no damage was detected in soft tissues of colonies exposed for 2 h to air, a prolific secretion of mucus and distention of the tentacular crown of the polyps was observed after applying this treatment. These are signs of adaptive behavior to avoid desiccation stress reported for cnidarians inhabiting tidal pools that frequently remain exposed to the air at low tide (Ottaway 1979; Stabili et al. 2015). In this study we observed physical deterioration in *Tubastraea* sp. due to desiccation after at least 4 h of exposure to air, a period that must exceed the resistance threshold in this species. Despite this, there was no severe damage to soft tissues of tentacles, mouth, or gastrovascular cavity of the polyps in this treatment (Figures 7 and S2) and we recorded complete recovery of the colonies after a few weeks (Figure 4). Partial mortality due to desiccation was observed in colonies treated for 8 h or more, in which some polyps lost a large proportion of soft tissue, with no further recovery (Figures 5, 7 and S3). By applying the desiccation method described here, 50% mortality (LC50) is achieved in sun corals exposed to air during a period between 12 and 20 h (Figure 7), but only after 96 h of desiccation all colonies died completely (Figures 7 and S9).

Several studies reported on tissue repair in cnidarians after some type of injurious trauma (Holstein et al. 2003; Henry and Hart 2005; Bosch 2007). Wound healing ability has been linked to asexual reproduction and dispersal potential of stony corals because they generally break into parts after structural damage. The fragments derived from the parental colonies regenerate the damaged areas and adhere to the substrate by tissue proliferation, resulting in new recruitment (Heyward and Collins 1985; Highsmith 1982; Smith and Hughes 1999; Lirman 2000). Rapid regeneration in sublethal wounds plays an important role in the survival of long-lived corals, because such mechanism prevents inter- and intraspecific competition, predation and diseases caused by pathogenic endolytic fungi (Wahle 1985; Brown and Howard 1985; Bentis et al. 2000; Brandt et al. 2013). In addition, overgrowth of barnacles, hydroids, sponges, ascidians, and algae on injured corals indicates loss of competitive potential due to the decrease in the emission of allelopathic substances (Peyrot-Clausade and Brunel 1990; Titlyanov and Titlyanova 2008). Thus, competitive abilities related to chemical defense in sun corals (Creed 2006; Lages et al. 2011) could be significantly diminished due to the allocation of energy to heal wounds suffered after desiccation. Here, sun corals showed a greater potential for regeneration during the first 2–3 weeks after suffering desiccation injuries (Figure 4), which correlates with the survival strategies and high energy costs involved in tissue recovery proposed by other authors for phylogenetically related corals.

Several papers detail the responses in cnidarians to reduce the size of lesions (Bak 1983; Meesters and Bak 1993; Kramarsky-Winter and Loya 2000; Oren et al. 2001; Titlyanov et al. 2005; Denis et al. 2011). For example, manipulation experiments with *Porites compressa* allowed estimation of the effect of wound size on energy costs of healing, as well as ultimate effects on its growth rate (Jayewardene 2010). Short-term regeneration rates in *Favia favus* depend primarily on wound perimeter, but wound area becomes more important in later healing stages (Oren et al. 1997). *Favia* can heal few and small wounds with resources provided only by polyps surrounding the damaged areas, but several large injuries require the integration of energetic inputs from the entire colony, which represents a considerable metabolic demand that compromises fertility (Oren et al. 2001). Our observations concur with this, since sun coral regeneration rates varied with the intensity, size, and quantity of lesions. Colonies of *Tubastraea* sp. subjected to desiccation for 4 h suffered slight damages on few polyps, which recovered completely (Figures 4, 7 and S2). This shows the full resilience of this coral after exposure to desiccation for periods equivalent to the duration of spring low tides in the study area. Colonies removed from seawater for 8 h had the highest tissue regeneration rate, with 24% of polyps recovered to full health condition (X_4). However, healing was not complete due to the stress caused by this treatment, and permanent sequelae, with partial mortality, affected a considerable proportion of the colonies (Figure 7). Incomplete recovery from wounds in scleractinians was previously reported by Meesters et al. (1994), who showed that more intense damage and prolonged stress over time caused deviations in the typical regeneration response, which in extreme cases led to the partial or total death of the colony. Our results show that sun coral progressively loses its healing abilities as exposure to the air is extended for longer periods. In extreme cases, polyps become incapable of repairing the lesions inflicted by desiccation (result for 72 h treatment: Figures 6, 7 and S8).

Regeneration in cnidarians improves the chances of immediate survival but involves high-energy costs and requires redirection of metabolic pathways from processes such as growth, reproduction, and chemical defense (Hall 1997; Oren et al. 2001; Anthony et al. 2002; Titlyanov et al. 2005). Depending on the location and intensity of the wounds, vital functions can be affected in different ways and tissue repairing can be uneven, even within the same colony. In cases in which the structures and mechanisms needed for incorporation of matter and energy are affected, healing regeneration becomes deficient. The experimental design applied in this study showed that sun corals exposed to air for shorter periods had a higher proportion of healthy or slightly affected polyps (X_4 and X_3), which retained functional tentacles, mouths, and gastrovascular cavities, and were able to feed on plankton and assimilate energy, repairing their wounds faster and more efficiently. On the contrary, longer treatments led to a greater number of dead or seriously damaged polyps (X_1 and X_2) so that the corals lost the means to incorporate energy resources for tissue repairing. Damaged polyps showed a greater ability to regenerate tissue when they retained the structures necessary to capture plankton, periodically offered as food (Figure 5).

The proportion of polyps that partially lost soft tissue after desiccation trauma (X_3/X_2) varied significantly (Figure 7) between treatments, leading to different rates of healing regeneration in *Tubastraea* sp. (Figure 6). This suggests that the feeding capacity of *Tubastraea* polyps is a key factor for the recovery of the entire colony. Complementary observations assisted us to understand the importance of specialized tissues for feeding in the survival of the entire colony: in cultures of sun corals deprived of food for several months, we noticed progressive loss of soft tissues (leading to skeletal exposure), from the base to the top of the corallites (Figure 8). Once food supply was resumed, the polyps fed by everting the remaining soft tissue in the mouth and tentacles. After a few weeks of offering a regular zooplankton supply, the coral colonies fully recovered their soft tissues, even at their base, re-attaching to the substrate (i.e., bottom of culture tanks in this case). However, probably the variation of the feeding capacity of the polyps is not the only determining factor of the speed and type of regeneration of the corals. Some investigations have demonstrated, through manipulative experiments, the existence of regulatory factors for tissue regeneration, which are present in the mouth of cnidarian polyps, such as in *Fungia* spp. (Kramarsky-Winter and Loya 1996). After trauma, coral fragments retaining oral structures managed to repair damaged tissues and rebuild the original polyps. However, when mouths are separated from the polyps, a complete reorganization of soft tissues occurs, and new mouths develop. This is a process associated with bud formation, which is also verified for coral species when polyp mouths are removed or covered with putty. After this type of manipulation, instead of recovering damaged tissues, small new mouths appear next to the original ones (*e.g.*, Boschma 1923; Chadwick and Loya 1990; Jokiel and Bigger 1994). Although there is some evidence of budding after soft tissue retraction and reorganization in sun corals (Luz et al. 2018), we were unable to observe these processes, but it should not be ruled out that this may occur after desiccation stress in these corals.

Figure 8. Colony of *Tubastraea* sp. deprived of food for several months, with loss of soft tissues and exposure of the calcareous skeleton at the base of its polyps. The open mouths and extended tentacles of corallites during the supply of zooplankton for food show that these structures are functional. Photographs by Milena C. Silva.

We recorded in the present study resistance to acute stress due to desiccation, as well as healing abilities through tissue repair in *Tubastraea* sp. Although the results of this research suggest that soft tissue preservation in the mouth of sun coral polyps plays a central role in curative regeneration after desiccation stress, further studies are needed to test whether this process is mediated by regulatory signals of cell replication (budding versus healing regeneration) or simply responds to the energy absorption capacity of polyps. The information obtained about gradual variation in soft tissue damage in sun corals exposed to air for different time intervals, the capacity of tissue regeneration of these organisms, and the identification of the minimum period (96 h) necessary to completely kill *Tubastraea* sp. colonies by desiccation offer general biosecurity subsidies for possible management operations using exposure of these organisms to air. It is important to reinforce that the data here reported were collected under controlled laboratory conditions. In field scenarios, under the action of sun, wind and rain, colony mortality could be faster. However, attention should be paid to shaded locations and areas with potential for seawater accumulation, where sun coral colonies may have a longer survival than under the conditions described here.

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Authors' contribution

Damián Mizrahi: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Validation; Visualization; Writing – original draft; Writing – review and editing. Milena C. Silva: Investigation. Maurício L. Fonseca: Conceptualization; Writing – review and editing. Rubens M. Lopes: Funding acquisition; Supervision; Project administration; Resources; Writing – review and editing.

References

Altvater L, de Messano LV, Andrade M, Apolinário M, Coutinho R (2017) Use of sodium hypochlorite as a control method for the non-indigenous coral species *Tubastraea coccinea* Lesson, 1829. *Management of Biological Invasions* 8: 197–204, https://doi.org/10.3391/mbi.2017.8.2.07

Anthony K, Connolly S, Willis B (2002) Comparative analysis of energy allocation to tissue and skeletal growth in corals. *Limnology and Oceanography* 47: 1417–1429, https://doi.org/10.4319/lo.2002.47.5.1417

Bak RPM (1983) Neoplasia, regeneration and growth in the reefbuilding coral *Acropora palmata. Marine Biology* 77: 221–227, https://doi.org/10.1007/BF00395810

Bak RPM, Luckhurst E (1980) Constancy and change in coral reef habitats along depth gradients at Curacão. *Oecologia* 47: 145–155, https://doi.org/10.1007/BF00346812

Bastos N, Calazans SH, Altvater L, Neves EG, Trujillo AL, Sharp WC, Hoffman EA, Coutinho R (2022) Western Atlantic invasion of sun corals: incongruence between morphology and genetic delimitation among morphotypes in the genus *Tubastraea*. *Bulletin of Marine Science* 98: 187–210, https://doi.org/10.5343/bms.2021.0031

Begossi A (1996) The fishers and buyers from Búzios Island: Kin ties and modes of production. *Ciência e Cultura* 48: 142–147

Bentis CJ, Kaufman L, Golubic S (2000) Endolithic fungi in reef-building corals (Order: Scleractinia) are common, cosmopolitan, and potentially pathogenic. *Biological Bulletin* 198: 254–260, https://doi.org/10.2307/1542528

Bosch TCG (2007) Why polyps regenerate and we don't: towards a cellular and molecular framework for hydra regeneration. *Developmental Biology* 303: 421–433, https://doi.org/10.1016/j.ydbio.2006.12.012

Boschma H (1923) Expenmental budding in *Fungia fungites. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* 26: 88–96

Brandt ME, Smith TB, Correa AMS, Vega-Thurber R (2013) Disturbance driven colony fragmentation as a driver of a coral disease outbreak. *PLoS ONE* 8: e57164, https://doi.org/10.1371/journal.pone.0057164

Brito A, Lopez C, Ocaña O, Herrera R, Moro L, Monterroso O, Rodrígues A (2017) Colonización y expansión en Canarias de dos corales potencialmente invasores introducidos por las plataformas petrolíferas. *Vieraea* 45: 65–82, https://doi.org/10.31939/vieraea.2017.45.04

Brown BH, Howard LS (1985) Assessing the effects of 'stress' on reef corals. *Advances in Marine Biology* 22: 1–63, https://doi.org/10.1016/S0065-2881(08)60049-8

Cairns SD (2000) A revision of the shallow-water azooxanthellate *Scleractinia* of the western Atlantic. *Studies on the Natural History of the Caribbean Region* 75: 1–240

Castro CB, Pires D (2001) Brazilian coral reefs: what we already know and what is still missing. *Bulletin of Marine Science* 69: 357–371

Chadwick NE, Loya Y (1990) Regeneration after experimental breakage in the solitary reef coral *Fungia granulosa*, Klutzinger 1879. *Journal of Experimental Marine Biology and Ecology* 142: 221–234, https://doi.org/10.1016/0022-0981(90)90093-R

Creed JC (2006) Two invasive alien azooxanthellate corals, *Tubastraea coccinea* and *Tubastraea tagusensis*, dominate the native zooxanthellate *Mussismilia hispida* in Brazil. *Coral Reefs* 25: 350–350, https://doi.org/10.1007/s00338-006-0105-x

Creed JC, Fenner F, Sammarco P, Cairns S, Capel K, Junqueira AOR, Cruz I, Miranda RJ, Carlos-Junior L, Mantelatto MC, Oigman-Pszczol S (2017a) The invasion of the azooxanthellate coral *Tubastraea* (Scleractinia: Dendrophylliidae) throughout the world: history, pathways and vectors. *Biological Invasions* 19: 283–305, https://doi.org/10.1007/s10530-016-1279-y

Creed JC, Junqueira AOR, Fleury BG, Mantelatto MC, Oigman- Pszczol SS (2017b) The Sun-Coral Project: the first social environmental initiative to manage the biological invasion of *Tubastraea* spp. in Brazil. *Management of Biological Invasions* 8: 181–195, https://doi.org/10.3391/mbi.2017.8.2.06

Creed JC, Masi BP, Mantelatto MC (2019) Experimental evaluation of vinegar (acetic acid) for control of invasive corals (*Tubastraea* spp.) and a review of knowledge for other aquatic pests. *Biological Invasions* 21: 1227–1247, https://doi.org/10.1007/s10530-018-1895-9

Creed JC, Casares AF, Oigman-Pszczol SS, Masi BP (2021) Multi-site experiments demonstrate that control of invasive corals (*Tubastraea* spp.) by manual removal is effective. *Ocean and Coastal Management* 207: 105616, https://doi.org/10.1016/j.ocecoaman.2021.105616

Crivellaro MS, Silveira TCL, Custódio FY, Battaglin LC, Dechoum MdS, Fonseca AC, Segal B (2021) Fighting on the edge: reproductive effort and population structure of the invasive coral *Tubastraea coccinea* in its southern Atlantic limit of distribution following control activities. *Biological Invasions* 23: 811–823, https://doi.org/10.1007/s10530-020-02403-5

De Paula AF (2007) Biologia reprodutiva, crescimento e competição dos corais invasores *Tubastraea coccinea* e *Tubastraea tagusensis* (Scleractinia: Dendrophylliidae) com espécies nativas. DSc. Dissertation, Universidade Federal do Rio de Janeiro. Rio de Janeiro, 87 pp

De Paula AF, Creed JC (2004) Two species of the coral *Tubastraea* (Cnidaria, Sclerectinia) in Brazil: a case of accidental introduction. *Bulletin of Marine Science* 74: 175–183

De Paula A, Creed JC (2005) Spatial distribution and abundance of non-indigenous coral genus *Tubastraea* (Cnidaria, Scleractinia) around Ilha Grande, Brazil. *Brazilian Journal of Biology* 65: 661–673, https://doi.org/10.1590/S1519-69842005000400014

De Paula AF, Pires DO, Creed JC (2014) Reproductive strategies of two invasive sun corals (*Tubastraea* spp.) in the southwestern Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 94: 481–492, https://doi.org/10.1017/S0025315413001446

De Paula AF, Fleury BG, Lages BG, Creed JC (2017). Experimental evaluation of the effects of management of invasive corals on native communities. *Marine Ecology Progress Series* 572: 141–154, https://doi.org/10.3354/meps12131

Denis V, Debreuil J, De Palmas S, Richard J, Guillaume MMM, Bruggemann JH (2011) Lesion regeneration capacities in populations of the massive coral *Porites lutea* at Reunion Island: environmental correlates. *Marine Ecology Progress Series* 428: 105–117, https://doi.org/10.3354/meps09060

Fenner D (2001) Biogeography of three Caribbean corals (Scleractinia, Milleporidae, and Stylasteridae) species of Belize (Central America) and Cozumel (Mexico). *Bulletin of Marine Science* 64: 143–154

Fenner D, Banks K (2004) Orange cup coral *Tubastraea coccinea* invades Florida and the Flower Garden Banks, northwestern Gulf of Mexico. *Coral Reefs* 23: 505–507, https://doi.org/10.1007/s00338-004-0422-x

Hall VR (1997) Interspecifc diverences in the regeneration of artifcial injuries on scleractinian corals. *Journal of Experimental Marine Biology and Ecology* 212: 9–23, https://doi.org/10.1016/S0022-0981(96)02760-8

Henry LA, Hart M (2005) Regeneration from injury and resource allocation in sponges and corals - a review. *International Review of Hydrobiology* 90: 125–158, https://doi.org/10.1002/iroh.200410759

Heyward AJ, Collins JD (1985) Coral reefs fragmentation in *Montipora ramosa*: the genet and ramet concept applied to a reef coral. *Coral Reefs* 4: 35–40, https://doi.org/10.1007/BF00302202

Highsmith RC (1982) Reproduction by fragmentation in corals. *Marine Ecology Progress Series* 7: 207–226, https://doi.org/10.3354/meps007207

Hilliard R, Polglaze J, Leprovost I (2006) Review and evaluation of the biofouling protocol for vessels less than 25 m in length. URS Australia Pty Ltd prepared for Australian Quarantine and Inspection Service. Report R1216, Perth, Australia, 149 pp

Holstein TW, Hobmayer E, Technau U (2003) Cnidarians: an evolutionarily conserved model system for regeneration? *Developmental Dynamics* 226: 257–267, https://doi.org/10.1002/dvdy.10227

Hopkins GA, Forrest BM (2010) Challenges associated with pre-border management of biofouling on oil rigs. *Marine Pollution Bulletin* 60: 1924–1929, https://doi.org/10.1016/j.marpolbul.2010.07.015

Hopkins GA, Prince M, Cahill PL, Fletcher LM, Atalah J (2015) Desiccation as a mitigation tool to manage biofouling risks: trials on temperate taxa to elucidate factors influencing mortality rates. *Biofouling* 32: 1–11, https://doi.org/10.1080/08927014.2015.1115484

Hughes TP, Jackson JBC (1985) Population dynamics and life histories of foliaceous corals. *Ecological Monographs* 55: 141–166, https://doi.org/10.2307/1942555

Hughes TP, Ayre D, Connell JH (1992) The evolutionary ecology of corals. *Trends in Ecology and Evolution* 7: 292–295, https://doi.org/10.1016/0169-5347(92)90225-Z

Inglis G, Floerl O, Woods C (2012) Scenarios of vessel biofouling risk and their management. An evaluation of options. MAF Technical Paper No: 2012/07, 126 pp

Jayewardene D (2010) Experimental determination of the cost of lesion healing on *Porites compressa* growth. *Coral Reefs* 29: 131–135, https://doi.org/10.1007/s00338-009-0560-2

Jokiel PL, Bigger CH (1994) Aspects of histocompatability and regeneration in the solitary reef coral *Fungia scutaria. Biological Bulletin* 186: 72–80, https://doi.org/10.2307/1542037

Kramarsky-Winter E, Loya Y (1996) Regeneration versus budding in fungiis corals: a trade-off. *Marine Ecology Progress Series* 134: 179–185, https://doi.org/10.3354/meps134179

Kramarsky-Winter E, Loya Y (2000) Tissue regeneration in the coral *Fungia granulosa*: the effect of extrinsic and intrinsic factors. *Marine Biology* 137: 867–873, https://doi.org/10.1007/s002270000416

Lages BG, Fleury BG, Menegola C, Creed JC (2011) Change in tropical rocky shore communities due to an alien coral invasion. *Marine Ecology Progress Series* 438: 85–96, https://doi.org/10.3354/meps09290

Lirman D (2000) Fragmentation in the branching coral *Acropora palmata* (Lamarck): growth, survivorship, and reproduction of colonies and fragments. *Journal of Experimental Marine Biology and Ecology* 251: 41–57, https://doi.org/10.1016/S0022-0981(00)00205-7

Luz BLP, Capel KCC, Zilberberg C, Flores AAV, Migotto AE, Kitahara MV (2018) A polyp from nothing: The extreme regeneration capacity of the Atlantic invasive sun corals *Tubastraea coccinea* and *T. tagusensis* (Anthozoa, Scleractinia). *Journal of Experimental Marine Biology and Ecology* 503: 60–65, https://doi.org/10.1016/j.jembe.2018.02.002

Mantelatto MC, Pires LM, de Oliveira GJG, Creed JC (2015) A test of the efficacy of wrapping to manage the invasive corals *Tubastraea tagusensis* and *T. coccinea. Management of Biological Invasions* 6: 367–374, https://doi.org/10.3391/mbi.2015.6.4.05

Meesters EH, Bak RPM (1993) Effects of coral bleaching on tissue regeneration potential and colony survival. *Marine Ecology Progress Series* 96: 189–198, https://doi.org/10.3354/meps096189

Meesters EH, Noordeloos M, Bak RPM (1994) Damage and regeneration: link to growth in the reef-building coral *Montastrea annularis. Marine Ecology Progress Series* 112: 119–128, https://doi.org/10.3354/meps112119

Mizrahi D (2008) Influência da temperatura e luminosidade na distribuição da espécie invasora *Tubastraea coccinea* na região de ressurgência de Arraial do Cabo, RJ. MSc Dissertation, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil, 85 pp

Mizrahi D, Navarrete AS, Flores AAV (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, https://doi.org/10.1016/j.jembe.2013.11.013

Mizrahi D, Pereira SF, Navarrete AS, Flores AAV (2017) Allelopathic effects on the sun-coral invasion: facilitation, inhibition and patterns of local biodiversity. *Marine Biology* 164: 139, https://doi.org/10.1007/s00227-017-3164-3

Moreira PL, Ribeiro FV, Creed JC (2014) Control of invasive marine invertebrates: an experimental evaluation of the use of low salinity for managing pest corals (*Tubastraea* spp). *Biofouling* 30: 639–650, https://doi.org/10.1080/08927014.2014.906583

Oren U, Benayahu Y, Loya Y (1997) Effect of lesion size and shape on regeneration of the Red Sea coral *Favia favus. Marine Ecology Progress Series* 146: 101–107, https://doi.org/10.3354/meps146101

Oren U, Benayahu Y, Lubinevsky H, Loya Y (2001) Colony integration during regeneration in the stony coral *Favia favus. Ecology* 82: 802–813, https://doi.org/10.1890/0012-9658(2001)082[0802:CIDRIT]2.0.CO;2

Ottaway JR (1979) Population Ecology of the Itertidal Anemone *Actinia tenebrosa*. III. Dynamics and Environmental Factors. *Marine and Freshwater Research* 30: 41–62, https://doi.org/10.1071/MF9790041

Peyrot-Clausade M, Brunel JF (1990) Distribution patterns of macroboring organisms on Tuléar reef flats (SW Madagascar). *Marine Ecology Progress Series* 61: 133–144, https://doi.org/10.3354/meps061133

Rajagopal S, van der Gaag M, van der Velde G, Jenner HA (2002) Control of brackish water fouling mussel, *Mytilopsis leucophaeata* (Conrad), with sodium hypochlorite. *Archives of Environmental Contamination and Toxicology* 43: 296–300, https://doi.org/10.1007/s00244-002-1203-6

Ryland J S, Warner GF (1986) Growth and form in modular animals: ideas on the size and arrangement of zooids. *Philosophical Transactions of the Royal Society B* 313: 53–76, https://doi.org/10.1098/rstb.1986.0025

Sampaio CLS, Miranda RJ, Maia-Nogueira R, de Anchieta CC, Nunes J (2012) New occurrences of the nonindigenous orange cup corals *Tubastraea coccinea* and *T. tagusensis* (Scleractinia: Dendrophylliidae) in Southwestern Atlantic. *Check List* 8: 528–530, https://doi.org/10.15560/8.3.528
Savio LA, Dias GM, Leite KL, Godoi SN, Figueiroa AC, Neto, GFO, Correa EC, Francini CLB, Shintate G, Kitahara MV (2021) Sun coral management effectiveness in a wildlife refuge from south-eastern Brazil. *Aquatic Conservation: Marine and Freshwater Ecosystems* 31: 2830–2841, https://doi.org/10.1002/aqc.3657
Silva R, Vinagre C, Kitahara MV, Acorsi I, Mizrahi D, Flores AAV (2019) Sun coral invasion of shallow rocky reefs: effects on mobile invertebrate assemblages in Southeastern Brazil. *Biological Invasions* 21: 1339–1350, https://doi.org/10.1007/s10530-018-1903-0
Smith LD, Hughes TP (1999) An experimental assessment of survival, re-attachment and fecundity of coral fragments. *Journal of Experimental Marine Biology and Ecology* 235: 147–164, https://doi.org/10.1016/S0022-0981(98)00178-6
Stabili L, Schirosi R, Parisi MG, Piraino S, Cammarata M (2015) The Mucus of *Actinia equina* (Anthozoa, Cnidaria): An Unexplored Resource for Potential Applicative Purposes. *Marine Drugs* 13: 5276–5296, https://doi.org/10.3390/md13085276
Titlyanov EA, Titlyanova TV (2008) Coral-algal competition on damaged reefs. *Russian Journal of Marine Biology* 34: 199–219, https://doi.org/10.1134/S1063074008040019
Titlyanov EA, Titlyanova TV, Yakovleva IM, Nakano Y, Bhagooli R (2005) Regeneration of artificial injuries on scleractinian corals and coral/algal competition for newly formed substrate. *Journal of Experimental Marine Biology and Ecology* 323: 27–42, https://doi.org/10.1016/j.jembe.2005.02.015
Underwood AJ (1997) Ecological experiments: their logical design and interpretation using analysis of variance. Cambridge University Press, 504 pp, https://doi.org/10.1017/CBO9780511806407
Vaughan TW, Wells JW (1943) Revision of the suborders, families, and genera of the Scleractinia. Vol. 44. Geological Society of America, 363 pp, https://doi.org/10.1130/SPE44-p1
Vinagre C, Silva R, Mendonça V, Flores AAV, Baeta A, Marques JC (2018) Food web organization following the invasion of habitat-modifying *Tubastraea* spp. corals appears to favor the invasive borer bivalve *Leiosolenus aristatus*. *Ecological Indicators* 85: 1204–1209, https://doi.org/10.1016/j.ecolind.2017.11.056
Wahle CM (1985) Habitat-related patterns of injury and mortality among Jamaican gorgonians. *Bulletin of Marine Science* 37: 905–927

Web sites and online databases

Brasil (2018) Portaria Nº 3.642, de 10 de dezembro de 2018 - Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis http://www.ibama.gov.br/phocadownload/biodiversidade/coral-sol/2019-08-02-Plano-Nacional-de-Prevencao-Controle-e-Monitoramento-do-Coral-sol-Tubastraea-spp-no-Brasil.pdf (accessed 10 November 2022)

Supplementary material

The following supplementary material is available for this article:

Figure S1. Sun coral colonies exposed to 2 h of dessication.
Figure S2. Sun coral colonies exposed to 4 h of dessication.
Figure S3. Sun coral colonies exposed to 8 h of dessication.
Figure S4. Sun coral colonies exposed to 12 h of dessication.
Figure S5. Sun coral colonies exposed to 20 h of dessication.
Figure S6. Sun coral colonies exposed to 38 h of dessication.
Figure S7. Sun coral colonies exposed to 52 h of dessication.
Figure S8. Sun coral colonies exposed to 72 h of dessication.
Figure S9. Sun coral colonies exposed to 96 h of dessication.

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