Emergent properties in the responses of tropical corals to recurrent climate extremes

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Summary

The frequency, intensity and spatial scale of climate extremes is changing rapidly due to anthropogenic global warming.[1,2] A growing research challenge is to understand how multiple climate-driven disturbances interact with each other over multi-decadal timeframes, generating combined effects that cannot be predicted from single events alone.[3,4,5] Here we examine the emergent dynamics of five coral bleaching events along the 2,300km length of the Great Barrier Reef, that affected >98% of the Reef between 1998 and 2020. We show that the bleaching responses of corals to a given level of heat exposure differed in each event, was strongly influenced by contingency, and by the spatial overlap and strength of interactions between events. Naïve regions that escaped bleaching for a decade or longer were the most susceptible to bouts of heat exposure. Conversely, when pairs of successive bleaching episodes were close together (1-3 years apart), the thermal threshold for severe bleaching increased because the earlier event hardened regions of the Great Barrier Reef to further impacts. In the near future, the biological responses to recurrent bleaching events may become stronger as the cumulative geographic footprint expands further, potentially impairing the stock-recruitment relationships among lightly- and severely bleached reefs with diverse recent histories. Understanding the emergent properties and collective dynamics of recurrent disturbances will be critical for predicting spatial refuges and cumulative ecological responses, and for managing the longer-term impacts of anthropogenic climate change on ecosystems.

Results and Discussion

We no longer have the luxury of studying climate extremes as single, unprecedented events. Rather, scientists need to better understand the ecological dynamics of multi-decadal sequences of climate-related disturbances, and the emergent properties of multiple biological responses.

In theory, interactions between chains of repeated disturbances can be inhibitory, neutral, or reinforcing.[4] In the past three decades, three global coral bleaching events have been triggered by anthropogenic heating, each affecting 50-70% of the world's coral reefs.[1,2,6,7] Global and regional-scale mass bleaching of corals is a stress response to spikes in sea temperatures, disrupting the symbiotic relationship between corals and their dinoflagellate endosymbionts, which causes a loss of colour and elevated mortality.[8] Bleaching can be measured directly,[8,9] which is the approach we use here, or it can be inferred or predicted from levels of thermal exposure, most commonly quantified as Degree Heating Weeks (DHW, ºC-weeks).[6,7] DHW is a satellite-based metric that integrates both the duration and intensity of heat exposure.[10] A common benchmark in bleaching models, which underpins the IPCC's sobering predictions for the future fate of coral reefs[11] is that exceeding a threshold of 8 ºC-weeks DHWs twice per decade could trigger severe beaching and mortality, overwhelming the resilience of coral-dominated ecosystems.[12,13] Here we examine temporal shifts in the observed biological responses of coral assemblages to a given level of heat exposure (DHW), and test for interactions between pairs of events that were close together or further apart in time. We also quantify key emergent spatial features of multiple events - the cumulative spatial footprint of mild and severe bleaching, spatial heterogeneity in return-times of disturbances, and the emergence and subsequent decline of spatial refuges on the Great Barrier Reef, one of the world's largest coral ecosystems. In principle, establishing a judiciously placed network of well-protected, climate-resistant locations could help to repopulate or restore the broader land- and sea-scape, if greenhouse gas emissions are sufficiently curtailed to stabilize temperatures later this century.[14,15] On coral reefs, the utility of this emerging approach depends on the ability to accurately identify contemporary and future spatial refuges from bleaching[15,16,17], on the production, dispersal and recruitment of coral larvae,[18,19] and on the extent to which the responses of corals to heat stress changes as they experience more and more bouts of temperature extremes.[4,20,21,22,23,24,25]

The amount of bleaching on the Great Barrier Reef that was triggered by a given level of heat exposure has changed markedly over the past three decades, contingent on interactions between successive episodes (Figure 1). Each bout of extreme thermal exposure in 1998, 2002, 2016, 2017 and 2020 elicited a unique, non-linear bleaching response. In each event, Degree Heating Week exposure in that summer correctly predicted severe bleaching in 82.4-90.0% of cases (Table 1), in a statistical model that accounted for spatial autocorrelation (Supplementary Materials). Compared to the first mass bleaching in 1998, the response curve in 2002 flattened and moved strongly to the right, i.e. it took much more heat exposure in the second event to produce the same incidence of bleaching as the first event four years earlier (Figure 1A). Consequently, in 1998, 6.6 ^{o}C-weeks triggered a ~50% probability of severe bleaching (affecting >30% of corals), whereas the same 50% probability occurred at approximately 10.9 ^{o}C-weeks in 2002. After a further 14 years, the bleaching response curve re-set again to the left in the third mass bleaching in 2016 (Figure 1A). Then, in the fourth event only one year later in 2017, the response curve shifted sharply once more to the right, repeating the increased resistance to bleaching seen earlier in 1998-2002. Finally, Reef-scale bleaching responses in 2020 moved again to the left, intermediate to the responses in 2016 and 2017 (Figure 1A).

These temporal back and forth shifts in bleaching responses to heat exposure were even more marked at a regional scale - in the northern, central and southern Great Barrier Reef (Figure 1B-F). Different regions were more resistant to bleaching in each event, depending in part on history. In 1998 and 2002, regional differences in responses were small (Figure 1B,C), reflecting the relatively low levels of heat exposure compared to 2016, 2017 and 2020, especially in the northern region where only a handful of reefs experienced severe bleaching (Figure 2A,B). In 2002, it took roughly double the levels of DHW exposures to trigger a 50%

probability of severe bleaching for a second time in the central and southern sections compared to 1998 (Figure 1B,C), and the north escaped bleaching again (Figure 2A). Fourteen years later, in 2016 the response curve for the central and southern regions shifted back to the left (Fig. 1D), and the north bleached severely for the first time. A year later in 2017 and again in 2020, the northern region was the most resistant region to bleaching, even at exposure levels of 8-10 ^{o}C-weeks (Figure 1E,F). The south escaped with little thermal heat stress or bleaching in both 2016 and 2017 (Figure 2A, B). However, in 2020, 8 ^{o}C-weeks in the southern region triggered a 99% probability of severe bleaching, compared to 38% in the central region, and only 4% in the northern third of the Great Barrier Reef (Figure 1F). Consequently, we attribute the relatively high sensitivity of corals in 2020 at the scale of the entire Reef, (Figure 1A) to the severe bleaching that occurred that year in thermally naïve coral assemblages in the southern region, which were relatively unscathed during the 18-year period since 2002 (Figure 2A). In contrast, heat-sensitive corals in the north were severely depleted by mass mortality caused by bleaching in 2016,[26] and the depleted coral assemblages there were the most resistant to bleaching in both 2017 and 2020 (Figure 1E, F). The extent of the back and forth temporal variation in the bleaching responses during the five events (Figure 1) was unexpected, and suggests that bleaching and mortality thresholds will continue to rise and fall between future successive events, depending on the gap and interaction between them. Currently, models for predicting the temporal and spatial dynamics of bleaching assume either a constant bleaching and mortality response to a specific level of DHW exposure,[11,12,13] or a gradually increasing threshold (to mimic the potential for adaptive processes).[20]

To further investigate the potential for interactions between pairs of bleaching events, for each of the four bleaching episodes following 1998, we examined whether the model fits between heat exposure (DHW) and the bleaching responses on each reef were improved by incorporating DHW values for the preceding event as well as the current one (Table 1). An ecological memory of earlier events can be generated by a broad range of biological mechanisms operating over different spatial and time-scales, including acclimation, adaptation and shifts in species composition.[4,18,21,22] In 1998 and 2002, the incidence of severe bleaching on individual reefs across all regions was correctly predicted by DHW exposures in each year alone in 77.8% and 78.9% of cases, respectively (Table 1). Incorporating the comparatively mild 1998 DHW exposures into a model that included spatial eigenvectors (Supplemental Materials) did not significantly improve the model fit for 2002 ($Z=1.87$, $P=0.06$). Similarly, DHW values for 2016 alone predicted 80.4% of severe bleaching cases that year (Table 1) and heat exposures from 14 years earlier in 2002 did not change the model fit ($Z=-0.528$, $P=0.598$). In contrast, a year later, including the DHW values from 2016 improved the prediction accuracy in 2017 from 66.7% to 71.2%, and yielded very strong statistical support for an effect of prior heat exposure ($Z=-8.275$, $P<<0.0001$). Similarly, in 2020, incorporating the 2017 DHW levels increased the prediction accuracy due to the DHW variables from 63.0% to 72.1%, again with a highly significant historical effect ($Z=-8.069$, $P<<0.0001$, Table 1). Indeed, the shape of the fitted bleaching response curve in 2020 (Figure 1A) shifted strongly not only in response to heat exposure in 2017, but also to heat exposure in 2016: Reefs that experienced low levels of heat exposure in either 2016 or 2017 exhibited markedly higher sensitivity to bleaching in 2020 (Figure S1). These results strongly suggest that predictions of bleaching responses could be significantly improved by accounting for the shifting impacts of a succession of temperature extremes. Interaction occurred between events that were stronger and close together (2016, 2017, and 2020), but not after relatively weak bleaching (1998) or a longer interval (2002-2016) (Table 1). Consequently, we can realistically expect the combined effects of consecutive events to strengthen as temperatures continue to rise and the return-time of bleaching shortens.[1]

Next, we consider the spatial dynamics of refuges from recurrent heat extremes, as an emergent outcome of the overlapping footprints of repeated episodes of mass bleaching (Figure 2). The sequential depletion of spatial refuges is strongly scale-dependent: While the Great Barrier Reef has recorded five bouts of mass bleaching, the northern region so far has been affected severely (defined as >50% of reefs with >30% bleaching) only once in 2016, the south also once in 2020, and the central region three times in 2016, 2017 and 2020 (Figure 2A, Figure S2). Consequently, the bleaching severity varies asynchronously among regions (Log-linear test, $P<0.001$, Table S1, Figure S2). Similarly, at the scale of individual reefs, 20% to 55% of reefs experienced severe bleaching in each of the five mass bleaching events, while 14% to 48% of reefs have escaped bleaching each time (Pearson's Chi-squared = 567.76, df = 16, $p < 0.001$).

Of the 145 reefs that have been scored in all five mass bleaching events, 80.7% have bleached severely at least once, 21% twice, 19% three times, 4% four times, and only 1% five times (Figure 2C). Similarly, fewer than 2% of the 573 individual reefs that were assessed repeatedly in 2016, 2017 and 2020 have escaped bleaching entirely during the three latest events (Figure 3). So far, almost all reefs that have escaped with minimal or no bleaching are located in a single aggregation, approximately 200-250 km offshore, close to latitude 22°S on the southern Great Barrier Reef (Fig. 2E). This area has remained consistently cool during summer months (<4 °C-weeks) during all five mass bleaching events (Fig. 2F), possibly due to tidal movements and upwelling at the edge of the continental shelf (Figure S3). However, other offshore upwelling areas[27] with episodic intrusion of cool water in the northern and southern Great Barrier Reef (Figure S3) have experienced unusually warm summer periods and severe bleaching repeatedly since 1998 (Figure 2), suggesting that favorable hydrodynamic conditions are intermittent, and may not always coincide with extended periods of hot summer temperatures.[28]

Our results provide important insights into the contemporary responses of coral reefs to anthropogenic heating over multiple decades. Firstly, the milestone of two mass bleaching events per decade, highlighted in the Intergovernmental Panel on Climate Change's assessment of the future trajectory of reefs[11] is already emerging at larger spatial scales; Of the five mass bleaching episodes we examined on the Great Barrier Reef, three have followed within 1-4 years of the previous one, and we have already seen the first example of back-to-back severe bleaching in two consecutive summers in 2016 and 2017 (Figure 2). Our findings also highlight the critical importance of spatial scale (e.g. the entire Great Barrier Reef, regions within the Reef, and individual reefs within regions) when considering return-times and spatial refuges. While the Great Barrier Reef system has experienced five mass bleaching events since 1998, the northern, central and southern regions have each been severely bleached only 1-3 times, and 19.3% of the individual reefs we assessed five times have not yet experienced severe bleaching (Figure 3). Consequently, due to this scale-dependency, we can expect smaller-scale locations to escape from severe bleaching for substantially longer and to have lengthier gaps for re-building depleted populations in coming decades.

Secondly, our results point to the limitations of using satellite-derived Degree Heating Weeks as a proxy for bleaching severity across repeated events, and for identifying future spatial refuges. While DHW exposure during individual mass bleaching episodes (or pairs of them) since 1998 successfully predicted the probability of severe bleaching in ~82-90% of cases (Table 1), the shape of the bleaching response curves triggered by a particular level of heat stress varied substantially from one event to the next (Figure1). Our results strongly suggest that projections of future impacts of temperature extremes that are founded on historical or contemporary bleaching responses and on fixed heat stress thresholds will not accurately predict the fate of world's coral reefs over the rest of this century. At a global scale, the onset of bleaching in 2007 to 2017 has already been triggered by significantly higher temperatures than in the preceding decade (1998 to 2006),[2] and there is growing evidence that bleaching thresholds also vary geographically among locations with different bleaching histories.[23,29,30] Our finding that non-linear bleaching thresholds increase or decrease from one event to the next depending on recent history (Figure 1), has important implications for modelling future bleaching events,[31] and for the design of spatially-based interventions to protect coral reefs in the face of an increasingly unpredictable and hotter future.

Thirdly, we show that the extent of spatial refuges from coral bleaching – locations that could potentially re-seed nearby damaged reefs in future decades - has steadily declined on the Great Barrier Reef (Figure 2E). Following the latest mass bleaching event in 2020, only 1.7% of individual reefs (spanning fourteen degrees of latitude) have escaped with no bleaching since 1998, and 19.3% have so far avoided severe bleaching (Figure 3). Even the most stringent marine protected areas have bleached severely, and there is little evidence that deeper, mesophotic reefs are a source of resilience for species that primarily occur in shallower habitats.[7,24,32] Following the fifth event in 2020, regions and reefs that were earmarked earlier as candidate refuges[15,16] have now also experienced severe or moderate bleaching at least once. Nonetheless, while coral populations are depleted,[26,33] adult brood stock still persist throughout the Great Barrier Reef, even after five bleaching events. Recurrent climate extremes have generated an increasingly complex mosaic of reefs and sites within reefs with different histories of bleaching (Figure 2C, D). Bleached and unbleached reefs are spatially clustered in every event, reflecting local patterns of heat exposure, leading to sub-regional and inshore-offshore gradients in bleaching severity (Figure 2, Figure S4). Given the low to modest dispersal capacity of coral larvae compared to many marine invertebrates and fishes,[34,35] the remaining unbleached southern reefs (Figure 2F), which lie downstream from the rest of the Great Barrier Reef (Fig. S3), are unlikely to make a demographically significant contribution to replenishment of coral populations spread for >2,000km to the north.[19] As temperatures continue to rise in coming decades, we predict that the patchy local production and dispersal of coral larvae, recovering locally after the most recent bleaching event before crashing at the next, is more likely to re-build coral populations than the long-distance influence of a dwindling proportion of unbleached or lightly bleached reefs. Ultimately, however, the multi-decadal accumulation of bleaching impacts (Figure 2, Figure 3) highlights the grave risk that without immediate global action on greenhouse gas emissions, more frequent and more severe bleaching events will continue to undermine the resilience of coral reef ecosystems.

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Author Contributions

This study was conceptualized and led by T.H., who also wrote the first draft of the paper. All authors contributed to writing subsequent drafts. T.H and J.K conducted the aerial bleaching surveys in 2016, 2017 and 2020. S.FH and CME provided satellite data on heat exposure. J.A-R. contributed to spatial analysis and mapping, and S.C., M.G. and J.M. provided statistical and modelling expertise.

Declaration of Interests

The authors declare no competing interests.

Main Text Figures and Table legends

Figure 1. Temporal and regional variation in mass bleaching responses of corals on the Great Barrier Reef, 1998-2020. The x-axis is heat exposure, Degree Heating Weeks (ºC-weeks), experienced by individual reefs during each of five mass bleaching events. The y-axis is the resulting probability of severe bleaching (affecting >30% of corals) calculated from aerial bleaching scores. (A) Bleaching response curves for the entire Great Barrier Reef, with 95% confidence limits, in each of five consecutive mass bleaching events, in 1998, 2002, 2016, 2017 and 2020, for a model including an interaction between DHW and year. The number of reefs surveyed each year was 587 (in 1998), 630 (2002), 1,135 (2016), 742 (2017) and 1,036 (2020). (B-F) Bleaching response curves during each event for the northern, central and regions of the Great Barrier Reef, from a model including interactions between DHW, year, and region. (B) 1998, (C) 2002, (D) 2016, (E) 2017, (F) 2020. Fitted curves are plotted only over the range of DHW values observed for each year or region. See also Figure S1.

Figure 2. Cumulative coral bleaching and heat exposure on the Great Barrier Reef, 2016-2020. (A) Geographic extent and severity of coral bleaching during major events in 1998, 2002, 2016, 2017 and 2020, measured by extensive aerial scores: 0 (<1% of corals bleached), 1 (1-10%), 2 (10-30%), 3 (30-60%), 4 (>60%). The number of reefs surveyed in each year was 587 (in 1998), 630 (2002), 1,135 (2016), 742 (2017) and 1,036 (2020). (B) Spatial pattern of heat stress (Degree Heating Weeks, ºC-weeks) measured from satellites during each mass bleaching event. Dark blue represents 0 ºC-weeks and red is 15 ºC-weeks (the maximum recorded, in 2017 and 2020). (C) Map of the frequency of bleaching (0-5 times) on 145 reefs that were surveyed repeatedly during mass bleaching events in 1998, 2002, 2016, 2017 and 2020. (D) Map showing the most recent occurrence of severe bleaching. (E) Heatmap of maximum bleaching scores during mass bleaching events in 2016, 2017 and 2020, measured

by repeated aerial surveys of 573 reefs, using the same bleaching scores as (A). (F) Maximum Degree Heating Weeks (ºC-weeks) measured from satellites during each of the latest three bleaching events, showing the contraction of spatial refuges from heat stress to a relatively small southern, offshore region. See also Figure S2-S4 and Table S1.

Figure 3. Accumulating extent of recurring mass bleaching events, 1998-2020. Blue trajectory: Decline in the percentage of reefs that remained unbleached (category 0) through time since 1998. Red: Accumulation of severely bleached reefs (>30% of colonies bleached) through time. Black: Accumulation of reefs experiencing all non-zero categories of bleaching.

Table 1. Bleaching responses depend on interactions among successive events. The percentage of reefs correctly predicted as severely bleached, based on a model fit between Degree Heating Week (DHW) exposure and bleaching scores, in each year alone (left column), or in a model that combined heat exposures in the current and previous event (e.g. bleaching in 2020 as a function of DHW values in both 2020 and 2017, right column). In each case, the first number represents the prediction accuracy using only the heat stress covariates from the model, whereas the second number in parenthesis represents the prediction accuracy of the full model (including the components of the model that account for spatial autocorrelation -- see Supplementary Materials). "NA" marks the absence of an historical effect prior to 1998 (the first recorded mass bleaching event). "ns" indicates that the effect of historical heat exposure on the next event was not statistically significant. See also Figure S1.

RESOURCE AVAILABILITY

Lead Contact

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, terry.hughes@jcu.edu.au

Materials availability

This study did not generate new reagents.

Data and code availability

- Coral bleaching and Degree Heat Weeks data have been deposited at Mendeley Data, and are publically available as of the date of publication. The DOI is listed in the key resources table.
- All original code has been deposited at Mendeley Data, and is publically available as of the date of publication. The DOI is listed in the key resources table.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

METHOD DETAILS

Coral Bleaching

Aerial assessments to measure the location and intensity of coral bleaching were conducted throughout the Great Barrier Reef from an elevation of approximately 150 m during five mass bleaching events in 1998, 2002, 2016, 2017 and 2020. Each reef was assigned by visual assessment to one of five categories of bleaching severity: (0) <1% of corals bleached, (1) 1-10%, (2) 10-30%, (3) 30-60%, and (4) > 60% of corals bleached.[9] Severely bleached reefs in category 3-4 have high levels of mortality, whereas lower levels of bleaching are generally sub-lethal.[25] The sample sizes in each event were 587, 630, 1,135, 742 and 1,036 reefs, respectively. The surveyed reefs extended from the coast to the edge of the continental shelf up to 250km offshore, between latitudes 9 to 24°S. To examine regional scale patterns, we distinguished between the northern (9-15°S), central (15-19°S), and southern (19-24°S) regions. The archived dataset (doi:10.17632/tncdys47mh.1) provides the reef IDs, longitude, latitude and bleaching score in each year. In 2016, we demonstrated the accuracy of the aerial scores by simultaneous underwater ground-truthing on 104 reefs that exhibited the full spectrum of bleaching.[19]

One hundred and forty-five reefs were censused in all five bleaching events, and 573 reefs were scored three times in 2016, 2017 and 2020. We use these two subsets of repeatedly censused reefs to investigate the depletion through time of unbleached or lightly bleached reefs (categories 0, 1 and 2) and the accumulation of severely bleached reefs (categories 3 and 4). (Figure 3). The aerial bleaching scores for each year are shown in Figure 2A as heat-maps created using inverse distance weighting interpolation (Power: 2, Cell Size: 1000, Search Radius: variable, 100 points) in ArcGIS 10.6.

Degree Heating Week exposure

Heat exposure throughout the Great Barrier Reef during each mass bleaching event (Figure 2B), and the maximum across all five events (Figure 2D), was quantified using the Degree Heating Week metric (DHW, °C-weeks) derived from Optimal Interpolation Sea Surface Temperature (OISST) records for 1998 and 2002, and from the blended Geostationary Orbiting Environmental Satellite and Polar-orbiting Operational Environmental Satellites (OES-POES Blended 5km sea surface temperatures) for 2016, 2017 and 2020, as reported by NOAA's Coral Reef Watch.[10] For 1998 and 2002, the coarser 25km resolution data from OISST was interpolated to 5km pixels to map the spatial distribution of DHW each year (Figure 2). For 1998, 2002 and 2020, we used the maximum DHW for each year because bleaching was recorded after the peak. In 2016 and 2017, when bleaching was recorded prior to the maximum DHW for those years, we used the accumulated DHW on the date when bleaching was observed. In each event, we recorded the DHW value for the 5km pixel that overlapped with the centroid of each reef where the severity of bleaching was recorded. We calibrated the relationship between the probability of severe bleaching (>30% of colonies bleached) and heat exposure in each mass bleaching event, to assess if the responses of coral assemblages differed among each bout of heat stress.

QUANTIFICATION AND STATISTICAL ANALYSIS

Bleaching responses to heat exposure

We used General Linear Models (GLMs) with binomial error structure to account for interannual, regional, and historical effects on the relationship between the probability of severe bleaching (aerial score categories 3 and 4) and degree-heating weeks (DHW: ^{o}C-weeks). Using the statistical package R[36], we fit one model with year as a second (categorical) explanatory variable, alongside DHW (Figure 1A), and another model with both year and region as additional explanatory variables, dividing the Great Barrier Reef into three regions (northern, central, southern; Figure 1B-E). To account for spatial autocorrelation, we employed spatial eigenvector filtering (ESF).[37,38,39] This approach involves constructing a spatial weighting matrix in which matrix elements are (generally decreasing) functions of the distance between pairs of sites (e.g., the value in row *i,* column *j* is a decreasing function of the distance between sites *i* and *j*).

Constructing a GLM using ESF requires several steps. The first is to decide on a distance weighting function and associated parameter values; the second is to adopt a protocol for the selection of eigenvectors to use in the model. In our analyses, we assembled candidate models using the function "listw.candidates" in package adespatial[37] and we undertook eigenvector selection using the "ME" function in package spatialreg[38]. Specifically, we assembled a spatial weighting matrix using the concave-up function in "listw.candidates":

$$w_{ij} = \begin{cases} \frac{1}{d_{ij}^{y}} & d_{ij} \leq d_{\ hresh} \\ 0 & d_{ij} > d_{\ hresh} \end{cases}$$

where d_{ij} is the distance between sites *i* and *j*, and *y* and d_{thresh} are parameters that varied among candidate models depending on the apparent spatial scale of spatial autocorrelation for each year, based on visual inspection of variograms (Table S2).

Function ME takes each of these candidate models (i.e., spatial weights matrices with a unique combination of *y* and d_{thresh}), and uses a forward selection algorithm to add eigenvectors of the spatial weighting matrix to the explanatory variables in the original GLM until Moran's *I* decreases beyond the threshold of statistical significance. Following convention, we used a threshold of a=0.05. The selected model was the one that achieved this level of non-significance of spatial autocorrelation with the fewest number of eigenvectors. In the case of ties, we selected the model with the lowest-magnitude value of Moran's *I*. We considered only eigenvectors with corresponding eigenvalues that were positive in this model selection procedure, given that the spatial autocorrelation was positive.

Because the spatial patterning of DHW, and the spatial structure of residual autocorrelation, was different in each bleaching event, we conducted eigenvector selection separately for each year. Consequently, we fit GLMs separately by year (using DHW as the predictor for the analysis of interannual variation in bleaching responses (Figure 1A). We also incorporated an interaction between DHW and region for the analyses of regional variability (Figure 1B-F). To test for significant differences between years in these two analyses, we then combined all years into a single GLM analysis including a DHW x year interaction, and a DHW x year x region interaction, respectively, alongside main effects of DHW and year. Each eigenvector only affected the observations for the year for which it was selected. For example, in the case of an eigenvector selected in the analysis of 1998 bleaching, values of zero were entered for this predictor for observations from all other years, to ensure that this eigenvector had no effect on the fitted bleaching curve for any years other than 1998.

Ecological memory

We investigated how heat exposure in the preceding bleaching event affected subsequent bleaching responses in 2002, 2016, 2017 and 2020 (Table 1). We fit GLM models with binomial error structure, to examine the difference in how well current-year DHW alone versus current year and historical DHW explain the percentage of reefs that were severely bleached. For instance, for 2002, we modeled bleaching probability with both a main effect of DHW in 2002, and an interaction term between DHW values from 1998 and 2002. We calculated the prediction accuracy using only the fitted DHW effects from the full model, as well as the overall accuracy (Table 1). The former allowed us to calculate a prediction accuracy that is analogous to a partial R-squared, and thereby to compare the variation explained only by the DHW components of the different models (Table 1). For the 2020 bleaching event, we explored both the interaction between 2017 and 2020 heat stress, 2016 and 2020 heat stress and the maximum heat stress from 2016 and 2017 and 2020 heat stress (Figure S1). In these models, we omitted the fixed effect of the preceding event DHW, to capture our hypothesis that past heat stress would alter the sensitivity of bleaching to concurrent heat stress (technically, this approach ensures that all thresholds have the same intercept at 0^{o} C-weeks of the bleaching year, but that the rate at which bleaching probability increases with increasing concurrent heat stress may differ depending on the historical heat stress). To further examine how these regional differences affected bleaching responses through time, we modelled regional and temporal bleaching history outcomes by fitting a log-linear model, with variables: region, year, and bleaching outcome (Table S1).

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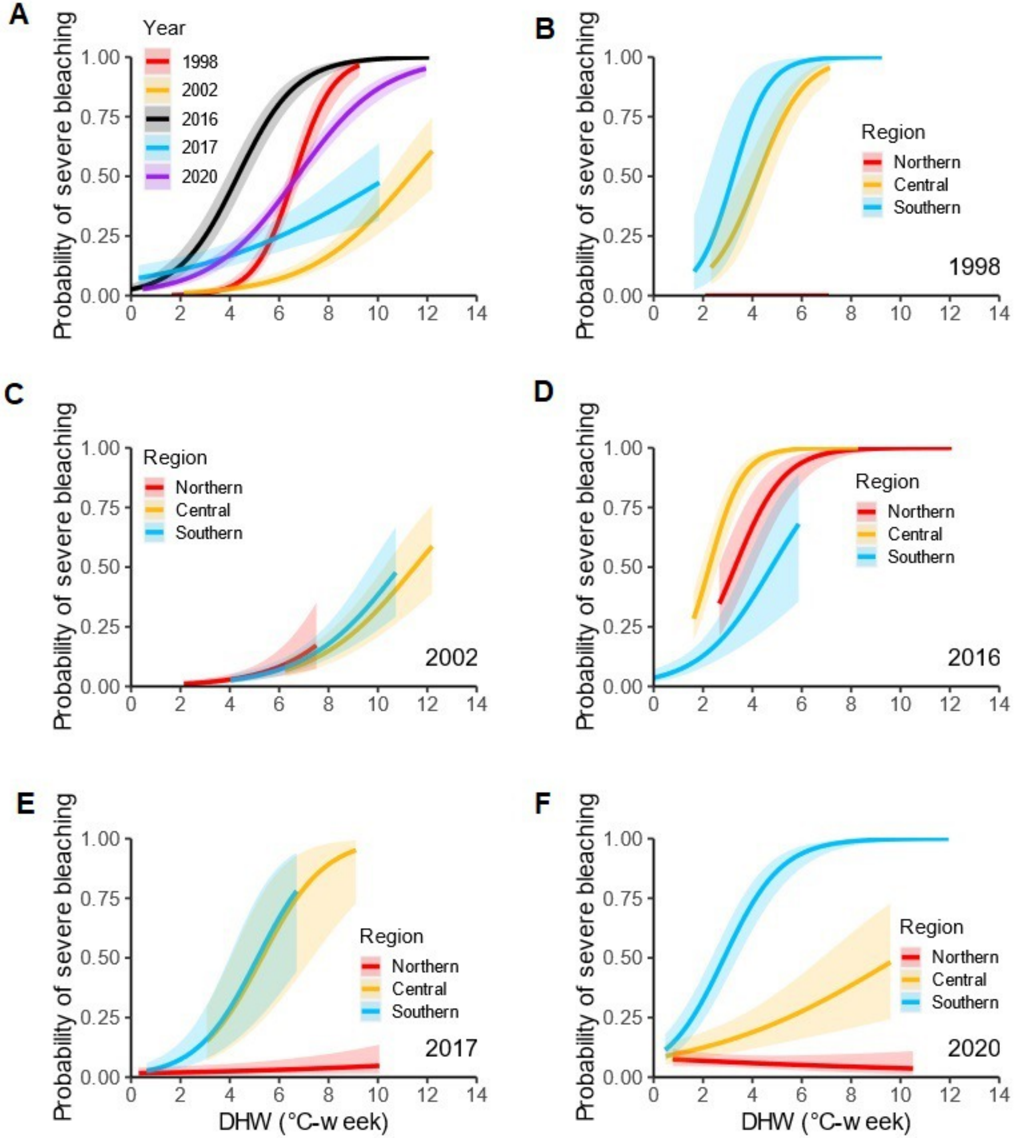
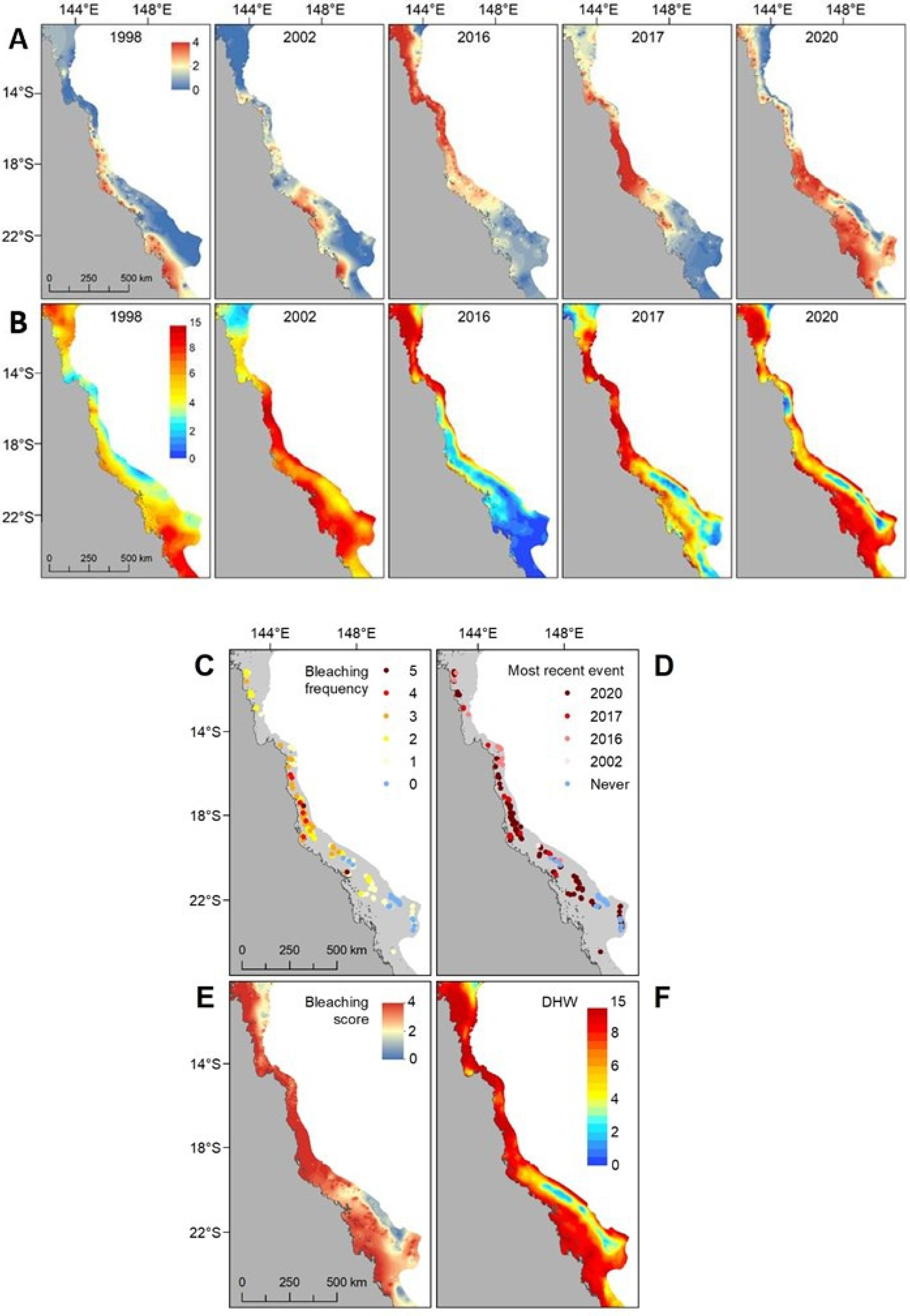
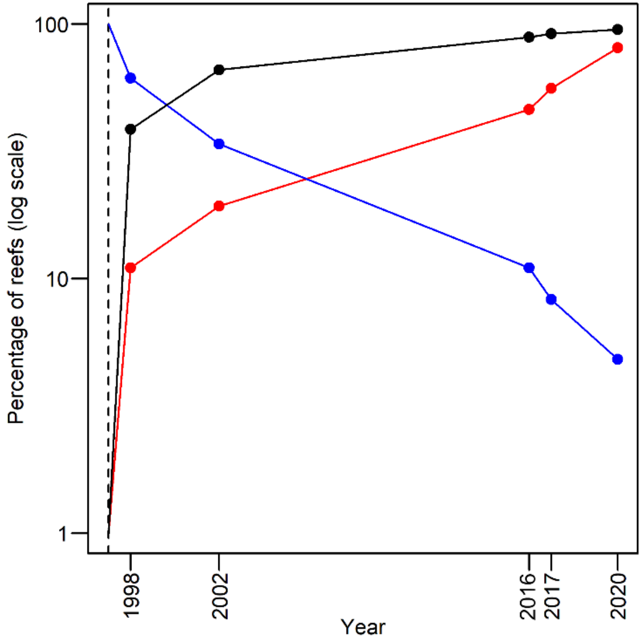


A
Year
1998
2002
2016
2017
2020
Probability of severe bleaching
1.00
0.75
0.50
0.25
0.00
0
2
4
6
8
10
12
14
B
Region
Northern
Central
Southern
1998
C
2002
D
2016
E
2017
F
2020
DHW (°C-w eek)


A
B
C
D
E
F
144°E
148°E
14°S
18°S
22°S
1998
2002
2016
2017
2020
0
250
500 km
Bleaching frequency
5
4
3
2
1
0
Most recent event
2020
2017
2016
2002
Never
Bleaching score
DHW
15
8
6
4
2



100
10
1
Percentage of reefs (log scale)
1998
2002
2016
2017
2020
Year

Year	% of reefs correctly predicted in each event alone	% of reefs correctly predicted in consecutive events
1998	77.82% (85.49%)	NA
2002	78.89% (89.05%)	ns
2016	80.42% (90.04%)	ns
2017	66.71% (84.37%	71.16% (88.41%)
2020	63.03% (81.76%)	72.10% (82.63%)