



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

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Abstract The detection and control of invasive alien species in marine ecosystems is especially challenging because it is difficult to visualize the full extension of an invasion, while control options are often limited. The invasive scleractinian coral *Tubastraea coccinea* have spread over 8000 km of the Atlantic coastline, from Florida in the USA to southern Brazil, mainly in association with oil and gas platforms. This invasive coral threatens endemic species, reduces native coral recruitment, and modifies communities and trophic interactions, posing a relevant threat to shallow

Atlantic reefs. The main aim of our study was to assess the effectiveness of an ongoing *T. coccinea* control program by analyzing the results of control interventions on population structure and cover of the target species in its southern Atlantic limit of distribution. We also describe the reproductive effort of *T. coccinea* in a 12-month time span. Between 2012 and 2019, almost 14,000 colonies were removed, most of them of small size (< 5 polyps). The highest reproductive effort was observed in September. Changes in *T. coccinea* cover, population structure and potential local propagule supply were observed. Control activities led to a reduction in up to half the cover of the invaded area, maintained the majority of the population in non-reproductive sizes, and consequently lowered the potential local propagule supply. Our paper highlights the fundamental role of control in preventing the local spread of *T. coccinea*. Recommendations on management frequency and timing are also discussed in order to contribute to the improvement of management efficiency.

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Introduction

As a consequence of the expansion of international trade, the number of translocated and introduced species is continuously increasing (Seebens et al. 2017). Most introductions in marine ecosystems are related to shipping and aquaculture (Molnar et al. 2008), while the global artificialization of habitats is the main driver of success in marine invasions (Bishop et al. 2017). Invasive non-native species can alter ecosystem functions. The introduced clam *Corbula amurensis*, for example, has caused the decline of phytoplankton biomass, consequently reducing primary production in the San Francisco Bay in California, USA (Alpine and Cloern 1992). Moreover, invasive species can impact human health and the economy, as when human pathogens are dispersed by ballast water (Ruiz et al. 2000). An estimated loss of 250 million dollars/year in the anchovy fishery industry is correlated with the introduction of the ctenophore *Mnemiopsis leidyi* (Zaitsev 1992).

Prevention is the most effective strategy to avoid future impacts of biological invasions (Bax et al. 2001). When prevention fails, early detection and rapid response are the next best opportunity for eradication (Wittenberg and Cock 2001; Simberloff et al. 2013). A well-designed eradication program must have enough funds for long-term work and monitoring possible recolonization (Wittenberg and Cock 2001). Therefore, technical and financial limitations hinder the possibilities of eradication. In such cases, control efforts to reduce species abundance or limit spread can protect the natural ecosystem on a local scale as long as they are not discontinued, and may in due course increase the feasibility of eradication (Green et al. 2014).

There are several methods to contain spread using mechanical, chemical and/or biological control (Wittenberg and Cock 2001). Biological control requires close monitoring of host specificity, which can be limited in marine ecosystems. Chemical control has been successfully used under certain conditions (*Mytilopsis sallei* in Australia—Bax et al. 2002; *Caulerpa taxifolia* in California—Anderson 2005) that weighed the benefits against potential impacts such as fast dilution in water and impact on non-target species. Although mechanical control can be labor-intensive and time-consuming, it is highly specific to the target (Wittenberg and Cock 2001).

Complementarily, information on the biology of the target species is important to support the definition of control strategies (Dommissse and Hough 2004; Anderson 2005). In Australia, a “ballast window” was defined for ships to fill up with ballast water only in larvae-free periods of the *Asterina* starfish in order to reduce propagule pressure and mitigate spread (Dommissse and Hough 2004).

Two azooxanthellate scleractinian corals, *Tubastraea coccinea* Lesson 1829, native to the Indo-Pacific, and *T. tagusensis* Wells 1982, from the Galapagos Islands, successfully invaded Atlantic shallow reefs. These corals do not seem to have substrate settlement preferences (Creed and De Paula 2007). Their introduction has been mostly associated with structures translocated between regions, such as oil and gas platforms (please see Creed et al. 2017a for more details on *T. coccinea* invasion pathways). The invasion started in the Caribbean (1943) (Cairns 2000) and spread throughout the Gulf of Mexico (Fenner 2001), the Atlantic coast of Brazil (Castro and Pires 2001), Florida in the USA (Fenner and Banks 2004), and the Canary Islands of Spain (López et al. 2019). The first record of the coral on the Brazilian coast was made on an offshore oil platform in the late 1980s, in the Campos Basin, in Rio de Janeiro (RJ) state (Castro and Pires 2001). It spread fast along natural substrates on the rocky shores of Ilha Grande, also in RJ state, in the 1990s (Castro and Pires 2001; De Paula and Creed 2004). Nowadays, several disjunct populations are present along 3800 km of the Brazilian coastline, from North (Ceará state, Soares et al. 2016) to South (Santa Catarina state, Capel 2012).

These corals, popularly known as “sun corals”, are spreading fast (~ 2 km/year, Da Silva et al. 2014) mainly due to early maturity, and sexual and asexual reproduction (Glynn et al. 2008; De Paula et al. 2014; Capel et al. 2017; Luz et al. 2020). In the Ilha Grande Bay (Rio de Janeiro state), *T. coccinea* reproduces many times throughout the year. Different stages of propagule development occur simultaneously in a polyp. Two reproductive peaks were observed, one from September to December and the other one from February to May (De Paula et al. 2014). Larvae were alive for ~ 4 months in artificial conditions (Mizrahi et al. 2014; Luz et al. 2020), but they usually settle and metamorphose fast (1–3 days), displaying gregarious behavior near parental colonies (Glynn et al. 2008; De Paula et al. 2014; Luz et al. 2020). Invasive

Tubastraea corals impact trophic interactions (Miranda et al. 2018a; Silva et al. 2019), modify communities (Lages et al. 2011), damage endemic species (Creed 2006; Santos et al. 2013; Barbosa et al. 2019), and reduce native coral recruitment (Miranda et al. 2018b).

Several initiatives based on mechanical methods to control *Tubastraea* spp. have been locally implemented by environmental government agencies, non-governmental organizations, researchers and volunteers in Brazil (Creed et al. 2017b), as well as by local managers in the Flower Garden Banks Marine Sanctuary (Florida, USA) (Precht et al. 2014). Although a National Plan for Prevention, Control and Monitoring (NPPCM) for *Tubastraea* spp. was published in Brazil by the Ministry of Environment in 2018 (MMA 2018), no control actions have been implemented on a national scale so far. However, one of the goals of the NPPCM is to define priority areas for control and monitoring, as well as to eradicate small, isolated, and initial populations. Albeit manual removal using a chisel and hammer has proven effective to reduce *Tubastraea* spp. cover (De Paula et al. 2017), sun corals grow at high regeneration rates and can grow back from remaining tissue that is not completely detached from the substrate (Luz et al. 2018), which can undermine the effectiveness of control.

The main aim of our study was to assess the effectiveness of an ongoing *T. coccinea* control program by analyzing the results of control interventions on population structure and cover of the target species in its southern Atlantic limit of distribution. We also assessed the outcome of control activities conducted by local managers and volunteer researchers. In the same region, we investigated propagule production of *T. coccinea* for 13 months to determine the most appropriate time interval for control interventions. In addition, we combined information on reproduction and cover to estimate the potential of local propagule release. We assumed that control activities would reduce cover and maintain populations with small individuals, reducing the local population propagule supply. Considering the data available and the threat of invasion by *T. coccinea* in southern Atlantic ecosystems, we expect our study to contribute with relevant information to support and improve the ongoing control program.

Materials and methods

Study system

This study was carried out on rocky shores of the Arvoredo Marine Biological Reserve (Rebio Arvoredo from now on), a no-take, no-entry protected area (176 km²) on the coast of Brazil, in the southwestern Atlantic (between 28° 36' 16.94" S and 28° 13' 43.18" S). Rebio Arvoredo comprises an archipelago formed by three islands (Arvoredo, Deserta, and Galé) of rocky shores surrounded by a highly productive pelagic ecosystem. Oceanographic conditions vary seasonally, with temperatures ranging from ~ 15 to 29 °C (Faria-Junior and Lindner 2019). In the summer, tropical hot and nutrient poor waters dominate the continental shelf. In winter, waters are cold, generating much higher primary production on the ocean surface due to the influence of the La Plata River and Patos Lagoon discharges (Freire et al. 2017). Given these conditions, Rebio Arvoredo plays a key biological role in the region. The area includes the most southern coralline algal bank on the Brazilian coast (Rocha et al. 2006), serves as refuge to commercial fish species (Anderson et al. 2019), and is a transitional area between tropical and temperate fauna for many benthic species. The Reserve is the southern distribution limit of *T. coccinea* in the Atlantic Ocean (Capel 2012; Lindner et al. 2017). This occurrence is at least 450 km away from the nearest known population, located farther north (Alcatrazes islands, São Paulo state).

The first record of *T. coccinea* on the rocky shores of Arvoredo island was made in 2012, outside the limits of Rebio Arvoredo, in a site called Engenho (EG, Fig. 1) (Capel 2012). Subsequently, invasion patches were observed in two other sites, Saco do Farol (SF) and Saco do Vidal (SV), in 2013 and 2014, respectively (Fig. 1). Still in 2014, the invader was found within the limits of Rebio Arvoredo in Rancho Norte (RN). Judging by the large size of colonies, this seems to be the site that was invaded first in the area (Fig S1a). In 2015, two colonies were found in a shipwreck by Galé Island (GI), also within the limits of Rebio Arvoredo. Currently, invasion patches are still scattered, outside and within the limits of Rebio Arvoredo. Invasion is generally restricted to vertical surfaces, caves and crevices. These substrates are mostly occupied by calcareous and turf algae,

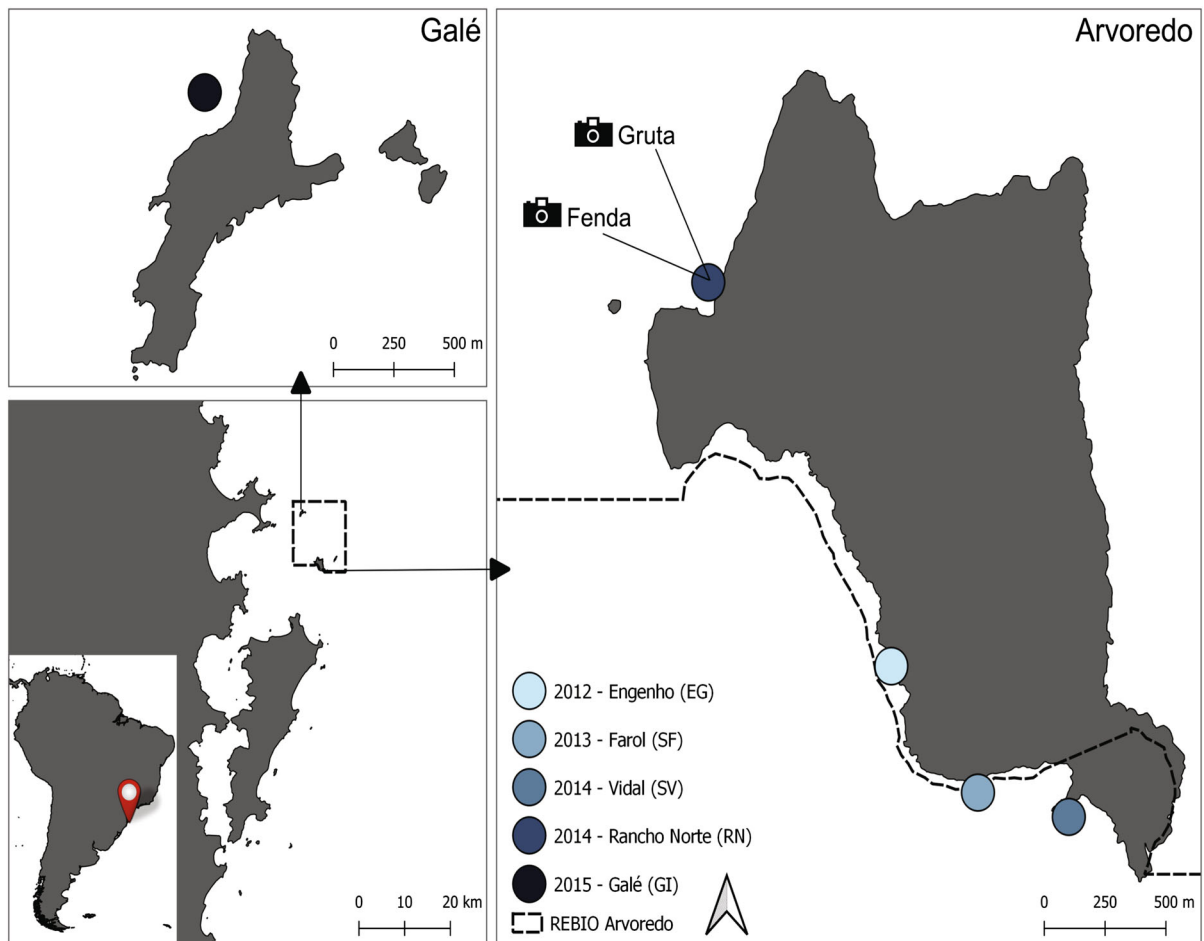


Fig. 1 Map of the study area showing sites of occurrence of *Tubastraea coccinea* and areas of photographic sampling. Sites are chronologically ordered by successive observations of the invasive coral. The dotted line shows the limits of Rebio Arvoredo

sponges, ascidians, the octocoral *Carijoa riisei*, the zoanthids *Parazoanthus swiftii* and *Palythoa caribaeorum* (only on horizontal surfaces, see Almeida Saá et al. 2019), and the scleractinians *Astrangia rathbuni*, *Phyllangia americana* and *Madracis decatis* (a rare species) (Capel 2012; Lindner et al. 2017).

Control activities

In 2012, the federal environmental agency in charge of Rebio Arvoredo, Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), in partnership with researchers of the Federal University of Santa Catarina (UFSC), established a program to control and monitor invasions by *T. coccinea*. Current control activities consist in two 50-min dives performed by two pairs of divers, each pair working on a site. While

one diver manually removes colonies with a chisel and hammer, the other inserts them in a plastic bag to prevent dispersal of larvae or colony fragments. The removal of larger colonies was prioritized because of the larger number of polyps and likely higher reproductive potential. Control activities were undertaken outside (Engenho, Saco do Farol and Saco do Vidal) and within the limits of Rebio Arvoredo (Galé Island and Rancho Norte). The numbers of control actions in each site and of colonies removed since the beginning of the control program were recorded and analyzed. All colonies were classified in five size classes according to the number of polyps: I (1–5 polyps), II (6–10 polyps), III (11–20 polyps), IV (21–40 polyps), and V (41 or more polyps). Figures were produced using the package *ggplot2* (Wickham 2016) in RStudio software (2020).

Reproductive effort

To describe the yearly reproductive effort of sun corals, we collected five colonies of similar sizes in each campaign between January, 2018, and June, 2019 (January to April, and July to November, 2018, and January, February, April and June, 2019). Collections were made by scuba divers at 2–8 m depth on rocky shores of Arvoredó Island. Colonies were fixed in 4% formalin solution, decalcified in 10% formic acid and 2% formalin for 48 h, then cleaned up in running tap water for 24 h (Glynn et al. 2008; De Paula et al. 2014). We measured the diameter, maximum oral disc diameter and distance between the oral and aboral ends of polyps to evaluate colony and polyp area (circle formula) and polyp volume (cylinder formula). We dissected two central polyps ($N = 126$) in each colony, and, when present, we counted all propagules under a stereomicroscope. As the development stages of embryos can only be differentiated through histological analysis (Glynn et al. 2008), we used the term propagule to refer to all stages. We only selected central polyps because larvae are more abundant in central polyps than on colony edges (Chornesky and Peters 1987). We extrapolated the number of propagules observed per polyp area to total colony area (propagules $\text{cm}^2 \cdot \text{colony}^{-1}$) in order to establish a correlation with cover (explained in the next section). We considered solely the central (fertile) part of the colonies for the extrapolation. Descriptive analyses were performed in RStudio software (2020) and figures were produced using the package *ggplot2* (Wickham 2016).

T. coccinea cover, population size structure and propagule supply

Between January, 2018, and June, 2019, we monitored two invaded sites where frequent control actions were conducted in REBIO Arvoredó (Rancho Norte, sites “Fenda” and “Gruta”) approximately every four months (5 sampling efforts in Gruta and 6 in Fenda, Table S1). Both sites occupy an area of approximately 5 m in length by one and a half in width at a depth of three meters. Accessibility to invasion patches for mechanical control differed between sites. Although a crevice in “Fenda” is inaccessible (Fig. S1c), a vertical surface in this site is easier to access than in “Gruta”, where sun corals were growing on the

negative surface of a cave. The invaded surfaces were photographed in the format of photo quadrats (25×25 cm). To evaluate cover and assess population size structure, we outlined the area of each colony in ImageJ Software (Schindelin et al. 2012) on five photographs taken in each site ($N_{\text{total}} = 55$). For this evaluation, we classified each colony according to five size classes based on surface area ($< 0.3 \text{ cm}^2$; $0.3\text{--}1 \text{ cm}^2$; $1\text{--}5 \text{ cm}^2$; $5\text{--}10 \text{ cm}^2$; $>10 \text{ cm}^2$) and determined their relative frequency (%). Classes $< 0.3 \text{ cm}^2$ (recruit size 4 mm, see Mizrahi 2008) and $0.3\text{--}1 \text{ cm}^2$ represent non-reproductive individuals, since propagules were observed in colonies larger than 1.2 cm^2 or more (De Paula 2007). Descriptive statistics were performed in RStudio software (2020) and figures were produced using the package *ggplot2* (Wickham 2016).

To estimate the local potential propagule supply of sun coral populations in our samples, we combined the data obtained on propagule production (propagules $\text{cm}^2 \cdot \text{colony}^{-1}$) and coral cover (cm^2). We used the median of propagules per cm^2 from the month of September ($200 \text{ propagules cm}^2 \text{ colony}^{-1}$) to extrapolate to the coral cover (cm^2) measured in each sample. Data from the month of September were used because it was the period of highest reproductive effort observed in our analysis. In the absence of control actions, all colonies would probably have reached an equivalent reproductive condition. Polyps located on the edge of colonies produce less larvae due to potential defense activity that is common along the edges (Chornesky and Peters 1987). Therefore, we measured the total area of 30 colonies on photographic samples and excluded the area of the peripheral (infertile) polyps from each of the colonies. We considered peripheral polyps as those not entirely inside the colony (with a free border). As a result, we obtained a fraction of 44.37% of potentially reproductive tissue in relation to total colony area. The cover of non-reproductive colonies/recruits ($< 0.3 \text{ cm}^2$ and $0.3\text{--}1 \text{ cm}^2$ classes) was excluded from the extrapolation.

Results

Control activities

Between February, 2012, and October, 2019, 59 control actions were conducted in Rebio Arvoredó,

resulting in the removal of 13,986 colonies (Fig. 2). The majority of these colonies belonged to the smallest size classes I (6872; 49.1%) and II (4611; 33%), with less colonies in classes III (1865; 13.3%), IV (468; 3.4%), and V (170; 1.2%). A considerable number of large colonies was eliminated shortly after discovery (Rancho Norte, site “Fenda”, 2014), with the removal of 108 and 75 colonies in classes IV and V, respectively. Only small colonies remain since then. Another large group of class V colonies was eliminated in Saco do Farol 2019 (43 colonies), and a few more colonies of size V (maximum 7) were removed in other 20 control efforts from scattered areas.

Rancho Norte was the site where more control actions (21) were conducted and the highest number of colonies was removed (6239), mainly because it contained the two largest invasion patches (in “Fenda” and “Gruta”). The highest number of colonies eliminated in a single control action was 876 (class I; 437; II: 264; III: 128; IV: 40; V: 7) at Engenho (2019). The smallest number of colonies eliminated refers to only two colonies immediately removed when discovered in a shipwreck by Galé island in 2015. Despite this early detection and rapid response effort, 23 colonies were found and eliminated

in the same shipwreck in 2019. The years with the largest numbers of colonies removed were 2018 (4595) and 2019 (3805); conversely, 2012 (324) and 2015 (137) were the years with the lowest number of colonies removed. The years 2018 (15) and 2019 (11) were also those with more control campaigns, while 2013 (3) and 2015 (2) were the years with less control campaigns.

Reproductive effort

Samples were collected during 13 months, between January, 2018, and June, 2019 (Appendix Table 1). Colony diameter ranged between 2.1 and 7.3 cm (mean = 4 cm \pm 1.2), while polyp diameter ranged between 0.6 and 1.6 cm (mean = 1 cm \pm 0.16). Polyp volume ranged between 250 and 5069 mm³ (mean = 1205 \pm 757 mm³). The number of propagules per polyp varied widely (mean = 153.8 \pm 165.6 SD). Propagules were present throughout the year except in January, 2018, and were observed in low numbers in August, 2018 (44 \pm 56.3 SD propagules.polyp⁻¹), January, 2019 (39.8 \pm 42.5 SD propagules.polyp⁻¹), February, 2019 (37.6 \pm 26.8 SD propagules.polyp⁻¹) and June, 2019 (78.6 \pm 47.7 SD propagules.polyp⁻¹) (Fig. 3,

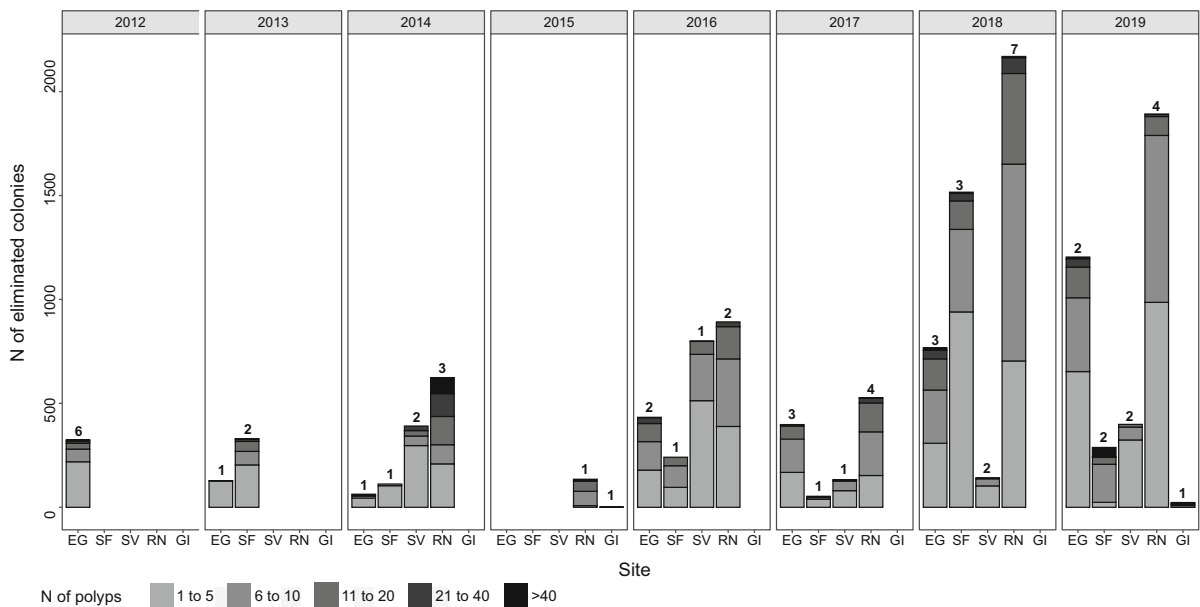


Fig. 2 Number of control activities (labels on top of the bars) and colonies eliminated in each class of polyp numbers (vertical axis on the left) in each site. EG = Engenho; GI = Galé Island;

RN = Rancho Norte; SF = Saco do Farol; SV = Saco do Vidal. Zero indicates the absence of control activities

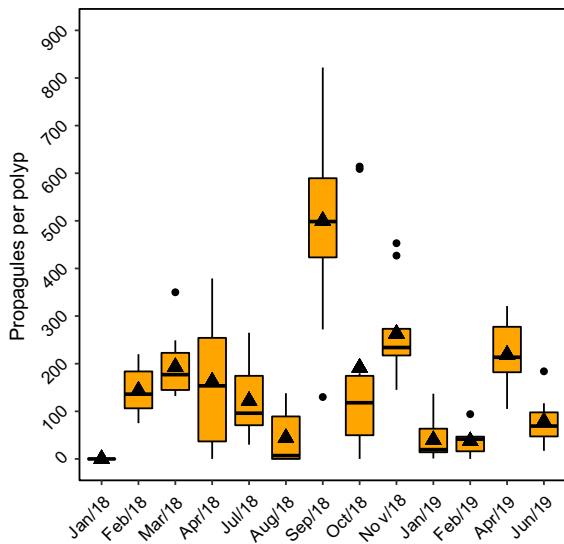


Fig. 3 Variation and mean (black triangle) of *T. coccinea* propagules per month (2 polyps each, 5 colonies/month). The horizontal black line inside box-plots represents the median

Appendix Table 1). The absence and low number of propagules in summer (January and February) may indicate events of larvae release, as propagules were clearly observed in an advanced larvae development stage only in January, 2019, which coincides with the peak reproductive period observed in Ilha Grande Bay, in Rio de Janeiro (600 km north of Santa Catarina). The highest numbers of propagules per polyp were observed in September (822 max; 500 ± 205 SD) and November, 2018 (453 max; 263 ± 102.3 SD). Polyps in October, 2018, also contained a large number of propagules (614 max; 191 ± 229.3 SD), with the exception of one colony in which no propagules were observed.

Cover, population size structure and propagule supply

In both invaded areas, our first sampling effort (January 2018) was conducted 167 days after a control action. During the period of sampling, both areas were submitted to control actions six times, with similar total numbers of colonies removed (Fenda—1673; Gruta—1614). Most colonies eliminated (83%) contained between 1 and 10 polyps (classes I and II), with only three of them having more than 41 polyps.

Figure 4 shows the estimated propagule supply (4a), population structure (4b), and the number of

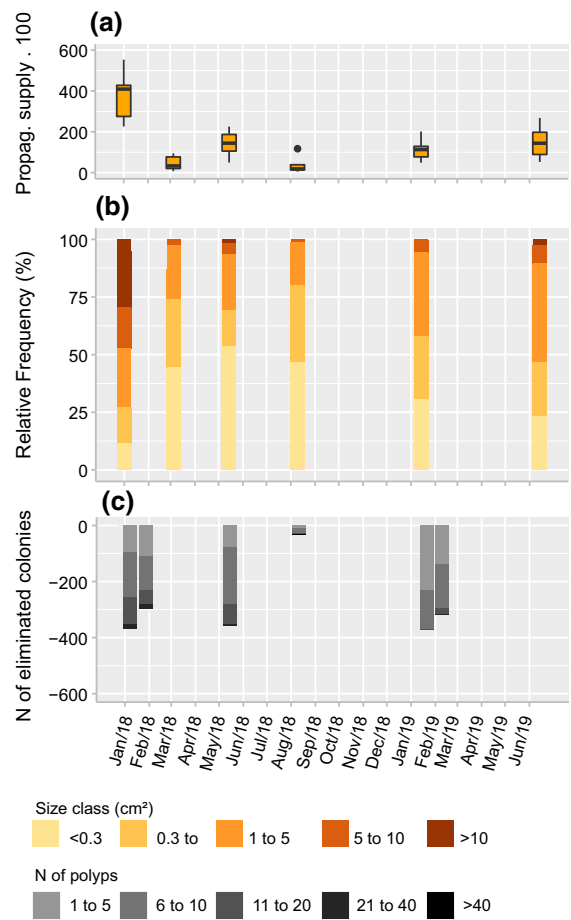


Fig. 4 Changes in population structure after control actions in Fenda. **a** Estimated propagule supply (value of y axis was divided by 100 to adjust figure dimensions; the horizontal black line inside box-plots represents the median); **b** relative frequency of colonies in each size class, and **c** number of colonies eliminated in each class of polyp numbers per control action

eliminated colonies in each control action (4c) in Fenda. The highest mean cover 30.6 ± 10.35 SD % (Fig S2a) and mean estimated propagule supply of $37,913 \pm 12,811$ SD propagules per 0.06m^2 were observed in the first sampling effort (January, 2018). Population structure was almost evenly distributed ($< 0.3\text{ cm}^2$ —11.5%; 0.3 – 1 cm^2 —15.8%; 1 – 5 cm^2 —25.1%; 5 – 10 cm^2 —17.9%; and $> 10\text{ cm}^2$ —29.4%), with by far the highest proportion of reproductive colonies observed. By January, 2018, 664 colonies had been removed in two control actions (classes I, 204; II, 285; III, 142; IV: 33). These efforts led to a reduction in cover from 30.6 ± 10.35 SD % to 5 ± 3 SD % (Mar 2018), or almost eight times less potential

production of propagules (from $37,913 \pm 12,811$ SD to 5047 ± 3758 SD propagules per 0.06 m^2). Only 2.3% of colonies were larger than 5 cm^2 . In August, 2018, mean cover was 4.9 ± 3.2 SD %, and propagule supply, 4438 ± 4545 SD propagules per 0.06 m^2 , with 80.4% of colonies probably non-reproductive and only 0.9% of colonies larger than 5 cm^2 . A low proportion of large colonies was also observed in the following control actions. Only 9 colonies with more than 20 polyps (class IV) were removed in control actions in May (5 colonies) and August (2 colonies), 2018, and in two actions in January, 2019 (2 colonies). In June, 2019, cover was 12.9 ± 7 SD %, propagule supply, $15,273 \pm 8,639$ SD propagules per 0.06 m^2 , and the proportion of reproductive colonies, 52.8%.

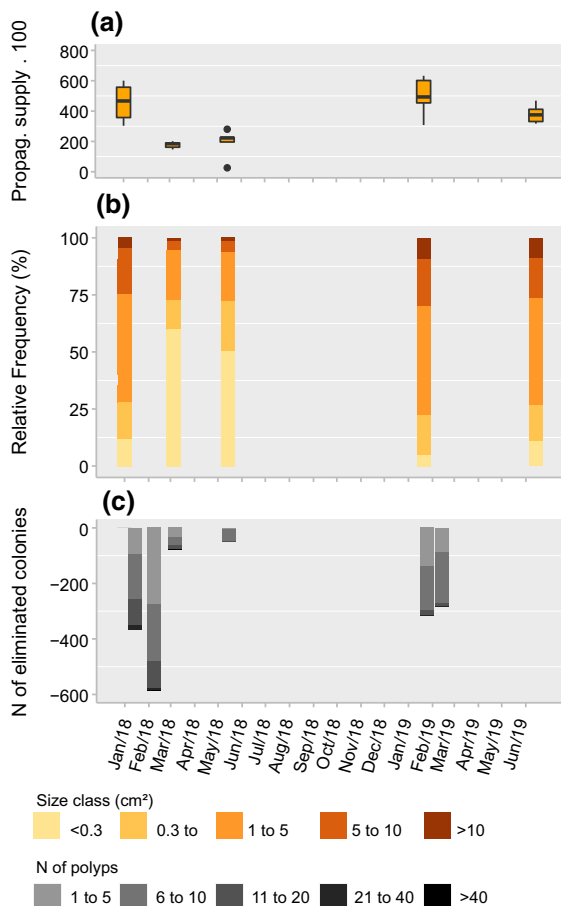


Fig. 5 Changes in population structure after control actions in Gruta. **a** Estimated propagule supply (value of y axis was divided by 100 to adjust figure dimensions; the horizontal black line inside box-plots represents the median); **b** relative frequency of colonies of each size class, and **c** number of colonies eliminated in each class of polyp numbers per control action

Figure 5 shows the estimated propagule supply (5a), population structure (5b), and the number of colonies eliminated in each control action (5c) in Gruta. In January, 2018, mean cover was 37.9 ± 10.6 SD % (Fig S2b), and propagule supply, $46,019 \pm 12,811$ SD propagules per 0.06 m^2 (Fig. 5b). These were smaller compared with colonies in Fenda ($< 0.3 \text{ cm}^2$ —12%; 0.3 – 1 cm^2 —15.9%; 1 – 5 cm^2 —47.6%; 5 – 10 cm^2 —19.9%; and $> 10 \text{ cm}^2$ —4.5%). Afterwards, 955 colonies were removed in two control actions (classes I, 370; II, 366; III, 193; IV, 25; V, 1). In March, 2018, cover and propagule supply were 15.9 ± 2.6 SD % and $18,254 \pm 2,342$ SD propagules per 0.06 m^2 , respectively, with 72.8% of colonies non-reproductive. In the 2018 control actions (March and May), only 130 colonies were removed (classes I, 38; II, 71; III, 17; IV, 3; V, 1). There was an interval of 252 days between control efforts in 2018 (May) and 2019 (January), when the highest cover (41 ± 10.4 SD %), propagule supply ($49,912 \pm 12,947$ SD propagules per 0.06 m^2), proportion of reproductive colonies (77.3%) and colonies larger than 10 cm^2 (9%) were observed. Shortly after, 599 colonies (classes I, 226; II, 342; III, 28; IV, 3) were removed in two control actions conducted in January, 2019. In June, 2019, cover was 31.2 ± 5 SD %, propagule supply, $38,247 \pm 6,130$ SD propagules per 0.06 m^2 , and 73.3% of the colonies were reproductive.

Discussion

Our results support the importance of ongoing control actions to slow the spread of *T. coccinea*. Even if manual removal is not the ideal control method because of the high regenerative capacity of *T. coccinea* (Luz et al. 2018), the current advantage of manual removal is to restrain populations to a large proportion of small, non-reproductive individuals, therefore reducing propagule supply, and consequently restricting spread. The current status of relatively small invasion patches in the Arvoreda marine reserve and surroundings is due to the results of ongoing control. Although eradication is not feasible with the control methods currently in use, the maintenance of populations in restrained sizes with individuals in small size classes increases future possibilities of eradication (Myers et al. 2000), buying

time until better solutions for more effective control are identified.

Some biological traits of *T. coccinea* explain its high invasiveness. The species reproduces mostly asexually (Capel et al. 2017), and colonies as small as two polyps are already mature (Glynn et al. 2008; De Paula et al. 2014). In artificial conditions, larvae can metamorphose in the water column and form clusters that settle and start benthic life as a colony (Mizrahi et al. 2014; Luz et al. 2020). Although larvae of large colonies may be viable for a long time (~ 90 days, Luz et al. 2020), they usually show gregarious behavior and settle fast (1–3 days, Glynn et al. 2008; De Paula et al. 2014). The complexity of recruitment in corals is well known. Estimates show that only 1% of marine benthic invertebrates successfully survive the several bottlenecks in this early stage of life (Gosselin and Qian 1997). In this sense, considering our extrapolation of the propagule supply at the beginning of sampling, populations of *T. coccinea* in “Fenda” and “Gruta” may potentially produce approximately 80 thousand propagules. Considering a survival rate of ca. 1%, this means that a release event at that moment may generate almost 1000 new settled individuals with capacity to establish new invasion patches on their own. The reproductive data generated in our study are extremely important for planning the timing of control activities, which should be conducted before reproductive peaks and before recruits or regenerative colonies reach maturity. Based on these data, we recommend that control activities are preferentially carried out between May and September in the southern Atlantic coast of Brazil. Although we cannot precise the relative contribution of larval recruitment versus regeneration for the maintenance of the *T. coccinea* population in the Rebio Arvoredo, it is important to highlight that limiting local production of propagules is key to contain spread to new sites and the establishment of new invasion foci.

Despite the high number of colonies removed (~ 14 thousand), the invasion observed in our study sites can be considered small compared to those in the Brazilian southeastern coast. In the Ilha Grande Bay (Rio de Janeiro), for instance, more than $\sim 220,000$ colonies had been removed in more than 150 control actions by 2017 (Creed et al. 2017b). Furthermore, a *T. coccinea* distribution and abundance survey in a port area influenced by upwelling in Arraial do Cabo (Rio de Janeiro) fifteen years after its first record showed

that more than 50% of the total population was formed by colonies larger than 30 cm^2 (Batista et al. 2017). During the 18 months in which we conducted sampling work, colonies larger than 5 cm^2 never made up more than 50% of the populations. Sun coral is assumed to change communities completely when cover reaches 45% (Lages et al. 2011). Even with inaccessible crevices in Rebio Arvoredo (Fig S1c), there are not any known invasion patches in the region of our study with such levels of cover, which emphasizes the relevance of the ongoing control program to contain the invasion and consequential impacts on local communities and ecosystems.

De Paula et al. (2017) suggested that, after the first control effort of *T. coccinea*, follow-up within a 6–12-month interval may be sufficient. Our results corroborate this indication. From the discovery of invasion in Fenda (2014, Fig S1a) until now (Fig S1b), the effectiveness of control activities undertaken so far is palpable. Besides, immediately after control actions, regenerating colonies are flattened and virtually lack the calcareous skeleton (Fig S3b, S3e), becoming very difficult to detach from the substrate (Luz et al. 2018). Thus, the energy used on mechanical control should be invested when colonies have regenerated enough to be effectively removed, before reaching maturity. The combination of initial efforts of manual removal with a revisit to scratch/suction the remaining regenerating tissue may produce interesting results. Other methods to eliminate sun corals include the use of acetic acid (Creed et al. 2018), sodium hypochlorite (Altvater et al. 2017), freshwater (Moreira et al. 2014), and wrapping (Mantelatto et al. 2015), the last of which requires specific conditions or isolation of colonies for application and is extremely difficult to implement with success in tridimensional natural rocky reefs.

Regulatory frameworks for preventing the introduction and spread of sun corals must be established on all scales (global, regional and local) (Hewitt et al. 2008). There are 158 active offshore oil platforms, 23 drill ships, and expectations that 18 new structures will be installed by 2022 (Mafra 2018) in Brazil alone. A large part of these oil platforms (42%) are 20–25 years old, which means they must be decommissioned soon (Mafra 2018). Additionally, projections indicate that oil production will double in the next decade, generating more than 250 billion dollars in investments (MME 2018). The relevance of the expansion of these activities to the Brazilian economy is undeniable, but

they are also a threat to marine ecosystems. While specific regulations on the decommissioning of such structures do not exist at present, the oil industry claims that having to clean all structures offshore would render the business unviable. The complexity of the issue must be acknowledged, but it is essential to prevent the transit of contaminated structures. There is an urgent need for the development of specific regulatory frameworks by policy makers. The commitment of the governments of Australia and New Zealand are good examples to follow (see Hewitt et al. 2008). In a similar way to using the “ballast window” proposed to reduce the spread of the starfish *Asterina* in Australia (Dommissie and Hough 2004), structures potentially contaminated with *Tubastraea* corals should be moved only in periods of lowest reproductive potential (winter in the southern hemisphere). Furthermore, it is very important that these structures are immediately sent for clean-up (exposure to air or freshwater), avoiding docking for long periods in sheltered environments suitable to sun coral development.

In order to generate an effective response to marine invasions, different technical components must be integrated, such as data on the biology of the target species, agencies in charge of invaded areas, field expertise, and financial and human resources (Anderson 2005). Successful marine eradications have been achieved based on these premises (*Mytilopsis sallei* in Australia—Bax et al. 2002; *Caulerpa taxifolia* in California—Anderson 2005). However, the early detection and rapid response of environmental agencies and scientists in the southern distribution limit of *T. coccinea* were insufficient for eradication to be achieved. This is explained mainly because sun corals have occupied crevices inaccessible to manual removal (Fig S1c), and most importantly, because a formal eradication program with sufficient funding to eliminate all individuals and monitor recolonization in the following years (such as recommended by Simberloff 2003) has not been implemented. The recently published National Plan for the Prevention, Control and Monitoring for *Tubastraea* spp. (MMA 2018) must be put into action. The small, isolated invasion in the southern Atlantic limit of distribution in Rebio Arvoredo, an important Marine Reserve, must be prioritized for eradication. We agree with Oigman-Pszczol et al. (2017) on the claim that invasion by *T. coccinea* is not a lost cause.

Citizen-science may be helpful to increase *T. coccinea* control efforts. Positive results were obtained by citizen engagement in the detection and control of lionfish (*Pterois volitans*) in the Gulf of Mexico (see Scyphers et al. 2015). *Tubastraea coccinea* was actually first reported for Arvoredo island by recreational divers (Capel 2012). In 2013, the federal environmental agency (ICMBio), in partnership with the Marine Biodiversity Lab at UFSC, organized a workshop with staff from dive schools in the region to explain the threats and impacts of invasion by *T. coccinea* and provided training for the identification of colonies. Since then, some invasion patches around Arvoredo island were detected and reported by trained divers. However, controlling *T. coccinea* is not technically simple, requiring well-trained and qualified scuba divers to prevent the propagation of fragments. Creed et al. (2017b) involved local communities to collect corals by snorkeling and sell coral skeletons as a craftwork on a highly invaded site (Ilha Grande, RJ). Because invasion is restricted in Rebio Arvoredo, citizen engagement would be best used for the early detection of new invasion patches.

Given the challenges of controlling invasive marine species (Williams and Grosholz 2008) and global predictions of increase in the number of non-native species (Seebens et al. 2017), our work provides relevant information to support and improve ongoing control of *Tubastraea* spp. Our data show that control efforts reduced the population propagule supply of *T. coccinea* by maintaining a large portion of the population in small, non-reproductive sizes. We also highlight the urgent need for new techniques that might lead to eradication. Furthermore, the NPPCM for *Tubastraea* spp. must be implemented and prioritize the southern Atlantic limit of distribution including Rebio Arvoredo. Finally, even in the lack of a formal eradication program with ensured funding, control activities have successfully slowed the spread of *T. coccinea*. With the use of more effective techniques and the commitment of federal policies, eradication can be feasible.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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