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# Frequent Disease Intervention on the Largest Corals Prolongs Colony Life During Coral Disease Outbreaks

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# Thesis of
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NOVA SOUTHEASTERN UNIVERSITY

HALMOS COLLEGE OF ARTS AND SCIENCES

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By

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**Abstract**

Stony coral tissue loss disease (SCTLD) is a highly contagious coral disease, causing rapid colony mortality and local extinctions. Conducting disease interventions on all corals in a region during an outbreak is virtually impossible therefore, prioritizing corals must be considered. In 2015, we identified and monitored 78 of southeast Florida's largest (>2m in diameter) living *Orbicella faveolata* colonies. In 2018, all corals were revisited, and those with the greatest living tissue area and largest colony size were grouped as priority corals (n=42) and the remainder were grouped as non-priority corals (n=36). Priority corals received additional monthly monitoring with disease interventions starting immediately, whereas non-priority corals did not. All SCTLD lesions were treated beginning in 2018 with chlorinated epoxy and amoxicillin paste after 2019. Our results highlight that on average priority corals lost significant amounts of tissue (-6.07 % ± 4.34 % SE) before disease interventions began (2015-2018), while tissue loss was not significant (-2.93 % ± 4.93% SE) once monthly monitoring and disease interventions started (2018-2022) and no complete colony mortality occurred. In contrast, non-priority corals experienced significant losses (-33.22 % ± 5.06 % SE) between 2015-2018, and (-5.72 % ± 2.07 % SE) between 2018-2021, leading to the death of 66.7% (24/36) corals. Priority corals continually developed new lesions, and while disease interventions were highly successful at reducing the amount of tissue lost to disease, treatments were still required nearly every month. Frequent treatments have prolonged the lives of priority colonies, allowing them to spawn for several more seasons.

**Keywords:** SCTLD, Disease Intervention, Frequent Monitoring, *Orbicella faveolata*, Amoxicillin, Base2B, Southeastern Florida.

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## Introduction

Coral diseases are a naturally occurring phenomenon, even in the most remote parts of the ocean where human populations are low (< 20 people) and major anthropogenic impacts are absent (Williams et al., 2008, Williams et al., 2011). Coral disease is often the result of a complex interplay between the host, pathogen, and environment (Williams et al., 2010; Work et al., 2008) and an increase in global climate change and local anthropogenic stressors have exacerbated disease prevalence and severity, threatening the persistence of coral reefs (Burke et al., 2023; Maynard et al., 2015; Paseka et al., 2020). Coral disease is particularly problematic in the Caribbean, contributing to mass mortality of corals in recent decades and reducing coral cover and density (Garzón-Ferreira et al., 2001; Hayes et al., 2022). In 1972, black band disease was the first biotic coral disease identified in the Caribbean (Antonius, 1973). Since then, Caribbean coral reefs have suffered from many diseases, including but not limited to, white band disease (Gladfelter, 1982), white pox disease (Holden, 1996), white plague disease type II (Richardson et al., 1998), yellow band disease (Korrubel & Riegl, 1998), and dark spot disease (Goreau et al., 1998). In 2014, stony coral tissue loss disease (SCTLD) emerged as one of the most virulent and persistent coral diseases recorded (Hawthorn et al., 2024; Precht et al., 2016).

SCTLD was first documented in southeast Florida after a severe and prolonged coral bleaching event (Heres et al., 2021; Jones et al., 2021; Manzello, 2015; Precht et al., 2016). The disease spread quickly through the entirety of Florida's Coral Reef (Dobbelaere et al., 2020) and many locations throughout the Tropical Western Atlantic (Rosenau et al., 2021). SCTLD affects at least 22 species of Scleractinian coral and can spread through direct contact and the water column (Aeby et al., 2019; Alvarez-Filip et al., 2019; Landsberg et al., 2020; Muller et al., 2020; Thome et al., 2021). Coral species range in SCTLD susceptibility. Some are highly susceptible (e.g., *Dendrogyra cylindrus*, *Dichocoenia stokesii*, *Meandrina meandrites*), moderately susceptible (e.g., *Orbicella* spp., *Montastraea cavernosa*, *Siderastrea siderea*), and others appear tolerant (e.g., *Acropora* spp.) (Muller et al., 2020; *Stony Coral Tissue Loss Disease Response, (n.d.)*. Presently in Florida, the highly susceptible species exist in low abundances, while moderately susceptible species have higher abundances with persistent disease infection rates (Thome et al., 2021; Toth et al., 2024).

While white plague diseases (WPDs: WPD-I, II, and III) and SCTLD have similar signs making them difficult to separate in the field. But, SCTLD has a more comprehensive case definition. SCTLD lesions are visually characterized by a 1-5 cm wide disease margin of necrotic tissue with a bleached boarder (a unique diagnostic feature of SCTLD), which rapidly spreads and progresses away from the denuded skeleton at 3.6 to 5.3 $cm^2$ per day (Aeby et al., 2019; Cróquer et al., 2021). Lesions can originate at the colony's base, periphery, or center, and a coral can have single or multiple coalescent lesions that spread across the colony (Aeby et al., 2019). Histopathology has revealed that lesions form in a bottom-up process beginning in the basal body wall extending to the calicodermis and into the surface body wall, resulting in cell death and tissue sloughing (Landsberg et al., 2020). As tissue along the disease lesion sloths off, the newly denuded skeleton can become colonized by opportunistic benthic groups such as turf algae and macroalgae (Cróquer et al., 2021). If untreated, SCTLD often results in whole coral mortality, which reduces coral density regionally and is suspected to lead to a reduced population fitness through an Allee effect (i.e., a reduced reproductive potential due to low density or a large distance between colonies) (Hayes et al., 2022; Rippe et al., 2019; Walton et al., 2018).

Up to the time of this publication, the pathogen(s) responsible for SCTLD has not yet been identified. Evidence suggests that SCTLD is a viral infection attacking certain Symbiodiniaceae communities with a secondary bacterial infection, eventually leading to coral host death (Beavers et al., 2023; Landsberg et al., 2020; Work et al., 2021). Endosymbionts within SCTLD infected tissues exclusively contained anisometric viral-like particles (VLPs), and experienced morphological changes such as intracellular cavities filled with debris, loss of thylakoid membranes, and gigantism of chloroplasts (Howe-Kerr et al., 2023; Work et al., 2021). Coral host cells had massive proliferation and lysis of mucous cells, the first line of defense against foreign particles and microbes (Work et al., 2021). Beavers et al., (2023) revealed that corals exposed to disease had an induced expression of genes involved in immunity, apoptosis, and extracellular matrix. Interestingly, infected corals consistently had increased expression of the *rab7* protein, a marker responsible for in situ degradation of dysfunctional Symbiodiniaceae, suggesting SCTLD is a virus of the symbionts (Beavers et al., 2023). The susceptibility and severity of the disease is influenced by Symbiodiniaceae species, with *Breviolum*, *Cladocopium*, and *Durisdinium* being more susceptible, and more likely to contain VLPs and produce lesions (Dennison et al., 2021; Howe-Kerr et al., 2023; Work et al., 2021).

The inability to identify disease pathogens makes it especially hard to design effective interventions. Many coral disease intervention methods were proposed and trialed to find the most effective and appropriate technique to treat various coral diseases, including mechanical (removal of the diseased tissue, creating trenches, smothering), chemical (antiseptics or antibiotics), or biological (phage therapy, probiotics) techniques (Neely et al., 2021). Each method varied in success, measured by the proportion of quiesced disease lesions, but required individual colony treatments and continued monitoring. For example, a cut in the live tissue and skeleton isolating the disease lesion from healthy-looking tissue (now termed a disease break by Walker et al., 2021) was successful at reducing the rate and amount of tissue lost to Caribbean Yellow Band Disease by 31% in *Orbicella* spp., while aspiration and shading were not (Randall et al., 2018). Growth anomaly removal with a hammer and chisel was an effective treatment for *Acropora acuminata* but not *Monitpora efflorescens* (Williams, 2013). Black band disease was effectively treated in-situ using chlorinated epoxy on a margin treatments with a disease break; treated corals lost 30% less tissue on average than untreated controls (Aeby et al., 2015). Antibiotics successfully arrested the progression of white band disease in *Acropora cervicornis* ex-situ, but not dark spot disease (Aeby et al., 2019; Gil-Agudelo et al., 2004; Sweet et al., 2014). While many disease interventions were trialed to treat SCTLD (Neely et al., 2020, Neely et al., 2021), chlorinated epoxy was quickly permitted for use ex-situ on Florida's Coral Reef in 2018. The rapid approval of chlorinated epoxy is because it effectively treated black band disease in Hawaii (Aeby et al., 2015). However, the success of using chlorinated epoxy to treat and quiesce SCTLD lesions is species-specific, with ~70-75% effective on *O. faveolata* and ~20% effective on *M. cavernosa* (Shilling et al., 2021; Walker et al., 2021).

The most effective SCTLD intervention to date is covering the lesion with amoxicillin trihydrate and CoralCure Ointment Base2B at a ratio of 1:8, heretofore called CoralCure (*Coral ointment information*). CoralCure was designed to adhere to the coral skeleton and release amoxicillin into the coral at a fixed dosage rate over three days and was used in place of chlorinated epoxy once permitted for experimental use in 2019. Studies have found using CoralCure to quiesce SCTLD lesions on *O. faveolata* and *M. cavernosa* to be ~80% effective, and the disease-break combination can be ~95% effective after one application (Neely et al., 2020; Shilling et al., 2021; B. K. Walker et al., 2021). While CoralCure treatments are more successful than chlorinated epoxy, about 20% of amoxicillin treatments fail to stop disease progression, making retreatments

necessary. Furthermore, CoralCure treatments do not prevent new lesions from forming, prompting recommendations that corals should be visited monthly or bi-monthly to monitor and treat SCTLD lesions on the most valuable corals while SCTLD remains prevalent (Neely et al., 2021; Shilling et al., 2021; Walker et al., 2021).

Currently, there are two main regional response efforts for in-situ SCTLD interventions: broadscale strike team interventions and prioritized coral interventions. Strike team interventions involve conducting thorough searches for diseased corals in densely coral populated areas and administering one-time treatments. Zummo (2024) found that broadscale disease intervention were 87% effective at keeping corals alive 4 years after treatments were administered on small (<1m) *M. cavernosa* corals in southeast Florida. However, the effectiveness of broadscale disease interventions relies on the ability to find and treat diseased individuals, treatment efficacy, and coral reinfection rates.

In contrast, prioritized coral interventions focus on providing frequent and repeated monitoring and treatments on specific coral colonies. This approach allows for early disease identification, immediate treatment administration, and subsequent retreatments if failure occurs. Additionally, treatment effectiveness can be assessed and determined for each species. Therefore, frequent monitoring could reduce the amount of tissue lost to SCTLD (Neely et al., 2020, 2021; Toth et al., 2024; Walker et al., 2021), lessen the pathogen load in the environment (Forrester et al., 2022; Toth et al., 2024), and potentially decrease the chances of a nearby coral becoming infected. Colonies with large surface areas have an increased exposure to waterborne pathogens, and an increased chance of multiple lesions appearing (Downs et al., 2019; Sharp et al., 2020), making frequent disease interventions necessary for larger corals.

Corals prioritized for interventions focused on the largest and oldest colonies due to their significant ecological functions. Larger colonies can have a higher reproductive output and potential fertilization success due to their greater number of polyps able to release gametes (Hughes, 1984; Szmant, 1986) and greater fitness compared to younger and smaller colonies (Hughes et al., 1992). Southeast Florida's reefs are characterized by many small colonies (<1 m) aging to a few decades. However, there are a few hundred, large (>2 m) *O. faveolata* corals that have been discovered and that are hundreds of years old (Walker & Brunelle, 2018). One large *Orbicella* measured 7.5m in diameter and was dated to over 320 years old (Banks et al., 2008). In South Florida, *O. faveolata* colonies have a mean annual linear extension of 0.79 cm (±0.07 cm

SD) per year (Helmle et al., 2011). Using their size as a proxy for age, a colony that is >2 m in diameter can be hundreds of years old. Therefore, these colonies could be some of the most resilient corals on Florida's Coral Reef, having survived the many natural and anthropogenic impacts over the past several hundred years of coastal development and climate change. Preserving these large colonies' genetic diversity is extremely important for the natural repopulation and persistence of the bouldering species along Florida's Coral Reef.

Given their critical ecological roles, but limited resources, it was imperative to prioritize these corals for disease interventions. Since large scale disease interventions are a new proactive response in coral reef management, little is known about the longer-term effectiveness of intervention strategies. This study used data collected over seven years (2014-2021) to examine the effectiveness of monthly interventions on large *O. faveolata* colonies in southeast Florida. It specifically compares the rate of tissue loss and whole colony mortality between colonies that had prioritized disease interventions by repeated, and frequent disease interventions (priority corals) with colonies that did not (non-priority corals). Past and present rate of tissue loss was used to forecast future prioritized colony fates under present conditions.

## Methods

*Spatial Mapping and Reconnaissance*

In 2014, a nearshore mapping project in southeast Florida was completed using high-resolution Light Detection and Ranging (LIDAR) bathymetry (<4 m resolution), NOAA's Office of Coast Survey Hydrographic Division bathymetry (1 m resolution), and aerial photography (0.3 m resolution) (Walker & Klug, 2014). This revealed the presence of previously undocumented, unusually large corals (>2 m diameter) for the area, in the shallow (<7 m) Nearshore Ridge Complex habitats (Walker & Klug, 2015). Scuba divers visited and photographed each potential coral seen in the remote sensing data, finding 115 living and 70 dead massive coral colonies, predominately from the species *O. faveolata* (Walker & Klug, 2014).

*Prioritization of Colonies for In-Situ Monitoring*

In 2015, these newly found living corals (n=115) were revisited, assessed, and documented (Table 1) by a diver floating 1-2 m above the colony to visually estimate the percentage of old mortality, recent mortality, living tissue, and bleached tissue, and state if diseased tissue was

present or absent from the colony. Each coral was measured using a rigid 1-meter stick to measure the maximum colony height, maximum diameter, and perpendicular width were measured on each coral. Photographs of the colony were taken at each cardinal direction: North (0°), East (90°), South (180°), West (270°), and from directly above for quality assessment and quality control of tissue percentage estimates. Photographs of up-close disease lesions were taken with a scale bar to visually confirm disease presence, type, and progression.

**Table 1:** Summary of morphological statistics of corals found in 2015 during nearshore mapping project in south Florida. Adapted from Walker and Klug (2015).

| **Statistic** | **All Corals** | ***O. faveolata*** | ***M. cavernosa*** | ***S. siderea*** | ***O. annularis*** | ***P. strigosa*** | ***C. natans*** |
|---|---|---|---|---|---|---|---|
| n | 115 | *90* | *12* | *7* | *2* | *2* | *2* |
| Mean Length (m) | 2.73 ± 0.81 SD | 2.88 ± 0.82 SD | 2.15 ± 0.50 SD | 2.44 ± 0.30 SD | 3.25 ± 0.07 SD | 1.45 ± 0.07 SD | 1.60 ± 0.28 SD |
| Height (m) | 1.37 ± 0.48 SD | 1.38 ± 0.49 SD | 1.24 ± 0.22 SD | 1.50 ± 0.41 SD | 2.10 ± 0.71 SD | 0.93 ± 0.04 SD | 0.93 ± 0.25 SD |
| Mean Width (m) | 2.28 ± 0.68 SD | 2.40 ± 0.68 SD | 1.70 ± 0.32 SD | 2.24 ± 0.35 SD | 2.35 ± 0.35 SD | 1.20 ± 0.28 SD | 1.20 ± 0.28 SD |
| Mean Surface Area ($m^2$) | 7.58 ± 4.58 SD | 8.23 ± 4.83 SD | 4.55 ± 1.37 SD | 6.74 ± 1.69 SD | 10.27 ± 0.79 SD | 2.23 ± 0.40 SD | 2.41 ± 0.40 SD |
| Mean Living SA ($m^2$) | 4.02 ± 3.54 SD | 4.51 ± 3.79 SD | 2.22 ± 0.94 SD | 2.23 ± 1.64 SD | 4.84 ± 2.04 SD | 1.81 ± 0.09 SD | 0.59 ± 0.69 SD |
| Mean Depth (m) | 6.36 ± 0.80 SD | 6.38 ± 0.86 SD | 6.20 ± 0.48 SD | 6.40 ± 0.68 SD | 6.40 ± 0.43 SD | 6.10 ± 0.00 SD | 6.55 ± 0.22 SD |
| % colonies with Recent Mortality | 37% (42/115) | 30% (27/90) | 58% (7/12) | 43% (3/7) | 100% (2/2) | 50% (1/2) | 100% (2/2) |
| % colonies w/ Bleaching | 23% (27/115) | 21% (19/90) | 42% (5/12) | 14% (1/7) | 50% (1/2) | 0% (0/2) | 50% (1/2) |
| % colonies w/ Paling | 21% (24/115) | 17% (15/90) | 67% (8/12) | 0% (0/7) | 50% (1/2) | 0 % (0/2) | 0 % (0/2) |
| % colonies w/ disease | 23% (27/115) | 22% (20/90) | 17% (2/12) | 43% (3/7) | 0 % (0/2) | 0 % (0/2) | 100% (2/2) |
| % colonies w/ no disease, bleaching or paling | 49% (56/115) | 54% (49/90) | 0% (0/12) | 57% (4/7) | 0 % (0/2) | 100% (2/2) | 0 % (0/2) |

During the 2015 assessments, over half (51%) of the colonies had at least partial bleaching and disease (Table 1). 23% of the colonies had active disease, 23% had some bleaching, and 21% percent had some paling. 8% of the colonies had both disease and bleaching. The observed diseases were white plague (likely SCTLD), white band, black band, dark spot and possibly Caribbean yellow band. Diseases were not noted in the initial 2014 reconnaissance photo and video

documentation but were obvious during the 2015 in-situ monitoring. Specifically, dark spot disease developed in two large *S. siderea* colonies between 2014 and 2015 (Walker & Klug, 2015). At least 30% of the live tissue on an *O. faveolata* colony (LC-025) was lost that appeared healthy in 2014 (Figure 1).

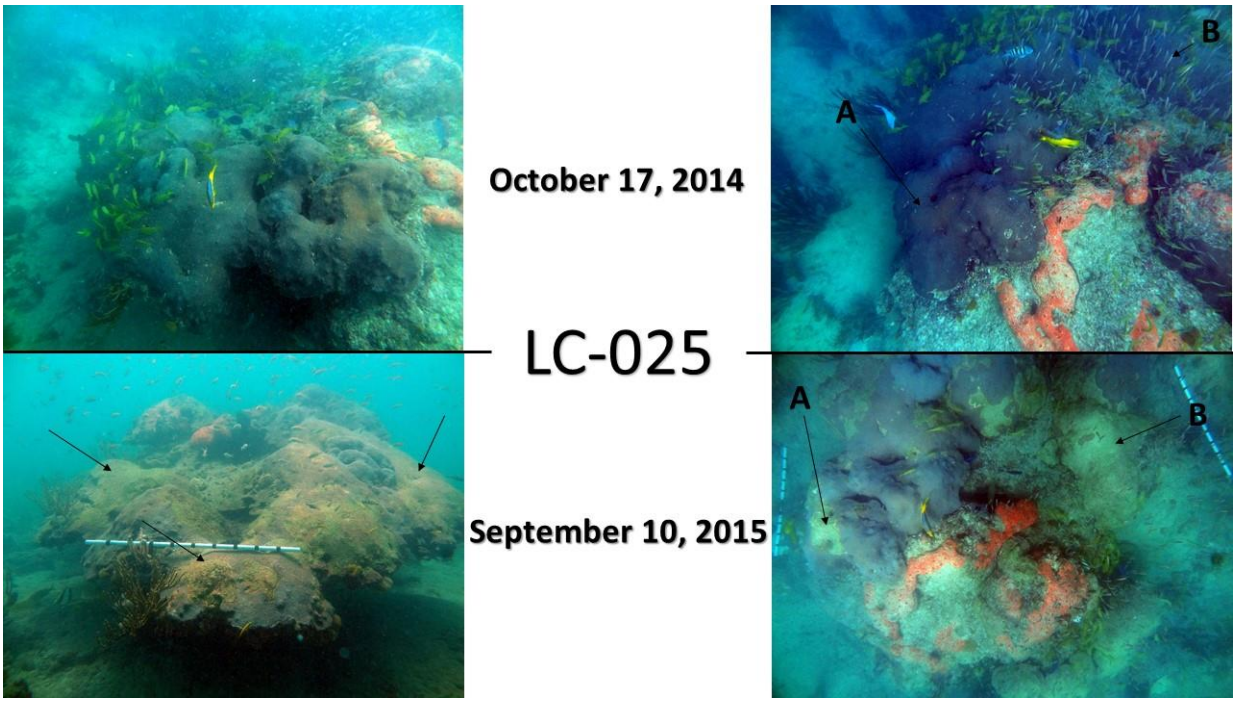


**Figure 1.** Photographs of a large *Orbicella faveolata* colony that lost over 30% live tissue between October 17, 2014 and September 10, 2015. The left panel is the side view of the colony, and the right is the top down. Letters in right images indicate the same location on the colony between image where tissue loss occurred. Tissue loss is evident in 2015 by the lightly colored skeleton. The arrows in the lower left photo represent areas where there was tissue loss since 2014.

In 2018, after three years of persistent SCTLD, two historical thermal stress events (2014 and 2015), and the passing of a major hurricane (Irma in 2017), funding was received to reassess, monitor, and treat disease on all the 115 living colonies that were originally assessed in 2015 (Walker & Brunelle, 2018). Initial disease intervention funding was only sufficient to regularly treat 54 colonies, therefore the colonies were divided into priority (corals that received monthly monitoring and disease interventions) and non-priority (corals that did not receive additional monitoring and disease interventions). The largest colonies of each species with the most estimated live tissue area and the least estimated percent mortality, based on condition from 2018, were selected as priority corals, leaving 61 non-priority corals (Table 2). This yielded 54 priority corals

with either >4 m² of live tissue remaining or colonies with <10% mortality to receive monthly monitoring and disease interventions beginning in April 2018. Non-priority corals were only revisited in 2021.

**Table 2:** Initial coral species assigned to priority and non-priority corals (n=115). Due to the low number of replicates of other species, only *O. faveolata* corals were used for statistical testing.

| Species | Priority | Non-Priority |
|---|---|---|
| *O. faveolata* | 46 | 44 |
| *M. cavernosa* | 6 | 6 |
| *S. siderea* | 1 | 6 |
| *O. annularis* | 0 | 2 |
| *P. strigosa* | 1 | 1 |
| *C. natans* | 0 | 2 |
| **Total** | **54** | **61** |

Priority coral monitoring involved the corals being assessed and monitored at the beginning of each month. Assessments followed similar methods as the initial 2015 monitoring, with photos of the colony and visual estimations of tissue levels, and the addition of disease treatments. As additional funding was received, more corals were added to the priority monitoring. As of 2024, there were 107 large priority corals consisting of 7 species, with *O. faveolata* highly represented, and ranging in location. Priority and non-priority corals are found spanning 55 km between Pompano and Biscayne National Park, with clusters of corals found in the most northern and southern extent (Figure 2).

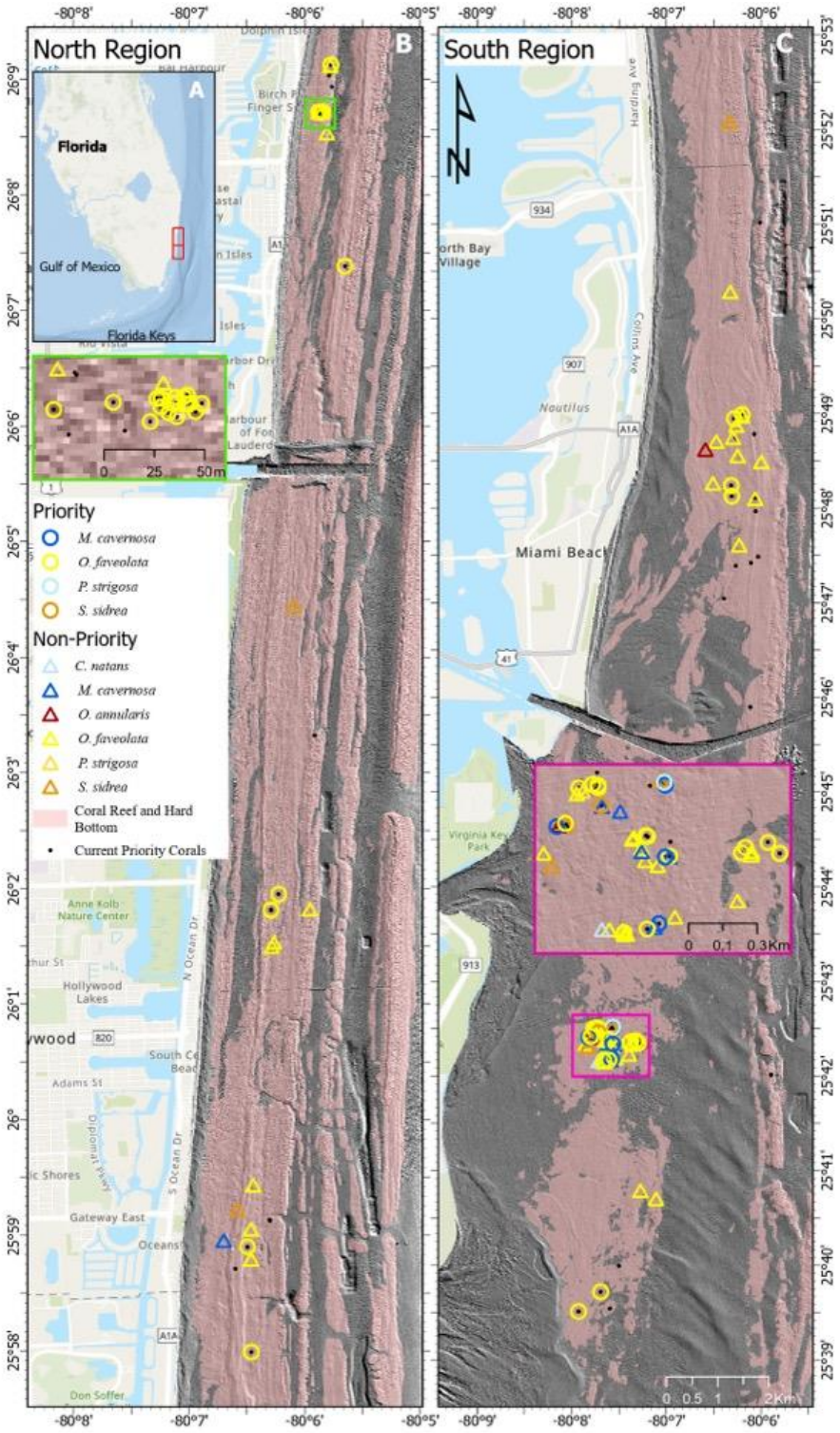


**Figure 2.** (A) Southeast Florida including the Gulf of Mexico and the Florida Keys; the study area is outlined in red. (B, C) Corals visited for priority or non-priority monitoring separated by species and current priority corals (all colonies with priority corals status as of 2024 (n=107)), overlaying Florida's Coral Reef, with green and pink rectangles showing a zoomed in view of the respective area.

Of the 115 corals identified by the nearshore mapping project of South Florida and monitored in 2015, 101 of them were visited in 2015, 2018, and 2021. Of those, 78 were *O. faveolata* colonies, making up 77% of the data. Due to the low number of replicates of other species, only *O. faveolata* corals were used for statistical testing comprising of 42 corals that received monthly visits and SCTLD treatments (priority) and 36 no-treatment control corals that were not regularly visited and treated (non-priority).

*Disease Interventions*

SCTLD interventions began in April 2018, and until August 2019, interventions consisted of applying chlorinated epoxy treatments to margins and disease breaks (Figure 3). Margin treatments were applied to the live and dead polyps adjacent to and ~2 cm beyond the active disease margin. Disease breaks were created using a Nemo underwater grinder (AG-22-5Li-50) with a 4.5-inch masonry grinding blade to isolate healthy tissue ~5 cm from the margin and ~1 cm deep, then filled the trench with treatment. Approximately 50 mL of Part A of a two-part marine epoxy, ZSPAR A-788 Splash Zone™, was premixed with 15 g Poolife™ Turboshock® chlorine powder (Aeby et al., 2015). Equal parts of Part A epoxy (with chlorine powder) and Part B epoxy were kept separate and mixed underwater before application (hereafter referred to as chlorinated epoxy). These interventions yielded 68% effectiveness in stopping lesions on *O. faveolata* (Walker & Brunelle, 2018).

After August 2019, CoralCure was used as the disease intervention treatment. CoralCure is an antibiotic paste comprised of a mixture of amoxicillin trihydrate (from PhytoTechnology Laboratories) and a silicone-based paste labeled Base2B (from Ocean Alchemists) designed to release antibiotics over 72 hours. Base2B and amoxicillin were mixed by a weight ratio of 8:1 and combined well (hereafter referred to as CoralCure). The resulting paste was left for at least 15 minutes to allow any ethanol-based preservative in the Base2B to evaporate. Then, the CoralCure paste was transferred into 60 mL catheter-tip syringes, with the tips cut off to facilitate application, and kept refrigerated and used within 48 hours of mixture. CoralCure was applied as a margin or disease break (Figure 3). However, the increased success of CoralCure treatments allowed for the reduction of using disease breaks except in circumstances of very fast lesion progression evident by a wide margin of freshly dead skeleton. Interventions using CoralCure yielded >87% effectiveness in stopping lesions on *O. faveolata* (Walker et al., 2022).

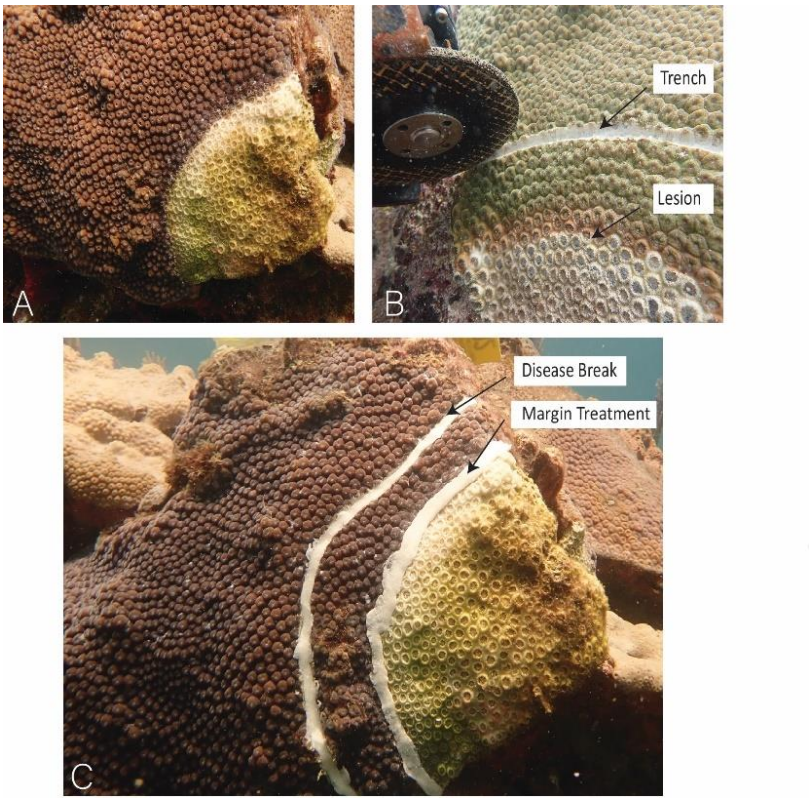


**Figure 3**. Stony coral tissue loss disease (SCTLD) treatment involves a diver assessing the coral disease lesion to decide to apply a margin treatment by smothering the lesion with disease treatment, and/or creating a disease break using an angle grinder and filling in the area with disease treatment. Disease treatment can be chlorinated epoxy or CoralCure. (A) shows the untreated disease lesion. (B) shows an angle grinder creating a disease break in the coral above the lesion. (C) shows the final treated coral using a disease break and margin treatment with CoralCure.

*Statistical Analysis*

Survival of the treated and non-treated control colonies was determined by the number of colonies with >1% live tissue for each monitor period. A coral was considered dead if it had less than 1% of living tissue remaining. The R package glmmTMB was used to fit a generalized linear mixed model (GLMM) with a beta binomial distribution (Brooks et al., 2017) to test the effect of treatment (fixed factor, 2 levels: treated and control) on the percent/proportion of living tissue at each monitor year (fixed factor, 3 levels: 2015, 2018, 2021), using individual colonies as replicates. Colony depth, length, height, colony surface area (CSA) **(1)**, and live tissue area (LTA) **(2)** (all continuous factors) were included in the model.

Colony surface areas (CSA) were calculated using the following formula, which is a modified version (Walton et al., 2018) of the Knud Thomsen (Klamkin, 1971, 1976) approximation for the surface area of an ellipsoid:

**(1)**

$$CSA = \left( 4\pi \left( \frac{(ab)^p + (ac)^p + (bc)^p}{3} \right)^{\frac{1}{p}} \right) (0.5)$$

Live tissue area (LTA) for each colony was calculated to estimate tissue loss by multiplying the individual CSA by the proportion or percentage of the living tissue, as:

**(2)**

$$Live\ Tissue\ Area\ (LTA) = CSA \times Living\ Tissue\ Proportion\ (LTP)$$

Model selection was completed by fitting the interaction between treatment and years, and cofactors, by assessing AIC (multiple candidate models fitted (Table 3)). In the event of equivalent models (i.e., within an AIC score of 2; Burnham & Anderson, 2004), the less complex model was selected. Model validation was performed using the R package DHARMa, with residual diagnostics, including overdispersion, heterogeneity and temporal autocorrelation (Hartig, 2022). Model validation indicated no problems. Marginal and conditional $R^2$ was calculated using the performance package (GLMM, marginal $R^2$= 0.8, conditional $R^2$= 1.0, where the marginal $R^2$ considers only the variance of the fixed effects and the conditional $R^2$ accounts for both the fixed and random effects), however, due to a large Z statistic, the model's variance cannot be accurately calculated, making the $R^2$ values not reliable (Table 3). The minimum adequate model for change in living tissue proportion contained monitor period, priority status, depth, and colony ID as a random factor (AIC= -396.1). A *post hoc* Tukey-adjusted pairwise comparison with a 95% familywise confidence level analysis was completed using the emmeans package to assess the significant factors in the fitted model (Lenth, 2022), particularly to determine temporal variation on tissue between 2015-2018 and 2018-2021 within the control and treated groups.

**Table 3:** Candidate models for variation in living tissue percent. The fitted model is in bold, which was the chosen candidate model with low AIC and acceptable model residuals. The conditional $R^2$ was calculated using fixed and random effects from the fitted model, and the marginal $R^2$ was calculated only from fixed effects. Due to a large Z statistic, the $R^2$ values are not reliable.

| Response | Candidate Model | AIC | Conditional $R^2$ | Marginal $R^2$ |
|---|---|---|---|---|
| **Living Tissue** | Year + (1\| ColonyID) | -216.3 | | |
| **Percent** | Year + Priority + (1\| ColonyID) | -318.9 | | |
| | Year × Priority + (1\| ColonyID) | -393.3 | | |
| | Year × Priority + Coral Surface Area+ (1\|ColonyID) | -395.6 | | |
| | Year × Priority + Coral Surface Area + Depth + (1\|ColonyID) | -395.9 | | |
| | **Year × Priority + Depth + (1\| ColonyID)** | **-396.9** | **1.0** | **0.8** |

Future projections of mean living tissue percentage were created using data from all *O. faveolata* priority colonies (n=82) that were visited as of June 2018. Only *O. faveolata* colonies were used in the projections to limit species interactions. Mean living tissue percentage were calculated each month. We omitted corals that were not continuously visited from June 2018 to October 2023; However, if a colony was missed for a month or multiple months, but there was no change in tissue coverage, we assumed that the colony remained at the same tissue level during the months that it was not visited. Projections were created using R-studio's forecast package (Hyndman & Khandakar, 2008). Models were run and validated by checking for residual standard deviation and autocorrelation. The exponential smoothing model fit the data best with the smallest residual standard deviation (Residual SD = 0.0241) and lacked autocorrelation.

## Results

*Survival*

No priority corals died during the length of the study, whereas 66.7% (24) of the non-priority corals died (Figure 4). 47.2% (17) of the non-priority colonies died between 2015 and 2018, and 19.4% (7) died between 2018 and 2021.

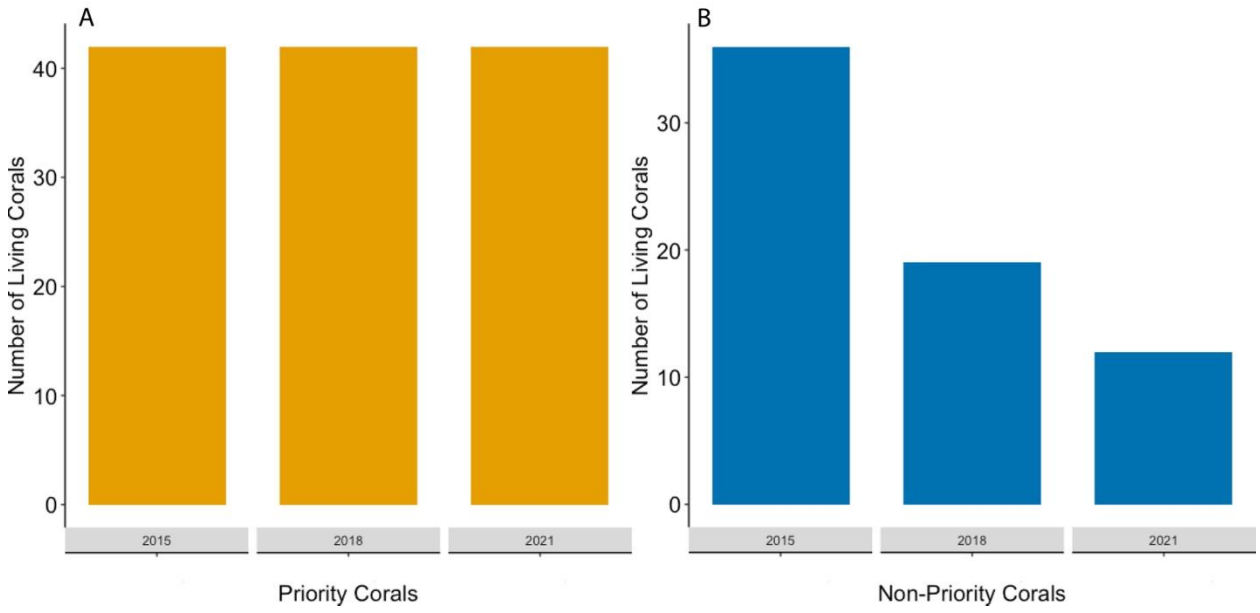


**Figure 4.** Number of living corals at each monitoring period (2015, 2018, 2021) for priority (A) and non-priority corals (B). A coral was considered alive if it had >1% living tissue remaining.

*Priority Coral Temporal Change*

Before monthly monitoring and disease intervention began (2015 – 2018), priority corals significantly declined in percentage of living tissue (p= 0.048) (Figure 5). In 2015, the mean amount of living tissue on priority corals was 74.1% (± 3.0% SE) and dropped to 68.1% (± 3.2 % SE) in 2018, losing on average 6.1% (± 4.3% SE). 14 colonies (33.3%) lost tissue during this time (Figure 6 (D&E)), one colony (2.4%) gained 5% tissue, and 27 colonies (64.3%) remained with consistent tissue coverages (Figure 6 (A&B)), equivalating to losing a total of -26.8 $m^2$ of living tissue.

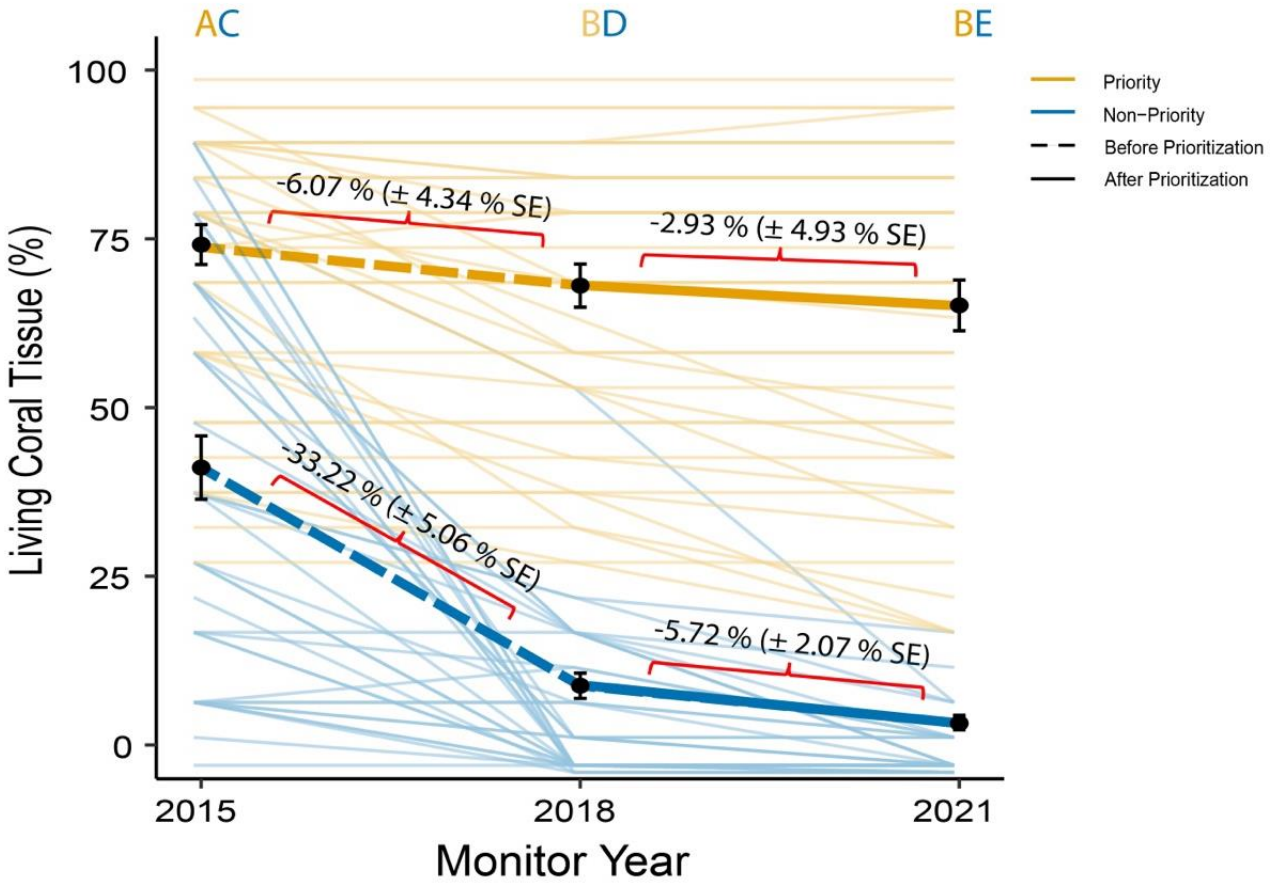


**Figure 5.** The percent living tissue (%) by priority status for each monitor year. The blue lines indicate priority corals and yellow lines indicate non-priority corals. The large bars show the mean percentage of living tissue with standard error bars and the difference between the means and standard error between each monitor period is labeled above. The dashed portion of the thick lines show before the groups were prioritized, while the large solid lines show after prioritizing. The thin lines show the live tissue of a single coral over time. Letters indicate test results significances which are color coded to show priority status. Priority corals do not have a significant decline in live tissue once frequent monitoring began. Non-priority corals have a significant decline in live tissue between all monitor years. There is a significant difference between priority and non-priority corals at all monitor years.

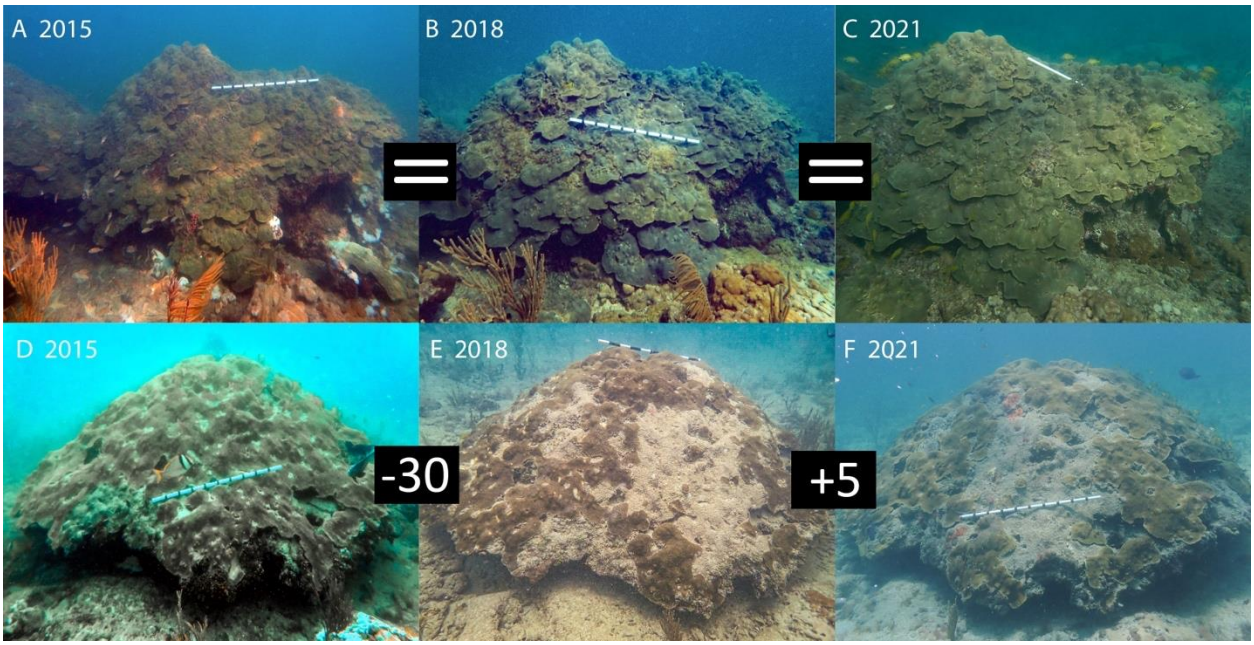


**Figure 6.** (A-C) Priority coral that had consistent live tissue cover throughout monitor periods. (D-E) shows a priority coral that lost 30% tissue between 2015-2018, and (E-F) shows the same coral with a 5% growth of living tissue from 2018-2021.

The amount of tissue loss and the number of priority corals that experienced tissue loss significantly declined once monthly monitoring and disease interventions began (Figure 5). During the monthly monitoring and disease interventions period (2018 – 2021), priority corals did not have a significant decline in amount of living tissue (p= 0.583), losing an average of -2.9% (± 4.9% SE) of living tissue. 10 colonies (23.8%) lost tissue during this time (Figure 6 (E&F)), 2 colonies (4.8%) gained 5% tissue, and 30 colonies (71.4%) remained with consistent tissue coverage (Figure 6 (B&C)), losing a total of 13.6 $m^2$ of living tissue. After disease interventions began, priority corals lost 52% less mean tissue (2.9% ± 4.9 SE), compared to the period before disease interventions (6.1% ± 4.3 SE).

*Non-Priority Coral Temporal Change*

Between 2015–2018, the non-priority corals significantly declined in living tissue (p= <0.0001) (Figure 5). In 2015, the mean living tissue on non-priority corals was 41.1% (± 4.7% SE), losing on average 33.2% (± 5.06% SE). During this time, 32 colonies (88.9%) lost living tissue resulting in 17 colonies (47.2%) dying (Figure 4B, Figure 7 (A&B)), 1 colony (2.7%) gained

5% tissue, and 3 colonies (8.3%) remained consistent tissue percentage, equivalating to losing a total of 135.7 $m^2$.


**Figure 7. (**A-B) shows a non-priority coral that lost 15% live tissue between 2015-2018. (B-C) shows the same coral with an additional 15% living tissue lost between 2018-2021.

Then, the non-priority corals significantly declined in living tissue between 2018-2021 ($p= 0.0196$), losing on average 5.7% (± 2.1% SE). 20 colonies (55.6%) lost tissue during this time resulting in 7 colonies (19.4%) dying (Figure 4B, Figure 5, Figure 7 (B&C)), 2 colonies (5.6%) remained consistent, and no colonies gained living tissue, equivalating to losing a total of 26.9 $m^2$ of living tissue.

Living tissue percentage declined over time in both priority and non-priority colonies, but the rate of decline was significantly greater in non-priority colonies. The priority and non-priority groups had dramatic differences in tissue loss between the two groups before interventions began. Between 2015-2018, non-priority corals lost 5.5 times more tissue compared to priority corals, indicating they were perhaps more susceptible to SCTLD. Interestingly, within these groups, some *O. faveolata* colonies displayed chronic disease lesions, while others nearby appeared unaffected.

*Intervention Efforts*

SCTLD prevalence was high during the study period. Priority corals had a high disease prevalence nearly every month they were visited (Figure 8). The priority corals were treated every time disease was present, totaling 623 new treatments and 62 retreatments (Figure 9). Disease on the priority corals followed a cyclical pattern with the most disease prevalent in the warm, wet summer months and the least in the cool, dry winter months. Between April 2018- December 2021,

only 2 priority colonies never had a disease lesion, 5 colonies had 1 disease lesion, 13 colonies had between 2-5 disease lesions, and 21 colonies had >6 lesions.

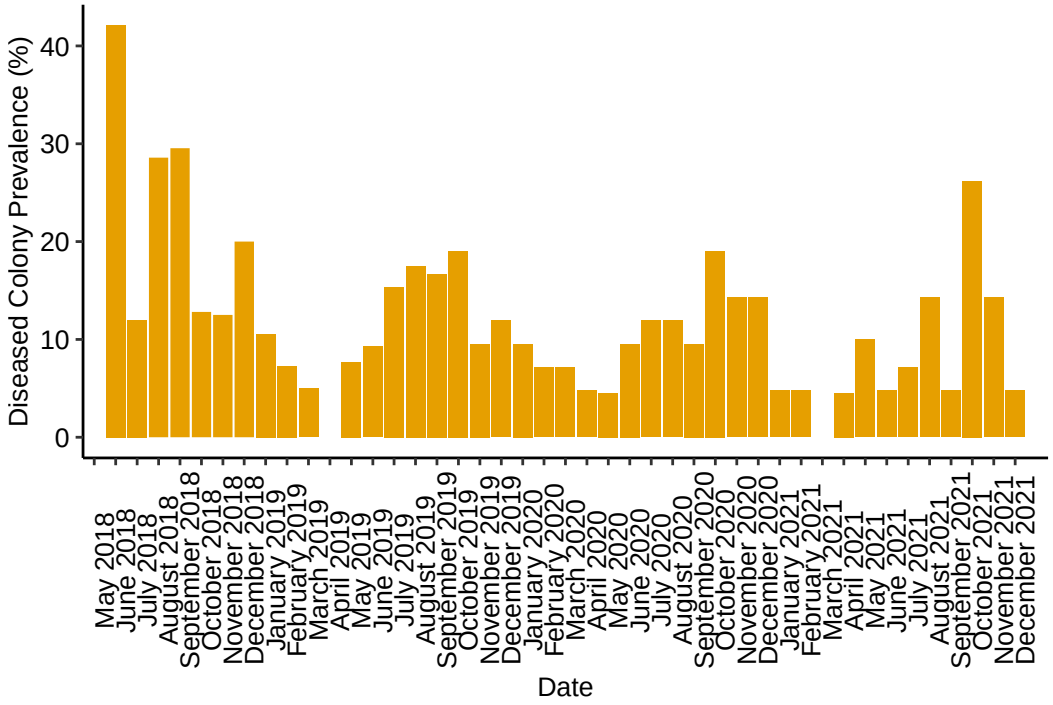


**Figure 8.** Percentage of priority corals that had disease prevalent each month once CoralCure treatments began. Nearly all months (except 2 months) have SCTLD prevalent in the priority corals requiring treatment. Seasonality variability is noticeable with higher SCTLD prevalence in the warmer wet months and lower variability in the cooler drier months.

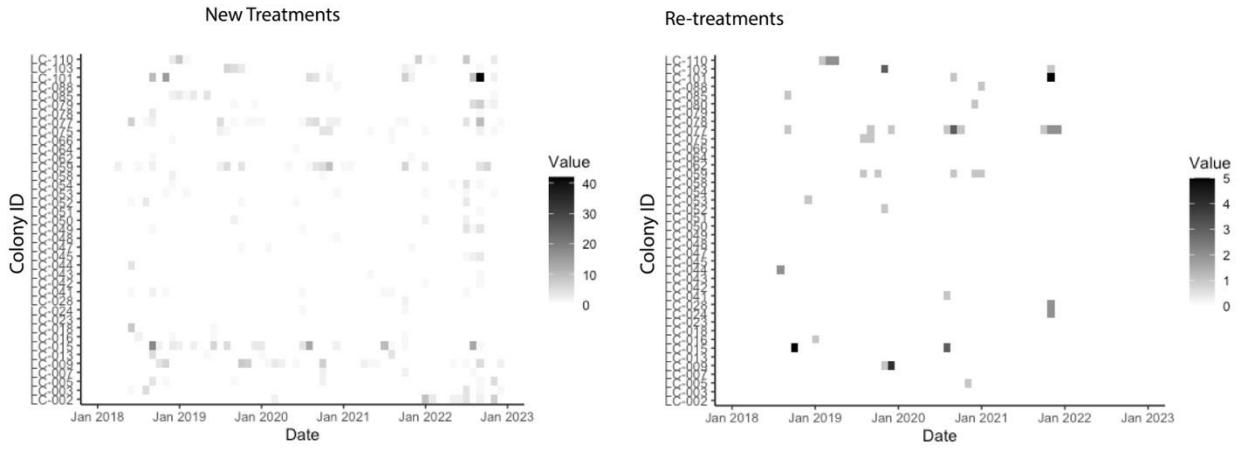


**Figure 9.** Priority colony SCTLD treatment (left) from January 2018- December 2022 for each colony ID. Priority colony SCTLD retreatment (right) from failed initial treatments for each colony ID from January2018- December 2022.

Forty of the non-priority corals had disease during the study. However, only 7 corals were treated when visited in May and June 2018, totaling 23 new treatments. Since the non-priority corals were not visited each month, it is unknown if they were diseased when they were not monitored. But there was disease prevalent on the colonies each time they were monitored.

*Projections*

Future projections of priority *O. faveolata* corals showed a decrease in living tissue proportion through time losing 1.6% (±2.2% SE) per year on average (Figure 10). By January 2026, priority *O. faveolata* corals were projected to lose approximately 3.3%, 95% CI [55.8%, 60.2%] living tissue and reach 0%, 95% CI [-9.0 %, 9.1%] living tissue by 2061. However, there are some outlier corals that may not follow the predictions of the projections. Two corals have grown and increased living tissue by 5% since initial monitoring in 2015, and 11 other corals have maintained consistent living tissue percentage.

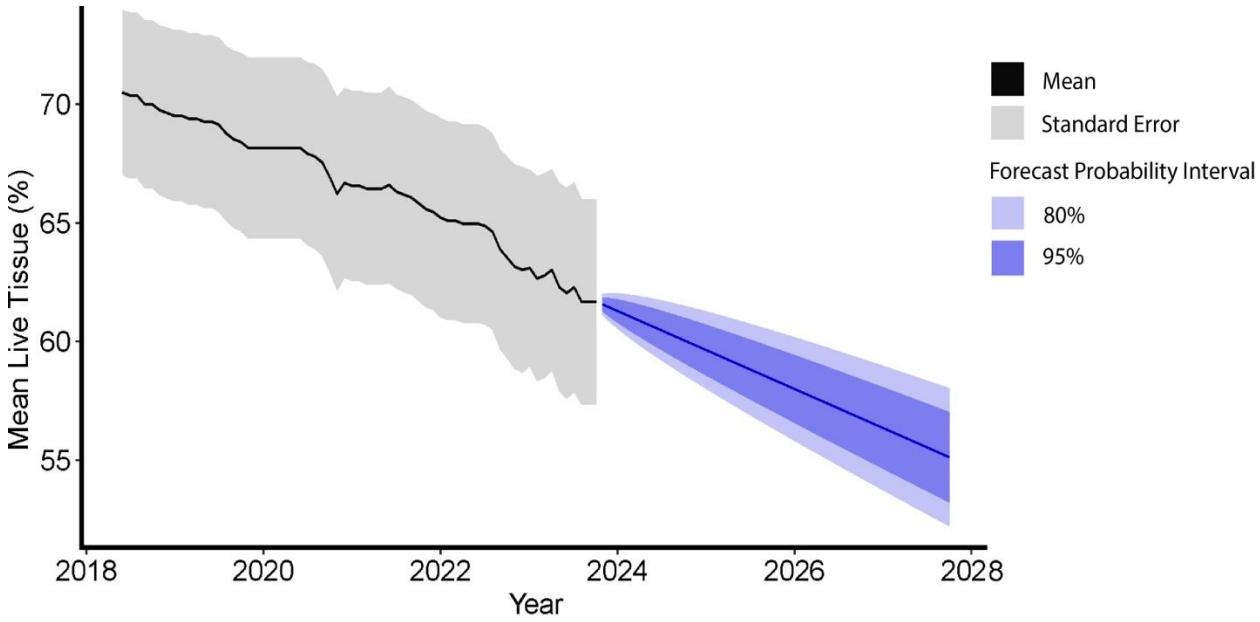


**Figure 10.** Mean proportion of living coral tissue black line with standard error shaded in grey, in all *O. faveolata* priority corals added since 2018. The dark purple line represents the mean point forecast of coral tissue, the dark shaded purple represents the 95% confidence interval, and the light purple represents the 80%.

In 2021, the last time the non-priority corals were visited, they had average living tissue percentages very close to zero (3.0% ± 1.0% SE), negating the need for future projection of their

live tissue cover. However, there are some outlier non-priority corals that have not reached critically low levels of living tissue. For example, a coral had ~20% and another ~15% living tissue as of 2018. Additionally, there were three colonies with ~10% living tissue. These corals may have different tissue levels than the projections can predict and should be reassessed.

**Discussion**

This study demonstrated that disease intervention prioritization is an effective strategy in endemic areas to preserve the largest, intermediately susceptible corals on the reef. Monthly monitoring and CoralCure disease interventions reduced tissue loss from SCTLD on *Orbicella faveolata* corals, potentially extending their lifespan by decades. Priority corals lost significant amounts of tissue before disease interventions began (2015-2018), and they lost significantly less tissue once monthly monitoring and disease interventions started (2018-2021) even though new lesions required treatments nearly every month. Without regular interventions, 66.7% (24/36) of the non-priority corals had <1% living tissue after 3 years. A similar decline in tissue might be expected of the priority corals, but frequent visitations caught disease lesions early and highly effective treatments halted progression, reducing the mean percent tissue loss by 52%. Suggesting that treatments were responsible for the reduction in priority coral tissue loss.

Disease interventions are a proactive response to SCTLD that saves existing coral genetic diversity, reducing the need for *post hoc* reef restoration (e.g. artificial reefs, outplanting corals, and assisted fertilization). Prior to disease intervention implementation (2015 to 2018), the priority corals lost a total of 26.8 $m^2$ of living tissue. Following intervention, tissue loss was drastically reduced, with colonies losing only 13.6 $m^2$. This represents more than a 50% decrease in tissue loss compared to the pre-intervention period. Assuming the colonies would have continued losing tissue at the previous rate without intervention, disease interventions saved 13.2 $m^2$ of coral tissue. Restoring the equivalent tissue area saved by disease intervention would require approximately 165,000 coral fragments (assuming a fragment size of 1 $cm^2$ and an 80% survival rate (Page et al., 2018)). Post hoc coral restoration is costly (Bayraktarov et al., 2019). This proactive response highlights the importance of disease intervention as a cost-effective strategy to conserve coral reefs, while post hoc restoration efforts can focus on replenishing species that disease interventions cannot save.

In the priority and non-priority coral groupings, some colonies displayed chronic disease lesions, while other colonies nearby seemed unaffected. Both disease exposure and host susceptibility are factors dictating why some individuals die of disease, while others remain healthy (Hawley & Altizer, 2011; Sheldon & Verhulst, 1996; Stewart Merrill et al., 2019, 2021; Sweeny & Albery, 2022). SCTLD transmission in the Florida Keys was deemed independent of coral density and the distance to a neighboring colony (Sharp et al., 2020), and the disease has since spread through the entirety of Florida's Coral Reef. While we cannot determine if disease exposure was consistent at all sites, we can assume that exposure was present (Dobbelaere et al., 2020). The fast and far pathogen spread suggests that susceptible corals have a weak defense mechanism against the causative agent (Dobbelaere et al., 2020). Factors contributing to varying disease resistance in colonies could be immune defenses, stress, genetics, or algal symbiont communities, and environmental conditions (Darling et al., 2012; Kelley et al., 2021; Klein et al., 2024; Palmer et al., 2010).

Corals possess innate immune mechanisms that provide the first line of internal defense and could contribute to their ability to resist disease (Palmer et al., 2008, 2010; Shnit-Orland & Kushmaro, 2009). In response to foreign organisms or physical injury, scleractinian corals can activate the melanin-synthesis pathway (Mydlarz et al., 2008; Palmer et al., 2008). Once activated, the deposition of encapsulating melanin (Bull, 1970) and highly cytotoxic intermediates (Nappi & Christensen, 2005) provide antimicrobial defense and wound healing. However, there are physiological costs involved with coral immunity. The evolution of a species' life history can cause trade-offs with investments in other life history traits, resulting in individualistic immunity levels (Rinkevich, 1996; Darling et al., 2012). There is mounting evidence implicating that SCTLD is a viral infection with a secondary bacterial infection (Beavers et al., 2023; Landsberg et al., 2020; Work et al., 2021). High bacterial growth is present in diseased colonies (Rosales et al., 2022), which could be caused by a weakened immune system (Palmer et al., 2010), potentially explaining why antibiotics are successful in halting a viral disease.

SCTLD lesions can quiesce without interventions, but this is species and colony dependent. Shilling et al., (2021) found that 40% of untreated *Montastraea cavernosa* corals halted SCTLD lesions after 46 weeks. Aeby (et al., 2019) found that 60% halted lesions after 52 weeks. While there are no specific studies on the natural quiescent rate of SCTLD in *O. faveolata* colonies, the percentage of non-priority corals that did not lose much tissue could be an indicator of natural

quiescence rates in *O. faveolata*. Between 2018-2021, 17% of the non-priority colonies lost minimal tissue (decline by 0-10%, but not reaching death). This could indicate that *O. faveolata* colonies have a lower natural quiescent rate compared to *M. cavernosa*, but more definitive studies would need to be done to know for sure. What is known, is it takes a long time for a coral colony to naturally quiesce a disease lesion, resulting in high tissue loss, which is apparent in the drastic tissue loss seen in the colonies before intervention began. Therefore, relying on a colony's natural ability to halt disease lesions is not practical, as they would lose too much tissue, making interventions a necessity.

One-time treatments on small *M. cavernosa* colonies can be effective at reducing the amount of tissue lost to SCTLD. Zummo (2024) found 94% survival and 2% disease prevalence in small *M. cavernosa* colonies receiving one-time treatments from one to four years prior. 19% of non-priority corals received one-time treatments in 2018, which may have reduced the rate of tissue loss from 2018 to 2021. However, due to the large size of the non-priority corals, and a difference of species, the rates of success between the study are distinct and may not apply to other species like *Orbicella faveolata*.

CoralCure treatments can fail, and even with regular, monthly treatments, 19% (8/42) of the priority corals lost between 8-20% living tissue area. This could be due to many factors such as user error, environmental factors such as high waves, or incorrect disease identification. During preparation of CoralCure, the amoxicillin becomes stuck together when initially mixed into the base. If not properly mixed, these clumps could alter the effectiveness of the release of amoxicillin at a steady rate uniform throughout the treatment, leaving gaps open for disease to cross the amoxicillin barrier (Walker et al., 2021). If a treatment was applied and wavy, surgy conditions follow, the disease treatment could be washed off the lesion, leaving the diseased coral untreated for the appropriate time (Walker et al., 2021). Despite divers' training in identifying coral diseases, some diseases are undistinguishable by the naked eye, posing risk of misidentification and improper disease treatment (Cróquer et al., 2021). Therefore, ongoing research is crucial to improve treatment efficacy, refine disease identification techniques, and develop strategies to mitigate the effects of environmental factors on CoralCure application.

There are many factors contributing to the steady decrease in coral living tissue area in southeast Florida, such as increased storm activity, continued declines in water quality, anchor damage, fishing damage, and increasing ocean temperatures (Jones & Gilliam, 2024). Our models

were used to create predictions of future coral tissue levels using the past decline of priority corals. This assumes linear future local and global human impacts, which may not be the case. Every increment of global warming will intensify climate change, making adverse impacts more frequent, severe, and widespread (Intergovernmental Panel on Climate Change, 2023). The oceans could continue to get warmer, ocean levels will continue to rise, and stressors from human actions could continue to increase (Intergovernmental Panel on Climate Change, 2023; van Hooidonk et al., 2016; Vermeer & Rahmstorf, 2009). Combined, these conditions could increase the chances of corals becoming bleached, diseased, and damaged by storms, and a lower coral recruitment rate, resulting in a less diverse and functional coral reef (Hoegh-Guldberg et al., 2007; Jones & Gilliam, 2024; Williams & Graham, 2019). Therefore, my predictive models are likely underestimating the decrease in coral tissue over years, which might decrease exponentially, like the non-priority corals, instead of linearly. For Florida's Coral Reef to have a functional future, it is essential to immediately mitigate environmental pressures to allow natural population recovery while these corals still exist, the small window of opportunity for a sustainable future is rapidly closing (Intergovernmental Panel on Climate Change, 2023).

Prioritization of corals with monthly monitoring and disease intervention is highly successful at reducing the amount of tissue lost to SCTLD and prolonging the lives of *O. faveolata* corals on Florida's Coral Reef. SCTLD is still very prevalent on the reef, with colonies getting new lesions and requiring treatments continuously (Toth et al., 2024). Monthly visits to 107 priority corals (of many species) have occurred since 2018, with a 100% survival rate and reduced tissue loss. This delayed the death of the few remaining corals to continue to contribute to spawning seasons and repopulation of the reefs with genetically diverse coral recruits. It is important to understand that disease interventions act as a technique to minimize the amount of coral tissue loss and colony morbidity due to SCTLD, but do not necessarily protect the coral from reinfection (Williams, 2013). Therefore, it is vital to continue to monitor priority corals monthly and perform CoralCure treatments. As SCTLD progresses through the reefs, management should prioritize large, susceptible, important corals for frequent, monthly disease interventions to save the most important corals on the reef. Finally, minimizing the anthropogenic stressors affecting the ocean is crucial, as there could be a time when disease interventions will no longer be effective.

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