

GULF AND CARIBBEAN

R E S E A R C H

Volume 34
2023
ISSN: 2572-1410



Published by

**THE UNIVERSITY OF
SOUTHERN MISSISSIPPI**

GULF COAST RESEARCH LABORATORY

Ocean Springs, Mississippi

GULF AND CARIBBEAN FISHERIES INSTITUTE PARTNERSHIP

DYNAMICS OF THE BENTHIC COMMUNITIES OF PIGEON ISLETS (GUADELOUPE ISLAND, LESSER ANTILLES) FROM 2012 TO 2021 MONITORED BY A PHOTO—QUADRATS TECHNIQUE[§]

Hanna—May Malahel^{1,2*}, Camille Freschet³, Simone Mège³, and Claude Bouchon^{2,4}

¹UMR BOREA, CNRS 7208, MNHN, UPMC, UCBN, IRD 207, Université des Antilles, Campus de Fouillole, 97157 Pointe-à-Pitre, Guadeloupe – France; ²Laboratoire d'Excellence "CORAIL", 66100 Perpignan – France; ³National Park of Guadeloupe, 97122 Baie-Mahault, Guadeloupe – France; ⁴ÉcoRécif Environnement, 97122 Baie-Mahault, Guadeloupe – France; *Corresponding author, email; hannamay.malahel@gmail.com

ABSTRACT: Since 2012, the benthic communities of the Pigeon Islets (Guadeloupe Island, Lesser Antilles) have been monitored biannually by the National Park of Guadeloupe using photo—quadrats. This monitoring was carried out at 12 coral reef stations distributed around the islets. The data collected from 2012 to 2021 highlight the significant events that disrupted the coral communities of Guadeloupe. Among these remarkable phenomena, an episode of coral bleaching occurred in 2019, followed by the appearance of a new coral disease, Stony Coral Tissue Loss Disease (SCTLD), in 2020. As a result of these threats, a drop of 54% of coral cover was observed in the monitored sites, accompanied by a rise of 16% of the surface occupied by macroalgae. The protocol set up by the National Park of Guadeloupe was found to be efficient to follow the temporal dynamics of benthic reef communities.

KEY WORDS: Coral communities, temporal dynamics, coral bleaching, coral disease, SCTLD

INTRODUCTION

With 67 coral species, 66 gorgonian species and hundreds of sponge species, Guadeloupe Island has one of the richest reef fauna of the Lesser Antilles (Philippot 1987, Bouchon and Laborel 1990, Bouchon et al. 2016). This high biodiversity is an important economic driver for the local population. Reef fishing represents 25 million euros per year, while blue tourism (i.e., nautical activities, scuba diving, boat lagoon visits) brings in about 62 million euros per year (Batailler et al. 2021).

However, the coral reefs of Guadeloupe are subjected to many natural and anthropogenic pressures, namely, overfishing, rising sea temperatures, and coral diseases (Wilkinson and Souter 2008, Eakin et al. 2010, Jackson et al. 2014, Batailler et al. 2021). These pressures result in the substrate becoming more available for the development of macroalgae, already boosted by terrigenous inputs rich in nutrients caused by coastal degradation (building and industrial activities, mangrove destruction, and poor wastewater management; McManus and Polsenberg 2004, Bouchon et al. 2008).

The Guadeloupe National Park is a public institution founded in 1989 to preserve biodiversity and establish a balance in the relationship between man and nature in Guadeloupe. In 2009, the National Park of Guadeloupe established a territorial charter that defines the projects and objectives pursuing sustainable development. It delineates areas such as the "core" (21,000 ha) where the preservation of biodiversity is strictly regulated, and the "membership area" (90,000 ha) which includes all the municipalities that have an ecological

and geographical continuity with the spaces classified in the core of the park. Islets listed in the core of the park are surrounded by the adjacent maritime area (130,000 ha). One of the missions of the National Park is to monitor the evolution of the ecosystems for which it is responsible.

The present study deals with the benthic reef communities located around Pigeon Islets, which have been classified as a Guadeloupe National Park core since 2009. The coral communities of Pigeon islets are an integral part of the Guadeloupean heritage and represent one of the most protected sites of the island (Bouchon—Navaro and Bouchon 2000). This site includes coral species listed on the IUCN (International Union for Conservation of Nature) red list, such as the coral genus *Acropora* as well as the presence of corals belonging to the list of protected species in Guadeloupe, Martinique and Sint—Marteen Islands, according to the national decree of 25 April 2017.

In recent years, activities such as scuba diving, snorkeling, kayaking, or boat trips have multiplied and intensified the anthropogenic pressure on the islets. Nevertheless, regulations are in place in order to perpetuate economic activity in harmony with the protection of the environment (Mège et al. 2023). Moreover, professional and recreational fishing, the use of jet—skis, and boat mooring are prohibited, although mooring buoys have been deployed for visiting boats.

In addition to other anthropogenic activities that cause marine pollution, Pigeon Islets are located 1.15 km away from

[§] This article is based on a presentation given in November 2022 at the 75th meeting of the Gulf and Caribbean Fisheries Institute, Ft. Walton Beach, FL.

wastewater treatment plants of medium (between 2,000 and 10,000 population equivalent) and small (between 20 and 2,000 population equivalent) capacity. According to an assessment established in 2019 by the Direction de l'Environnement, de l'Aménagement et du Logement (DEAL, Department of the Environment, Development and Housing) of Guadeloupe, these plants do not meet treatment standards. Poor wastewater management enhances eutrophication in the coastal marine environment.

Another factor favoring the intense proliferation of macroalgae is the decrease in the abundance of herbivores, either due to epizootics affecting herbivorous sea urchins or to the overexploitation of herbivorous fish. These phenomena result in a decrease in grazing pressure on algal communities (McCook 1999, McCook et al. 2001, Cheal et al. 2010). However, recent studies do not suggest a significant decline in herbivorous fish around Pigeon Islets (Batailler et al. 2021). In contrast, the populations of diadem sea urchins (*Diadema antillarum*) on the site were affected by an epizootic that devastated them in 1983 (Lessios 1988) and, more recently in 2022 (pers. obs.). As a result, the areas occupied by macroalgae may become even larger on reefs, stimulated by eutrophication conditions in coastal waters and reduced herbivory.

The National Park of Guadeloupe initiated a temporal study of the benthic communities of Pigeon Islets using photo-quadrats in 2012. The objective of the study was to monitor the long-term dynamics of coral communities. The benthic organisms within quadrats were photographed twice a year and then analyzed by photo-interpretation. The results obtained were compiled in a database. The study focused on the abundance of benthic organisms and the dynamic of their coverage rate of the substratum, as well as on the stressors likely to impact the balance of the coral community through time.

MATERIALS AND METHODS

The Pigeon Islets are located on the leeward coast of Guadeloupe Island, 1,200 m offshore. They consist of 2 islets of volcanic origin. The bedrock does not support coral reefs *sensu stricto* but is occupied by flourishing coral communities nonetheless (Bouchon-Navaro 1997).

In order to monitor the changes in the benthic communities, 12 monitoring sites were chosen around the islets (Figure 1). On each site, a photo-quadrat was permanently marked on the bottom by four stainless steel rods driven into the rocky substrate. The photo-quadrats were located in areas where benthic biodiversity was maximal. The quadrats were photographed twice a year, during the wet and the dry seasons, from 2012 to 2021. In Guadeloupe, the wet season extends from December to April with rainfall reaching 800 mm per month and the dry season from May to November during which rainfall does not exceed 200 mm per month. Field trips were conducted during the month of December for the wet seasons and during May for the dry season according to the sea conditions. A total of 240 photographs were taken.

The benthic organisms settled in the quadrats were photographed with a Canon PowerShot G7 X Mark II camera placed in a waterproof housing and mounted on a PVC frame (Figure 2). The photo-quadrats measured 80x60 cm. This size corresponds to a compromise between the maximum size to investigate while maintaining fine observable details in each photograph. Several photos of each quadrat were taken during the survey campaigns in order to select the best photograph. Adobe Photoshop 2022 photo editing software was used to correct the images from distortions due to a possible lack of parallelism of the camera with the substrate and optical defects of its photographic lens (distortion tool). Then, the colorimetry of the images was adjusted using the same software

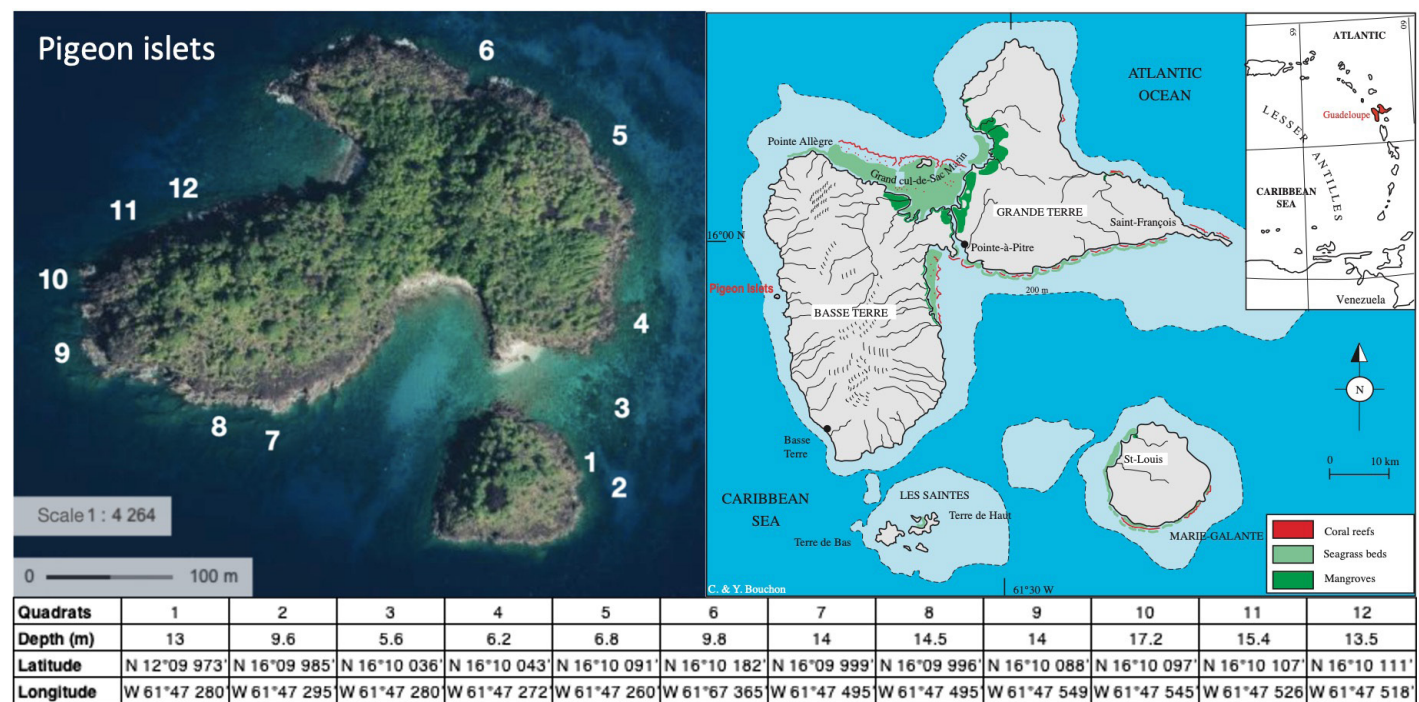


FIGURE 1. Guadeloupe Island in the Lesser Antilles. Distribution of monitoring stations at Pigeon Islets, including depth, latitude and longitude of each quadrat.



Figure 2. Photographic device used to record substrate at each quadrat. (Photo: C. Bouchon).

(color adjustment tool), so that all the elements were visible and usable for data processing. The total area of each sessile organism present in a quadrat was measured using the software Coral Point Count with Excel extensions (CPCe). Mobile animals were not taken into consideration, given their motility and random presence in the quadrats.

The sessile organisms taken into consideration were corals, including Scleractinians and also Hydrocorals of the genus *Millepora*, gorgonians, other sessile invertebrates, and algae. Corals were identified at the species level. In addition to the measure of their surface area, the state of health of each colony was evaluated by estimating the percentage of necrotic tissue surface area of the animal. We defined a 100% necrotic coral as a freshly dead animal of which the (white) skeleton has not yet been recolonized by other organisms; otherwise it is considered as dead substrate. Corals affected by the phenomenon of “bleaching” were subjected to special consideration, as a bleached coral is not dead and remains likely to recover its original condition in many cases. The bleaching phenomenon was noted and the surface of bleached tissues was estimated for each colony. Coral diseases were also identified and monitored. The surface of dead tissue was measured. The recruitment of young corals was assessed by counting all young colonies < 1 cm in diameter (\approx corals < one year old). At the beginning of the study (2012 – 2016), there was a lack of precision in the data concerning tissue damage, coral recruitment and mortal-

ity. Consequently, the results for those 3 variables presented hereafter concern the period 2017 to 2021.

The percentage coverage of the substrate by algae was estimated, distinguishing between the algal turf and the macroalgae. Empirically, turf encompasses all (short) algae from which an individual cannot be separated with certainty (Connell et al. 2014). These algae play a vital role on reefs, as a preferred food source for herbivorous animals. The macroalgae were separated into green, brown and red macroalgae. Cyanobacteria were also taken into account.

Gorgonians hold a special place among the sessile benthic organisms, insofar as they enter very little into competition with the other sessile organisms for the occupation of the bottom due to their erect bearing. Estimating the recovery rate of gorgonians is difficult and does not have much ecological significance. Therefore, gorgonians were simply identified at the species level and counted inside the quadrats. An exception was made for *Erythropodium caribbaeorum*, the only encrusting species of gorgonian in the Caribbean region. For this species, the surface area was measured as for any other benthic organism likely to occupy a significant area on the bottom. Other sessile benthic invertebrates that occupy a significant surface area on the bottom were identified at the species level (i.e., Sponges, Actinarians, Zoantharians, etc.) and their bottom cover was also measured.

Data concerning the main biological groups were analyzed using the statistical software XLSTAT. Hydrozoans and Gorgonians (except for *E. caribbaeorum*) were excluded from the analyses because of their erect form which cannot be translated into a measure of the coverage rate of the substrate. Due to the small sample size of the temporal series, nonparametric statistical tests were used to process the data.

Significant temporal trends (negative or positive) in the percent coverage of the benthic organisms present in the photo-quadrats were evaluated using the Spearman rank correlation coefficient. The changes in the ranks of dominance (in terms of percent coverage of the substratum) between the main groups of organisms or between coral and sponge species over time was tested using Friedman rank analysis of variance. When a statistically significant overall difference was revealed, a *post-hoc* Nemenyi test of multiple comparisons (Hollander et al. 2013) was used to determine which samples were responsible for the heterogeneity in the data.

The Friedman Rank Analysis of Variance was used to test if the ranks of dominance, i.e. the structure of species assemblages, changed over time. The variable taken into consideration is the dominance of each group of organisms or species in term of coverage of the bottom.

RESULTS

Composition of the benthic communities (2012 – 2021)

The percent coverage of the different groups of benthic organisms for all the quadrats over the period covered by the study is presented in Figure 3. The Pheophyceae dominated the benthic community with 45.6 % (\pm 1.9% se) coverage. Algal

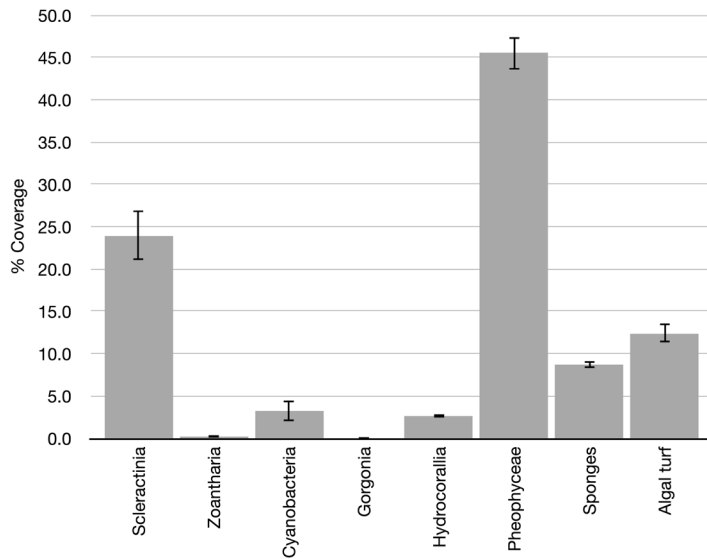


FIGURE 3. Mean \pm se percent coverage of substrate by main groups of benthic organisms at Pigeon Islets, Guadeloupe in all pooled quadrats during the 2012–2021 study period.

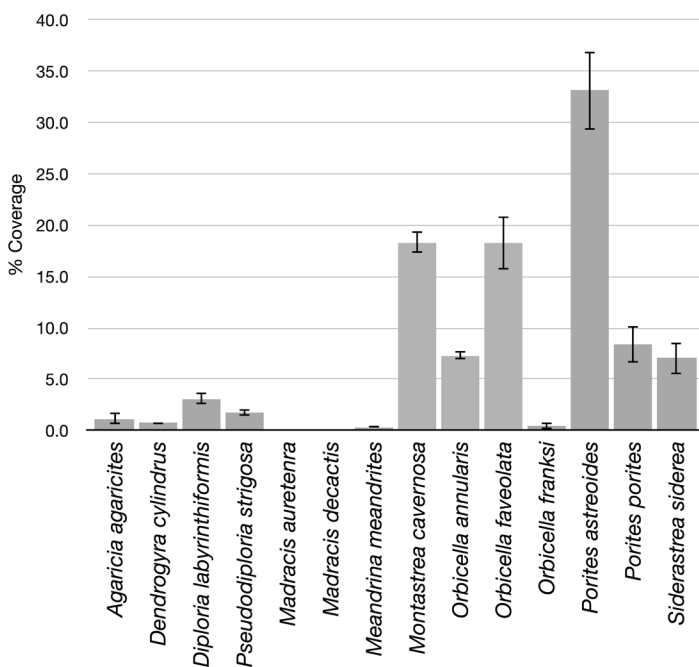


FIGURE 4. Mean \pm se percent coverage of Scleractinian corals at Pigeon Islets, Guadeloupe in all pooled quadrats during the 2012–2021 study period.

turf was the second group of Algae ($12.4 \pm 1.1\%$). Animals were dominated by Scleractinian corals ($24.0 \pm 2.9\%$) and sponges ($8.7 \pm 0.4\%$). The assemblage of Cnidaria over all the quadrats was composed by 14 species of Scleractinians, one species of Zoantharian and one species of Hydrocoral.

Figure 4 presents the relative dominance (percent coverage) of the Scleractinian coral species in all the quadrats over the study period. *Porites astreoides* dominated the assemblage with $33.1 \pm 3.8\%$, followed by *Montastrea cavernosa* ($18.3 \pm 1.1\%$) and

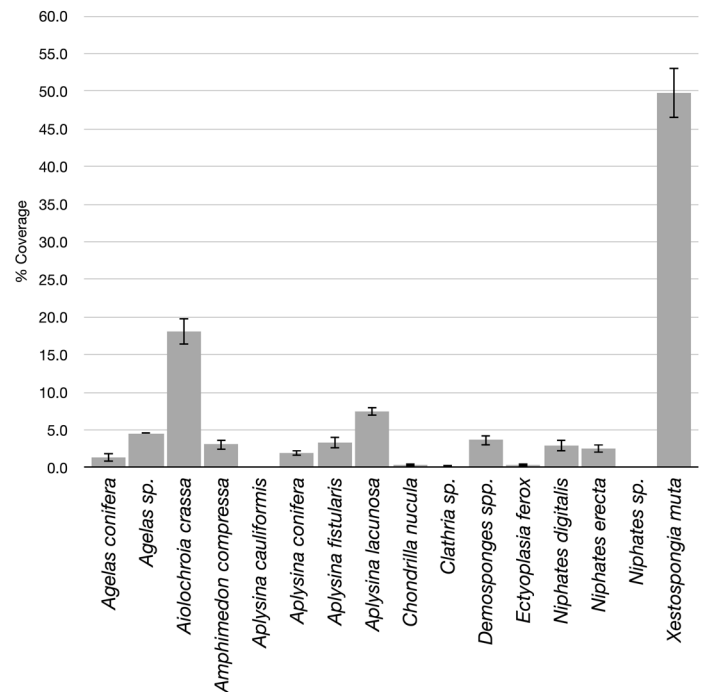


FIGURE 5. Mean \pm se percent coverage of sponges at Pigeon Islets, Guadeloupe in all pooled quadrats during the 2012–2021 study period.

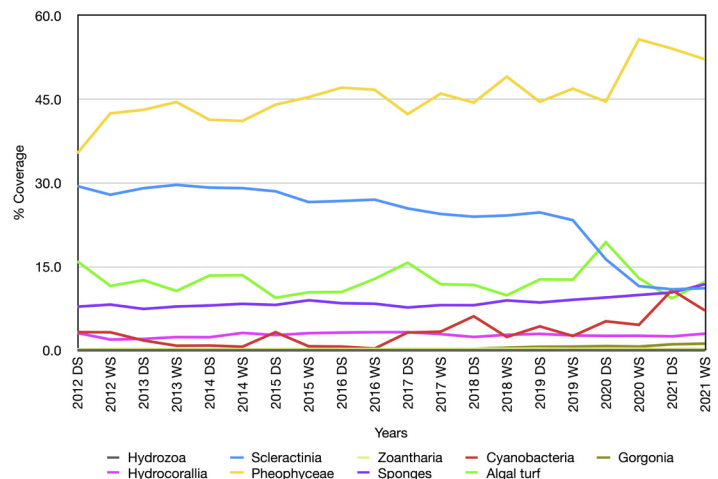


FIGURE 6. Changes in the substrate percent coverage by the main groups of benthic organisms at Pigeon Islets, Guadeloupe in all pooled quadrats, by season and by year, 2012–2021. WS–wet season; DS–dry season.

Orbicella faveolata ($18.2 \pm 2.6\%$).

Sponges, the second group of animals, included 16 species (Figure 5). *Xestospongia muta* accounted for $49.8 \pm 3.4\%$ of the sponge cover on all quadrats and periods pooled. *Aiellochroia crassa* and *Aplysina lacunosa* were the second and third most dominant species with $18.2 \pm 1.8\%$ and $7.5 \pm 0.6\%$, respectively.

Temporal changes in the benthic community

The changes in the percent coverage of the different groups of organisms over all quadrats by season and by year are presented in Figure 6. Beginning in the dry season of year 2020,

the Scleractinians showed a decrease due to the Stony Coral Tissue Loss Disease (SCTLD) that also affected the rest of the Caribbean. That decline was accompanied by an increase in the percent coverage of Pheophyceae algae and Cyanobacteria.

The evolutionary trends in taxonomic groups were an-

alyzed using the Spearman correlation coefficient. The tests revealed that Scleractinians ($S = -0.946$; $p < 0.0001$) were affected by a significant negative trend over the study period. Conversely, the Pheophyceae ($S = 0.776$; $p < 0.0001$), the Cyanobacteria ($S = 0.595$; $p = 0.007$), the Zoantharians ($S = 0.817$; $p < 0.0001$) and the Sponges ($S = 0.780$; $p < 0.0001$) showed a significant positive trend during the same period (Table 1). The other groups presented no significant changes: Hydrocorallians ($S = 0.110$; $p = 0.644$), Gorgonians ($S = 0.176$; $p = 0.457$) and algal turf ($S = -0.051$; $p = 0.831$; Table 1). A Friedman ranks analysis of variance did not reveal a significant change in the order of dominance of the different groups of organisms in the benthic community for the study period ($F = 17.420$; $p = 0.561$), despite the coral disturbance observed in 2020.

Global coral species richness in the quadrats was 13 in 2012 and 12 in 2021. The data presented no significant tendency ($R = -0.155$; $p = 0.512$). The temporal evolution of coral cover percentage is presented in Figure 7. Data on coral assemblages were submitted to 3 searches for trends with the Spearman's rank correlation: one covering the total survey period (2012–2021), the second considered the surveys carried out before the arrival of the SCTLD (2016–2019) and finally post-SCTLD (2019–2021). The objective of these tests was to check the stability of coral cover before the arrival of the disease and to discern the species sensitive to SCTLD. For the total period, 8 species showed a significant negative trend: *Dendrogyra cylindrus* ($S = -0.865$; $p < 0.0001$), *Diploria labyrinthiformis* ($S = -0.862$; $p < 0.0001$), *Madracis decactis* ($S = -0.656$; $p = 0.002$), *Meandrina meandrites* ($S = -0.937$; $p < 0.0001$), *Orbicella annularis* ($S =$

TABLE 1. Temporal trends of the different taxonomic groups in Pigeon Islets, Guadeloupe between 2012 and 2021. WS—percent coverage of the substrate in the wet season; DS—percent coverage of the substrate in the dry season. S—Spearman Rank statistic. P values in bold are significant.

Years	2012		2013		2014		2015		2016		2017		2018		2019		2020		2021		S	P
Seasons	DS	WS	DS	WS	DS	WS	DS	WS	DS	WS	DS	WS	DS	WS	DS	WS	DS	WS	DS	WS		
Scleractinia	29.4	27.9	29.1	29.7	29.2	29.1	28.5	26.6	26.8	27.0	25.4	24.4	24.0	24.2	24.7	23.3	16.3	11.5	10.9	11.1	-0.946	<0.0001
Zoantharia	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.3	0.2	0.3	0.3	0.3	0.2	0.3	0.3	0.3	0.2	0.817	<0.0001
Cyanobacteria	3.3	3.2	1.8	0.8	0.8	0.6	3.2	0.7	0.7	0.3	3.2	3.3	6.1	2.4	4.3	2.6	5.2	4.6	10.8	7.1	0.595	0.007
Gorgonia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.176	0.457
Hydrocorallia	3.1	1.9	2.0	2.4	2.3	3.1	2.7	3.1	3.2	3.2	3.2	2.9	2.4	2.8	2.9	2.7	2.6	2.6	2.5	3.0	0.110	0.644
Pheophyceae	35.3	42.5	43.1	44.5	41.3	41.1	44.1	45.4	47.1	46.7	42.3	46.0	44.4	49.1	44.6	46.9	44.6	55.8	54.1	52.2	0.776	<0.0001
Sponges	7.8	8.2	7.4	7.8	8.0	8.3	8.1	9.0	8.4	8.3	7.7	8.1	8.1	8.9	8.6	9.1	9.5	9.9	10.4	11.8	0.780	<0.0001
Algal turf	15.9	11.5	12.6	10.6	13.4	13.5	9.4	10.4	10.4	12.8	15.7	11.8	11.7	9.9	12.7	12.7	19.4	12.9	9.3	12.3	-0.051	0.8

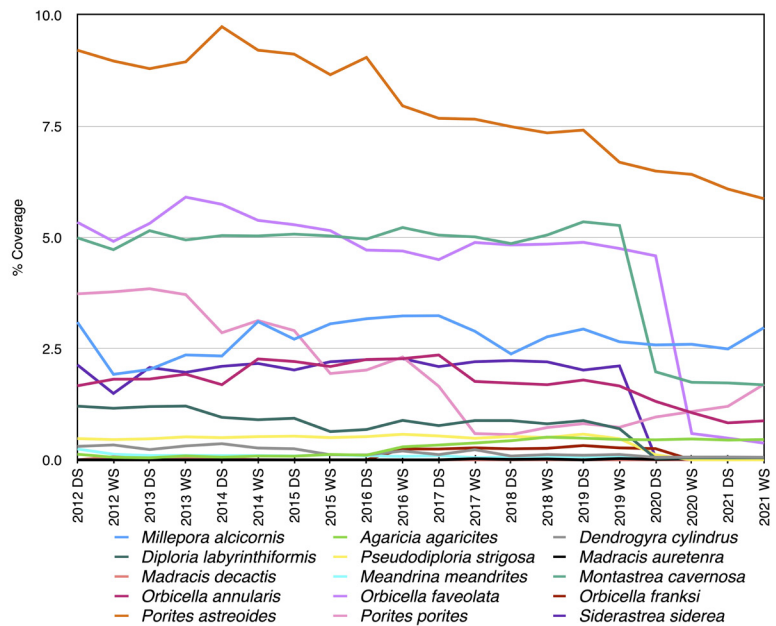


FIGURE 7. Annual variation of the global coral percent coverage at Pigeon Islets, Guadeloupe in the quadrats from 2012–2021. WS—wet season; DS—dry season.

TABLE 2. Results of the Spearman correlation tests (S) for coral species in Pigeon Islets, Guadeloupe between 2012 and 2021. WS—percent coverage of the substrate in the wet season; DS—percent coverage of the substrate in the dry season. P values in bold are significant.

Years	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2012–2021 (overview)		2012–2019 (before SCTLD)		2019–2021 (post SCTLD)	
Seasons	DS	WS	DS	WS	DS	WS	DS	WS	DS	WS	S	P	S	P	S	P
<i>Millepora alcicornis</i>	3.1	1.9	2.0	2.4	2.3	3.1	2.7	3.1	2.7	3.1	0.110	0.644	0.357	0.192	−0.086	0.919
<i>Madracis decactis</i>	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	−0.656	0.002	−0.668	0.008	0	0
<i>Madracis auretenra</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.805	<0.0001	0.569	0.029	0.543	0.356
<i>Agaricia agaricites</i>	0.1	0.1	0.0	0.1	0.1	0.1	0.4	0.5	0.5	0.5	0.865	<0.0001	0.836	0.000	−0.371	0.497
<i>Siderastrea siderea</i>	2.1	1.5	2.1	2.0	2.1	2.2	2.2	2.2	2.0	2.1	−0.298	0.202	0.421	0.119	−0.714	0.136
<i>Porites astreoides</i>	9.2	9.0	8.8	8.9	9.7	9.2	7.7	7.5	7.4	6.7	−0.922	<0.0001	−0.814	0.000	−1.000	0.003
<i>Porites porites</i>	3.7	3.8	3.8	3.7	2.9	3.1	2.9	1.9	0.9	0.6	−0.792	<0.0001	−0.929	<0.0001	0.943	0.017
<i>Diploria labyrinthiformis</i>	1.2	1.2	1.2	1.2	1.0	0.9	0.9	0.8	0.9	0.7	−0.862	<0.0001	−0.757	0.002	−0.486	0.356
<i>Pseudodiploria strigosa</i>	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.0	−0.264	0.260	0.646	0.011	−0.941	0.017
<i>Orbicella annularis</i>	1.7	1.8	1.8	1.9	1.7	2.3	2.4	1.8	1.7	1.7	−0.565	0.011	0.029	0.923	−0.943	0.017
<i>Orbicella faveolata</i>	5.3	4.9	5.3	5.9	5.7	5.4	4.5	4.9	4.8	4.8	−0.832	<0.0001	−0.686	0.006	−1.000	0.003
<i>Orbicella franksi</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.3	0.2	0.3	0.445	0.051	0.870	<0.0001	−0.941	0.017
<i>Montastrea cavernosa</i>	5.0	4.7	5.2	4.9	5.0	5.0	5.1	5.0	5.2	5.1	−0.259	0.270	0.336	0.221	−0.845	0.003
<i>Meandrinia meandrites</i>	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	−0.937	<0.0001	−0.875	<0.0001	−0.845	0.003
<i>Dendrogya cylindrus</i>	0.3	0.3	0.2	0.3	0.4	0.3	0.2	0.1	0.1	0.1	−0.865	<0.0001	−0.796	0.001	−0.543	0.297
<i>Palythoa caribbaeorum</i>	0.2	0.2	0.2	0.2	0.2	0.2	0.3	0.2	0.3	0.2	0.817	<0.0001	0.864	<0.0001	−0.657	0.175

−0.565; $p = 0.011$), *Orbicella faveolata* ($S = -0.832$; $p < 0.0001$), *P. astreoides* ($S = -0.922$; $p < 0.0001$) and *Porites porites* ($S = 0.792$; $p < 0.0001$). In contrast, *Agaricia agaricites* ($S = 0.865$; $p < 0.0001$) and *Madracis auretenra* ($S = 0.805$; $p < 0.0001$) were the only coral species presenting a significant positive trend. The other species remained stable over the period (Table 2).

Before the occurrence of SCTLD, from 2012 to 2019, the coverage of the different coral species changed significantly, with the exception of 4 species. The percent coverage of *D. cylindrus* ($S = -0.796$; $p = 0.001$), *D. labyrinthiformis* ($S = -0.757$; $p = 0.002$), *M. decactis* ($S = -0.668$; $p = 0.008$), *M. meandrites* ($S = -0.875$; $p < 0.0001$), *O. faveolata* ($S = -0.686$; $p = 0.006$), *P. astreoides* ($S = -0.814$; $p < 0.0001$) and *P. porites* ($S = 0.929$; $p < 0.0001$) decreased significantly. However, *A. agaricites* ($S = 0.836$; $p < 0.0001$), *Pseudodiploria strigosa* ($S = 0.646$; $p = 0.011$), *M. auretenra* ($S = 0.569$; $p = 0.029$) and *Orbicella franksi* ($S = 0.870$; $p < 0.0001$) showed a significant positive trend (Table 2).

After the occurrence of SCTLD, *P. porites* was the only species with a positive trend ($S = 0.943$; $p = 0.017$). In contrast, the percent coverage of 7 species decreased significantly: *P. strigosa* ($S = -0.941$; $p = 0.017$), *M. meandrites* ($S = -0.845$; $p = 0.033$), *M. cavernosa* ($S = -1.000$; $p = 0.003$), *O. annularis* ($S = 0.943$; $p = 0.017$), *O. faveolata* ($S = -1.000$; $p = 0.003$), *O. franksi* ($S = -0.941$; $p = 0.017$), and *P. astreoides* ($S = -1.000$; $p = 0.003$; Table 2). The remaining coral species did not show significant trends in percentage of cover change following SCTLD. Thus, coral cover was mostly impacted after the arrival of the disease. Based on the results of Friedman ranks variance analysis, the order of dominance between coral species changed significantly over the study period ($F = 43.935$; $p < 0.0001$). *Post-hoc* multiple comparison tests showed that the 2020 and 2021 surveys, carried out after the arrival of the disease, are responsible for this disparity.

Four sponge species presented a significant positive trend in percent coverage over the study period: *A. conifera* ($S = 0.950$; $p < 0.0001$), *Chondrilla nucula* ($S = 0.936$; $p < 0.0001$), *Clathria* sp. ($S = 0.703$; $p = 0.001$) and *X. muta* ($S = 0.968$; $p < 0.0001$). In contrast, the percentage cover of *Agelas conifera* ($S = -0.783$; $p < 0.0001$), *Agelas* sp. ($S = -0.759$; $p < 0.0001$) and *Ectyoplasia ferox* ($S = -0.534$; $p < 0.017$) significantly decreased during the period (Table 3). Considering the dominance of species, a Friedman analysis of variance of ranks did not reveal changes in the order of dominance of sponge species over the study period ($F = 11.980$; $p = 0.886$).

Coral tissue damage (2017–2021)

Two events impacted the coral community on all the quadrats. First, a bleaching phenomenon occurred in 2019 due to an abnormal warming of the sea temperature (Figure 8). The bleached coral tissue represented a total surface area of 1545.2 cm², i.e., 16% of the total coral tissue damage. Nevertheless, all the bleached colonies recovered during the next year. Secondly, in 2020, the arrival of SCTLD resulted in the necrosis of 8212.3 cm² of coral tissue within all the quadrats, and accounted for 83% of tissue damage (Figure 8). Other tissue necrosis caused by predation (worms, molluscs, fish, etc.) represented only a small area (89.7 cm²) i.e., 1% of all lesions observed. No

TABLE 3. Results of the Spearman correlation tests (S) for the sponge species in Pigeon Islets, Guadeloupe between 2012 and 2021. WS—percent coverage of the substrate in the wet season; DS—percent coverage of the substrate in the dry season. P values in bold are significant.

Years	2012		2013		2014		2015		2016		2017		2018		2019		2020		2021		S	P
Seasons	DS	WS	DS	WS	DS	WS	DS	WS	DS	WS	DS	WS	DS	WS	DS	WS	DS	WS	DS	WS		
<i>Chondrilla nucula</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.02	0.02	0.02	0.03	0.05	0.07	0.06	0.09	0.09	0.09	0.08	0.936	<0.0001
<i>Agelas conferta</i>	0.38	0.24	0.12	0.14	0.18	0.15	0.27	0.17	0.13	0.16	0.18	0.04	0.02	0.03	0.02	0.03	0.03	0.03	0.02	0.02	−0.783	<0.0001
<i>Agelas</i> sp.	0.73	0.52	0.57	0.54	0.51	0.58	0.61	0.55	0.59	0.55	0.35	0.22	0.18	0.19	0.21	0.20	0.20	0.20	0.23	0.20	−0.759	0.000
<i>Clathria</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01	0.03	0.03	0.27	0.02	0.01	0.02	0.00	0.01	0.01	0.703	0.001
<i>Ectyoplasia ferox</i>	0.01	0.04	0.03	0.03	0.05	0.08	0.00	0.10	0.08	0.07	0.06	0.08	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	−0.534	0.017
<i>Niphates erecta</i>	0.21	0.16	0.14	0.13	0.14	0.31	0.26	0.41	0.28	0.33	0.23	0.35	0.24	0.28	0.26	0.23	0.11	0.11	0.10	0.14	−0.222	0.344
<i>Amphimedon compressa</i>	0.30	0.59	0.07	0.20	0.27	0.25	0.23	0.24	0.29	0.37	0.35	0.08	0.13	0.14	0.11	0.24	0.20	0.30	0.39	0.65	0.065	0.787
<i>Xestospongia muta</i>	3.24	3.17	2.54	3.49	3.48	3.60	3.40	4.03	3.90	3.76	3.79	4.55	4.82	5.02	4.96	5.27	5.54	5.63	5.92	6.30	0.968	<0.0001
<i>Aplysina cauliformis</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.02	0.01	0.02	0.02	0.03	0.01	0.00	0.00	0.00	0.00	0.319	0.170
<i>Aplysina fistularis</i>	0.09	0.36	0.31	0.25	0.44	0.43	0.31	0.58	0.11	0.07	0.08	0.11	0.12	0.17	0.22	0.28	0.34	0.42	0.50	0.59	0.189	0.422
<i>Aplysina lacunosa</i>	0.61	0.63	0.69	0.71	0.71	0.69	0.69	0.64	0.79	0.76	0.53	0.67	0.42	0.47	0.53	0.48	0.55	0.69	0.76	0.94	−0.099	0.677
<i>Aplysina conferta</i>	0.07	0.06	0.06	0.07	0.08	0.08	0.08	0.08	0.09	0.13	0.18	0.21	0.24	0.25	0.21	0.16	0.36	0.30	0.25	0.29	0.950	<0.0001
<i>Aiolochroia crassa</i>	1.44	1.75	2.38	1.70	1.64	1.73	1.73	1.56	1.38	1.41	1.40	1.12	1.17	1.30	1.21	1.55	1.56	1.74	1.68	2.01	−0.192	0.414
<i>Demosponges</i> spp.	0.69	0.37	0.25	0.36	0.31	0.17	0.27	0.22	0.39	0.34	0.16	0.24	0.22	0.19	0.13	0.34	0.41	0.35	0.37	0.53	0.003	0.992

other coral diseases, such as “white band”, “black band”, or “white plague” were observed within the quadrats during the course of the study.

Young coral and adult colony recruitment and mortality (2017–2021)

Between 2017 and 2021, 24 young corals recruited and 76 colonies died among 169 coral colonies monitored. *Millepora alcicornis* and *A. agaricites* presented the highest level of larvae recruitment over the study period (6 recruits each), followed by *P. astreoides* (5 recruits). In contrast, *M. alcicornis* and *P. astreoides* were the species with the highest mortality of colonies during the study (14 and 18, respectively). *Montastrea cavernosa* was also among the species presenting a high mortality (10 colonies lost during the study). Two peaks of mortality were remarkable in the wet season in 2017 (15 out of 127 colonies died) and in the dry season in 2020 (15 out of 101 colonies), when SCTLD disease appeared (Table 4).

From an overall perspective, the recruitment of all species reached a maximum in the wet season of 2017 (6 recruits). The Spearman rank correlation coefficient did not reveal any significant trend in coral recruitment ($S = -0.043$; $p = 0.917$), nor for colony mortality ($S = 0.379$; $p = 0.282$).

DISCUSSION

Events affecting the benthic community (2012–2021)

Coral bleaching is an event that is increasingly affecting tropical areas in response to climate change. Rising sea temperatures is the main factor responsible for this phenomenon (Jokiel and Coles 1977, Jokiel and Coles 1990, Glynn and D'Croz 1990, Eakin et al. 2010).

In the lesser Antilles, corals tolerate a maximum sea temperature of 29°C (Bouchon et al. 2008). Above this threshold, corals experience thermal stress and expel zooxanthellae from their tissue. However, coral bleaching is reversible if sea temperatures decrease rapidly below the 29°C tolerance. The final coral mortality therefore depends on both amount of the increase as well as the duration of elevated water temperatures (McClanahan et al. 2007).

The year 2019 was marked by an episode of coral bleaching, corresponding to a 122 d period during which the water temperature exceeded 29°C and reached a maximum of 30.5°C in Pigeon Islets, recorded by a thermograph at 3 m depth (Malahel 2020). Another thermograph placed at 23 m depth near Pigeon Islets recorded a 77 d period above 29°C with a maximum of 29.2°C. Nevertheless, there was no loss of corals in Guadeloupe as a result of this phenomenon, since all the bleached corals had re-

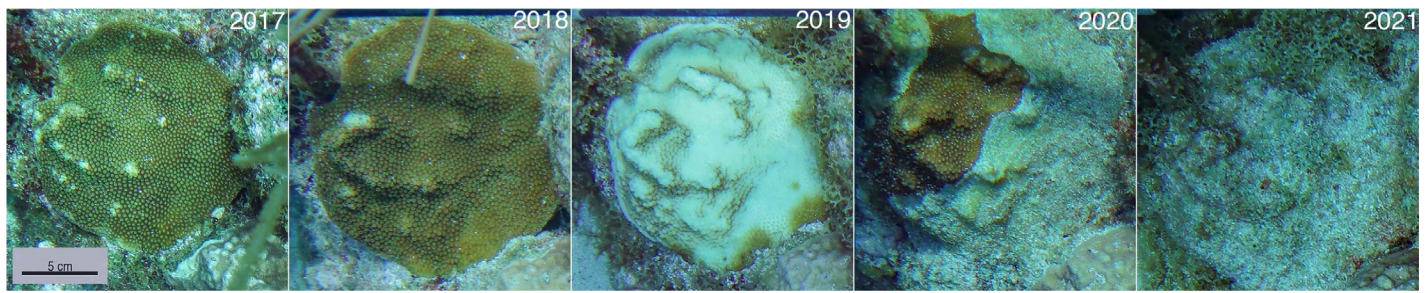


FIGURE 8. Example of tissue damage observed in an *Orbicella faveolata* colony over time. 2017: the colony was observed with “coral biting”. 2018: The colony healed from previous necroses. 2019: Bleached colony due to thermal stress. 2020: SCTLD observed on *O. faveolata*, leading to the death of the colony. 2021: Dead colony covered with algal turf and macroalgae. (Photos: D. Baltide).

covered their zooxanthellae the following season. There had not been such a severe episode of bleaching since 2005 in Guadeloupe and the West Indies (Wilkinson and Souter 2008). In Guadeloupe, 76% of the corals bleached in 2005 and the induced mortality reached 45% in 2006 (Bouchon et al. 2008). In the Caribbean, the year 2005 was the warmest in over 150 years and this phenomenon was the source of the most important coral bleaching observed in the region (Eakin et al. 2010).

In May 2020, the first case of SCTLD observed in Guadeloupe was on Pigeon Islets (Bouchon et al. 2023). SCTLD is the latest coral disease, first appearing in Florida in 2014, and showed a 30% coral mortality rate (Precht et al. 2016, Walton 2018). The agent was first supposed to be bacterial, but recent research suggests a viral origin (Work et al. 2021). The disease is not linked to anthropogenic actions. Transmission of the pathogen appears to occur through direct contact between colonies (Aeby et al. 2019), and currents constitute the main transport vector (Sharp et al. 2020). The consequences of SCTLD are a progressive loss of living tissue that leads to the death of the affected coral in a short time. The total necrosis of a colony varies between 4 and 7 days, depending on colony size (Dobbelaere et al. 2020, Meiling et al. 2021).

Many corals present in our study quadrats died because of SCTLD. In 2019, the percentage coverage of Scleractinians represented 24% of all quadrats; this decreased to 13.9% in 2020, and finally to 11% in 2021. In contrast, although Caribbean sponges are prone to diseases such as “orange band” and “red band” (Webster 2007), no diseased or bleached sponges were found in any quadrat during the course of the study.

Among the 21 coral species affected by SCTLD in the Caribbean, the mortality rate is quite variable, from < 10% to 94% according to reef sites (Alvarez-Filip et al. 2022). For example, in the Bahamas coral mortality fluctuated from 31.5% to 42.7% depending on the island (Dahlgren et al. 2021).

Coral death generates free substratum for colonization. As a consequence, the percent coverage of other benthic organisms increased from 45.7% to 53.1% for Pheophyceae, from 3.4% to 9% for Cyanobacteria and from 8.8% to 11.1% for sponges. These 3 groups of organisms had not exhibited significant variations in their abundance prior to the arrival of coral disease. Similar observations have been previously described in the Ca-

ribbean region (McCook et al. 2001, McManus and Polsenberg 2004) as well as than in the Indo-Pacific area (Diaz-Pulido et al. 2002, Nugues and Bak 2006).

SCTLD was the major cause of tissue damage (83%) in the quadrats. All the affected corals died without exception. The coral cover dropped by 54.2% due to the SCTLD. This disease led to an accelerated deterioration of the health of the reefs of Guadeloupe Island.

The necrosis of coral tissue due to predation by worms, mollusks and fish represent only 1% of tissue damage over all quadrats. Furthermore, the tissues of the coral colonies affected by this type of necrosis eventually healed. In a comprehensive review of the literature concerning coral predators, Renzi et al. (2022) suggested that the invertebrate predators may interfere with coral diseases and so enhance their impact on the corals.

Overview of 2012–2021 results

The dominant groups of organisms were Pheophyceae ($45.6 \pm 1.9\%$), Scleractinians ($24.0 \pm 2.9\%$) and algal turf ($12.4 \pm 1.1\%$). Our study was characterized by a drastic decrease in the percent coverage of Scleractinians and by an increase of Pheophyceae, Cyanobacteria and sponges around the year 2020. Additionally, macroalgae dominated the substrate and prevented the development of minor groups such as Zoantharians and Hydrocorallians.

Despite a decrease in coral percent coverage, the species richness of coral assemblages increased during the period with the appearance of *O. franksi* (in 2016) and *M. auretenra* (in 2017) recruits in the quadrats. In terms of occupation of the substrate, *P. astreoides* was the dominant coral species throughout all the study (2012 – 2021). Overall, it appears that the coral species richness was not significantly affected by SCTLD. However, the coral assemblage was already showing some species with negative trends due to anthropogenic conditions around Pigeon islets prior to the advent of SCTLD, although this did not appear to impact its stability.

The order of dominance of coral species changed significantly during the years 2020 and 2021, i.e. at the onset of SCTLD that showed a significant loss of corals. The disease disrupted the stability of the coral community. However, *P. porites* appeared to be less sensitive to SCTLD, with a significant increase in percent coverage between 2019 and 2021. Furthermore, it should

TABLE 4. Young coral recruitment and adult colony mortality in Pigeon Islets, Guadeloupe between 2017 to 2021. WS—wet season; DS—dry season; Recr.—Recruitment)

Years Species	2017						2018						2019						2020						2021						TOTAL	
	DS		WS		Recr.	Dead	DS		WS		Recr.	Dead	DS		WS		Recr.	Dead	DS		WS		Recr.	Dead	DS		WS		Recr.	Dead		
Recr.	Dead	Recr.	Dead	Recr.			Dead	Recr.	Dead	Recr.			Dead	Recr.	Dead	Recr.			Dead	Recr.	Dead	Recr.			Dead	Recr.	Dead	Recr.			Dead	Recr.
Millepora alicornis	1	0	2	4	0	3	0	0	0	2	0	2	0	0	2	0	0	1	2	0	1	2	0	1	0	0	0	6	14			
Madracis decactis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
Madracis auretenra	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	5			
Agaricia agaricites	1	0	2	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	6	5	0			
Siderastrea siderea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	2	1			
Porites astreoides	0	1	0	3	0	2	1	3	0	1	2	1	0	0	1	2	1	0	1	0	1	0	1	0	0	0	4	5	18			
Porites porites	0	0	0	4	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	3	6	0			
Diploria labyrinthiformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0			
Pseudodiploria strigosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	2	0			
Orbicella annularis	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0			
Orbicella faveolata	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	6	0			
Orbicella franki	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0			
Montastrea cavernosa	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	1	1	10	0			
Meandrina meandrites	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0			
Dendrogyra cylindrus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0		
Palythoa caribbaeorum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0			
TOTAL	2	1	6	15	0	5	2	5	3	3	2	4	1	15	3	14	4	7	1	7	4	7	1	7	24	76						

also be noted that *P. astreoides* did not develop any lesions due to SCTLD in any quadrat, likely because this species has better adaptation strategies in the environment than other Scleractinians against coral bleaching and diseases (Bove et al. 2019, Claquin et al. 2021). Overall, changes among the dominant species were observed in massive corals with similar growth rates ($\pm 1\text{cm/year}$).

The maximum mortality of Scleractinians was reached in 2020 (15 colonies), due to SCTLD. However, an important mortality event was reached in 2017 because of mechanical destruction observed in one quadrat, assumed to be caused by a boat anchor. In total, 76 coral colonies died during the study, including 43 (57%) due to the SCTLD. Thus, despite recruitment of 24 young coral colonies during the course of the study, coral mortality was not compensated by coral recruitment in the quadrats.

Sponges are also in competition with corals for the colonization of substrate. Some sponge species are bioindicators of a healthy environment, while others are bioindicators of pollution by organic matter. For instance, *Chondrilla nucula* is a bioindicator of organic matter pollution (Alcolado 2007). This species was present in the quadrats and its percent surface cover increased significantly during the course of the study. Additionally, *Aplysina cauliformis* thrives in areas of high sedimentation (Alcolado 2007), and this was also a common species collected in our study. The congener, *Aplysina fistularis*, is an indicator of areas in good ecological condition (Alcolado and Herrera—Moreno 1987, Alcolado 2007). However, both these species showed no significant trends in the quadrats. The dominant sponge in our study was *Xestospongia muta*, one of the dominant species in the Caribbean, especially on healthy reefs (McMurray et al. 2008). Due to its large size, it is an important competitor for access to the substrate.

One of the main objectives of this study was to establish a monitoring protocol of the benthic communities around the Pigeon Islets. Secondly, our objective was to assess the health of the organisms present in the quadrats, with a particular focus on the corals that constitute the “key-stone” species of the reef ecosystem. A decade of monitoring has highlighted the significant environmental changes that have affected the coral communities in Guadeloupe Island. Considering the loss of biodiversity observed in the quadrats, it would be advisable to add other monitoring sites around the Pigeon Islets, which would increase the scope of the observations. Parallel studies in other areas of the National Park of Guadeloupe would also reinforce this monitoring program. The photo—quadrat method allowed an efficient analysis of the dynamics of the temporal evolution of benthic communities. The drastic decrease of the surface occupied by corals, keystone species of the reef ecosystem, is a major problem that requires the greatest attention for the economic sustainability of the island and for the preservation of the natural heritage.

ACKNOWLEDGMENTS

The authors acknowledge the technical staff of the National Park of Guadeloupe and in particular D. Baltide, who facilitated the photographs of the quadrats throughout the study.

LITERATURE CITED

- Aeby, G.S., B. Ushijima, J.E. Campbell, S. Jones, G.J. Williams, J.L. Meyer, C. Häse, and V.J. Paul. 2019. Pathogenesis of a tissue loss disease affecting multiple species of corals along the Florida Reef Tract. *Frontiers in Marine Science* 6:678. <https://doi.org/10.3389/fmars.2019.00678>
- Alcolado, P. 2007. Reading the code of coral reef sponge community composition and structure for environmental biomonitoring: Some experiences from Cuba. In: M.R. Custódio, G. Lobo-Hajdu, E. Hajdu, and G. Muricy, eds. *Porifera Research. Biodiversity, Innovation and Sustainability*. Livros de Museu Nacional 28, Rio de Janeiro, Brazil, p. 3–10.
- Alcolado, P. and A. Herrera-Moreno. 1987. Efectos de la contaminación sobre las comunidades de esponjas en el Litoral de La Habana, Cuba. *Academia de Ciencias de Cuba, Reporte de Investigación del Instituto de Oceanología* 68:1–17.
- Alvarez-Filip, L., F.J. González-Barrios, E. Pérez-Cervantes, A. Molina-Hernández, and N. Estrada-Saldivar. 2022. Stony coral tissue loss disease decimated Caribbean coral populations and reshaped reef functionality. *Communications Biology* 5(1):440. <https://doi.org/10.1038/s42003-022-03398-6>
- Batailler, C., C. Bouchon, Y. Bouchon-Navaro, F. Kerninon, and S. Mège. 2021. La Guadeloupe. In: IFRECOR, ed. *État de santé des récifs coralliens, herbiers marins et mangroves des outre-mer français. Bilan 2020. Final Report*. IFRECOR, Paris, France, p. 85–107.
- Bouchon, C. and J. Laborel. 1990. Les peuplements coralliens du Grand Cul-de-Sac Marin de Guadeloupe (Antilles françaises). *Annales de l'Institut Océanographique* 66:19–36. https://kolibris.univ-antilles.fr/permalink/33UAG_INS-T/6pkts6/alma991000641069705746
- Bouchon, C., P. Portillo, M. Louis, F. Mazeas, and Y. Bouchon-Navaro. 2008. Évolution récente des récifs coralliens des îles de la Guadeloupe et de Saint-Barthélemy. *Revue Écologie (Terre et Vie)* 63:45–65. <https://doi.org/10.3406/rev.2008.1398>
- Bouchon, C., C. Batailler, Y. Bouchon-Navaro, R. Garnier, F. Mazeas, P. Portillo, F. Kerninon, and M. Windstein. 2016. Guadeloupe. In: IFRECOR, ed. *État des récifs coralliens et des écosystèmes associés des Outre-mer français en 2015. Final report*. IFRECOR, Paris, France, p. 67–77.
- Bouchon, C., S. de Lavigne, S. Cordonnier, and Y. Bouchon-Navaro. 2023. Bilan de l'impact de la maladie corallienne « Stony Corals Tissue Loss Disease » (SCTLD) sur les récifs coralliens de Guadeloupe. Final report. Parc National de la Guadeloupe, Guadeloupe, France. 40 p.
- Bouchon-Navaro, Y. 1997. Les peuplements ichthyologiques récifaux des Antilles. *Distribution spatiale et dynamique temporelle*. Ph.D thesis. Université des Antilles et de la Guyane, Guadeloupe, France, 247 p.
- Bouchon-Navaro, Y. and C. Bouchon. 2000. Dossier de création de la réserve marine et terrestre des îlets Pigeon (Guadeloupe). Part 1: Présentation générale et milieu marin. Technical report. Parc National de la Guadeloupe, Université des Antilles, Guadeloupe, France. 71 p.
- Bove, C.B., J.B. Ries, S.W. Davies, I.T. Westfield, J. Umbanhowar, and K.D. Castillo. 2019. Common Caribbean corals exhibit highly variable responses to future acidification and warming. *Proceedings of the Royal Society B* 286(1900):20182840. <https://doi.org/10.1098/rspb.2018.2840>
- Cheal, A.J., M.A. MacNeil, E. Cripps, M.J. Emslie, M. Jonker, B. Schaffelke, and H. Sweatman. 2010. Coral-macroalgal phase shifts or reef resilience: Links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. *Coral Reefs* 29:1005–1015. <https://doi.org/10.1007/s00338-010-0661-y>
- Claquin, P., M. Rene-Trouillefou, P.J. Lopez, A. Japaud, Y. Bouchon-Navaro, S. Cordonnier, and C. Bouchon. 2021. Singular physiological behavior of the Scleractinian coral *Porites astreoides* in the dark phase. *Coral Reefs* 40:139–150. <https://doi.org/10.1007/s00338-020-02023-4>
- Connell, S., M.S. Foster, and L. Airoidi. 2014. What are algal turfs? Towards a better description of turfs. *Marine Ecology Progress Series* 495:299–307. <https://doi.org/10.3354/meps10513>
- Dahlgren, C., V. Pizarro, K. Sherman, W. Greene, and J. Oliver. 2021. Spatial and temporal patterns of stony coral tissue loss disease outbreaks in the Bahamas. *Frontiers in Marine Science* 8:82114. <https://doi.org/10.3389/fmars.2021.682114>
- Díaz-Pulido, G. and L. McCook. 2002. The fate of bleached corals: Patterns and dynamics of algal recruitment. *Marine Ecology Progress Series* 232:115–128. <https://doi.org/10.3354/meps232115>
- Dobbelaere, T., E.M. Muller, L.J. Gramer, D.M. Holstein, and E. Hanert. 2020. Coupled epidemio-hydrodynamic modeling to understand the spread of a deadly coral disease in Florida. *Frontiers in Marine Science* 7:591881. <https://doi.org/10.3389/fmars.2020.591881>
- Eakin, C.M., J.A. Morgan, S.F. Heron, T.B. Smith, G. Liu, L. Alvarez-Filip, B. Baca, E. Bartels, C. Bastidas, C. Bouchon, M. Brandt, A.W. Bruckner, Bunkley-Williams, A. Cameron, B.D. Causey, B. D. M. Chiappone, T.R.L. Christensen, M.J.C. Crabbe, O. Day, E. de la Guardia, G. Díaz-Pulido, D. DiResta, D.L. Gil-Agudelo, D.S. Gilliam, R.N. Ginsburg, S. Gore, H.M. Guzmán, J.C. Hendee, E.A. Hernández-Delga-

- do, E. Husain, C.F.G. Jeffrey, R.J. Jones, E. Jordán–Dahlgren, L.S. Kaufman, D.I. Kline, P.A. Kramer, J.C. Lang, D. Lirman, J. Mallela, C. Manfrino, J.P. Maréchal, K. Marks, J. Mihaly, W.J. Miller, E.M. Mueller, E.M. Muller, C.A. Orozco Toro, H.A. Oxenford, D. Ponce–Taylor, N. Quinn, K.B. Ritchie, S. Rodríguez, A.R. Ramirez, S. Romano, J.F. Samhouri, J.A. Sánchez, G.P. Schmahl, B.V. Shank, W.J. Skirving, S.C.C. Steiner, E. Villamizar, S.M. Walsh, C. Walter, E. Weil, E.H. Williams, K.W. Roberson, and Y. Yusuf. 2010. Caribbean corals in crisis: Record thermal stress, bleaching, and mortality in 2005. *PLoS One* 5(11):e13969. <https://doi.org/10.1371/journal.pone.0013969>
- Lessios, H.A. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: What have we learned? *Annual Review of Ecology and Systematics* 19:371–393. <https://doi.org/10.1146/annurev.es.19.110188.002103>
- Glynn, P.W. and L. D’Croz. 1990. Experimental evidence for high temperature stress as the cause of El Niño–coincident coral mortality. *Coral Reefs* 8:181–191. <https://doi.org/10.1007/BF00265009>
- Hollander, M., D.A. Wolfe, and E. Chicken. 2013. *Nonparametric Statistical Methods*. John Wiley & Sons, New York, NY, USA, 848 p.
- Jackson, J.B.C., M.K. Donovan, K.L. Cramer, and V.V. Lam. 2014. Status and trends of Caribbean coral reefs: 1970–2012. *Global Coral Reef Monitoring Network*, IUCN, Gland, Switzerland, 304 p. <https://doi.org/10.13140/2.1.4868.6726>
- Jokiel, P.L. and S.L. Coles. 1977. Effects of temperature on the mortality and growth of Hawaiian reef corals. *Marine Biology* 43:201–208. <https://doi.org/10.1007/BF00402312>
- Jokiel, P.L. and S.L. Coles. 1990. Response of Hawaiian and other Indo–Pacific reef corals to elevated temperature. *Coral Reefs* 8:155–162. <https://doi.org/10.1007/BF00265006>
- Malahel, H. 2020. Suivi de la température de la mer et de ses impacts sur le blanchissement corallien de 2017 à 2019 à l’aide de thermographes. Technical report. Parc National de la Guadeloupe. Guadeloupe, France. 19 p.
- McClanahan, T.R., M. Ateweberhan, C.A. Muhando, J. Maina, and M.S. Mohammed. 2007. Effects of climate and sea-water temperature variation on coral bleaching and mortality. *Ecological Monographs* 77:503–525. <https://doi.org/10.1890/06–1182.1>
- McCook, L.J. 1999. Macroalgae, nutrients and phase shifts on coral reefs: Scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18:357–367. <https://doi.org/10.1007/s003380050213>
- McCook, L., J. Jompa and G. Diaz–Pulido. 2001. Competition between corals and algae on coral reefs: A review of evidence and mechanisms. *Coral Reefs* 19:400–417. <https://doi.org/10.1007/s003380000129>
- McManus, J. and J. Polsenberg. 2004. Coral–algal phase shifts on coral reefs: Ecological and environmental aspects. *Progress in Oceanography* 60:263–279. <https://doi.org/10.1016/j.pocean.2004.02.014>
- McMurray, S.E., J.E. Blum, and J.R. Pawlik. 2008. Redwood of the reef: Growth and age of the giant barrel sponge *Xestospongia muta* in the Florida Keys. *Marine Biology* 155:159–171. <https://doi.org/10.1007/s00227–008–1014–z>
- Mège, S., M. Robert, G. Van Laere, D. Begot, D. Bonnissent, C. Bouchon, J. Breton, C. Dessert, D. Imbert, M. Louis, D. Monti, F. Pagey–Benito, and A. Rousteau. 2023. Politique scientifique du Parc National de la Guadeloupe. Mode d’acquisition de la connaissance et de participation à la recherche 2013 – 2023. Technical report. Parc National de la Guadeloupe. Guadeloupe, France. 54 p
- Meiling, S.S., E.M. Muller, D. Lasseigne, A. Rossin, A.J. Veglia, N. MacKnight, B. Dimos, N. Huntley, A.M.S. Correa, T.B. Smith, D.M. Holstein, L.D. Mydlarz, A. Apprill, and M.E. Brandt. 2021. Variable species responses to experimental stony coral tissue loss disease (SCTLD) exposure. *Frontiers in Marine Science* 8:670829. <https://doi.org/10.3389/fmars.2021.670829>
- Nugues, M. and R.P.M. Bak. 2006. Differential competitive abilities between Caribbean coral species and a brown alga: A year of experiments and a long–term perspective. *Marine Ecology–Progress Series* 315:75–86. <https://doi.org/10.3354/meps315075>
- Philippot, V. 1987. Annotated checklist of the Gorgonacea from Martinique and Guadeloupe Islands (F.W.I.). *Atoll Research Bulletin* 303:1–16. <https://doi.org/10.5479/si.00775630.303>
- Precht, W.F., B.E. Gintert, M.L. Robbart, R. Fura, and R. van Woesik. 2016. Unprecedented disease–related coral mortality in southeastern Florida. *Scientific Reports* 6:31374. <https://doi.org/doi:10.1038/srep31374>
- Renzi, J.J., E.C. Shaver, D.E. Burkepile, and B. Silliman. 2022. The role of predators in coral disease dynamics. *Coral Reefs* 41:405–422. <https://doi.org/10.1007/s00338–022–02219–w>
- Sharp, W.C., C.P. Shea, K.E. Maxwell, E.M. Muller, and J.H. Hunt. 2020. Evaluating the small–scale epidemiology of the stony–coral–tissue–loss–disease in the middle Florida Keys. *PLoS One* 15:e0241871. <https://doi.org/10.1371/journal.pone.0241871>
- Walton, C.J., N.K. Hayes, and D.S. Gilliam. 2018. Impacts of the regional multi–years, multispecies coral disease outbreak in southern Florida. *Frontiers in Marine Science* 5:323. <https://doi.org/10.3389/fmars.2018.00323>
- Webster, N.S. 2007. Sponge disease: A global threat? *Environmental Microbiology* 9:1363–75. <https://doi.org/doi:10.1111/j.1462–2920.2007.01303.x>
- Wilkinson, C. and D. Souter. 2008. Status of Caribbean coral reefs after bleaching and hurricanes in 2005. *Global Coral Reef Monitoring Network*, and Reef and Rainforest. Research Centre, Townsville, Australia, 152 p.
- Work T.M., T.M. Weatherby, J.H. Landsberg, Y. Kiryu, S.M. Cook, and E.C. Peters. 2021. Viral–like particles are associated with endosymbiont pathology in Florida corals affected by stony coral tissue loss disease. *Frontiers in Marine Science* 8:750658. <https://doi.org/10.3389/fmars.2021.750658>