PLOS CLIMATE

RESEARCH ARTICLE

A century of warming on Caribbean reefs

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Abstract

The world's oceans are warming at an unprecedented rate, causing dramatic changes to coastal marine systems, especially coral reefs. We used three complementary ocean temperature databases (HadISST, Pathfinder, and OISST) to quantify change in thermal characteristics of Caribbean coral reefs over the last 150 years (1871–2020). These sea surface temperature (SST) databases included *in situ* and satellite-derived measurements at multiple spatial resolutions. We also compiled a Caribbean coral reef database identifying 5,326 unique reefs across the region. We found that Caribbean reefs have been warming for at least a century. Regionally reef warming began in 1915, and for four of the eight Caribbean ecoregions we assessed, significant warming was detected for the latter half of the nineteenth century. Following the global mid-twentieth century stasis, warming resumed on Caribbean reefs in the early 1980s in some ecoregions and in the 1990s for others. On average, Caribbean reefs warmed by 0.18˚C per decade during this period, ranging from 0.17˚C per decade on Bahamian reefs (since 1988) to 0.26˚C per decade on reefs within the Southern and Eastern Caribbean ecoregions (since 1981 and 1984, respectively). If this linear rate of warming continues, these already threatened ecosystems would warm by an additional ~1.5˚C on average by 2100. We also found that marine heatwave (MHW) events are increasing in both frequency and duration across the Caribbean. Caribbean coral reefs now experience on average 5 MHW events annually, compared to 1 per year in the early 1980s, with recent events lasting on average 14 days. These changes in the thermal environment, in addition to other stressors including fishing and pollution, have caused a dramatic shift in the composition and functioning of Caribbean coral reef ecosystems.

Citation: Bove CB, Mudge L, Bruno JF (2022) A century of warming on Caribbean reefs. PLOS Clim 1(3): e0000002. https://doi.org/10.1371/journal.pclm.0000002

Editor: Andrea Storto, National Research Council, ITALY

Received: May 28, 2021

Accepted: February 1, 2022

Published: March 9, 2022

Peer Review History: PLOS recognizes the benefits of transparency in the peer review process; therefore, we enable the publication of all of the content of peer review and author responses alongside final, published articles. The editorial history of this article is available here: https://doi.org/10.1371/journal.pclm.0000002

Data Availability Statement: HadISST data can be accessed at www.metoffice.gov.uk/hadobs/hadisst/, Pathfinder data can be accessed at www.ncei.noaa.gov/data/oceans/pathfinder/Version5.3/L3C/, and OISST data can be accessed at www.ncdc.noaa.gov/oisst/data-access. All data and code

Introduction

Greenhouse gas emissions are warming the planet, intensifying natural disturbances (e.g., fires and cyclonic storms), and modifying countless other aspects of the environment [1–3]. This is causing extinctions, altering species composition, and degrading nearly every ecosystem on earth [4, 5]. Although we tend to think of surface warming as a terrestrial phenomenon, the oceans have stored about 93% of the additional retained heat since 1955 [6, 7].

The impacts of warming on marine communities are widespread, affecting a large range of taxa [8, 9]. Most marine species are ectothermic, so their body temperature matches that of the

compiled for this manuscript can be freely accessed on GitHub (github.com/seabove7/CaribbeanSST) and Zenodo (DOI: 10.5281/zenodo.4751658), including links to the compiled databases used here from the three sources listed above.

Funding: This paper was funded in part by a grant from the National Science Foundation to JFB (OCE 1737071). CBB was funded through this grant. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors declare no conflicts of interest.

surrounding seawater. Therefore, warming increases their metabolism and subsequently alters physiological processes such as caloric demands, growth rates, and behaviors [10–12]. This in turn has widespread effects on species interactions and the structure of marine food webs [13–15] driven by warming-related disease outbreaks, loss of foundation species that provide habitat structure (e.g., corals and kelps), and reductions in primary production [16]. The recent National Climate Assessment [17] described the well-documented effects of climate change as an "ecosystem disruption" and concluded it will "intensify as ocean warming, acidification, deoxygenation, and other aspects of climate change increase."

Anthropogenic warming is altering the biodiversity and ecosystem functioning of coral reefs around the world [18–25]. Reef degradation is particularly evident in the Caribbean, where dramatic ecological shifts have occurred over the past several decades [26–32]. Warming is causing mass coral mortality events due to bleaching [31] and increased disease severity [33], and alterations to metabolic processes across marine taxa [34, 35]. Additionally, losses of countless reef-dependent taxa including fishes, seaweeds, and invertebrates, due to both direct and indirect effects of warming, have been caused by acute warming events (heatwaves) globally [36–38]. These and other effects of warming are not the only causes of these changes. Other aspects of climate change (e.g., ocean acidification, stratification, and increasing storm intensity and frequency), and in some cases localized stressors (particularly fishing and pollution), can also play a role in Caribbean reef degradation [29, 39–44].

The purpose of this study was to quantify the long-term (150 year) spatiotemporal trends in ocean temperature across the Greater Caribbean, and specifically on Caribbean coral reefs, to provide an easily interpretable synthesis of Caribbean ocean warming that can be used to better understand how temperatures are impacting these ecosystems. We compiled three open-access sea surface temperature (SST) datasets (HadISST, Pathfinder SST, and OISST) for all mapped coral reef locations across the Greater Caribbean. Numerous previous studies have documented the anthropogenic heating of the ocean generally [7, 45], and of coral reefs in particular [46–53]. Our study builds on this work by focusing on coral reefs of the Greater Caribbean, updating the analysis through 2020, and by adding an assessment of coral reef marine heatwaves (MHW) to the standard focus on spatiotemporal temperature trends.

Methods

Reef locations

We compiled a Caribbean coral reef location database by sourcing latitude and longitude coordinates for known coral reef locations from the following sources: UNEP World Conservation Monitoring Center [54], the Global Coral Reef Monitoring Program [55], the Atlantic and Gulf Rapid Reef Assessment (AGRRA) [56], Reef Check (reefcheck.org), Florida's Coral Reef Evaluation and Monitoring Program (CREMP) [57], the US Virgin Islands Territorial Coral Reef Monitoring Program (TCRMP) [58], and previously published survey data for the region [32]. Sites were considered duplicates if they had the same GPS coordinates. In total, we identified 5,326 unique reefs across the Caribbean basin that were assigned to eight ecoregions based on the World Wildlife Fund (WWF) marine ecoregion classifications [59]. Ecoregions contained between 84 (Gulf of Mexico) and 1,277 (Greater Antilles) reef locations (**Fig 1**). This database was used to assess SST and MWH trends across Caribbean coral reefs.

Sea surface temperature datasets

In this study, we calculated the rate of SST change through time, the total warming for the Caribbean basin, and more specifically on coral reefs (**Table 1**). Additionally, we quantified the frequency, duration, and return time of marine heatwave events (MHW) across the basin

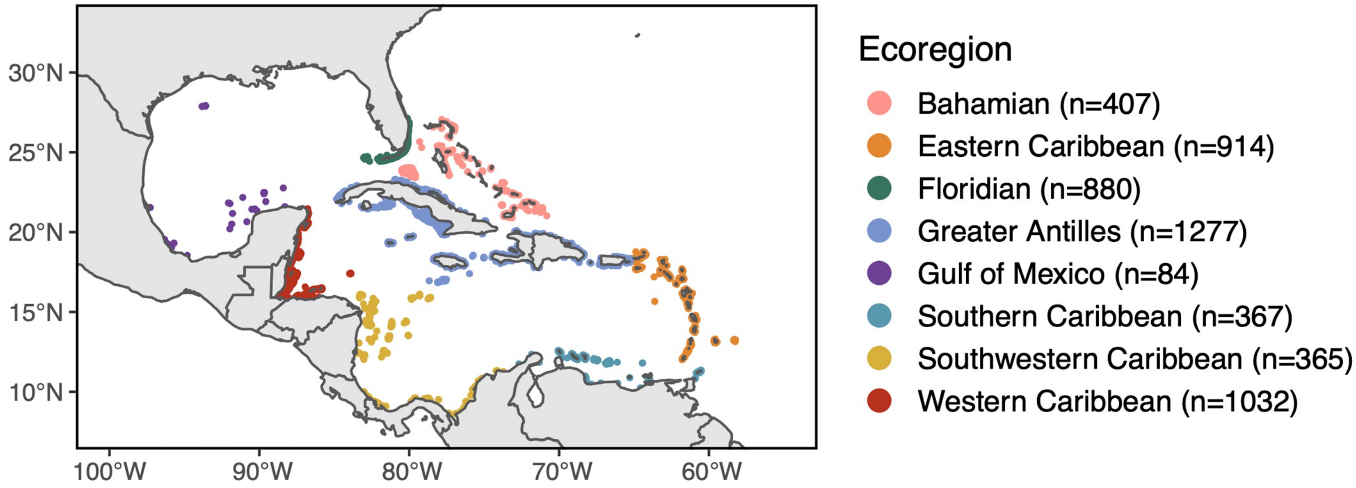

Fig 1. Caribbean coral reef site locations and ecoregion designation. The colour of each reef represents the designated ecoregion and n denotes the number of unique reef locations within that ecoregion. Map layer was acquired from Natural Earth (https://www.naturalearthdata.com).

https://doi.org/10.1371/journal.pclm.0000002.g001

(**Table 1**) and on coral reefs (**Table A in S1 Text**). Our characterization of the thermal history of the Caribbean was based on three complementary ocean temperature datasets: HadISST from the United Kingdom Met Office [60], the Pathfinder satellite temperature records from NOAA/NASA [61–63], and NOAA's daily Optimum Interpolation Sea Surface Temperature (OISST) [64]. These SST products were selected to represent different temporal ranges and spatial resolutions, with the HadISST database containing the longest record of SST for the region (1870-present), however, at a lower resolution (1˚ vs. 0.25˚ grids). The OISST database was used for all MHW analyses since these metrics were developed using this database [65]. Finally, the Pathfinder database was used for all other SST metrics because it has been widely used to assess SST on coral reefs and is available at a higher resolution [66].

We obtained monthly SST from 1871 to 2020 from the HadISST database [67, 68] at a resolution of 1˚ grids across the Caribbean (0˚N–40˚N; 100˚W–55˚W). The HadISST data are based on a combination of temperature reconstruction and observational data to produce a long-term record of *in situ* measurements (typically from ships and buoys) and satellite-derived temperatures. HadISST uses *in situ* SST data from the Met Office Marine Data Bank (MDB) and is supplemented with data from the Comprehensive Ocean-Atmospheric Data Set (ICOADS) when missing from the MDB between the years 1871 and 1995. Satellite SST data from the Global Telecommunications System are included in the HadISST dataset after 1982, making this database ideal for long-term SST assessments [52, 68].

Table 1. Estimated warming rates from both HadISST and Pathfinder databases for different temporal ranges. Coral reef values are means of all 5,326 reef locations included in the study. The year 1994 was estimated as the beginning of the most recent period of significant warming across all Caribbean coral reefs (**see Fig 2B**). The HadISST data can be accessed at www.metoffice.gov.uk/hadobs/hadisst/, the Pathfinder can be accessed at www.ncei.noaa.gov/products/avhrr-pathfinder-sst, and the OISST can be accessed at www.ncei.noaa.gov/products/optimum-interpolation-sst.

Temperature parameter	HadISST			Pathfinder		OISST
	1871–2020	1981–2020	1994–2020	1981–2019	1994–2019	1981–2019
Caribbean Basin (˚C per decade)	0.04	0.17	0.20	0.17	NA	NA
Caribbean Basin (total ˚C for period)	0.60	0.68	0.54	0.66	NA	NA
Caribbean Reefs (˚C per decade)	0.04	0.15	0.17	0.19	0.18	NA
Caribbean Reefs (total ˚C for period)	0.60	0.60	0.46	0.74	0.47	NA
Caribbean Basin (increasing frequency of MHW per year)	NA			NA		0.05

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Additionally, we calculated monthly mean SST at 4 km resolution from September 1981 to December 2019 using the twice daily (night and day) Pathfinder Version 5.3 database [61, 62]. Pathfinder SST data were clipped to the Greater Caribbean (i.e., including the Gulf of Mexico, Florida, and Bahamas; see maps for full extent of area) constraints and quality filtered (quality four or greater [62, 63]) before the mean monthly SST value was calculated per grid cell and concatenated into a single netCDF file. The Pathfinder database is derived from measurements made by the Advanced Very High Resolution Radiometer (AVHRR) instruments aboard NOAA's polar orbiting satellites that combine multiple passes of data. These data were provided by GHRSST and the NOAA National Centers for Environmental Information.

We used NOAA's AVHRR 0.25° daily OISST data to determine sea surface temperature climatology and detect MHW events across the Caribbean basin from 1981 to 2019 [64, 69]. OISST data are constructed by combining *in situ* (collected via ships and buoys) and infrared satellite (AVHRR instruments) SST measurements. A bias adjustment is applied to satellite and ship observation data, and gaps are filled as necessary through interpolation [70].

Historic SST assessment

We examined the rate of SST change through time for the Greater Caribbean region using the HadISST (1871–2020) and Pathfinder (1981–2019) databases (described above) to evaluate historic SST trends. A linear model using generalized least squares (GLS) with temporal autocorrelation (*nlme* package; version 3.1.151 [71]) was applied to each grid cell through time (months each year) of both datasets to calculate the slope and significance of SST increases over time for the full region [46]. A linear relationship between SST and time was assumed for these analyses for simple approximation of direction and magnitude of change [72]. Additionally, we extracted SST from the HadISST and Pathfinder datasets using a compiled Caribbean coral reef location database (*raster* package; version 2.9–23 [73]). These data were compared between the two databases to assess the relationship between the recorded SST values and resulted in a linear relationship (**S2 Fig**). Because these databases, including the OISST database, are collected on different time scales, spatial resolutions, and slightly differing methodologies, the minor differences observed between the databases is not unexpected.

The use of satellite-derived SST measurements to represent benthic temperature patterns has been frequently assessed via comparisons of different databases with *in situ* logger measurements at the same locations. While these studies report that satellite-derived measurements often underestimate *in situ* temperatures [74, 75], the consensus is that satellite databases accurately reflect temperature conditions on many coral reefs at depth [21, 75, 76] and are a useful tool for identifying global warming signals [67]. Monthly SST measurements were averaged across all reef locations to assess historic SST trends on Caribbean coral reefs per sampling period (month) as well as within individual ecoregions. We assessed annual SST on coral reefs since 1871 using a generalized additive model (GAM) with a cubic regression spline for year and a cyclic cubic regression spline for month to smooth temperature variability through time for better assessment of temporal SST trends on reefs (*mgcv* package; version 1.8.36 [77]). We then identified periods in which annual warming rates significantly increased (i.e., significant warming) based on the first derivative of the GAM curve for the entire region as well as each ecoregion [78]. The initial years of significant warming were then used to calculate the mean warming rate since the identified inflection points for the entire basin and within the eight ecoregions. All analyses and visualizations were conducted using R version 3.6.1 [79] and a table describing the assessed metric, SST database, and statistical analysis can be found in the supporting information [80] (see **Table B in S1 Text** for description of statistical methods for each metric) [81].

Marine heatwaves classification

Marine heatwaves (MHW) are defined as anomalously warm sea-surface temperature events, with temperatures warmer than historical climatology for that specific time and location, lasting for at least a 5 day period [65]. Although technically different, effectively the MHW metric is very similar to the temperature anomaly metrics reef scientists have been using for a quarter century to quantify acute thermal disturbance on reefs, e.g., Degree Heating Weeks and Thermal Stress Anomalies [19, 51, 82–86]. A recent study demonstrated a positive correlation between MHW duration and the frequency of coral bleaching across the Caribbean and Gulf of Mexico [87]. We used NOAA's OISST data (described above) to identify and assess MHWs across the Greater Caribbean from 1981–2019 [88]. If successive events had less than two days between them, we considered them to be the same event. We used the *heatwaveR* package in R (version 0.4.4) [87] and code provided from the marine heatwave working group (www.marineheatwaves.org) to identify marine heatwave events from our OISST dataset and calculate heatwave metrics (**Table A in S1 Text**).

For each pixel (0.25˚ x 0.25˚), we aggregated a list of distinct MHW events between 1981 and 2019, which included the start and end date of the event (see **Table A in S1 Text** for all MHW properties obtained). We then calculated a history of MHW events for each coral reef location using a nearest neighbor analysis to match reef locations to MHW events identified from the OISST grids. A MHW event was assigned to a coral reef location if the reef occurred in the grid that had the MHW event (i.e., coordinates of coral reef sites were matched to the centroid location of a MHW pixel). We assessed the temporal trends for each MHW metric using ordinary least squares (OLS) models, except for event frequency and total number of MHW days, as these variables are count data and best analyzed using generalized linear models (GLM) (package *lme4*; version 1.1–23) [89]. The response variables for OLS models were log transformed to meet model assumptions when necessary. For MHW trends on coral reefs, the level of observation was each unique MHW pixel that overlapped coral reef habitat and we modelled trends for each ecoregion to account for potential spatial differences in MHW metrics across the Caribbean basin. Significance and R^2 values were obtained to evaluate the strength of each trend. For GLM trends, we report the Nagelkerke pseudo R^2 value, a commonly used pseudo R2 for GLM models in similar analyses [80] (see **Table B in S1 Text** for description of statistical methods for each metric).

Results and discussion

Our results indicate that Caribbean reefs began warming in 1915 (i.e., the statistically estimated infection point for reefs across the region, **Fig 2B**). However, four of the eight Caribbean ecoregions we assessed warmed significantly even earlier; during the latter half of the nineteenth century (**Fig 3**). For example, the southern Caribbean ecoregions (i.e., Western, Southwestern, Southern, and Eastern Caribbean) warmed significantly as early as 1871, while reefs across the Gulf of Mexico did not begin warming until 1925 (**Fig 3; Table C in S1 Text**).

The initial period of anthropogenic Caribbean reef warming was followed by two to three decades (depending on the ecoregion) when ocean temperatures varied from year-to-year, but there was no warming trend (**Fig 2B**). This mid-20th century stasis, observed for the global surface [90], was due to the reflection of solar radiation from sulphate aerosols which counteracted anthropogenic warming [91, 92]. Several studies have documented this broad pattern for the tropical oceans, and specifically for coral reefs (including early twentieth century warming and mid-century stasis). Tropical sea surface temperature increased rapidly in the 1920s and 1930s, and in some regions, including the tropical North Atlantic, there was more warming early in the twentieth century than in the latter half [93]. Lough et al. [52] found that globally,

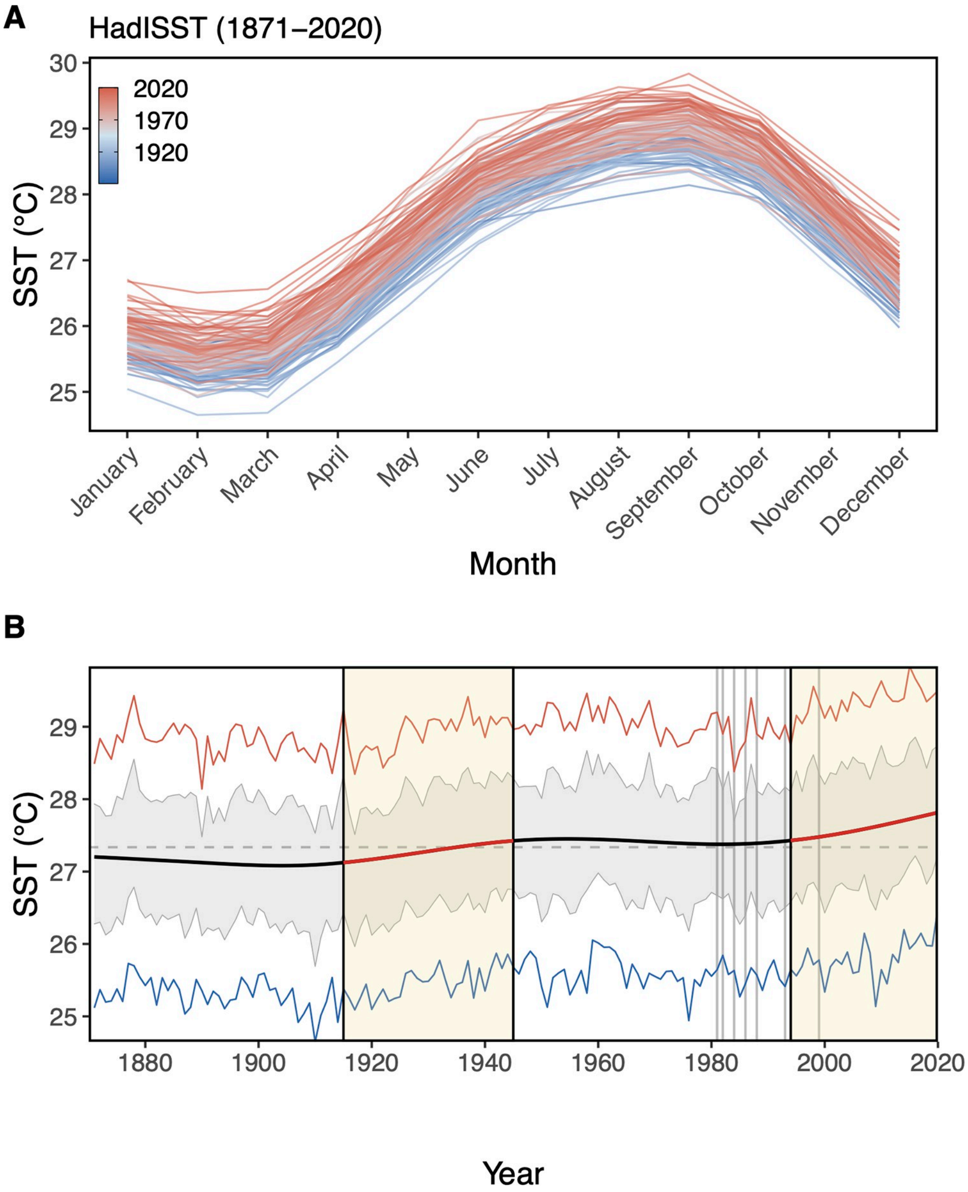

Fig 2. Historic SST trend on Caribbean coral reefs (1871–2020). Long-term SST records (HadISST) on Caribbean coral reefs depicting **A)** mean monthly SST each year (represented by line colour: blue to red) and **B)** annual mean SST with significant warming based on the first derivative of the GAM slope (1915 and 1994 highlighted in the yellow boxes). The GAM smoothed annual mean SST over time is represented by the black line with significantly warming periods (red) identified over the curve. The annual maximum (red line) and annual minimum (blue line) SST are also depicted, along with the overall mean SST for all sites over the entire period (27.3˚C; grey dashed line). The grey ribbon represents the 95% confidence interval around the annual SST mean through time. Vertical grey lines represent year of significant warming across ecoregions.

https://doi.org/10.1371/journal.pclm.0000002.g002

coral reefs began warming around 1915, with nearly as much warming before the mid-century stasis as after it. Additionally, numerous climate proxy studies based on coral cores [94–97] also found evidence for long-term (i.e., beginning in the nineteenth or early twentieth centuries) anthropogenic warming of Caribbean reefs. For example, Saenger et al. [95] reported that anthropogenic forcing caused much of the SST warming of the Bahamas since 1900. While

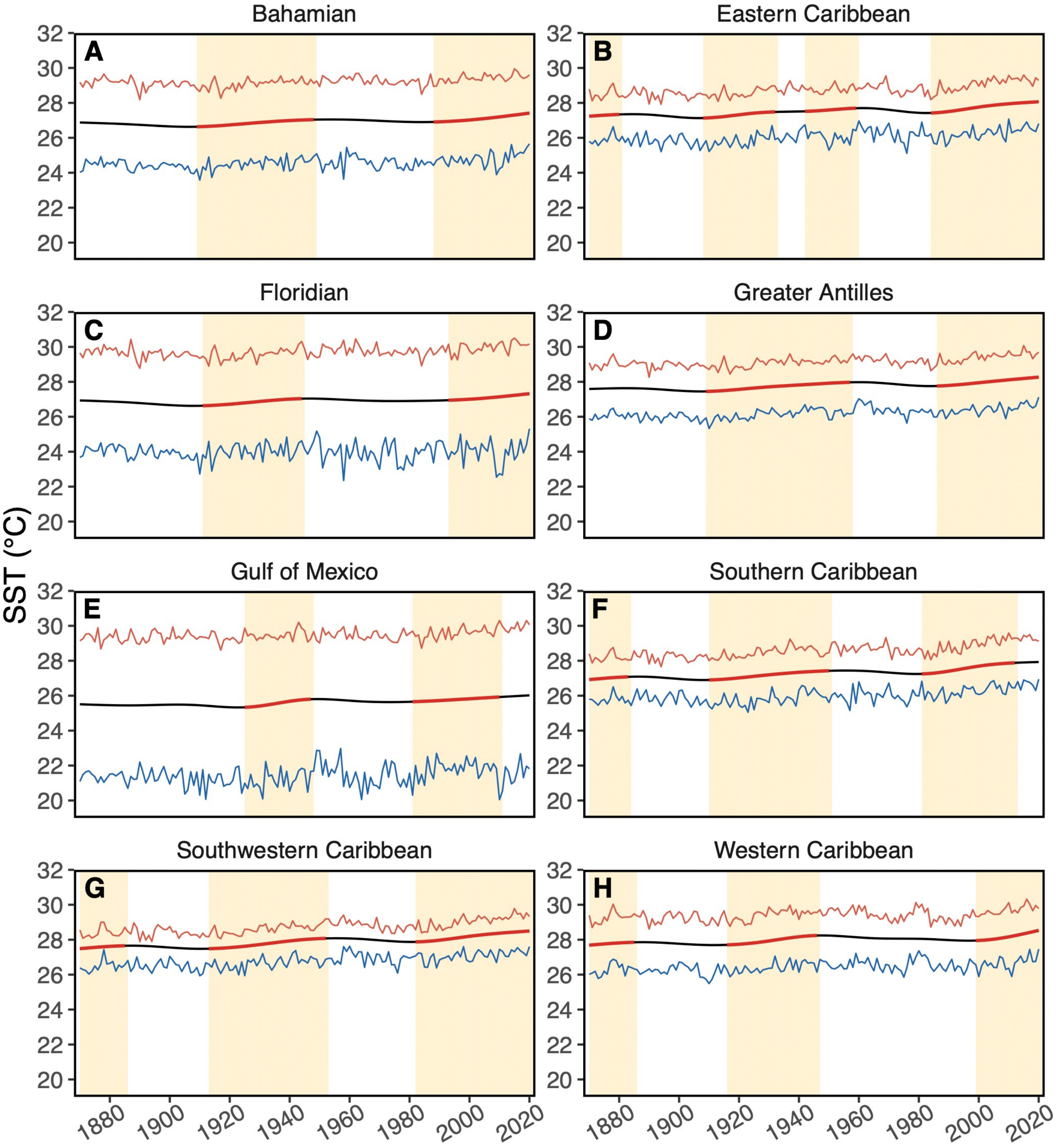

Fig 3. Historic SST trends on coral reefs within ecoregions (1871–2020). Long-term SST records (HadISST) on Caribbean coral reefs separated by ecoregion depicting the GAM smoothed annual mean SST through time (black line) with significantly warming periods (red line and yellow background; see **Table C in** S1 Text) identified over the curve. The grey dashed horizontal line denotes the mean SST over the entire period, the red line depicts the annual maximum SST, the blue line depicts the annual minimum SST, and the grey ribbon represents the 95% confidence interval around the true annual SST mean for each ecoregion.

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reports of warming vary slightly based on source of data and region assessed, these overall warming patterns are evident across the Caribbean.

Whether or how early twentieth-century warming affected coral reefs is unknown. But given the sensitivity of Cnidarians (including corals), fishes, macroalgae, bacteria, and other reef inhabitants to thermal anomalies [9, 22, 25, 38, 98], it is hard to imagine there were no effects. There are no reports of widespread coral bleaching during the 1920s or 1930s. However, the short-term consequences of early twentieth-century warming could have been sublethal, including negative effects on growth, reproduction, energy stores, and other fitness components [9, 22]. Over the longer term, when coral mass bleaching was first observed in 1982 [99], temperatures had been elevated by ~0.3˚C for nearly 70 years. Did this warming reduce resistance of coral reef inhabitants to the marine heatwaves of the early and mid-1980s [47, 100–104]? In some locations, local factors including nutrient pollution are believed to play an important role in coral mortality [43, 105, 106]. It is generally believed that these localized stressors make coral colonies and populations more sensitive to ocean warming [44, 107] (but see [108, 109]). However, the sequence of this potential synergism is more likely to work in the opposite direction, with warming making corals more susceptible to pollution, negative interactions with seaweeds, pathogens, and other causes of coral mortality. In this scenario, ocean heating should not be considered the final straw, but rather, the underlying environmental driver of coral loss, even when the proximate causes are local human activities. If true, the burden for reef conservation largely shifts from local communities (who are frequently blamed for reef demise) to the wealthy northern nations responsible for global warming through centuries of greenhouse gas emissions [28].

The timing of the post-stasis resumption of Caribbean reef warming varied substantially among ecoregions; ranging from 1981 to 1999 (**Fig 3, Table C in S1 Text**). Locations that warmed earlier (e.g., Puerto Rico and the Bahamas) generally experienced severe bleaching and mass mortality in the mid-1980s [47, 100, 102–104]. In contrast, mass bleaching and coral mortality in the Western Caribbean, where warming resumed substantially later, did not occur until 1998 [110] (**Fig 3 and S4 Fig**; **Table C in S1 Text**).

Overall, we found that the average linear warming rate for Caribbean reefs during the most recent anthropogenic warming period (1994–2020) was 0.17˚C per decade (**Figs 2 and S9**; **Table 1**; HadISST database). Based on satellite data alone (**S1 and S3 Figs**; Pathfinder database), the average coral reef warming rate during this period (1994–2019) was 0.18˚C per decade (**Table 1**), resulting in 0.47˚C of warming. The slight difference in warming rate between these two databases is likely due to the time period assessed, temporal and spatial resolution, and differences in SST calculations between databases [111]. While the HadISST is valuable for its long-term record of SST across the Caribbean, the Pathfinder database more accurately represents in situ temperatures due to the higher temporal and spatial resolution observations [111, 112]. At this rate, the mean temperature on Caribbean reefs would be roughly 1.5˚C higher by 2100 assuming continued linear warming—and that is in addition to already realized warming.

The observed warming rates of Caribbean coral reefs in this and previous studies report similar values (see [50–52, 113]), however, these rates are somewhat greater than estimates for the global ocean surface (**Table 2**). Winter et al. [47] reported a warming rate of about 0.25˚C per decade for the reef off La Parguera, southwestern Puerto Rico (1966–1995). Similarly, Hoegh-Guldberg [53] found the warming rate was 0.23˚C per decade (1981–1999) off the south coast of Jamaica. Kuffner et al. [49] described a remarkable temperature record collected by lighthouse keepers for five coral reefs off the Florida Keys starting in 1878 that also observed SST warming at 0.25˚C per decade between 1975 and 2006. It is reassuring (if surprising) that studies of vastly different scales and based on disparate methods, including *in situ*

Table 2. Published reports of global ocean surface warming rates.

Study	˚C per decade	Years
Casey and Cornillon 2001 [48]	0.14	1960–1990
Lawrence et al. 2004 [116]	0.09 and 0.13	1985–2000
Good et al. 2007 [90]	0.17	1985–2004
Burrows et al. 2011 [117]	0.07	1960–2009
USGCRP 2017 [118]	0.15	1900–2016

https://doi.org/10.1371/journal.pclm.0000002.t002

measurements (i.e., filling a bucket with seawater then measuring temperature by hand with a thermometer) [47], remote sensing via satellite [46], and databases based on both (this study) report similar warming rates. Moreover, Caribbean reef warming rates are approaching the CMIP5 RCP 8.5 model prediction of about 0.3˚C per decade [114]. This "business as usual" emissions model is now viewed by many climate scientists as "unlikely", especially for the end of this century [115]. Yet, our results and previous work suggest that Caribbean coral reefs are already warming far more quickly than scenarios considered to be more likely (e.g., RCP 4.5).

Our results indicate that reefs within all ecoregions are warming (**Figs 3 and S4**), albeit at somewhat different rates. Warming rates during the most recent period ranged from 0.17˚C per decade for Bahamian reefs to 0.26˚C per decade for reefs in the Southern and Eastern Caribbean (**Figs 1 and 3**; **Table C in S1 Text**). These rates translate to an increase of 0.53 to 0.99˚C during this period (which has lasted from 21 to 39 years, depending on the ecoregion).

Subregional patterns of warming across the Caribbean calculated here are similar to other SST parameters used for assessing thermal risk on coral reefs, such as degree heating weeks (accumulation of temperature anomalies exceeding the monthly maximum mean SST [82]; DHW). Ecoregions within the Caribbean with faster rates of warming (e.g., Southern and Eastern Caribbean [mean 0.26˚C per decade], **Table C in S1 Text**) have also been reported to have some of the highest occurrences of weekly SST anomalies [119], maximum DHWs [82], and coral bleaching or mortality risk events [50]. The spatiotemporal variability in warming parameters across ecoregions has important implications for conservation [50, 120, 121]. However, because these spatial patterns are temporally variable, caution should be applied when basing policy on recent warming trends.

While increasing SST on Caribbean coral reefs is clearly a major concern, warming is not limited to reef locations. Sea surface temperatures are rising across the entire Caribbean basin at a mean rate of 0.04˚C per decade since 1871 (HadISST data; **S7 Fig**) and more rapidly since 1981 at 0.17˚C per decade (Pathfinder SST data; **Figs 4A and S7**). This recent rate of ocean warming (0.17˚C per decade from 1981–2019) is similar to those previously calculated for the Caribbean basin. For example, Chollett et al. [46] reported a rate for the entire Caribbean and southeastern Gulf of Mexico of 0.27˚C per decade (1985–2009). Additionally, rapid increases in ocean heat content across the region has been apparent [122], driving increases in other severe events such as increased storm activity and MHWs.

We complemented our analyses of increasing Caribbean SST with an assessment of changes in marine heatwaves on Caribbean coral reefs. Marine heatwaves (MHW) are discrete warming events characterized by rate of onset, duration of event (five days or longer), and the intensity of warming [65]. Over the past several decades, MHW have increased in both frequency and duration globally [123]. Likewise, we found that heatwaves are occurring more frequently across the entire Caribbean basin (**Figs 4B and S5**) and specifically on Caribbean coral reefs (**Fig 5A; Tables D and E in S1 Text**). The average frequency of MHW events on Caribbean coral reefs has increased from about 1 per year in the 1980s to almost 5 per year in the 2010s (**Fig 5A; Table E in S1 Text**), with current events lasting on average about 14 days each (**Fig**

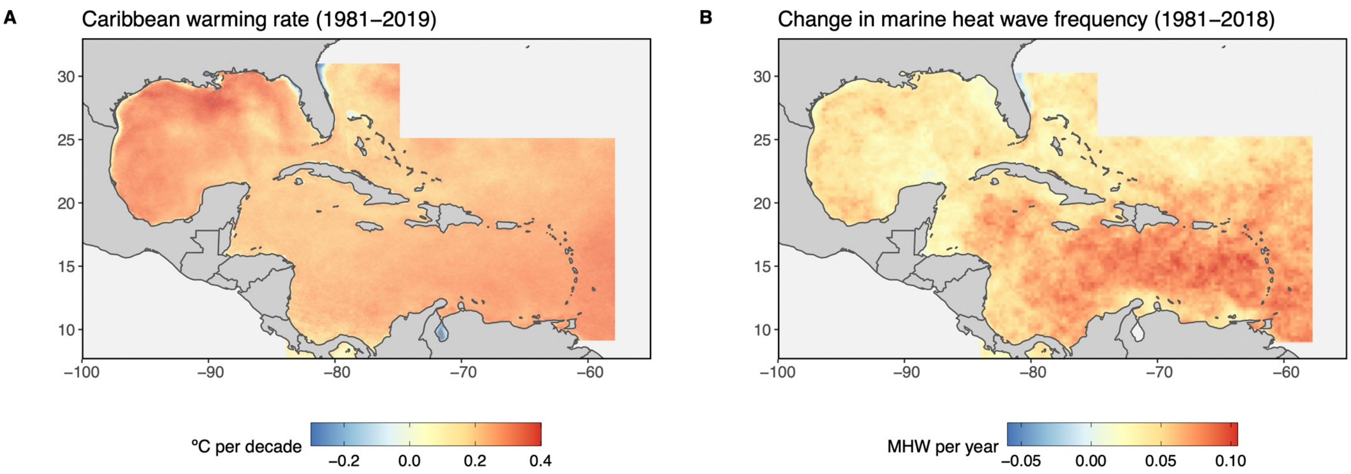

Fig 4. Warming patterns throughout the Caribbean sea. Increasing warming events across the Caribbean depicted through **A)** rate of SST change (˚C per decade) from 1981 to 2019 (Pathfinder; mean slope 0.17˚C per decade) and **B)** increasing marine heatwave events (slope of counts per year). Grey ocean area was not included in these analyses. Map layer was acquired from Natural Earth (https://www.naturalearthdata.com).

https://doi.org/10.1371/journal.pclm.0000002.g004

5B; **Table E in** S1 Text). Additionally, the decadal mean return time (number of days elapsed since the last MHW event) has steadily declined from 377 days in the 1980s to just 111 days in the 2010s (Fig 5C; **Table E in** S1 Text), suggesting that Caribbean reef organisms have approximately one third the time to recover from such thermal events.

MHW trends are fairly consistent across Caribbean ecoregions (S9 Fig), however, coral reefs within the Eastern Caribbean are experiencing the greatest increase in MHW duration compared to the 1980s (S9 Fig; **Table E in** S1 Text), while the change in frequency of MHWs was the lowest on Western Caribbean reefs (S9 Fig; **Table E in** S1 Text). Such variations in MHW events across ecoregions further highlight differences in subregional warming patterns that impact the future success of coral reefs on both regional and local scales.

Conclusions

Caribbean coral reefs have been heating up at remarkable rates over the last century (Fig 6), resulting in total warming of 0.5 to 1˚C. Additionally, the frequency and duration of acute

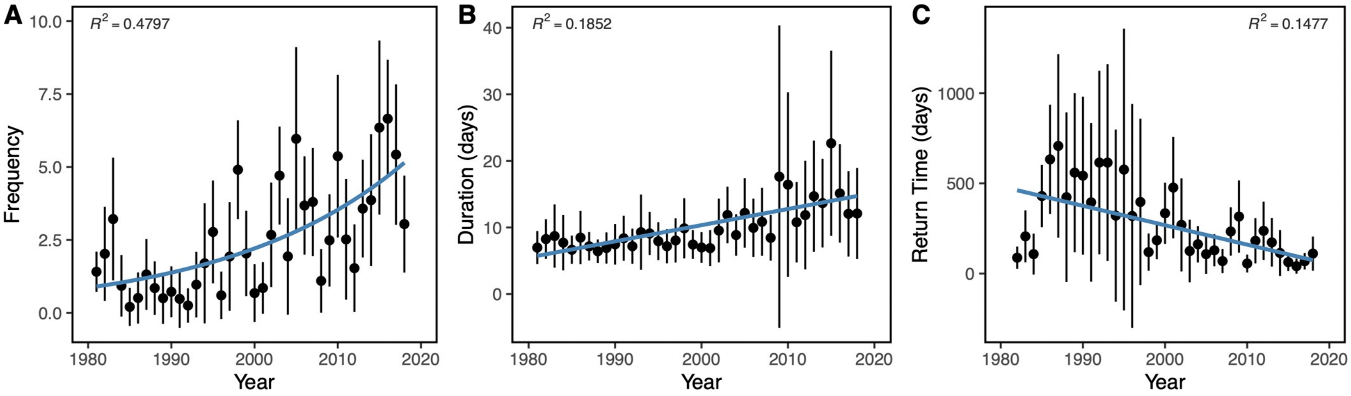

Fig 5. MHW trends (1981–2019) across Caribbean coral reefs. Temperature data are based on OISST gridded data to determine **A)** marine heat wave (MHW) frequency (number events per year) with Nagelkerke pseudo R^2; **B)** MHW duration (number days per event) with linear model R^2; and **C)** return time (number days per event) since the previous MHW event with linear model R^2 reported. Points denote annual mean values (±SD) and blue lines represent linear (lm or glm) trends.

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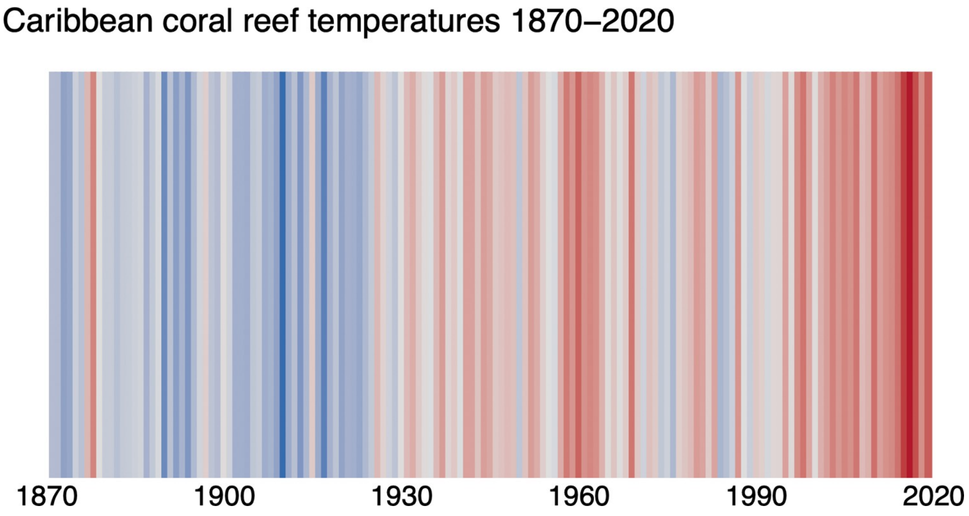

Fig 6. Climate stripe diagram depicting the mean annual temperature recorded on Caribbean coral reefs based on the HadISST database. Warmer temperatures are depicted in red (maximum annual SST of 28.0) and cooler annual temperatures are in blue (minimum annual SST of 26.6) (figure inspired by Professor Ed Hawkins [131]).

https://doi.org/10.1371/journal.pclm.0000002.g006

marine heatwaves increased markedly, particularly since 2010. This manifestation of increased temporal variability in ocean temperature is believed to be an important cause of many of the observed (and predicted) changes to these threatened habitats.

Not only has warming been one of the primary drivers of widespread coral mortality [19, 22, 52, 82, 84, 124], but it has indirectly (via habitat loss) and directly affected countless non-coral reef inhabitants when their own thermal tolerances were exceeded [36–38, 125]. However, there are numerous other important drivers of coral reef degradation. Fishing is by far the primary cause of dramatic Caribbean-wide fish population declines [40, 42, 126]. Additionally, the die off of the herbivorous sea urchin *Diadema antillarum* (especially coupled with coral mortality) caused widespread increases in the cover of benthic macroalgae [127]. In some locations, pollution may have further contributed to coral declines [39, 44]. And the worst current coral epizootic, stony coral tissue loss disease [128–130], might not be related to ocean warming, pollution, or any human activities. We urgently need to reduce greenhouse gas emissions while simultaneously addressing these and other local and regional stressors to protect the remnant Caribbean coral reefs and similarly at-risk global ecosystems.

Supporting information

S1 Text.
(DOCX)

S1 Fig. Historic SST record on Caribbean coral reefs (1981–2019). Historic SST records (Pathfinder) on Caribbean coral reefs depicting A) mean monthly SST each year (represented by line colour: blue to red) and B) GAM smoothed annual mean SST time (black line), annual maximum (red line), and annual minimum (blue line) SST. The grey dashed horizontal line denotes the overall mean SST for all sites over the entire period (27.23˚C) and the grey ribbon represents the 95% confidence interval around the true annual SST mean through time.
(PDF)

S2 Fig. Comparison of monthly SST (˚C) recorded in the HadISST and Pathfinder databases from 1982–2019. SST values were regressed against one another for the same time for

comparison of the relationship between the databases. Points are depicted by month (cooler months in blue and warmer months in red) and the black line represents the resulting linear regression model ($R^2 = 0.97$; $P < 0.001$).
(PDF)

S3 Fig. Comparison of HadISST (1871–2020) and Pathfinder (1981–2019) SST recorded on Caribbean coral reef locations. The high-resolution Pathfinder is represented as darker data over the long-term HadISST. Both datasets are represented by GAM smoothed annual mean SST time (solid line), annual maximum (red line), and annual minimum (blue line) SST. The dashed horizontal line denotes the overall mean SST for all sites over the entire period and the grey ribbon represents the 95% confidence interval around the true annual SST mean through time.
(PDF)

S4 Fig. Historic SST trends on coral reefs within Caribbean ecoregions. Long-term SST trends on Caribbean coral reefs by ecoregion (1871–2020; see **Figs 1 and 3** in the main text). The colour of each reef location and box around long-term SST (HadISST) plots represent the designated ecoregion. Plots depict SST data with GAM smoothed annual mean SST time (black line), annual maximum (red line), and annual minimum (blue line) SST. The grey dashed horizontal line denotes the mean SST over the entire period and the grey ribbon represents the 95% confidence interval around the true annual SST mean for the A) Bahamian, B) Eastern Caribbean, C) Floridian, D) Greater Antilles, E) Gulf of Mexico, F) Southern Caribbean, G) Southwestern Caribbean, and H) Western Caribbean ecoregions. Map layer was acquired from Natural Earth (https://www.naturalearthdata.com).
(PDF)

S5 Fig. Significance of A) rate of SST change (˚C per decade) and B) number of marine heatwave events per year across the Caribbean depicted in Fig 4. Grey ocean area was not included in these analyses. Map layer was acquired from Natural Earth (https://www.naturalearthdata.com).
(PDF)

S6 Fig. A) Rate of SST change (˚C per decade) over the duration of the HadISST database across the Caribbean from 1871 to 2020 (mean slope 0.04 ± 0.014˚C per decade) and B) significance of rate of SST change. Grey ocean area was not included in these analyses. Map layer was acquired from Natural Earth (https://www.naturalearthdata.com).
(PDF)

S7 Fig. A) Rate of SST change (˚C per decade) across the Caribbean from 1981 to 2020 (HadISST; mean slope 0.16 ± 0.054˚C per decade) and B) significance of rate of SST change. Grey ocean area was not included in these analyses. Map layer was acquired from Natural Earth (https://www.naturalearthdata.com).
(PDF)

S8 Fig. MHW trends (1981–2018) across Caribbean coral reefs by ecoregion. Temperature data are based on OISST gridded data to determine frequency (number events per year), duration (number days per event), return time (number days per event) since the previous event, onset rate (˚C per day) from start until peak intensity, peak intensity (˚C), and total days reefs experience MHWs per year. Points denote annual mean values (±SD) and blue lines represent linear (lm or glm) trends within each ecoregion (see **Figs 1 and S4** for ecoregion locations). Frequency, duration, and return time across all Caribbean coral reefs are depicted in **Fig 5** in

the main text.
(PDF)

S9 Fig. GIF of long-term SST records (HadISST) on Caribbean coral reefs depicting mean monthly SST each year (represented by line colour: Blue to red).
(GIF)

Acknowledgments

We thank the following data providers: Atlantic Gulf Rapid Reef Assessment (AGRRA) contributors and data managers; the Reef Check Foundation, UNEP World Conservation Monitoring Center, the Global Coral Reef Monitoring Program, Florida's Coral Reef Evaluation and Monitoring Program (CREMP), and the US Virgin Islands Territorial Coral Reef Monitoring Program (TCRMP). We thank Matthew Kendall for his assistance with cluster development and support with acquiring satellite data, and S. Williams, H. Reich, J. Rippe, and J. Baumann for their helpful feedback on early drafts of the manuscript.

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