Cumulative bleaching undermines systemic resilience of the Great Barrier Reef

Mandy W.M. Cheung[1,2,6*], Karlo Hock[1,2], William Skirving[3,4], Peter J. Mumby[1,2,5,7*]

[1] Marine Spatial Ecology Lab, School of Biological Sciences, The University of Queensland, St Lucia, QLD 4072, Australia
[2] Australian Research Council Centre of Excellence for Coral Reef Studies, The University of Queensland, St Lucia, QLD 4072, Australia
[3] Coral Reef Watch, U.S. National Oceanic and Atmospheric Administration, College Park, MD 20740, USA
[4] ReefSense Pty Ltd, Cranbrook, QLD 4814, Australia
[5] Lead Contact
[6] Twitter: @mandywmcheung
[7] Twitter: @petemumby
* Correspondence: mandy.cheung@uq.net.au (M.W.M.C.); p.j.mumby@uq.edu.au (P.J.M.)

Highlights

- The Great Barrier Reef is being damaged by expanding coral bleaching events
- The recent cumulative bleachings may have reduced coral larval supply by 71%
- Bleaching events are unique but predictable warm spots and cooler refugia exist
- Refugia have the potential to deliver coral larvae to 58% of the GBR

In Brief

Cheung *et al.* quantify the cumulative ecological disruption of coral bleaching to the Great Barrier Reef. They also reveal predictable thermal stress patterns that allow managers to target interventions specifically to facilitate ecosystem resilience and coral adaptation to a warming climate.

Summary: Climate change and ENSO have triggered five mass coral bleaching events on Australia's Great Barrier Reef (GBR), three of which occurred in the last five years[1-5]. Here, we explore the cumulative nature of recent impacts and how they fragment the Reef's connectivity. The coverage and intensity of thermal stress has increased steadily over time. Cumulative bleaching in 2016, 2017, and 2020 is predicted to have reduced systemic larval supply by 26%, 50%, and 71% respectively. Larval disruption is patchy and can guide interventions. The majority of severely bleached reefs (75%) are predicted to have experienced an 80-100% loss of larval supply. Yet, restoration would not be cost-effective in the 2% of such reefs (~30) that still experience high larval supply. Managing such climate change impacts will benefit from emerging theory on the facilitation of genetic adaptation[6,7], which requires the existence of regions with predictably high or low thermal stress. We find that a third of reefs constitute warm spots that have consistently experienced bleaching stress. Moreover, 13% of the GBR are potential refugia that avoid significant warming more than expected by chance, with a modest proportion (14%) within highly protected areas. Coral connectivity is likely to become increasingly disrupted given the predicted escalation of climate-driven disturbances[8], but the existence of thermal refugia, potentially capable of delivering larvae to 58% of the GBR, may provide pockets of systemic resilience in the near-term. Theories of conservation planning for climate change will need to consider a shifting portfolio of thermal environments over time.

Keywords: spatial patterns, coral reefs, coral bleaching, sea surface temperature, thermal stress

Results and Discussion

Australia's Great Barrier Reef (GBR) has experienced an unprecedented sequence of three mass coral bleaching events in the last five years, intensifying concerns over the impacts of climate change on the ecosystem[3]. Coral bleaching is one of the most striking manifestations of marine heatwaves and can cause mass coral mortality over thousands of hectares within a few months[9-12]. While no two bleaching events are ever identical, the cumulative nature of their impacts is unclear. For example, if successive events are highly correlated then some reefs will become untenable under repeated stress whereas others will persist with relatively little damage, at least in the near-term. Resolving these questions will provide a clearer insight into how hastening climate change impacts will unfold[8].

The first global bleaching event occurred during the 1998 El Niño-Southern Oscillation (ENSO), though the effects on the GBR were relatively modest[13]. A second event impacted the GBR only four years later (2002) after which there was a 14 year hiatus before a rapid succession of events in 2016, 2017 and 2020. Using satellite measurements of cumulative thermal stress anomalies during each event (Degree Heating Weeks, DHWs)[14], we see that both the areal coverage and intensity of stress has increased from one event to the next (Figure 1A). Notably, the area affected by severe warming (DHW≥8), that can elicit mass coral mortality exceeding 66%[15], has increased rapidly to cover 40% of the entire GBR in 2020 (Figure 1A). Moreover, individual patches of severe stress, delineated as contiguous pixels exceeding DHW8, have evolved from a dominance of a few small patches in 1998 and 2002, averaging 630 km^2, to an order of magnitude increase in average patch size of 5200 km^2 by 2017 and 2020 (Figure 1B). Where thermal stress does not exceed DHW4, coral mortality varies from virtually nonexistent (DHW≤3), to modest (<<40%), particularly on the reef slope[15,16]. By 2020, the majority of the Reef experienced at least mild bleaching, albeit with a small number of large patches (Figure 1A and 1C).

We first asked how the cumulative impacts of three recent bleaching events has disrupted the system-wide supply of larvae, which is important for reef recovery[17]. Bleaching can disrupt larval supply by reducing fecundity[18] and killing adult corals outright[19]. Successive bleaching events have significantly and cumulatively disrupted connectivity of the GBR. Larval supply was estimated to decline by 26% after the 2016 event. The decline continued to 50% after the 2017 bleaching, and cumulatively reached 71% after the most recent event in 2020, assuming that no recovery had taken place in 2018 and 2019. Yet these statistics mask strong differences between areas that bleached severely versus those that did not. By 2020, 75% of severely bleached reefs were estimated to have suffered a major (80-100%) loss of larval supply and less than 1% experienced a minor (0-20%) loss (Figure 2A). In contrast, 6% of those reefs experiencing mild bleaching (DHW<4) were predicted to experience a severe loss of larvae and most mildly bleached reefs (70%) experienced between 20-60% losses of connectivity (Figure 2B). We note that this analysis only focuses on spawning corals and while it takes advantage of all available data on the impacts of recent bleaching events[15,20], it necessarily makes some simplifying assumptions (see STAR Methods). To explore the sensitivity of our results to assumptions, we altered the relationships between heatwaves (DHW) and both fecundity and the probability of bleaching over successive events (Figure S1 and S2). The percentages of reefs experiencing each category of connectivity loss (0-20%, 21-40%, etc) were treated as response variables. We found that the sensitivity of results to model choice (i.e., assumptions) was only one sixth of that attributable to the main treatment of thermal stress (Figure S3, and STAR Methods), implying that our conclusions are robust.

While we consider our results indicative rather than precise estimates of larval supply loss, the existence of a diversity of local impacts are crucially important for targeting reef management. For example, while restoration might be considered for some recently-bleached reefs, it would be ineffective and inadvisable to attempt this in the 30 severely bleached reefs that are still predicted to have fairly high larval supply (i.e. 60-100%)[21].

Climate change impacts like coral bleaching present a formidable management challenge. A central concern is the ability of corals to adapt to a warming environment[22]. Fortunately, an emerging body of theory considers the design of marine protection in order to facilitate the process of adaptation[6,7,23]. Such theory assumes the existence of predictable heterogeneity in the environment including regions that are routinely exposed to severe thermal stress versus those that remain relatively cool and provide refugia (at least for now). Strategies might focus protection on refugia, warm areas, or perhaps a portfolio of stress exposures[24]. While every bleaching event is unique, our second objective asked whether spatial variability in stress was predictable over time, as required by current theory.

We compared the spatial patterns of thermal stress among bleaching events to a random model. In essence, the random model collected the observed stress values in all reef cells (DHW≥3, DHW≥4, etc) and redistributed them randomly across the seascape, repeating the process for each bleaching event (See STAR method and Figure 3). Taking severe stress as an example, this approach yields the probabilities that reefs will not experience DHW≥8 in any of the five bleaching events (41%), in only one out of five events (43%), two out of five events (15%), and so on to include all five events (0%) (Figure 4A). The comparison of observed frequencies to those expected by chance allowed us to determine whether some reefs could be considered ‘warm spots’ in that they warmed more often than expected by chance; ‘potential refugia’, which experienced fewer warming events than expected; or simply conformed to the random distribution of stress. We found evidence of warm spots, random patterns, and refugia (Figure 4).

There was little evidence of warm spots across the full 23 year period from 1998-2020 (Figure 4A). However, the drivers of bleaching are likely changing from ENSO events (e.g., 1998, 2016)[25] to include global warming (2017, 2020)[5]. With that in mind we repeated the spatial analysis of bleaching for the three events since 2016. This recent set of bleaching events exhibit strong non-random behaviour (Figure 4B). A third of reefs (33%) can be considered potential warm spots in having experienced consistent exposure to at least moderate bleaching stress (DHW≥4) during all three recent events, which exceeds the random expectation (Figure 4B).

Warm spots likely experience relatively limited vertical mixing during bleaching events[13]. Their existence implies that some areas of the reef have predictably higher stress – and therefore higher selection pressure – than others. The evolutionary importance of such areas is complicated by the higher risk of coral mortality that may constrain adaptation owing to smaller population size[23]. We speculate that a favourable environment for genetic adaptation may occur where reefs routinely experience stress of sufficient intensity to cause only modest mortality; i.e., DHW 4-6. Less than 1% of reefs consistently experienced this range of stress across all recent events, although approximately 40% of reefs experienced these conditions in one of the three recent events, a pattern that is virtually identical to that expected by chance (Figure 4D). In other words, bleaching events do create 'evolutionarily desirable' ranges of stress but we are unlikely to find sites that consistently experience such characteristics over time. Thus, targeting management specifically for 'evolutionarily desirable' thermal regimes would be challenging.

While some areas experienced severe stress (DHW≥8) multiple times, such as in three of five bleaching events (Figure 4A), their frequency was similar to that expected by chance (2.2% vs 1.7%). In practice, a random pattern implies that the locations of severe stress were sufficiently variable over time that they were unpredictable. This does not necessarily imply that such patches of stress are found in random locations. Rather, there may be a limited set of locations that exhibit severe stress but they have occurred too infrequently to depart from a random expectation. As future bleaching events unfold some of these locations may experience severe stress sufficiently often to become warm spots. The warm spots identified here (Figure 4C) have exhibited sufficiently frequent repeat warming that they have already departed from a random expectation.

Importantly, both the five year and three year analyses of bleaching find potential refugia from thermal stress. Refugia can be inferred when stress is absent more often than expected by chance. For example, the observed probabilities of a reef never experiencing stress (0 events) at all four DHW thresholds were higher than that expected under a null model at 5%, 13%, 25% and 46% (Figure 4A and 4E). Taking the point where bleaching begins (DHW≥4)[26-28], the DHW<4 potential refugia equate to 16,800 km^2 (13%) of the GBR (Table S1). We use the term 'potential refugia' because we do not know which parts of that area exceed the null model; only that the expected and observed exposure probabilities differ and some individual sites would still have been expected by chance.

Although it is not possible to mitigate heatwaves, managers can take steps to safeguard critically important source populations from other impacts like coral-consuming crown-of-thorns starfish[29]. A previous analysis sought the most connected reefs of the GBR and included areas of relatively low heat stress, albeit prior to the 2017 and 2020 bleaching events[30]. Here we took a statistical approach to identifying potential refugia that considered all bleaching events and ignored connectivity. Yet once again we find evidence of moderate systemic resilience: the 568 potential bleaching refugia have the potential to connect 58% of the entire GBR (2,185 reefs). At present, 14% of the potential DHW<4 refugia are located in highly protected zones of the GBR Marine Park (Figure S4 and Table S1). Continued analysis of future bleaching events will help resolve which of these 'potential' refugia are the specific areas that warm less than expected by chance. Downscaled climate models will also help resolve the persistence of such refugia as the ocean continues to warm.

The emerging picture is that cumulative bleaching events will continue to disrupt functioning of the GBR and reduce the opportunity for recovery in susceptible areas. We predict that brooding corals, which only comprise 15% of scleractinian taxa[31], are likely to increase their dominance in the extensive areas identified as experiencing severe bleaching with a profound reduction in spawner larval supply. Like spawners, many brooders are highly sensitive to bleaching[16] but their recovery rate can exceed spawners because of rapid maturation and local release of planulae[32]. The ecological consequences of such community shifts are not yet clear, although similar trends in the Caribbean have reduced ecosystem functions[33].

Management efforts can be targeted according to thermal regime and connectivity, perhaps adopting a portfolio approach because investing purely in refugia may limit the evolutionary potential of the ecosystem[7]. Moreover, as we anticipate a shifting portfolio of thermal stress environments over time, theory will need to evolve and consider such dynamism.

ACKNOWLEDGEMENTS

We thank Selina Ward, Robert Mason, George Roff, Taison Chang and Gerard Ricardo for comments and discussion. W.S. is supported by NOAA grant NA19NES4320002 (Cooperative Institute for Satellite Earth System Studies) at the University of Maryland/ESSIC, and the U.S. Department of Defense's Strategic Environmental Research and Development Program. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the author(s) and do not necessarily reflect the views of NOAA or the Department of Commerce. P.J.M. was funded by an ARC Discovery Grant.

AUTHOR CONTRIBUTIONS

P.J.M., K.H., and M.W.M.C. designed the study, while W.S. provided critical review. M.W.M.C. conducted the analysis and both M.W.M.C. and P.J.M. wrote the manuscript. All authors edited the manuscript.

DECLARATION OF INTERESTS

P.J.M. declares that he is a member of the editorial advisory board for Current Biology.

INCLUSION AND DIVERSITY

One or more of the authors of this paper self-identifies as an underrepresented ethnic minority in science.

FIGURES

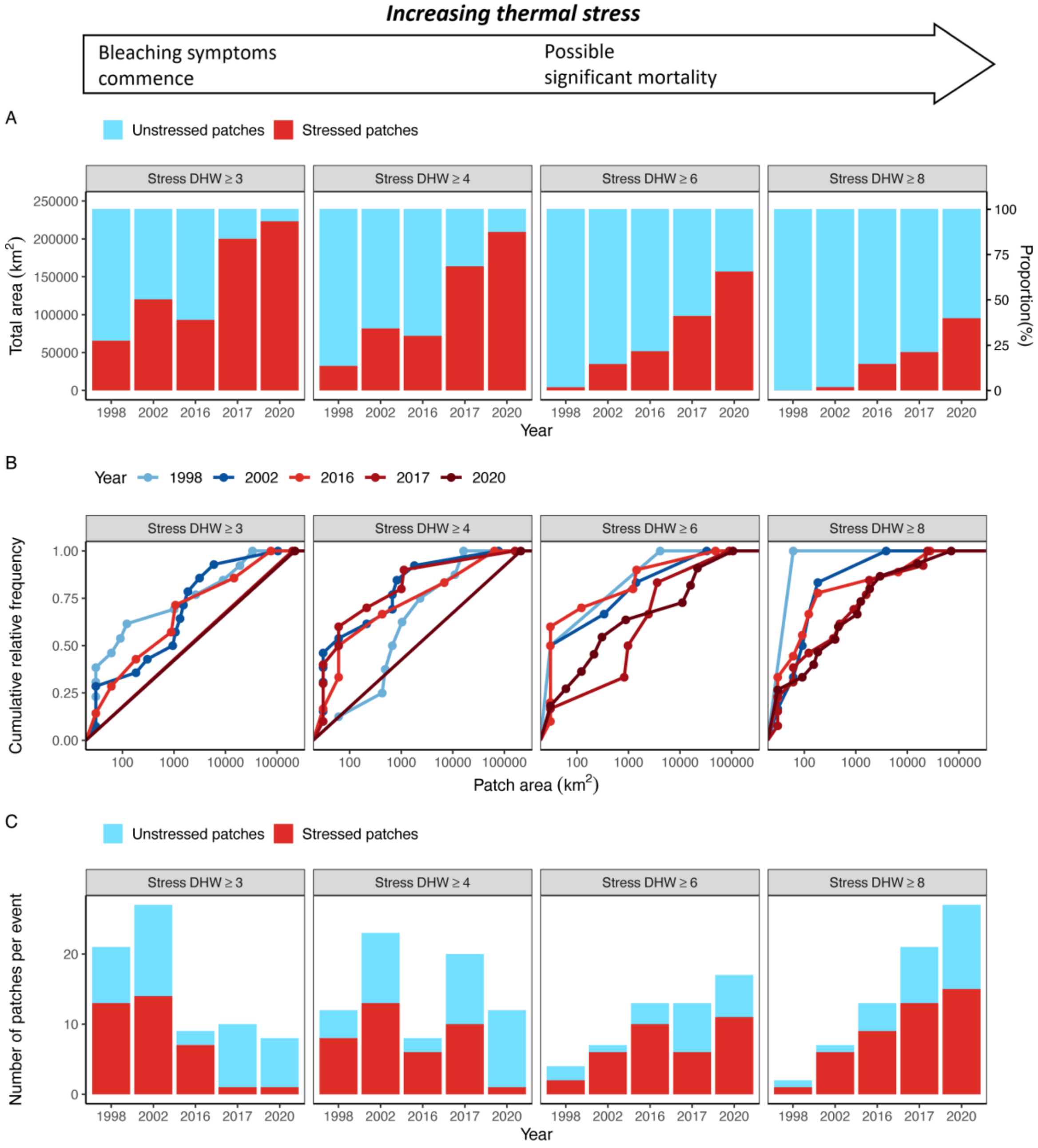

Figure 1. Spatial patterns of heat stress in major GBR bleaching events
(A) Overall area of stressed vs unstressed regions of the GBR. (B) Cumulative relative frequency of the sizes of individual stressed patches disaggregated by the magnitude of stress (note log-transformation of x-axis). (C) Number of stressed and unstressed patches disaggregated by magnitude of stress.

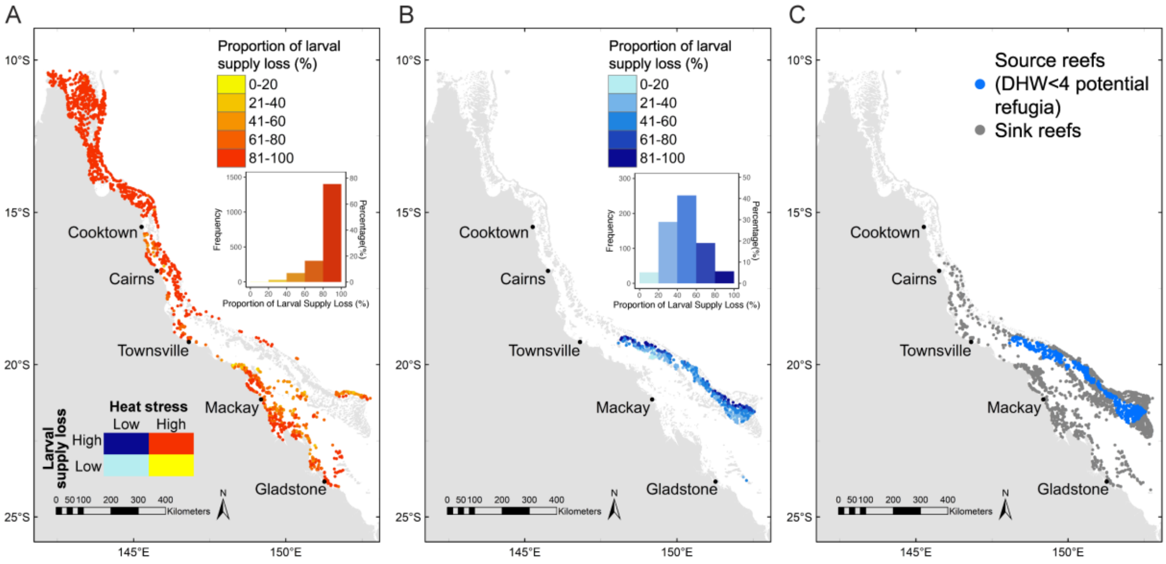

Figure 2. Impacts of bleaching on larval supply after the cumulative bleaching in 2016, 2017 and 2020 as well as the connectivity of bleaching refugia

(A) Loss of larvae to severely bleached reefs (DHW≥8). (B) Loss of larvae in reefs experiencing low thermal bleaching stress. High heat stress signifies at least DHW8 since 2016 whereas low has never experienced DHW8 in that time. (C) Linkages between the 568 source reefs in refugia and their sinks (2,185 reefs). Map legend defines high larval supply loss as >80% and low as <20%. See also Figure S3.

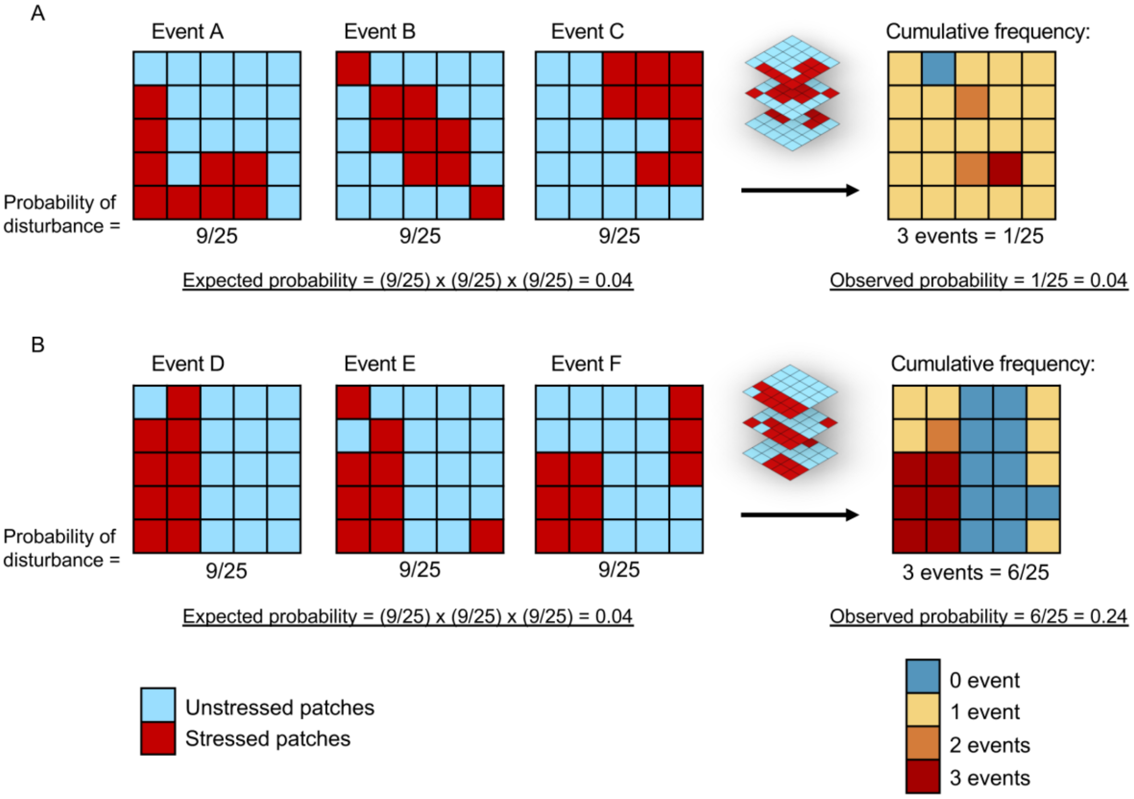

Figure 3. Conceptual diagram describing the expected and observed probabilities for an inconsistent scenario (random), and a consistent scenario (non-random)

(A) In an inconsistent scenario, the expected probability is the same as or very close to the observed probability. Hence, the disturbance spatial patterns conform a random model. No ‘warm spots’ of the disturbance events is identified because no pixels experience disturbance more than expected by chance. The mechanism driving the disturbance event may be different for each event, or the same mechanism will not produce consistent impacts at the same location.

(B) In a consistent scenario, the expected probability is different from the observed probability. Reef pixels that experience 3 times of disturbance events, more than it will be expected in the null model, are potential ‘warm spots’ of the disturbance event. Reef pixels that never experience disturbance events, on the other hand, are potential refugia of the disturbance event, escaping the disturbance more than expected by chance. The events are likely driven by a mechanism that acts on the same locations across multiple events.

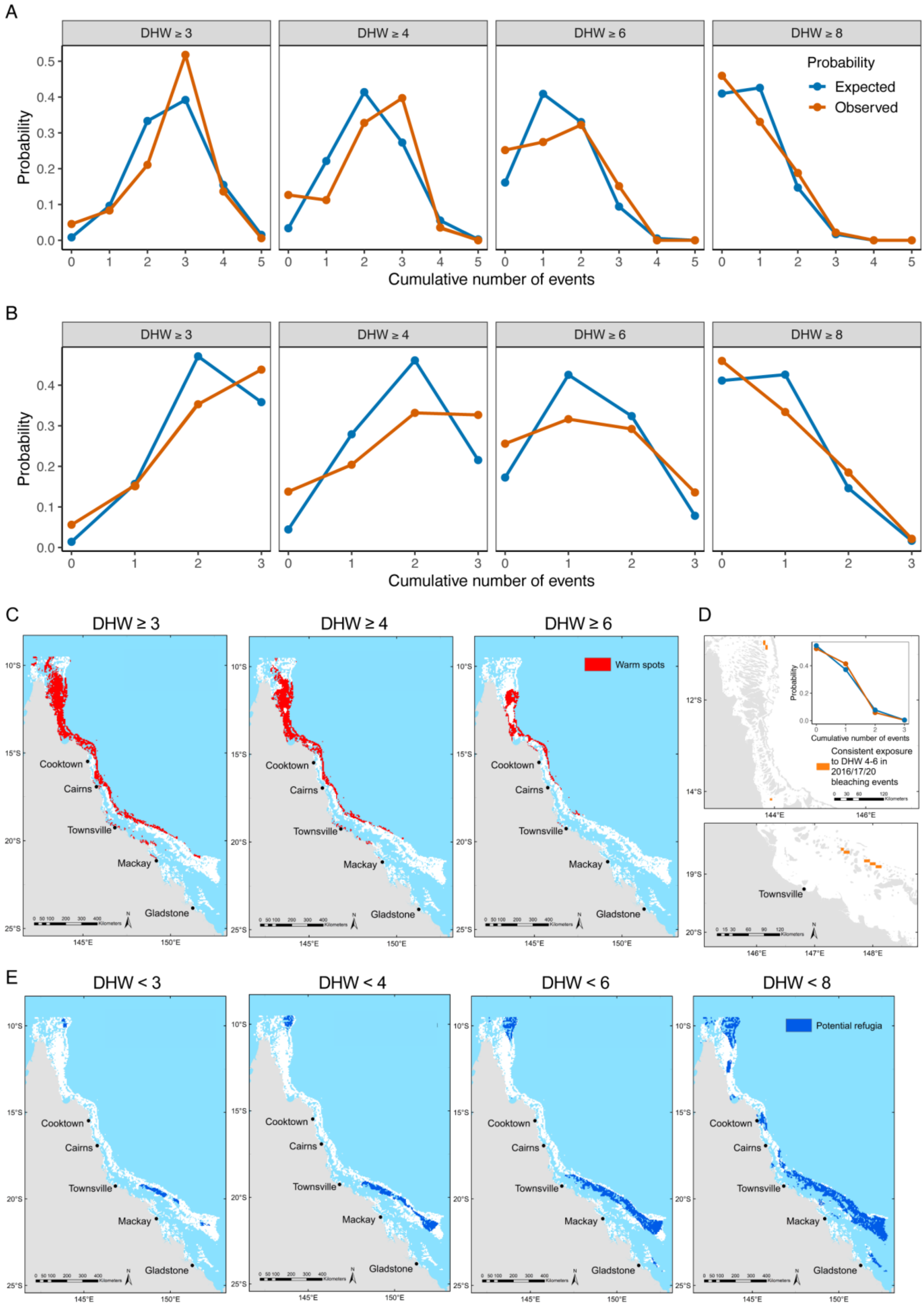

Figure 4. Predictable patterns of thermal stress

Comparisons of observed frequencies of repeated bleaching stress to that expected by chance. Comparison for all five events in 1998, 2002, 2016, 2017, and 2020 (A) and the last three bleaching events only (B). (C) Locations of warm spots where reef pixels were consistently exposed to modest level of heat stress in the three recent bleaching events. (D) Location of reefs exhibiting frequent mild bleaching stress of DHW 4-6 in all recent events with an inset showing observed vs random expectation. (E) Locations of potential refugia where reef pixels consistently escaped from heat stress during all five events. See also Figure S4.

STAR METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
NOAA Coral Reef Watch 5km satellite-derived annual maximum DHW metric	NOAA – Coral Reef Watch	https://coralreefwatch.noaa.gov/product/5km/index.php
GBR *Acropora* larval connectivity model	[34]	10.5281/zenodo.2653244
Percentage change in coral cover and DHW data from the 2016 coral bleaching event on the GBR	[15]	https://doi.org/10.4225/28/5a725ee7548a7
Aerial bleaching scores and DHW for surveyed reefs in 2016 and 2017	[20]	https://doi.org/10.25903/5beb6e4173f88
Code for connectivity and probability analysis	This study	http://dx.doi.org/10.17632/rmdstjb7j3.1
Software and Algorithms		
R version 3.6.3	R Development Core Team	https://www.cran.r-project.org/
MATLAB R2020b	MathWorks, Inc.	https://www.mathworks.com/
ArcMap	Esri	https://www.esri.com/en-us/home
Other		
GIS layer of reef and reef centroids of GBR	[35]	http://www.gbrmpa.gov.au/geoportal/
GIS layer of GBR Marine Park Zoning	[36]	http://www.gbrmpa.gov.au/geoportal/
Queensland continental shelf	[37]	https://eatlas.org.au/data/uuid/25685ba5-6583-494f-974d-cce2f3429b78

RESOURCE AVAILABILITY

Lead Contact

Further information and requests for code and data should be directed to and fulfilled by the Lead Contact, Peter Mumby (p.j.mumby@uq.edu.au).

Materials Availability

This study did not generate new unique materials.

Data and Code Availability

The satellite-derived heat stress data is available from NOAA Coral Reef Watch, https://coralreefwatch.noaa.gov/product/5km/index.php. All original codes are deposited at Mendeley Data (http://dx.doi.org/10.17632/rmdstjb7j3.1). All datasets analysed are publicly available and listed in the key resource table.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Historical thermal stress data

We conducted our study using publicly available satellite-derived thermal stress data of historical mass coral bleaching events on the entire spatial extent of the GBR. Although variabilities in coral bleaching and mortality responses exist within reefs, potentially due to light level[34,35], water flow[36,37], nutrient enrichment[38-40], water depth[16], and thermal history[20], heat stress is a widely used proxy to predict mass coral bleaching event[14,26,28]. The degree heating weeks (DHW) metric closely aligned to mortality on the GBR[3], but other metrics work well elsewhere[12].

Mass coral bleaching has been associated with prolonged heat stress which can be measured using the satellite-derived DHW metric. The DHW metric measures the cumulative anomalies of thermal stress above 1°C in a 12-week rolling window[14,26,28]. The annual maximum DHW data were obtained from the National Oceanic and Atmospheric Association Coral Reef Watch (NOAA CRW) at a spatial resolution of 0.05°[14,26,28]. The metric was used to characterise historical heat stress patterns for the five documented mass coral bleaching events in 1998, 2002, 2016, 2017, and 2020 on the GBR[1-5]. Specifically, the maximum DHW for 2020 was derived from the months of southern hemisphere summer of 2020. The annual maximum DHW per pixel were extracted using a 0.03°-buffered Queensland continental shelf layer[41], to include all reefs within the continental shelf. The study extent for the spatial analysis corresponded to 8,234 pixels of which 4,546 are reef pixels.

Two studies have acquired sufficient data to examine the relationship between DHW and coral mortality. The first was carried out in the Caribbean after the 2005 bleaching event [9]. That study found a positive linear relationship between DHW and the percentage of corals bleached and a positive, but non-linear relationship, with coral mortality. Here, significant coral mortality did not occur until DHW exceeded 10, then rose sharply.

The second study was carried out on the GBR in 2016[15]. Here again the relationships between DHW and both coral bleaching and mortality were positive, though both were non-linear. Working on shallow reef flats (~2 m), Hughes et al[15] found virtually no loss of coral cover at up to DHW3. This rose to 40% loss at DHW4, 66% at DHW8 and >80% at DHW9 or above. Much of the Great Barrier Reef occurs at depths greater than 2 m[42]. For the most abundant corals, in the genera *Acropora*, *Porites* and *Pocillopora*, the percentage of bleaching declined significantly with greater depth[16]. For example, comparing a depth of 2 m on the reef flat[15] to 7 m on the reef slope, the percentage of *Acropora* bleached halved from around 95% to 50%. These were the bleaching frequencies where DHW was greatest. Where DHW was lower (though unspecified), the depth effect became even stronger with bleaching rates falling from ~40% at 2 m to <10% at 7 m. Indeed, there was still an overall positive impact of DHW on the percentage corals bleached at depth[16]. The key point here is that higher DHW is associated with increased severity of bleaching and intensity of coral mortality. This applies within the range of DHW reported in our study such that bleaching and mortality are minimal at DHW3, modest to low at DHW4 (particularly at depths exceeding 2 m), and high at DHW≥8.

METHOD DETAILS

Heat stress patterns spatial analysis

The heat stress patterns from the five mass coral bleaching events were characterised based on indicators of coral bleaching and mortality risks using the annual maximum DHW metric at DHW thresholds of 3, 4, 6, and 8. Thermal stress levels of DHW≥3 and ≥4 were associated with significant bleaching risk[3,9,26,27]. Thermal stress levels of DHW≥6 and ≥8 were linked with not only extensive bleaching but also significant mortality risk[15,26,27]. Although the real effect of heat stress could be more nuanced, not all corals above the threshold would bleach or die, these DHW thresholds were widely used to predict bleaching and mortality risks[26,28]. For each threshold level, stressed pixels were defined based on the exposure to annual maximum DHW equal to or above the thresholds in that event. Pixels with annual maximum DHW values below the thresholds were defined as unstressed. Both stressed and unstressed patches were delineated based on the eight-cell rule of contiguity, where pixels sharing adjacent sides or corners, will be defined as a patch[43-45]. Patches were defined using the Region Group tool to connect eight nearest neighbours of same-valued pixels in ArcMap 10.7.1. This was done separately for each threshold in each event.

QUANTIFICATION AND STATISTICAL ANALYSIS

Spatial extents of thermal stress on the GBR

The three main metrics calculated for all five mass coral bleaching events were: a) the total area of stressed patches and unstressed patches, measured in km^2, b) the size of all individual patches, measured in km^2, and c) the number of patches, at each of the four DHW threshold levels. The raster layers were projected into the Australia Albers Equal Area projection to preserve the patch areas in ArcMap. The patch areas were calculated using the Calculate Geometry function. To identify the differences in heat stress extent, the total area of stressed patches was compared across events for each DHW threshold. The size distribution, mean patch sizes and number of unstressed and stressed patches were compared to understand the variation of spatial patterns across events. Analysis was conducted in R version 3.6.3. Our finding of increasing spatial extent of bleaching over time, based on SST data, is consistent with a recent analysis of extent from 1998-2017 based on aerial surveys[46].

Effects of thermal stress on larval supply

To investigate the impacts of successive bleaching events on coral replenishment given the lack of recovery time among events, we measured the potential cumulative loss of larval supply for 2016, 2017, and 2020 when three mass coral bleaching events were documented within five years. Our model analysis uses available data on the effects of thermal stress (DHW) on both coral mortality and fecundity. The model is presented as (i) impacts of DHW on fecundity, (ii) impacts of DHW on coral mortality, allowing for legacies of earlier bleaching, (iii) integration with larval connectivity matrices, (iv) key assumptions, (v) sensitivity analyses.

Fecundity

Few studies have studied the impacts of coral bleaching on the fecundity of corals, yet each show profoundly negative impacts. Working on the GBR during the 1998 bleaching event, Ward et al[47] found an average reduction of 67% in both egg number and the percentage of fecund polyps, which collectively reduced fecundity by 78%. This was for a relatively modest stress event of DHW6. In the Caribbean, one of the main reef builders – *Orbicella annularis* – experienced a reduction in the percentage of colonies spawning in bleaching years[48]. The reductions were considerable at 79% and 95% depending on event. In Hawaii, the impact of bleaching on the subsequent early mortality of coral larvae changed from 3% under non-bleaching conditions to 57% during the 2015 event[49]. We created a putative relationship between fecundity and DHW (Figure S1) by assuming (a) that fecundity was unimpaired at mild thermal stress, DHW≤3, where mortality is negligible[15], (b) that fecundity is reduced by 0.8 at DHW6[47], and (c) that fecundity reaches zero at DHW≥8 where bleaching is severe[50].

Coral mortality and the legacy of bleaching

Because the larval output of reefs will be determined by the number of surviving corals and their fecundity, we also estimated the relative effects of thermal stress on coral mortality. We first fitted an empirical relationship between the percentage change in coral cover and DHW from the 2016 coral bleaching event[15]. For every reef of the GBR, we used the observed annual maximum DHW to estimate the percentage loss of coral. Note that the MATLAB code for the entire model is deposited at Mendeley Data so we only describe the steps in pseudo-code here. Importantly, resurveys of reefs in 2017 found that the likelihood of severe bleaching declined as a function of the historical thermal stress[20]. The authors' pointed out that more thermally sensitive individuals would likely have been lost in 2016 so the remaining coral populations in 2017 exhibited less intense responses to thermal stress (i.e., lower probabilities of severe bleaching). We refitted the statistical models of Hughes et al[20] to estimate the dependency of severe bleaching in 2017 on both the stress experienced in 2017 and the historical exposure to stress in 2016 (Figure S2). Thus, we calculated the degree to which the probability of severe bleaching declined in 2017 given its historical exposure. In practice, this yielded a percentage reduction in the probability of severe bleaching. We then used this legacy effect to adjust the expected mortality of corals on each reef in 2017. For example, if the stress experienced in 2017 suggested 60% coral mortality, but the legacy of thermal stress suggested that the probability of severe bleaching in 2017 had declined from 40% to 30% (i.e., a reduction of 25%), then the adjusted coral mortality rate for 2017 would be 45% (i.e., a 25% reduction from 60%). This approach reduction of the rate expected in 2017 if we had ignored the stress experienced in 2016. Lastly, we repeated this procedure for each reef for the 2020 event but rather than conditioning the legacy effect on the 2016 DHW we used the annual maximum DHW experienced in either 2016 or 2017.

Integration through connectivity

We utilised a larval dispersal connectivity network describing the larval supply between source and sink reefs for 3,806 reefs on the GBR. This network accounted for the greatest number of larval supply connections for *Acropora* corals during seven spawning seasons in 2008, 2010, 2011, 2012, 2014, 2015, and 2016 (developed by Hock et al[51]). The network described larval supply from both other reefs and self-retention. For each year, we excluded the weakest 10th percentile of larval supply connections under the assumption that not all of the modelled larval exchanges were necessarily demographically relevant for replenishment. Reefs with no thermal stress data were also excluded in the connectivity network analysis.

The impacts of bleaching on reef larval supply were determined cumulatively for each successive bleaching event. The larval output from each reef was reduced (weighted) according to the cumulative mortality of coral and its proportional fecundity for a given year (i.e., larval output weighting = proportional coral cover remaining × proportional fecundity). These weights were then applied to the aggregated connectivity matrix to determine the reef-to-reef reductions in larval supply compared to a counterfactual in which no loss of coral or fecundity takes place (a weight of 1). We then quantified the overall change in larval supply across the entire GBR and categorised the losses of larval supply into 20% bands (0-20%, 21-40%, etc) for individual reefs.

Key assumptions

Like any model we make a number of simplifying assumptions. We focus on spawning corals because these dominate recruitment on the GBR[52] and are the taxa most likely to create systemic resilience among reefs. Moreover, more than 80% of the coral taxa on the GBR exhibit this reproductive mode. We comment on the implications of our results for brooders in the main text. Models of coral larval dispersal are parameterised for acroporids, which are the best understood taxa and major contributors to recruitment. However, the larval behaviours of coral taxa were recently reviewed[53]. Of the 58 taxonomic records available, 90% would have a competency window within that used in our model of *Acropora* (i.e., 4-120 days). The main exceptions stemmed from records at higher latitudes where longer pre-competency times are often observed[54]. Of the remaining tropical studies only one had a competency window incompatible (shorter) than ours (*Goniastrea australensis*) and five species had mixed results such that at least one study reported an earlier competency time whereas others of the same species had reported compatible competency to our model (*Pectinia lactuca*, *Platygyra sinensis*, *Goniastrea aspera, Acropora digitifera*, and *Acropora tenuis*). In short, we feel that the use of *Acropora* with a broad competency window should be representative of the majority of spawner behaviour.

We assume that corals do not have sufficient time for substantial recovery to maturity between successive bleaching events, which vary from 1 year to 3 years. Long-term monitoring revealed that full recovery took approximately 7-12 years, and the initial recovery was slow following disturbances[10,55,56]. Although the recovery rate may change in time[57], we argue that it is reasonable to assume that the short recovery windows between successive events will impede coral recovery to reproductive states. We assume that the CONNIE model of coral larval dispersal, combined with empirical larval behaviour, is a reasonable approximation of systemic connectivity[51,58] (https://connie.csiro.au/). While we acknowledge that all models have weaknesses, it predicts the observed genetic structure of multiple corals on the GBR[59]. Bleaching susceptibility is taxon-specific and community structure could be changed among events[12,60]. While we cannot include this here, our approach mitigates some of these concerns because we assume there is insufficient time for effective community reorganisation on scales of a few years.

Sensitivity analyses

We recognise that the putative relationship for the impact of DHW on fecundity is uncertain. We created an alternative calibration which was less pessimistic and enabled 10% fecundity at DHW8 rather than zero (here, fecundity declines to zero at DHW9). This is a reasonable alternative scenario given that GBR data already found an 80% reduction in fecundity at DHW6 and very high levels of coral mortality occur at DHW9[15]. The calibration functions are plotted in Figure S1 and the equations are present in the MATLAB code.

The conditional analysis of the probability of severe coral bleaching according to both present stress and historical stress allowed us to estimate the upper and lower confidence intervals (CIs) of each probability (adjusted for the binomial distribution). While our main results used the mean probabilities of bleaching, we also ran cases that only used the lower CIs for all years or only used upper CIs for all years.

Thus, we created three alternative model scenarios, Severe Bleaching F=10%, Bleaching history LCL (F=0%), Bleaching history UCL (F=0%). For each we quantified the distribution of larval supply loss among reefs (see Figure S3). We estimated two forms of variation: that attributable to assumptions and that associated with the main effect of the study, the impacts of heatwaves on lost larval supply. The standard model run with mean bleaching probabilities and fecundity=0 at DHW≥8 yielded an estimated percentage of reefs in each class of larval supply loss (see Figure 2A and 2B). We then recalculated these percentages for each of the three alternative scenarios. The absolute difference in the percentages of reefs were calculated between the standard run and each of the alternatives. We then quantified the mean value of difference across the three scenarios (within each connectivity class) as the variability associated with model assumptions. The variability of main effects was quantified as the mean difference across connectivity classes holding model scenario constant. The relative magnitudes of variability enabled the overall effects of altering some key model assumptions to be compared to that of the main analysis within a single model scenario. Taking the mildly bleached reefs as an example, the mean variability in percentage of reefs among model scenarios was 3%. In contrast, the mean variability in percentage of reefs among connectivity classes (of the same model) was 19%.

Probability analysis of cumulative bleaching

To understand whether the spatial patterns of thermal stress conform to a random model, we compared the null expected and observed probabilities of thermal stress. We have scaled down the study extent to reef pixels only. The study extent for the probability analysis corresponded to 4,546 reef pixels. The expected probabilities of having cumulative number of disturbance events were computed by modelling the Poisson trials, where a series of Bernoulli trials with unequal probabilities of independent events reflected the fact that disturbance probabilities differed between events[61]. The probabilities of each independent disturbance event were measured as the proportion of reef pixels with annual maximum DHW above the DHW thresholds of 3, 4, 6 and 8 in the study extent. All possible combinations of obtaining each cumulative frequency of event, in this case from a minimum of 0 to a maximum of 5 events, were enumerated. The products of all possible combinations of Poisson trials for each event frequency were summed to obtain the null expected probabilities of having 0 to 5 events being above the DHW threshold. This was done separately for each DHW threshold. Computations were performed using MATLAB R2020b, with the following equation:

$$P(x=k)=\binom{n}{k}{p_i}^{k}(1-p_i)^{n-k}, \qquad for\ k=0,1,2,\ldots,n;\ p_i\ =\ (p_1\,,\ldots,p_n\,)$$

where n is the number of heat exposure events, k is the number of events with DHW above thresholds, and p_i is the probability of DHW above thresholds, which varies across different events. At each DHW threshold, the five bleaching event layers were summed to determine the cumulative frequency of events per reef pixel using the Raster Calculator tool in ArcMap. The observed probabilities were calculated as the proportion of reef pixels experiencing zero to five disturbance events in the study extent. The null expected probabilities were then compared to the observed probabilities at each DHW threshold to identify consistent and inconsistent patterns (Figure 3). To investigate the existence of regions that experience modest but not severe stress, we repeated the analysis using DHW 4-6. The study extent covered the entire reef population of interest; therefore, statistical tests were not required.

Using the comparisons of observed and expected disturbance patterns, we identified two types of regions as warm spots and potential refugia. Reef pixels that experienced multiple times of bleaching or mortality risk, more than it would be expected in the null model, were classified as warm spots. Reef pixels that never experienced bleaching or mortality heat stress were identified as potential refugia if their prevalence were higher than the null expectation. To assess the current protection levels on potential refugia, we also calculated the proportion of potential refugia falling into the Marine National Park (Green) Zone and Preservation (Pink) Zone, according to the Great Barrier Reef Marine Park Authority (GBRMPA) Zoning Plan[62] in ArcMap using the Calculate Geometry function. Spatial information was obtained from GBRMPA[63] (https://eatlas.org.au/data/uuid/ac8e8e4f-fc0e-4a01-9c3d-f27e4a8fac3c).

Replenishment ability of potential refugia

To understand the potential replenishment ability of the thermal refugia identified in the probabilistic analysis, we estimated the possible connectivity of all the reefs within the potential refugia to other sink reefs using the cumulative connectivity network of the seven spawning seasons[51]. Reefs that received larvae from more than one refugia source were only counted once. The proportion of sink reefs represented all the possible connections from the thermal refugia source reefs within the seven spawning seasons. Self-replenishment was excluded from the result because we were interested in seeing the proportion of sink reefs receiving benefits from the refugia reefs. This was done separately for the DHW<3, <4, <6 and <8 potential refugia (See Table S1).

References

1. Berkelmans, R., and Oliver, J.K. (1999). Large-scale bleaching of corals on the Great Barrier Reef. Coral Reefs *18*, 55-60.
2. Berkelmans, R., De'ath, G., Kininmonth, S., and Skirving, W.J. (2004). A comparison of the 1998 and 2002 coral bleaching events on the Great Barrier Reef: spatial correlation, patterns, and predictions. Coral Reefs *23*, 74-83.
3. Hughes, T.P., Kerry, J.T., Alvarez-Noriega, M., Alvarez-Romero, J.G., Anderson, K.D., Baird, A.H., Babcock, R.C., Beger, M., Bellwood, D.R., Berkelmans, R., et al. (2017). Global warming and recurrent mass bleaching of corals. Nature *543*, 373-377.
4. Great Barrier Reef Marine Park Authority (GBRMPA) (2017). Final report: 2016 coral bleaching event on the Great Barrier Reef, GBRMPA, Townsville.
5. Great Barrier Reef Marine Park Authority (GBRMPA), Australian Institute of Marine Science (AIMS), and CSIRO (2020). Reef snapshot: summer 2019-20, GBRMPA, Townsville.
6. Wilson, K.L., Tittensor, D.P., Worm, B., and Lotze, H.K. (2020). Incorporating climate change adaptation into marine protected area planning. Global Change Biology *26*, 3251-3267.
7. Walsworth, T.E., Schindler, D.E., Colton, M.A., Webster, M.S., Palumbi, S.R., Mumby, P.J., Essington, T.E., and Pinsky, M.L. (2019). Management for network diversity speeds evolutionary adaptation to climate change. Nature Climate Change *9*, 632-636.
8. Frieler, K., Meinshausen, M., Golly, A., Mengel, M., Lebek, K., Donner, S.D., and Hoegh-Guldberg, O. (2012). Limiting global warming to 2°C is unlikely to save most coral reefs. Nature Climate Change *3*, 165-170.
9. Eakin, C.M., Morgan, J.A., Heron, S.F., Smith, T.B., Liu, G., Alvarez-Filip, L., Baca, B., Bartels, E., Bastidas, C., Bouchon, C., et al. (2010). Caribbean corals in crisis: record thermal stress, bleaching, and mortality in 2005. PLoS One *5*, e13969.
10. Baker, A.C., Glynn, P.W., and Riegl, B. (2008). Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. Estuarine, Coastal and Shelf Science *80*, 435-471.
11. Guest, J.R., Baird, A.H., Maynard, J.A., Muttaqin, E., Edwards, A.J., Campbell, S.J., Yewdall, K., Affendi, Y.A., and Chou, L.M. (2012). Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. PLoS One *7*, e33353.
12. McClanahan, T.R., Darling, E.S., Maina, J.M., Muthiga, N.A., D'agata, S., Leblond, J., Arthur, R., Jupiter, S.D., Wilson, S.K., Mangubhai, S., et al. (2020). Highly variable taxa-specific coral bleaching responses to thermal stresses. Marine Ecology Progress Series *648*, 135-151.
13. Skirving, W., Heron, M., and Heron, S. (2006). The hydrodynamics of a bleaching event: Implications for management and monitoring. In Coastal and Estuarine Studies. Coral Reefs and Climate Change: Science and Management Volume 61, J.T.H.-G. Phinney, O.; Kleypas, J.; Skirving, W.; Strong, A., ed. (Washington, DC: American Geophysical Union), pp. 145-161.
14. Skirving, W., Marsh, B., De La Cour, J., Liu, G., Harris, A., Maturi, E., Geiger, E., and Eakin, C.M. (2020). CoralTemp and the Coral Reef Watch Coral Bleaching Heat Stress Product Suite Version 3.1. Remote Sensing *12*, 3856.
15. Hughes, T.P., Kerry, J.T., Baird, A.H., Connolly, S.R., Dietzel, A., Eakin, C.M., Heron, S.F., Hoey, A.S., Hoogenboom, M.O., Liu, G., et al. (2018). Global warming transforms coral reef assemblages. Nature *556*, 492-496.
16. Baird, A.H., Madin, J.S., Álvarez-Noriega, M., Fontoura, L., Kerry, J.T., Kuo, C.Y., Precoda, K., Torres-Pulliza, D., Woods, R.M., Zawada, K.J.A., et al. (2018). A decline in bleaching suggests that depth can provide a refuge from global warming in most coral taxa. Marine Ecology Progress Series *603*, 257-264.

17. Hughes, T.P., Bellwood, D.R., Folke, C., Steneck, R.S., and Wilson, J. (2005). New paradigms for supporting the resilience of marine ecosystems. Trends in Ecology and Evolution *20*, 380-386.
18. Ward, S., Harrison, P., and Hoegh-Guldberg, O. (2002). Coral bleaching reduces reproduction of scleractinian corals and increases. Proceedings 9th International Coral Reef Symposium, Bali, Indonesia. 23-27 October 2000.
19. Hughes, T.P., Kerry, J.T., Baird, A.H., Connolly, S.R., Chase, T.J., Dietzel, A., Hill, T., Hoey, A.S., Hoogenboom, M.O., Jacobson, M., et al. (2019). Global warming impairs stock-recruitment dynamics of corals. Nature *568*, 387-390.
20. Hughes, T.P., Kerry, J.T., Connolly, S.R., Baird, A.H., Eakin, C.M., Heron, S.F., Hoey, A.S., Hoogenboom, M.O., Jacobson, M., Liu, G., et al. (2019). Ecological memory modifies the cumulative impact of recurrent climate extremes. Nature Climate Change *9*, 40-43.
21. Edwards, A.J., Guest, J.R., Heyward, A.J., Villanueva, R.D., Baria, M.V., Bollozos, I.S.F., and Golbuu, Y. (2015). Direct seeding of mass-cultured coral larvae is not an effective option for reef rehabilitation. Marine Ecology Progress Series *525*, 105-116.
22. Cote, I.M., and Darling, E.S. (2010). Rethinking ecosystem resilience in the face of climate change. PLoS Biol *8*, e1000438.
23. Mumby, P.J., Elliott, I.A., Eakin, C.M., Skirving, W., Paris, C.B., Edwards, H.J., Enriquez, S., Iglesias-Prieto, R., Cherubin, L.M., and Stevens, J.R. (2011). Reserve design for uncertain responses of coral reefs to climate change. Ecology Letters *14*, 132-140.
24. Webster, M.S., Colton, M.A., Darling, E.S., Armstrong, J., Pinsky, M.L., Knowlton, N., and Schindler, D.E. (2017). Who Should Pick the Winners of Climate Change? Trends in Ecology and Evolution *32*, 167-173.
25. McClanahan, T.R., Darling, E.S., Maina, J.M., Muthiga, N.A., ’agata, S.D., Jupiter, S.D., Arthur, R., Wilson, S.K., Mangubhai, S., Nand, Y., et al. (2019). Temperature patterns and mechanisms influencing coral bleaching during the 2016 El Niño. Nature Climate Change *9*, 845-851.
26. Liu, G., Heron, S., Eakin, C., Muller-Karger, F., Vega-Rodriguez, M., Guild, L., De La Cour, J., Geiger, E., Skirving, W., Burgess, T., et al. (2014). Reef-Scale Thermal Stress Monitoring of Coral Ecosystems: New 5-km Global Products from NOAA Coral Reef Watch. Remote Sensing *6*, 11579-11606.
27. Skirving, W.J., Heron, S.F., Marsh, B.L., Liu, G., De La Cour, J.L., Geiger, E.F., and Eakin, C.M. (2019). The relentless march of mass coral bleaching: a global perspective of changing heat stress. Coral Reefs *38*, 547-557.
28. Liu, G., Skirving, W., Geiger, E.F., De La Cour, J.L., Marsh, B.L., Heron, S.F., Tirak, K.V., Strong, A.E., and Eakin, C.M. (2017). NOAA Coral Reef Watch’s 5km satellite coral bleaching heat stress monitoring product suite version 3 and four-month outlook version 4. Reef Encounter *32*, 39-45.
29. Condie, S.A., Plaganyi, E.E., Morello, E.B., Hock, K., and Beeden, R. (2018). Great Barrier Reef recovery through multiple interventions. Conservation Biology *32*, 1356-1367.
30. Hock, K., Wolff, N.H., Ortiz, J.C., Condie, S.A., Anthony, K.R.N., Blackwell, P.G., and Mumby, P.J. (2017). Connectivity and systemic resilience of the Great Barrier Reef. PLoS Biol *15*, e2003355.
31. Baird, A.H., Guest, J.R., and Willis, B.L. (2009). Systematic and Biogeographical Patterns in the Reproductive Biology of Scleractinian Corals. In Annual Review of Ecology Evolution and Systematics, Volume 40. pp. 551-571.
32. Doropoulos, C., Ward, S., Roff, G., Gonzalez-Rivero, M., and Mumby, P.J. (2015). Linking demographic processes of juvenile corals to benthic recovery trajectories in two common reef habitats. PLoS One *10*, e0128535.
33. Alvarez-Filip, L., Carricart-Ganivet, J.P., Horta-Puga, G., and Iglesias-Prieto, R. (2013). Shifts in coral-assemblage composition do not ensure persistence of reef functionality. Scientific reports *3*, 3486.

34. Mumby, P.J., Chisholm, J.R.M., Edwards, A.J., Andrefouet, S., and Jaubert, J. (2001). Cloudy weather may have saved society island reef corals during the 1998 ENSO event. Marine Ecology Progress Series *222*, 209-216.
35. Skirving, W., Enríquez, S., Hedley, J., Dove, S., Eakin, C., Mason, R., De La Cour, J., Liu, G., Hoegh-Guldberg, O., Strong, A., et al. (2018). Remote Sensing of Coral Bleaching Using Temperature and Light: Progress towards an Operational Algorithm. Remote Sensing *10*, 18.
36. Nakamura, T., and van Woesik, R. (2001). Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. Marine Ecology Progress Series *212*, 301-304.
37. McClanahan, T.R., Maina, J., Moothien-Pillay, R., and Baker, A.C. (2005). Effects of geography, taxa, water flow, and temperature variation on coral bleaching intensity in Mauritius. Marine Ecology Progress Series *298*, 131-142.
38. Wiedenmann, J., D'Angelo, C., Smith, E.G., Hunt, A.N., Legiret, F.-E., Postle, A.D., and Achterberg, E.P. (2012). Nutrient enrichment can increase the susceptibility of reef corals to bleaching. Nature Climate Change *3*, 160-164.
39. Vega Thurber, R.L., Burkepile, D.E., Fuchs, C., Shantz, A.A., McMinds, R., and Zaneveld, J.R. (2014). Chronic nutrient enrichment increases prevalence and severity of coral disease and bleaching. Global Change Biology *20*, 544-554.
40. DeCarlo, T.M., Gajdzik, L., Ellis, J., Coker, D.J., Roberts, M.B., Hammerman, N.M., Pandolfi, J.M., Monroe, A.A., and Berumen, M.L. (2020). Nutrient-supplying ocean currents modulate coral bleaching susceptibility. Science Advances *6*, eabc5493.
41. Beaman, R. (2012). Project 3DGBR: Great Barrier Reef and Coral Sea Geomorphic Features. R.S.o.E.a.E.S. Beaman, James Cook University ed. (eAtlas).
42. Roelfsema, C.M., Kovacs, E.M., Ortiz, J.C., Callaghan, D.P., Hock, K., Mongin, M., Johansen, K., Mumby, P.J., Wettle, M., Ronan, M., et al. (2020). Habitat maps to enhance monitoring and management of the Great Barrier Reef. Coral Reefs *39*, 1039-1054.
43. With, K. (1997). The application of neutral landscape models in conservation biology. Conservation Biology *11*, 1069-1080.
44. Turner, M.G., Gardner, R.H., O'neill, R.V., and O'Neill, R.V. (2001). Landscape ecology in theory and practice, Volume 401, (New York, NY: Springer).
45. Girvetz, E.H., and Greco, S.E. (2007). How to define a patch: a spatial model for hierarchically delineating organism-specific habitat patches. Landscape Ecology *22*, 1131-1142.
46. Dietzel, A., Connolly, S.R., Hughes, T.P., and Bode, M. (2021). The spatial footprint and patchiness of large-scale disturbances on coral reefs. Glob Chang Biol.
47. Ward, S., Harrison, P., and Hoegh-Guldberg, O. (2000). Coral bleaching reduces reproduction of scleractinian corals and increases. Proceedings 9th International Coral Reef Symposium, Bali, Indonesia. 23-27 October 2000.
48. Levitan, D.R., Boudreau, W., Jara, J., and Knowlton, N. (2014). Long-term reduced spawning in Orbicella coral species due to temperature stress. Marine Ecology Progress Series *515*, 1-10.
49. Hagedorn, M., Carter, V.L., Lager, C., Camperio Ciani, J.F., Dygert, A.N., Schleiger, R.D., and Henley, E.M. (2016). Potential bleaching effects on coral reproduction. Reproduction, Fertility and Development *28*, 1061-1071.
50. Donner, S.D., Skirving, W.J., Little, C.M., Oppenheimer, M., and Hoegh-Guldberg, O. (2005). Global assessment of coral bleaching and required rates of adaptation under climate change. Global Change Biology *11*, 2251-2265.
51. Hock, K., Doropoulos, C., Gorton, R., Condie, S.A., and Mumby, P.J. (2019). Split spawning increases robustness of coral larval supply and inter-reef connectivity. Nature Communication *10*, 3463.
52. Hughes, T., Baird, A.H., Dinsdale, E.A., Moltschaniwskyj, N.A., Pratchett, M., Tanner, J.E., and Willis, B.L. (1999). Patterns of recruitment and abundance of corals along the Great Barrier Reef. Nature *397*, 59-63.

53. Jones, R., Ricardo, G.F., and Negri, A.P. (2015). Effects of sediments on the reproductive cycle of corals. Mar Pollut Bull *100*, 13-33.
54. Wilson, J.R., and Harrison, P.L. (1998). Settlement-competency periods of larvae of three species of scleractinian corals. Marine Biology *131*, 339-345.
55. Halford, A., Cheal, A.J., Ryan, D., and Williams, C.M. (2004). Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. Ecology *85*, 1892-1905.
56. Robinson, J.P.W., Wilson, S.K., and Graham, N.A.J. (2019). Abiotic and biotic controls on coral recovery 16 years after mass bleaching. Coral Reefs *38*, 1255-1265.
57. Ortiz, J.-C., Wolff, N.H., Anthony, K.R.N., Devlin, M., Lewis, S., and Mumby, P.J. (2018). Impaired recovery of the Great Barrier Reef under cumulative stress. Science Advances *4*, eaar6127.
58. Condie, S.A., Hepburn, M., and Mansbridge, J. (2012). Modelling and visualisation of connectivity on the Great Barrier Reef. Proceedings of the 12th International Coral Reef Symposium, Cairns, Australia. 9-13 July 2012.
59. Riginos, C., Hock, K., Matias, A.M., Mumby, P.J., Oppen, M.J.H., Lukoschek, V., and Treml, E. (2019). Asymmetric dispersal is a critical element of concordance between biophysical dispersal models and spatial genetic structure in Great Barrier Reef corals. Diversity and Distributions *25*, 1684-1696.
60. Baird, A.H., and Marshell, P.A. (2002). Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. Marine Ecology Progress Series *237*, 133-141.
61. Nedelman, J., and Wallenius, T. (1986). Bernoulli trials, poisson trials, surprising variances, and Jensen's inequality. The American Statistician *40*, 286-289.
62. Great Barrier Reef Marine Park Authority (GBRMPA) (2004). Great Barrier Reef Marine Park Zoning Plan 2003. (Townsville, QLD, Australia.), p. 211.
63. Great Barrier Reef Marine Park Authority (GBRMPA) (2004). Great Barrier Reef Marine Park Zoning (Version 1) [Dataset] EC12E1A4-36AE-4D5A-AB53-89D662FDF34E.

SUPPLEMENTAL INFORMATION

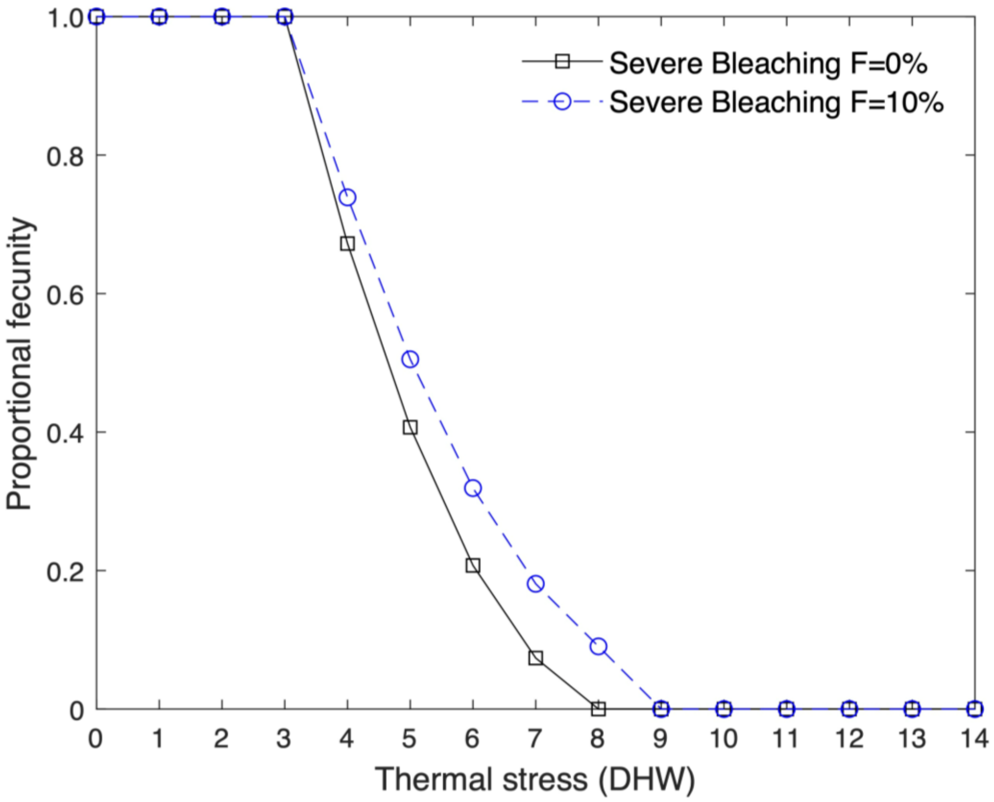

Figure S1. Relationship of coral fecundity and thermal stress (DHW). Related to Figure 2 and STAR methods.
Calibration functions of impacts of thermal stress on proportional reduction in coral fecundity. The solid black line represents relationship with fecundity of 0% at DHW8, and the blue dashed line represents the relationship with fecundity of 10% at DHW8 and 0% at DHW9.

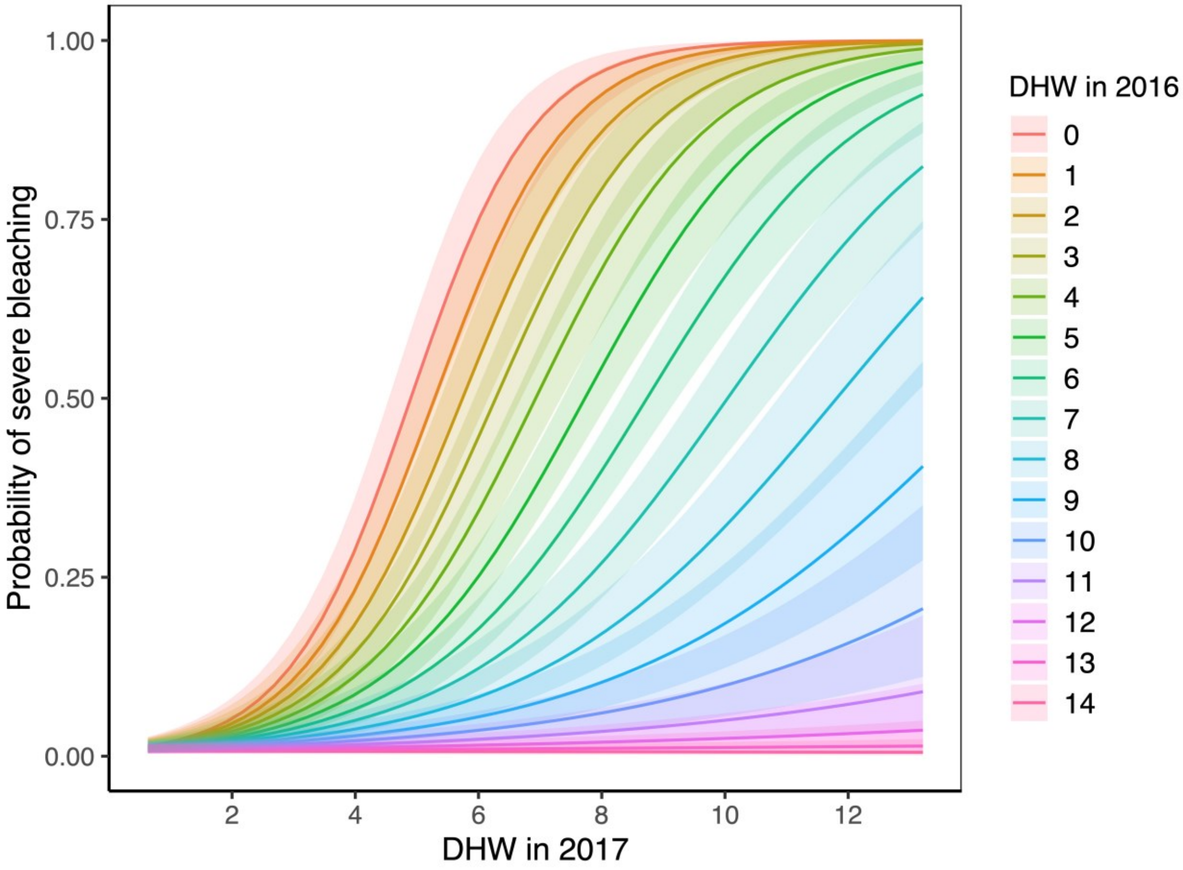

Figure S2. Decline likelihood of severe bleaching in 2017 as a function of the historical thermal stress in 2016 at different DHW levels (data from Hughes et al[S1]). Related to STAR methods.

Refitted relationship of legacy effect of thermal stress and severe coral bleaching probability in 2016 and 2017 from Hughes et al[S1]. Historical exposure to thermal stress in 2016 has reduced the probability of severe bleaching in 2017.

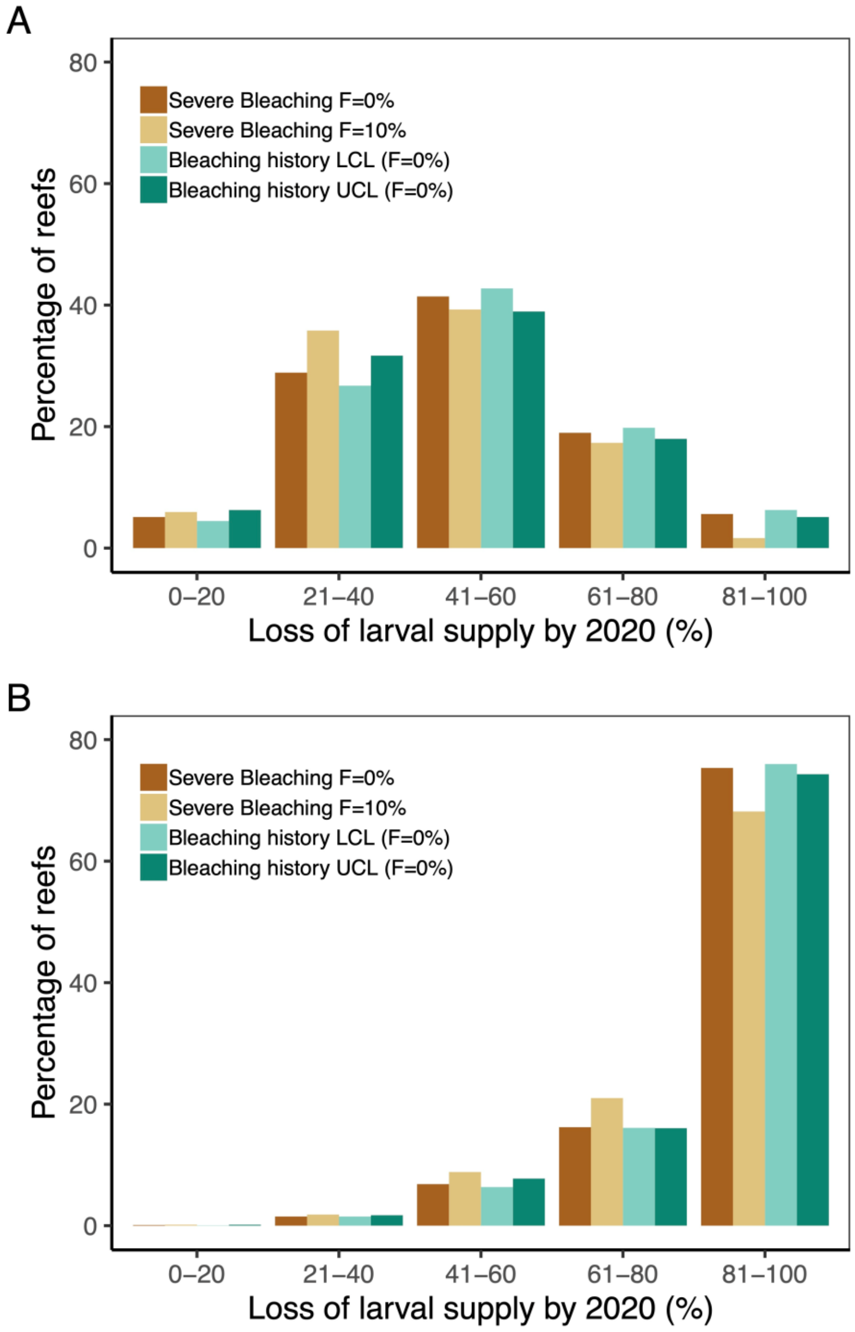

Figure S3. Sensitivity analysis of cumulative impacts of thermal stress on larval supply loss after three successive bleaching events in 2016, 2017, and 2020. Related to Figure 2 and STAR methods.

Bar plots showing the percentage of unbleached reefs (DHW<4) experiencing loss of larval supply by 2020 (A), and the percentage of bleached reefs (DHW≥8) experiencing loss of larval supply by 2020 (B). Four model scenarios were used, including severe bleaching with fecundity of 0% at DHW8, severe bleaching with fecundity of 10% at DHW8, lower confidence intervals of bleaching probability and upper confidence intervals of bleaching probability.

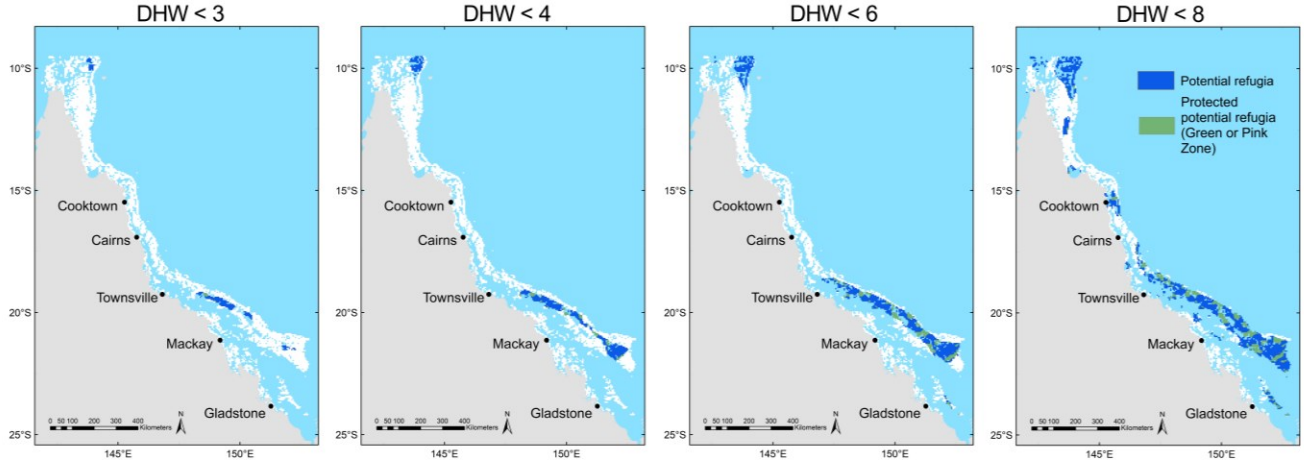

Figure S4. Potential thermal refugia under protection. Related to Figure 4. Potential thermal refugia currently under protection as Marine National Park (Green) Zone and Preservation (Pink) Zone are shown in green. The protected areas constitute 7%, 14%, 22% and 22% of the DHW<3, DHW<4, DHW<6, and DHW<8 potential refugia respectively.

	Warm spots		Potential refugia				
DHW threshold	Area (km^2)	% of the GBR	No. of reefs	Area (km^2)	% of the GBR	% of potential refugia overlapping with Green/Pink Zone (under protection)	No. of reefs receiving larval supply from refugia reefs
3	59529	44%	167	6048	5%	7%	1624 (43%)
4	44410	33%	568	16860	13%	14%	2185 (58%)
6	18479	13%	1105	33476	25%	22%	2570 (68%)
8	--	--	1884	60995	46%	22%	3290 (87%)

Table S1. The area and proportion of warm spots and potential refugia on the GBR based on historical thermal stress exposure. Related to Figure 2 and Figure S4.

Supplemental Reference

S1. Hughes, T.P., Kerry, J.T., Connolly, S.R., Baird, A.H., Eakin, C.M., Heron, S.F., Hoey, A.S., Hoogenboom, M.O., Jacobson, M., Liu, G., et al. (2019). Ecological memory modifies the cumulative impact of recurrent climate extremes. Nature Climate Change *9*, 40-43.