

Article

Validation of Reef-Scale Thermal Stress Satellite Products for Coral Bleaching Monitoring

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Abstract: Satellite monitoring of thermal stress on coral reefs has become an essential component of reef management practice around the world. A recent development by the U.S. National Oceanic and Atmospheric Administration's Coral Reef Watch (NOAA CRW) program provides daily global monitoring at 5 km resolution—at or near the scale of most coral reefs. In this paper, we introduce two new monitoring products in the CRW Decision Support System for coral reef management: Regional Virtual Stations, a regional synthesis of thermal stress conditions, and Seven-day Sea Surface Temperature (SST) Trend, describing recent changes in temperature at each location. We describe how these products provided information in support of management activities prior to, during and after the 2014 thermal stress event in the Commonwealth of the Northern Mariana Islands (CNMI). Using *in situ* survey data from this event, we undertake the first quantitative comparison between 5 km satellite monitoring products and coral bleaching observations. Analysis of coral community characteristics, historical temperature conditions and thermal stress revealed a strong influence of coral biodiversity in the patterns of observed bleaching. This resulted in a model based on thermal stress and generic richness that explained 97% of the variance in observed bleaching. These findings illustrate the importance of using local benthic characteristics to interpret the level of impact from thermal stress exposure. In an era of continuing climate change, accurate monitoring of thermal stress and prediction of coral bleaching are essential for stakeholders to direct resources to the most effective management actions to conserve coral reefs.

Keywords: coral reef; coral bleaching; sea surface temperature; SST; satellite; thermal stress; NOAA Coral Reef Watch; Commonwealth of the Northern Mariana Islands; CNMI; coastal and marine management; coral diversity

1. Introduction

Global, near real-time satellite monitoring of environmental conditions linked to coral bleaching has supported coral reef management efforts for nearly 20 years. Throughout this period, the U.S. National Oceanic and Atmospheric Administration's Coral Reef Watch (NOAA CRW) program developed and released coral-specific satellite-based tools and successfully monitored thermal stress causing mass bleaching events around the world [1–8]. These products have been instrumental in aiding reef managers and other stakeholders to prepare for and respond to coral bleaching events.

Bleaching is a stress response of corals whereby the symbiotic zooxanthellae, which under usual conditions provide up to 90% of energy requirements of corals, are expelled from the coral host [9]. Zooxanthellae contain colorful pigments—their departure leaves the white calcium carbonate skeleton of the coral visible through the translucent tissue; the coral appear “bleached”. Environmental stressors including low salinity (fresh water), unusually cold temperature and increased exposure to light can result in localized coral bleaching. However, mass coral bleaching events have been linked to warm oceanic temperature anomalies, which occur on the scale of hundreds to thousands of kilometers [10].

Initially developed in the mid-1990s, CRW's heritage coral bleaching Decision Support System (DSS) consists of a suite of operationally supported (*i.e.*, 24/7 production/delivery/maintenance) products in near real-time twice each week [11,12]. The basis of the satellite product suite is a global *Sea Surface Temperature (SST) field* at 0.5° (~50 km) resolution. Comparison of this SST field with a long-term monthly climatology provides the SST Anomaly product, identifying conditions that differ from the expected temperatures for each location at that time of year. The first coral-specific product released by CRW was the *Coral Bleaching HotSpot*, reporting positive temperature anomalies above the warmest monthly climatology value and therein indicating the current magnitude of thermal stress. The *Degree Heating Week (DHW)* is the accumulation of HotSpots of 1 °C or greater through a rolling 12-week period and has been the strongest predictor of mass coral bleaching (*e.g.*, [2]). Summarizing the information of the HotSpot and DHW products into a single management-oriented product, the *Bleaching Alert Area* provides reef stakeholders with a categorized stress level on a reef, indicating presence or absence of bleaching thermal stress and predicted coral bleaching severity. *Virtual Stations* at over 200 reef locations provide managers with summarized information on current thermal conditions accompanied by historical time series of CRW SST and DHW products. These underpin the free, automated email system providing *Satellite Bleaching Alerts* to subscribers whenever thermal conditions traverse established thermal stress thresholds. These 50 km products have served the global coral reef community for well over a decade.

A recent major development has been the release of next-generation global thermal stress products at 5 km (0.05°) spatial and daily temporal resolution, which resulted in a dramatic improvement in near-shore reef coverage and responded to the most-frequent request from reef managers and other stakeholders for higher resolution [13]. Underpinning the suite is a 5 km SST field that blends data from instruments on multiple geostationary and polar-orbiting satellites, with current input streams resulting in as much as a 50-fold increase in the amount of data for most of the global ocean each day, as compared with the heritage SST. Derived products, matching those described for the 50 km resolution, are calculated by comparing the 5 km SST field with a customized, long-term climatology [14] derived using the current NOAA Climate Data Record for SST—the Pathfinder dataset [15]. The one distinction is that the 5 km Bleaching Alert Area product reports the maximum alert from the prior seven-day period, updated on a daily basis. This was necessitated by rapid daily fluctuations that result from the

increased spatial and temporal resolution. This next-generation 5 km DSS was initially released in July 2012, with updated versions culminating in the official release in February 2015.

Since its inception, the CRW 5 km DSS has monitored thermal stress globally and identified reef locations at risk of bleaching. CRW has received anecdotal and, in some cases, quantitative reports of coral bleaching from partner observers at several of these locations. The 5 km DSS showed that the Commonwealth of the Northern Mariana Islands (CNMI) was exposed to high levels of thermal stress in both 2013 and 2014 [13]. Other reef locations where the 5 km DSS reported thermal stress and where mass bleaching was observed in the past 2–3 years include the Hawaiian archipelago, the central and South Pacific, the Coral Triangle, the Florida Keys and Bermuda.

In this paper we introduce two new monitoring products developed within the 5 km DSS that support management efforts prior to, during, and after a bleaching event: *Regional Virtual Stations* and *Seven-day SST Trend*. Using these and other CRW products, we describe the development of thermal stress in CNMI (Figure 1a) during 2014; discuss how the CRW 5 km DSS was used to inform local managers and other stakeholders as stress developed; present data from *in situ* observations of coral bleaching during this event; and undertake the first quantitative comparison of the 5 km DSS products with observations of coral bleaching.

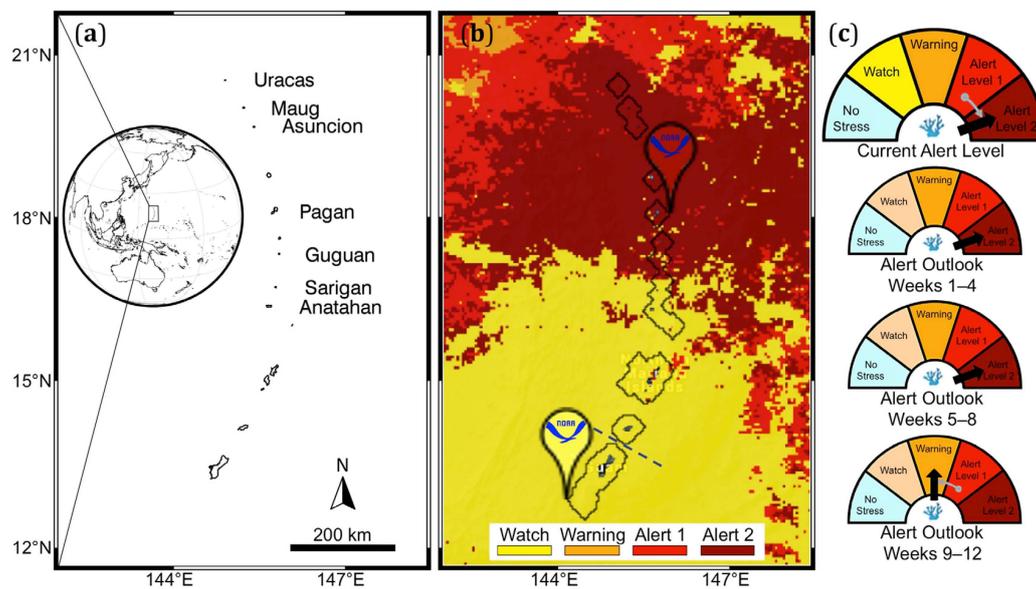


Figure 1. (a) Map of the study region identifying islands at which surveys were undertaken; (b) Spatial coverage of the Regional Virtual Stations for CNMI (north of dashed line) and Guam include satellite pixels within 20 km of reef-containing pixels (outlined by polygons). The color of customized Google Maps pins (inverted teardrops) indicates the 90th percentile Bleaching Alert Area level for pixels within each Regional Virtual Station. The background image shows the Bleaching Alert Area level on 13 August 2014 displayed in Google Maps [16]); (c) Regional Virtual Station gauges for CNMI showing the Bleaching Alert level on 13 August 2014 (top gauge) and the forecast stress levels in the subsequent three months. Grey arrows indicate change from the previous gauge reading.

2. Materials and Methods

2.1. CRW Product Expansion

2.1.1. Regional Virtual Stations

Reef managers and other stakeholders have benefited from the capacity to track localized conditions through time afforded by the heritage Virtual Stations. CRW has developed a set of 5 km Regional Virtual Stations (211 at the time of writing) to replace the heritage Virtual Stations

and take advantage of higher resolution data. These provide comprehensive information for reefs in a jurisdiction or predetermined sub-region. The Regional Virtual Stations represent a change in methodology from the heritage Virtual Stations. Rather than constructing each Virtual Station using a single pixel, as in the heritage 50 km Virtual Stations [12], Regional Virtual Stations were based on data from all of the 5 km pixels within each regional jurisdiction (e.g., CNMI, Guam; polygons in Figure 1b). While data from a single 5 km pixel provide much higher spatial detail, they may not be generally representative of thermal conditions for reefs across each jurisdiction. The new Regional Virtual Stations are more representative of regions at the expense of any localized spatial variability.

In a further enhancement from the heritage Virtual stations and because of the regional nature, the new Regional Virtual Stations include all coral reef locations around the world. Global coral reef locations were compiled from several data sources. The multi-source compilation by the United Nations Environment Programme–World Conservation Monitoring Centre (UNEP-WCMC) and the WorldFish Centre, in collaboration with the World Resources Institute (WRI) and The Nature Conservancy (TNC) [17], includes the Millennium Coral Reef Mapping Project and the World Atlas of Coral Reefs. This was augmented using other local marine atlases (e.g., refs [18,19]) and several in-house reef location sources (*i.e.*, where reef observation surveys had been reported). Reef-containing 5 km pixels were identified and augmented with a 20 km buffer around each 5 km reef pixel to define the extent for each Regional Virtual Station (black polygons in Figure 1b). The product provides regionally representative statistics based on all pixels contained within the Regional Virtual Station. The number of water pixels contained within each Regional Virtual Station varies due to the geo-political definition of the jurisdictions, ranging from 39 (Easter Island) to 12,014 (Papua New Guinea), with an average of 1156. The examples in Figure 1b contain 813 (CNMI) and 275 water pixels (Guam).

The Regional Virtual Stations are used in a series of products including new *Regional Bleaching Thermal Stress Gauges*; a Satellite Bleaching Alert email system; time series graphs; interactive Google Maps and Google Earth interfaces showing locations of Regional Virtual Stations; and associated data. Bleaching Thermal Stress Gauges use the 90th percentile value among pixels in the designated region to report the regional thermal stress alert level (No Stress, Bleaching Watch, Bleaching Warning, Alert Level 1, and Alert Level 2). For example, if 5% of the pixels for CNMI were at Alert Level 2 and a further 8% at Alert Level 1, the status for CNMI would be Alert Level 1. This methodology alerts users to regional thermal stress exposure while preventing exaggeration of bleaching risk. Satellite Bleaching Alerts for a region are emailed when the alert level changes, prompting users to look at CRW's map products for details on which specific locations within the region are affected by thermal stress. The "current" Bleaching Thermal Stress Gauge is augmented with three further gauges showing the predicted stress level for the coming one-to-three months (Figure 1c), based on CRW's Four-Month Coral Bleaching Thermal Stress Outlook product [20].

Time series reveal the temporal evolution of SST and thermal stress metrics for each Regional Virtual Station. Time series data of the 90th percentile value of SST, SST Anomaly, HotSpot, DHW and Bleaching Alert Area level within each region are published online. In addition, the temperature at the location of the 90th percentile HotSpot value from among 5 km pixels of each Regional Virtual Station is provided each day, corresponding to the thermal stress indicated by the HotSpot value for that day. It is this SST value that is shown on the time series figure for each Regional Virtual Station (Figure 2), along with representative monthly climatological SST values for each region (the average of climatology values across the pixels within each region) and the 90th percentile DHW within the region. Regional Virtual Station time series summary information and graphs are accessible directly from the interactive Google Maps interface on the CRW website by clicking on the Google Maps pins (Figure 1b), the color of which reflect the current bleaching alert level for each jurisdiction.

The new Regional Virtual Stations provide an indication of regional conditions pertaining to entire reef jurisdictions; however, the method lessens the geographic specificity of the data for monitoring individual islands and reefs. Information from the Regional Virtual Stations is intended to lead users to the CRW product maps, where spatial patterns of thermal stress are found.

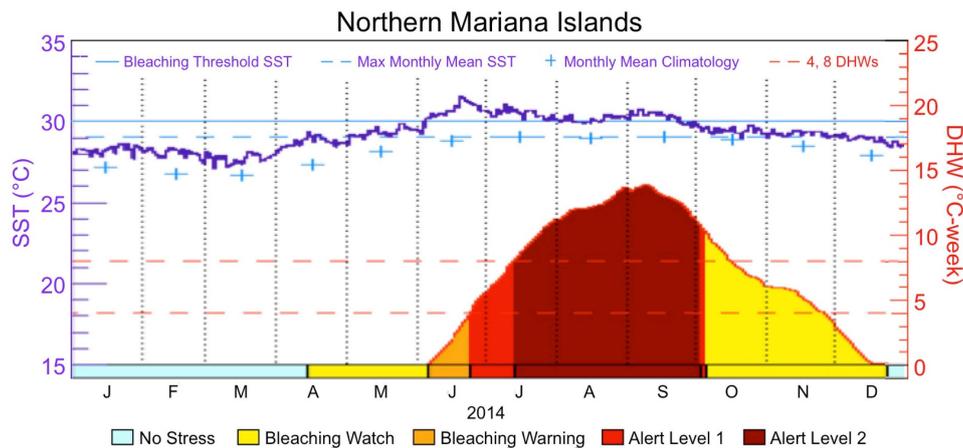


Figure 2. Regional Virtual Station time series for CNMI in 2014. The purple SST trace is the temperature at the location of the 90th percentile HotSpot value from among 5 km pixels for CNMI (see Figure 1b) for each date. Similarly, the red DHW trace is the 90th percentile DHW value and the color under this trace reflects the 90th percentile Bleaching Alert Area value. For each pixel, DHW accumulates when the SST value exceeds the maximum (blue dashed, MMM) of the monthly mean climatology values (blue plus) by at least 1 °C (blue solid, Bleaching Threshold)—the time series shows the spatial average of each of these values. DHW thresholds of 4 and 8 °C-weeks (red dashed) have been associated with significant coral bleaching, and widespread bleaching and significant mortality, respectively.

2.1.2. Seven-Day SST Trend

Dramatic and rapid changes in SST, particularly during summer months, can alert reef managers and other stakeholders to increased likelihood of ecosystem impacts. The Seven-day SST Trend product at 5 km resolution was recently developed, providing reef managers with the capacity to track the rate of SST change (slope of the linear regression) during the prior seven days. The seven-day period was chosen as it is within the spring-neap tidal cycle (typically ~14 days), while providing sufficient values ($n = 7$) for testing trend significance. A two-tailed Student's t -test with five degrees of freedom at the 20% significance level was incorporated to test for trend significance. Updated daily, the product was designed to mask trends insignificant at the 20% level, as well as those within the range -0.2 to 0.2 °C per week. SST Trend products can provide distinctive information on short-term changes associated with significant weather events (e.g., the passing of a tropical storm); change in upwelling strength; and warming caused by persistent doldrum conditions. While describing the changes in SST during the past seven days, trend products can also point to the trajectory of SST changes in the upcoming days. This product is useful to distinguish short-term thermal variations from the longer-term signals, lasting on the order of weeks to months, that lead to mass bleaching.

2.2. CNMI Field Work

The Mariana Archipelago consists of nine emergent volcanic islands to the north and five geologically older, raised limestone islands to the south (Figure 1a). The CNMI consists of all islands of the archipelago north of Guam (a separate US commonwealth from CNMI). Reef structure increases from north, where the underlying benthos consists of boulders surrounding the volcano, to south, where more-developed fringing reef areas are present. Reef managers and other stakeholders monitored the 5 km CRW DSS products during the development of thermal stress in 2014. From 26 June to 20 July 2014 members of the CNMI Bureau of Environmental and Coastal Quality's (BECQ) marine monitoring team collected bleaching data at 62 shallow (2–6 m), inshore sites across seven of the remote northern volcanic islands. The islands visited, from north to south (Figure 1a), were Uracas, Maug and Asuncion in June; and Pagan, Guguan, Sarigan and Anatahan in July. For each island, survey sites were selected using a stratified random sampling design with stratification based

on distance along the coastline. At each site, surveys were conducted on snorkel with an average of 79 (range: 66–104) 0.25 m² photoquadrats from 1 m above the substrate taken across an approximately 200 m × 10 m belt transect. The number of photoquadrats depended upon the availability of hard bottom habitat within the prescribed depth range and ocean conditions. Using the computer program CPCe v4.1 [21], five random points (after [22]) were digitally overlaid on each photoquadrat frame and the substrate or biota under each point was recorded. Hard corals were identified to the genus level (allowing determination of generic richness at each site) following the Corals of the World taxonomy [23]. Bleaching and mortality were noted for each recorded coral point.

A separate, collaborative project provided the opportunity to revisit the island of Maug from 10–13 August 2014 and survey three relatively deeper (7–10 m) reef sites on SCUBA. For these surveys, three to five 50 m transects were laid out sequentially along the depth contour, along which 0.25 m² photoquadrats were taken every meter. Photoquadrats were processed as described above.

2.3. Analysis of Field Observations and Comparison with Satellite Products

Field data for the northern section of the Mariana Archipelago provided an opportunity to undertake a quantitative comparison between satellite thermal stress monitoring and observed bleaching. Time series of the CRW products were extracted for satellite pixels containing or directly adjacent to the field survey sites. For each survey site and date, thermal stress values were extracted. While the 5 km products are at higher resolution than previously available, sub-pixel variability can remain due to localized effects (e.g., bathymetry, turbidity, shading). To reduce effects of between-site variability in the comparisons, survey and satellite data were averaged for each island (island-scale), with the two Maug surveys in June and August kept distinct. The two periods of field observations at Maug (24–27 June and 12–13 August 2014) provided an opportunity to evaluate the progression in bleaching at that island as the thermal stress continued to develop.

To investigate any influence of site characteristics on bleaching, island-scale coral cover, generic richness and bleaching susceptibility were also determined. Coral taxa bleaching susceptibility were extracted from the summary for the CNMI in [24], averaging the five-point scale of specific susceptibility (1–5, low-high) to give genus-level values (Table 1). Site and island-scale susceptibilities were determined as the weighted average of genus-level susceptibilities, based on the predominant coral taxa (*i.e.*, those genera with at least 1% benthic cover) at each site. Generic richness, the number of coral genera present, is an effective predictor variable for coral species richness [25].

Table 1. Susceptibility of coral genera with at least 1% benthic cover in Commonwealth of the Northern Mariana Islands (CNMI) surveys, after Maynard *et al.* [24]—species susceptibility (1–5, low-high) averaged to genus level.

Genus	Susceptibility	Genus	Susceptibility
<i>Stylophora</i>	5.0	<i>Leptoria</i>	3.0
<i>Astreopora</i>	4.0	<i>Montastrea</i>	3.0
<i>Montipora</i>	4.0	<i>Platygyra</i>	3.0
<i>Acropora</i>	3.8	<i>Pavona</i>	2.8
<i>Goniastrea</i>	3.8	<i>Acanthastrea</i>	2.0
<i>Pocillopora</i>	3.7	<i>Leptastrea</i>	2.0
<i>Favia</i>	3.1	<i>Porites</i>	1.3
<i>Favites</i>	3.0	<i>Goniopora</i>	1.0
<i>Cyphastrea</i>	3.0	<i>Heliopora</i>	1.0
<i>Galaxea</i>	3.0	<i>Millepora</i>	1.0

Historical temperature conditions for individual sites were also considered. The 5 km products for 2013 revealed substantial thermal stress levels across the CNMI. The maximum DHW value in 2013 for each island was used in the analysis to incorporate impacts of the prior year's thermal stress. Bleaching has also been linked to the SST variability for the warm season [26] and frequency of past

thermal disturbance. Past temperature variability has also been identified as a key factor for reef resilience [27]. Due to the short temporal domain of the 5 km products, each of these metrics was calculated using the Pathfinder version 5.2 SST dataset (1985–2012), an official NOAA Climate Data Record for SST [15]. SST variability was calculated as the standard deviation about the mean from temperatures during the warmest three-month period, reflecting the likely acclimation to extreme warm temperature and, therefore, capacity for reduced impact during extremes. This parameter was recently included in a resilience assessment for the southern islands of CNMI [24]. Past thermal disturbance is represented here by the number of thermal stress events of 4 °C-weeks or greater (corresponding with the established CRW threshold for ecologically significant bleaching [3]).

Direct relationships between bleaching, thermal stress, coral community characteristics and historical temperature conditions were investigated through linear regression and correlation analysis to demonstrate which variables affect bleaching response. Combined linear effects from several factors were investigated using multiple correlation analysis, which led to multi-factor modeling of bleaching response. The form of the model was dependent upon which factors showed the strongest relationship with bleaching. Model fit was assessed using linear regression of modeled predictions with observed bleaching.

3. Results

Field observations were analyzed for each site individually and grouped by island and survey month (June–August). Coral cover varied between 0 and 34% at the sites surveyed. When averaged by island and month (“island-scale”) the cover ranged from 2%–22%, with variability (standard deviation) between sites on the same order as and scaling with the average value (Figure 3a). Bleaching at sites ranged from 0%–94% of coral present. Island-and-month average bleaching varied within 0%–90%, with variability about the averages within 1%–34% (Figure 3b). Spatial variation in bleaching was particularly apparent for Maug, for which the June survey sites were distributed inside (six sites) and outside (seven sites) the volcanic caldera. While the coral cover (average \pm SD) was fairly consistent inside and outside ($11.1\% \pm 8.7\%$ and $7.1\% \pm 3.3\%$, respectively), the observed bleaching was markedly greater but with less variability inside the caldera ($52.2\% \pm 22.0\%$) than outside ($13.8\% \pm 33.1\%$). Generic richness of corals (with at least 1% benthic cover) ranged from 0–9 genera across the surveyed sites and 0.86–3.88 genera when averaged for island/month, with variability on the same order as and scaling with average values (Figure 3c). Bleaching susceptibility at sites ranged within 1.25–3.96 (on a scale from 1 to 5); susceptibilities were 1.75–3.44 at the island-scale with fairly consistent variability across the islands (Figure 3d).

Comparisons between the field survey data and satellite thermal stress revealed that observed bleaching increased with increasing DHW (Figure 4). Comparisons for each site individually (dots in Figure 4) were weakly correlated ($r^2 = 0.142$, linear regression), as was anticipated given that localized effects that may have influenced bleaching were not included. Grouping the surveys by island and month (squares in Figure 4) resulted in only one group having less than six observations (Maug, August; see Figure 3). This island-scale grouping reduced the effect of between-site variability and considerably enhanced the goodness-of-fit of the linear relationship ($r^2 = 0.411$), demonstrating with these data the established link between thermal stress and bleaching [2].

Consideration of the influence of benthic coral characteristics (cover, generic richness, susceptibility) and historical temperature conditions (number of bleaching-level stress events during 1985–2012, warm-season SST variability from 1985–2012, maximum DHW from 2013) was incorporated with thermal stress exposure (DHW) and bleaching response through pair-wise correlations of variables (Table 2). These revealed that cover, generic richness and DHW ($r = 0.9423$, 0.8166 and 0.6410 , respectively) had the strongest correlations with percent bleaching. Strong positive correlations were observed between coral cover and generic richness ($r = 0.7345$) and between bleaching susceptibility and the number of bleaching-level stress events ($r = 0.8293$), the latter being the second highest correlation calculated.

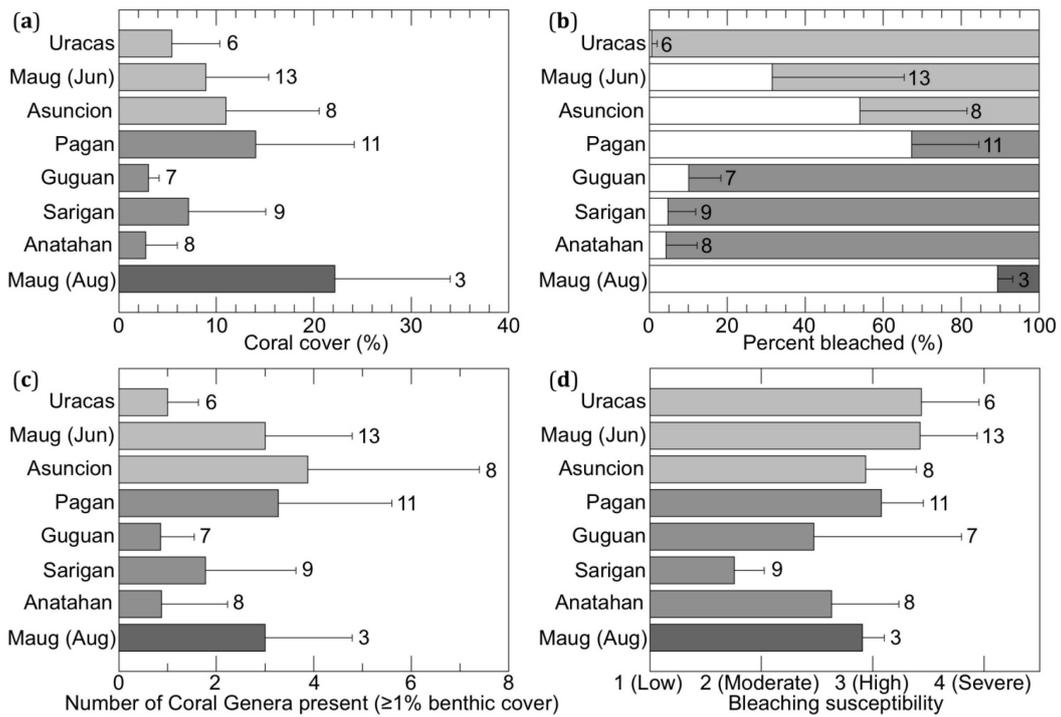


Figure 3. Observed (a) coral cover; (b) percent of coral bleached (white shading); and (c) number of coral genera present; with calculated (d) bleaching susceptibility, compiled by island and survey month. Bars show the island-and-month average, while whiskers show 1 SD. Numbers of sites for each island/month grouping are shown. Grey shading in all panels indicates the survey month (light-dark: June–August); white shading in (b) indicates percent bleached. Note that Maug was surveyed twice (in June and August 2014).

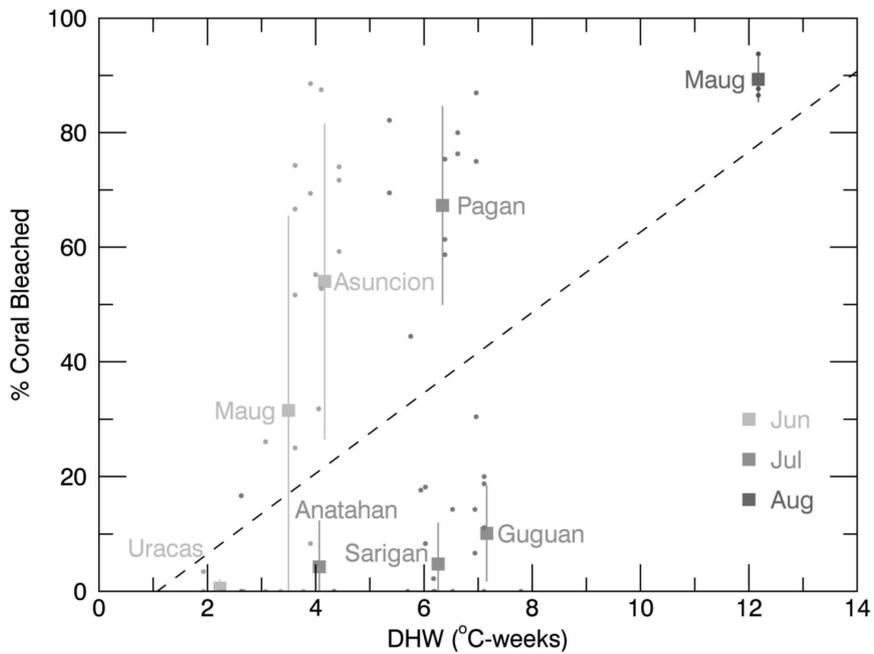


Figure 4. Comparison of percent coral bleached against Degree Heating Weeks (DHW). Site data (dots) were averaged by island and date (filled square), with the whiskers showing 1 SD. Symbol shading indicates the month of observation. The dashed line shows the linear regression of the island-scale data ($y = 7.0177x - 7.5183, r^2 = 0.411$).

Table 2. Correlations (r) between percent Bleaching (B), Degree Heating Week (DHW) (thermal stress accumulation, D), Coral cover (C), Generic richness (G), Susceptibility (S), Number of DHW ≥ 4 °C-week events during 1985–2012 (N), Warm-season sea surface temperature (SST) variability during 1985–2012 (W) and the Maximum 5 km DHW from 2013 (M). All parameters were calculated for each island-and-month grouping ($n = 8$). Emboldened numbers are referenced in the text. Where no plausible correlation should be expected, values were not calculated.

	Impact/Exposure			Benthic			SST History		
	B	D	C	G	S	N	W	M	
Bleaching (%)	1	0.6410	0.9423	0.8166	0.2980	0.3580	−0.1851	−0.0227	
Max. DHW in 2014		1	-	-	-	0.0091	−0.5526	0.2643	
Coral cover			1	0.7345	0.2267	0.4651	−0.1050	0.0394	
Generic richness				1	0.3095	0.2558	0.0720	−0.0430	
Susceptibility					1	0.8293	0.1332	−0.1839	
Number of DHW ≥ 4 events						1	0.0695	−0.0373	
Warm-season SST variability							1	−0.4715	
Max. DHW in 2013								1	

Multiple correlations of bleaching response with DHW exposure and various other parameters were used to identify the best combination of predictors for the 2014 northern CNMI bleaching (Table 3). With the small size of the island-scale data ($n = 8$), the number of contributing variables in determining the multiple correlations was limited to a maximum of three (in addition to DHW). The high correlation between bleaching and coral cover suggested the importance of cover; however, the combination of generic richness with DHW exposure provided the highest two-factor correlation with bleaching ($r = 0.9455$). Unsurprisingly, using all three further increased the correlation but not greatly ($r = 0.9660$), suggesting considerable overlap in the explanatory power of these variables. Adding susceptibility resulted in small improvements to each of the multivariate models. Combining current thermal stress with historical temperature parameters also improved the predictive capacity for bleaching from DHW exposure alone (Table 3).

Table 3. Multiple correlations between bleaching (dependent variable) and combinations of location-specific variables.

Correlation with Bleaching	0.9428	0.9455	0.8286	0.9660	0.9470	0.9821	0.9827	0.7314	0.6724	0.7514
Max. DHW in 2014	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Coral cover	✓			✓	✓		✓			
Generic richness		✓		✓		✓	✓			
Susceptibility			✓		✓	✓	✓			
Number of DHW ≥ 4 events								✓		✓
Warm-season SST variability									✓	✓

4. Discussion

The new Regional Virtual Station (Figure 2) provided BECQ reef managers and other stakeholders in CNMI with the capacity to easily track the development of thermal stress in 2014. Regional long-term monthly climatology values illustrate the normal seasonal cycle of temperatures, with the warmest period for CNMI typically in July–September (Figure 2). The SST trace was above the regional monthly climatology values from the beginning of 2014. SST briefly exceeded the regional maximum monthly mean (MMM) climatology in April and was consistently above the MMM from the first week of May until November. A rapid increase in regional SST in the first week of June resulted in accumulation of thermal stress (*i.e.*, DHW) in at least 10% of CNMI pixels. Regional SST values stayed above the Bleaching Threshold through June and July, with regional stress accumulation exceeding

4 °C-weeks (associated with ecologically significant coral bleaching [3]) in late-June and 8 °C-weeks (associated with widespread bleaching and mortality [3]) in mid-July. Stress accumulation resulted in the 90th-percentile DHW value for CNMI peaking at 13.9 °C-weeks in early September. SST values returned below the regional Bleaching Threshold by the end of September and below the MMM by December. As Regional Virtual Stations represent the 90th-percentile conditions in each region, they do not necessarily reflect conditions at individual satellite pixels but rather the upper range of thermal stress conditions within the region. This event was part of a large-scale warm anomaly affecting the northwestern Pacific Ocean, whose epicenter was located just to the north of the CNMI [13].

The rapid increase in regional SST in early June was reflected in the Seven-day SST Trend product for 4–10 June 2014 (Figure 5a), with some locations at the northern extent of the archipelago experiencing an increase of more than 2.5 °C during this single week. This was the most rapid large-scale increase in thermal stress during the event and occurred while final preparations for the planned monitoring expedition to the northernmost islands of the CNMI were being undertaken [28]. A second rapid increase in SST peaked on 21 June (Figures 2 and 5b), exacerbating thermal stress. Based on the CRW satellite products, the field monitoring team was anticipating coral bleaching in the survey area and re-assessed their methods to ensure that bleaching information was captured. Throughout their surveys, BECQ staff provided regular status updates to CRW. A rapid decrease in SST occurred at the end of June (Figure 5c) during the first stages of the fieldwork, possibly related to an intensifying storm or frontal system. While SST trends that occurred in the northern CNMI were large in magnitude, the trend magnitudes were consistently less in the southern CNMI during the entire event.

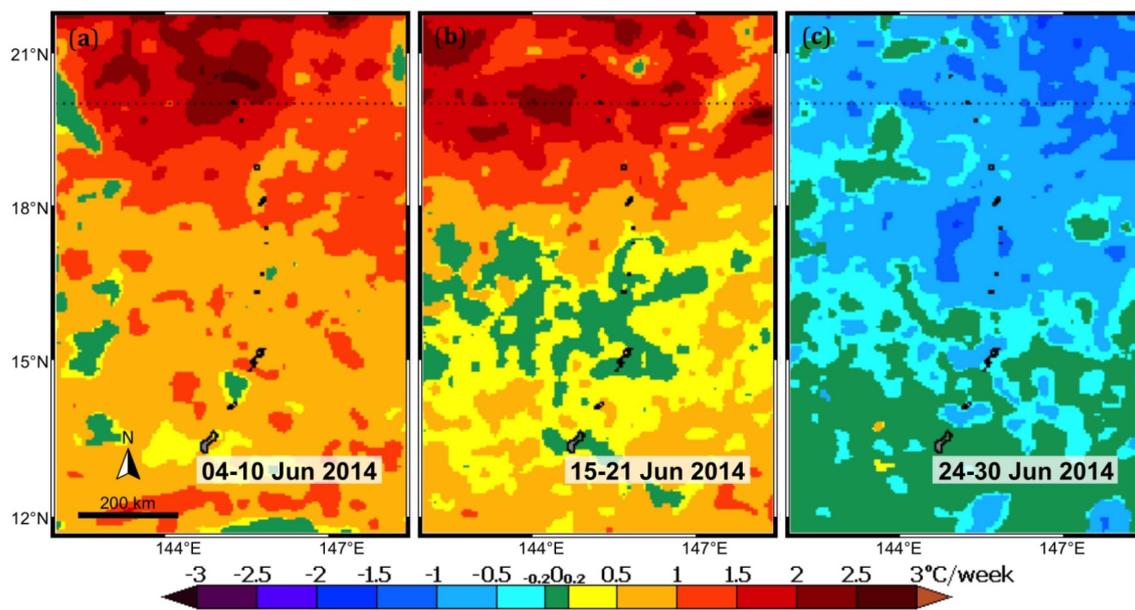


Figure 5. Maps of 5 km Seven-day SST Trend for the Mariana Archipelago during June 2014. Regional SST peaked on (a) 10 June 2014 and (b) 21 June 2014, with a rapid cooling event culminating on (c) 30 June 2014 (see also Figure 2).

Spatial and temporal patterns in the SST Trend appeared to be associated with short-term weather events in the region, emphasizing the weather-related nature of bleaching events [7] superimposed upon broad-scale warm ocean anomalies [10].

By the end of June 2014, coincident with the first group of BECQ field surveys, thermal stress along the entire Mariana Archipelago (Figure 6a) had exceeded the DHW threshold of 4 °C-weeks that has historically been connected with ecologically significant bleaching [3]. By mid-July (Figure 6b), when most of the sites were surveyed, thermal stress had intensified to the level where widespread

bleaching and significant mortality could be expected (8 °C-weeks [3]). By the mid-August visit to Maug, thermal stress there had increased to 12.3 °C-weeks (Figure 6c).

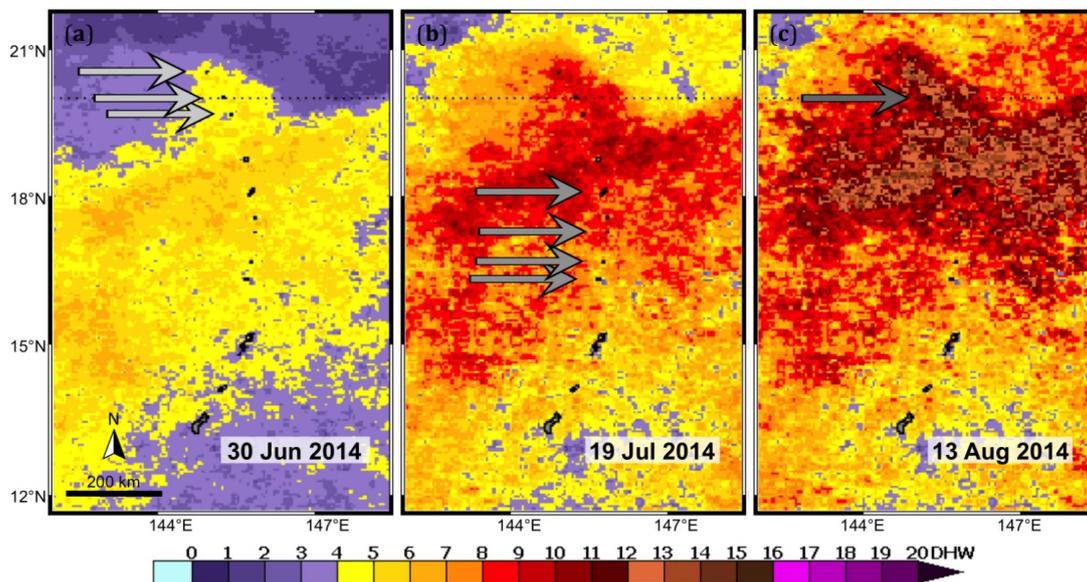


Figure 6. Maps of 5 km Degree Heating Week (DHW) for the Mariana Archipelago when bleaching observation surveys were conducted. (a) 30 Jun 2014; (b) 19 Jul 2014; (c) 13 Aug 2014. Arrows indicate locations of surveys taken within 1–11 days prior to the date shown. Shade of arrows corresponds to the different survey months (also in Figures 3 and 4).

While the remote and unpopulated nature of the surveyed locations in CNMI minimizes localized anthropogenic impacts, it also greatly reduces the capacity for pro-active and responsive management actions. However, having information on the development of thermal stress meant that field observers could anticipate likely conditions during the surveys and target monitoring efforts and protocols accordingly. Targeting research opportunities is a significant benefit afforded by satellite remote sensing and predictive models of thermal stress. In more accessible and populated places, the capability of predicting and monitoring thermal stress can lead to implementation of management actions that enhance reef resilience, minimize impacts from other potential stressors and support recovery of reefs following disturbance. In all locations, satellite monitoring of thermal stress provides effective support for communication with governments and other stakeholders, including the public, about potential ecosystem impacts.

Variability in bleaching among sites at each island is unsurprising given that variations in physical exposure (*i.e.*, windward *vs.* leeward sides) and coral community structure (*i.e.*, coral diversity) across sites are likely to influence thermal response characteristics. This is exemplified by the volcanic caldera at Maug. The semi-enclosed nature of the caldera and reduced circulation may have resulted in a greater temperature increase within the caldera as compared with temperature in the open-ocean during the 2014 event, with a corresponding increase in average bleaching observed inside the caldera. A volcanic vent inside the caldera acidifies the waters, affecting the abundance and diversity of corals [29] and may also have influenced the susceptibility of corals to thermal stress; however, recent evidence indicates little effect of acidified waters on bleaching sensitivity [30]. The increased bleaching variability outside the caldera is driven by one site that had distinctly different coral composition and was predominated by corals of greater susceptibility (80% *Pocillopora* spp.) than were present at the other outer caldera sites. This example emphasizes the importance of local knowledge in interpreting the broad-scale (even at 5 km resolution) satellite products for impacts on specific reef sites.

That observed bleaching increased with increasing DHW was consistent with past analyses using the CRW heritage (50 km) products (*e.g.*, [2]). Acknowledging the conspicuous variation among

site conditions in and around the Maug caldera, the island-scale bleaching for the June survey was re-calculated excluding sites inside the caldera. This revised the data point to just below the determined linear regression (at DHW = 3.43 °C-weeks, % Coral Bleached = 13.8% ± 33.1%) and resulted in a marginal improvement to the correlation ($r^2 = 0.465$). Even with this adjustment, it is clear that there remains considerable scatter of the island-and-month values about the line of best fit.

Performance evaluation of how the satellite products monitored the development of bleaching through time was hampered in that a return visit during the event occurred only at one island. Furthermore, the August survey at Maug consisted of only three sites and only one of these was at the same location (albeit deeper) as the June survey. This lack of replication makes direct comparisons between the June and August surveys and the analysis of event development difficult. At the one repeated site, inside the caldera, bleaching had increased from 74% (June) to 88% (August).

It is important to note that the 2014 thermal stress and bleaching was not an isolated event. The CNMI experienced significant thermal stress during 2013 [13] with multiple reports of significant coral bleaching and mortality in the field [31]. Based on the 2014 field observations, corals in Anatahan, Sarigan and Guguan appeared to have suffered extremely high mortality of bleaching susceptible corals during 2013 (Figure 3d), consistent with the highest observed thermal stress in the region during 2013 [13]. This may explain why the bleaching response for these three islands was substantially lower than the linear regression in Figure 6. Comparing the proportion of high susceptibility (≥ 3 in Table 1) taxa observed at Anatahan, Sarigan and Guguan (42.8% ± 18.5%) with those from Uracas, Maug (June survey), Asuncion and Pagan (82.9% ± 7.4%) revealed they were distinct (Student's $t = 4.01$, $df = 5$, $p = 0.0102$). Colonies present at Anatahan, Sarigan and Guguan in 2014 were either new recruits or had tolerated and survived thermal stress in 2013. The presence of more tolerant corals may explain why the observed bleaching response in 2014 was below what might otherwise have been expected. More susceptible coral taxa or genotypes were probably the first to die in 2013. Considering only data from the four northernmost islands in June/July (*i.e.*, excluding locations with prior effects of thermal stress) considerably strengthened the correlation between thermal stress and bleaching ($r^2 = 0.871$). While it is useful to examine this relationship in the absence of prior effects, bleaching prediction may be improved by considering other relevant factors.

The influence of benthic coral characteristics and historical temperature conditions demonstrated the importance of using coral community characteristics in interpreting bleaching likelihood due to thermal stress (Table 2). The positive correlation of generic richness with bleaching was somewhat surprising, given that coral diversity has been described as an important indicator of reef resilience, associated with both resistance to and recovery from bleaching [27]. This correlation may have resulted from the mortality of the most-susceptible taxa from thermal stress in 2013 leaving only the hardest corals to be surveyed in 2014 (though there is no correlation between generic richness and maximum DHW from 2013). All else being equal, higher susceptibility should result in higher bleaching; however, the correlation between percent bleaching and susceptibility was unexpectedly low ($r = 0.2980$). We note that thermal stress levels varied across the surveys (Figure 4), so the true contribution of susceptibility to bleaching response may not have been realized in all locations. The strong positive correlation between cover and generic richness suggested that greater coral cover generally included more taxa for these locations.

Historical temperature conditions were generally less correlated with bleaching than coral characteristics. However, the correlation of bleaching with the number of bleaching-level stress events during 1985–2012 suggests the potential for this metric to combine with thermal stress exposure (DHW) to improve the prediction of bleaching. The association of past exposure with bleaching may be a result of past disturbance influencing coral characteristics, demonstrated by the correlations between the number of events and each of the coral characteristics. Notably, the strong positive correlation between number of stress events and susceptibility suggested that disturbance history had increased thermal tolerance of susceptible taxa for these CNMI locations. This is consistent with patterns between prior stress exposure and current bleaching impacts previously reported [26,32]. One possible

explanation is that the higher growth rates and shorter generation times of the more susceptible genera infer a relatively higher capacity to adapt and/or acclimatize to thermal stress (*i.e.*, a locally reduced susceptibility). Prior-year DHW exposure showed little correlation with coral characteristics, indicating that short-term disturbance history was less informative. The negative correlation between bleaching and warm-season SST variability supports past findings that, *ceteris paribus*, reefs acclimated to more variable summer temperatures experience less bleaching [26,27]. Additionally, the negative correlation between DHW (in both 2013 and 2014) and warm-season SST variability ($r = -0.4715$ and -0.5526 , respectively) appears to suggest that less thermal stress is accumulated in highly variable locations; physically this could result from more variable SST being more likely to drop below the accumulation threshold for DHW, adding a stress mitigation mechanism to the reduced sensitivity through coral acclimation.

Multi-variable correlations (Table 3) of bleaching with combinations of thermal stress and benthic characteristics confirmed the value in interpreting thermal stress using knowledge of reef conditions. While the multi-variable correlations using historical temperature parameters were not as high as observed with the benthic characteristics, the combined effects of temperature history could prove useful in enhancing the capability of remotely sensed prediction of bleaching. This is especially so for the number of past stress exposure events, which might be considered a proxy for benthic characteristics (noting the correlations in Table 2).

Based on multiple correlations, a model for bleaching response was developed using only the thermal stress accumulation (DHW) and generic richness (GR). That bleaching occurred where both DHW and generic richness were high suggested an interactive model for these factors. Furthermore, no bleaching would be expected for zero thermal stress (irrespective of coral biodiversity). This led to a model that multiplied these factors to predict percent bleaching (B):

$$B = a \text{ DHW GR} + c \quad (1)$$

where a and c are constants. This model format represents the linear relationship of each independent variable with bleaching (as used in the multiple correlation), for a fixed value of the other variable. A least squares fit of this model to the island-and-month data ($a = 2.818$, $c = -4.935$) provided a strong predictor for bleaching (Figure 7a, $r^2 = 0.8788$). The negative intercept suggests that bleaching does not occur below a threshold of DHW exposure (as a function of generic richness).

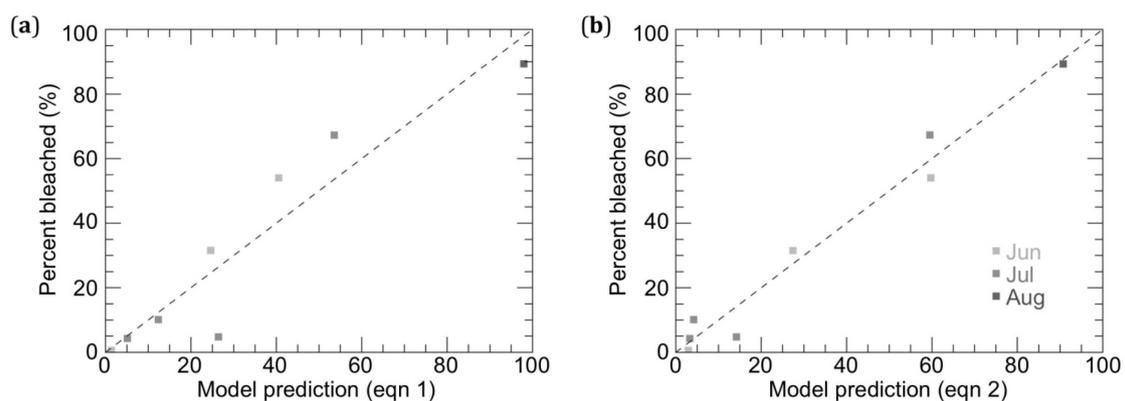


Figure 7. Modeled predictions of percent bleaching, as functions of thermal stress accumulation (DHW) and generic richness. Models based on (a) the product of DHW and generic richness (Equation (1)); and (b) the product of exponential factors of DHW and generic richness (Equation (2)). Symbol color indicates the month of observation. The line of unity is also shown (dashed).

A second model considered non-linearity in the effects of DHW and generic richness on bleaching; *viz.*,

$$B = a DHW^d GR^g + c \quad (2)$$

The least squares fit of this model (Figure 7b, $a = 0.4640$, $d = 0.9995$, $g = 2.509$, $c = 1.920$, $r^2 = 0.9696$) revealed the exponent of DHW was very close to unity, the presumptive value in Equation (1).

This supports the past use of linear comparisons between thermal stress and resultant bleaching (e.g., [2,33]). In contrast, the magnitude of the exponent g is substantially different from unity (as was presumed in Equation (1)). This stronger weighting of variations in the generic richness identifies its importance in describing the bleaching during this event.

The results here provide the first validation of the performance of reef-scale monitoring using satellite products, showing the clear relationship between thermal stress and bleaching. Furthermore, the study demonstrates that complex relations exist among various coral characteristics in describing bleaching. However, it does not automatically ensue that all mass bleaching events will necessarily follow the presented models for bleaching that incorporate generic richness and thermal stress accumulation. Given the limited geographic domain and the relatively small number of observations analyzed, these results should be tested more broadly. The analysis does emphasize the importance of interpreting thermal stress exposure using locally specific reef conditions.

5. Conclusions

The 5 km Decision Support System continues the legacy of Coral Reef Watch products in providing timely information about thermal stress conducive to mass coral bleaching events. The new Regional Virtual Stations enable reef managers and other stakeholders to track the potential for mass bleaching events and underpin the automated emails notifying managers of changes in the Bleaching Alert level. Spatial patterns in stress are revealed through CRW's mapped products, including the newly released Seven-day SST Trend. The analysis of bleaching observations from the 2014 CNMI event, undertaken here, has validated the use of reef-scale monitoring products in monitoring conditions likely to result in bleaching. Analysis of benthic data and historical thermal conditions has shown the importance of interpreting thermal stress exposure using locally specific information. A model for observing bleaching based only on accumulated thermal stress (explaining 41% of variance in bleaching) was greatly improved by the inclusion of generic richness (97%). Where available, benthic coral characteristics can be used to refine the vulnerability of reef areas to bleaching and lead to improved robustness of the models demonstrated here. The potential for historical temperature conditions to prove useful in fine-tuning the level of impact on corals, particularly in remote and/or infrequently visited areas, was also indicated. Together with CRW's Four-Month Thermal Stress Outlook product, the 5 km DSS provides reef managers and other stakeholders with tools to respond to potential and apparent thermal stress exposure, taking appropriate management action to minimize ecosystem impacts before, during and following bleaching. In an era of changing climate, improved understanding and monitoring of threats to coral reef ecosystems will guide the management and conservation of reef resources.

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Steven Johnson, Denise I. Perez, David Benavente, and John Iguel undertook the fieldwork planning, surveys and data processing. Scott F. Heron, Lyza Johnston, and Jeffrey A. Maynard analyzed the data. Scott F. Heron, Lyza Johnston, Gang Liu, Erick F. Geiger, Jeffrey A. Maynard, Jacqueline L. De La Cour, and C. Mark Eakin wrote the paper with input and revision from all other co-authors.

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References

1. Brandt, M.E.; Smith, T.B.; Correa, A.M.S.; Vega-Thurber, R. Disturbance driven colony fragmentation as a driver of a coral disease outbreak. *PLoS ONE* **2013**, *8*, e57164. [[CrossRef](#)] [[PubMed](#)]
2. Eakin, C.M.; Morgan, J.A.; Heron, S.F.; Smith, T.B.; Liu, G.; Alvarez-Filip, L.; Baca, B.; Bartels, E.; Bastidas, C.; Bouchon, C.; *et al.* Caribbean corals in crisis: Record thermal stress, bleaching, and mortality in 2005. *PLoS ONE* **2010**, *5*, e13969. [[CrossRef](#)] [[PubMed](#)]
3. Liu, G.; Strong, A.E.; Skirving, W. Remote sensing of sea surface temperature during 2002 Barrier Reef coral bleaching. *EOS Trans. AGU* **2003**, *84*, 137–144. [[CrossRef](#)]
4. Liu, G.; Strong, A.E.; Skirving, W.; Arzayus, L.F. Overview of NOAA Coral Reef Watch program's near-real time satellite global coral bleaching monitoring activities. In Proceedings of the 10th International Coral Reef Symposium, Okinawa, Japan, 28 June–2 July 2004; pp. 1783–1793.
5. Liu, G.; Eakin, C.M.; Rauenzahn, J.L.; Christensen, T.R.L.; Heron, S.F.; Li, J.; Skirving, W.; Strong, A.E.; Burgess, T. NOAA Coral Reef Watch's Decision Support System for coral reef management. In Proceedings of the 12th International Coral Reef Symposium, Cairns, Australia, 9–13 July 2012.
6. Moore, J.A.Y.; Bellchambers, L.M.; Depczynski, M.R.; Evans, R.D.; Evans, S.N.; Field, S.N.; Friedman, K.J.; Gilmour, J.P.; Holmes, T.H.; Middlebrook, R.; *et al.* Unprecedented mass bleaching and loss of coral across 12° of latitude in Western Australia in 2010–2011. *PLoS ONE* **2012**, *7*, e51807. [[CrossRef](#)] [[PubMed](#)]
7. Skirving, W.J.; Strong, A.E.; Liu, G.; Liu, C.; Arzayus, F.; Sapper, J.; Bayler, E. Extreme events and perturbations of coastal ecosystems: Sea surface temperature change and coral bleaching. In *Remote Sensing of Aquatic Coastal Ecosystem Processes: Science and Management Applications*; Richardson, L.L., LeDrew, E.F., Eds.; Springer: New York, NY, USA, 2006; pp. 11–25.
8. Thomas, C.R.; Heron, S.F. *South-East Asia Coral Bleaching Rapid Response: Final Report*; Commonwealth Scientific and Industrial Research Organisation (CSIRO): Campbell, ACT, Australia, 2011; p. 24.
9. Marshall, P.; Schuttenberg, H. *A Reef Manager's Guide to Coral Bleaching*; Great Barrier Reef Marine Park Authority: Townsville, Australia, 2006; p. 164.
10. Heron, S.F.; Pressey, R.L.; Skirving, W.J.; Rauenzahn, J.L.; Parker, B.A.A.; Eakin, C.M. Identifying oceanic thermal anomalies in the Coral Triangle Region. In Proceedings of the 12th International Coral Reef Symposium, Cairns, Australia, 9–13 July 2012.
11. Eakin, C.M.; Lough, J.M.; Heron, S.F. Climate variability and change: Monitoring data and evidence for increased coral bleaching stress. In *Coral Bleaching: Patterns, Processes, Causes and Consequences*; Lough, J., van Oppen, M., Eds.; Springer: Berlin, Germany, 2009; pp. 41–67.
12. Liu, G.; Rauenzahn, J.L.; Heron, S.F.; Eakin, C.M.; Skirving, W.J.; Christensen, T.R.L.; Strong, A.E.; Li, J. NOAA Coral Reef Watch 50 km Satellite Sea Surface Temperature-Based Decision Support System for Coral Bleaching Management; NOAA Technical Report NESDIS 143; NOAA/NESDIS: College Park, MD, USA, 2013; p. 33.
13. Liu, G.; Heron, S.F.; Eakin, C.M.; Muller-Karger, F.E.; Vega-Rodriguez, M.; Guild, L.S.; de la Cour, J.L.; Geiger, E.F.; Skirving, W.J.; Burgess, T.F.R.; *et al.* Reef-scale thermal stress monitoring of coral ecosystems: New 5-km global products from NOAA Coral Reef Watch. *Remote Sens.* **2014**, *6*, 11579–11606. [[CrossRef](#)]
14. Heron, S.F.; Liu, G.; Eakin, C.M.; Skirving, W.J.; Muller-Karger, F.E.; Vega-Rodriguez, M.; De La Cour, J.L.; Burgess, T.F.R.; Strong, A.E.; Geiger, E.F.; *et al.* *Climatology Development for NOAA Coral Reef Watch's 5-km Product Suite*; NOAA Technical Report NESDIS 145; NOAA/NESDIS: College Park, MD, USA, 2015; p. 21.
15. Casey, K.S.; Brandon, T.B.; Cornillon, P.; Evans, R. The past, present and future of the AVHRR Pathfinder SST program. In *Oceanography from Space: Revisited*; Barale, V., Gower, J.F.R., Alberotanza, L., Eds.; Springer: Berlin, Germany, 2010; pp. 323–341.
16. NOAA Coral Reef Watch. Bleaching Alert Area for 13 August 2014 Displayed in Google Maps. Available online: <http://coralreefwatch.noaa.gov/vs/map.php> (accessed on 13 August 2014).

17. UNEP-WCMC; WorldFish Centre; WRI; TNC. *Global Distribution of Warm-Water Coral Reefs, Compiled from Multiple Sources Including the Millennium Coral Reef Mapping Project. Version 1.3*; UNEP World Conservation Monitoring Centre: Cambridge, UK, 2010.
18. UNEP/IUCN. *Coral Reefs of the World. Volume 1: Atlantic and Eastern Pacific. UNEP Regional Seas Directories and Bibliographies*; IUCN: Gland, Switzerland, 1988.
19. UNEP/IUCN. *Coral Reefs of the World. Volume 3: Central and Western Pacific. UNEP Regional Seas Directories and Bibliographies*; IUCN: Gland, Switzerland, 1988.
20. Eakin, C.M.; Liu, G.; Chen, M.; Kumar, A. Ghost of bleaching future: Seasonal outlooks from NOAA's operational Climate Forecast System. In Proceedings of the 12th International Coral Reef Symposium, Cairns, Australia, 9–13 July 2012.
21. Kohler, K.E.; Gill, S.M. Coral Point Count with Excel extensions (CPCe): A visual basic program for the determination of coral and substrate coverage using random point count methodology. *Comput. Geosci.* **2006**, *32*, 1259–1269. [[CrossRef](#)]
22. Houk, P.; van Woesik, R. Coral reef benthic video surveys facilitate long-term monitoring in the Commonwealth of the Northern Mariana Islands: Toward an optimal sampling strategy. *Pac. Sci.* **2006**, *60*, 177–189. [[CrossRef](#)]
23. Veron, J.E.N. *Coral Reefs of the World*; Australian Institute of Marine Science: Cape Ferguson, QLD, Australia, 2000; p. 1382.
24. Maynard, J.A.; McKagan, S.; Raymundo, L.; Johnson, S.; Ahmadi, G.; Johnston, L.; Houk, P.; Williams, G.; Kendall, M.; Heron, S.F.; *et al.* Assessing relative resilience potential of coral reefs to inform management. *Biol. Conserv.* **2015**, *192*, 109–119. [[CrossRef](#)]
25. Richards, Z.T.; Hobbs, J.-P.A. Predicting coral species richness: The effect of input variables, diversity and scale. *PLoS ONE* **2014**, *9*, e83965. [[CrossRef](#)] [[PubMed](#)]
26. Guest, J.R.; Baird, A.H.; Maynard, J.A.; Muttaqin, E.; Edwards, A.J.; Campbell, S.J.; Yewdall, K.; Affendi, Y.A.; Chou, L.M. Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. *PLoS ONE* **2012**, *7*, e33353. [[CrossRef](#)] [[PubMed](#)]
27. McClanahan, T.R.; Donner, S.D.; Maynard, J.A.; MacNeil, M.A.; Graham, N.A.J.; Maina, G.; Baker, A.C.; Alemu I., G.B.; Beger, M.; Campbell, S.G.; *et al.* Prioritizing key resilience indicators to support coral reef management in a changing climate. *PLoS ONE* **2012**, *7*, e42884. [[CrossRef](#)] [[PubMed](#)]
28. Johnson, L.; (CNMI Bureau of Environmental and Coastal Quality Coral Reef Watch, College Park, MD, USA). Personal Communication, 2014.
29. Enochs, I.C.; Manzello, D.P.; Donham, E.M.; Kolodziej, G.; Okano, R.; Johnston, L.; Young, C.; Iguel, J.; Edwards, C.B.; Fox, M.D.; *et al.* Shift from coral to macroalgae dominance on a volcanically acidified reef. *Nat. Clim. Chang.* **2015**. [[CrossRef](#)]
30. Noonan, S.H.C.; Fabricius, K.E. Ocean acidification affects productivity but not the severity of thermal bleaching in some tropical corals. *ICES J. Mar. Sci.* **2015**. [[CrossRef](#)]
31. Reynolds, T.; Burdick, D.; Houk, P.; Raymundo, L.; Johnson, S. Unprecedented coral bleaching across the Marianas archipelago. *Coral Reefs* **2014**, *33*, 499. [[CrossRef](#)]
32. Maynard, J.A.; Anthony, K.R.N.; Marshall, P.A.; Masiri, I. Major bleaching events can lead to increased thermal tolerance in corals. *Mar. Biol.* **2008**, *155*, 173–182. [[CrossRef](#)]
33. Maynard, J.A.; Turner, P.J.; Anthony, K.; Baird, A.H.; Berkelmans, R.; Eakin, C.M.; Johnson, J.; Marshall, P.A.; Packer, G.R.; Rea, A.; *et al.* ReefTemp: An interactive monitoring system for coral bleaching using high-resolution SST and improved stress predictors. *Geophys. Res. Lett.* **2008**, *35*, L05603. [[CrossRef](#)]

