Research Article

Contrasting color loss and restoration in survivors of the 2014–2017 coral bleaching event in the Turks and Caicos Islands

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Abstract

Coral cover throughout the Caribbean region has declined by approximately 80% since the 1970s (Gardner et al. in Ecology 86(1):174–184, 2005) attributed to a combination of environmental and anthropogenic factors, including ocean acidification, rising sea surface temperatures, increased susceptibility to disease, as well as increased frequency and strength of storms, development stress, and increased sediment and nutrient loads. Three Global Bleaching Events (GBE) coincide directly with El Niño warming phases in El Niño-Southern Oscillation cycle (1997–1998, 2009–2010, and 2014–2017). This study focuses the effects of anomalously high sea surface temperatures on Turks and Caicos Islands coral taxa during the 2014–2017 GBE. Interannual and interspecific variability in coral health offshore of South Caicos Island were evaluated between 2012 and 2018 using the CoralWatch citizen science Coral Health Chart method along belt transects at four dive survey sites. The study includes 104 site surveys conducted from 15 October 2012 to 18 July 2018. Coral health was assessed for the 35 principal coral taxa and 5646 individual corals. Data indicates that all coral taxa at the study sites were resilient to the maximum regional thermal stress during the 2014–2017 GBE, with boulder-type corals showing no significant bleaching as a result of the peak thermal stress in late 2015 and plate-type corals responding with a significant ($p < 0.05$) bleaching signal (i.e., coral color reductions), rebounding to pre-GBE pigmentations within months of the anomalously-high thermal stress. Boulder coral types were significantly healthier in 2017 than in 2014 when using coral color as a health diagnostic.

Keywords Global bleaching events · Coral bleaching · Citizen science · NOAA Coral Reef Watch · Turks and Caicos Islands · CoralWatch

1 Introduction

Climate-change induced increases in sea surface temperatures (SSTs) and the frequency of extreme thermal stress events have resulted in widespread coral bleaching [1–6]. For instance, when SSTs surpass a coral's thermal threshold, bleaching may occur. Coral bleaching mechanisms are linked with the unique endosymbiotic relationship between the host coral and single-celled dinoflagellates known as *Symbiodinium* (zooxanthellae), living within the coral polyps that provide corals with their color and 90% of their total energy through photosynthesis [7]. When corals become stressed, they expel their algal symbionts, losing both their pigmentation and primary source of nutrients [7, 8].

Approximately 90% of Caribbean coral reef systems are likely to experience severe bleaching in response to climate-change induced thermal stress by 2040 [9–11]. Over the past three decades, coral cover throughout the Caribbean has declined by approximately 80% [12]. Health

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declines of these reef biomes are largely attributable to major Global Bleaching Events (GBEs) that have occurred most recently in 1997–1998, 2009–2010, and 2014–2017, coinciding with El Niño warming phases in the El Niño-Southern Oscillation (ENSO) cycle [2, 6, 13]. Lough et al. [14] found that the level of thermal stress on coral reefs was about 3 times greater in the GBE of 1997–1998 than the level of thermal stress in pre-industrial El Niño of 1878, hinting that temperatures have been rising steadily with the Caribbean and Atlantic oceans experiencing the most severe stress. Although thermal stress in the Caribbean has been influencing coral health in years outside of major GBEs, the 2014–2017 event was detrimental to Caribbean reef ecosystems, particularly given the two extreme hurricanes in 2017 that damaged both shallow and deep reefs by dislodging coral colonies and turning them to rubble [15].

Seasonality of the environmental stressors, such as increases in water temperature, may impact coral susceptibility to bleaching [16]. Symbiont density responds to higher water temperatures negatively causing decreases in *Symbiodinium* [16]. However, recent studies reveal that the specific lineages, or clades, of *Symbiodinium* may influence the resistance and abilities of individual coral taxa to recover from environmental and thermal stress [7, 17]. Consequently, when evaluating the resistance of coral taxa and reefs to thermal stress, it is important to consider the multiple environmental, geographical, and physiological factors that can impact coral resistance and recovery from stress events such as the recent 2014–2017 GBE.

With SSTs predicted to increase in the coming years, a simple methodology of determining coral health is vital to gain a wide-spread assessment of bleaching and recovery [10]. The CoralWatch (CW) citizen science monitoring program enables non-specialists to assess coral health using a color chart (Fig. 1), providing a health diagnostic tool with the potential to expand global coral bleaching and health datasets, providing a low-cost proxy for evaluating and documenting natural coral color variability and health [18]. CW color health charts have been used in

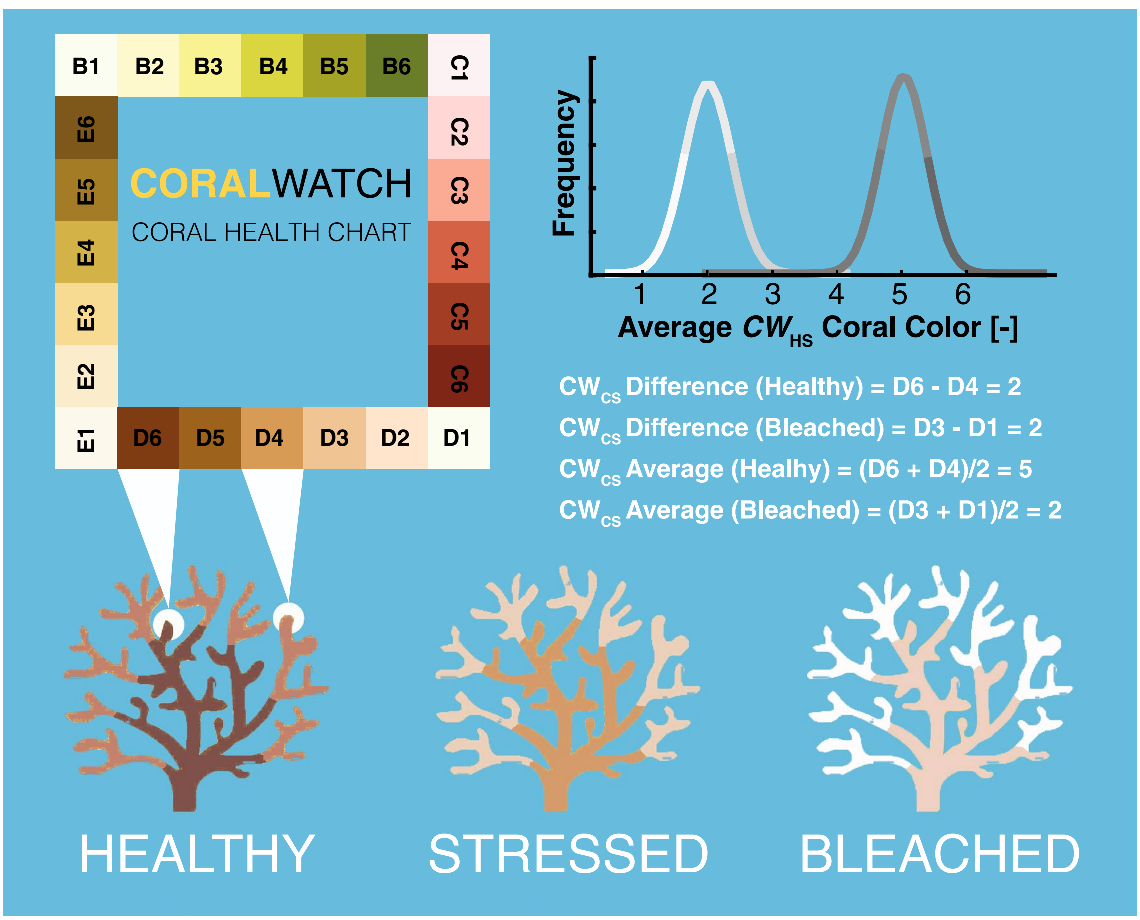

Fig. 1 CoralWatch Coral Health Chart sampling methodology, used to sample 5646 corals in the Turks and Caicos from 2012 to 2018 over 104 surveys. An example measurement of a darker, healthier coral is depicted, with hue $\boldsymbol{CW}_{HS}$ difference and average shown. Schematic based on "What is coral bleaching?" schematic, published by NOAA (2019)

over 25 published scientific papers to help validate, in part, remotely-sensed methods of monitoring thermal stress and coral bleaching threats [19]. Following Siebeck et al. [20], CW coral health score, CW_{HS}, can be used as a diagnostic to monitor coral health over time and coral sensitivity to regional thermal stress. Specifically, lighter CW_{HS} values (closer to 1) represent decreased densities of *Symbiodinium* associated with stress and bleaching, while darker CW_{HS} values (closer to 6) represent higher densities of *Symbiodinium* and therefore healthier or recovering corals [18, 20] (Fig. 1). According to Siebeck et al. [20], a shift in CW_{HS} distributions to lighter color hues over time indicates reductions in zooxanthellae density.

This study investigates the interannual and interspecific variability in Turks and Caicos coral taxa stress and subsequent recovery, evaluated using the CW Coral Health Chart method, in response to the 2014–2017 Global Bleaching Event. South Caicos Island, historically dominated by *Montastraea* spp., *Siderastrea* spp., *and Porites* spp., has seen a drop in average coral cover from 32.5% in 1995 to 21.9% in 2004 with signs of increased coral bleaching and disease [21]. Compared to neighboring countries in the Caribbean, South Caicos has reasonably healthy reefs, perhaps in part due to lower density tourism and minimal anthropogenic drivers of coral stress [13]. South Caicos Island fringing reefs are characterized as narrow, discontinuous, with shelf-edges dominated with macroalgae, corals, and gorgonians, with the reef dropping off into the deep ocean at approximately 15 meters, as seen in Fig. 1 [13]. As sea surface temperatures continue to rise, susceptibility to bleaching is increasing. This increase in coral bleaching causes physiological distress leading to increased incidence of coral disease, coral death, and growth of macroalgae [22]. It is essential to understand the extent of thermal stress and its impacts on corals around South Caicos so that effective conservation methods may take place.

An assessment of coral color loss and restoration was conducted using 104 surveys of CW coral color variability offshore of South Caicos Island (Fig. 2) for 35 coral taxa from 2012 to 2018, along with NOAA Coral Reef Watch (CRW) monitoring products. Our study questioned if coral color, a coral health proxy, in the Turks and Caicos was

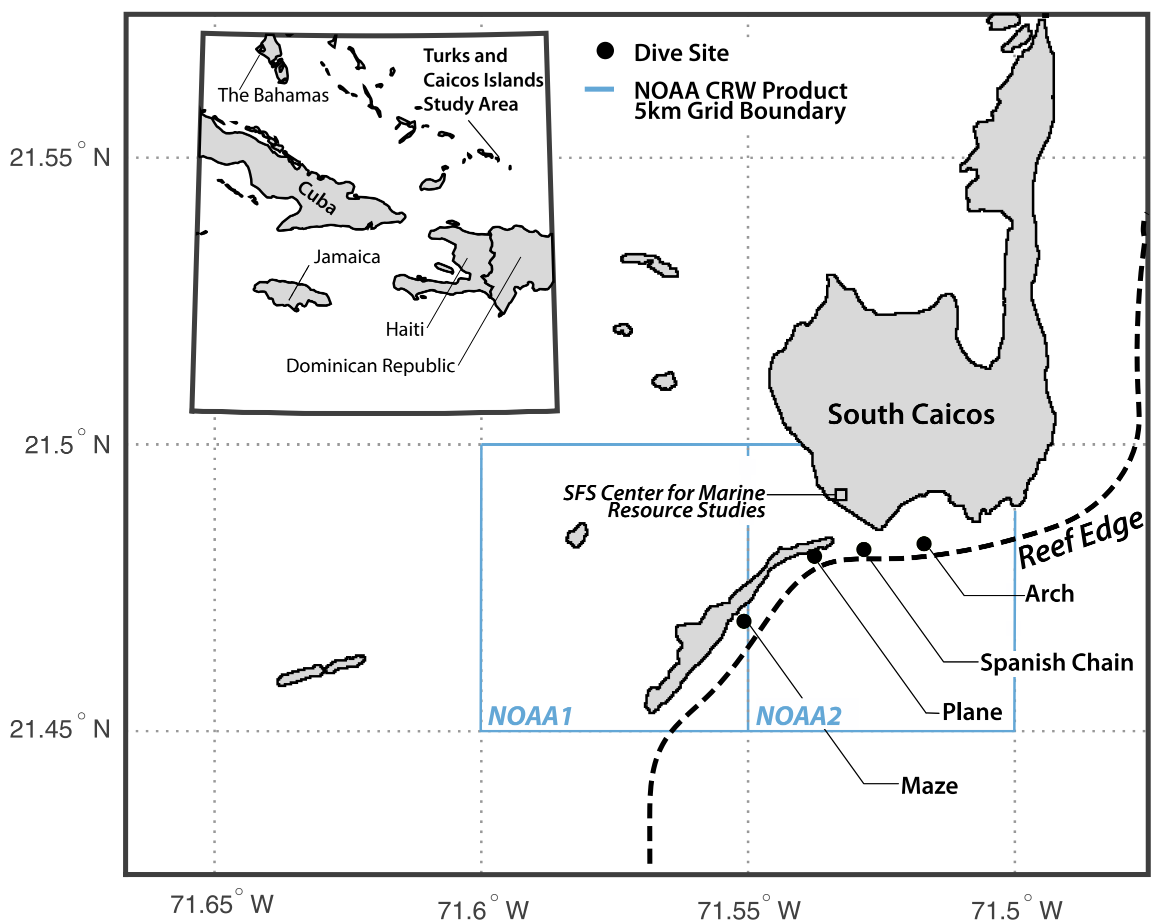

Fig. 2 Location of four Coral Reef Survey dive sites monitored by the students and staff at the School for Field Studies (SFS) Center for Marine Resource Studies in the Turks and Caicos Islands

significantly affected by the late 2015 thermal stress event as part of the 2014–2017 GBE? In addition, were different coral species in this region more resilient to the 2014–2017 bleaching event? If so, what was the interspecific variability in coral rebound and healing from this major thermal stress event? Specifically, to what extent did corals that survived the 2014 event lose and regain their color? And finally, does coral color decline linearly in response to repeated thermal stress, or are coral color and bleaching stress signals nonlinear and more strongly coupled with longer wavelength regional sea surface temperature (SST) signals?

2 Materials and methods

2.1 Data collection

The CW_{HS} data assessed in this study was collected by students, interns, and researchers at The School for Field Studies Center for Marine Resource Studies (SFS) on South Caicos Island (Fig. 2). Members of the SFS field station assessed coral health using the CoralWatch method (Fig. 1) from 15 October, 2012 to 18 July, 2018 across multiple dive study sites in the Admiral Cockburn Land and Sea National Park off South Caicos Island, TCI. Coral reef sampling locations in this study include four dive sites greater than 10 m in depth, i.e., Arch, Chain, Plane, and Spanish Maze (Fig. 2).

At each study site, a 100 m long line-intercept transect was established as part of SFS' long-term monitoring of reef health in South Caicos. At 2-m intervals, two corals were randomly selected, the diver recorded the lightest and darkest CW_{HS} values of a coral using the CW color card chart, from which average CW_{HS} for the specific coral species were determined (Fig. 1). Water temperature, time of the day, depth, coral species, and CW_{HS} values were also recorded. CW_{HS} values were then averaged by individual coral species and by coral types (boulder and plate).

2.2 NOAA Coral Reef Watch (CRW) data

NOAA Coral Reef Watch (CRW) products were extracted for the study area to diagnose thermal stress variability over the study period, and to determine when the environmental stress during the 2014–2017 GBE began. Specifically, the 4 coral reef sampling sites in this study are encompassed by two (2) NOAA CRW 5-km grids (0.05°), i.e., *NOAA-1* and *NOAA-2* grids (Fig. 1). NOAA CRW products from 1985 to 2018, including the 2012–2018 study interval, were extracted to help establish a long-term record of thermal stress in the TCI region, including: (a) SST Anomaly (SSTA), (b) Coral Bleaching HotSpot, and (c) Degree Heating Week (DHW). The Coral Bleaching HotSpot represents the maximum of the monthly mean SST climatology, as outlined by Strong et al. [23], Liu et al. [24], and Skirving et al. [25]. A description of the data products can be found on NOAA's, "Description for 5 km Regional Virtual Stations, Time Series Data, and Graphs," webpage (https://coralreefwatch.noaa.gov/vs/description.php).

2.3 Statistical analysis

In order to estimate differences in CW_{HS} over time and to diagnose coral stress and response during and after the 2014–2017 GBE, three time intervals were established using NOAA SSTA data: (1) 28 April, 2014–28 April, 2015–pre-GBE conditions, (2) 28 April 2015–31 October 2016–maximum thermal stress during the GBE as indicated by the SSTA time series, and (3) 1 November 2016–18 July 2017–post GBE recovery time window, corresponding with the return of SSTA levels to pre-GBE conditions.

Gaussian Probability Density Functions (PDFs) of CW_{HS} data for coral species and type were fitted using MATLAB®'s Statistical Toolbox for each of the three-time windows, according to Johnson et al. [26, 27] and Bowman and Azzalini [28]. MATLAB's Statistics and Machine Learning Toolbox was used to conduct the ANOVA analyses to determine statistical significance of coral color response during and after the 2014–2017 GBE. Using ANOVA, two CW_{HS} distributions were determined to be statistically significant from one another if the ANOVA returned a p value < 0.05.

Interspecific variability coral response to the 2014–2017 GBE was then evaluated by comparing, the change in average CW_{HS} before significant thermal stress impacted the region to the average CW_{HS} during significant thermal stress in the region, as established by the NOAA SSTA data products. Coral species recovery was then compared from the thermal stress after the April 2015 SSTA maximum by quantifying change in average CW_{HS} during the GBE to the average CW_{HS} after significant thermal cooling region.

The average CW_{HS} time series for each coral species was cross-correlated with SSTA in order to understand which coral taxa are most sensitive to changes in water temperature and thermal stress. Cross-correlation coefficients, R_{xy}, between the discrete average CW_{HS} and SSTA time series were computed as:

$$R_{xy}(m) = E\{x_{n+m}y_n^*\} = E\{x_{n+m}y_{n-m}^*\}, \quad (1)$$

where $-\infty < n < \infty$, the asterisk represents complex conjugation, and E is the expected value operator [29, 30], as implemented in MATLAB®'s Signal Processing Toolbox. In our cross-correlation of the species-species, average CW_{HS} time series and SSTA time series over the 2012–2018 study period, R_{xy} values closer to 1 would therefore indicate that coral color coral bleaching of a given coral taxa resulted likely from increased thermal stress according to the SSTA record. Alternately, lower R_{xy} values closer to 0 would indicate coral insensitivity to thermal stress and changes in sea water temperature.

Finally, in order to investigate the potential correlation between coral growth habit (boulder vs. plate-type) and thermal stress, a dendrogram analysis (hierarchical binary cluster tree) was performed in MATLAB® for the dominant seven coral species, in which the species-specific CW_{HS} time series were included in the analysis.

3 Results

NOAA SSTAs averaged over the two TCI 5 km (0.05°) grid cells, from 1985 to present show a clear increasing (warming) trend (Fig. 3). The 1997–1998, 2009–2010, and 2014–2017 mass Global Bleaching Events (GBEs) are indicated. The 2012–2018 study interval was used to analyze TCI sensitivity to the 2014–2017 GBE (Fig. 3). Maximum SSTA and DHW across the entire Caribbean region in late 2015 during the 2014–2017 GBE is shown in Fig. 4. While the TCI site is located in the NE Caribbean and generally cooler with its closer proximity to Atlantic currents, maximum 2015 SSTA and DHW for the study site were comparable with the Caribbean regions experiencing higher thermal stress, but not at the extremes found in other regions in 2015 (Fig. 4).

The dominant coral taxa in South Caicos Island include: plate-type *Agaricia* spp. (29%), boulder-type *Porites astreoides* (16%), and boulder-type *Siderastrea* spp. (12%), as seen in Table 1. A time series for boulder and plate-type corals represents the average boulder or plate-type coral CW_{HS} values for each survey (Fig. 5). The NOAA Degree Heating Week (DHW) in Fig. 5c illustrates the interannual variability in SST over the study period, averaged over the NOAA-1 and NOAA-2 5 km grid cells (Fig. 2). An ANOVA analyses of annual DHW trends reveals that 2013, 2015, and 2016 were significantly warmer than 2012, 2014, and 2017–2018 ($p < 0.05$) due to abnormally high SSTA in these years compared with the remainder of the years included in the analysis.

The CW_{HS} time series visually depicts an apparent coupling between coral color (coral health) and thermal stress, as the average CW_{HS} time series declines in magnitude during the GBE event (Fig. 5). Although boulder and plate coral types generally drop in value, indicating bleaching during the GBE, data indicate a general recovery in CW_{HS} values after the GBE to pre-GBE (April 2014-April 2015) CW_{HS} averages within 1 year following the end of the GBE (Fig. 5).

While the CW_{HS} trends appear to suggest a coral bleaching stress response to, and recovery from the late 2015 DHW peak thermal stress associated with the GBE, one-way ANOVA analyses of the fitted CW_{HS} distributions (Fig. 6) for boulder and plate-type corals provides more meaningful insight into the bleaching response. In our analysis, only plate-type corals exhibited significant color reduction during the 2014–2017 GBE, indicated by a statistically significant ($p < 0.05$) shift in color distributions. Average CW_{HS} trends for both types increased after the GBE, with boulder-type corals darkening significantly (higher average CW_{HS}, $p < 0.05$) more than pre-GBE color distributions in the post-GBE recovery (2017 +) time window (Table 2).

Results from our cross-correlation analyses (Eq. 1) of species-specific CW_{HS} and SSTA signals (Fig. 7) reveal strong coupling between coral color and SSTA for the dominant coral taxa sampled between 2012 and 2018 during the 104 surveys. As seen in Fig. 7, even though boulder corals are most strongly correlated with changes in SSTA, the correlation appears to be dominated by post-GBE coupling, given boulder-type corals did not significantly bleach during the GBE. Cross-correlation analyses over each of the 3 analysis periods (pre-GBE, GBE, and post-GBE) could help devolve which coral color

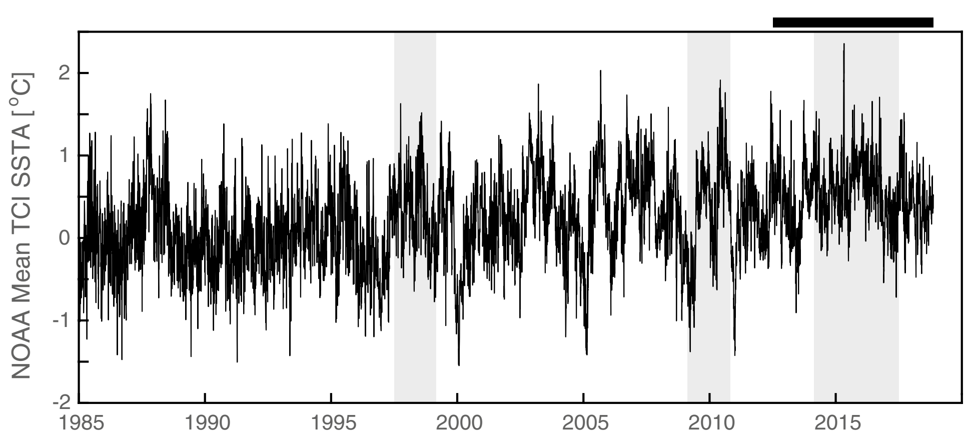

Fig. 3 NOAA Sea Surface Temperature Anomalies (SSTAs), averaged over the three Turks and Caicos Islands 5 km grid cells, 1985 to present. The 1997–1998, 2009–2010, and 2014–2017 mass Global Bleaching Events (GBEs) are bracketed in gray. The 2012–2018 study interval, used in this paper to analyze TCI sensitivity to the 2014–2017 GBE, is bracketed by the black bar at the top-right of the figure

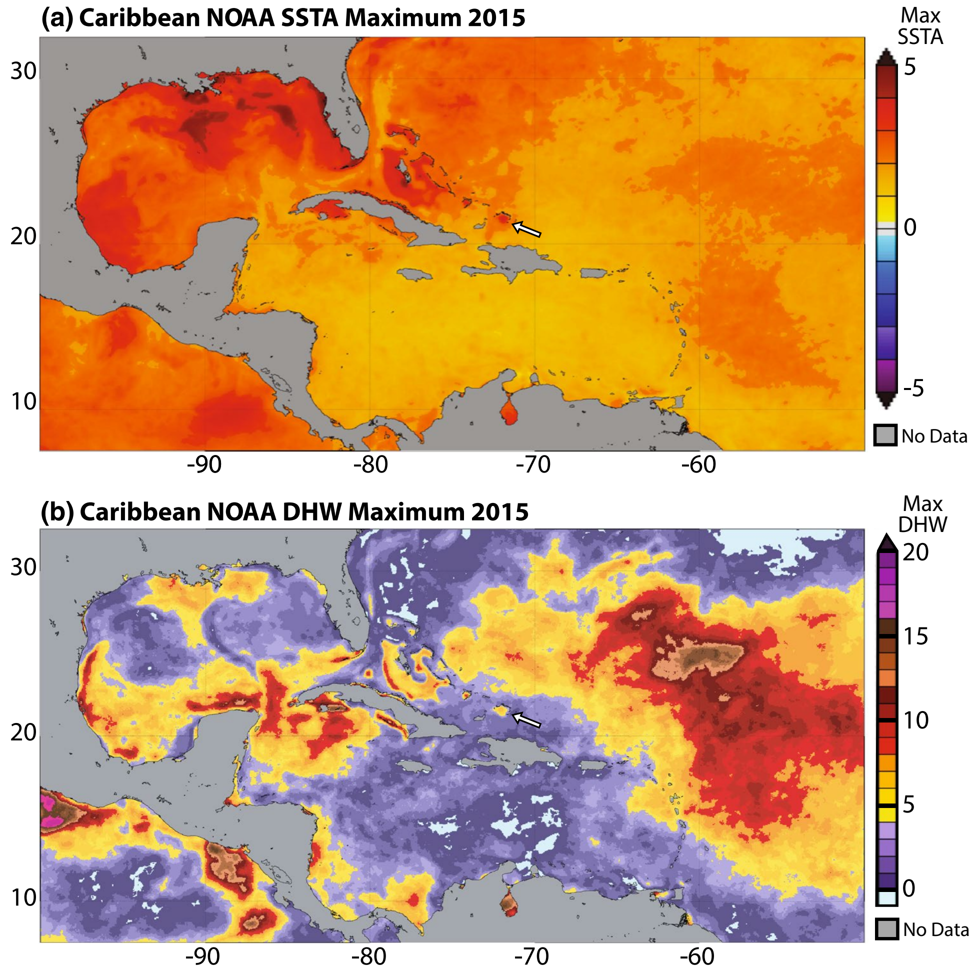

Fig. 4 Interannual variability in CoralWatch Coral Health Chart color for **a** boulder type and **b** plate type corals all survey sites between 2012 and 2018. Average lighter colors (1–2) indicate stressed corals whereas average darker coral colors (4+) indicate healthier, less stressed coral habitats. NOAA Degree Heating Week (DHW) depicted in (c)

signals were most correlated with SSTA over each of these intervals versus the entire study period. The dominating coral species in the TCI appear to be the most influenced by rising SSTA. Similarly, the R_{xy} values for corals not sampled frequently (e.g., < ~ 5% of overall dataset) may not yield as much insight into species-specific coupling of coral-color to water temperature variability.

The dendrogram analysis (Fig. 8) reveal that coral color and pigmentation variability for the principal coral taxa surveyed offshore of South Caicos during the 2012–2018 study period is independent of coral growth habit. As shown on Fig. 8, color variability of plate-type *Agaricia sp*. is most correlated with boulder-types *Porites astreoides* (R_{xy} = 0.82) and *Siderastrea sp.* (R_{xy} = 0.65). The CW_{HS} signals for boulder-types corals *Meandrina meandrites* and *Siderastrea sp.* were found to be strongly coupled (R_{xy} = 0.7). In summary, the dendrogram analysis of CW_{HS} signals adds to our understanding of coral response to thermal stress by revealing that coral response to thermal stress in the TCI region is independent of coral growth habit.

4 Discussion

Our study revealed that significant coral bleaching and restoration of coral color occurred offshore of South Caicos Island during, and after the 2014–2017 GBE for plate-type corals. Instead of a linear decline in average coral color over the 2012–2018 time window, principal coral taxa in our analysis exhibited strong coupling with longer wavelength regional sea surface temperature (SST) signals. We recognize a multitude of factors influence the susceptibility of a coral to bleach or its ability to recover. Such influences are the coral community composition, geography, endosymbiont type, and multiple temperature metrics [31].

However, while our study found temperature to play a direct role in coral color decline, many studies have found *Symbiodinium* to have a large impact on coral recovery from increased ocean temperatures [7, 17]. Interestingly, plate-type corals contain a different type of *Symbiodinium* that is not as resilient to thermal stress

Table 1 Coral species, grouped by type, sampled between 2012 and 2018 at the 4 SFS dive sampling locations (10–30 m) offshore of South Caicos Island

Coral species	Percentage	Counts
Plate-type		
Agaricia spp.	28.9	1632
Agaricia agaricites	4.5	253
Agaricia tenuifolia	1.6	93
Agaricia humilis	0.5	31
Agaricia fragilis	0.2	11
	Subtotal	2020
Boulder-type		
Porites astreoides	16.4	925
Siderastrea spp.	11.5	647
Siderastrea siderea	8.3	471
Meandrina meandrites	5.2	292
Favia fragum	4.4	246
Siderastrea radians	4	226
Diploria labyrinthiformis	3.1	177
Eusmilia fastigiata	2.3	129
Diploria strigosa	1.9	107
Dichocoenia stokesi	1.5	82
Colpophyllia natans	1.2	65
Orbicella annularis	1.2	66
Stephanocoenia intersepta	0.8	44
Madracis mirabilis	0.7	42
Montastraea cavernosa	0.7	42
Montastraea franksi	0.3	15
Isophyllastrea rigida	0.2	10
Manicina areolata	0.2	10
Porites spp.	0.2	10
Mycetophyllia lamarckiana	0.1	6
Palythoa caribaeorum	0.1	4
Stephanocoenia mechelinii	0.1	7
Diploria spp.	0	0
Montastraea faveolata	0	0
Montastraea sp.	0	1
Mussa angulosa	0	0
Scolymia spp.	0	2
Solenastrea intersepta	0	0
	Subtotal	3626
	Total	5646

which may explain why plate-type corals experienced significant bleaching in response to the anomalously high SSTAs in 2015 and 2016 (Figs. 5, 6) [32, 33]. Whereas boulder-type corals did not significantly respond to the GBE, many studies have found *P. astreoids* and *Siderastrea* spp., two dominant boulder-type corals in our study, to have resilient *Symbiodinium* clades (Clades A4a, B1, C3) that have made them resilient to intense bleaching events [32, 34, 35].

Nonetheless, while *Symbiodinium* clades may explain the resilience and recovery differences across plate and boulder-type corals, the three South Caicos reef-dominating corals, *Agaricia* spp., *P. astreoids* and *Siderastrea* spp., all share opportunistic life history traits that allow them to monopolize and persist in degraded reef habitats [34, 36–38]. Overall, supporting research seems to conclude that *Symbiodinium* types and life history traits are important determinants in the survival of corals in degrading reef habitat with multiple environmental stressors [34–36, 39].

While our study only found plate-type corals to bleach significantly, both plate-type and boulder-type significantly rebounded to pre-GBE health by the beginning of 2017 with boulder-type corals darkening even more post-GBE (Figs. 5, 6). However, looking outside the physiological processes impacting recovery, environmental factors influence the recovery process. For example, Fig. 3 shows a large decrease in SSTA in 2017 due to the two hurricanes, Irma and Maria that passed through the Caribbean and reduced SST, inducing local upwelling and a reduction in light stress. Furthermore, as indicated by the dendrogram analysis (Fig. 8), coral color response to thermal stress is independent of coral growth habit.

Our cross-correlation analysis of CW_{HS} with thermal stress indicated that, not only was the bleaching of plate type corals during the GBE directly attributable to increases in water temperature, but that cooler, post-GBE regional water temperatures resulted in coral health recovery for both boulder and plate-type corals, albeit with less coral color variability post-GBE than pre-GBE. The cross-correlation analysis of coral color and SSTA variability (Fig. 7) suggested which coral species and taxa are most susceptible to bleaching and stress during GBEs. Furthermore, corals most strongly correlated with SSTA variability may be the most likely to experience widespread mortality in the Caribbean with more frequent, more extreme GBEs associated with climate change. It is important to note, however, that coral vulnerability to bleaching may be due to different stressors, including multiple temperature metrics. Specifically, McClanahan et al. [31] find that, "Corals experience temperatures that differ from those measured by satellites, and their responses also integrate acclimation, adaptation and histories of stress," and exercise caution when interpreting products like DHW due to the spatial complexities and need for additional ground truthing of satellite-derived products to properly represent the thermal history at any given site. Pernice and Hughes [40] highlight the need for proper representation of thermal history, as fluctuations of extreme temperatures may

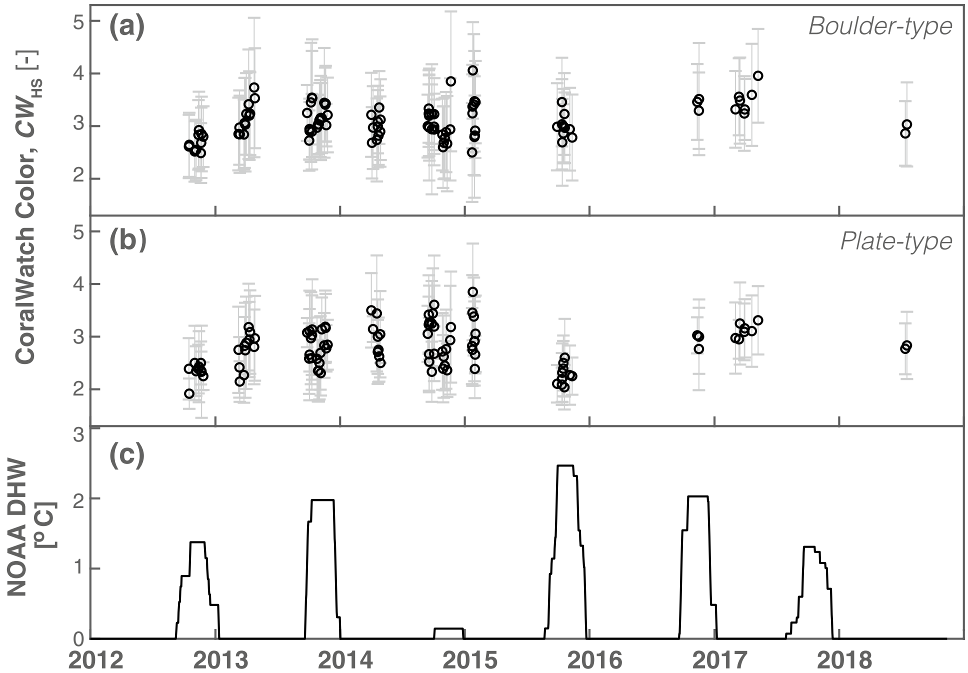

Fig. 5 Regional maximum SSTA (a) and DHW (b) for the Caribbean for 2015. The black arrow indicates the South Caicos Island study site

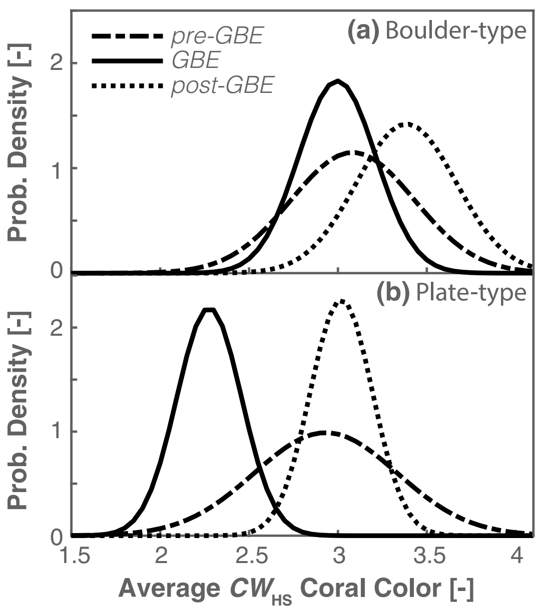

Fig. 6 Impact of thermal stress on average coral color variability pre, during, and post-GBE using fitted distributions for boulder and plate-type coral CW_{HS} averages

improve certain coral species' ability to withstand thermal stress, as found by Oliver and Palumbi [41].

Our results support Muñiz-Castillo et al. 's [42] finding that the TCI belong in the Caribbean ecoregion least exposed to heat stress and with the greatest percentage of its area without bleaching and mortality risk. Whereas our results reveal coral color darkening, i.e., statistically-significant shift of mean color distribution from lighter to darker hues, in response to thermal stress offshore of South Caicos Island, the relatively low thermal stress experienced in this region compared with other Caribbean regions more stressed during the 2014–2017 GBE (i.e., Central and eastern Venezuelan, Honduran and Nicaraguan Miskito Cays and nearby islands, etc., [42]), adds important regional context.

While coral bleaching in the Caribbean has been documented since the 1980s [43, 44], the increase in frequency and intensity of GBEs with climate change has added unprecedented stress on coral habitats regionally and globally. Recent studies assess the rapid decline in scleractinian corals and the transformation of dominant reef-building corals to reefs covered in macroalgae [43–45]. An ecological study by Dikou et al. [46] revealed that South Caicos benthic substrate was dominated by turf algae and dead coral rubble with live coral cover only encompassing approximately 2–7% of benthic space. Of the live coral found in the benthic space the dominating species were *Agaricia* spp., *Montastraea* spp., and *Siderastrea* spp. [46]. Thus, in general, the greater Caribbean reefs are shifting, as a result, from historically large, slow-growing scleractinian colonies of *Acropora* and *Montastraea* to smaller colonies of 'weedy' species, such as *P. astreoides* [45, 47, 48].

5 Conclusion

In summary, assessing coral health using the CoralWatch health chart methodology as described by Siebeck et al. [20] has proven to be an efficient diagnostic tool in

Table 2 Site-specific relative abundance of major coral species sampled at each SFS Center for Marine Resource Studies site between 2012 and 2018

Coral species	Relative abundance by site 2012–2018 (%)			
	Arch	Chain	Plane	Maze
Agaricia agaricites	5.3	4.4	4.0	4.1
Agaricia fragilis	0.0	0.7	0.1	0.1
Agaricia humilis	0.4	0.1	0.1	1.4
Agaricia spp.	28.6	28.3	30.8	28.2
Agaricia tenuifolia	2.7	3.8	0.0	0.3
Colpophyllia natans	1.5	1.4	0.0	1.5
Dichocoenia stokesi	0.9	1.9	2.1	1.1
Diploria labyrinthiformis	2.2	3.3	3.6	3.5
Diploria spp.	0.0	0.0	0.0	0.0
Eusmilia fastigiata	2.7	2.9	2.0	1.6
Favia fragum	3.0	5.4	5.7	3.7
Isophyllastrea rigida	0.2	0.2	0.2	0.1
Madracis mirabilis	0.7	0.5	0.7	1.1
Manicina areolata	0.1	0.2	0.1	0.3
Meandrina meandrites	4.1	5.2	5.2	6.1
Montastraea cavernosa	0.6	1.2	0.7	0.6
Montastraea faveolata	0.0	0.0	0.0	0.0
Montastraea franksi	0.1	0.0	0.0	0.9
Montastraea spp.	0.0	0.0	0.0	0.1
Mussa angulosa	0.0	0.0	0.0	0.0
Orbicella annularis	1.6	1.9	1.1	0.2
Mycetophyllia lamarckiana	0.0	0.0	0.0	0.4
Palythoa caribaeorum	0.0	0.2	0.1	0.0
Porites astreoides	18.3	12.0	19.4	15.7
Porites spp.	0.0	0.0	0.0	0.6
Pseudodiploria strigosa	1.6	2.1	1.1	2.7
Scolymia spp.	0.1	0.0	0.0	0.1
Siderastrea radians	4.5	3.6	3.9	4.0
Siderastrea siderea	6.6	10.5	9.4	7.4
Siderastrea spp.	13.0	9.9	9.1	13.1
Stephanocoenia intersepta	1.5	0.3	0.5	0.7
Stephanocoenia mechelinii	0.0	0.0	0.0	0.4
Solenastrea intersepta	0.0	0.0	0.0	0.0

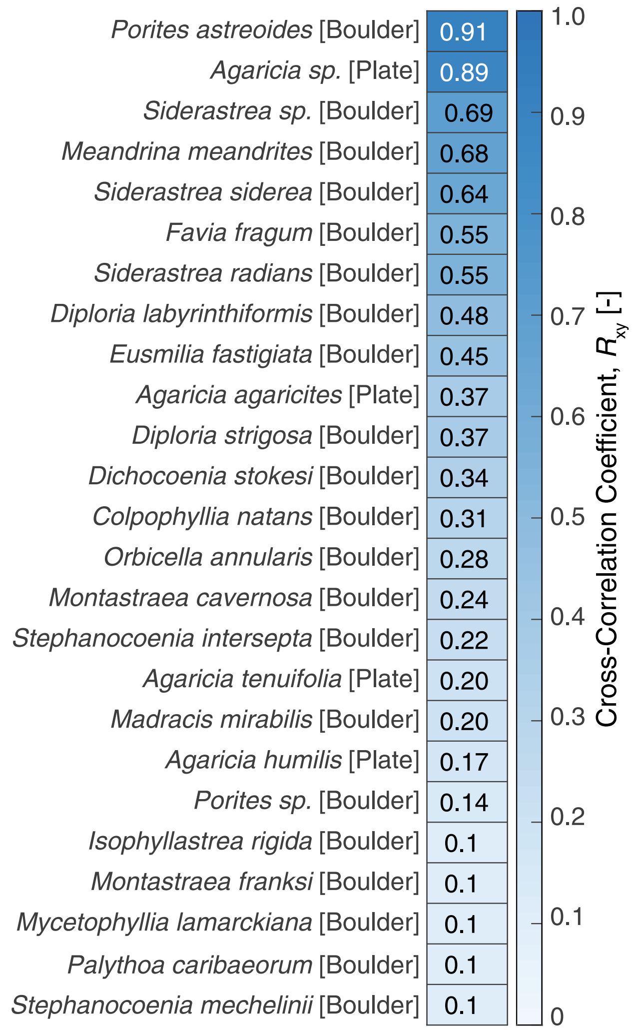

Fig. 7 Cross-correlation of Turks and Caicos coral taxa with SSTA, showing coral species most sensitive to thermal stress and exhibiting bleaching in response to the 2014–2017 Global Bleaching Event. Sample sizes for each species can be found on Table 1

diagnosing coral reef bleaching and recovery in response to regional thermal stress. Results from this study suggest a change in the composition of modern reefs, moving from massive colonies of scleractinian corals to 'weedy' scleractinian corals. Future studies in this region should examine the resilient endosymbiont types and life history traits of corals that have assisted in the survival of dominant reef species, representing a key factor for the emerging assisted evolution science as outlined by van Oppen et al. [49]. Further investigations of Turks and Caicos coral habitats are imperative to help understand specific coral response mechanisms and therefore predict how Caribbean region coral reefs may respond to more frequent, and more intense GBEs in the coming decades. This research is important not only to understand the mechanisms behind survival in high stress environments but in order to prioritize conservation efforts, such as establishing effective Marine Protected Areas.

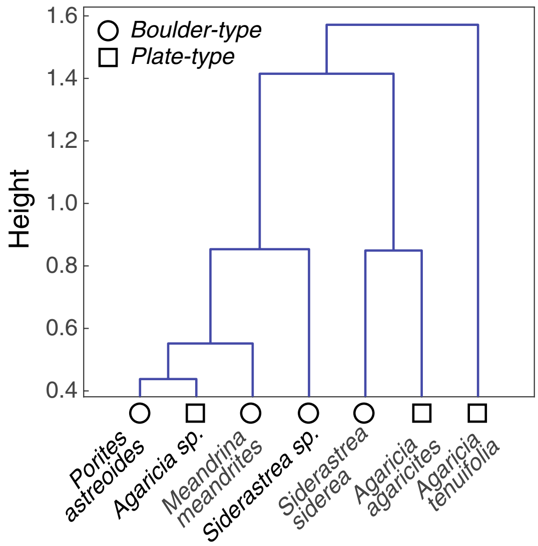

Fig. 8 Dendrogram of interspecific color and pigmentation variability for principal coral taxa surveyed offshore of South Caicos during the 2012–2018 study period using cross-correlation analysis of average CW_{HS} signals. As seen, coral color coupling to thermal stress is not dependent upon coral growth habit, as the dendrogram analysis reveals close correlation between coral species of differing growth habits

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Compliance with ethical standards

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

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