

# Global warming transforms coral reef assemblages

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Global warming is rapidly emerging as a universal threat to ecological integrity and function, highlighting the urgent need for a better understanding of the impact of heat exposure on the resilience of ecosystems and the people who depend on them<sup>1</sup>. Here we show that in the aftermath of the record-breaking marine heatwave on the Great Barrier Reef in 2016<sup>2</sup>, corals began to die immediately on reefs where the accumulated heat exposure exceeded a critical threshold of degree heating weeks, which was 3–4 °C-weeks. After eight months, an exposure of 6 °C-weeks or more drove an unprecedented, regional-scale shift in the composition of coral assemblages, reflecting markedly divergent responses to heat stress by different taxa. Fast-growing staghorn and tabular corals suffered a catastrophic die-off, transforming the three-dimensionality and ecological functioning of 29% of the 3,863 reefs comprising the world's largest coral reef system. Our study bridges the gap between the theory and practice of assessing the risk of ecosystem collapse, under the emerging framework for the International Union for Conservation of Nature (IUCN) Red List of Ecosystems<sup>3</sup>, by rigorously defining both the initial and collapsed states, identifying the major driver of change, and establishing quantitative collapse thresholds. The increasing prevalence of post-bleaching mass mortality of corals represents a radical shift in the disturbance regimes of tropical reefs, both adding to and far exceeding the influence of recurrent cyclones and other local pulse events, presenting a fundamental challenge to the long-term future of these iconic ecosystems.

Extreme weather events due to anthropogenic global warming are rapidly emerging as major contemporary threats to almost all ecosystems<sup>1</sup>. On coral reefs, severe heatwaves trigger episodes of mass bleaching<sup>4–7</sup>, which occur when the relationship between corals and their photosynthetic symbionts (zooxanthellae, *Symbiodinium* spp.) breaks down, turning the coral pale. Bleached corals are physiologically damaged and nutritionally compromised, and they can die if the bleaching is severe and the recovery time of their symbionts is prolonged<sup>8,9</sup>. However, the relationship between heat exposure, bleaching and the initial and longer term mortality of different taxa is not well understood or quantified. Although the concept of winners versus losers has been widely applied to describe inter-specific differences in the degree of bleaching<sup>10–14</sup>, predicting the definitive losers, namely those corals that fail to regain their colour and ultimately die following heat stress, is key to understanding how climate change affects biodiversity, species composition and ecosystem function. To date, no study has, to our knowledge, examined the quantitative relationship between a broad range of heat exposures and the response of coral assemblages. Establishing the shape of this response curve is essential for identifying the critical levels of heat exposure that trigger bleaching and mass mortality, and for predicting the amount of heat exposure that could drive a transformation in species composition and the widespread collapse of ecological functions. Here, we examine geographical patterns of heat exposure and the resultant mortality of coral assemblages along the 2,300 km

length of the Great Barrier Reef, following the record-breaking marine heatwave of 2016<sup>2</sup>. We show that taxonomic patterns of bleaching did not predict the identity of the corals that ultimately died, that many corals succumbed immediately from heat stress, and that others died more slowly following the depletion of their zooxanthellae. The die-off of corals drove a radical shift in the composition and functional traits of coral assemblages on hundreds of individual reefs, transforming large swaths of the Great Barrier Reef from mature and diverse assemblages to a highly altered, degraded system.

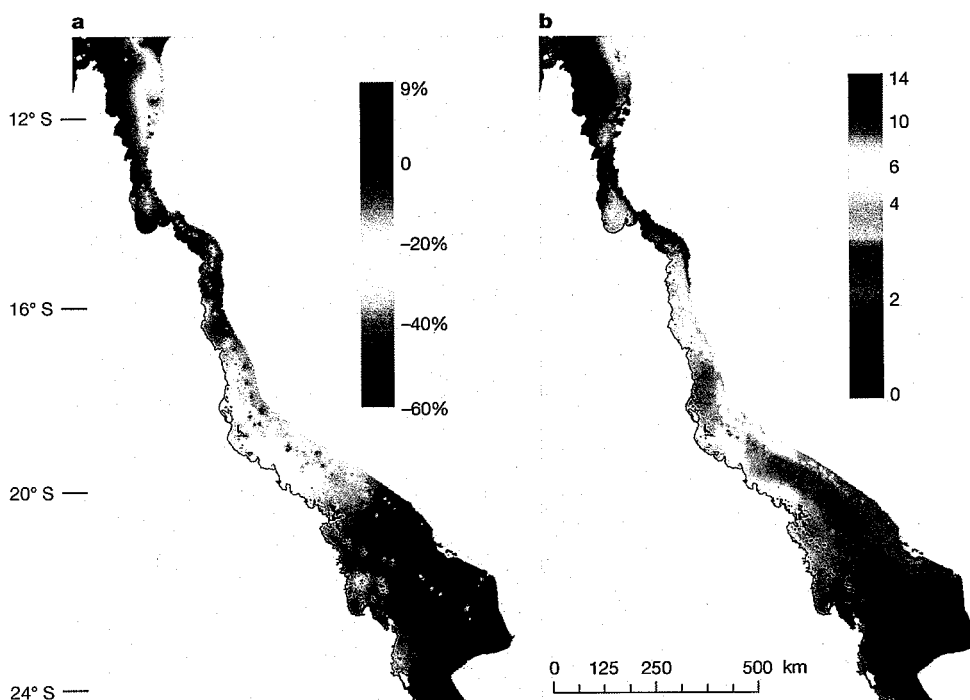
The 2016 bleaching event triggered an unprecedented loss of corals on the northern third of the Great Barrier Reef, and to a lesser extent, the central third, with almost no heat-stress mortality occurring further south (Fig. 1a and Extended Data Figs. 1–3). The geographical footprint and intensity of the coral die-off (Fig. 1a) closely matched the observed north–south pattern in accumulated heat (Fig. 1b), measured as satellite-derived degree heating weeks (DHW in °C-weeks), a commonly used measurement that incorporates both the duration and intensity of heat stress<sup>15,16</sup>. The 5-km-resolution DHW values (Fig. 1b) were significantly correlated with independently estimated losses of corals (Fig. 1a;  $r^2 = 0.50$ ,  $P < 0.001$ ,  $n = 1,156$  reefs). In the northern, 700-km-long section of the Great Barrier Reef (from 9.5–14.5 °S), in which the heat exposure was the most extreme, 50.3% of the coral cover on reef crests was lost within eight months (Fig. 1b). More broadly, throughout the entire Great Barrier Reef, including the southern third, in which the heat exposure was minimal (Fig. 1b), the cover of corals declined by 30.0% between March and November 2016. In comparison, the massive loss of corals from the 2016 marine heatwave was an order of magnitude greater and more widespread than the patchier, localized damage that typically occurs on reef sites within the track of a severe tropical cyclone<sup>17</sup>.

At the scale of individual reefs, the severity of coral mortality was also highly correlated with the amount of bleaching, and with the level of heat exposure (Fig. 2). Initially, at the peak of temperature extremes in March 2016, many millions of corals died quickly in the northern third of the Great Barrier Reef over a period of only 2–3 weeks (Fig. 2a). These widespread losses were not due to the attrition of corals that slowly starved because they failed to regain their symbionts<sup>9</sup>. Rather, temperature-sensitive species of corals began to die almost immediately in locations that were exposed to heat stress of more than 3–4 °C-weeks (Figs. 1b, 2a). The amount of initial mortality increased steadily with increasing heat exposure ( $r^2 = 0.50$ ,  $P < 0.001$ ,  $n = 63$  reefs); on reefs which were exposed to less than 4 °C-weeks, fewer than 5% of the corals died, whereas an initial median loss of 15.6% of corals was recorded on reefs with 4–8 °C-weeks exposure, and a median loss of 27.0% of corals at locations that experienced 8 °C-weeks or more (Fig. 2a). Across the entire Great Barrier Reef, 34.8% of individual reefs experienced at least 4 °C-weeks, and 20.7% of reefs were exposed to 8 °C-weeks or more of accumulated heat stress in 2016 (Fig. 1b). The amount of initial mortality at the peak of summer varied strikingly among different groups of corals (Extended Data Fig. 4a).

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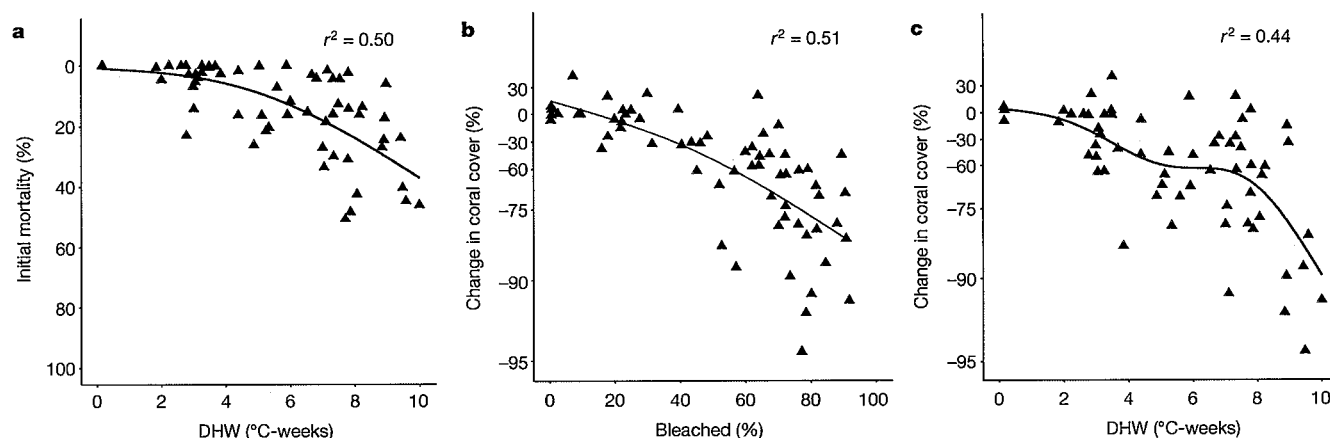
**Fig. 1 | Large-scale spatial patterns in change in coral cover and in heat exposure on the Great Barrier Reef, Australia. a, Change in coral cover between March and November 2016. b, Heat exposure, measured**

in DHW (in °C-weeks) in the summer of 2016. Map template is provided by Geoscience Australia (© Commonwealth of Australia (Geoscience Australia) 2018).

During the ensuing Austral winter, the bleached corals in the northern and central Great Barrier Reef either slowly regained their colour and survived or they continued to die at unprecedented levels. Less than 1% of surviving colonies remained bleached after eight months. The severity of the longer term loss of corals, measured in situ as the decline in coral cover between March and November, was accurately predicted by the percentage of corals that were initially bleached (Fig. 2b;  $r^2 = 0.51$ ,  $P < 0.001$ ,  $n = 63$  reefs). Specifically, reefs that experienced less than 25% bleaching in March typically had almost no loss of cover after eight months (Fig. 2b). By contrast, above this threshold, the loss of coral cover increased progressively, indicating that fewer of the bleached corals survived. Furthermore, the longer term loss of coral cover also intensified with increasing levels of heat exposure (DHW)

experienced by each reef ( $r^2 = 0.44$ ,  $P < 0.001$ ,  $n = 63$  reefs; Fig. 2c). Consequently, we recorded almost no loss of coral cover for reefs exposed to 0–3 °C-weeks, compared to a 40% decline at 4 °C-weeks, 66% for 8 °C-weeks, and extreme declines of > 80% for exposures of 9 °C-weeks or more. The nonlinear responses to heat exposure varied significantly among coral taxa (Extended Data Figs. 5, 6), illustrating a spectrum of survivorship among winners versus losers, driving a radical shift in species composition.

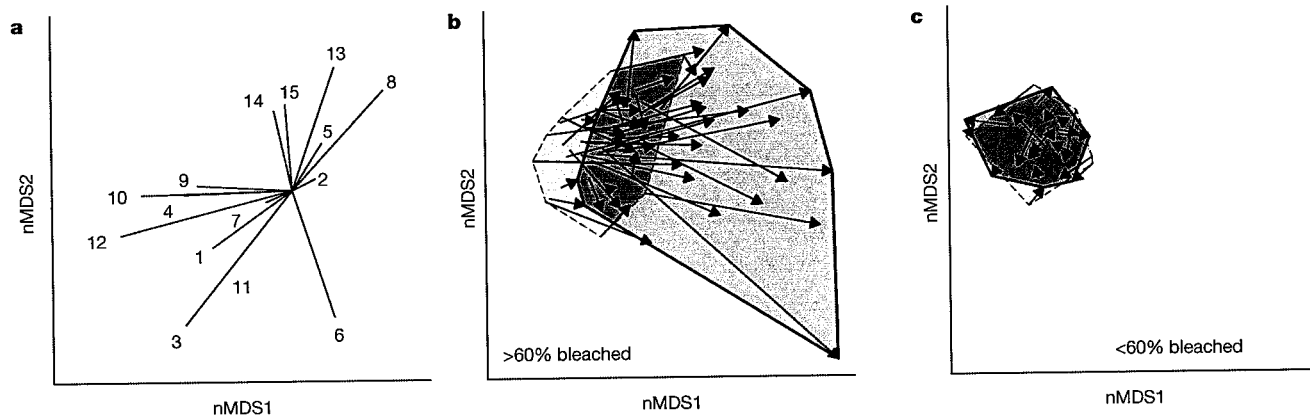
Post-bleaching mortality has disproportionately transformed the assemblage structure and functional diversity of corals on reefs that experienced high levels of bleaching (affecting more than 60% of colonies), as illustrated by a non-metric multi-dimensional scaling (nMDS) analysis (Fig. 3). The abundances of all categories of corals



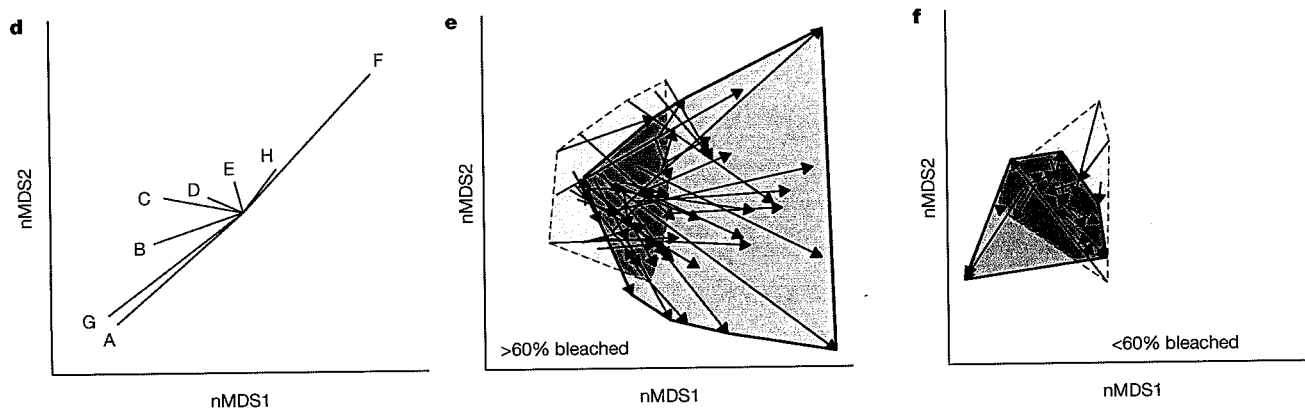
**Fig. 2 | The initial and longer term response of coral assemblages to heat exposure.** Regression curves were fitted using generalized additive models, with 95% confidence limits (ribbons). Data points represent individual reefs. a, Initial coral mortality measured at the peak of bleaching ( $n = 63$  reefs), versus the heat exposure each reef experienced

(satellite-based DHW (in °C-weeks)). b, Longer term change in coral cover ( $\log_{10}$ ) between March and November 2016 on 63 individual reefs, versus the initial amount of bleaching recorded underwater. c, Longer term change in coral cover ( $\log_{10}$ ) between March and November 2016, versus heat exposure (DHW) on the same individual reefs.

## Assemblage structure



## Functional traits



**Fig. 3 | Changes in assemblage structure and functional traits of corals following mass bleaching.** a–c, nMDS analyses of shifts in coral assemblages between March and November 2016. a, Fifteen nMDS vectors indicate the responses of individual taxa: 1, other *Acropora*; 2, faviids; 3, *Isopora*; 4, *Montipora*; 5, *Mussidae*; 6, other *Pocillopora*; 7, *Pocillopora damicornis*; 8, *Poritidae*; 9, *Seriatopora hystrix*; 10, staghorn coral (*Acropora* spp.); 11, *Stylophora pistillata*; 12, tabular coral (*Acropora* spp.); 13, soft corals; 14, other scleractinia; 15, other sessile fauna (see Methods). b, The grey polygon bounds the ordination space occupied by coral assemblages on each reef in March. Red arrows connect the before–after pairs of data points for each location to show changes in composition on severely bleached reefs (> 60% of colonies bleached,  $n = 43$  reefs) after eight months (in November), bounded by the red polygon. c, Blue arrows

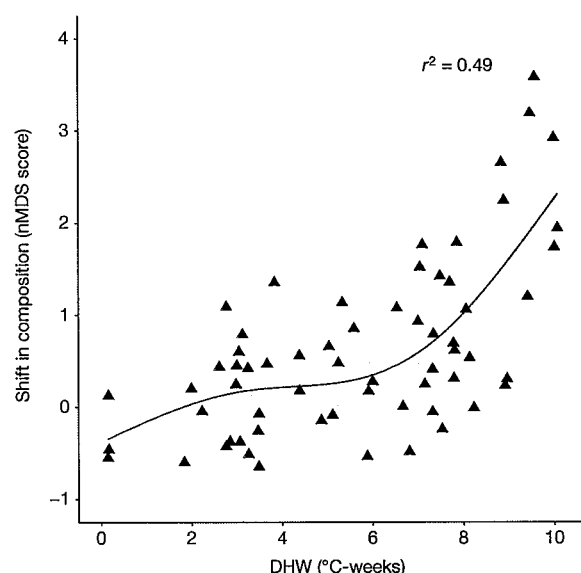
connect the before–after pairs of data points for each location on reefs ( $n = 20$ ) that were moderately (< 60% bleached), bounded by the grey (March) and blue polygons (November). d–f, nMDS analyses of shifts in assemblage trait composition between March and November 2016 at the same locations. d, The eight vectors indicate the absolute contribution of traits to coral assemblages: A, surface area to volume ratio; B, growth rate; C, colony size; D, skeletal density; E, colony height; F, corallite width; G, interstitial space size; H, reproductive mode (see Methods and Extended Data Table 1). e, The shift in abundance-weighted trait space coordinates for coral assemblages over eight months to show changes in composition on severely bleached reefs (> 60% bleaching). f, The shift in abundance-weighted trait space coordinates for coral assemblages on reefs with < 60% bleaching.

decreased to varying degrees on these heavily bleached reefs, shown by the orientation of the nMDS vectors (Fig. 3a) and the directional shift in the before–after assemblages (Fig. 3b). Tabular and staghorn *Acropora*, *Seriatopora hystrix* and *Stylophora pistillata*—fast-growing, three-dimensional species that dominate many shallow Indo-Pacific reefs—all declined by > 75% (Extended Data Fig. 4b). In contrast to the radical shifts on heavily bleached reefs, assemblages changed very little between March and November on reefs that experienced moderate (30–60%) or minor (0–30%) bleaching (Fig. 3c).

The response of coral assemblages on reefs exposed to a broad range of heat stress, ranging from 0 to 10 °C-weeks, was strikingly nonlinear (Fig. 4). The changes in assemblage structure after eight months (measured as the Euclidean distance between before and after compositions on each reef; Fig. 3b, c) were small on reefs that were exposed to less than 6 °C-weeks, whereas reefs subjected to more than 6 °C-weeks lost over 50% of their corals (Fig. 2c) and shifted markedly in composition (Fig. 4). Satellite-derived DHW data indicate that 28.6% of the 3,863 reefs comprising the Great Barrier Reef experienced thermal exposures of more than 6 °C-weeks during the 2016 bleaching event, and 20.7%

(800 reefs) were exposed to more than 8 °C-weeks (Fig. 1). Individual reefs with this severity of heat exposure have undergone an unprecedented ecological collapse, extending southwards from Papua New Guinea for up to 1,000 km (Fig. 1). Reefs that were exposed to less than 6 °C-weeks were located predominantly in the southern half of the Great Barrier Reef, and in a narrow northern patch at the outer edge of the continental shelf where temperature anomalies in 2016 above the local long-term summer maximum were small (Fig. 1b).

The abrupt, regional-scale shift in coral assemblages has also radically reduced the abundance and diversity of species traits that facilitate key ecological functions (Fig. 3d, e and Extended Data Tables 1, 2). A before–after analysis of the multi-dimensional trait space of coral assemblages, weighted by the absolute abundance of taxa contributing to each trait, reveals a transformation in the functional-trait composition of assemblages on heavily bleached reefs (affecting over 60% of colonies) in the eight-month period after March 2016 (Fig. 3e). In most cases, reefs shifted away from the dominance of fast-growing, branching and tabular species that are important providers of three-dimensional habitat, to a depauperate assemblage dominated by taxa



**Fig. 4 | Change in coral assemblages in response to heat exposure.** The regression curve is fitted using a generalized additive model, with 95% confidence limits. Each data point represents the shift in composition ( $n = 63$  reefs), based on the Euclidean distance in a non-metric multi-dimensional scaling analysis of assemblages on individual reefs sampled at the peak of bleaching and eight months later. Heat exposure for each reef was measured as satellite-derived DHW (in °C-weeks).

with simpler morphological characteristics and slower growth rates. By contrast, on less-bleached reefs the weighted abundances of functionally important traits typically showed small gains (Fig. 3f).

In conclusion, our analyses show that acute heat stress from global warming is a potent driver of a 1,000 km-scale transformation of coral assemblages, affecting even the most remote and well-protected reefs within an iconic World Heritage Area. Forecasts of coral bleaching made continuously by the US National Oceanic and Atmospheric Administration are accompanied with guidance that a DHW exposure of 4 °C-weeks is expected to cause significant bleaching, and 8 °C-weeks may also result in mortality of corals<sup>15,16,18</sup>. Similarly, a model for predicting the locations of resilient reefs on the Great Barrier Reef assumed that coral mortality starts to occur only once thermal exposure exceeds 6 °C-weeks<sup>19</sup>. However, we show that substantial mortality occurred on the Great Barrier Reef in 2016 well below 6 °C-weeks, beginning instead at 3–4 °C-weeks, and with typical losses exceeding 50% at 4–5 °C-weeks (Fig. 2c). Furthermore, the threshold that we have identified for the breakdown of assemblage structure, approximately 6 °C-weeks (Fig. 4), was transgressed in 2016 throughout most of the northern, as well as much of the central, region of the Great Barrier Reef (Fig. 1). The prospects for a full recovery to the pre-bleaching coral assemblages are poor, for several reasons. First, many of the surviving coral colonies continue to die slowly even after recovery of their algal symbionts, because they have lost extensive patches of tissue, are injured and fragmented, and because corals weakened by bleaching are susceptible to subsequent outbreaks of disease<sup>20,21</sup>. Second, the replacement of dead corals by larval recruitment and subsequent colony growth will take at least a decade even for fast-growing, highly fecund corals, such as species of *Acropora*, *Pocillopora*, *Seriatopora* and *Stylophora*<sup>22,23</sup>. The success of future recruitment will depend on an adequate supply of larvae from lightly bleached locations, the rapid break down of many millions of dead coral skeletons to provide a more enduring and stable substrate for settling larvae and the availability of suitable settlement cues and conditions for survival of juvenile corals<sup>24</sup>. Third, for longer-lived, slow-growing species, the trajectory of replacement of dead corals on heavily damaged reefs will be far more protracted, almost certainly decades longer than the return-times of future bleaching events. The

recurrence of mass bleaching during the recovery period will be critical, in view of the global rise in the frequency of bleaching events<sup>4–6</sup>.

The 2015–2016 global bleaching event is a watershed for the Great Barrier Reef, and for many other severely affected reefs elsewhere in the Indo-Pacific Ocean<sup>4</sup>. Furthermore, the Great Barrier Reef experienced severe bleaching again in early 2017, causing additional extensive damage<sup>25,26</sup>. The most likely scenario, therefore, is that coral reefs throughout the tropics will continue to degrade over the current century until climate change stabilizes<sup>7,27</sup>, allowing remnant populations to reorganize into novel, heat-tolerant reef assemblages. The 2016 marine heatwave has triggered the initial phase of that transition on the northern, most-pristine region of the Great Barrier Reef (Figs. 1, 4), changing it forever as the intensity of global warming continues to escalate. The large-scale loss of functionally diverse corals is a harbinger of further radical shifts in the condition and dynamics of all ecosystems, reinforcing the need for risk assessment of ecosystem collapse<sup>3</sup>, especially if global action on climate change fails to limit warming to 1.5–2 °C above the pre-industrial base-line.

### Online content

Any Methods, including any statements of data availability and Nature Research reporting summaries, along with any additional references and Source Data files, are available in the online version of the paper at <https://doi.org/10.1038/s41586-018-0041-2>.

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**Author contributions** The study was conceptualized by T.P.H., who also wrote the first draft of the paper. All authors contributed to writing subsequent drafts. J.T.K. coordinated data compilation, analyses and graphics. Aerial bleaching surveys were conducted by T.P.H. and J.T.K. Underwater bleaching and mortality censuses were undertaken by A.H.B., A.D., A.S.H., M.O.H., M.J.M., R.J.P., M.S.P., J.S.S. and G.T. C.M.E., S.F.H., G.L. and W.J.S. provided satellite data on heat stress. M.J.M. undertook the functional trait analysis and S.R.C. provided statistical advice and modelled loss of coral cover among different taxa.

**Competing interests** The authors declare no competing interests.

#### Additional information

**Extended data** is available for this paper at <https://doi.org/10.1038/s41586-018-0041-2>.

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## METHODS

**Initial mortality and heat stress.** We used aerial surveys, conducted in March–April 2016, to measure the geographical extent and severity of bleaching on the Great Barrier Reef, and subsequently converted the bleaching scores into mortality estimates (Fig. 1a) using a calibration curve based on underwater measurements of coral losses (Extended Data Fig. 1). The aerial surveys were conducted throughout the Great Barrier Reef Marine Park and the Torres Strait between Australia and Papua New Guinea, from the coast of Queensland to the outermost reefs, and along the entire Reef from latitudes 9.5 °S to 23.5 °S. Each of 1,156 individual reefs was scored into one of five bleaching categories: 0, less than 1% of corals bleached; 1, 1–10%; 2, 10–30%; 3, 30–60%; 4, more than 60% of corals bleached. The accuracy of the aerial scores was ground-truthed by measuring the extent of bleaching underwater on 104 reefs, also during March–April 2016<sup>14,28</sup>.

We assessed underwater the initial mortality of different taxa due to heat stress, at the same time as the aerial surveys, on 63 reefs that spanned the full spectrum of heat exposures and bleaching. On each reef, the extent of bleaching and mortality on individual coral colonies was measured at two sites using five 10 × 1 m<sup>2</sup> belt transects placed on the reef crest at a depth of 2 m. We identified each colony (at the species or genus level) and recorded a categorical bleaching score for each one ( $n = 58,414$  colonies): 1, no bleaching; 2, pale; 3, 1–50% bleached; 4, 51–99% bleached; 5, 100% bleached; 6, recently dead. The dead colonies, which had suffered whole-colony mortality, were white with fully intact fine-scale skeletal features, typically still had patches of rotting coral tissue and were experiencing the initial week or two of colonization by filamentous algae, features which distinguished them from corals that had died earlier. The timing of our initial underwater censuses, at the peak of the bleaching in March–April 2016, was critical for identifying corals that were dying directly from heat stress, and for measuring the baseline composition of the assemblages.

Heat stress on the Great Barrier Reef in 2016 was quantified at 5-km resolution, using the NOAA Coral Reef Watch version 3 DHW metric<sup>16</sup>. DHW values are presented in Fig. 1b as a heat map (stretch type: histogram equalize) using inverse distance weighting (power: 2, cell size: 1000, search radius: variable, 100 points) in ArcMap 10.2.1.

**Longer term mortality.** To measure longer term coral loss (decrease in coral cover after eight months) and its relationship to the level of bleaching and heat exposure, we also conducted detailed before–after assessments of taxon-specific abundances by re-visiting the 63 reefs. We measured abundances in March–April and eight months later at the same locations in October–November, allowing us to compare changes in coral cover for 15 ecologically and taxonomically distinct components of benthic assemblages, on reefs exposed to a broad spectrum of heat stress. These measurements were conducted at the same two geo-referenced sites per reef, on reef crests at a depth of 2 m, using five 10-m long line-intercept transects per site. There were no cyclones or flood events on the Great Barrier Reef during the March–November period (Austral winter) in 2016. Unbleached reefs typically showed small increases in cover due to growth, which we included in the regression analyses. Analysis of change in coral cover was undertaken using the log<sub>10</sub>-transformed ratio of final to initial cover. To improve readability of Fig. 2 and Extended Data Fig. 1, changes in coral cover are presented as percentages calculated from the log-scale.

We compared the initial and final composition of corals using a non-metric multi-dimensional scaling (nMDS) analysis based on a Bray–Curtis similarity matrix of square-root transformed data, and quantified the shift over time using the Euclidean distance between before–after assemblages at each location. We then estimated the relationship between the shift in composition at each reef versus the level of heat exposure experienced there (Fig. 4). To include all species, the majority of which are too rare to analyse individually, we pooled them into 15 ecologically cohesive groups depending on their morphology, life history and taxonomy. Three of the fifteen groups are ubiquitous species or species complexes: *Pocillopora damicornis*, *Seriatopora hystrix* and *Stylophora pistillata*. In each of the multi-species groups, the dominant species or genera on reef crests were: other *Acropora* (*A. gemmifera*, *A. humilis*, *A. loripes*, *A. nasuta*, *A. secale*, *A. tenuis* and *A. valida*); faviids (that is, species and genera from the formerly recognized family Faviidae: *Cyphastrea*, *Favia*, *Favites*, *Goniastrea*, *Leptastrea*, *Montastrea* and *Platygyra*); Mussidae (*Lobophyllia* and *Symphylia*); *Isopora* (*I. palifera* and *I. cuneata*); other *Pocillopora* (*P. meandrina* and *P. verrucosa*); other sessile animals (sponges, tunicates, molluscs); *Porites* (*P. annae* and *P. lobata*); *Montipora* (*M. foliosa*, *M. grisea*, *M. hispida*, *M. montasteriata* and *M. tuberculosis*); staghorn *Acropora* (*A. florida*, *A. intermedia*, *A. microphthalma*, *A. muricata* and *A. robusta*); soft corals (alcyonaceans and zooanthids); tabular *Acropora* (*A. cytherea*, *A. hyacinthus* and *A. anthocercis*).

We calculated longer term mortality for all species combined at the scale of the entire Great Barrier Reef in three ways, all of which yielded consistent results. The first approach, which provided the best spatial resolution (Fig. 1a), was based on a comparison of the observed loss of total coral cover on 63 reefs that extend along the entire Great Barrier Reef measured underwater between March and November, with aerial bleaching scores of the same locations in March–April (Extended Data

Fig. 1). This calibration allowed us to convert the aerial scores of bleaching that we recorded for 1,156 reefs into mortality estimates for each of the five aerial score categories, and to map the geographic footprint of losses of corals throughout the Great Barrier Reef (Fig. 1a). The spatial patterns of coral decline (Fig. 1a) are presented as a heat map of the calibrated scores (stretch type: histogram equalize) using inverse distance weighting (power: 2, cell size: 1000, search radius: variable, 100 points) in ArcMap 10.2.1.

The second methodology for estimating large-scale mortality is independent of aerial surveys of bleaching, and based on the loss of total coral cover on 110 reefs (Extended Data Fig. 2), including the 63 reefs that were re-censused for change in composition. The median cover on these reefs declined between March and November from 34% to 20% (Extended Data Fig. 3). For method two, the observed loss of coral cover was averaged for replicate reefs surveyed within each of eight sectors of the Great Barrier Reef Marine Park and the Torres Strait, corrected for differences in reef area for each sector based on GIS data provided by the Great Barrier Reef Marine Park Authority, and then summed to calculate the total loss. For method three, we used the fitted relationship between satellite-derived DHW and observed change in cover (Fig. 2c) to score the losses or gains on all 3,863 individual reefs comprising the Great Barrier Reef, and averaged the total. These two alternative approaches for estimating large-scale loss of cover, both based on before–after underwater surveys (Extended Data Figs. 2 and 3) yielded consistent results with Fig. 1a—a 29.0% and 27.7% decline, respectively, after eight months.

**Differential mortality among coral taxa.** To estimate how exposure to heat (measured as DHW) affects loss of cover differentially among taxa, we used a linear mixed effects model. The fixed effect was DHW and we allowed for a random effect of taxonomic grouping on both the intercept and slope of the relationship between coral cover change and DHW. We excluded from the analysis observations with zero initial coral cover of a particular taxonomic group. Change in coral cover was transformed before analysis by calculating the  $\log\left(\frac{C_f + \epsilon}{C_i + \epsilon}\right)$  where  $C_f$  and  $C_i$  were the final and initial coral cover, respectively, and  $\epsilon$  was the minimum observed value of coral cover. The estimated random effect on intercepts was approximately zero, so we eliminated it from our final model. Thus, in the final model, there was a common intercept, but differences between taxa in sensitivity to DHW (that is, there was a random effect of taxonomic group on the slope). To illustrate these differences, Extended Data Fig. 5 plots the estimated slope of the coral cover response variable for each taxon versus DHW as the overall mean effect of DHW plus the taxon-specific random effect. Conditional standard errors plotted in Extended Data Fig. 5 are the standard errors on each random effect.

**Shifts in functional traits.** To calculate how differential mortality affected the mix of traits in the coral assemblages, we scored eight traits for 12 of the 15 functional groupings (excluding soft corals, other Scleractinia, and other sessile fauna, Extended Data Tables 1, 2). We chose traits that are likely to influence ecosystem functions. For example, corals with fast growth rates and high skeletal density strongly influence calcification, colony shape affects photosynthesis and the provision of three-dimensional habitat, and the size of corallites is a measure of heterotrophy. The traits were scored using the Coral Trait Database<sup>29</sup>, with the exception of colony size, which we measured directly for each group on reef crests using the geometric mean of intercept lengths for each taxon from our initial transects. For multi-species groups, the traits were generally identical for all species, except for *Montipora* and *Porites*, for which we used the mean score across the reef crest species that we encountered. To measure the depletion of traits based on changes in absolute abundances between March and November (Fig. 3e, f), we used a community weighted mean (CWM) analysis of each trait:

$$CWM = \sum_{i=1}^n a_i \text{trait}_i$$

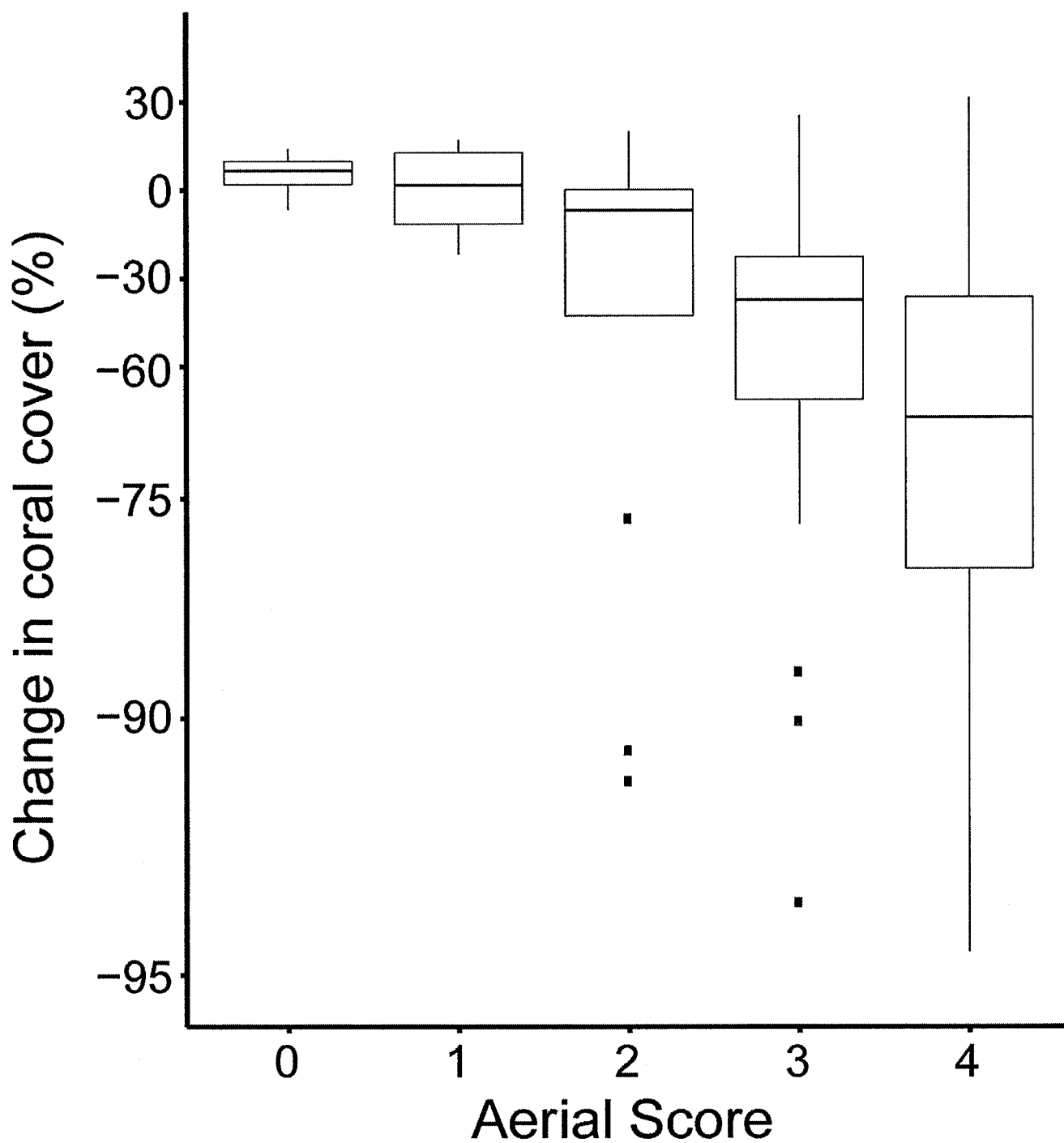
where  $a_i$  is the abundance of coral taxa  $i$  and  $\text{trait}_i$  is the trait value of coral taxa  $i$ . This metric provides a trait value for each reef weighted by the total abundance of each taxa. To visualize the overall shift in functional composition, we used a nMDS analysis based on a Bray–Curtis dissimilarity matrix of square-root transformed data for each trait community weighted mean, creating a multi-dimensional trait space in which reefs are positioned according to the value and abundance of critical traits.

**Reporting summary.** Further information on experimental design is available in the Nature Research Reporting Summary linked to this paper.

**Data availability.** All heat exposure data used in this study are publicly available from the US National Oceanic and Atmospheric Administration. Source data for coral bleaching, mortality and abundances are available online at the Tropical Data Hub: <https://doi.org/10.4225/28/5a725ee7548a7>.

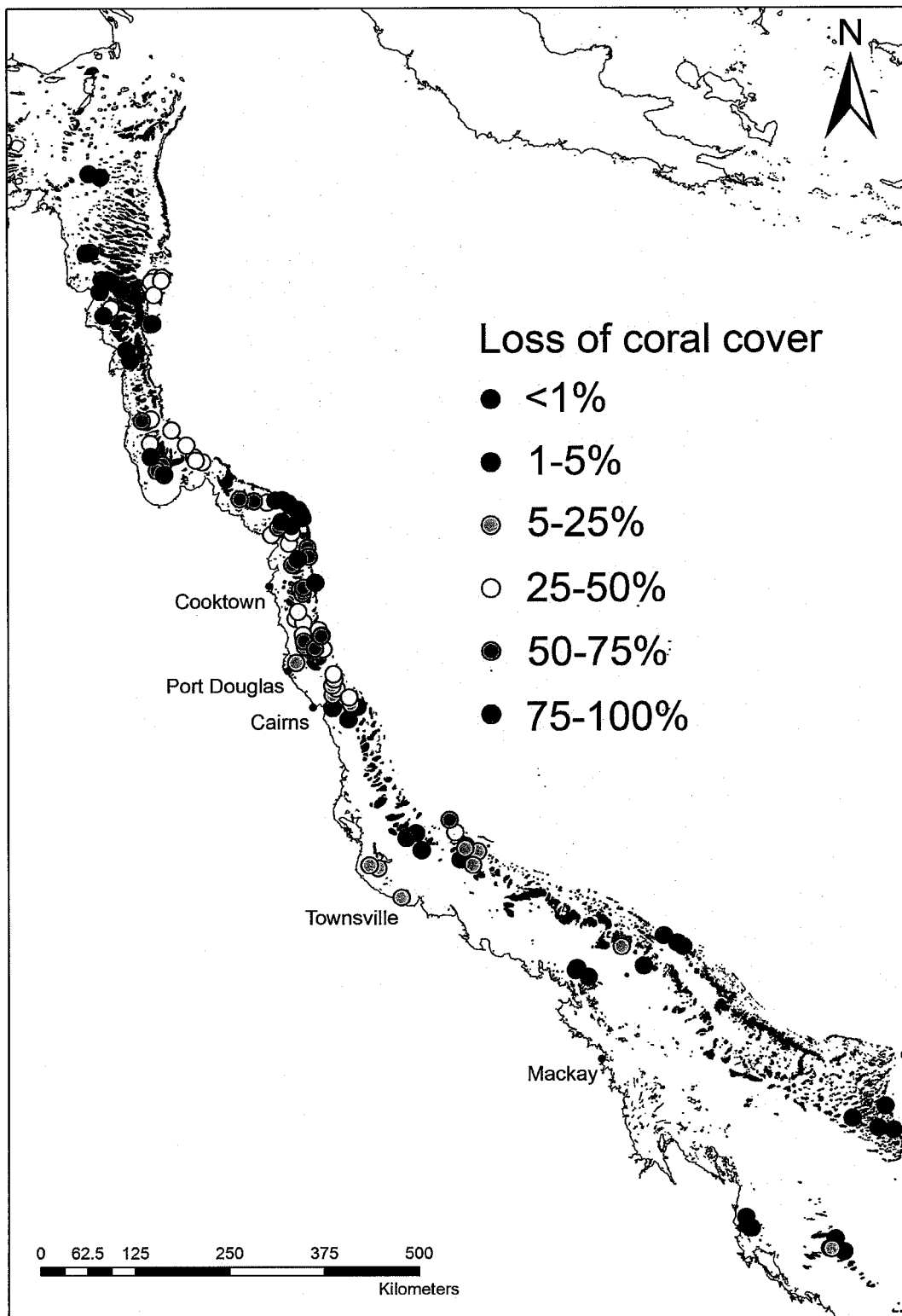
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29. Madin, J. S. et al. The Coral Trait Database, a curated database of trait information for coral species from the global oceans. *Sci. Data* **3**, 160017 (2016).



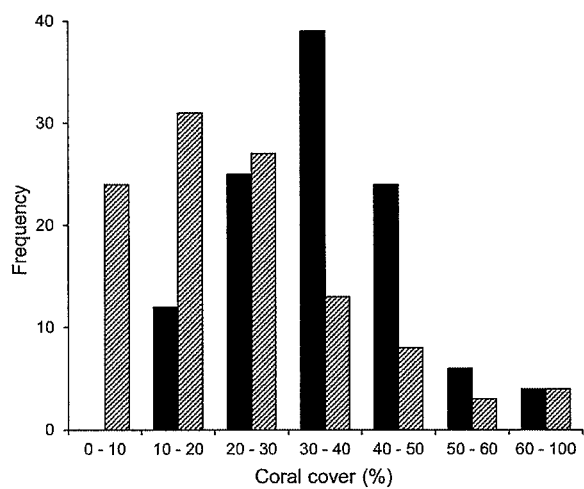
**Extended Data Fig. 1 | Relationship between aerial bleaching scores and change in coral cover.** Aerial scores of bleaching on the x axis are: 0 (< 1% of colonies bleached), 1 (1–10%), 2 (10–30%), 3 (30–60%) and 4 (60–100%). Change in coral cover on the y axis was measured in situ between March and November 2016 on 98 reefs that were also scored

from the air. Box plots are shown for each aerial category, showing median values (horizontal lines), boxes for values in the 25th–75th percentiles, vertical lines for values less than the 25th percentile and greater than the 75th, and data points for outliers. Medians were used when calibrating change in cover for each aerial category (see Fig. 1a).

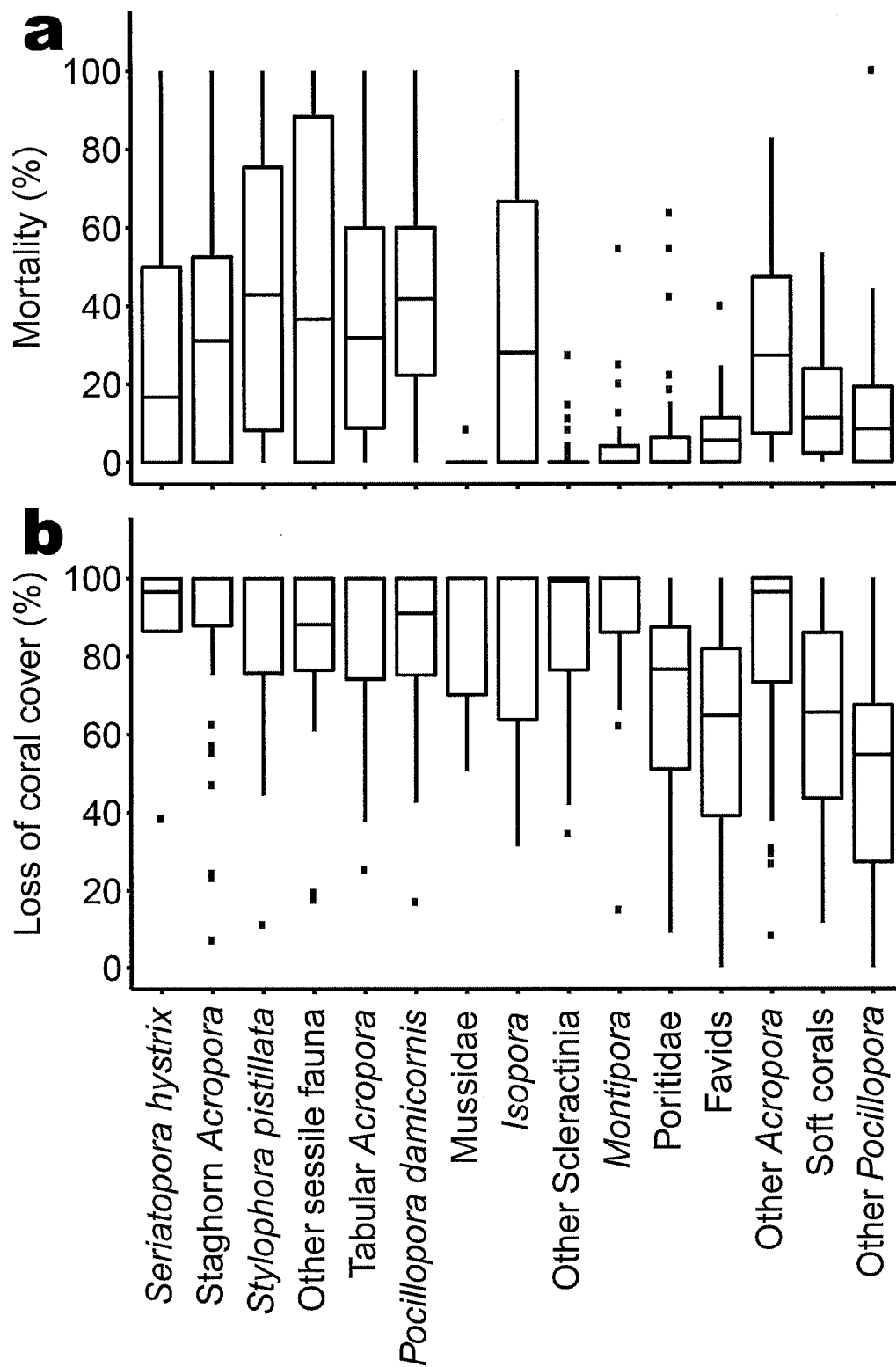


**Extended Data Fig. 2 | Loss of coral cover along the Great Barrier Reef in 2016.** Losses, measured on 110 reefs between March and November 2016, range from 0 (dark green) to 100% (1-5% (green), 5-25% (light

green), 25-50% (yellow), 50-75% (orange) and 75-100% (red)). Map template is provided by Geoscience Australia (Commonwealth of Australia (Geoscience Australia) 2018).

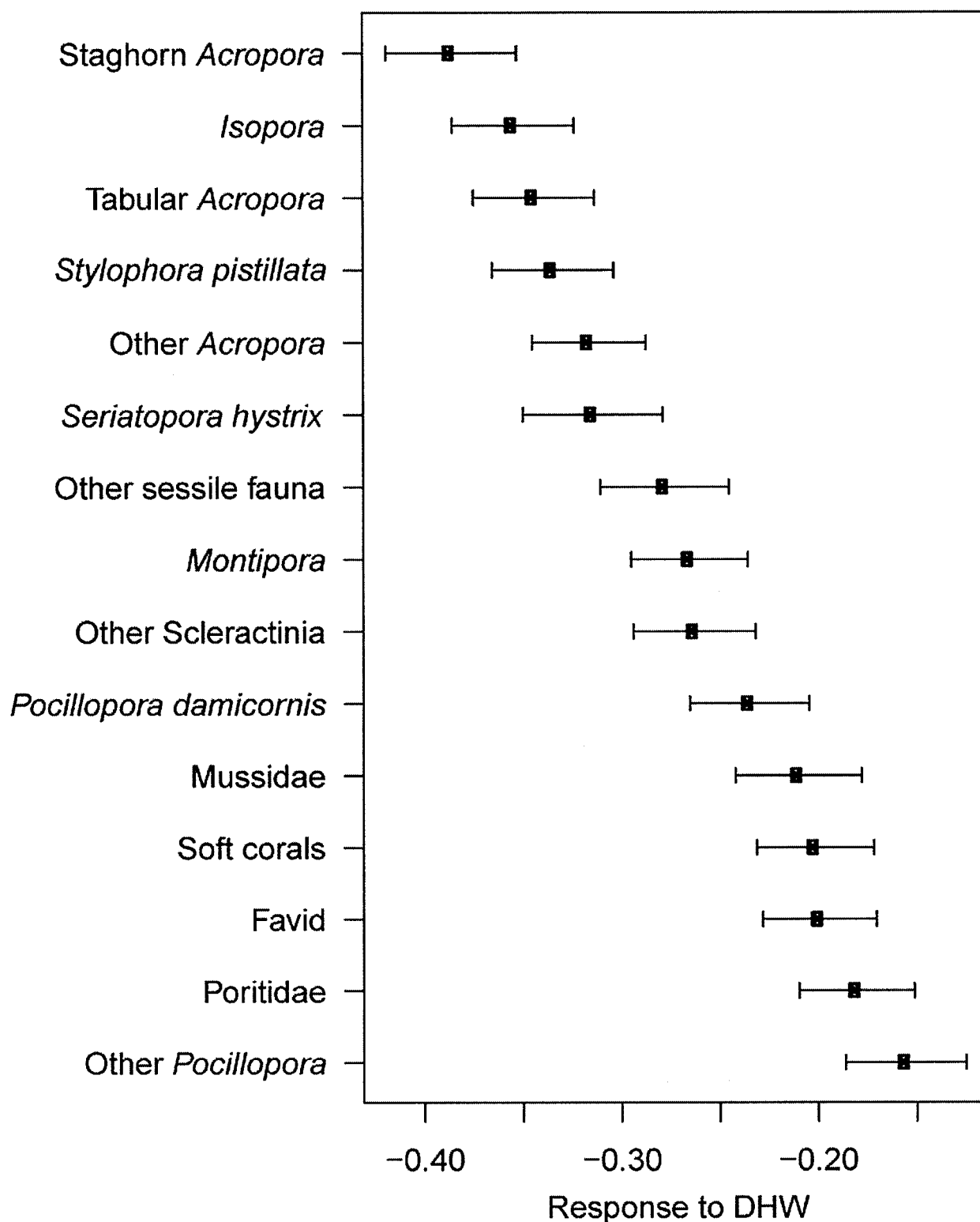


**Extended Data Fig. 3 | Shifts in coral cover following coral bleaching.**  
The frequency distribution of coral cover on 110 reefs, measured in March 2016 (solid bars) and again in November 2016 (hashed bars). Reef locations are shown in Extended Data Fig. 2.



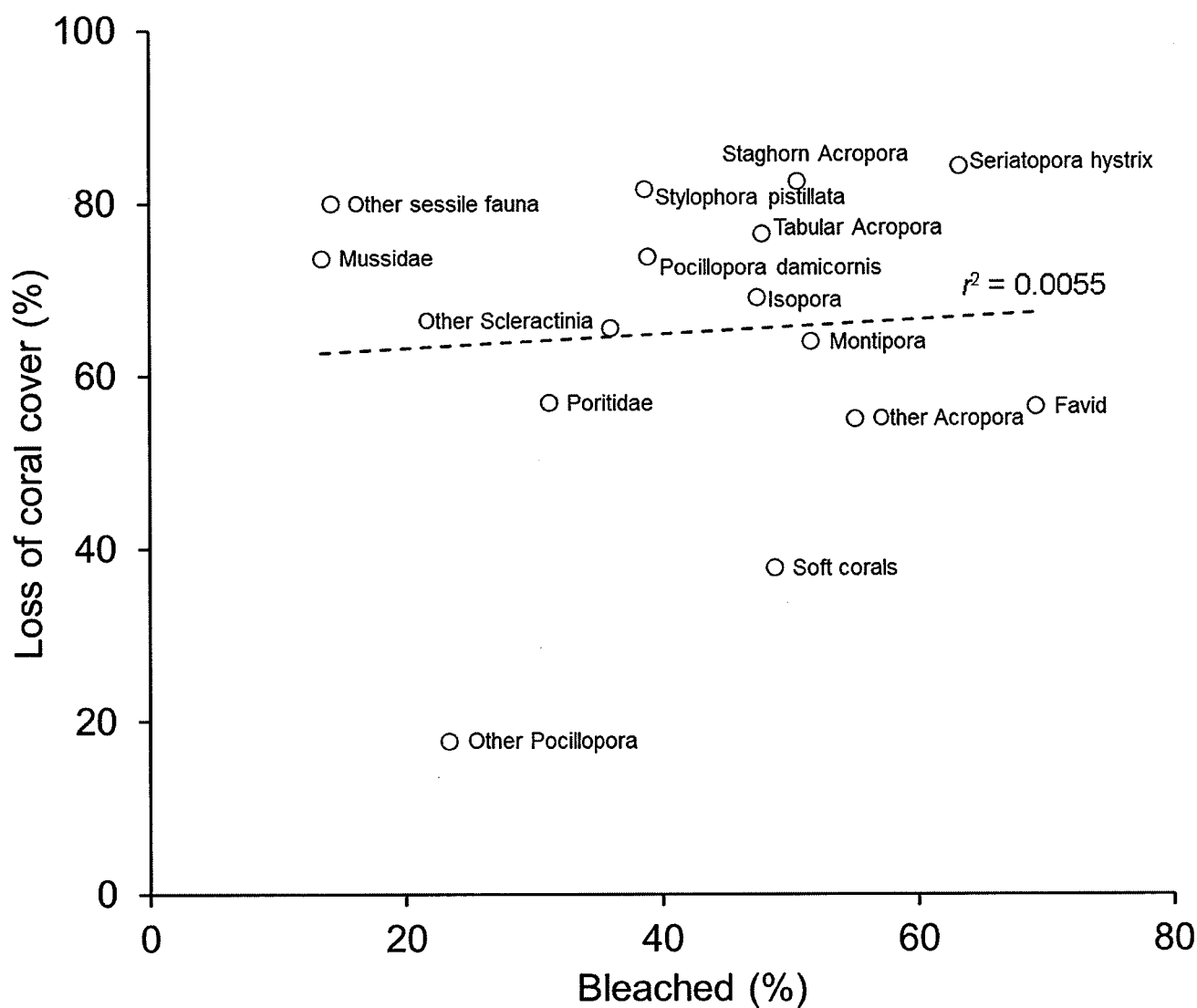
**Extended Data Fig. 4 | Mortality rates differ among coral taxa.** Box plots are shown for each taxon, showing median mortality (horizontal lines), boxes for the middle two quartiles, vertical lines for the first and fourth quartiles, and data points for outliers. **a**, The initial mortality of corals recorded on belt transects on 43 reefs with > 60% bleaching. **b**, Longer

term loss of cover for taxonomic categories recorded between March and November 2016 on the 43 remeasured reefs with > 60% bleaching. Taxa in **a** and **b** are plotted in rank order along the *x* axis, from highest to lowest decreases in mean cover between March and November 2016.



Extended Data Fig. 5 | Differential sensitivity of coral taxa to temperature stress. Sensitivity is estimated from the loss of cover on 63 reefs for different groups of corals between March and November 2016, as a function of heat exposure (DHW). The horizontal axis is the slope

of the relationship between the log-ratio of final and initial coral cover (response variable) and DHW (explanatory variable). Values plotted for each taxonomic grouping (ordered from most sensitive to least sensitive) are random effects estimates, with conditional standard errors.



**Extended Data Fig. 6 | Bleaching extent is unrelated to mortality.** The regression shows the relationship between the levels of bleaching by individual coral taxa on severely bleached reefs (where >60% of all colonies were affected,  $n = 43$  reefs), and their subsequent loss of cover

eight months later. The non-significant correlation indicates that the winners-losers spectrum of bleaching among taxa is a poor predictor of which ones ultimately die.

Extended Data Table 1 | Eight traits of coral species and their key functional roles

| Trait                        | Trait scores                                                             | Reef function                                    |
|------------------------------|--------------------------------------------------------------------------|--------------------------------------------------|
| Growth rate                  | In mm/year: 0-10 (1), 10-20 (2), 20-40 (3), 40-60 (4), >60 (5).          | Carbonate framework accretion; reef regeneration |
| Skeletal density             | In g/cm <sup>3</sup> : <1 (1), 1-1.4 (2), 1.4-1.7 (3), 1.7-2 (4), >2 (5) | Carbonate framework accretion                    |
| Corallite width              | In mm: <1 (1), 1-2 (2), 2-5 (3), 5-15 (4) ; <15 (5)                      | Filter feeding; nutrient capture                 |
| Interstitial space size      | (1-5) Based on morphological categories.                                 | Habitat provision                                |
| Colony height                | (1-5) Based on morphological categories.                                 | Carbonate framework accretion; habitat provision |
| Surface area to volume ratio | (1-5) Based on morphological categories                                  | Primary productivity; nutrient cycling           |
| Colony size                  | Rank (1-12) measured from reef crest transects                           | Carbonate framework accretion; habitat provision |
| Reproductive mode            | Brooders (1), Mixed (2), Spawners (3)                                    | Reef connectivity and regeneration               |

Extended Data Table 2 | Trait scores for each of 12 groups of corals

| Taxon                         | Corallite size | Growth rate | Colony size | Skeletal density | Colony height | Tissue area | Interstitial space size | Reproductive mode |
|-------------------------------|----------------|-------------|-------------|------------------|---------------|-------------|-------------------------|-------------------|
| Bushy <i>Acropora</i>         | 2              | 3           | 7           | 3                | 3             | 5           | 3                       | Spawner           |
| Favids                        | 4              | 1           | 4           | 3                | 2             | 1           | 1                       | Spawner           |
| <i>Isopora</i>                | 2              | 2           | 10          | 3                | 2             | 2           | 1                       | Brooder           |
| <i>Montipora</i>              | 2              | 3           | 9           | 5                | 1             | 1           | 1                       | Spawner           |
| <i>Mussidae</i>               | 5              | 1           | 3           | 2                | 2             | 1           | 1                       | Spawner           |
| Other <i>Pocillopora</i>      | 1              | 3           | 8           | 3                | 3             | 4           | 3                       | Spawner           |
| <i>Pocillopora damicornis</i> | 1              | 3           | 2           | 4                | 2             | 4           | 3                       | Brooder           |
| <i>Poritidae</i>              | 2              | 2           | 6           | 2                | 4             | 1           | 1                       | Mix               |
| <i>Seriatopora hystrix</i>    | 1              | 3           | 1           | 5                | 2             | 3           | 3                       | Brooder           |
| Staghorn <i>Acropora</i>      | 2              | 5           | 11          | 4                | 5             | 3           | 5                       | Spawner           |
| <i>Stylophora pistillata</i>  | 2              | 3           | 5           | 4                | 2             | 3           | 3                       | Brooder           |
| Tabular <i>Acropora</i>       | 2              | 4           | 12          | 4                | 3             | 5           | 5                       | Spawner           |

Spawners release eggs and sperm that fertilize externally, whereas brooders release internally fertilized planulae larvae.

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## ► Experimental design

## 1. Sample size

Describe how sample size was determined.

No statistical methods were used to predetermine sample size of experimental treatments - the study was observational (non-manipulative). For aerial scoring of bleaching, a sample size of 1,156 reefs was sufficient to map bleaching throughout the Great Barrier Reef, and to demonstrate a statistically significant correlation ( $p < 0.001$ ) with a satellite-based measures of heat exposure on each reef. For underwater observations, a sample size of 63 reefs was sufficient to demonstrate relationships between heat exposure, bleaching and mortality (all with  $p < 0.001$ )

## 2. Data exclusions

Describe any data exclusions.

No data were excluded

## 3. Replication

Describe whether the experimental findings were reliably reproduced.

The study is observational rather than experimental. See #1 for justification of sample sizes.

## 4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.

There were no experimental treatments. Therefore, reefs were selected randomly from throughout the Great Barrier Reef to assess their condition.

## 5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

There were no experimental treatments. Therefore, investigators were not blinded to allocation during experiments and outcome assessment.

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

## 6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

n/a Confirmed

- ☒ The exact sample size ( $n$ ) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
- ☐ ☒ A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- ☒ ☐ A statement indicating how many times each experiment was replicated
- ☐ ☒ The statistical test(s) used and whether they are one- or two-sided (note: only common tests should be described solely by name; more complex techniques should be described in the Methods section)
- ☐ ☒ A description of any assumptions or corrections, such as an adjustment for multiple comparisons
- ☐ ☒ The test results (e.g.  $P$  values) given as exact values whenever possible and with confidence intervals noted
- ☐ ☒ A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
- ☐ ☒ Clearly defined error bars

See the web collection on statistics for biologists for further resources and guidance.

## ► Software

Policy information about availability of computer code

### 7. Software

Describe the software used to analyze the data in this study.

R coding for statistical analysis. ArcGIS (ArcMap) for graphical interpolation of data

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). *Nature Methods* guidance for providing algorithms and software for publication provides further information on this topic.

## ► Materials and reagents

Policy information about availability of materials

### 8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.

No unique materials were used

### 9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).

No antibodies were used

### 10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.

No cell lines were used

b. Describe the method of cell line authentication used.

No cell lines were used

c. Report whether the cell lines were tested for mycoplasma contamination.

No cell lines were used

d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by ICLAC, provide a scientific rationale for their use.

No cell lines were used

## ► Animals and human research participants

Policy information about studies involving animals; when reporting animal research, follow the ARRIVE guidelines

### 11. Description of research animals

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No animals were used

Policy information about studies involving human research participants

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Study did not involve human research participants

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# Patterns of bleaching and mortality following widespread warming events in 2014 and 2015 at the Hanauma Bay Nature Preserve, Hawai'i

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\* These authors contributed equally to this work.

† Deceased.

## ABSTRACT

Drastic increases in global carbon emissions in the past century have led to elevated sea surface temperatures that negatively affect coral reef organisms. Worldwide coral bleaching-related mortality is increasing and data has shown even isolated and protected reefs are vulnerable to the effects of global climate change. In 2014 and 2015, coral reefs in the main Hawaiian Islands (MHI) suffered up to 90% bleaching, with higher than 50% subsequent mortality in some areas. The location and severity of bleaching and mortality was strongly influenced by the spatial and temporal patterns of elevated seawater temperatures. The main objective of this research was to understand the spatial extent of bleaching mortality in Hanauma Bay Nature Preserve (HBNP), O'ahu, Hawai'i to gain a baseline understanding of the physical processes that influence localized bleaching dynamics. Surveys at HBNP in October 2015 and January 2016 revealed extensive bleaching (47%) and high levels of coral mortality (9.8%). Bleaching was highly variable among the four HBNP sectors and ranged from a low of ~31% in the central bay at Channel (CH) to a high of 57% in the area most frequented by visitors (Keyhole; KH). The highest levels of bleaching occurred in two sectors with different circulation patterns: KH experienced comparatively low circulation velocity and a low temperature increase while Witches Brew (WB) and Backdoors (BD) experienced higher circulation velocity and higher temperature increase. Cumulative mortality was highest at WB (5.0%) and at BD (2.9%) although WB circulation velocity is significantly higher. HBNP is minimally impacted by local factors that can lead to decline such as high fishing pressure or sedimentation although human use is high. Despite the lack of these influences, high coral mortality occurred. Visitor impacts are strikingly different in the two sectors that experienced the highest mortality evidenced by the differences in coral cover associated with visitor use however, coral mortality was similar. These results suggest that elevated temperature was more influential in coral bleaching and the associated mortality than high circulation or visitor use.

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page 11

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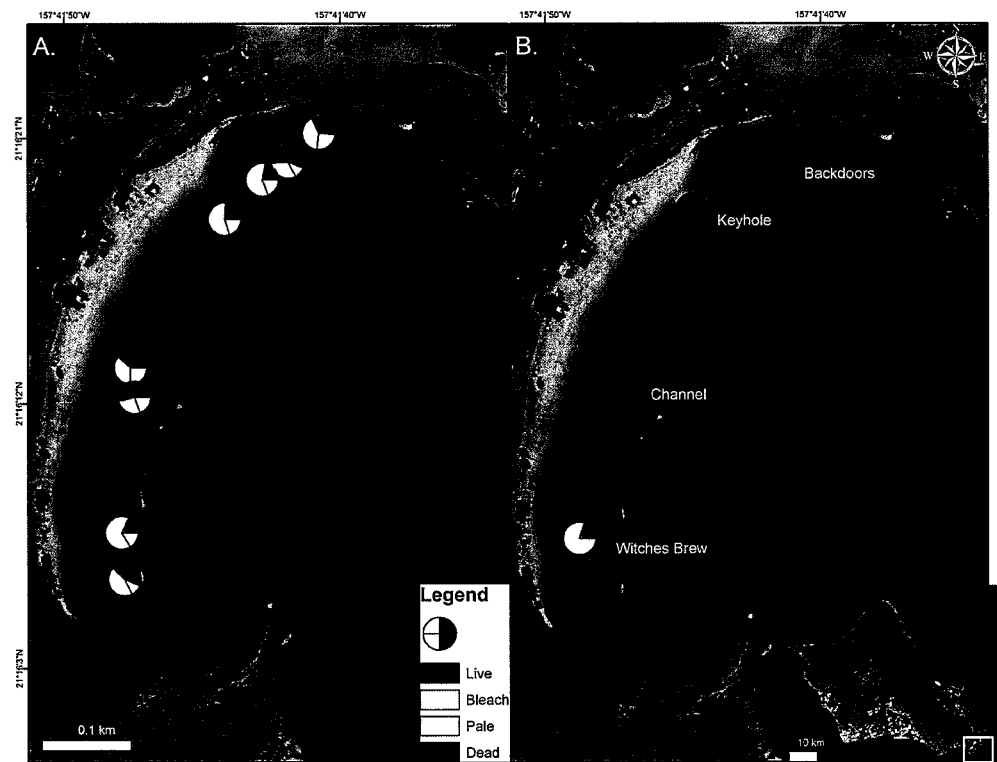
**Keywords** Coral bleaching, Global climate change, Marine protected area, Elevated seawater temperature, Marine life conservation district, Currents, Hanauma Bay

## INTRODUCTION

Global sea surface temperatures (SSTs) have increased an average 0.9 °C in the past century due to an increase in anthropogenic atmospheric gases resulting mainly from fossil fuel burning (Sabine *et al.*, 2004). The greatest increases of 0.06–0.11 °C decade<sup>-1</sup> have occurred since 1970 (EPA, 2016) and have resulted in mass coral bleaching events worldwide. Scientific documentation of these events began nearly a decade later (Jaap, 1979). Since then, large-scale bleaching has occurred worldwide with increasing frequency and severity, and is projected to continue (Hoeke *et al.*, 2011; Mora *et al.*, 2014; Bahr, Jokiel & Rodgers, 2015). Nearly half of the corals in the western Indian Ocean were lost following widespread bleaching in 1998. By 2005, SSTs in the Caribbean had surpassed any previously reported temperatures and caused unprecedented coral mortality (Eakin, Lough & Heron, 2009). The year 2014 marked the beginning of the longest global bleaching event on record, which currently continues and has affected more reefs than any previous worldwide bleaching event (Eakin *et al.*, 2014). Australia's Great Barrier Reef (GBR) recently experienced catastrophic bleaching and mortality with over 90% of its 2,300 km reef tract affected (ARC, 2016). The pristine reefs of the northern GBR were thought to be resistant to bleaching due to their remote location and low fishing and tourism pressure, however, over 99% of these reefs were observed bleached along a 1,000 km stretch (Normile, 2016). On Kiritimati atoll, over 80% mortality occurred during a record 15 months with SSTs above local bleaching thresholds. By November 2016, up to 90% of corals were dead (Baum Lab, 2016). This devastating loss of coral occurred on the relatively undisturbed reefs in the southeastern part of the atoll as well as in the degraded northwest (Sandin *et al.*, 2008; Watson, Claar & Baum, 2016). The full extent of worldwide coral mortality has not yet been quantified, however, NOAA climate models predict another year of warming for the GBR, Kiritimati, and other Pacific Islands, particularly in the southern hemisphere (NOAA Coral Reef Watch, 2017). The negative influence of prolonged elevated seawater temperature on coral reefs is not selective and appears to affect protected, pristine, and degraded reefs, equally.

Coral reefs of the Hawaiian Islands have not been exempt, experiencing extensive bleaching in recent years. Significant heating in the offshore waters statewide (+1.15° over the past 58 years) has led to an increase in frequency of coral bleaching events (Jokiel & Brown, 2004; Bahr, Jokiel & Rodgers, 2015). The bleaching events that affected the Hawaiian Islands in 1996, 2002, and 2004 were relatively short in duration and thus coral recovery was high (Jokiel & Brown, 2004). Conversely, Hawaiian reefs experienced unsurpassed bleaching on a statewide scale during the multi-year bleaching events in 2014 and 2015 (Bahr, Jokiel & Rodgers, 2015).

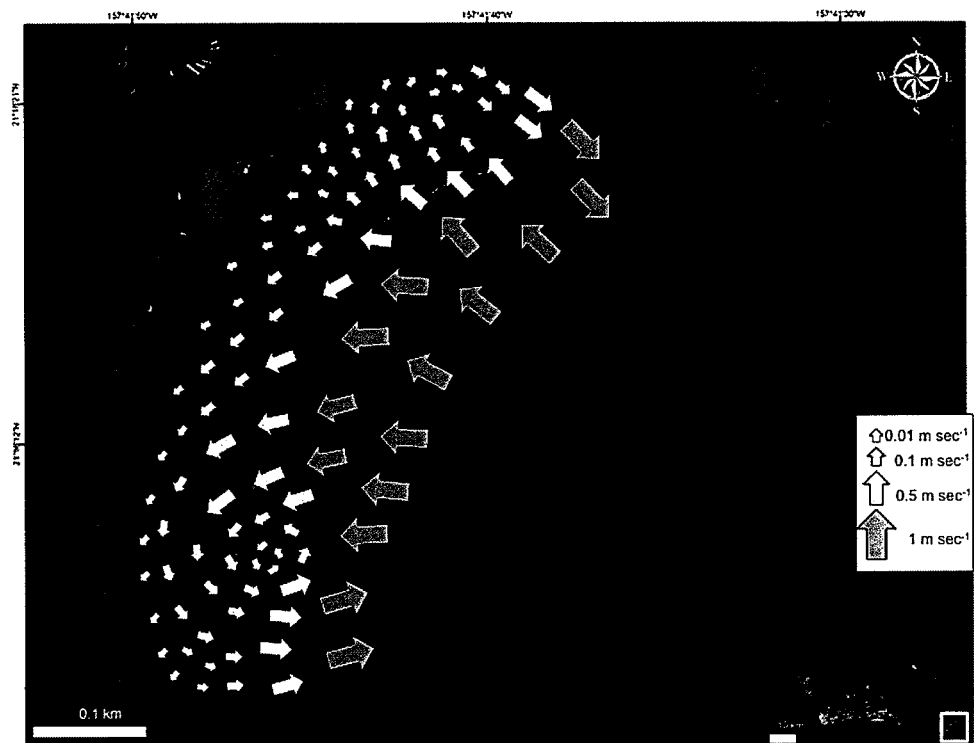
The Hanauma Bay Nature Preserve (HBNP), a 40 ha fully protected Marine Life Conservation District (MLCD) established in 1967, is the most popular snorkeling location in the Hawaiian Islands with close to one million visitors annually (Fig. 1). The Coral Reef Assessment and Monitoring Program (CRAMP) began surveys here in 2000 and has shown a significant decline in shallow water coral cover with the majority of the decrease occurring after 2002 (Brown *et al.*, 2004; Rodgers *et al.*, 2015). The recent and predicted bleaching (Jokiel & Brown, 2004; Hoeke *et al.*, 2011; Eakin *et al.*, 2014) poses an imminent



**Figure 1** Coral condition on map of Hanauma Bay Nature Preserve. Coral condition in the Hanauma Bay Nature Preserve, O'ahu, Hawai'i in October 2015 (A) and January 2016. (B) Proportion of surveyed corals are shown as normal (red), bleached (white), pale (yellow), and dead (black). Surveys were conducted and temperature loggers deployed at each of the two stations within the four sectors. Photo credit: Quickbird Digital Globe.

threat to the biological sustainability of the HBNP ecosystem and a significant economic threat to the state of Hawai'i. Tourism expenditures provided over 15 billion USD to the state's economy in 2015 (DBEDT, 2016). Of the over eight million annual visitors to the state of Hawai'i, it is estimated that 80% participate in ocean recreational activities and over 1,000 ocean recreation companies exist to accommodate them (Clark, 2016).

The HBNP is located adjacent to the strong open-ocean, westward current referred to as the Moloka'i Express. The outer section of this 40 ha (100 ac) bay can at times experience strong surges, ocean currents, and high wave energy while the protected 8 ha (20 ac) inner reef, located shoreward of the reef crest is relatively calm (Brock & Kam, 2000). The overall circulation pattern within Hanauma Bay moves shoreward and westerly from the northeast Toilet Bowl side of the bay towards the southwest Witches Brew side (Fig. 2). This pattern prevails during all tide phases (incoming, outgoing, and mixed) and during both tradewind and calmer south wind conditions. The mean velocity is  $3.1 \text{ cm sec}^{-1}$  with a range of  $0.8\text{--}6.5 \text{ cm sec}^{-1}$  with higher average velocities near the outer mouth of the bay and decreasing in shallower inner waters (Whittle, 2003). Under typical tradewind conditions water continuously enters the inner reef across the reef and boulder boundary.



**Figure 2** Map of current flow at Hanauma Bay Nature Preserve. Generalized map of current flow in Hanauma Bay Nature Preserve, O'ahu, Hawai'i. Red dots indicate surveyed sites. Photo credit: Quickbird Digital Globe.

Travelling parallel to shore it exits at high velocities (up to  $50 \text{ cm sec}^{-1}$ ) near the ledges on the extreme opposite sides of the bay (Fig. 2) and through the mid-bay channel during outgoing tide at lower speeds.

In 2014, the State of Hawai'i Division of Aquatic Resources (DAR) coral bleaching assessments determined 47% of corals exhibited signs of bleaching in the HBNP; however, mortality was not subsequently quantified (Neilson, 2014). The main objective of this study was to quantify bleaching prevalence and subsequent mortality within the four major sectors of the HBNP and define how they relate to temperature and currents. These scientific data form a benchmark for the local environmental patterns that can be used to predict the extent and distribution of future bleaching events and aid management preparation strategies.

## METHODS & MATERIALS

### Coral surveys

In 2015, surveys were conducted to characterize coral bleaching extent and severity in the four major inshore sectors of the Hanauma Bay Nature Preserve (HBNP) ( $21.2690^{\circ}\text{N}$ ,  $157.6938^{\circ}\text{W}$ ). These areas are locally known as Backdoors (BD), Keyhole (KH), Channel (CH), and Witches Brew (WB) (Fig. 1). To define the extent of bleaching, two  $15 \text{ m} \times 5 \text{ m}$

transects were surveyed in each sector. Transect lines were placed on the reef flat at depths <1 m and all coral colonies within the transect area (75 m<sup>2</sup>) were counted. To quantify the severity of the bleaching and mortality, we recorded coral species, colony size, and percent of colony that was live, pale, bleached, and recently dead. Redundant methodologies were used to provide accurate locations for subsequent resurveys using a handheld Garmin Geko 201 GPS unit, graphic and written documentation of positions using triangulation, and underwater photographic imagery of distinct initial and concluding coral colonies on each transect. To avoid error from observer variation, one surveyor collected data in all sectors during both initial bleaching and recovery surveys.

### Temperature

From June 2015 to January 2016, seawater temperature at all four sectors within the HBNP was recorded at fifteen-minute intervals using replicate HOBO Water Temperature Pro v2 Data Loggers (Onset, Wareham, MA, USA). The loggers were secured in 6" × 12" hand-poured concrete "rocks" that mimic the benthic substrate and protect the loggers from solar irradiance and associated heating (Bahr, Jokiel & Rodgers, 2016) while providing concealment from human disturbance. The loggers at BD, KH, and CH were placed at 1 m depth, whereas at WB, a somewhat deeper site, the loggers were placed at 3 m to determine temperatures at a long-term monitoring station. To adjust for depth and to determine whether there were finer scale variations, an additional short-term deployment of 32 loggers were deployed at all transect locations on 19 April 2016 from 08:00 (low tide) to 15:00 (high tide). These data were used to calculate mean mid-day differences among transects.

### Currents

Current patterns characterized by Whittle (2003) primarily covered the region seaward of the reef boundary. To determine the nearshore current patterns, drogues were released and tracked in the water by surveyors. Twenty 2.5" soft plastic balls were deployed and followed in each of the four sectors ( $n = 80$ ). Drogues were identified by color and numbers written on 4" × 4" underwater paper attached with a cable tie through small holes in the plastic. These holes also allowed the drogues to fill with water and remain positioned just below the water surface where wind effects are negligible. The position of each drogue was determined by GPS (Garmin eTrex 10) at initial deployment and at each subsequent sighting for eight consecutive hours spanning both low (−0.05 ft) and high (1.15 ft) tides. Drogues were deployed shoreward ( $n = 40$ ) and seaward ( $n = 40$ ) of the reef boundary. Researchers swam parallel to shore in a creeping line pattern from one end of the designated sector to the next dropping each drogue approximately 10 m apart horizontally with 5 m between each deployment line. After eight hours, drogues were retrieved and final location recorded. Drogues reaching shore prior to the end of the final retrieval were randomly redeployed in their original sector. To determine the original sector when drogues moved to another sector, each sector had different colored drogues.

Most of the drogues deployed at BD were carried outside the bay and were not followed by swimmers thus current patterns for this sector remained unclear. Additionally, nearshore areas in the CH sector were not fully covered. Thus, a second deployment was conducted

**Table 1 Coral condition by sector in October 2015 and January 2016.** Coral condition in October 2015 and January 2016 in the Hanauma Bay Nature Preserve, O'ahu, Hawai'i (mean  $\pm$  SE). Mean coral condition in 75 m<sup>2</sup> surveyed area.

| Sector              | Live         | Bleach        | Pale          | Dead          |
|---------------------|--------------|---------------|---------------|---------------|
| <b>October 2015</b> |              |               |               |               |
| BD                  | 37 $\pm$ 6.3 | 38 $\pm$ 6.2  | 22 $\pm$ 4.1  | 2.9 $\pm$ 1.7 |
| CH                  | 47 $\pm$ 6.4 | 31 $\pm$ 5.3  | 22 $\pm$ 4.6  | 0.3 $\pm$ 0.3 |
| KH                  | 23 $\pm$ 6.1 | 57 $\pm$ 7.1  | 20 $\pm$ 4    | 0.8 $\pm$ 0.6 |
| WB                  | 30 $\pm$ 5.2 | 53 $\pm$ 5.6  | 13 $\pm$ 2.9  | 3.9 $\pm$ 2   |
| <b>January 2016</b> |              |               |               |               |
| BD                  | 94 $\pm$ 3   | 0.5 $\pm$ 0.4 | 0.7 $\pm$ 0.7 | 0             |
| CH                  | 77 $\pm$ 4.8 | 0             | 0.2 $\pm$ 0.2 | 0.5 $\pm$ 0.5 |
| KH                  | 85 $\pm$ 4.6 | 0             | 0             | 0.3 $\pm$ 0.3 |
| WB                  | 85 $\pm$ 3.6 | 8 $\pm$ 3.1   | 2.5 $\pm$ 1.7 | 1.1 $\pm$ 0.5 |

during an incoming tide beginning at low tide ( $-0.23$  ft). In the smaller BD sector, five drogues were released approximately 5 m apart along the eastern boundary. These were deployed over the reef in a perpendicular path to shore from the channel marker buoys. In the larger CH sector, five drogues were released approximately 10 m apart following a path parallel to shore. All drogues were deployed shoreward of the reef boundary and retrieved after three hours with final locations recorded.

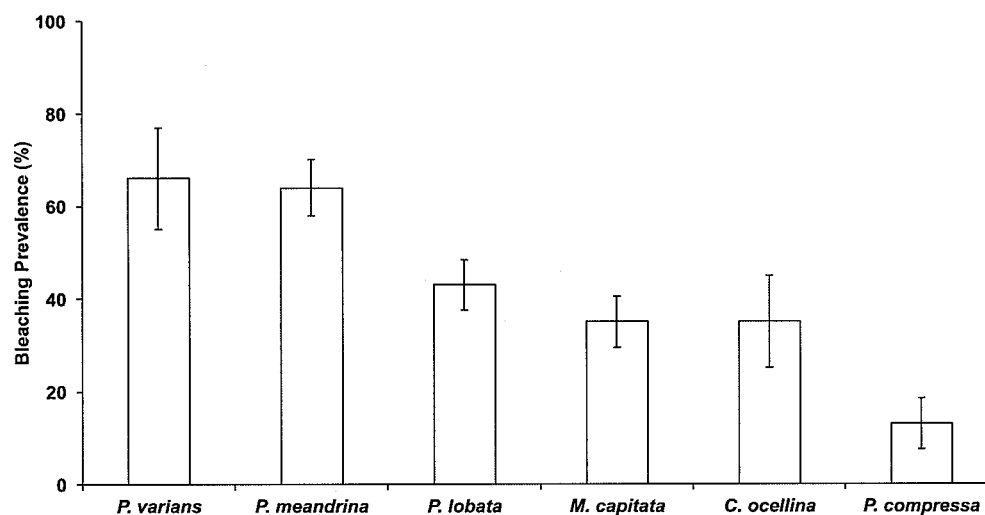
### Statistical analyses

Bleaching prevalence was analyzed using a General Linear Model (GLM) with sector as a fixed factor and transect nested within sector. Temperature was treated with a repeated measures mixed model by location with transect nested within location. Assumptions of normal distribution, homoscedasticity, and multivariate normality were assessed through graphical analyses of the residuals. All statistical analyses and descriptive statistics were conducted using JMP Pro 12. Calculations of location, distance, and time were determined in ArcGIS 10 and Excel 2010 to characterize current patterns (Fig. 2).

## RESULTS

### Bleaching prevalence

In October 2015,  $45\% \pm 3.2\%$  (mean  $\pm$  SE) of corals in the Hanauma Bay Nature Preserve (HBNP) showed signs of bleaching (Table 1). The highest bleaching prevalence was observed in *Pavona varians* and *Pocillopora meandrina* (Fig. 3). Bleaching prevalence was significantly different among sectors (GLM;  $F_{(7,143)} = 3.4239$   $p = 0.0020$ ) with highest levels at Keyhole (KH;  $56.6 \pm 7.1\%$ ) and Witches Brew (WB;  $52.7 \pm 5.6\%$ ) compared to Backdoors (BD;  $38.4 \pm 6.2\%$ ) and Channel (CH;  $30.9 \pm 5.3\%$ ) (Fig. 1). A further 13–22% of corals were paling in all sectors. Coral colony size was not a factor in bleaching prevalence ( $R^2 = 0.0246$ ;  $p = 0.0611$ ) whereas number of colonies was. While colony size in all locations was similar (Oneway ANOVA  $F_{(3,290)} = 0.7229$ ,  $p = 0.5391$ ), number of colonies at WB was higher ( $28 \pm 2.9$ ) (Oneway ANOVA;  $F_{(3,12)} = 7.4677$   $p < 0.0044$ ) compared to the average number of colonies at BD ( $15.25 \pm 2.65$ ), CH ( $19 \pm 1.8$ ), and KH ( $11 \pm 0.8$ ).



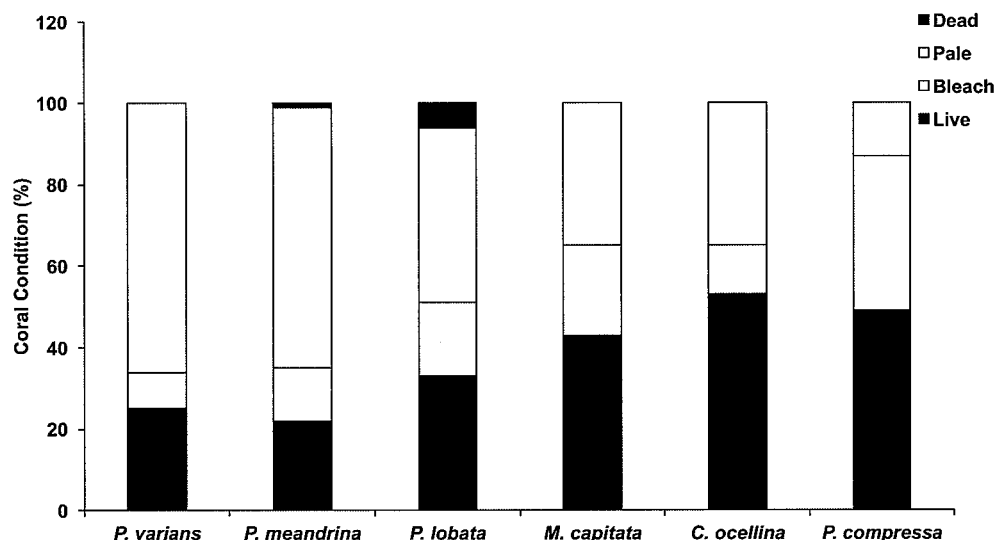
**Figure 3 Bleaching prevalence by coral species.** Mean bleaching prevalence by coral species in October 2015 in Hanauma Bay Nature Preserve, O'ahu, Hawai'i. Error bars represent standard error.

### Coral mortality

In October 2015, the highest average levels of coral mortality occurred at WB ( $3.9 \pm 2\%$ ) and BD ( $2.9 \pm 1.7\%$ ). Lower mortality rates were observed at KH ( $0.8 \pm 0.6\%$ ) and CH ( $0.3 \pm 0.3\%$ ). In January 2016, average coral mortality rates by sector were near or below 1% (WB =  $1.1 \pm 0.5\%$ ; BD =  $0\%$ ; KH =  $0.3 \pm 0.3\%$ ; and CH =  $0.5 \pm 0.5\%$ ), although recovery was slowest in WB. Highest mortality rates were observed in *Porites lobata* and *Pocillopora meandrina* (Fig. 4). Total coral mortality inside the HBNP due to elevated SSTs was calculated with a cumulative value of 9.8% (October = 7.9%; January = 1.9%). Cumulative mortality rates also varied by sector (sum of Oct and January surveys: WB = 5.0%; BD = 2.9%; KH = 1.1%; and CH = 0.8%). No overlap in recently dead corals occurred between October and January determined by rapid algal turf growth over the coral skeleton.

### Environmental drivers

The patterns of coral bleaching prevalence and mortality in the four sectors in HBNP are linked to localized heating, due to circulation patterns. Incoming currents show a great reduction in flow velocity as oceanic water ( $1 \text{ m s}^{-1}$ ) flows over the reef boundary into the shallow, sandy areas ( $0.5 \text{ m s}^{-1}$ ). Here, residence time and temperatures increase and the warmer water follows a westerly direction ( $0.1 \text{ m s}^{-1}$ ) along shore to the far end (WB) where it turns seaward and flows either to a small gyre or over the reef boundary and out of the bay (Fig. 2). Because water exits the bay at WB, water flow into the sector comes strictly from slow, alongshore currents. A similar small gyre is located at the far eastern end (BD), whereas at the adjacent KH, water flows slowly to shore at  $0.01 \text{ m s}^{-1}$  (Fig. 2). Inshore currents were faster in CH ( $0.075 \pm 0.011 \text{ m s}^{-1}$ ) and WB ( $0.055 \pm 0.011 \text{ m s}^{-1}$ ) compared to KH ( $0.008 \pm 0.011 \text{ m s}^{-1}$ ) and BD ( $0.019 \pm 0.011 \text{ m s}^{-1}$ ) (One Way ANOVA;  $F_{(3,7)} = 7.717$ ;  $p = 0.0386$ ). Notably, the relatively high current velocities at CH and WB



**Figure 4 Graph of coral condition in October 2015.** Coral condition in October 2015 in Hanauma Bay Nature Preserve, O‘ahu, Hawai‘i across all sectors. Mean proportion of surveyed corals are indicated by color (Live, brown; pale, yellow; bleach, white; and black, dead).

are substantially different in character. At CH cooler water flows into the shallows from outside the reef boundary, whereas at WB, slow-moving, warm water from as far as KH sector increases in velocity only as it is exiting the shallows.

Analysis of temperature gradients in HBNP revealed temperatures were significantly different throughout the bay (Mixed Model;  $R^2 = 0.30$ ;  $F_{(3,4)} = 454.97$ ;  $p < 0.0001$ ). WB experienced significantly higher mean mid-day temperatures ( $26.46 \pm 0.014$  °C) compared to BD ( $26.05 \pm 0.014$  °C), CH ( $26.01 \pm 0.014$  °C), and KH ( $25.99 \pm 0.014$  °C). Additionally, temperatures are variable within locations (Mixed Model;  $R^2 = 0.43$ ;  $F_{(1,2)} = 23.27$ ;  $p < 0.0001$ ). Overall, the largest differences within site occurred at WB ( $\pm 0.58$  °C) and BD ( $\pm 0.26$  °C), while KH ( $\pm 0.10$  °C) and CH ( $\pm 0.08$  °C) were more similar. The effects of the localized heating revealed higher bleaching prevalence in KH ( $56.6 \pm 7.1\%$ ) and WB ( $52.7 \pm 5.6\%$ ) compared to BD ( $38.4 \pm 6.2\%$ ) and CH ( $30.9 \pm 5.3\%$ ) (Fig. 1).

## DISCUSSION

Bleaching and recovery rates and species tolerance in 2015 were highly variable across islands of the Hawaiian archipelago. In 2015, the warm water approached the islands from the south and this resulted in a maximum 18 DHW for Hawai‘i Island and 10 DHWs for eastern shores of O‘ahu (NOAA Coral Reef Watch, 2016). Extensive surveys in 2015 found between 30 and 86% bleaching on Hawai‘i Island with reported mortality at nearly 50% on the island’s west coast (Kramer et al., 2016). Results of the current study revealed nearly half (47%) the corals surveyed at HBNP were found to exhibit signs of severe bleaching and associated mortality was ~9.8%. It appears localized heating and circulation patterns inside HBNP are driving differences in bleaching-associated mortality. Variation in spatial and temporal temperature patterns account for the differences in bleaching between islands.

Accompanying rates of coral mortality may slow predicted recovery rates of Hawaiian corals and shape future reefs (Jokiel & Brown, 2004; Bahr, Jokiel & Rodgers, 2015).

The Hanauma Bay Nature Preserve (HBNP) has shown decline in coral cover in shallow waters since 2002 (Brown *et al.*, 2004; Rodgers *et al.*, 2015) however, global climate change may drive this management-protected reef into more rapid decline. Increasing length, severity, and frequency of coral bleaching events pose an imminent threat to the biological sustainability of the HBNP ecosystem and a significant economic threat to the state of Hawai'i. Of the total area surveyed (600 m<sup>2</sup>) in the HBNP in 2015, cumulative coral mortality was 9.8%. This Marine Life Conservation District reflects the fish populations in more remote areas distant from anthropogenic impacts due to management restrictions that prohibit any take of marine organisms. However, the organic and nutrient levels at HBNP are much higher than at 60 other sites statewide due to high fish biomass (Rodgers, 2005). Minimal levels of fine sediments due to a low contribution of terrigenous material from the influencing watershed are found here. In addition, nearly one million people visit HBNP annually but the majority of visitors using the ocean resources remain on the northern end of the bay in the BD and KH regions. The southern section where WB lies has relatively minimal human use (Fig. 1). Nonetheless, these two areas experienced similar mortality following the bleaching event. These results support global reports of high mortality following bleaching in remote regions removed from anthropogenic influences such as the northern GBR and at Lisianski in Papahānaumokuakea in the Northwestern Hawaiian Islands (NWHI) (Couch *et al.*, 2016).

Reef recovery after major disturbances depends not only on the prevailing environmental conditions but also on the species affected. For example, *Pocillopora meandrina* is considered a "competitive" species (Darling *et al.*, 2012) and is far more likely to recolonize a degraded reef than longer-lived "stress-tolerant" species such as *Porites lobata* and *Porites evermanni*. This study revealed bleaching prevalence and mortality to vary by species and location. The highest bleaching prevalence was observed in *Pavona varians* (66%), and *P. meandrina* (64%) while highest mortality occurred in *P. lobata* (5.3%) and *P. meandrina* (1.3%). No mortality was observed in *P. varians*. Bleaching prevalence was highly variable within HBNP due to localized environmental gradients. The highest levels of bleaching and mortality were observed in WB, which is characterized as the sector where warm water accumulates before exiting the bay.

Additionally, WB has the greatest number of coral colonies, particularly *Porites lobata* colonies. *Porites lobata* was also the most abundant species at BD. This sector is characterized as having low water velocity and relatively high temperatures. Cumulative bleaching was relatively low compared to other sectors but mortality was second highest. KH has the lowest number of coral colonies and *P. meandrina* was the most abundant species. Currents head directly from beyond the reef boundary to shore presumably bringing colder water with considerable reduction in velocity into KH. Temperature is lower here than at WB and BD, which may explain why mortality was low although cumulative bleaching was high. Lastly, CH had the lowest bleaching and mortality due to high water circulation and high oceanic input with associated lower temperatures. This sector had the second highest coral abundance, mainly dominated by *P. lobata* and *Montipora capitata*. Because *P. lobata*

is the most abundant species in three of four sectors, the observed mortality indicates an important vulnerability that cannot be overcome by circulation or conservation effort. With repeated mortality of the more vulnerable species, shifts in coral composition are likely to occur.

Temperature and circulation are difficult to separate. These two factors are highly correlated with one another since circulation can increase or ameliorate temperatures and account for localized heating differences. Our results suggest circulation patterns facilitate localized heating and influence bleaching dynamics in HBNP. Incoming oceanic water flows shoreward to the reef boundary then follows a counterclockwise pattern west before exiting the bay. Significant heating occurs as incoming water moves over the shallow reef flat and accumulates in the WB sector. This explains the observed  $\sim 0.5$  °C difference in temperatures between WB and other sectors of HBNP. The observed high circulation rates appear to be movement and accumulation of warm water in WB. This accumulation of warm water likely facilitated increased bleaching prevalence and associated mortality in that area. A similar, but less severe pattern was observed in the BD sector (Fig. 2). The cumulative heating associated with these circulation patterns correlates with the observed high levels of bleaching in these two sectors. Even in the absence of direct anthropogenic stressors (e.g., fishing pressure, pollution, and sedimentation) coral mortality can be high as temperatures increase. Corals live within 1–2 °C of their summer maximum temperatures and will bleach at this threshold whether they inhabit cooler, deeper waters or live on warmer shallow reefs (Coles, Jokiel & Lewis, 1976).

## CONCLUSION

In summary, bleaching and mortality were highly variable across the main Hawaiian Islands. Differing spatial patterns of warming greatly influence the location and severity of bleaching and associated mortality. Results of this study indicate variability in bleaching and associated mortality can be described by species-specific tolerances, number of colonies, localized environmental patterns of heating, and currents. This study of the marine protected HBNP results determined:

- Bleaching and mortality varied by species and location.
- Bleaching prevalence and associated mortality were the highest in the sectors where warm water accumulated (i.e., BD and WB).
- Regardless of anthropogenic influences, temperatures beyond the thermal tolerances for corals can result in mortality.

Oceans will continue to absorb a significant amount of carbon even once emissions are reduced but we must slow the increase to begin addressing the impacts of climate change. Sound management strategies based on scientific research will increasingly play a more important role. Data from this research will serve as a baseline for future research to better understand the environmental patterns in HBNP and elsewhere. Data on species tolerances, circulation patterns and temperatures can assist managers in predicting the spatial extent, bleaching severity, and distribution of future bleaching events to support planning efforts.

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## ADDITIONAL INFORMATION AND DECLARATIONS

### Funding

The authors received no funding for this work.

### Competing Interests

The authors declare there are no competing interests.

### Author Contributions

- Ku'ulei S. Rodgers conceived and designed the experiments, performed the experiments, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Keisha D. Bahr conceived and designed the experiments, performed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Paul L. Jokiel conceived and designed the experiments, performed the experiments, contributed reagents/materials/analysis tools, provided historical bleaching research.
- Angela Richards Donà performed the experiments, wrote the paper, reviewed drafts of the paper.

### Data Availability

The following information was supplied regarding data availability:

The raw data was provided as Data S1.

### Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.3355#supplemental-information>.

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## Warming Trends and Bleaching Stress of the World's Coral Reefs 1985–2012

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Coral reefs across the world's oceans are in the midst of the longest bleaching event on record (from 2014 to at least 2016). As many of the world's reefs are remote, there is limited information on how past thermal conditions have influenced reef composition and current stress responses. Using satellite temperature data for 1985–2012, the analysis we present is the first to quantify, for global reef locations, spatial variations in warming trends, thermal stress events and temperature variability at reef-scale (~4 km). Among over 60,000 reef pixels globally, 97% show positive SST trends during the study period with 60% warming significantly. Annual trends exceeded summertime trends at most locations. This indicates that the period of summer-like temperatures has become longer through the record, with a corresponding shortening of the 'winter' reprieve from warm temperatures. The frequency of bleaching-level thermal stress increased three-fold between 1985–91 and 2006–12 – a trend climate model projections suggest will continue. The thermal history data products developed enable needed studies relating thermal history to bleaching resistance and community composition. Such analyses can help identify reefs more resilient to thermal stress.

Record warm temperatures in recent years have been extremely stressful to coral reefs. At the time, 2014 set the record for the warmest global surface temperature. The year 2015 was 0.16°C warmer than 2014, setting not only the record for the warmest year ever but also the record for the largest single year increase<sup>1</sup>. So far, 2016 has been warmer than 2015 was. Ocean warming, exacerbated by one of the strongest El Niño events on record (comparable with 1997/98 and 1982/83) on top of a general warming trend, has resulted in the longest global coral bleaching event on record. Since mid-2014, reef stakeholders (scientists, managers) have reported observations of bleached corals near-continuously and from across all three tropical ocean basins<sup>2</sup>. As of late-2016 the event was ongoing, with more than 40% of global reef locations having been exposed to temperature stress levels that cause bleaching (G. Liu, pers. comm.).

Reefs are among the most sensitive of all ecosystems to climate change. Stony 'reef-building' corals live in a symbiotic relationship with microscopic algae called zooxanthellae (*Symbiodinium spp.*), whose photosynthesis provides corals with up to 90% of their energy<sup>3</sup>. Environmental stressors can disrupt this relationship. The main driver of contemporary stress on coral reefs is high temperature, which together with high irradiance results in an accumulation of damage to photosystem II<sup>4,5</sup>. Under extreme stress the coral expels algae<sup>4,6</sup>, leaving its bright white aragonite skeleton visible through a thin translucent layer of coral tissue and appearing 'bleached'. Anomalously warm sea temperatures across broad scales have been closely linked to spatially extensive 'mass' coral bleaching events in recent decades<sup>7–9</sup>.

There is a bleaching continuum. Some coral paling is common in many coral species during warm-season months, and bleached corals can survive mild thermal stress and recover their algae<sup>10</sup>. However, severely bleached

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corals can and have died in great numbers when exposed to persistent stressful conditions<sup>11,12</sup>. Thermally stressed corals have higher disease susceptibility<sup>13–15</sup>; and reduced reproductive output<sup>10</sup> and skeletal growth<sup>16</sup>. Eventual impacts of bleaching (over years to decades) can include reduced reef rugosity, coral cover and biodiversity<sup>10</sup>; and perhaps local extinction of coral species<sup>17–18</sup>. Reefs affected by bleaching provide a lower quality habitat for fish and invertebrate species, and provide fewer ecosystem goods and services for dependent human communities<sup>19,20</sup>. As ocean waters warm under climate change, bleaching events are expected to become both more frequent and more severe<sup>21–24</sup>.

Historical temperature variation and the cumulative effects of past disturbance events influence not only the condition of reefs but also their capacity to respond to subsequent stress events<sup>25</sup>. Corals are known to have adapted or acclimated to local environmental conditions<sup>26,27</sup>; e.g., temperature thresholds for bleaching vary spatially and have been linked to local summertime conditions<sup>7</sup>. Impacts from thermal stress have been lower at sites where short-term pulses of low-level temperature stress preceded higher thermal stress later in summer<sup>24</sup> or that had been affected by a prior but recent thermal stress event (e.g., Thompson & van Woessik<sup>28</sup>, Heron *et al.*<sup>29</sup>). Reef sites dominated by high-frequency variability (5.7-year period) over low-frequency variability (>54-year period) were observed to experience more intense thermal stress and severe bleaching<sup>28</sup>. High SST variability year-round and during the warm season has also been suggested to proffer protection for reefs from bleaching<sup>30–32</sup>. Knowledge of thermal history can shape the lens through which managers and researchers view the current condition of reefs, and how they anticipate and respond to bleaching impacts on reefs. However, until now, high-resolution spatial data on key thermal history characteristics has not been available for all global coral reef locations.

Our objective here is to assess and provide tools to understand thermal history trends and patterns for reefs worldwide at the approximate scale of reefs using 4-km SST archives. Satellite remote sensing using Advanced Very High Resolution Radiometers (AVHRR) provides the capacity to undertake analysis of sea surface temperature (SST)-based metrics over spatially vast areas at high-resolution (4 km) through recent decades. Our period of analysis, 1985–2012, spans the two previous global bleaching events confirmed to have impacted all three tropical ocean basins (i.e., global events) in 1998<sup>11</sup> and 2010<sup>33–38</sup>. We quantify and compare the following metrics for all coral reef areas: (1) rates of change in annual and warm-season SST; (2) the frequency of exposure to and onset timing of bleaching-level thermal stress events; (3) the percentage of reefs exposed to bleaching-level thermal stress each year during the study period; and (4) warm-season temperature variability. Previous studies<sup>32,39–43</sup> included only some of these descriptors of thermal history, were conducted at lower spatial resolution, used shorter time periods and/or were regional in nature. We present spatial analyses of these thermal history metrics globally and for the six reef regions within *Reefs at Risk-Revisited*<sup>44</sup>: Middle East (MID), Indian Ocean (IND), Southeast Asia (SEA), Australia (AUS), Pacific Ocean (PAC) and Atlantic Ocean (ATL). The context of future thermal exposure is included using stress projections based on the latest available global modelling.

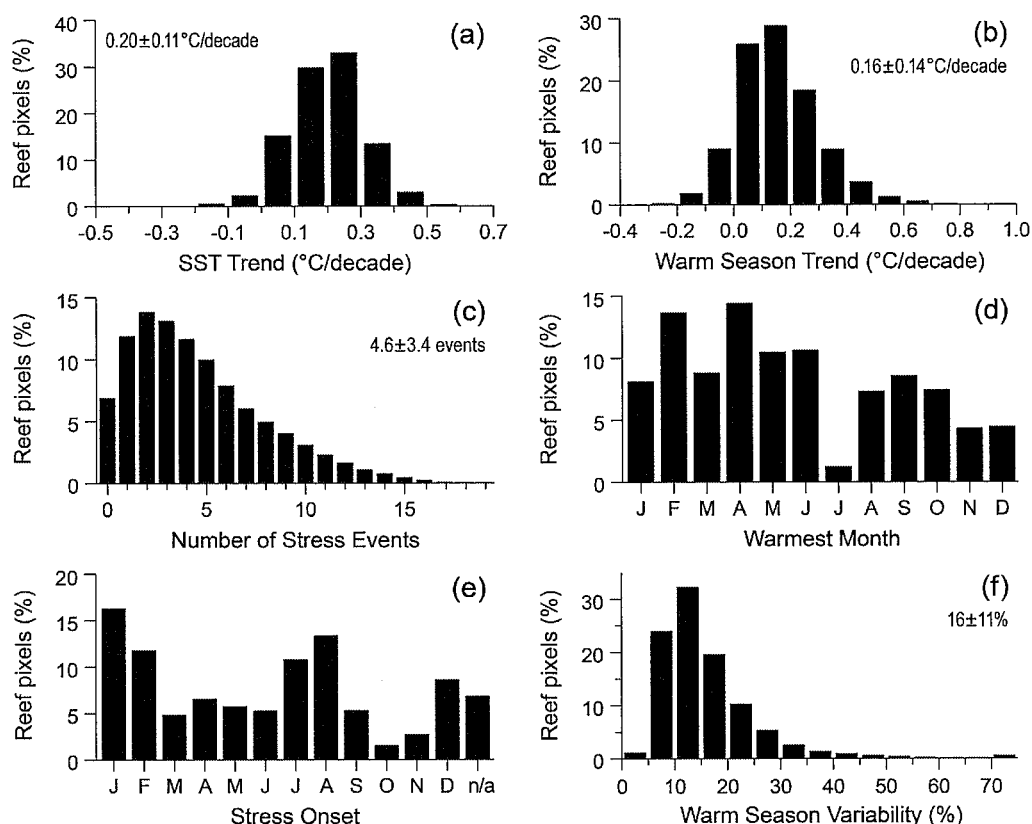
## Results

In summary, our analysis of thermal history at global coral reef locations revealed warming at almost all reefs in recent decades; summertime temperature increased through the record at the great majority of reefs. One-third of the world's reefs were exposed to bleaching-level thermal stress less than once per decade, with one-third of reefs exposed between once and twice per decade, and the remaining one-third exposed more than twice per decade. The global percentage of reefs impacted by bleaching stress tripled through the 28-year record, explaining the increase in observed bleaching. While the onset of thermal stress mostly coincided with the warmest part of the year, we found that at nearly one-quarter of reefs it did not. The following key points were identified from each set of thermal history parameters.

**SST Trends.** Coral reef SST warmed during the 28-year period, with cool seasons warming faster than warm seasons. Annual average temperature increased during the study period at nearly all 4-km reef pixels (97% or 58,847 pixels). Globally, coral reefs warmed an average of  $0.20 \pm 0.11$  (spatial SD) °C/decade (Fig. 1a, Table S1a). Reefs across all reef regions warmed but rates varied considerably (Figure S1) with the most rapid warming (Middle East,  $0.32 \pm 0.13$  °C/decade) nearly four times greater than the slowest (Australia,  $0.08 \pm 0.09$  °C/decade; Table S2). The distribution of values is demonstrated by annual average temperature time-series (Fig. 2) for five reef locations for the approximately 99<sup>th</sup>, 75<sup>th</sup>, 50<sup>th</sup>, 25<sup>th</sup> and 1<sup>st</sup> percentiles for SST trend. Annual-average SST trend was positive and significant ( $p < 0.05$ ) at 60% of reefs (36,308 pixels), while negative and significant at less than 0.01% of reefs (4 pixels). Locations with cooling temperatures are all in the Atlantic region north of Grand Bahama Island (Fig. 2e), which is in contrast to the general warming across the Atlantic region ( $0.17 \pm 0.12$  °C/decade).

Bleaching stress typically occurs during the warm season. Reef SSTs warmed more slowly during the warm season (avg:  $0.16$  °C/decade) and had greater spatial variability (SD:  $0.14$  °C/decade) than the overall SST trend (Fig. 1b, Table S1b). Warm-season temperatures increased at 89% of reefs (53,768 pixels) and were significantly positive at 30% of reefs (18,362 pixels,  $p < 0.05$ ). In contrast, significantly negative trends occurred at only <0.03% of reefs (16 pixels). All regional-average warm-season trends were positive (Fig. 3). Across the regions, positive trends were observed at 68–99% of reefs (Table S3). The Atlantic (92%), followed by the Middle East (47%), had the greatest percentage of reefs with statistically significant ( $p < 0.05$ ) positive warm-season trends – consistent with the generally strong annual warming in these regions.

Annual SST warmed faster than the warm-season trend in 70% of locations and by  $+0.05$  °C/decade when averaged across global reefs (Fig. 4), indicating a suppression of seasonality at most reefs. The difference between annual and warm-season trends was greater than  $0.1$  °C/decade ( $\sim 1$ SD about the spatial average) at 37% of the reef pixels (Table S4). The Middle East and Atlantic were the only regions where warm-season trend predominantly

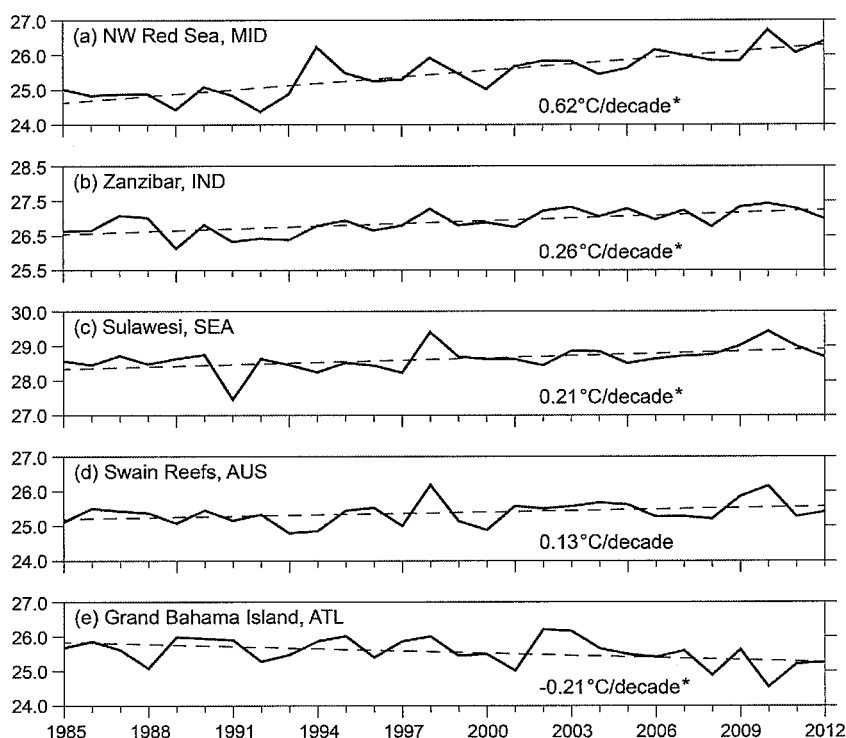


**Figure 1.** Histograms of thermal history metrics for global reef locations ( $n = 60,710$ ). Global summary of the data distribution for (a) annual and (b) warm-season trends; (c) bleaching-level thermal stress events; (d) warmest month; (e) stress onset; and (f) warm-season temperature variability, 1985–2012. Warm-season temperature variability is the standard deviation of warm-season temperatures expressed as a percentage of the climatological range. Global averages  $\pm$  one standard deviation are shown in plots (a,b,c and f. Data are provided for each histogram in Table S1.

exceeded annual SST trend (78% for MID and 94% for ATL, see Fig. 4). In all other regions, at least 68% of the pixels had an annual SST trend greater than the warm-season trend.

**Thermal Stress.** Most reefs (81%,  $n = 49,321$ ) were exposed to multiple thermal stress events that were at a level likely to cause bleaching<sup>12</sup> during the 28-year period ( $\text{DHW} \geq 4^\circ\text{C-weeks}$ ; Fig. 1c, 5). Globally, reefs were exposed to bleaching-level stress  $4.6 \pm 3.4$  times during the 28-year study period (Fig. 1c, Table S1c), and the regional average was above three events ( $\sim 1/\text{decade}$ ) in all reef regions (Fig. 5, Table S5). Bleaching stress on reefs occurred most frequently in the Middle East ( $9.1 \pm 3.6$ ) and least often in the Australia region ( $3.4 \pm 2.8$ ). Globally, 33% of reefs (19,794 pixels) experienced bleaching-level thermal stress two or fewer times during the record ( $< 1/\text{decade}$ ). The Australia, Indian Ocean and Southeast Asia regions had the highest proportions of infrequent exposure ( $< 1/\text{decade}$  at 43%, 41% and 38% of reefs, respectively). One-third (33%,  $n = 19,831$ ) of reefs globally experienced bleaching-level thermal stress events six or more times during the 28-year record ( $> 2/\text{decade}$ ), with most reefs in the Middle East and Atlantic affected (81% and 59%, respectively; Table S5, Fig. 5). Severe thermal stress ( $\text{DHW} \geq 8^\circ\text{C-weeks}$ ), linked to significant coral mortality<sup>12</sup>, affected 57% of global reef pixels at least once (Table S6). Just over 4% of reefs globally were exposed more than twice per decade to mortality-level thermal stress events. The Middle East and Atlantic regions had the highest proportions of reefs with frequent exposure to severe thermal stress (23% and 12%, respectively; Table S6, Figure S2).

**Temporal Patterns.** In each year of 1985–2012, thermal stress was observed somewhere across global reefs (Fig. 6–left panels; Table S7a). The greatest numbers of reefs were impacted in 1998 (48%), 2010 (48%) and 2005 (32%), corresponding to the two global bleaching events and largest Caribbean bleaching event during this period. In most regions, 1998 and 2010 were the two highest ranked (either 1<sup>st</sup> or 2<sup>nd</sup>) years for all reef regions with the exception of the Atlantic (2005, 2010) and Pacific (2009, 2000). When the record was divided into four 7-year periods, the global percentage of reef pixels that were stressed increased steadily (8, 14, 23 and 26%), tripling from 1985–91 to 2006–12 (Fig. 6–right, Table S7b). This increasing trend of bleaching-level stress events was consistent in the Middle East, Southeast Asia, Pacific and Atlantic regions. In contrast, there was no consistent temporal trend in the frequency of bleaching events in Indian Ocean and Australia reef pixels; the number of reef pixels affected in first or second 7-year period is comparable with that of the most recent period (within 1%).



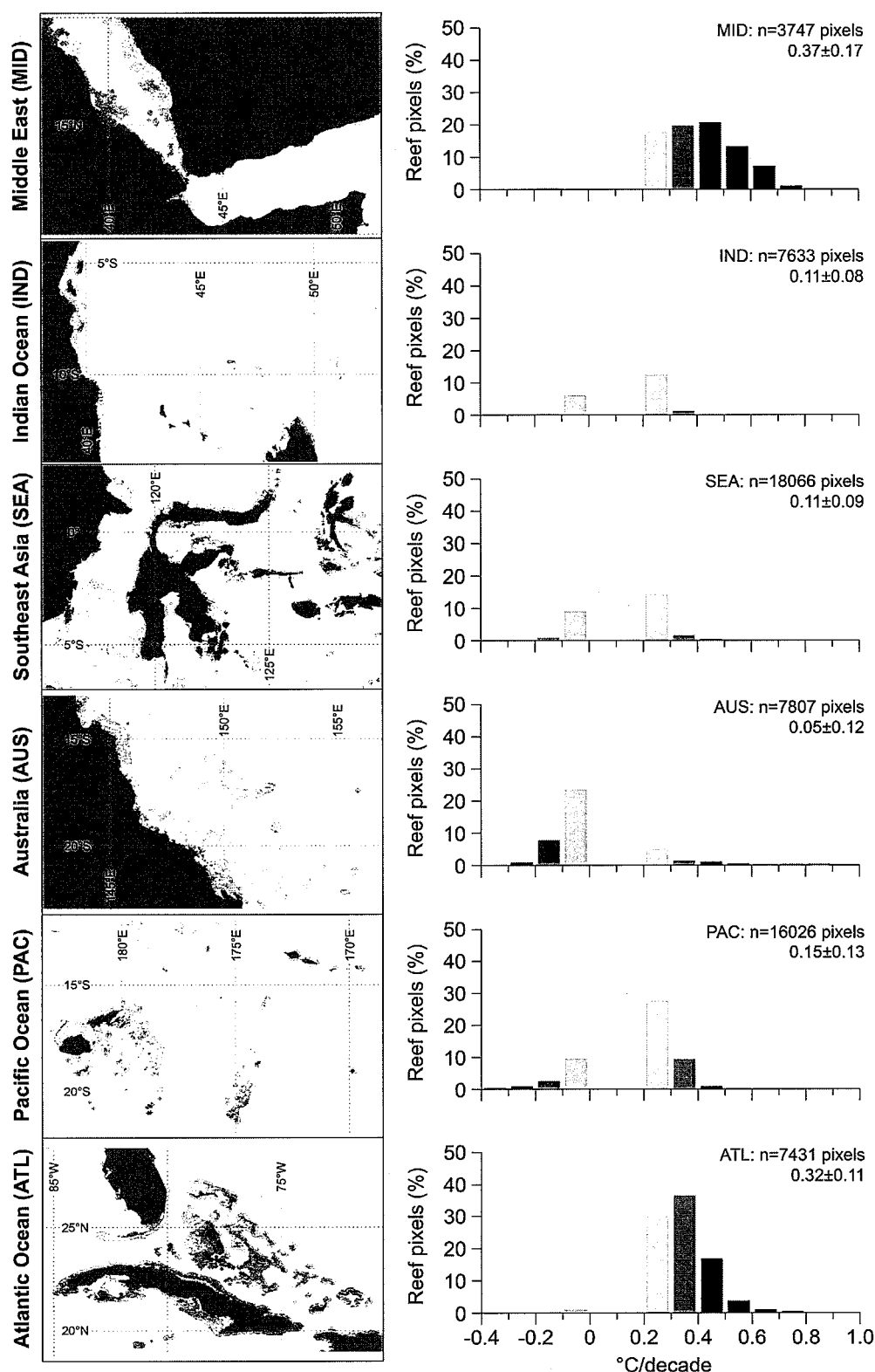
**Figure 2.** Trends in annual mean temperature at select coral reef locations. These locations approximate the 99<sup>th</sup>, 75<sup>th</sup>, 50<sup>th</sup>, 25<sup>th</sup>, and 1<sup>st</sup> percentiles (a–e, respectively) of the annual SST Trend values in the global dataset ( $n = 60,710$  reef pixels). Reef regions are MID = Middle East, IND = Indian Ocean, SEA = Southeast Asia, AUS = Australia and ATL = Atlantic Ocean). Trend values shown are significant ( $p < 0.05$ , denoted by\*) excepting for Swain Reefs, AUS.

The percentage of reef locations exposed to bleaching-level thermal stress events is projected by climate models<sup>22</sup> to continue to increase (Fig. 6–right, Table S7b). By 2050, more than 98% of reefs are expected to be exposed to bleaching-level thermal stress in each year<sup>21,22</sup>. Even in the Atlantic region, where projections suggest reduced bleaching around 2030, more than 91% of reefs are likely to experience bleaching-level thermal stress each year by 2050 (consistent with van Hooidonk *et al.*<sup>21</sup>).

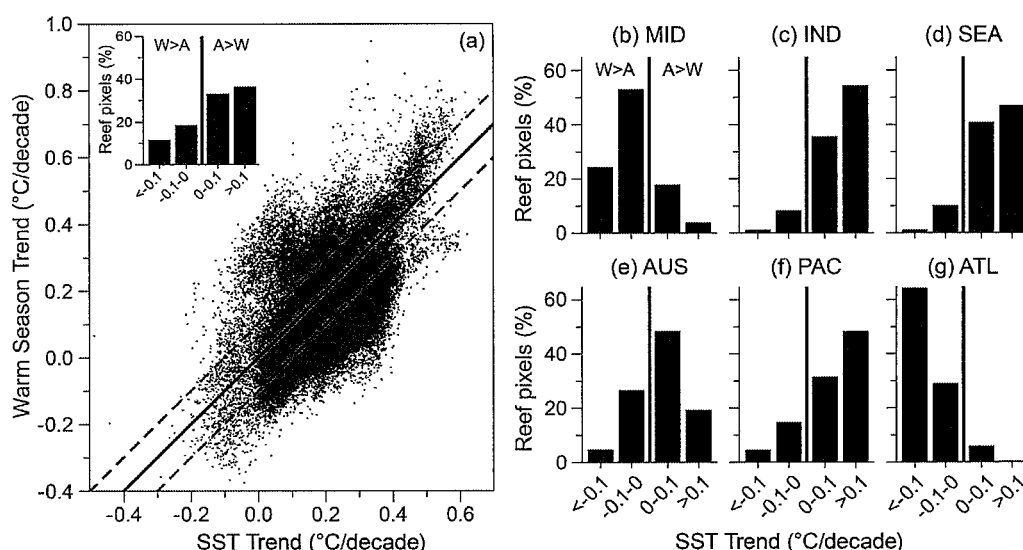
**Timing.** Each of the calendar months was the warmest on a reef somewhere across the globe (Fig. 1c,S3). Within each region, two or three consecutive months predominated as the warmest for reefs – e.g., April–June in Southeast Asia and August–October in the Atlantic. Sub-region maps (Figure S3–left panels) indicate that geographic/oceanographic physical separation and latitudinal variation were factors defining warmest month areas. When considered globally, peaks in the onset of stress were in January/February and July/August, following the astronomical solstice events (Fig. 1e). However, many locations had onset months between solstice events, particularly reefs near the equator (in the Indian Ocean, Southeast Asia and Pacific regions; Figure S4).

Of the 93% of reefs that experienced bleaching-level thermal stress (56,521 pixels), average stress onset coincided with the warmest month at 29% (16,383) of these and occurred in the preceding 1–2 months at a further 49% (27,824) of sites. The onset of bleaching stress did not coincide with or immediately precede the warmest month in nearly one quarter of reef locations. While some of these reefs were found in each of the six regions, most were in the Southeast Asia and Pacific regions. This may reflect timing delays due to the Southeast Asian monsoon cycle and the relatively high interannual variability in the equatorial Pacific (linked to El Niño–Southern Oscillation events), respectively. Understanding spatial patterns of stress onset timing can inform managers' preparations during broad-scale thermal events.

**Warm-season Variability.** High SST variability in summer has been linked with reduced sensitivity to thermal stress<sup>45</sup>. However, research to date has provided no clear threshold defining “high” variability. We considered the globally most-variable locations (approximately the upper quartile) as having high variability and examined the distribution of these reefs. Nearly one-quarter of global reefs (23%) had warm-season variability at or above 20% of the climatological range (Fig. 1f). There were no high-variability reef pixels in the Middle East, and very few in Australia (1%) and the Atlantic (9%); in contrast, between one- and two-thirds of reef pixels in Southeast Asia, the Indian Ocean and the Pacific Ocean were among the most variable (Figure S5, Table S8). Greater exposure to variable warm-season temperature may be important in stimulating adaptive responses in corals<sup>46</sup>.



**Figure 3.** Trend in three-month warm-season temperatures among reef regions, 1985–2012. Trend values are in °C/decade. Maps (left) show results for a subset of each region; histograms (right) show the distribution of results in the full region with the regional average  $\pm$  one standard deviation. Reef regions are as per Burke *et al.* 2011. Data are provided for each histogram in Table S3. Data visualisations produced using IDL [8.3] (Exelis Visual Information Solutions, Boulder, Colorado).



**Figure 4.** Scatterplot comparing annual SST and three-month warm-season trends globally and by reef region. Line of unity (solid) and  $\pm 0.1$  °C/decade about this (dashed) are shown. Dashed lines approximate one SD of the by-pixel difference between the trends (0.11 °C/decade). Histograms show the distribution of annual SST minus warm-season trends; the solid line (at zero) corresponding to the scatterplot line of unity. Reef regions are as per Burke *et al.* 2011 (MID = Middle East, IND = Indian Ocean, SEA = Southeast Asia, AUS = Australia, PAC = Pacific Ocean and ATL = Atlantic Ocean). Data are provided for each histogram in Table S4.

## Discussion

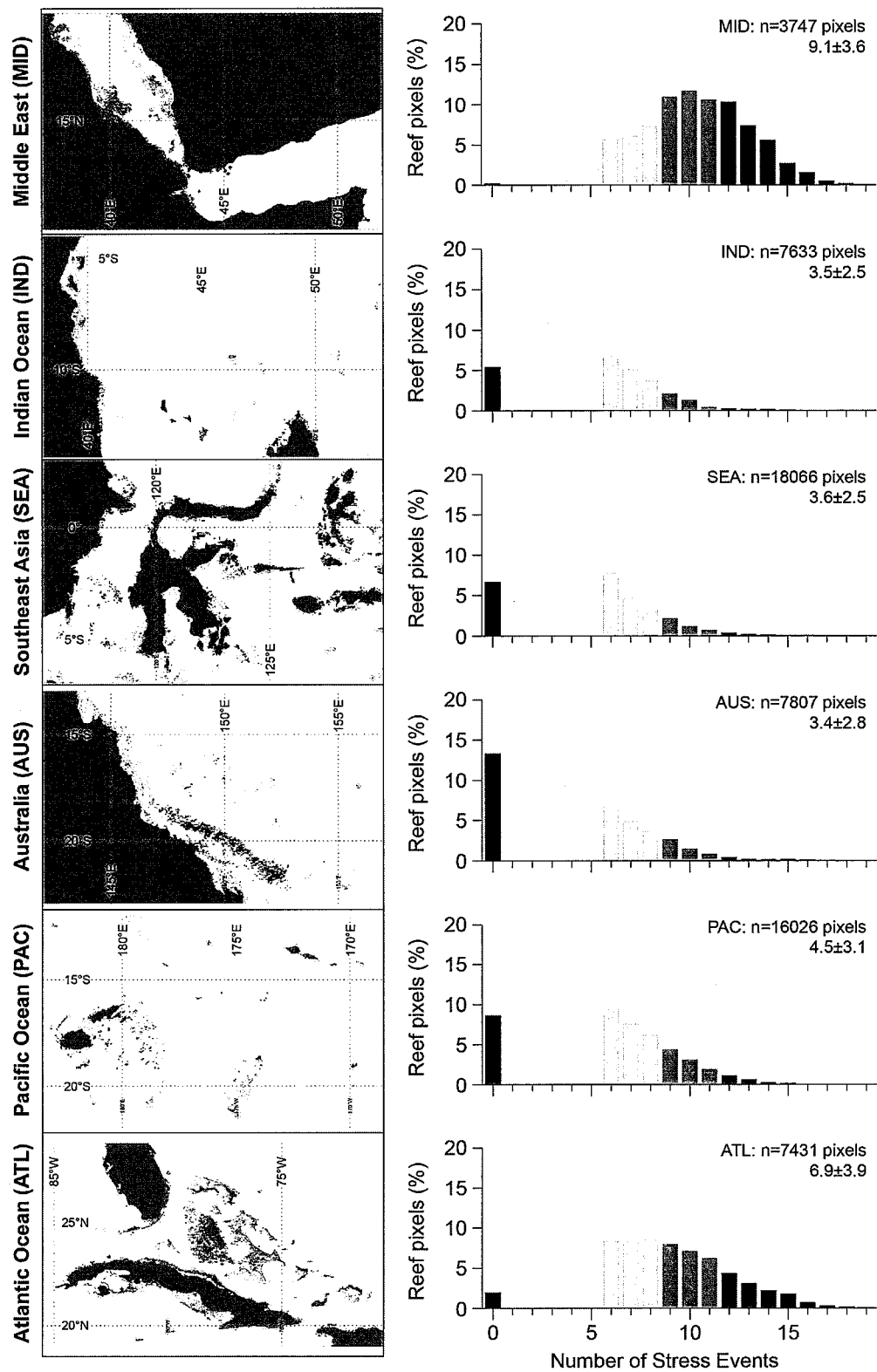
Temperature trends indicate accelerated warming in recent decades. Overall, reefs have been increasingly exposed to bleaching stress through this period. However, when comparing changes in exposure frequency across the record with the local summertime warming trend, some reefs experienced a lower-than-expected increase to stress exposure based on the global pattern, suggesting these locations as potential refugia. Using our analysis we identify reefs potentially more resilient to climate change impacts to inform conservation efforts.

**SST Trends.** Warming of coral reef waters (Fig. 1a, S1) was distinctly higher than that reported for ocean waters in general, both globally (0.10–0.12 °C/decade, 1971–2010<sup>47,48</sup>) and regionally (0.02–0.13 °C/decade, 1950–2009<sup>23</sup>). Consistent with IPCC findings, warming in the Indian Ocean (from the Middle East and Indian Ocean regions) exceeded that in the Pacific (from the Southeast Asia, Australia and Pacific Ocean regions), which in turn was greater than that in the Atlantic. Higher trends on reefs likely reflect the accelerated rate of warming from the most recent 28-year period (compared with the longer timeframes used in IPCC analyses), and potentially result from better resolution and improved accuracy of data closer to land<sup>39</sup>. Regional trends in annual and warm-season temperature (Fig. 3, S1) were consistent with earlier studies in the Atlantic<sup>40,41</sup> and in Southeast Asia<sup>42</sup>.

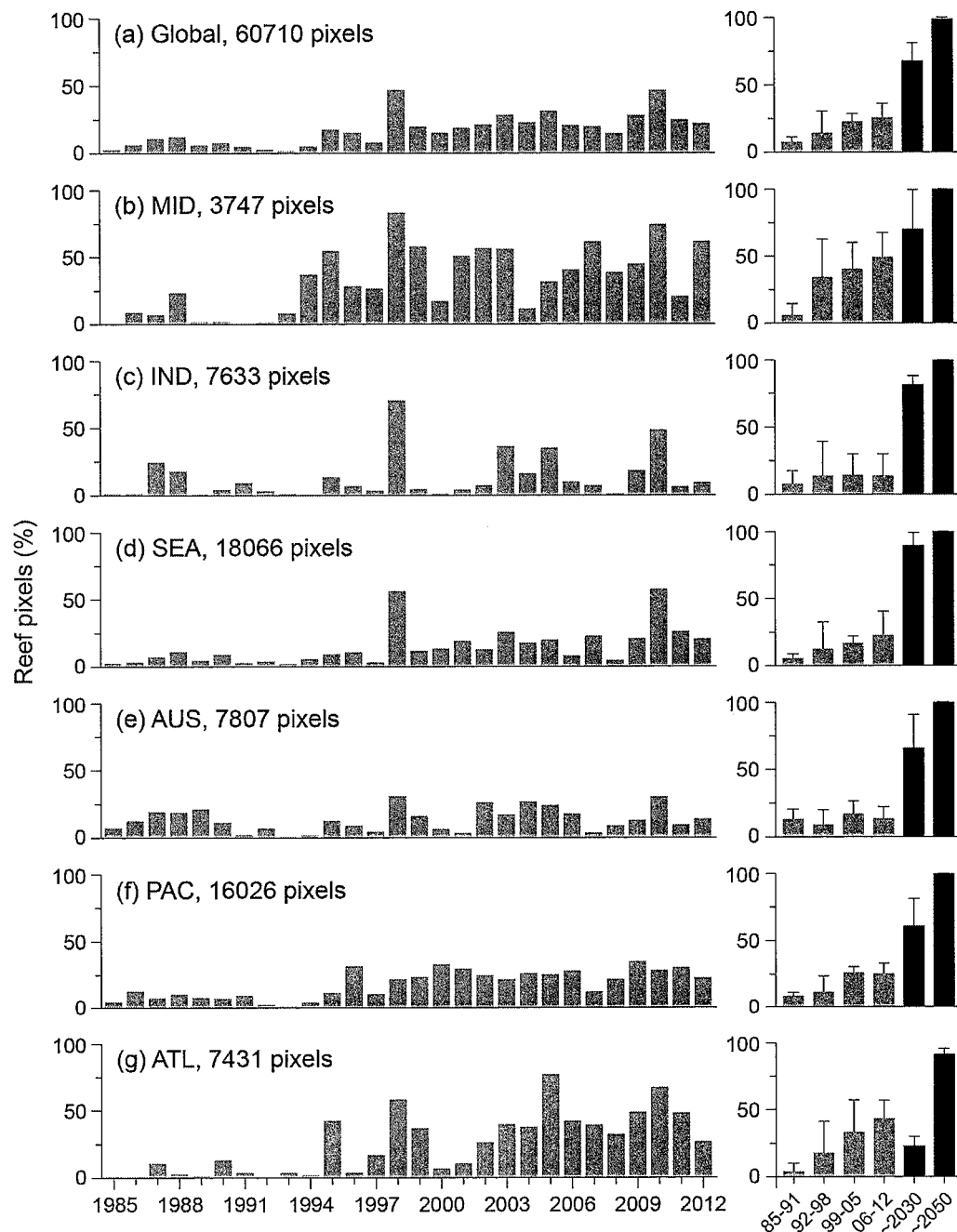
Warming trends vary broadly across reefs – annual average temperature in the northwestern Red Sea, Middle East (99<sup>th</sup> percentile) increased at approximately three times the global average. In contrast, temperature to the north of Grand Bahama Island in the Atlantic (1<sup>st</sup> percentile) declined at  $-0.21$  °C/decade – comparable to the rate of average global increase (Fig. 2). Recent cooling observations in parts of the Atlantic region have been linked to an increase in winter cold-air fronts from the North American continent since the 1990s<sup>49</sup>, including unusually cold weather causing coral mortality in Florida in 2010<sup>50</sup>. Warm-season trends in the Atlantic region were predominantly greater than annual SST trends (Fig. 4g), consistent with Chollett *et al.*<sup>41</sup>. Warm-season warming may have been driven by the negative- to positive-phase change of the Atlantic Multidecadal Oscillation around the mid-to-late 1990s<sup>51</sup>, also linked to increased oceanic heat content and Atlantic tropical storm activity in recent years<sup>52</sup>.

Faster warming in winter than in summer for 70% of global reefs (Fig. 4) is consistent with both observations through the past century and future predictions that winter temperatures are warming faster than summer temperatures<sup>53,54</sup>. The consequence for corals has been a steady reduction in the cool-season reprieve from warm-season temperatures, which can enhance disease outbreaks<sup>55,56</sup>. In contrast, reefs experiencing more rapid warming of their warm seasons may experience increased bleaching and infectious disease<sup>13–15</sup>.

**Thermal Stress.** Reefs with infrequent bleaching stress events (DHW  $\geq 4$  °C-weeks,  $< 1$ /decade; Fig. 1c, 5) would likely, all else being equal, have had sufficient time to recover between events<sup>10,57</sup>. This applies to 33% of reef pixels worldwide and to more than 41% of the pixels in the Indian Ocean and Australia regions, but to far fewer in the Atlantic (14%) and Middle East (4%). While low past exposure does not guarantee future refuge from stress,



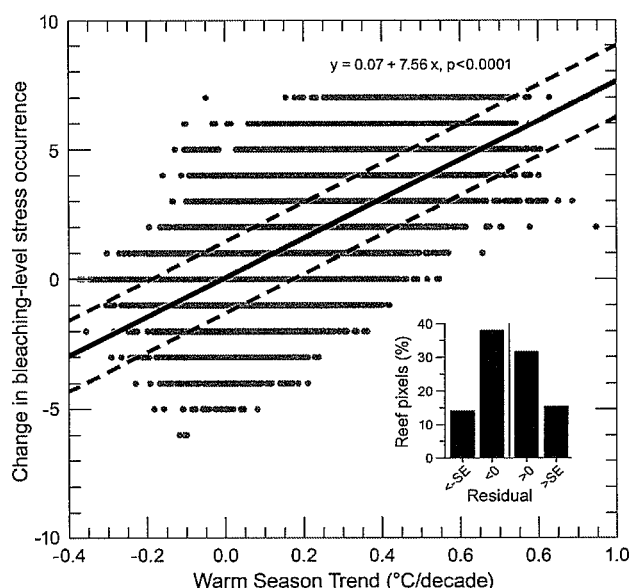
**Figure 5.** Frequency of bleaching-level thermal stress events among reef regions, 1985–2012. Bleaching-level stress is defined as DHW  $\geq 4^{\circ}\text{C}$ -weeks. Maps (left) show results for a subset of each region; histograms (right) show the distribution of results in the full region with the regional average  $\pm$  one standard deviation. Reef regions are as per Burke *et al.* 2011. Data are provided for each histogram in Table S5. Data visualisations produced using IDL [8.3] (Exelis Visual Information Solutions, Boulder, Colorado).



**Figure 6. Histograms of bleaching-level thermal stress events, 1985–2012.** Bleaching-level stress is defined as DHW  $\geq 4^{\circ}\text{C-weeks}$ ; plots refer to the % of reef pixels. The 28-year study period is divided into four 7-year periods in the histograms on the right (light grey), which show the average percentage of reef pixels affected by bleaching-level thermal stress across each period. The dark grey shade in the histograms show the average percentage of reef projected to experience bleaching-level thermal stress events under emissions scenario RCP8.5 for the 7-year periods centered on 2030 and 2050, following methods in van Hooidonk *et al.* 2014. Whiskers in the histogram are one standard deviation. Reef regions are as per Burke *et al.* 2011 (MID = Middle East, IND = Indian Ocean, SEA = Southeast Asia, AUS = Australia, PAC = Pacific Ocean and ATL = Atlantic Ocean). Data are provided for each histogram in Tables S7a,b.

it can indicate localised features (e.g., upwelling) that, if these persist, may provide some protection from thermal stress<sup>58,59</sup>. Alternatively, such locations may simply have been 'lucky so far' in escaping exposure to stress<sup>60</sup>.

In contrast, reefs with high frequency of bleaching-level exposure ( $>2/\text{decade}$ ) may have impaired function or may have already experienced shifts from susceptible to tolerant coral communities<sup>10,57</sup>. This applied to 33%



**Figure 7. Change in bleaching stress occurrence with warm-season temperature trend.** Difference in number of bleaching-level stress events ( $\text{DHW} \geq 4^\circ\text{C-weeks}$ ) between the 1985–1991 and 2006–2012 periods compared with warm-season trend for global reef pixels. Solid line shows linear regression; dashed lines are one standard error of estimate ( $\text{SE} = 1.37$ ) above and below this. Histogram shows the proportions of reef pixel residuals distinguished by the lines. Data are provided for the histogram in Table S9.

of reefs globally and >59% in the Middle East and Atlantic regions, but <21% of reefs in the Indian Ocean, Southeast Asia and Australia regions. Corals that have survived past frequent bleaching stress events may be among the hardier and more resistant species or may have acclimated to stressful conditions<sup>28</sup>. Such reefs may be the most likely to persist when exposed to future stress events, though probably with the cost of reduced species and genetic diversity of surviving corals (e.g., refs 10, 29 and 57). Reefs that have persisted despite frequent exposure to mortality-level stress ( $\text{DHW} \geq 8^\circ\text{C-weeks}$ , >2/decade) may prove critical for the continued existence of corals into the future. Nearly 24% of global reef locations ( $n = 14,672$ ) experienced mortality-level thermal stress in one or both of 1998 and 1999, suggesting that the reported 16% loss of reefs<sup>11</sup> from the first recorded global bleaching may have been substantially underestimated.

Temporal patterns in bleaching-level thermal stress (Fig. 6) show that reefs have been increasingly exposed to stress in recent decades, with variation across the regions. Dramatic increases in the regional percentage of stressed reefs were likely associated with switches in basin-scale oceanographic phenomena: in the Middle East region during 1992–98, coinciding with the switch in the Indian Ocean Dipole<sup>61</sup> and resulting in increased bleaching<sup>62</sup>; and in the Pacific region during 1999–2005, following the ca. 1998 phase shift in the Pacific Decadal Oscillation<sup>63</sup>.

Our assessment of both trends and stress exposure provides, for the first time, the opportunity to examine how these interact. We evaluated how summertime warming rate affected the frequency of bleaching stress events. The increase of bleaching-level events from 1985–91 to 2006–12 was associated with warm-season warming for many reefs (Fig. 7). For over 14% of reefs (8,704 pixels, Table S9), however, the change in stress exposure was more than one SE below the global linear regression. These reefs, present in all regions, had less increase to exposure than expected given their summertime warming rate.

**Warm-season Variability.** Several field studies<sup>45,46,64,65</sup> show that higher temperature variability reduces susceptibility to thermal stress on local scales; however, no variability threshold for or quantitative relationship with the mitigation of stress has been defined. To examine this, we considered the warm-season variability values at the reefs from these studies. With the exception of the study of Oliver & Palumbi<sup>45</sup>, each spanned multiple pixels. No absolute threshold value could be ascribed to distinguish sites (e.g., the “low variability” location from Carilli *et al.*<sup>65</sup> had a metric value greater than that of the “high variability” location in Castillo *et al.*<sup>64</sup>). This suggests that spatial patterns in temperature variability on a regional-to-local scale may be more important than a global threshold in identifying reefs resistant to thermal stress. The warm-season temperature variability data product enables broad-scale studies to test the hypothesis that high temperature variability reduces bleaching impacts<sup>66</sup>.

**Application to Conservation.** Identifying reefs with reduced exposure and/or less sensitivity can assist in identifying short-term target locations for conservation, which is critical given that projections of future bleaching indicate near-complete exposure of reefs to annual bleaching-level stress around 2050 (Fig. 6a–right, van Hooidonk *et al.*<sup>21</sup>). The production of the maps and spatial data presented here creates an opportunity to test

hypotheses of how bleaching impact may be influenced by thermal history. With the third global coral bleaching event in progress at the time of writing, observations from this event can be used to validate how aspects of thermal history influence the severity of bleaching responses and levels of bleaching-induced mortality.

Here, we consider three characteristics of thermal history to identify reefs potentially resilient to thermal stress: (i) the frequency of past exposure; (ii) how that frequency has changed in the context of warm-season trend; and (iii) the level of warm-season variability. For each, we provide high-resolution images of identified reefs to inform conservation and research efforts (Figures S6–S8).

There is potential for both low and high frequency of past thermal exposure to be important for conservation (Figure S6). Regions with low historical exposure (blue), which are potential thermal refugia, include the Maldives and the southern Great Barrier Reef. Those with high exposure (red), which may have developed resistance, include Zanzibar and the Meso-American Barrier Reef. Some areas had both low and high exposure reefs within tens of kilometres (e.g., New Caledonia, the Florida Keys). Magris *et al.*<sup>40</sup> identified reefs in southern Brazil as historical refugia due to relatively low past thermal exposure (among Brazilian reefs); our study found several reefs in this region that experienced relatively low exposure frequency (Figure S6).

Reefs with a lower increase in stress exposure (the number of bleaching stress events) than expected from their summertime warming rate (i.e., reefs with large negative residuals in Fig. 7) are potential refugia. While it is unknown if this may continue into the future, this characteristic warrants consideration of these sites as priorities for management action (Figure S7). This trait was apparent at reefs in the eastern Persian Gulf, the northern Great Barrier Reef, New Caledonia and around the Bahamas and Greater Antilles. Maina *et al.*<sup>67</sup> identified reefs along the southern African coast and east of Madagascar as among western Indian Ocean reefs with the lowest susceptibility to thermal stress; reef locations in this region were also identified in Figure S7.

Reef locations with the highest observed warm-season variability ( $\geq 20\%$  of the climatological range) were found in the Maldives, western Sumatra, the Solomon Islands and Micronesia, several islands in the south Pacific, and the Caribbean coast of Panama (Figure S8). Given the lack of information on a threshold for warm-season variability, we propose that these reefs, which have the highest variability globally, be considered as priority conservation sites. However, consideration might also be given to the most variable reefs within individual regions/sub-regions.

Reefs with slower future warming could also be valuable sites for conservation. These can be identified globally once downscaled model projections, such as those for the Caribbean presented in van Hooidonk *et al.*<sup>68</sup>, are available for all reef regions.

Understanding the capacity of corals to cope with thermal stress exposure may be the most important factor in predicting future reef trajectories<sup>69</sup>. Guided by remote sensing products that monitor thermal stress in near real-time<sup>29,70</sup> and modelled seasonal outlooks providing up-to-four-month advance warming<sup>71</sup>, observers are surveying reef impacts across global reef regions. The thermal history data products described here (and available at: [http://coralreefwatch.noaa.gov/satellite/thermal\\_history/](http://coralreefwatch.noaa.gov/satellite/thermal_history/)) enable studies relating thermal history to bleaching resistance and community composition. Such analyses are needed, especially in light of thermal exposure during the current global event, to expand on the efforts presented here in helping identify reefs more resilient to thermal stress.

## Conclusion

This study is the most comprehensive retrospective analysis of sea surface temperature and historical thermal stress in coral reef areas undertaken to date. Results from 1985–2012 show that: (i) 97% of reef pixels warmed through this period; (ii) cooler seasons represented less of a reprieve from warm-season stress; and (iii) more than three times as many reef pixels were exposed to bleaching-level thermal stress at the end of the record than was characteristic of the late 1980s, with even more drastic increases expected in coming decades. Importantly, the spatial heterogeneity seen in the analysis may identify locations that either represent refugia, or have reduced sensitivity to thermal stress and which could be less impacted during future disturbance. Coral bleaching events have become and will continue to become more frequent and severe – it is critical that we identify and conserve resilient reefs to help coral reefs survive while efforts are underway to control damaging anthropogenic global warming.

## Methods

We used the NOAA Pathfinder version-5.2 daily,  $1/24^\circ$  ( $\sim 4$  km) sea surface temperature (SST) dataset, derived from satellite remote sensing and an official NOAA Climate Data Record for SST<sup>72</sup>. This latest version of Pathfinder provides continuous and consistently derived reef-scale temperatures over recent decades, currently available through 2012. This product provides skin temperature whilst previous versions of Pathfinder reported bulk temperatures, which have an average offset of  $\sim 0.16^\circ\text{C}$ <sup>73</sup>. This offset can vary with wind speed, cloud cover and other atmospheric parameters<sup>73</sup>. However, the internal consistency of this dataset and the fact that it spans both previous global coral bleaching events in 1998 and 2010 (see introduction) are key considerations supporting its use. Pathfinder SST data were composited to weekly resolution and then gap-filled using temporal and spatial-comparison techniques for 1985–2012 following Heron *et al.*<sup>55</sup>.

We assessed which pixels contain coral reefs by combining three published global reef-locations datasets (ReefBase<sup>74</sup>, Millennium Maps<sup>75</sup>, Reefs at Risk–Revisited<sup>44,76</sup>). This was further augmented by other documented coral reef locations from collaborative reef studies; the reef-pixel dataset is available at [coralreefwatch.noaa.gov](http://coralreefwatch.noaa.gov). SST analysis was performed for 60,710 reef-containing pixels; maps presented here include pixels within  $\sim 9$  km of reefs (total  $n = 175,585$ ) to enhance visual interpretation of the results.

A range of thermal history metrics was developed in consultation with reef scientists and managers and arranged into six themes: 1. Trends (SST rates of change); 2. Climatology (long-term average conditions); 3. SST Variability (seasonal and annual); 4. Annual History (maximum SST, anomaly and DHW, by year); 5. Stress

Frequency (number of events for different stress levels); and 6. Onset Timing (expected onset and variability). From within these six themes, this study focused on seven metrics (numbered below).

*SST trend* in temperature [metric 1a] provides the long-term (28-year) historical trajectory of annual-mean temperature ( $SST_{ann}$ ) as the slope,  $\omega_{ann}$ , of a linear generalised least squares model (after Weatherhead *et al.*<sup>77</sup>):

$$SST_{ann} = \mu + \omega_{ann}t + N_t, \quad (1)$$

where  $\mu$  is constant,  $t$  is time in years and  $N_t$  is the residual assumed to be autoregressive of the order of 1. The residual at a given time is a linear function of the residual at the previous time step and a random variable,  $\varepsilon_t$  (i.e.,  $N_t = \phi N_{t-1} + \varepsilon_t$ ). Statistical significance of the trends was determined at the 5% level (i.e.,  $p < 0.05$ ). To ensure appropriate representation of global coral reef regions (see below), regional results were compiled for all trends as well as the subset that were statistically significant.

Expected intra-annual temperature variations on reefs can be described by long-term monthly averages (climatologies), developed here following Heron *et al.*<sup>78</sup>. The warmest of these, the Maximum of the Monthly Means (MMM, °C), is used by NOAA Coral Reef Watch (CRW) as the stress threshold for monitoring conditions conducive to bleaching<sup>79</sup>. The climatologically *warmest month* [2] varies across global reef locations and indicates the period when bleaching-level thermal stress is most likely.

To examine factors during the intra-annual period when there is potential for coral bleaching, we defined the three-month warm season as centred on the warmest month for each pixel. *Warm-season trend* in temperature [1b] is the slope,  $\omega_{ws}$ , of the generalised least squares model with autoregressive covariance (order 1) during the thermal stress period, calculated using three-month average temperature for the warm season,  $SST_{ws}$ , within each year, as:

$$SST_{ws} = \mu + \omega_{ws}t + N_t. \quad (2)$$

Parameters and statistical significance for warm-season trend are as described for the annual SST trend. The difference between SST trend and warm-season trend provides an indication of how the seasonality may have increased, or become suppressed, through the record. Reef locations for which SST trend exceeds warm-season trend indicate a suppressed seasonality, and therefore less respite from summertime temperature. Locations with a marked reduction in seasonality were identified by calculating the standard deviation of the trend difference across global reef pixels, and then determining where the trend difference was greater than approximately one standard deviation.

Bleaching-level thermal stress was calculated using Degree Heating Weeks (DHW), which combines magnitude and duration of temperature exceeding the MMM<sup>79</sup>. DHW of 4 °C-weeks has been linked to ecologically significant coral bleaching<sup>12</sup> and was used here to indicate bleaching-level thermal stress. DHW of 8 °C-weeks is associated with significant coral mortality<sup>12</sup> and was used as the threshold for mortality-level thermal stress. Knowledge of the likely onset timing of the bleaching season, and the spatial context of this information, can assist reef stakeholders in long-term planning, short-term preparation and monitoring. The mean timing of *stress onset* [3] (month) for thermal stress that reached 4 °C-weeks or greater was documented for all locations. Information on annual historical exposure can guide managers in understanding past thermal stress; identifying local DHW thresholds (i.e., if different from the broadly used values of 4 and 8 °C-weeks<sup>12</sup>); and distinguishing between thermal and non-thermal bleaching events. *Annual maximum DHW* [4] provides the highest accumulated thermal stress in each year. We quantified the *number of bleaching-level stress events* [5] through the 28-yr record, describing the historical incidence of annual maximum DHW at or above DHW of 4 °C-weeks. Reefs that experienced bleaching-level stress with frequency <1 event/decade (two or fewer occurrences) were defined as having had relatively low frequency of exposure to thermal stress, while those with >2 events/decade (six or more occurrences) were defined as having high frequency of exposure (see Donner *et al.*<sup>57</sup> and discussion therein). The number of mortality-level stress events through the record was determined using the DHW threshold of 8 °C-weeks.

The spatial distribution of the potential for increased thermal tolerance due to temperature variability was evaluated by defining *warm-season variability* [6], the standard deviation around the long-term mean of three-month warm-season temperature. This metric was calculated following the removal of the warm-season trend to separate the effects of long-term change and variability. Previous global mapping of SST variability at reduced resolution (0.5–1.0°) indicated strong influence of latitudinal variation<sup>32</sup>. To eliminate the effect of latitudinal variation, the warm-season variability was expressed here as a percentage of the climatological temperature range; i.e., the difference between the maximum (MMM) and minimum of the monthly mean climatologies. As the level of variability that confers bleaching resistance is unknown, we identified locations where the variability scaled by the local climatological range was in the approximately upper quartile of global values.

Spatial analysis of the aforementioned metrics was undertaken for reef locations globally ( $n = 60,710$ ). To provide further insight into regional (ocean basin/sub-basin) patterns of the metrics while aligning with existing conservation management knowledge, spatial analyses were also undertaken for the six regions defined by the World Resources Institute's Reefs at Risk—Revisited analysis<sup>44</sup>. These reef regions are as follows: Middle East (MID), Indian Ocean (IND), Southeast Asia (SEA), Australia (AUS), Pacific Ocean (PAC) and Atlantic Ocean (ATL). Global and regional summaries for each metric were calculated as the average and standard deviation (SD) across reef pixels within these regions and globally. Maps from within each region in the main text and supplementary material display within-region variation for each metric. The areas shown are centred on: the southern Red Sea (Middle East), Comoros (Indian Ocean), Sulawesi (Southeast Asia), the central Great Barrier Reef (Australia), Fiji/Samoas (Pacific Ocean) and the Bahamas (Atlantic Ocean). Distributions of data from reef locations globally and from across each region are presented as histograms, and the corresponding data are provided

in the supplementary material. Time-series and trends of annual-mean SST are displayed for five reef locations (across five of the six regions) that represent the ~99<sup>th</sup>, ~75<sup>th</sup>, ~50<sup>th</sup>, ~25<sup>th</sup> and ~1<sup>st</sup> percentiles of annual SST trend.

Temporal patterns in the historical incidence of bleaching- and mortality-level stress were considered annually and by dividing the 28-year period into four 7-year periods (1985–91, 1992–98, 1999–2005, 2006–12). Global and regional historical patterns were augmented using projections of thermal stress (DHW), based on monthly SST data from the World Climate Research Programme's Coupled Model Intercomparison Project Phase 5 (CMIP5) dataset<sup>79</sup>. Projected stress was calculated from 33 available GCMs under relative concentration pathway (RCP) 8.5 following the methods presented in van Hooidonk *et al.*<sup>21</sup> (model list in van Hooidonk *et al.*<sup>22</sup>). For the projections, the equivalent DHW value for bleaching-level thermal stress was 6 °C-weeks<sup>21</sup>. The median year for the start of annual bleaching conditions under RCP8.5 was reported as 2040<sup>21</sup>. To allow comparison with temporal patterns from the 7-year periods in the historical satellite data, we calculated the percentage of reef pixels with bleaching-level stress across 7-year periods centred on 2030 and 2050 (10 years prior and subsequent to the reported median year). We present regionally summarised information of projected thermal stress for comparisons with the four 7-year periods between 1985 and 2012; projections at full resolution are in refs 21, 22 and 56.

Remote sensing data collation, spatial analysis and data visualization was undertaken using Interactive Data Language (IDL) v8.1–3 and python 2.7.

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## Author Contributions

S.F.H. and J.A.M. conceived the study, with input from all authors. S.F.H. and J.A.M. wrote the text with assistance from and review by all other authors.

## Additional Information

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## **ANEXO IV**

Declarações de entidades internacionais  
renomadas (CHPA, PCPC)



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04 May 2018

# American Academy of Dermatology Association statement on sunscreen access

**ROSEMONT, Ill. (May 4, 2018)** — *Statement from Suzanne M. Olbricht, MD, FAAD, president, American Academy of Dermatology Association*

The American Academy of Dermatology Association is concerned that the public's risk of developing skin cancer could increase due to potential new restrictions in Hawaii that impact access to sunscreens with ingredients necessary for broad-spectrum protection, as well as the potential stigma around sunscreen use that could develop as a result of these restrictions. Sadly, the death rate from melanoma, the deadliest form of skin cancer, in Hawaii is already 30 percent higher than the national average.

The AADA wants the public to know that sunscreen remains a safe, effective form of sun protection. As one component of a daily sun protection strategy, sunscreen is an important tool in the fight against skin cancer. Claims that sunscreen ingredients currently approved by the U.S. Food and Drug Administration are toxic to the environment or a hazard to human health have not been proven. Furthermore, scientific evidence supports the benefits of applying sunscreen to minimize short- and long-term damage to the skin from the sun's harmful ultraviolet rays.

Research indicates that about 95 percent of melanoma cases are attributable to UV exposure, so the AADA encourages everyone to protect themselves from the sun by seeking shade, wearing protective clothing, and using a broad-spectrum, water-resistant sunscreen with an SPF of 30 or higher.

sunscreens with ingredients other than oxybenzone and octinoxate, such as zinc oxide or titanium dioxide. We also encourage the public to closely read product labeling, use products as directed, and contact a board-certified dermatologist if they have any questions.

Although there are many safe and effective sunscreen products on the market, the AADA continues to support the introduction of new sunscreen ingredients in the United States. The best sunscreen is the one that individuals will use every day. The more sun protection options consumers have at their disposal, the more likely they will be to find an option they like and will use regularly.

### **More Information**

[Find a Dermatologist \(/find-a-derm\)](#)

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[AADA letter to Hawaii State Legislature \(/File Library/Top navigation/Media/HI-AADA-Oppose-SB2571-House-and-Senate.pdf\)](#)

### **About the AADA**

*Headquartered in Rosemont, Ill., the American Academy of Dermatology, founded in 1938, is the largest, most influential and most representative of all dermatologic associations. A sister organization to the Academy, the American Academy of Dermatology Association is the resource for government affairs, health policy and practice information for dermatologists, and plays a major role in formulating policies that can enhance the quality of dermatologic care. With a membership of more than 19,000 physicians worldwide, the Academy is committed to excellence in the diagnosis and medical and surgical treatment of skin disease; advocating high standards in clinical practice, education and research in medical dermatology, surgical dermatology and dermatopathology; and supporting and enhancing patient care to reduce the burden of disease. For more information, contact the Academy at (888) 462-DERM (3376) or [aad.org](http://aad.org) (/home/home). Follow the Academy on [Facebook](https://www.facebook.com/AADskin) (<https://www.facebook.com/AADskin>)(American Academy of Dermatology), [Twitter](https://twitter.com/AADskin) (<https://twitter.com/AADskin>) (@AADskin) and [YouTube](https://www.youtube.com/user/AcademyofDermatology) (<https://www.youtube.com/user/AcademyofDermatology>)(AcademyofDermatology).*

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## **Statement from the Consumer Healthcare Products Association (CHPA) Regarding Hawaii Sunscreen**

19

“Today the health, safety and welfare of millions of Hawaii residents and tourists has been severely compromised by the passage of SB 2571 that will ban at least 70 percent of the sunscreens on the market today, based on weak science blaming sunscreens for damage to coral reefs. This irresponsible action will make it more difficult for families to protect themselves against the sun’s harmful ultraviolet rays, and it is contrary to the many concerns expressed by Hawaii’s medical doctors, dermatologists, and public health experts.”

“Overwhelming scientific evidence shows that excess sun exposure without effective sunscreen increases the risk of developing skin cancer in both adults and children. Banning oxybenzone and octinoxate – key ingredients in effective sunscreens on the market – will drastically and unnecessarily reduce the selection of safe and effective sunscreen products available to residents and visitors. Oxybenzone and octinoxate, found in the majority of sunscreens, are safe and effective over-the-counter (OTC) active ingredients recognized by the Food and Drug Administration (FDA) as important aides in decreasing the risk of developing skin cancer, the most common cancer in the U.S.”

“This ban also avoids the real causes of coral decline according to scientists in Hawaii and around the world: global warming, agricultural runoff, sewage, and overfishing. This ban creates false hope that banning sunscreen will restore the health of coral reef around the Hawaiian Islands, but it will have little to no positive impact on the health of coral reefs. Rather, it has the potential to create a public health crisis which is why the Hawaii Medical Association, Hawaii Dermatological Society, Hawaii Skin Cancer Coalition, and Hawaii Department of Health have also expressed concerns with this legislation.”

###

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*The Consumer Healthcare Products Association (CHPA) is the 137-year-old national trade association representing the leading manufacturers and marketers of over-the-counter (OTC) medicines and dietary supplements. Every dollar spent by consumers on OTC medicines saves the U.S. healthcare system \$6-\$7, contributing a total of \$102 billion in savings each year. CHPA is committed to empowering self-care by preserving and expanding choice and availability of consumer healthcare products. [chpa.org](http://chpa.org)*

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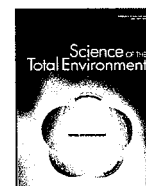
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# Examine all available evidence before making decisions on sunscreen ingredient bans

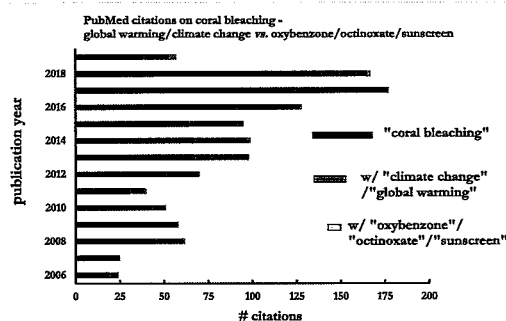
Jay Sirois

Regulatory & Scientific Affairs, Consumer Healthcare Products Association, 1625 I St NW, Suite 600, Washington, DC 20006, United States of America.

## HIGHLIGHTS

- Coral bleaching resulting from climate change has occurred worldwide for decades.
- Recent *in vitro* studies suggest sunscreen ingredients could cause coral to bleach.
- Sunscreen ingredient bans are likely to be ineffective in restoring coral health.
- Ingredient bans will likely result in decreased use and increased UV exposure.
- All scientific evidence needs to be considered before banning sunscreen ingredients.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Coral bleaching is a worldwide problem and more needs to be done to determine causes and potential solutions. A myopic focus on sunscreen ingredients as the proximate cause of coral bleaching provides consumers a false belief that enacted bans of these ingredients will erase decades of coral reef decline. Instead, these bans will likely only lead to decreased sunscreen use and exposure to potentially harmful UV radiation. A closer examination of all available evidence on the causes of coral reef bleaching needs to be undertaken, including a more thorough appraisal of studies conducted under artificial conditions using higher concentrations of sunscreen ingredients.

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Coral bleaching is a worldwide problem and more needs to be done to determine causes and potential solutions. To date, limited evidence generated in laboratory studies suggests that active ingredients in sunscreens are responsible for coral bleaching (Downs et al., 2016; Danovaro et al., 2008; He et al., 2019a; He et al., 2019b; Tsui et al.,

2017). Despite this, widespread media attention has focused on results from these studies often using single, unreplicated data points to suggest that ingredients in sunscreen pose a hazard to coral reefs and should thus be banned. Although results from these studies merit consideration, and suggest the need for further study, as with all scientific evidence, there are inherent limitations and results from these studies cannot be easily extrapolated to what might occur in a native coral reef setting. Instead of relying on results from isolated studies to

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promote proposed solutions to coral decline, a closer examination of all available evidence on the causes of coral reef bleaching should be undertaken. This should include a more thorough appraisal not only of these studies, conducted under artificial conditions using higher concentrations of sunscreen ingredients, but also of other evidence demonstrating the significant role that climate change and other factors have played in coral bleaching over the past 50 years.

Unfortunately, coral reef bleaching has occurred worldwide for the past several decades irrespective of whether a particular coral reef is impacted by a high level of human recreational activity (Bruno and Valdivia, 2016; Barkley et al., 2018). There is a vast amount of scientific evidence pointing to changes in ocean temperature resulting from climate change as a primary mediator of coral reef bleaching (Hughes et al., 2017; Heron et al., 2018; National Oceanic and Atmospheric Administration (NOAA), n.d.; National Aeronautics and Space Administration (NASA), n.d.; Heron et al., 2018). Further, results from other studies (Johnsen, 2018; et al., 2017; Reef Safe, 2016) suggest that exposure to sunscreens (including those that contain oxybenzone or octinoxate) does not negatively affect coral reef populations. In some cases, these experiments utilized exposure conditions which more closely reflected what might happen in a native coral reef setting and found no difference in the health of coral between sunscreen and control groups. Moreover, recent evidence demonstrating lower levels of sunscreen ingredients (including oxybenzone and octinoxate) in coral reef habitats (Mitchellmore et al., 2019) compared to earlier work suggests the need for careful examination of all available data.

Banning individual sunscreen ingredients based on preliminary results obtained under conditions which may not accurately reflect native coral reef settings is highly irresponsible, as it risks the diversion of resources towards efforts which will likely have no measurable effect. Further, reducing the number of available sunscreen ingredients will inhibit consumer choice of broad-spectrum sunscreen products shown to be effective in reducing skin cancer (Green et al., 2011; Van der Pols et al., 2006; Olsen et al., 2018; Watts et al., 2018).

One in five people will develop skin cancer in their lifetime and more than 5 million new cases of skin cancer were diagnosed in the U.S. in 2018 (American Cancer Society, Cancer Facts, and Figures, 2018). There are more new cases of skin cancer each year than breast, prostate, lung and colon cancer combined. Overwhelming evidence demonstrates that excess sun exposure without sunscreen increases the risk of developing skin cancer in both adults and children (Preston and Stern, 1992; English et al., 1998). Sun-protective behaviors to reduce exposure to harmful UVA and UVB radiation should be practiced whenever possible and sunscreens are one effective option. Dermatologists agree that the best sunscreen is the one that is used on a regular basis.

A broad array of healthcare professionals recommends using a broad-spectrum sunscreen daily to prevent against sunburn and skin cancer. Indeed, a recent survey of dermatologists (Farberg et al., 2016) found that 99% agreed that regular use of sunscreen helps lower skin cancer risk. Similarly, a diverse group of professional societies/expert bodies recommends use of a broad-spectrum sunscreen to help protect against the harmful effects of UV radiation and reduce the risk of skin cancer.

When viewed in its entirety, the currently available evidence on the causes of coral reef bleaching and mortality, in Hawaii, Florida and the world over, overwhelmingly demonstrates that climate change (Hughes et al., 2017) is primarily responsible. There is evidence suggesting that other factors such as ocean acidification (Cyronak et al., 2018), runoff (Brodie et al., 2010; De'ath and Fabricius, 2010; Fabricius, 2005) and sewage discharge also contribute to an overall decline in coral reef populations. Coral damage resulting from runoff or sewage discharge could be a consequence of numerous factors (Marques et al., 2019) including changes in salinity (Aguilar et al., 2019) or bacterial count (Staley et al., 2017).

An open, honest and unbiased discussion of the available science on the multifactorial causes of coral reef bleaching and possible solutions to this problem needs to be conducted. The current focus on implicating

chemical sunscreen ingredients as the proximate cause of coral bleaching provides consumers a false belief that enacted bans of these ingredients will erase decades of coral reef decline. Instead, these bans will likely only lead to decreased sunscreen use and increased exposure to potentially harmful UV radiation.

## Acknowledgements

The Consumer Healthcare Products Association (CHPA) is the 138-year-old national trade association representing the leading manufacturers and marketers of over-the-counter (OTC) medicines (including sunscreen manufacturers).

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# **Statement from the Consumer Healthcare Products Association (CHPA) and the Personal Care Products Council (PCPC) Regarding Sunscreen Ingredient Ban**

Feb 05, 2019

## **FOR IMMEDIATE RELEASE**

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**Lisa Powers, 202.466.0489, [powersl@personalcarecouncil.org](mailto:powersl@personalcarecouncil.org)**

“The Consumer Healthcare Products Association (CHPA) and Personal Care Products Council (PCPC) are disappointed with the action taken by the Key West City Commission to ban certain sunscreen ingredients found in numerous sunscreens, cosmetics, shampoos, lip balms, and other health and personal care products. While we respect the emotion around coral reef decline, the ban represents a bad policy that is not based on scientific evidence. This ban is unlikely to have a positive effect on Florida’s coral but it will have a profound negative impact on the health and wellbeing of residents and visitors in Key West.

“Oxybenzone and octinoxate contribute to broad-spectrum protection from the effects of both UVA and UVB rays. UVA and UVB rays contribute to skin damage, skin aging, and melanoma, the leading cause of skin cancer-related deaths. Manufacturers, health professionals, and many others are opposed to a ban on these ingredients which provide critical defense against excess ultraviolet (UV) radiation exposure. Banning these ingredients will drastically – and unnecessarily – reduce the

selection of safe and effective sunscreens and other products available to residents and visitors in Key West.

“There is no definitive scientific evidence that products containing oxybenzone or octinoxate damage coral in natural environments like Key West, nor any evidence that banning these ingredients improves the plight of coral. The ingredient ban in Key West ignores the real causes of coral decline according to scientists in Florida and from around the world: global warming, agricultural runoff, sewage, and overfishing. Public policy that will likely adversely impact public health should not be based on a limited number of exploratory lab-based studies alone.

“Oxybenzone and octinoxate, found in the majority of sunscreens in the U.S., are safe and effective over-the-counter (OTC) active ingredients recognized by the Food and Drug Administration (FDA) as an important aide in decreasing the risk of developing skin cancer – the most common cancer in the U.S.”

*The Consumer Healthcare Products Association (CHPA) is the 138-year-old national trade association representing the leading manufacturers and marketers of over-the-counter (OTC) medicines and dietary supplements. Every dollar spent by consumers on OTC medicines saves the U.S. healthcare system \$6-\$7, contributing a total of \$102 billion in savings each year. CHPA is committed to empowering self-care by preserving and expanding choice and availability of consumer healthcare products. [www.chpa.org](http://www.chpa.org)*

*Based in Washington, D.C., the Personal Care Products Council is the leading national trade association representing the global cosmetic and personal care products industry. Founded in 1894, PCPC's 600 member companies manufacture, distribute, and supply the vast majority of finished personal care products marketed in the U.S. As the makers of a diverse range of products millions of consumers rely on every day, from sunscreens, toothpaste and shampoo to moisturizer, lipstick and fragrance, personal care products companies are global leaders committed to product safety, quality and innovation.*

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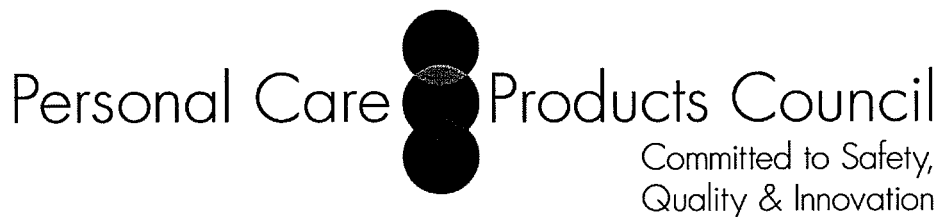
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**FOR IMMEDIATE RELEASE**  
**October 22, 2015**

**Contact: Lisa Powers, (202) 466-0489 or Lauren Brady, (202) 454-0316**

**Statement by Iain Davies, PhD, Senior Environmental Scientist  
The Personal Care Products Council  
In Response to Study on Sunscreens and Coral Reefs**

**Washington, D.C.** – “Benzophenone-3 (BP-3; oxybenzone) is an important sunscreen ingredient found in many personal care products and is designed to protect people against the damaging effects of ultraviolet (UV) light. In fact, according to the American Academy of Dermatology (AAD), oxybenzone is one of the few available sunscreen ingredients that effectively protect skin from both UVA and UVB rays that can contribute to skin cancer and premature skin aging.

“A study published recently in *Archives of Environmental Contamination and Toxicology* suggests that this common sunscreen ingredient could be harmful to coral and contributing to the decline of reefs around the world. This conclusion is based upon research conducted under laboratory conditions, which do not accurately reflect the complexity of the natural marine environment.

“Degradation of the world’s coral reefs is a serious concern. According to the U.S. National Oceanic and Atmospheric Administration’s (NOAA) Coral Reef Conservation Program, coral reefs are threatened by an increasing array of impacts – primarily from global climate change, unsustainable fishing and other factors. There is no scientific evidence that under naturally-occurring conditions, sunscreen ingredients, which have been safely used around the world for decades, are contributing to this issue.

“Our greatest concern is that this report may result in fewer people wearing sunscreens. In fact, a recent survey by the Centers for Disease Control and Prevention (CDC) published in the *Journal of the American Academy of Dermatology* found that approximately 43% of men and 27% of women never use sunscreen on their faces or other exposed skin. This is particularly concerning when we consider:

- Every year, there are more than 63,000 new cases of melanoma, the deadliest form of skin cancer, resulting in nearly 9,000 deaths;
- Skin cancer is the most commonly diagnosed cancer in the United States, with 5 million people treated each year;
- More than 1 out of every 3 Americans reports getting sunburned each year. Sunburn is a clear sign of overexposure to the sun’s UV rays, a major cause of skin cancer – a single bad burn in childhood doubles the risk of developing melanoma later in life.

**(MORE)**

"We all can play an important role in the fight against skin cancer. In addition to FDA, the Centers for Disease Control and Prevention (CDC), the U.S. Surgeon General, AAD, the Skin Cancer Foundation and health care professionals worldwide all emphasize that using sunscreens is a critical part of a safe sun regimen. The dangers of unprotected sun exposure are clear and universally recognized by public health professionals and dermatologists.

"As sunscreen manufacturers, our goal is to provide Americans with access to a wide variety of safe, effective and innovative sunscreens to use as an important part of an overall sun safe regimen."

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*For more information on cosmetic and personal care products, please visit [www.CosmeticsInfo.org](http://www.CosmeticsInfo.org).*

*Based in Washington, D.C., the Personal Care Products Council is the leading national trade association representing the global cosmetic and personal care products industry. Founded in 1894, the Council's more than 600 member companies manufacture, distribute, and supply the vast majority of finished personal care products marketed in the U.S. As the makers of a diverse range of products millions of consumers rely on every day, from sunscreens, toothpaste and shampoo to moisturizer, lipstick and fragrance, personal care products companies are global leaders committed to product safety, quality and innovation.*

###