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SHORT COMMUNICATION

Stony coral tissue loss disease (SCTLD) induced mass mortality at Arecibo, Puerto Rico

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Abstract

Stony coral tissue loss disease (SCTLD) is a highly contagious disease, causing mass coral mortalities in the Atlantic/Caribbean since 2014. In Puerto Rico, SCTLD was first reported in 2019 off the east coast, spreading to the north-central region by early February 2021. Benthic surveys were conducted at Cueva del Indio (CI) and Peñón de Mera (PM) off Arecibo to (1) quantify coral species-specific SCTLD prevalence using four $10 \times 1\text{-m}^2$ belt transects and (2) acquire time-series photo and video surveys to illustrate the impact of SCTLD, to evaluate coral species-specific susceptibilities, and estimate the timing of onset in Arecibo. A total of 650 corals in six species (*Pseudodiploria strigosa*, *P. clivosa*, *Montastraea cavernosa*, *Siderastrea siderea*, *Orbicella annularis*, *Porites astreoides*) were recorded inside the belt transects at both sites. SCTLD prevalence varied between 54% (*P. strigosa*) and 35.5% (*M. cavernosa*) at CI, and between 87.5% (*S. siderea*) and 25% (*O. faveolata*) at PM. Photo/video surveys revealed that SCTLD caused partial mortality in 11 species and full mortality in *P. strigosa*, *P. clivosa*, *S. siderea*, *M. cavernosa*, and *Dendrogyra cylindrus*. The results are discussed in view of prior research and contribute to understanding the spread and impact of SCTLD around Puerto Rico, which can be applied to predict its spread to other regions in the Caribbean.

Keywords Coral diseases · Biodiversity loss · Climate change · Caribbean corals · Marine protected area

Introduction

In 2014, coral reefs off Florida began experiencing yet another outbreak of an aggressive "white-type" (whitening syndrome) called stony coral tissue loss disease (SCTLD, hereafter). Since then, SCTLD has caused rapid, partial/total colony mortality in > 22 of the 45 coral species inhabiting the Florida Reef Tract (FRT, hereafter) (Precht et al. 2016; Walton et al. 2018; Aeby et al. 2019; Kramer et al. 2019). Overall, SCTLD has impacted > 30 species of corals in Florida and the northern Caribbean (Miller et al. 2006; AGRRA 2019; Kramer et al. 2019; Weil et al. 2019), similar to the white plague diseases (WPDs) of the early 2000s (Weil et al. 2009a, b; Weil and Rogers 2011; Cróquer et al. 2021; Morais et al. 2022). SCTLD is defined as focal, multifocal, locally extensive diffuse areas of acute to subacute tissue loss distributed basally, peripherally, or both (Meyer et al. 2019; Aeby et al. 2019). SCTLD was first observed in Virginia Key, FL, and within 1 year, it spread to southeast Florida near Miami, and by 2019, it has been documented from the northernmost reaches of the FRT in Martin County, down to Key West and in several other locations of the northern Caribbean, including Puerto Rico (Precht et al. 2016; Aeby et al. 2019; AGRRA 2019; Kramer et al. 2019; Meyer et al. 2019; Weil et al. 2019). The potential origin of SCTLD is associated with dredging and a thermal anomaly in Florida (Miller et al. 2016; Precht 2019; Dobbelaere et al. 2020a; Muller et al. 2020), but the connection between these events and the initial SCTLD outbreak in Florida have yet to be

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confirmed. The number of different coral species impacted, transmissibility, high prevalence, and incidence, with high mortality rates, indicate that SCTLD is a highly contagious and deadly disease, causing significant losses of live coral on every reef it infects (Weil et al. 2019; Cróquer et al. 2021; Alvarez-Filip et al. 2022).

SCTLD transmission is by direct contact, water currents, coral predators, and ship ballast water, which may explain the emergence of the SCTLD on coral reefs distant from Florida that do not follow prevailing ocean current patterns (Dobbelaere et al. 2020b; Dahlgren et al. 2021; Korein 2021). Within-reef scales, snails, fireworms, reef fish (Lucas et al. 2014; Aeby et al. 2019; Montano et al. 2022) and resuspended sediments are potential vectors of SCTLD (among other diseases) (Rosenau et al. 2021; Studivan et al. 2022). A study using 16S rRNA sequencing has shown that SCTLD is associated with a shift in the bacterial community of the host coral (Meyer et al. 2019) but the putative pathogen(s) have yet to be confirmed (Meyer et al. 2019; Muller et al. 2020). In contrast, research using transmission electron microscopy on healthy and SCTLD-infected corals indicated a possible viral disease of the algal symbionts (LaJeunesse et al. 2018) that lead to the host's death (Landsberg et al. 2020; Work et al. 2021). Coral tissues infected with SCTLD exhibit a breakdown of the host's cells and algal symbionts, rather than the bacterial communities associated with necrosis (Work et al. 2021). Additionally, biological and or chemical pollution cannot be ruled out as causative or antagonistic agents of SCTLD's severity. SCTLD has been documented in most of northern Caribbean countries, from the eastern Caribbean to Belize and Honduras (AGRRA 2019; Kramer et al. 2019). SCTLD was first observed in Puerto Rico's waters off the west coast of Culebra in November (2019) and has since moved westward along the northern and southern coasts (Kramer et al. 2019; Weil et al. 2019; Korein 2021). A few reports indicate SCTLD has been observed off Aruba, Bonaire, and Curaçao (see maps at AGRRA 2019; Kramer et al. 2019) but these accounts of SCTLD in the southern Caribbean need to be confirmed (Kramer et al. 2022).

Around Puerto Rico, the most extensive coral communities exist off the northeast and southwest coasts (Ballantine et al. 2008). In contrast, the northern coast of Puerto Rico's hard bottom coral communities are not as developed due to the narrow shelf-edge and high wave energy (Ballantine et al. 2008). Nonetheless, substantial nearshore coral communities occur off Hatillo, Arecibo, and Manati. Some are mono-specific, such as *Acropora palmata* reefs, while others are dominated by a few very abundant species, such as *Pseudodiploria strigosa*, *P. clivosa*, *Montastraea. cavernosa*, *Orbicella faveolata*, *O. annularis*, and *Porites* spp. Other coral species occurring off north-central Puerto Rico include *Dendrogyra cylindrus*, *Siderastrea siderea*, and to a much lesser extent, *Acropora cervicornis*. Despite these coral communities being less extensive, they serve as important habitat for a diverse range of keystone species and commercially important marine organisms. Although their close proximity to residential and commercial areas, land-based sources of pollution undoubtedly threaten the health of these coral communities. Other threats observed include coral diseases (WPD, black band disease (BBD), white band disease (WBD), dark spots disease (DSD)), and predation by snails and fireworms (personal observation, ML). The occurrence of coral diseases have been observed at seemingly low prevalence, but little is known historically about disease dynamics or bleaching events among the coral communities off the north-central coast of Puerto Rico. Numerous corals were first reported with SCTLD symptoms (personal observation, Miguel Mercado) at Cueva del Indio, a Marine Protected Area, off Arecibo in April 2021.

Because defining coral species-specific SCTLD susceptibility and transmission patterns are important for understanding the spread, ecological consequences, and management of SCTLD (Brandt and McManus 2009; Meiling et al. 2020; Costa et al. 2021; Korein 2021; Korein et al. 2023), the objectives of this study were to (1) quantify coral species-specific and coral community SCTLD prevalence and (2) study the spread and impact of SCTLD at Cueva del Indio (CI) and Peñón de Mera (PM), two coral communities off the coast of Arecibo. The collective goal of this study was to evaluate coral species-specific susceptibility patterns, estimate the potential onset of SCTLD in the Arecibo area, and assess the overall impact of SCTLD. The results are discussed in view of prior research and contribute to understanding the spread and geographic impact of SCTLD on coral communities around Puerto Rico.

Material and methods

Benthic assessments (belt transects) were first conducted on May 30, 2021, at CI (~ 18°29′35.53″ N, 66°38′34.42″ W) and on June 29, 2021 at PM (~ 18°29′19.37″ N, 66°40′37.91″ W) off Arecibo (Fig. S1). The area studied at PM (~ 5 m depth) is located on the backreef of the lagoon whereas the transect area studied at CI (~ 10 m depth) is located on the forereef (Fig. S1). To quantify SCTLD prevalence (proportion of infected colonies in the population) among coral species, data was recorded in situ by swimming four, randomly stratified 10×1 m^2 belt transects (Raymundo et al. 2008; Randall and van Woesik 2015; Jordán-Dahlgren et al. 2018), each separated by ~ 10 m, and counting the number of coral colonies for each species with SCTLD signs (white, tissue-devoid areas, tissue sloughing) and the number of healthy colonies (no SCTLD signs). Most SCTLD infected colonies had characteristic signs; however, given the similarity with WPD, it is possible that a few colonies were infected with

WPD (Cróquer et al. 2021). No statistical analyses were performed due to the small number of transects per treatment (survey dates, different habitats and depths, coral species composition between sites). Instead, prevalence data from each site was pooled for descriptive comparisons and plotted (XLStat 2007). Separate photo and video surveys at both sites were acquired using a Nikon W300. Photos and videos were analyzed on-screen to evaluate the potential onset of SCTLD and to illustrate the impact of SCTLD on Arecibo's coral communities.

Results

At the two study sites, a total of 650 coral colonies across six coral species were recorded inside the belt transects, together covering 160 m^2 of reef area (Table 1). A total of 263 coral colonies were recorded at CI, *P. strigosa* showed the highest disease prevalence (54%, $n=189$), *M. cavernosa* the lowest (35.5%), and *P. astreoides* had no infected colonies ($n=42$) (Table 1; Fig. 1). *Pseudodiploria clivosa* and *O. faveolata* were not observed in the transects at CI. At PM, 387 colonies were recorded, with *S. siderea* showing

Table 1 Coral species-specific SCTLD prevalence (%) at each site (four pooled transects), the number of colonies presenting SCTLD symptoms (+), the number of healthy colonies per species, total colonies per species, depth, and transect survey dates

Coral species	SCTLD (+) colonies	Healthy colonies	Total colonies	SCTLD prevalence (%)	Depth (m)	Transect survey dates
Cueva del Indio (CI), Arecibo						
Pseudodiploria strigosa	102	87	189	54.0%	10	30 May 2021
Montastraea cavernosa	11	20	31	35.5%	10	30 May 2021
Porites astreoides	0	42	42	0.0%	10	30 May 2021
Siderastrea siderea	0	1	1	0.0%	10	30 May 2021
Pseudodiploria clivosa	0	0	0	0.0%	10	30 May 2021
Orbicella faveolata	0	0	0	0.0%	10	30 May 2021
Peñón de Mera (PM), Arecibo						
Siderastrea siderea	7	1	8	87.5%	5	29 June 2021
Montastraea cavernosa	14	13	27	51.9%	5	29 June 2021
Pseudodiploria strigosa	127	134	261	48.7%	5	29 June 2021
Pseudodiploria clivosa	4	6	10	40.0%	5	29 June 2021
Orbicella faveolata	1	3	4	25.0%	5	29 June 2021
Porites astreoides	0	77	77	0.0%	5	29 June 2021

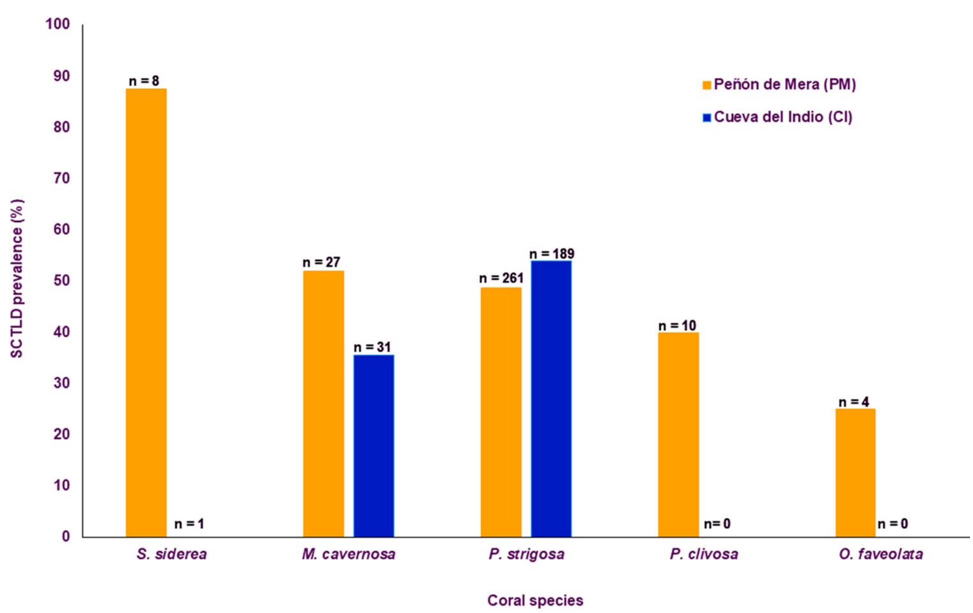

Fig. 1 SCTLD prevalence (%) in five of the most severely impacted coral species at (PM) Peñón de Mera (orange) and (CI) Cueva del Indio (blue) in 2021. $n=$ the total number of colonies of each species recorded in the band transects

the highest SCTLD prevalence (87.5%, $n=8$), *O. faveolata* the lowest (25%, $n=4$), and all *P. astreoides* were healthy (Table 1; Fig. 1). The impact of SCTLD in respect to tissue loss in four coral species is illustrated in Fig. 2. Similar impacts were observed in 11 coral species monitored at both sites (Fig. S2). Other coral species (*A. cervicornis*, *A. palmata*, *Agaricia* spp., *Madracis auretenra*, *M. decactis*, *P. porites*, and *P. astreoides*) did *not* present SCTLD signs at the time of these surveys. *Acropora palmata* colonies had small white patches of possibly white pox. At the end of 2021 field season (October 2021), numerous colonies *P. strigosa*, *P. clivosa*, *D. cylindrus*, *S. siderea*, and *M.*

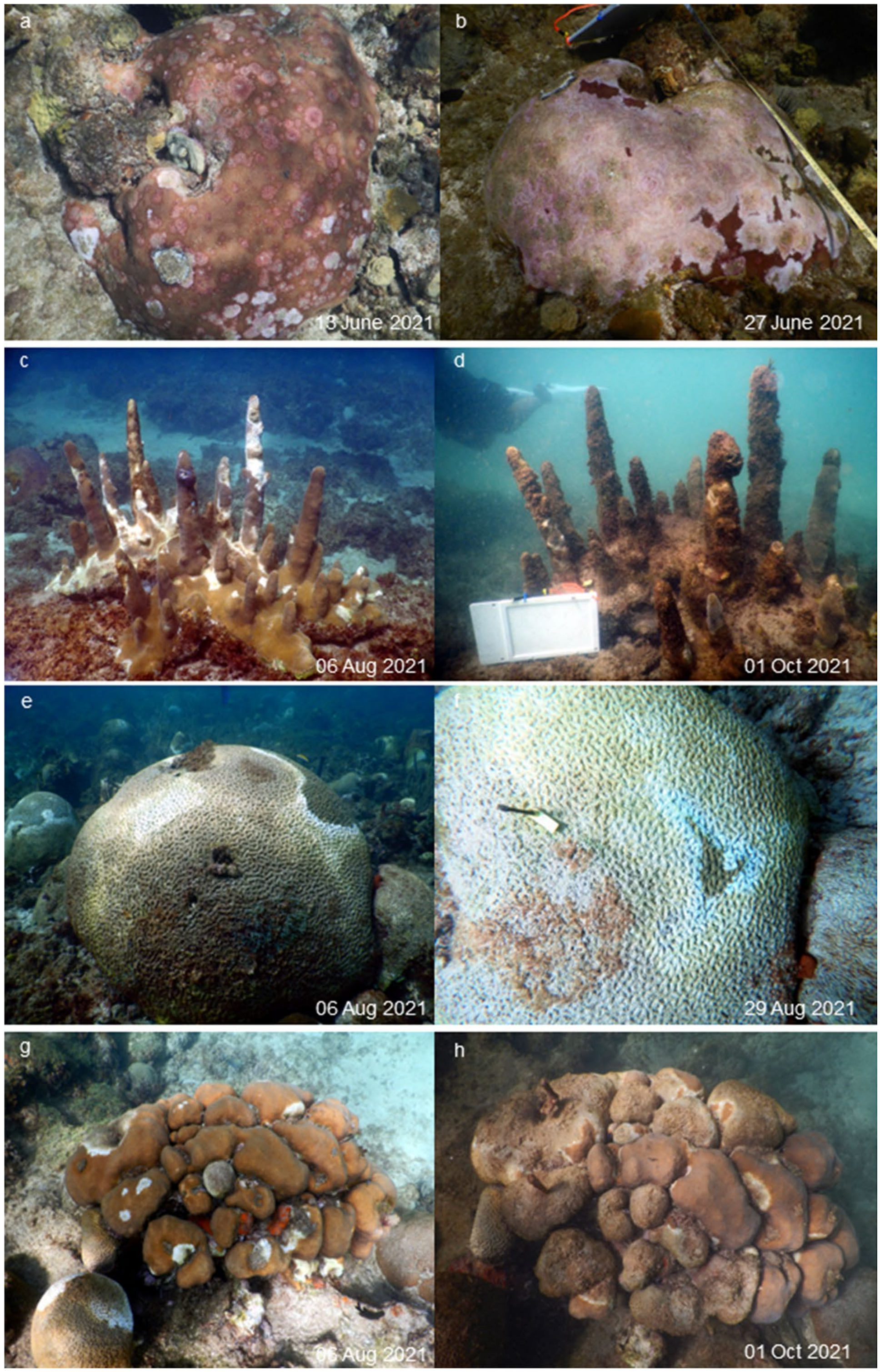

Fig. 2 Time-series photos (left to right) of four coral species presenting various levels of tissue-loss; **a**, **b** A colony of *S. siderea* was near full colony mortality in 15 days after SCTLD infection (CI); **c**, **d** A colony of *D. cylindrus* reached near full colony mortality in 57 days (~8 weeks) (PM); **e**, **f** A colony of *C. natans* was near full colony mortality at the first observation and died a few weeks later (PM); **e**, **f** A colony of *O. annularis* showing slower, but near full colony mortality (~2 months) (PM)

cavernosa from offshore to nearshore suffered near to full colony mortality at PM (Fig. S2; Fig. S3) and CI (Fig. S2; Fig. S4). By April 2022, SCTLD had spread and infected the coral community near the municipality of Hatillo, Puerto Rico (Fig. S5).

Discussion

This study combined coral species-specific SCTLD prevalence data and photo/video surveys to identify species susceptibility patterns, estimate the onset of SCTLD, and illustrate the overall impacts of SCTLD on the coral communities at Cueva del Indio and Peñón de Mera off the coast of Arecibo in 2021. Overall, we report 11 coral species impacted and SCTLD induced mass mortality in five coral species. Given the coral lesions observed in May 2021, we estimate that SCTLD arrived in Arecibo in early February to March 2021.

SCTLD prevalence data indicated that five coral species are most susceptible to SCTLD at the two sites (Table 1; Fig. 1). Although because of low sampling (only four transects per site), it is uncertain that coral species-specific SCTLD prevalence represented the entire coral community at either site. While we did not measure colony size or SCTLD progression (virulence = tissue loss rates) but observed different-sized coral colonies presenting variable levels of impact ranging from little to intermediate tissue loss, to near or full colony mortality (Fig. 2a–f; Fig. S2–S4). Because in highly SCTLD susceptible coral species, full mortality ranges from 1 week for smaller coral colonies to full mortality in 1–2 months for larger coral colonies (> 1 m), given the observed coral lesions at the time of our first observation (late April 2021 at Cueva del Indio), we estimate that SCTLD arrived on Arecibo's coral communities sometime between late February to mid-March 2021. By the end of the 2021 field season (October 2021) SCTLD had moved into shallow waters at both sites and 11 coral species were severely impacted (high prevalence, see Fig. 1) and where mass coral mortalities occurred from offshore to nearshore, and across depths (Fig. 2; Fig. S2–S4).

The coral species-specific SCTLD susceptibility patterns observed in this study are consistent with those in Florida (Precht et al. 2016; Aeby et al. 2019, 2021; Sharp et al. 2020), NE Brazil (Morais and Santos 2022), Mexico (Randazzo-Eisemann et al. 2022), and other localities in Puerto Rico (Weil et al. 2019). We observed highly susceptible coral species *P. trigosa*, *P. clivosa*, *D. cylindrus*, *D. stokesii*, and *D. labyrinthiformis* experiencing partial to full mortality throughout the study (Figs. 1 and 2; Figs. S2–S4). These coral species are the first to show rapid tissue loss and, in some colonies, full mortality due to SCTLD (Precht et al. 2016; NOAA 2018; Aeby et al. 2019, 2021; Meiling et al. 2020; Sharp et al. 2020). *Siderastrea siderea* and *M. cavernosa* are considered as intermediately susceptible to SCTLD (NOAA 2018). In the case of *S. siderea*, it often shows distinct disease signs, which produces confusion, and they show up before signs in other highly susceptible coral species, during and after a SCTLD outbreak has progressed through a coral community (NOAA 2018; Sharp et al. 2020; Cróquer et al. 2021; Morais et al. 2022). Furthermore, our observations revealed concurrent multiple infections in *S. siderea* populations (BBD, DSD, and SCTLD); however, after the onset of SCTLD, rapid tissue loss was followed by near full colony mortality in only a few weeks (Fig. 2a, b). A study in the Florida Keys monitored SCTLD prevalence in *P. strigosa* and *S. siderea* on nearshore and offshore reefs and found higher SCTLD prevalence in offshore colonies versus nearshore colonies (Sharp et al. 2020). Initially, our observations showed a similar nearshore–offshore pattern, with higher SCTLD prevalence in offshore versus nearshore colonies of *P. strigosa*, *P. clivosa*, and *M cavernosa* (13 June 2021; Figs. S2–S4); however, *S. siderea* seemed equally impacted across the nearshore–offshore gradient, and many colonies suffered full mortality (Fig. 1a, b; Figs. S2–S4). This result is also consistent with Sharp et al. (2020) who found differential SCTLD prevalence between the offshore and nearshore coral communities.

The species *M. cavernosa* has also been identified as an intermediately susceptible species in Florida (Shilling et al. 2021) and highly susceptible in Puerto Rico (Weil et al. 2019; Korein 2021). Our results are similar and *M. cavernosa* showed high susceptibility and near or full mortality in numerous colonies at both sites (Fig. 1; Fig. S2). Morais and Santos (2022) compared prevalence, the extent of bleaching, and diseases in *Siderastrea stellata* and *M. cavernosa* in shallow and at mesophotic depths and found high prevalence in *S. stellata* (75%) regardless of depth, but the colony area impacted was about two times greater in mesophotic than shallow reefs (14.4%) vs. (6.6%), respectively. While these authors were unable to compare *M. cavernosa* between shallow and mesophotic depths, *M. cavernosa* had lower prevalence than *S. stellata* at mesophotic depths. Incidentally, *M. cavernosa* consists of two ecomorphs that co-occur, but have differential depth distributions (Ruiz 2004; Budd et al. 2012). As a result, the reported geographic variation in SCTLD susceptibility (or resistance) (Korein 2021; Shilling et al. 2021; Korein et al. 2023) could be related to genotypic differences between *M. cavernosa* ecomorphs. Similar to other reports, our results indicate that *O. faveolata* is "intermediately" susceptible to SCTLD, but *O. faveolata* seems to be slightly more resistant than *O. annularis* (Fig. 1g, h; Figs. S2–S4).

SCTLD is one of the most devastating coral diseases on record and is rapidly decimating coral reefs across the northern Caribbean causing coral mass mortalities which significantly reduce live coral cover and species abundances, resulting in benthic community shifts, commonly to algae dominated assemblages (Alvarez-Filip et al. 2019; Estrada-Saldívar et al. 2021; Alvarez-Filip et al. 2022; Morais et al. 2022; Randazzo-Eisemann et al. 2022). Because of SCTLD, and the high potential for the emergence of more virulent coral diseases in the future, there is imminent need to take actions that rescue and protect genetic diversity as well as discover resistant genotypes that could aid in the adaptive capacity and resilience of foundational coral species.

Results of this short study, albeit lacking spatial and temporal observations, are particularly concerning because the coral communities off north-central Puerto Rico are not spatially extensive, have low density populations of a reduced number of species with presumably low genetic variability, and are also negatively impacted by human activities, storms, and thermal anomalies (Walton et al. 2018; Baums et al. 2019; Costa et al. 2021). Thus, these coral communities are perhaps highly susceptible to the emergence of new coral diseases and the impacts of thermally induced bleaching, which makes future recovery difficult and slow. Some mitigation protocols to reduce the impact of SCTLD on coral communities have been tested (Korein 2021; Neely et al. 2021; Walker et al. 2021; Korein et al. 2023). The most common is the use of a wide spectrum antibiotic paste that is applied to the edge of the lesion, which has some recognized caveats at different scales (*reviewed in* Kraemer et al. 2019; Weber et al. 2019; Neely et al. 2021; Shilling et al. 2021; Walker et al. 2021; Zheng et al. 2021; Connelly et al. 2022). Novel SCTLD treatments that use "human skin wound" treatment materials have been successfully used to cure coral lesions (Contardi et al. 2020) and a probiotic treatment has also recently shown promising results in treating SCTLD (Ushijima et al. 2023).

Continuing work should focus on the identity and origin of the SCTLD pathogen(s) to implement management strategies that mitigate and prevent SCTLD and other disease outbreaks. Coral restoration programs should focus on propagating surviving corals (SCTLD-resistant genotypes) in parallel with holistic and assisted evolutionary approaches that aim to increase survivorship of genetically diverse and more resilient corals to be outplanted to degraded reefs.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12526-023-01393-6.

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Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval No animal testing was performed during this study.

Sampling and field studies The study does not contain sampling material or data from field studies.

Data availability Data, photo, and video files are available without reservation: mlucas@arecibo.inter.edu.

Author contributions ML and EW drafted the report. All authors contributed by helping in the field, data collection, and reviewed the manuscript. Photo/video credits: ML and DCR.

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