Gulf and Caribbean Research

Volume 33 | Issue 1

2022

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## Recommended Citation

Croquer, A., S. Zambrano, S. King, A. Reyes, R. Sellares-Blanco, A. Valdez Trinidad, M. Villalpando, Y. Rodriguez-Jerez, E. Vargas, C. Cortes-Useche, M. Blanco, J. Calle-Trevino, R. García-Camps, A. Hernández-Orquet, R. Torres, I. Irazabal, L. Díaz, Y. Evangelista and E. Miyazawa. 2022. Stony Coral Tissue Loss Disease and Other Diseases Affect Adults and Recruits of Major Reef Builders at Different Spatial Scales in the Dominican Republic. Gulf and Caribbean Research 33 (1): GCFI1-GCFI13.
Retrieved from https://aquila.usm.edu/gcr/vol33/iss1/3
DOI: https://doi.org/10.18785/gcr.3301.03

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# GULF AND CARIBBEAN

# RESEARCH

Volume 33
2022
ISSN: 2572-1410

*Published by*

THE UNIVERSITY OF
SOUTHERN MISSISSIPPI

GULF COAST RESEARCH LABORATORY
Ocean Springs, Mississippi

Gulf and Caribbean Research Vol 33, GCFI 1-GCFI 13, 2022
DOI: 10.18785/gcr.3301.03
Manuscript received, December 21, 2021; accepted, April 12, 2022

GULF AND CARIBBEAN FISHERIES INSTITUTE PARTNERSHIP

# STONY CORAL TISSUE LOSS DISEASE AND OTHER DISEASES AFFECT ADULTS AND RECRUITS OF MAJOR REEF BUILDERS AT DIFFERENT SPATIAL SCALES IN THE DOMINICAN REPUBLIC§

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**Abstract:** Monitoring programs can help understand coral disease dynamics. Here, we present results from a national program in the Dominican Republic (DR) aimed at evaluating coral diseases 3 times a year following a nested spatial design. Prevalence of coral diseases in DR varied from sites to regions, suggesting that disease dynamics can be driven by local processes and/or across larger spatial scales. Three diseases were common: Dark Spot (DSD), Yellow Band (YBD) and Stony Coral Tissue Loss Disease (SCTLD). DSD and YBD were more prevalent across the western coast (north and south), whereas SCTLD was restricted for the study period to the northern coast. SCTLD has become endemic in the northwestern coast, epizootic in the northeastern, and absent in other sites across DR. SCTLD prevalence in the northwest was below 10% across sites, whereas in the northeast it varied from 2.13 ± 3.69% (mean ± sd) to 38.7 ± 13.55% in Galeras and from 1.9 ± 0.99% to 38.5 ± 19.8% in Samaná. Over 10 coral species were affected by SCTLD in DR, with *Pseudodiploria* spp, *Dendrogyra cylindrus, Eusmilia fastigiata, Siderastrea siderea, Montastraea cavernosa* and *Meandrina* spp, being the most susceptible. We observed SCTLD affecting recruits and juvenile corals with 5% prevalence on average. Furthermore, we observed *Oreaster reticulatus* climbing on 1% healthy and 27% SCTLD *P. strigosa* colonies in Samaná. We conclude that SCTLD is a serious problem in DR, producing rapid loss of coral cover of major reef builders that are locally used for propagation efforts. This monitoring plan will provide future insights to design more effective disease responses.

**Key words:** Coral diseases, SCTLD, prevalence, *Oreaster reticulatus*.

## Introduction

During the past 4 decades, different coral diseases have been reducing coral cover as they destroyed major reef–building coral populations across the Caribbean (Weil et al. 2006, Miller and Richardson 2015, Walton et al. 2018). Among other coral pathologies, Stony Coral Tissue Loss Disease (SCTLD) is an emergent coral disease that has produced devastating impacts on coral populations in Florida (Precht et al. 2016) and across the central, western, and eastern Caribbean Region (Croquer et al. 2021). The disease was first reported in 2014 in the Florida Keys, and in less than 7 years it had spread throughout the Caribbean region, particularly along the Florida Reef Track, Mexico, Mesoamerica, and the Greater Antilles (Aeby et al. 2019).

For decades, the identification of coral diseases has been focused on the description of macroscopic signs while often omitting proper case definitions based on veterinary framework and assuming that every observed sign is produced by infectious agents (Croquer et al. 2021). This approach has often led to confusion and problems in accurately identify coral diseases. For example, rapid loss diseases such as White Plague Disease I and II (WPDs) and SCTLD can be easily confused in the field as they produce similar gross signs (Croquer et al. 2021). However, the occurrence of an invasion, outbreak and endemic phases of SCTLD seem to differ from previous epizootic events produced by other diseases reported for the region (Lang 2021). Thus, continuous monitoring programs are an

*§This article is based on a presentation given in November 2021 at the virtual 74rd meeting of the Gulf and Caribbean Fisheries Institute.*

extremely important diagnostic tool to discern among diseases such as SCTLD and other rapid loss diseases (Croquer et al. 2021).

Information on coral disease prevalence in the Dominican Republic (DR) is limited. Coral diseases are mentioned in the last national report published by Reef Check in 2019 (Steneck and Torres 2019). However, diseases were not included, described, or listed in the most comprehensive review about the status of coral reefs in DR (Geraldes 2003). Irazabal and Rodriguez (2019) first reported a coral disease epizootic event in the DR, and described extensive mortality on corals affected by SCTLD in Cayo Arena, Punta Rucia. There are ongoing coral restoration efforts in the DR (Bayraktarov et al. 2020), but the paucity of information about coral disease epizootiology and the associated impact on reefs can affect decisions regarding coral reef restoration.

In 2020, The Nature Conservancy (TNC) and the Dominican Coral Network (RAD in Spanish) started to organize a series of virtual workshops to identify local stakeholders interested in determining the status of coral diseases in the DR and explore interest in participating in a national and inclusive monitoring program. During the initial phase, consultation and engagement with different NGOs (i.e., FUNDEMAR, CEBSE, Reef Check and TNC), governmental offices (The Ministry of Environment), academic institutions (CIBIMA IBC–UASD) and the private sector (Propagas Foundation, FGPC, FCC and Iberostar) was coordinated by RAD. Once engaged, a monitoring protocol was proposed, and a series of training sessions on coral disease identification were conducted virtually due to the Covid–19 pandemic. From this consultative and participative process, a coral disease action plan was published (TNC 2020) and the program officially started to collect data in 2021. In this paper, we introduce the structure and rationale of our coral disease monitoring program and present results from 2 initial coral disease surveys (March/May and June/August) completed in 2021 across the DR. We tested for spatial patterns on coral disease prevalence, whether these patterns were consistent among sampling periods and, finally, if species composition at each site explained these patterns. Furthermore, we present new observations in areas where SCTLD has become endemic and/or is at the outbreak phase.

## Material and Methods

### Study area

Surveys were conducted across the southern, eastern, and northern coasts of the DR, where reefs are well–developed (Figure 1). In the DR, the vast majority of reef habitats are found along the coastline (Geraldes 2003, Cróquer et al. 2021), as confirmed by recent mapping of reef habitats (Schill 2021). Major types of reefs include barrier, fringing and reef patches of different sizes with coral cover ranging from 5–22% on average (Geraldes 2003, Steneck and Torres 2019). Major reef builders include massive species such as *Orbicella* spp., *Colpophyllia natans*, branching species such as *Porites porites*, *Acropora cervicornis* and *A. palmata*, and foliose species such as *Agaricia* spp. among others (Geraldes 2003, Steneck and Torres 2018, 2019, Cortes–Useche et al. 2018). Higher diversity of corals is reported at depths from 5–15 m (Geraldes 2003, Cortes–Useche et al. 2018), although deeper reefs have not been formally described.

### Sampling design and coral disease surveys

We used a nested hierarchical design to test for spatial variation in the prevalence of coral disease and other conditions in

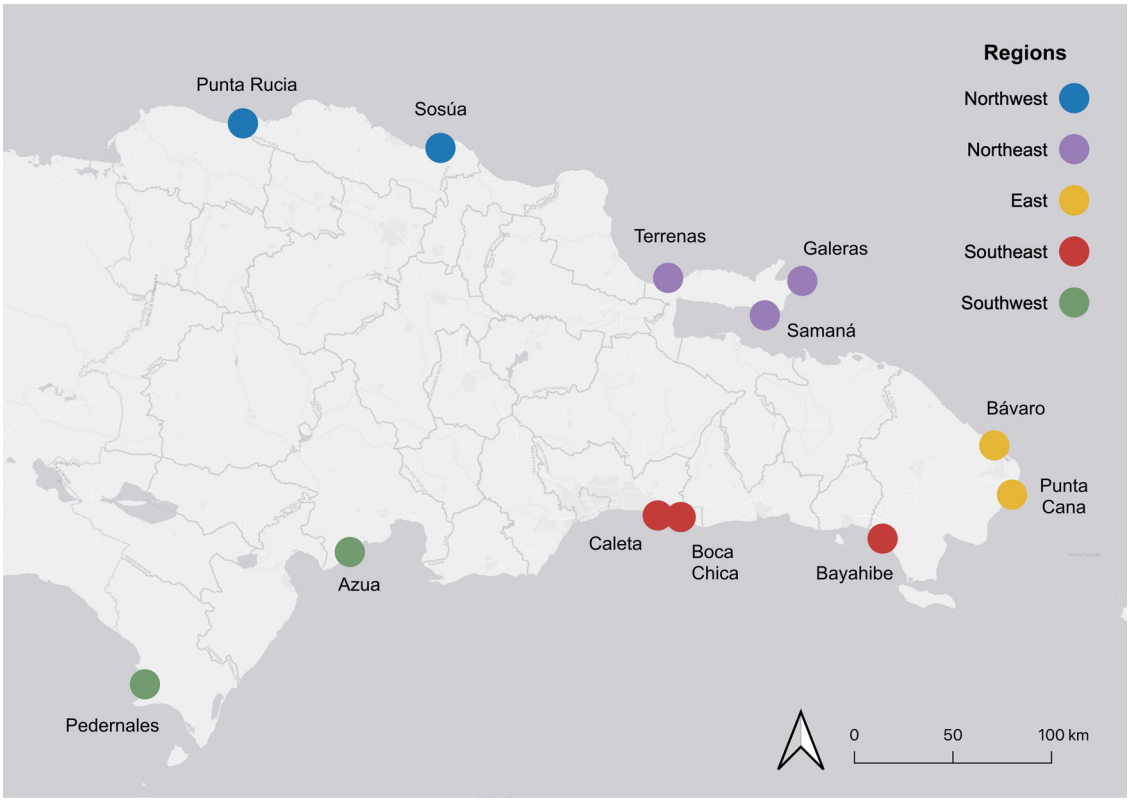


***FIGURE 1.*** *Geographic location of the 5 regions sampled across the Dominican Republic, with the localities within each region identified. Within each locality, 5–10 reef sites were sampled. Sites are listed in Table 1.*

3 reef sites (i.e., 100's of m), within 1–3 localities (10's of km), and within 5 subregions (100—1000's of km) across the DR. At each site, three 10 m—long x 2 m—wide belt transects (20 $m^2$) were haphazardly set onto the reef at 5–15 m depth for a total of 114 transects surveyed. The number of transects was set by considering the maximum sampling effort achievable at each site based on time constrains and logistics. The length and width of the transects were established following the recommendations provided by Jordán—Dahlgren et al. (2018). Within each belt transect, all hard corals (adults and juveniles < 2—4 cm in diameter) were identified to species level and their condition (healthy, diseased, bleached, paled, or predated) was annotated. For adult colonies, the belt transect was first surveyed at around 1 m above the substrate and for juveniles and recruits, the same observer surveyed the belt transect 20 cm above the substrate after the census for adult corals was completed. Each disease was identified from lesion gross morphology following the procedure outlined by Work and Aeby (2006) and using the field identification guide by Weil and Hooten (2008). The identification of SCTLD was guided by epizootiological criteria outlined by Aeby et al. (2020), AGRRA resources (AGRRA 2020), and Croquer et al. (2021). The first surveys began in March/May and were then repeated during June/August 2021. While depth has been reported as an important variable to determine change in coral disease prevalence across the Caribbean (Croquer and Weil 2009, Weil and Croquer 2009) we did not include this variable in our analysis for 2 reasons: 1) the aim is to report the status of diseases across spatial scales, and 2) our data only summarizes spatial trends from the first year in a Caribbean country where information on coral diseases is scarce; therefore, the data represents a baseline. As the program progresses and we expand our time series, a formal multivariate analysis including depth, other environmental—habitat as well as human—driven variables that could explain spatial and temporal variation of disease prevalence will be performed.

**Data analysis**

A rectangular matrix was constructed containing sites, localities, and subregions as rows (samples) and coral diseases/health conditions as columns (variables), with each cell representing the number of colonies recorded at each transect with a particular condition. The data was standardized by maximum number of colonies recorded for each column (disease/condition) to avoid more common diseases to drive the ordination and permutation analyses. Furthermore, by using this approach we avoided potential inaccuracies in the estimation of disease prevalence as not all species are equally common and therefore rare species or species seldom affected by coral diseases did not artificially decrease or increase disease prevalence. A nested permutation analysis of variance was performed from a Bray—Curtis similarity matrix. Three hierarchical factors were included in the analysis (i.e., sites, localities, and regions). We used untransformed data to determine the percentage of variance in the prevalence of different diseases and conditions explained by each spatial scale, since the data was previously standardized, with values ranging from 0 to 100%. Coral colonies that were disease free and coral species that were absent were represented as 0 in the analysis. To avoid confounding spatial and temporal patterns, we conducted 2 separate analyses: one in March/May and another in June/August because of the lack of temporal replication. Thus, we tested if spatial patterns of coral disease prevalence were consistent for these 2 sampling periods.

A non—metric multidimensional scaling (NMDS) based on a fourth root—transformed Bray—Curtis similarity matrix was performed to visualize patterns in the abundance of healthy corals across sites within regions. A test of similarity profiles (SIMPROF) was conducted to test if species composition across sites was homogenous. We then tested if the coral species composition of each site explained the patterns of prevalence for each disease. For this, from a list of 42 coral species, we screened the species that better explained the patterns of coral disease occurrence with the BEST tests (Clarke and Gorley 2006, Clarke et al. 2008). The selection of the most parsimonious BEST models were established by examining 1) the number of species added into the model, and 2) how much a new species addition improved the correlation between the coral disease and the coral species matrix. We therefore chose the model that maximized the correlation with the least number of variables included. We then ran a distance—based linear model (DistLM) using the abundance of a reduced list of coral species as predictor variables of prevalence for all coral diseases and conditions recorded across our sites. All analyses were performed with Primer + Permanova V6 (Anderson and Gorley 2008). Spatial patterns of coral disease occurrence recorded in March/May and June/August were represented in bubble charts designed in R using the package ggplot 2 (Wickham 2011).

## Results

**Spatial patterns in coral disease prevalence**

Coral disease prevalence in the DR was variable, ranging from <1% to 39% across sites (100's of m), localities (10's of km) and regions (100—1,000's of km; Table 1). Disease prevalence was significant at the scale of sites and localities in March/May, and across all spatial scales in June/August (Table 2). The factors regions, localities and sites combined explained about 80 and 75% of the total variance of coral disease prevalence in March/May and June/August, respectively (Table 2). Moreover, 20–24% of this variance is associated with the residual, further indicating large variability of coral disease prevalence between transects belonging to each site.

Out of many diseases reported in the Caribbean, only 3 are common in the DR: Dark Spot (DSD), Yellow Band (YBD), and SCTLD. We found different distributions of these coral diseases; DSD and YBD were more prevalent across the western coast of DR (north and south) whereas SCTLD is restricted to the northern coast of the island (Figure 2A). However, in northwestern reefs, the disease has become rare, seldom exceeding 10% of prevalence in areas such as Sosua where signs

***TABLE 1.*** *Mean (± sd) prevalence of coral diseases recorded across sites, localities, and sub regions during March–May (trimester 1) and June–August (trimester 2) in the Dominican Republic. See Figure 1 for regions and localities. Locality abbreviations: BAV–Bávaro; PTC–Punta Cana; GAL–Galeras; SAM–Samaná; TERR–Terrenas; PRU–Punta Rucia; SOSU–Sosúa; BYH–Bayahibe; BCH–Boca Chica; CALE–Caleta; AZU–Azua; PED–Pedernales. Disease abbreviations: BBD–black band disease; SCTLD–stony coral tissue loss disease; WPD–white plague I and II disease; YBD–yellow band disease; Other–other conditions; BL–bleaching; PL–pale; PRED–predation; DC–dead coral colonies.*

| Region | Locality | Site | Trimester | Healthy Mean ± sd | BBD Mean ± sd | DSD Mean ± sd | SCTLD Mean ± sd | WPD Mean ± sd | YBD Mean ± sd | OTH Mean ± sd | BL Mean ± sd | PL Mean ± sd | PRED Mean ± sd | DC Mean ± sd |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| East | BAV | Batato | 1 | 100.00 | | | | | | | | | | |
| | | Batato | 2 | 100.00 | | | | | | | | | | |
| | | Coco Loco | 1 | 97.93 ± 2.45 | | | | 2.39 ± 2.84 | 0.53 ± 1.42 | | | | | |
| | | Coco Loco | 2 | 1.00 | | | | | | | | | | |
| | | Coral Garden | 1 | 1.00 | | | | | | | | | | |
| | | Coral Garden | 2 | 98.99 ± 1.75 | | | | | | | 1.11 ± 1.75 | | | |
| PTC | | PC1 | 1 | 88.89± 1.92 | | 2.83 ± 5.13 | | | | 1.42 ± 1.2 | | 5.56 ± 8.67 | 3.47 ± 5.54 | |
| | | PC1 | 2 | 93.67 ± 6.87 | 0.53 ± 1.28 | 1.42 ± 2.55 | | | | | | 0.53 ± 1.28 | 3.22 ± 3.56 | |
| | | PC2 | 1 | 92.77 ± 2.89 | | | | | 0.13 ± 0.33 | | 0.25 ± 0.64 | 2.44 ± 2.69 | 4.43 ± 2.63 | |
| | | PC2 | 2 | 9.17 ± 4.68 | | | | 0.44 ± 1.74 | 0.67 ± 1.63 | 0.47 ± 0.20 | 0.25 ± 0.64 | 0.68 ± 1.12 | 7.83 ± 4.89 | |
| | | PC3 | 1 | 9.64 ± 5.86 | | | | | | | 0.23 ± 0.57 | 5.24 ± 6.96 | 4.54 ± 4.30 | |
| | | PC3 | 2 | 91.39 ± 4.95 | 0.11 ± 0.27 | 0.43 ± 0.64 | | | | | 0.17 ± 0.43 | 1.33 ± 2.12 | 6.65 ± 3.51 | |
| Northeast | GAL | Carriles 1 | 1 | 75.75 ± 11.57 | | 0.56 ± 0.87 | 22.77 ± 1.48 | | 0.48 ± 0.82 | 0.5 | 0.56 ± 0.87 | | | |
| | | Carriles 1 | 2 | 73.13 ± 2.56 | | | 2.13 ± 3.69 | | | | | 12.78 ± 17.98 | | 11.97 ± 6.74 |
| | | Carriles 2 | 1 | 64.54 ± 11.66 | | 0.63 ± 1.89 | 34.69 ± 13.55 | | 0.63 ± 1.89 | 0.72 ± 0.80 | | | | |
| | | Carriles 2 | 2 | 81.48 ± 6.15 | | 0.72 ± 1.26 | 5.14 ± 3.80 | | | | 1.11 ± 1.92 | 4.62 ± 4.66 | | 6.27 ± 2.72 |
| | | Fronton 1 | 1 | 71.43 ± 6.99 | | 9.78 ± 13.36 | 18.79 ± 8.86 | | | | | | | |
| | | Fronton 1 | 2 | 7.74 ± 6.12 | | 6.22 ± 3.83 | 19.67 ± 5.47 | | | | | | | 3.57 ± 3.16 |
| | SAM | Carenero | 1 | 98.46 ± 2.88 | | 0.20 ± 0.35 | | | | | | | 1.75 ± 3.39 | |
| | | Carenero | 2 | 96.22 ± 4.32 | | | 1.19 ± 0.99 | | | | | 0.79 ± 0.74 | 1.26 ± 2.18 | 0.63 ± 1.89 |
| | | Cayo arena | 1 | 27.95 ± 17.38 | | | 38.25 ± 19.76 | | | | | | | 33.84 ± 8.26 |
| | | Cayo arena | 2 | 72.00 ± 5.95 | | 1.28 ± 2.23 | 15.47 ± 6.97 | | | | | 3.85 ± 6.66 | | 7.83 ± 7.90 |
| | | Ferry | 1 | 9.64 ± 6.94 | | 0.84 ± 1.46 | 8.52 ± 8.27 | | | | | | | |
| | | Ferry | 2 | 92.81 ± 1.42 | | | 7.19 ± 1.42 | | | | | | | |
| | TERR | Cayo Jackson 1 | 1 | 98.13 ± 0.82 | | | 0.39 ± 0.68 | 1.40 ± 1.45 | | 0.33 ± 0.20 | | | 0.20 ± 0.34 | |
| | | Cayo Jackson 1 | 2 | 97.78 ± 1.64 | | | 0.55 ± 0.47 | | | | | | 0.54 ± 0.93 | 0.84 ± 0.88 |
| | | Cayo Jackson 2 | 1 | 94.42 ± 3.53 | | | 4.99 ± 4.14 | 0.36 ± 0.53 | 0.36 ± 0.53 | 0.26 ± 0.11 | | | | |
| | | Cayo Jackson 2 | 2 | 93.18 ± 4.24 | | | 1.78 ± 1.65 | | 0.25 ± 0.44 | | | 0.25 ± 0.44 | 2.75 ± 1.74 | 1.55 ± 2.56 |
| | | Cayo Jackson 3 | 2 | 96.94 ± 1.79 | | | 0.33 ± 0.57 | 1.60 ± 1.43 | | | | | 0.91 ± 0.79 | 0.22 ± 0.39 |
| Northwest | PRU | Barrera 1 | 1 | 94.74 ± 3.90 | | | | | 5.68 ± 4.32 | | | | 0.25 ± 0.44 | |
| | | Barrera 1 | 2 | 97.78 ± 1.93 | | 0.54 ± 0.93 | | | 1.69 ± 1.73 | | | | | |
| | | Barrera 2 | 1 | 94.33 ± 6.71 | | | 0.48 ± 0.82 | | 4.96 ± 7.25 | 0.78 ± 0.60 | | | 0.24 ± 0.41 | |
| | | Barrera 2 | 2 | 94.18 ± 1.34 | | 0.50 ± 0.86 | | | 4.27 ± 1.14 | | | | 0.43 ± 0.74 | |
| | | Barrera 3 | 1 | 92.19 ± 2.85 | | | | | 7.81 ± 2.85 | 0.40 ± 0.30 | | | | |
| | | Barrera 3 | 2 | 96.29 ± 0.79 | 0.35 ± 0.61 | | 1.81 ± 0.11 | | 2.14 ± 0.98 | | | | | |
| | | Cayo arena 1 | 1 | 88.17 ± 6.32 | | | 1.37 ± 2.26 | | 8.86 ± 3.39 | | | | 1.73 ± 1.63 | |
| | | Cayo arena 1 | 2 | 92.36 ± 5.94 | | | | | 5.49 ± 3.60 | | 2.23 ± 2.40 | | | |
| | | Cayo arena 2 | 1 | 93.93 ± 2.92 | | | | | 6.70 ± 2.92 | 0.48 ± 0.40 | | | | |
| | | Cayo arena 2 | 2 | 88.23 ± 5.37 | | | 0.95 ± 1.65 | | 6.96 ± 7.30 | | 0.48 ± 0.82 | 0.88 ± 1.52 | 2.32 ± 0.78 | |
| | | Cayo arena 3 | 1 | 94.70 ± 1.37 | | | 0.36 ± 0.68 | | 5.39 ± 1.87 | | | | | |
| | | Cayo arena 3 | 2 | 96.30 ± 1.42 | | | | | 3.25 ± 1.25 | | | | 0.50 ± 0.86 | |
| | SOSU | Aeropuerto 1 | 1 | 99.27 ± 0.72 | | | 0.79 ± 0.72 | | | 0.33 ± 0.2 | | | | |
| | | Aeropuerto 1 | 2 | 53.49 ± 14.78 | | 3.26 ± 3.34 | | | | | 1.11 ± 1.92 | | | 41.82 ± 1.78 |
| | | Aeropuerto 2 | 1 | 100.00 | | | | | | | | | | |
| | | Aeropuerto 2 | 2 | 15.21 ± 2.52 | | 1.11 ± 1.92 | | | | | | | | 83.68 ± 3.86 |
| | | CaÒon 1 | 1 | 95.56 ± 5.24 | | | | | 1.75 ± 1.86 | | | | 3.42 ± 5.92 | |
| | | CaÒon 1 | 2 | 38.60 ± 13.57 | | | | | | | | | 0.35 ± 0.61 | 61.55 ± 14.14 |
| | | CaÒon 2 | 1 | 99.48 ± 1.35 | | | 0.67 ± 1.15 | | 0.28 ± 0.49 | | | | | |
| | | CaÒon 2 | 2 | 3.40 ± 13.20 | | | | | | | 0.98 ± 1.70 | | | 68.62 ± 11.81 |
| | | CaÒon 3 | 1 | 99.62 ± 0.66 | | | 0.38 ± 0.66 | | | 0.39 ± 1.1 | | | | |
| | | CaÒon 3 | 2 | 7.56 ± 3.24 | | | 0.31 ± 0.54 | | 0.22 ± 0.35 | 1.28 ± 0.90 | | | | 91.68 ± 3.37 |
| Southeast | BAYH | Coco Reef | 1 | 92.88 ± 3.47 | | 0.47 ± 0.75 | | | | | 0.47 ± 0.75 | 5.49 ± 4.96 | 0.47 ± 0.75 | |
| | | Coco Reef | 2 | 85.88 ± 5.42 | | 0.72 ± 1.26 | | 1.85 ± 3.28 | | 0.38 ± 0.20 | 0.62 ± 1.69 | 5.77 ± 4.80 | 4.54 ± 2.78 | 0.62 ± 1.69 |

***TABLE 1.*** *Continued*

| Region | Locality | Site | Trimester | Healthy Mean ± sd | BBD Mean ± sd | DSD Mean ± sd | SCTLD Mean ± sd | WPD Mean ± sd | YBD Mean ± sd | OTH Mean ± sd | BL Mean ± sd | PL Mean ± sd | PRED Mean ± sd | DC Mean ± sd |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | BCH | BC 221 | 1 | 93.21 ± 2.32 | | 2.35 ± 2.39 | | | | | 0.51 ± 0.89 | 2.23 ± 0.45 | 1.91 ± 1.84 | |
| | | BC 224 | 1 | 93.68 ± 2.89 | | 3.49 ± 3.99 | | | | 0.45 ± 0.2 | 1.16 ± 1.12 | 1.68 ± 1.46 | | |
| | | BC 226 | 1 | 83.79 ± 6.16 | | 7.66 ± 1.84 | | | | | | 0.45 ± 0.78 | 7.66 ± 6.73 | |
| | CALE | 7 matas de coco | 2 | 97.14 ± 0.73 | | | | | 1.43 ± 0.82 | | 0.48 ± 0.84 | 0.26 ± 0.36 | 0.74 ± 0.43 | |
| | | La Bomba | 2 | 96.17 ± 0.70 | | | | 1.14 ± 0.33 | 1.93 ± 0.43 | | | | 0.52 ± 0.58 | 0.24 ± 0.42 |
| | | Paisanito | 2 | 97.62 ± 0.80 | | 0.11 ± 0.19 | | 0.15 ± 0.26 | 1.22 ± 1.57 | 0.93 ± 0.40 | 0.11 ± 0.19 | 0.11 ± 0.19 | 0.53 ± 0.12 | 0.15 ± 0.26 |
| Southwest | AZU | Arenita de Champ | 1 | 82.24 ± 6.30 | | 1.87 ± 1.20 | | | | | 0.93 ± 0.70 | 0.93 ± 0.20 | 13.84 ± 3.40 | |
| | | La Ray | 1 | 97.67 ± 3.29 | | | | | | 0.28 ± 0.3 | | 1.55 ± 2.19 | 0.78 ± 1.96 | |
| | | Muro Nuevo | 1 | 77.47 ± 1.78 | | 5.43 ± 2.66 | | | | | 0.57 ± 0.99 | 7.16 ± 3.48 | 9.58 ± 1.57 | |
| | PED | Cueva Pedernales | 1 | 97.33 ± 2.73 | | | | 0.33 ± 0.52 | 0.33 ± 0.52 | | | | 2.67 ± 1.87 | |
| | | Cueva Pedernales | 2 | 92.41 ± 5.19 | | | | 2.66 ± 1.54 | | | | | 2.63 ± 1.74 | 2.30 ± 3.55 |
| | | Torre Bahía | 1 | 98.66 ± 0.76 | | | | 1.11 ± 0.56 | 0.23 ± 0.39 | | | | | |
| | | Torre Bahía | 2 | 95.36 ± 2.16 | | 0.20 ± 0.34 | | 3.25 ± 2.90 | 0.24 ± 0.49 | 0.36 ± 0.20 | | | 0.78 ± 0.82 | 0.18 ± 0.31 |
| | | Yesos Cuevanjo | 1 | 79.84 ± 6.77 | | | | | | 1.93 ± 1.2 | | | 19.86 ± 7.46 | |
| | | Yesos Cuevanjo | 2 | 9.99 ± 6.63 | | | | | 2.45 ± 2.12 | | | | 1.22 ± 1.60 | 4.25 ± 6.00 |

***TABLE 2.*** *Comparison of coral disease prevalence using 3–way nested permutation of variance (Permanova) based on Bray Curtis similarity index for 2 periods of times. Lo–location; RE–region; Si–site; Res–residual; df–degrees of freedom; SS–sum of squares; MS–mean squares; CV–coefficient of variation.*

| Source | df | SS | MS | Pseudo—F | P(perm) | CV |
|---|---|---|---|---|---|---|
| **March—May 2021** | | | | | | |
| Region | 4 | 1364.30 | 341.08 | 3.15 | 0.06 | 35.73 |
| Lo(RE) | 6 | 640.46 | 106.74 | 2.69 | 0.01 | 16.77 |
| Si(Lo(RE)) | 26 | 1047.30 | 40.28 | 4.36 | 0.001 | 27.43 |
| Res | 83 | 766.62 | 9.24 | | | 20.08 |
| Total | 119 | 3818.68 | | | | 100.00 |
| **June—August 2021** | | | | | | |
| Region | 4 | 1417.54 | 354.39 | 3.26 | 0.02 | 44.42 |
| Lo(RE) | 5 | 270.08 | 54.02 | 1.92 | 0.03 | 8.46 |
| Si(Lo(RE)) | 25 | 709.06 | 28.36 | 2.82 | 0.001 | 22.22 |
| Res | 79 | 794.63 | 10.06 | | | 24.90 |
| Total | 113 | 3191.31 | | | | 100.00 |

of extensive mortality on *Pseudodiploria* spp., *Diploria labyrinthiformis* and meandrinid corals are clear. In the northeastern coast, however, SCTLD was in an outbreak phase from March–August 2021 with relatively high prevalence (5—38%) in Carriles and Fronton (Galeras) and Cayo Arena and Ferry (Samaná, Figure 2A). Prevalence of bleached and/or pale corals seldom exceeded 5% across sites, localities, and regions in the DR for the study period (Figure 2A).

Our results indicate that serious coral health problems are affecting major reef builders in the DR. While no evidence of massive mortality associated with DSD was recorded, the disease affected over 5–20% of *Siderastrea siderea* counted in southern and northwestern reefs of DR (Figure 2A). Furthermore, YBD was only recorded to affect species in the genus *Orbicella* spp. (*O. faveolata*, *O. annularis* and *O. franksi*) across the southwestern and northwestern sites of DR with prevalence ranging from 5–25% (Figure 2A). Over 10 species (about 50% of the host range) were affected by SCTLD along the northern coast of DR, with *Pseudodiploria strigosa*, *Dendrogyra cylindrus*, *Eusmilia fastigiata*, *P. clivosa*, *S. siderea*, *Montastraea cavernosa* and *Meandrina* spp. being the most susceptible (Figure 2B). We observed no colonies bearing macroscopic signs of SCTLD in other areas of the island; however, colonies with similar signs of former WPD—II were observed in reefs of Bayahibe and Pedernales in a few species (with prevalence below 2%): *D. cylindrus*, *P. strigosa* and *C. natans*.

**Species composition as predictor of coral disease distribution in the DR**

The NMDS plot showed some extent of overlapping in coral species composition across sites nested within regions, with 6 nonrandom statistically significant clusters sharing 32% of species in March/May ($\pi$ = 3.41, p = 0.01) and 9 significant clusters in June/August ($\pi$ = 2.71, p = 0.01, Figure 3A,B). We found a significant mild correlation between the abundance of susceptible corals and the spatial distribution of coral diseases in the DR for data collected in March/May (BEST, Rho 0.23, p = 0.04) and June/August (BEST, Rho = 0.33, p = 0.02; Table 3). According to the BEST model, the combination of species that better explained the association between coral disease prevalence and the abundance of corals were *D. labyrinthiformis*, *D. cylindrus*, *M. meandrites, E. fastigiata*, *Porites astreoides* and *S. siderea*. The DistLM analysis indicates that species composition explained about 31% and 37% of the total variance in coral disease prevalence recorded in March/May and June/August, respectively (Table 4). Results from this model are consistent with the BEST analysis, as the abundance of healthy

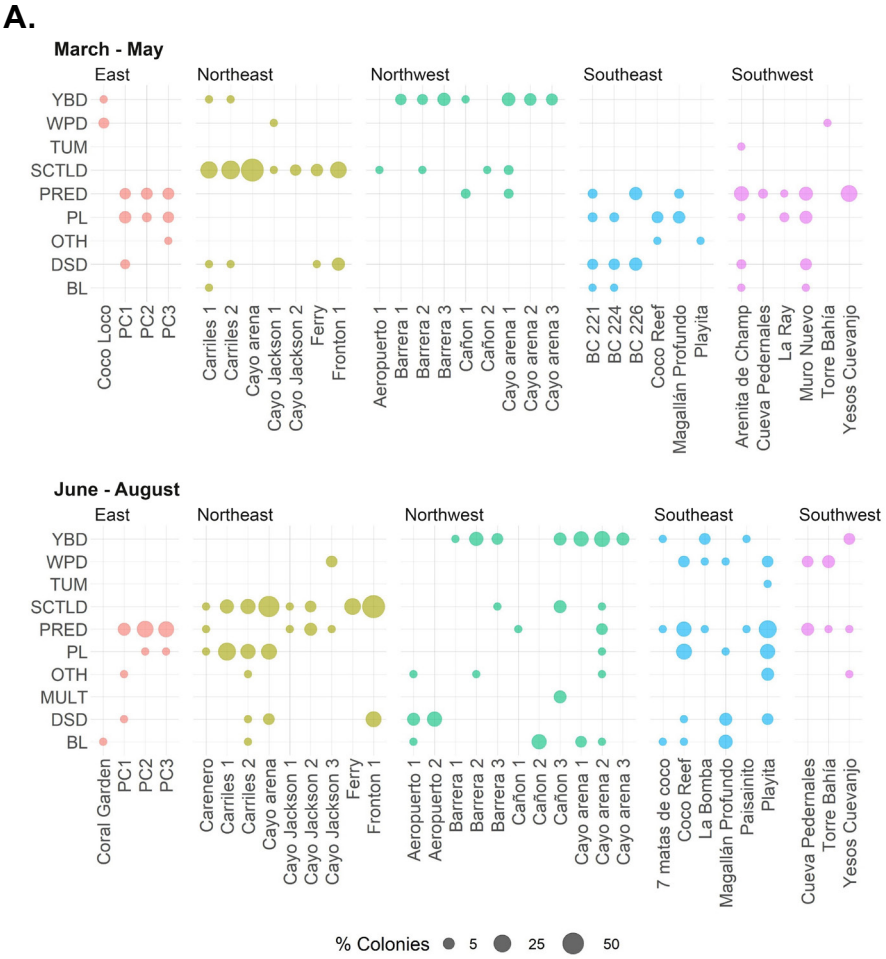


***FIGURE 2.*** *Distribution of coral diseases within the Dominican Republic by region and sampling site in 2021.* **A**. *Prevalence of different coral diseases and different conditions expressed as % of total colonies bearing a condition relative to the total number of colonies recorded at each site in March/May and June/August. YBD–yellow band disease; WPD–white plague disease; TUM–tumors or growth anomalies; SCTLD–stony coral tissue loss disease; PRED–predation; PL–paled; OTH–other conditions; DSD–dark spot disease; BL–bleached. DSD only recorded in* Siderastrea siderea. *YBD only recorded in* Orbicella *spp.* **B**. *Relative prevalence of SCTLD recorded by coral species in March/May and June/August at sites along the northern coast of the DR. Coral species: Aaga–*Agaricia agaricites*; Cnat–*Colpophyllia natans*; Dcyl–*Dendrogyra cilindrus*; Dlab–*Diploria labyrinthiformis*; Efast–*Eusmilia fastigiate*; Mcav–*Montastraea cavernosa*; Pcli–*Pseudodiploria clivosa*; Mmea–*Meandrina meandrites*; Pstr–*Pseudodiploria strigose*; Ofav–*Orbicella faveolata*; Oann–*Orbicella annularis*; Ofra–*Orbicella franksi,*; Past–*Porites astreoides*; Ssid–*Siderastrea siderea.

colonies of 5–7 coral reef builders significantly explained the occurrence of coral diseases across sites nested in locations and regions (Table 4). However, there were species that significantly explained coral disease prevalence in both sampling periods (i.e., *C. natans*, *M. meandrites*, *Orbicella annularis*, *P. astreoides* and *S. siderea*), while other species were only significant to explain patterns of occurrence in March/May (i.e., *O. faveolata* and *M. cavernosa*) and/or in June/August (i.e., *D. cylindrus*, *E. fastigiata* and *O. franksi*, Table 4).

**Coral recruits affected by SCTLD**

We observed coral recruits and juvenile corals affected by SCTLD in sites such as Carriles and Fronton in the northeast coast, where the disease became epizootic (Figure 4). When the substrate was closely explored on the same belt transects where the adult colonies were surveyed, recruits belonging to 10 coral species were recorded either showing macroscopic signs


***FIGURE 3.*** *nMDS with overlaying clusters from SIMPROF analysis based on Bray Curtis fourth–root transformed similarity matrix for coral species abundance (healthy colonies) recorded across sites nested within regions. Mean (± sd) depth along sites: Northwest = 7.8 ± 3.6 m; Northeast = 10.1 ± 7.8 m; East = 7.3 ± 3.4; Southeast = 9.6 ± 3.3 m; Southwest = 10.2 ± 5.8 m.*

of rapid tissue loss and/or were recently dead with denudated skeletons (Figure 4A–J). Overall, the prevalence of SCTLD on coral recruits was always below 3–5% regardless of the species. A clear overlapping of host ranges for adult and recruit/juvenile populations affected by SCTLD was observed during the study period. These results clearly indicate that counting coral recruits in areas where SCTLD is in an outbreak phase must be considered in monitoring protocols.

**Star fish feeding on SCTLD decaying tissues**

In March 2021 at Cayo Arena (Samaná), we recorded 43% of *Pseudodiploria* spp. (21/48) showing clear macroscopic signs that have been reported for SCTLD (Figure 5A–C). Over an about 60 m$^2$ area, about 30% of the *P. strigosa* showed active SCTLD lesions (n = 15/50), 48% were recently dead (n = 24/50) and only 22% (11/50) were apparently healthy. Within this area, we observed starfish, *Oreaster reticulatus,* that had climbed on 27% (4/15) of the *P. strigosa* colonies bearing the macroscopic signs reported for SCTLD (Figure 5D–F). Upon close inspection, these corals had multiple coalescent lesions with coral tissues detaching from the coral skeleton (Figure 5G, H). When one starfish was gently removed, we observed the ambulacra attached around the coral tissue (Figure 5I, J). We also observed *O. reticulatus* climbing on healthy–looking, recently dead, and long dead corals (Figure 5K, L). We did not observe this behavior in any other site surveyed.

## Discussion

This is the first study to survey coral disease prevalence in the Dominican Republic at the reef site, locality, and regional scale within the island. The study integrates coordinated and standardized monitoring efforts conducted by governmental, NGO, private and academic stakeholders to cover a large proportion of the island. We showed that prevalence of coral diseases in the DR is extremely variable in space, with different diseases occurring northwest, northeast, east, southeast, and southwest of the island. Our surveys show that the most prevalent coral diseases in the Dominican Republic are DSD, YBD, and SCTLD, all known to be widely spread across the Caribbean (Weil et al. 2006, Miller and Richardson 2015). While DSD does not seem to represent a serious problem because prevalence is normally below 3% and no extensive mortality associated with this disease was recorded, YBD and SCTLD are worrisome as they occur in high prevalence and affect major reef builders along the island. Together, these diseases are affecting and producing extensive mortality on coral species populations that are currently used by Dominican institutions implementing restoration efforts through sexual and asexual propagation. Therefore, epizootics events of any of these diseases could potently have negative effects on local restoration programs as noted by Moriarty et al. (2020) for other regions. Our results show that sites in Galeras and Samaná are clearly above baseline prevalence (0.3–4%) of coral diseases reported for the Caribbean Region from 2005 to 2010 (Ruiz–Moreno et al. 2012).

The etiology of both YBD and SCTLD remains unknown, similar to other coral diseases. However, for SCTLD, recent histopathological analysis indicates the presence of virus–like particles in diseased tissues, further suggesting SCTLD is an infectious disease likely produced by a virus targeting zooxanthellae (Work et al. 2021). Likewise, YBD has been regarded as a bacterial disease that targets the zooxanthellae as it affects and compromises its ultrastructure (Cervino et al. 2004, Bruckner and Rielg 2016). Yellow Band Disease is a persistent disease known to kill large colonies of *Orbicella* spp. (80–100 cm width) with rates of mortality in the order of cm per month (Bruckner and Bruckner 2006). On the other hand, SCTLD kills corals the fastest, with rates of tissue loss ranging from mm to cm a day (Aeby et al. 2019), making this disease the fastest

syndrome ever recorded to affect corals in the wider Caribbean (Brandt et al. 2021, Croquer et al. 2021). Both diseases have produced significant impacts on coral communities in different Caribbean countries, including the reduction of live coral cover, shifts in species composition and community structure (Bruckner and Hill 2009), shifts in population size structure (Bruckner and Bruckner 2006), and/or significant population reductions of endangered species, among other impacts (Bruckner and Rielg 2016, Alvarez–Fillip et al. 2019, Neely et al. 2021, Meiling et al. 2020, Thome et al. 2021).

The BEST analysis and the DistLM show that occurrence of coral diseases is partially explained by the abundance of susceptible hosts across reefs. Similar results were reported by Aeby et al. (2019) in the Florida Keys. Fewer species are affected by YBD compared to SCTLD, which is known to affect over 22 coral species, particularly *C. natans*, *D. cylindrus*, *Dichocoenia stokesii*, *D. labyrinthiformis*, *E. fastigiata*, *M. meandrites*, *M. jacksoni*, *P. strigosa*, *P. clivosa* and *M. cavernosa* (Aeby et al. 2019). Some species were important in explaining some of the variance in March/May but less so in June/August, suggesting potential high mortalities or seasonal behaviors, both beyond the scope of this study to infer. Our results indicate that reefs with higher abundance of these species along the northern coast of DR are more prone to suffer a SCTLD epizootic event. In fact, SCTLD is currently in an endemic phase along the northwestern coast and in outbreak phase in the northeastern coast of DR. We cannot explain the lack of SCTLD epizootic events along the southern coast of DR, despite the disease having been reported in La Parguera,

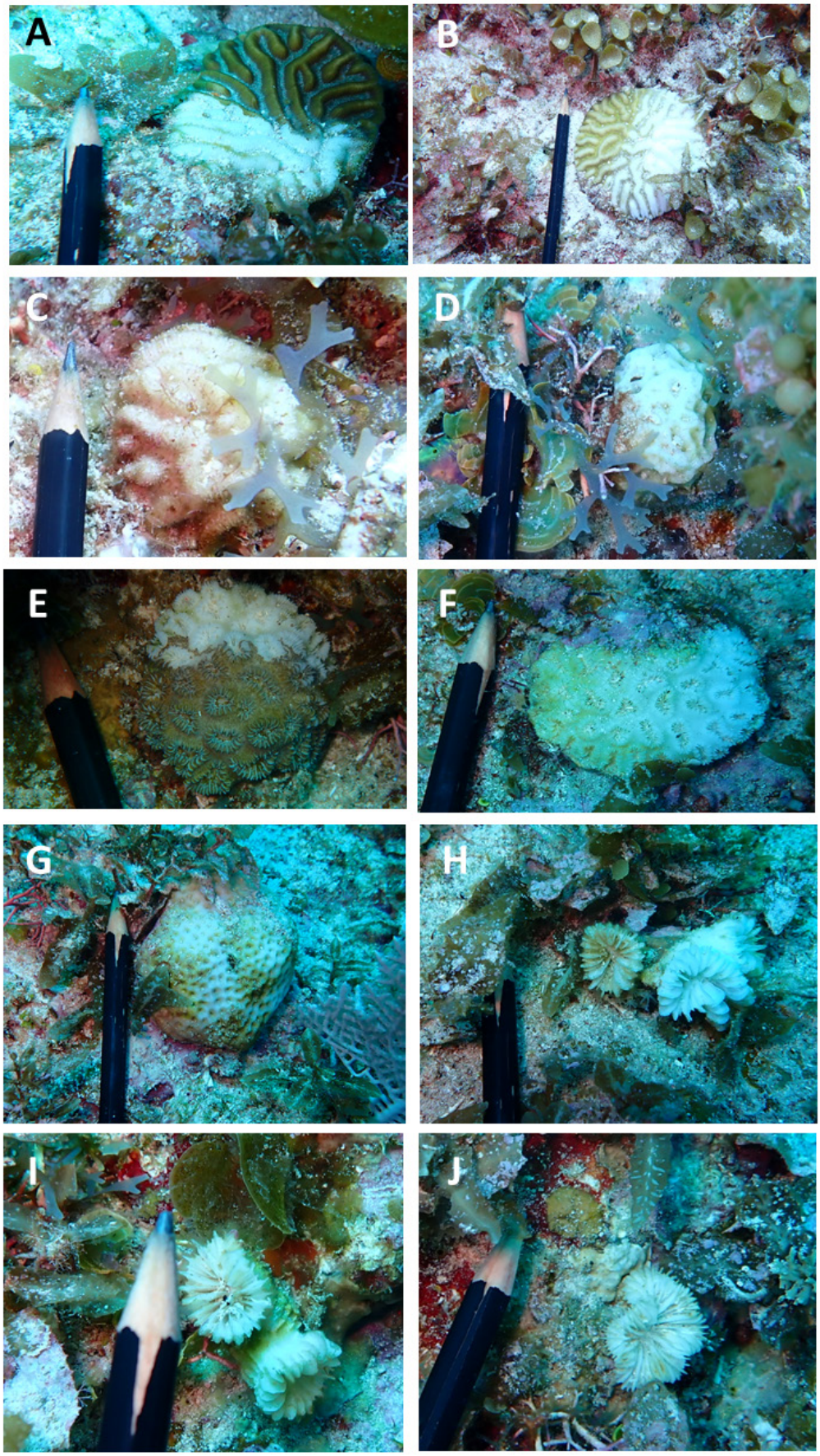


**Figure 4.** *Different coral species < 4 cm in diameter affected by stony coral tissue loss disease along the northerneastern coast of the Dominican Republic in Carriles and Fronton (Galeras) and Cayo Ferry (Samaná) during March 2021. See Figure 1 for location.* **A** *and* **B**. *Active tissue loss on* Pseudodiploria strigosa. **C** *and* **D**. *Recently dead* P. strigosa *and* Agaricia agaricites. **E.** Dichocoenia stockesi *with active tissue loss.* **F**. *Recently dead* D. stockesi. **G**. Siderastrea siderea *with active tissue loss.* **H** *and* **I.** *Recently dead* Eusmilia fastigiate. **J**. *Recently dead* Colpophyllia natans.

***TABLE 3.*** *The BEST model solution of combination of variables (coral species) that better explains the prevalence of coral diseases in the Dominican Republic. Cnat–* Colpophyllia natans*; Dcyl–*Dendrogyra cilindrus*; Dlab–*Diploria labyrinthiformis*; Efast–*Eusmilia fastigiate*; Mcav–*Montastraea cavernosa*; Mmea–*Meandrina meandrites*; Oann–*Orbicella annularis*; Ofra–*Orbicella franksi*; Past–*Porites astreoides*; Pcli–*Pseudodiploria clivosa*; Pstr–*Pseudodiploria strigose*; Ssid–*Siderastrea Siderea.

| MARCH/MAY | | | JUNE/AUGUST | | |
|---|---|---|---|---|---|
| Number of variables | Rho | Species BEST combination | Number of variables | Rho | Species BEST combination |
| 5 | 0.232 | Cnat, Dlab, Efast, Mmea, Past | 5 | 0.326 | Dlab, Mmea, Past, Pstr, Ssid |
| 5 | 0.231 | Cnat, Dcyl, Dlab, Mmea, Past | 5 | 0.326 | Dlab, Mmea, Ofra, Pstr, Ssid |
| 4 | 0.231 | Cnat, Dlab, Mmea, Past | 5 | 0.323 | Dcyl, Dlab, Mmea, Past, Ssid |
| 5 | 0.230 | Cnat, Dlab, Mmea, Mcav,Past | 4 | 0.323 | Dlab, Mmea, Past, Ssid |
| 5 | 0.230 | Cnat, Dlab, Mmea, Ofra,Past | 5 | 0.321 | Dlab, Mmea, Past, Pcli, Sisid |
| 5 | 0.228 | Cnat, Dcyl, Efas, Mmea,Past | 5 | 0.321 | Dcyl, Mmea, Ofra, Past, Sisid |
| 4 | 0.228 | Cnat, Efas, Mmea,Past | 5 | 0.321 | Cnat, Dlab, Mmea, Past, Ssid |
| 5 | 0.228 | Cnat, Efas, Mmea, Ofra,Past | 5 | 0.321 | Dlab, Ofra, Past, Pstr, Ssid |
| 5 | 0.227 | Cnat, Efas, Mmea, Oann,Past | 5 | 0.320 | Dcyl, Dlab, Past, Pstr, Ssid |

***TABLE 4****. Distance–based linear model marginal test showing total percentage of variance in the prevalence of coral diseases explained by the abundance of major reef builders across sites. SS–sum of squares; Prop.– proportion of variation explained; Aaga–*Agaricia agaricites*; Cnat–*Colpophyllia natans*; Dcyl–*Dendrogyra cilindrus*; Dlab–*Diploria labyrinthiformis*; Efast–*Eusmilia fastigiate*; Mcav–*Montastraea cavernosa*; Pcli–*Pseudodiploria clivosa*; Mmea–*Meandrina meandrites*; Pstr–*Pseudodiploria strigose*; Ofav–*Orbicella faveolata*; Oann–*Orbicella annularis*; Ofra–*Orbicella franksi*; Past–*Porites astreoides*; Ssid–*Siderastrea siderea. *Bolded values are significant ($p \leq 0.05$).*

| MARCH/MAY | | | | | JUNE/AUGUST | | | | |
|---|---|---|---|---|---|---|---|---|---|
| $r^2 = 0.37$ | | Adj $r^2 = 0.31$ | | | $r^2 = 0.43$ | | Adj $r^2 = 0.37$ | | |
| Variable | SS(trace) | Pseudo—F | p | Prop. | Variable | SS(trace) | Pseudo—F | p | Prop. |
| Aaga | 41.06 | 1.18 | 0.25 | 0.01 | Aaga | 24.56 | 1.26 | 0.281 | 0.01 |
| **Cnat** | **2604.10** | **3.92** | **0.02** | **0.03** | **Cnat** | **2150.80** | **4.03** | **0.013** | **0.03** |
| Dcyl | 937.43 | 1.38 | 0.23 | 0.01 | **Dcyl** | **1957.00** | **3.66** | **0.042** | **0.03** |
| Dlab | 1441.40 | 2.14 | 0.11 | 0.02 | Dlab | 549.45 | 1.00 | 0.332 | 0.01 |
| Efas | 701.78 | 1.03 | 0.301 | 0.01 | **Efas** | **2430.50** | **4.58** | **0.006** | **0.04** |
| **Mcav** | **1698.00** | **2.53** | **0.049** | **0.02** | Mcav | 163.97 | 0.30 | 0.921 | 0.00 |
| Pcli | 0.00 | 0.00 | 0.975 | 0.00 | Pcli | 12.91 | 0.66 | 0.54 | 0.01 |
| **Mmea** | **2935.20** | **4.44** | **0.009** | **0.04** | **Mmea** | **2553.90** | **4.82** | **0.002** | **0.04** |
| **Ofav** | **59.82** | **1.72** | **0.165** | **0.01** | Pstr | 34.90 | 1.80 | 0.137 | 0.02 |
| **Oann** | **1582.90** | **2.35** | **0.041** | **0.02** | **Oann** | **612.27** | **1.12** | **0.293** | **0.01** |
| Ofra | 1207.60 | 1.79 | 0.105 | 0.01 | **Ofra** | **1477.70** | **2.74** | **0.025** | **0.02** |
| **Past** | **5059.10** | **7.87** | **0.002** | **0.06** | **Past** | **5938.60** | **11.90** | **0.001** | **0.10** |
| **Ssid** | **511.49** | **16.53** | **0.001** | **0.12** | **Ssid** | **237.00** | **13.491** | **0.001** | **0.11** |

southwestern coast of Puerto Rico (Weil pers. comms). Understanding the mechanism of transmission of YBD and SCTLD and other diseases is extremely relevant to effectively track their dispersion. For YBD there is no information about transmission, whereas for SCTLD, spatial models suggest the disease is waterborne, and therefore oceanographic processes controlling currents and ballast water transport are presumably relevant (Muller et al. 2020, Sharp et al. 2020, Roseanu et al. 2021). Our goal is to continue monitoring diseases in the DR to better understand the environmental and biological drivers of SCTLD. Future steps will be improving our statistical models by adding other predictors such as distance to ports, cities, other human settlements, and rivers. We will also add depth and habitat type as predictor variables as they could determine the distribution of coral species across habitats within reefs, particularly for diseases with narrow host ranges. With this information in hand along with a clearer picture of the etiology of the disease, DR will evaluate to include available interventions to mitigate the effects of SCTLD outbreaks.

Our results also indicate that in outbreak areas, SCTLD does not only affect adult colonies, but also juveniles and recruits, clearly indicating the disease could have long–lasting effects for the most susceptible coral populations. We assume that recruits are affected by SCTLD because this condition was only recorded at sites where STCLD was in outbreak phase and not across areas where WPD was recorded. Regardless of the distinction between WPD and SCTLD, our observations show a rapid loss of tissue in recruit and juvenile corals.

Results from these surveys show that species currently being used for sexual and asexual propagation in the DR (Sellares et al. 2021) are currently being affected by coral diseases such as SCTLD and YBD across the island. Particularly, SCTLD was found killing adult and recruits of coral species that are used in local restoration efforts via microfragmentation and assisted

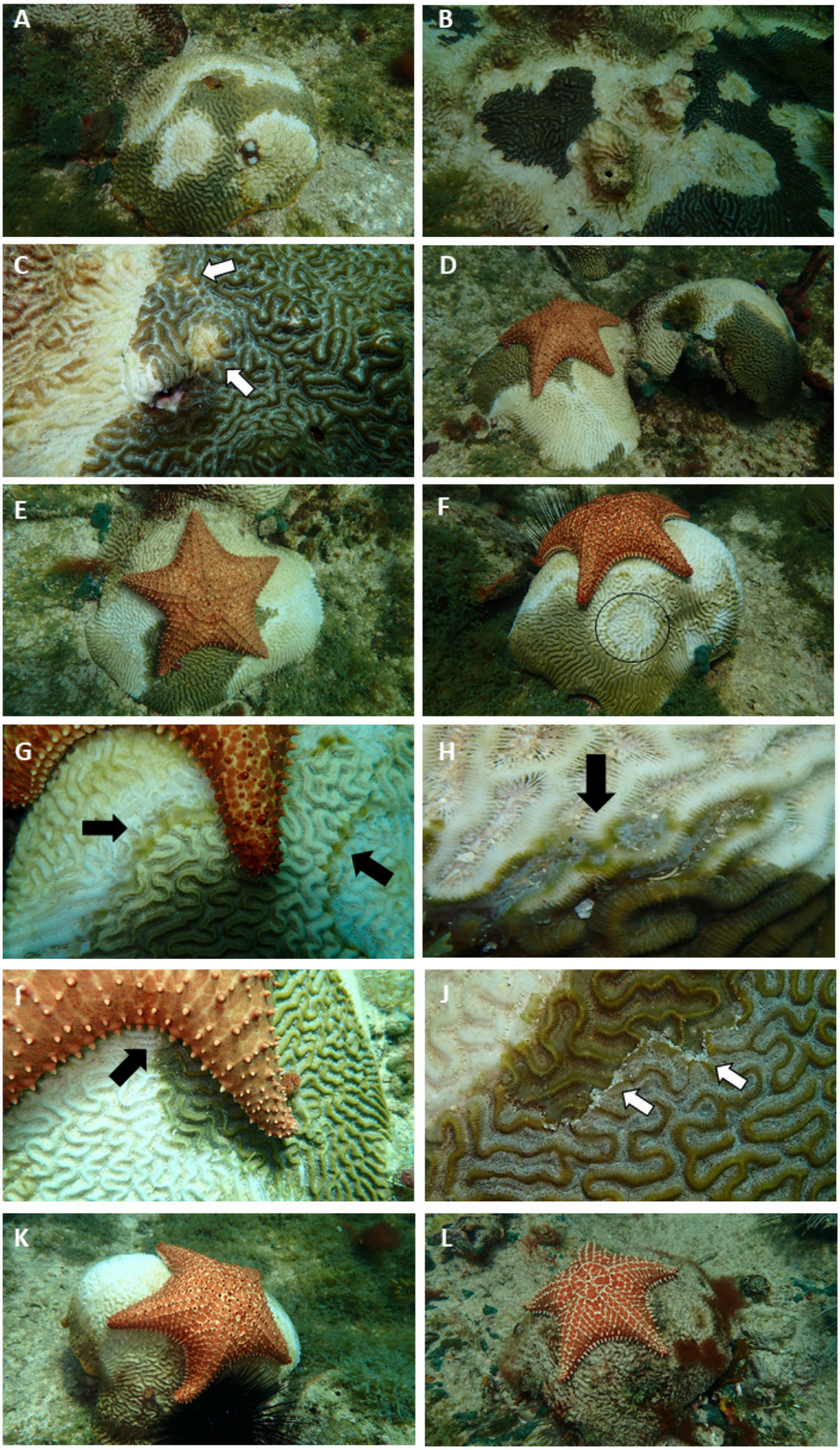


***FIGURE 5.*** *Photographic record of* Oreaster reticulatus *preying on decaying Stony Coral Tissue Loss Disease (SCTLD) tissue in Cayo Arena, Samaná in the northeast region of Dominican Republic during March 2021.* **A—C**. Pseudodiploria strigosa *and* P. clivosa *with multiple–coalescent SCTLD lesions.* **D—F.** O. reticulatus *climbing on top* P. strigosa *with sloughing tissues.* **G—H.** *Decaying coral tissue (black arrows).* **I.** *Details of the starfish arms attached to colonies with decaying tissue (black arrow).* **J**. *Starfish ambulacra after detachment (white arrows).* **K.** *A recently dead colony of* P. strigosa *with* O. reticulatus *on top.* **L.** *An old dead colony of* P. strigosa *with* O. reticulatus *on top.*

coral reproduction (Bayraktarov et al. 2020). In the future, the effect of coral disease outbreak on coral restoration outcomes in the DR must be formally evaluated.

Predated colonies with SCTLD were located in a patch reef located close to sandy bottoms and seagrass beds, where the starfish *O. reticulatus* is conspicuously found (Scheibling 1982). Based on our observations, and the described capacity of *O. reticulatus* to move across habitats (Wuff 1995, 2020), we hypothesize the species may be a potential vector of SCTLD in coral habitats near seagrass beds and/or sandy patches, but this hypothesis awaits formal testing. While it is possible that *O. reticulatus* may potentially act as a vector for this disease while feeding on decaying coral tissue, it could also prevent dispersion of SCTLD if the unknown pathogen is destroyed in the digestive system of the starfish. Generalist coral predators and/or scavengers such as the fireworm *Hermodice carunculata* and butterfly fish (Chaetodontidae) have also been inferred to be vectors of coral diseases, including SCTLD (Aeby et al. 2019).

## Acknowledgements

We thank our colleagues and collaborators for their assistance with this project, especially F. Nunez from TNC for supporting the coral disease action plan in the Dominican Republic and J. Lang from AGRRA for continuous counsel and support. We thank the Universidad Autonoma de Santo Domingo, Fundación Grupo Puntacana, Fundación Cap Cana, FUNDEMAR and Iberostar Group for supporting and financing their local monitoring programs. We thank P. Lamelas from CEBSE for logistic support and TNC for financing coral disease surveys along the northern coast of the country. We also thank Propagas Foundation for financing the coral disease monitoring in La Caleta and Pedernales. Finally, we extend our acknowledgment to Ministerio de Medio Ambiente y Recursos Naturales (MIMARENA) for providing the permits to complete the surveys at the national scale.

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