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The Loss of Beneficial Thermal Priming on Global Coral Reefs

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ABSTRACT

Warm-season marine heatwaves (MHWs) have greatly increased in frequency, severity, and extent over the last few decades, driving more frequent and severe coral bleaching episodes. Given the grave near-term threat to coral reefs imposed by MHWs, it is important to assess the mechanisms by which corals may acquire higher thermal tolerance. Recent field and laboratory studies have demonstrated that exposure to sublethal heat stress, known as "priming," can reduce bleaching susceptibility during a subsequent MHW. Little is known, however, about how often priming conditions occur, and how effective those conditions may be at protecting coral reefs. We employed a global historical coral bleaching database and a high-resolution sea surface temperature dataset to assess the frequency of priming and examine its effect on coral bleaching sensitivity on a global scale. The analysis showed that coral reefs in parts of the western to central tropical Pacific experienced priming on average over twice a decade and had a higher likelihood of priming protection. Mixed-effects regression models indicated that priming conditions could mitigate coral bleaching response by up to 12% in advance of a moderate MHW. However, the protective effect of priming decreased, and even became harmful, with more severe MHWs. We detected spatial variations in priming frequency that could provide insight for conservation planning and explain some variations in bleaching sensitivity to MHWs. Even so, our findings suggest that thermal priming will not be sufficient to protect most coral reefs from MHWs in the future, without substantial efforts to mitigate climate change.

1 | Introduction

Warmwater coral reefs are among the most diverse ecosystems in the world, housing up to 25% of marine biodiversity (Reaka-Kudla 1997; Spalding, Ravilious, and Green 2001). They provide essential ecosystem goods and services, such as food, coastline protection from storms, and tourism resources, to communities around the world (Costanza et al. 2014; Gattuso et al. 2015; Spalding et al. 2017). However, they are increasingly threatened by ocean warming and more frequent and severe warm-season marine heatwaves (MHWs) (Donner 2009; Eakin et al. 2010; Hughes et al. 2003; Hughes, Kerry et al. 2018; Hoegh-Guldberg et al. 2007). Heat stress as little as 1°C–2°C above the long-term average summer temperature can disrupt the symbiosis between corals and Symbiodiniaceae microalgae living in the coral tissue, leading to the paling of corals, a phenomenon known as coral bleaching (Glynn and D'Croz 1990; Hoegh-Guldberg 1999). Coral reefs worldwide have been exposed to bleaching-level heat stress over the past four decades (Hughes et al. 2017; Skirving et al. 2019), driving increasingly frequent and severe coral bleaching and mass mortality (Hughes, Kerry et al. 2018; Hughes, Anderson et al. 2018; Virgen-Urcelay and Donner 2023). The loss of living corals and the effects on reef ecosystems also threaten the associated cultures, fisheries, and incomes of local and Indigenous peoples (Cooley et al. 2022; Eddy et al. 2021; Stuart-Smith et al. 2018). Understanding the mechanisms by which the coral holobiont may acquire higher thermal tolerance temporarily or permanently is critical to helping corals persist in a rapidly warming climate.

Rapid response of organisms to environmental changes without genetic modifications, also known as stress memory, has been observed in terrestrial (Hilker et al. 2016) and marine plants (Jueterbock et al. 2021) and marine invertebrates (Ainsworth et al. 2016; Hackerott, Martell, and Eirin-Lopez 2021; Klein, Pitt, and Carroll 2017). For corals, exposure to sublethal heat stress followed by a recovery period without heat stress in advance of an MHW, known as "priming," can induce a higher tolerance to heat stress during a subsequent MHW (Hackerott, Martell, and Eirin-Lopez 2021). Recent studies have revealed that priming can protect corals from subsequent bleaching-level MHWs in laboratory experiments (Drury et al. 2022; Martell 2023), in the Florida Keys (Gintert et al. 2018) and on the Great Barrier Reef (Ainsworth et al. 2016). While these studies demonstrate that priming reduced bleaching severity in a controlled laboratory setting and in specific locations, we know little about how often priming conditions occur around the world, and how effective those conditions may be in protecting coral reefs. Importantly, coral reefs with a high frequency of priming conditions may have a greater potential for survival under continued climate change (Putnam et al. 2017), and be potential priorities for conservation and management.

In this study, we examined whether priming could alleviate coral bleaching severity on a global scale and assessed the spatial variations in the frequency of priming conditions. Using a historical global coral bleaching dataset and high-resolution sea surface temperature data, we examined the relationship between observed bleaching severity and the occurrence of priming. Next, we used mixed-effects models to quantify the extent to which priming of different durations and magnitudes mitigated bleaching severity. We then mapped the frequency of priming around the world over the past four decades, in order to identify coral reefs with a greater likelihood of protection via priming.

2 | Materials and Methods

2.1 | Coral Bleaching Database

Observed coral bleaching data were obtained from the most recent version of a high-resolution global mass coral bleaching observational database (Virgen-Urcelay and Donner 2023). In this database, each observed bleaching report includes geographical coordinates, date of observation, the percent of coral reefs bleached as a categorical variable (0–3), and in many cases, a continuous percent bleached value (0%–100%). Category [0] refers to $<1\%$ of coral bleached (henceforth referred to as no bleaching), Category [1] refers to 1%–10% of coral bleached (mild bleaching), Category [2] corresponds to 11%–50% of coral bleached (moderate bleaching) and Category [3] corresponds to $>50\%$ of coral bleached (severe bleaching).

The database contained 37,774 reports from 1963 to 2017. Detecting priming conditions and analyzing its effects on coral susceptibility to bleaching requires bleaching reports to feature a full calendar date (i.e., month–day–year) during the satellite era when daily SSTs are available (since 1985). We filtered the database to meet these criteria, resulting in 21,003 bleaching reports with the full dates during the satellite era. Out of the reports with full date, there were 17,284 reports (83%) with a continuous percent bleaching value, which were used for quantifying the contribution of priming conditions to bleaching severity via linear mixed-effects models (see more details in Section 2.4).

2.2 | Sea Surface Temperature and Heat Stress

The daily HotSpot (HS) for the 1985–2020 period was downloaded from the $0.05° \times 0.05°$ latitude–longitude global daily satellite-derived dataset CoralTemp (version 3.1) developed by the NOAA Coral Reef Watch (CRW) program (Skirving et al. 2020). The daily HS, a measure of heat stress in excess of the warm-season climatological baseline, is computed by NOAA CRW as the positive-only difference between the daily SST and the maximum monthly mean (MMM; maximum value in a monthly climatology) in a given grid cell. NOAA CRW centers the monthly climatology for computing the MMM in early 1988 in order to be consistent with its heritage climatology product (Liu et al. 2014).

To describe warm-season MHWs or heat stress that can cause coral bleaching, we used the daily HS values to calculate heat accumulation. Since thermal priming exposures that have been shown to confer coral bleaching resilience are on the scale of days to weeks (e.g., Ainsworth et al. 2016; Martell 2023; Gintert et al. 2018), heat accumulation was represented by degree heating days (DHD, °C·day), the daily equivalent of the accumulated heat stress metric degree heating weeks (DHW) used by the NOAA CRW program for real-time coral bleaching alerts (Kayanne 2017; Liu et al. 2014; Skirving et al. 2020). A 1985–2020 daily time series of DHD values was computed for each $0.05° \times 0.05°$ cell containing warmwater coral reefs according to the Millennium Coral Reef Mapping Project data (UNEP-WCMC, WorldFish Centre, and WRI 2021), as the accumulation of HS over the previous 84 days equivalent to the 12 weeks period employed in computing DHW (Liu et al. 2014).

NOAA CRW releases a Bleaching Alert Level I at the equivalent of DHD ≥ 28°C·day, indicating that moderate bleaching may occur, and Bleaching Alert Level II at the equivalent of DHD ≥ 56°C·day, indicating that severe coral bleaching and significant mortality may occur. Note that here the DHD calculation includes all positive HS values, whereas the NOAA CRW method only sums HS values greater than or equal to 1°C, which can lead DHD magnitudes in this study to be slightly greater than those computed by NOAA CRW. We purposely choose to include values of HS <1°C in the calculation of DHD for consistency with the calculation of priming conditions, which is based on analysis of HS <1°C in advance of MHW development (Section 2.3).

2.3 | Defining Priming Conditions

There were several obstacles in developing a globally robust method for identifying and characterizing priming conditions. First, the maximum or minimum duration of sublethal heat stress and recovery necessary to lead to priming for warm-water corals is not well known. Second, the method must delineate between true priming conditions—sublethal heat stress that occurs in advance of a warm-season MHW—and sublethal heat stress that occurs as a part of MHW development. In addition, because coral bleaching can be visible for weeks or months after the initial onset, the date of bleaching observations often do not align with the date of bleaching onset (Gonzalez-Espinosa and Donner 2021), which could lead to misidentifying priming conditions and the precise level of heat stress (e.g., DHD value) at which bleaching became prominent.

To address these obstacles, we developed metrics to characterize the duration of the priming period (D_p, in days), the duration of the postpriming recovery period (D_r, in days), and magnitude of priming (A_p, in°C·day) and methods to distinguish true priming conditions. The priming period was defined as a period with HS < 1°C (i.e., MMM < SST < MMM + 1°C) that occurred in advance of, at minimum, a moderate MHW (DHD ≥ 28°C·day) (Figure 1a). The postpriming recovery period (hereafter referred to as recovery period) was defined as a period with HS = 0 (i.e., SST < MMM) between the priming period and the MHW. Since the duration range of priming and recovery periods was not well constrained in the literature, we set broad limits for each: minimum duration of 7 days and maximum duration of 49 days. Such limits were necessary because an extended long period of recovery and priming could refer to two separate MHW events (Figure 1c), whereas a very short recovery period may actually be part of a longer MHW event (Figure 1d). To test the sensitivity of the results to these assumptions, we conducted sensitivity tests using a lower limit of 5 days and an upper limit of 35 days (see Section 2.4).

To control for possible mismatch between the date of bleaching reports and the date of bleaching onset as mentioned above, all priming and postpriming recovery periods were identified by analyzing the HS and DHD time series working backward from the date of annual peak heat stress (i.e., the peak of warm-season MHW) to avoid identifying sublethal heat stress that occurred during or after MHW development. The end of the recovery period was found by going backward from the date of annual peak heat stress to the first multiday period with no heat stress. Further backward examination of the time series of HS was then used to determine if priming occurred and to compute the associated metrics.

2.4 | Data Analysis

To test for the effects of priming conditions on coral bleaching sensitivity to heat stress, we calculated the priming and heat stress metrics (D_r, D_p, A_p, HS_{peak}, and DHD; Table 1) associated with each bleaching report. We then examined the differences in priming conditions between the reports with different levels of bleaching severity. For each bleaching severity category, we calculated the fraction of bleaching reports at different levels

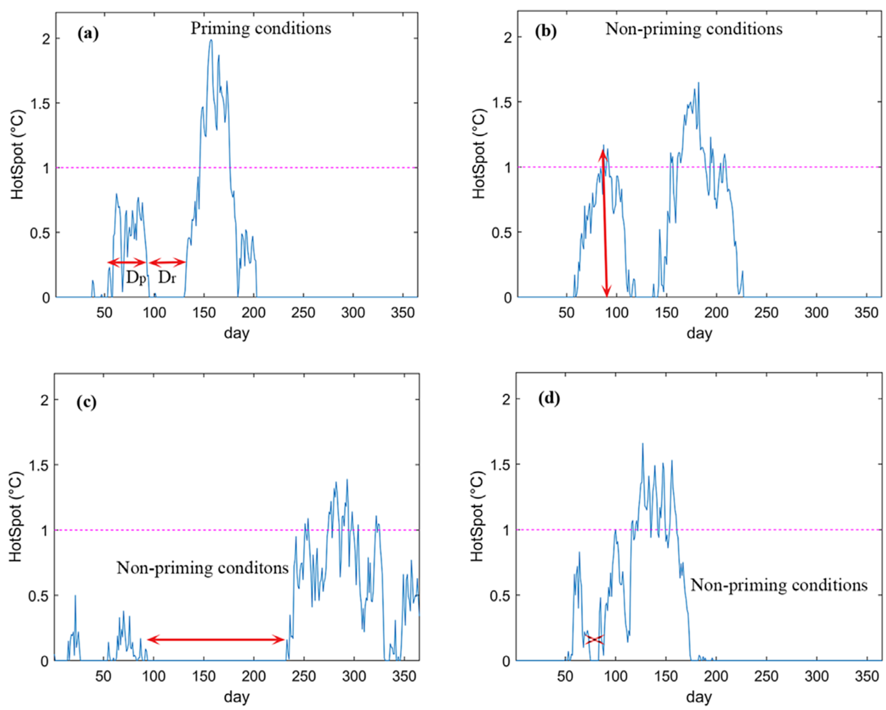

FIGURE 1 | Examples of daily HotSpot time series demonstrating examples of (a) priming conditions (6.2° S, 39.1° E, in 2016) and (b–d) nonpriming conditions, with (b) not classified as priming conditions due to HS > 1°C during the pre-marine heatwave (MHW) period (13.5° S, 48.3° E, in 2016), (c) not classified as priming conditions due to the recovery period exceeding the maximum duration of 49 days (4.8° N, 114.6° E, in 2010), and (d) not classified as priming conditions due to the recovery period being < 7 days (21.2° S, 55.3° E, in 2016). The dashed magenta horizontal line represents the priming thermal threshold (HS = 1°C), below which a period of HS prior to an MHW classifies as the priming period.

TABLE 1 | Heat stress and priming metrics.

Variable		Description
HotSpot (°C)	HS_{MMM}	Daily HotSpot in that grid cell using MMM threshold
	HS_{peak}	Maximum daily HS value that year
Duration (day)	D_r	Duration of the recovery period, the period with HS = 0 between the priming period and a bleaching-level MHW event
	D_p	Duration of the priming period, the period with sublethal heat stress prior to D_r and a bleaching-level MHW event
Accumulated heat stress (°C·day)	A_p	Accumulated sum of heat stress during the priming period D_p
	DHD	Maximum 84-day (3 months) continuous accumulated sum of positive HotSpot in the given year, measuring the magnitude of MHW that may drive coral bleaching
Heat stress level	Moderate	Bleaching Alert Level 1, defined as 28 ≤ DHD < 56°C·day
	Severe	Bleaching Alert Level 2, defined as DHD ≥ 56°C·day

of heat stress with and without priming conditions. This test was conducted using a DHD bin range of 2°C·day, from 28° to 70°C·day; the bin range of 2°C·day is sufficiently narrow to capture the sensitivity of priming to MHW magnitudes. For each DHD bin range, nonparametric Kruskal–Wallis test and Levene's test were used to test for statistical significance of the differences between the distribution of bleaching severity categories between groups with and without priming conditions. The nonparametric test was used because the sizes of the groups of reports without priming conditions are much larger than those with priming conditions for each DHD range. Kruskal–Wallis and Dunn's post hoc tests were used to identify differences in priming duration (D_p), magnitude (A_p), and recovery duration (D_r) between bleaching severity categories, in order to evaluate whether a higher level of priming exposure correlates with a lower bleaching severity.

To further quantify the effects of priming conditions on coral bleaching sensitivity to heat stress, we also fitted a series of linear mixed-effects regressions for bleaching severity (with the 17,284 reports containing a full date and continuous percent bleached value) using the DHD and the priming and recovery characteristics (D_p, A_p, and D_r). Following Equation 1, six models were constructed using different subsets of the bleaching reports (reports coinciding with Bleaching Alert Level I MHWs and reports coinciding with Bleaching Alert Level II MHWs) and one of each of three priming metrics (D_p, A_p, and D_r):

$$\text{Severity} = \beta_0 + \beta_1 DHD + \beta_2 P + \beta_3 DHD \times P \quad (1)$$

where severity is the percent bleaching from the bleaching database, β_x are the coefficients and P is the priming variable (A_p, D_p, and D_r) used in the particular model. In each case, the random effect structure was set as the latitude of the bleaching reports, as in previous research using the same bleaching database (Gonzalez-Espinosa and Donner 2021).

A second series of models were also constructed, using the same bleaching report data subset by bleaching alert levels, with DHD and a combination of the priming and recovery characteristics (A_p and D_r, respectively), including the interaction between DHD and the priming and recovery characteristics as explanatory variables:

$$\text{Severity} = \beta_0 + \beta_1 DHD + \beta_2 A_p + \beta_3 D_r + \beta_4 DHD \times A_p + \beta_4 DHD \times D_r \quad (2)$$

To test the sensitivity of the results to the assumptions about the minimum and maximum duration of the priming and recovery periods, the models were also repeated using a shorter (7–35 days) time limit range and a broader (5–49 days) time limit range. All models were performed using the function “lmer” from *lme4* R package (Bates et al. 2015).

Finally, to estimate the frequency with which priming occurred across the globe, we identified annual presence or absence of priming from 1985 through 2020 for all 0.05° × 0.05° latitude-longitude cells containing warmwater coral reefs, following the global coral reef map from the Millennium Coral Reef Mapping Project (UNEP-WCMC, WorldFish Centre, and WRI 2021). Given that the warm season in parts of the ocean can extend across 2 calendar years, we conducted the priming frequency analysis using a heat stress year (HSY) which begins in the coldest month in the climatology in each grid cell. The HSY extends from March to February in most of the Northern Hemisphere and from September to August in most of the Southern Hemisphere (Li and Donner 2022).

The computation of the priming and heat stress metrics was conducted in Matlab (version 2018b). All statistical analyses were conducted in R Studio (version 4.1.2).

3 | Results

3.1 | Role of Priming in Coral Bleaching Sensitivity to Heat Stress

Priming conditions occurred in advance of < 40% of the bleaching reports across all levels of moderate and severe MHWs, except for MHW events in the 30°C–32°C·day bin (Figure 2). For the 30°C–32°C, 32°C–34°C, and 34°C–36°C·day MHW events, the fraction of Category 0 (no bleaching) or 1 (mild bleaching) reports were significantly larger when priming conditions were present (Figure 3a; $p < 0.05$). By contrast, few higher-moderate

MHW events (e.g., 38°C–40°C·day) and some severe MHW bins (e.g., 60°C–62°C·day, roughly equivalent to NOAA CRW Bleaching Alert Level II events), the fraction of Category 0 (no bleaching) or 1 (mild bleaching), was significantly smaller in cells where priming occurred (Figure 3a, Figures S3 and S4, $p<0.05$). These results imply that bleaching of Categories 0 and 1 is more common among reports that featured priming conditions in advance of moderate MHWs.

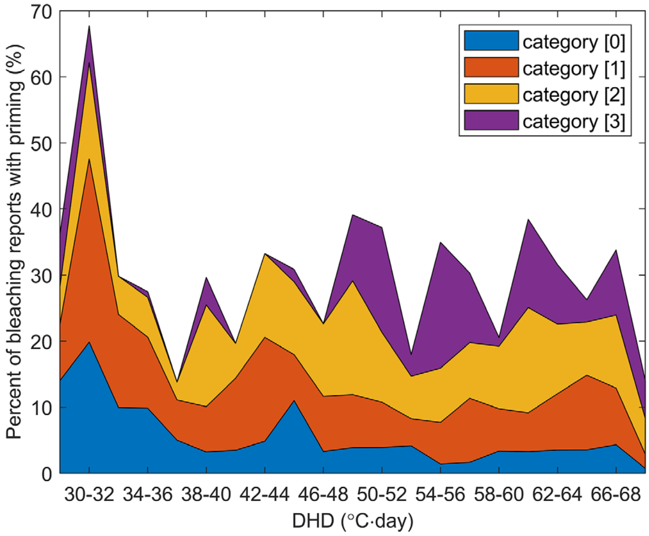

FIGURE 2 | Percent of bleaching reports which featured priming conditions, expressed for different marine heatwave (MHW) magnitudes. Data are sorted by MHW magnitude from 28°C to 70°C·day, in bins of 2°C·day. Colors indicate bleaching severity category, with blue representing Category 0 (no bleaching) reports and purple representing Category 3 (severe bleaching) reports. DHD, degree heating day.

For example, within the 34°C–36°C·day MHW range, the fraction of surveys reporting bleaching at the level of Categories 0 and 1 which experienced priming conditions was 10% and 9% higher, respectively, than those without priming conditions, and the fraction of surveys reporting bleaching at the level of Categories 2 and 3 with priming conditions was 6% and 14% lower than that without priming conditions (Figure 3). This pattern of a higher fraction of milder bleaching reports coinciding with priming conditions than that without priming conditions also appeared in reports with a 28°C–30°C or 36°C–38°C·day MHW (Figure 3), but the comparison was not statistically significant ($p>0.05$).

The duration (Kruskal–Wallis; $\chi 2=20.488$, $p<0.001$) and magnitude (Kruskal–Wallis; $\chi 2=23.507$, $p=0.001$) of the priming periods differed significantly between different categories of bleaching reports. There was a significant difference between reports of Category 0 ($n=77$) and that of Category 1 ($n=69$) (Dunn's post hoc test: $Z=3.75$, 3.67 and $p=0.001$, 0.001, respectively) and Category 2 ($n=34$) (Dunn's post hoc test: $Z=4.27$, 3.69 and $p=0.001$, 0.001, respectively), but not Category 0 and Category 3 ($n=4$) (Dunn's post hoc test: $Z=0.70$, 1.64 and

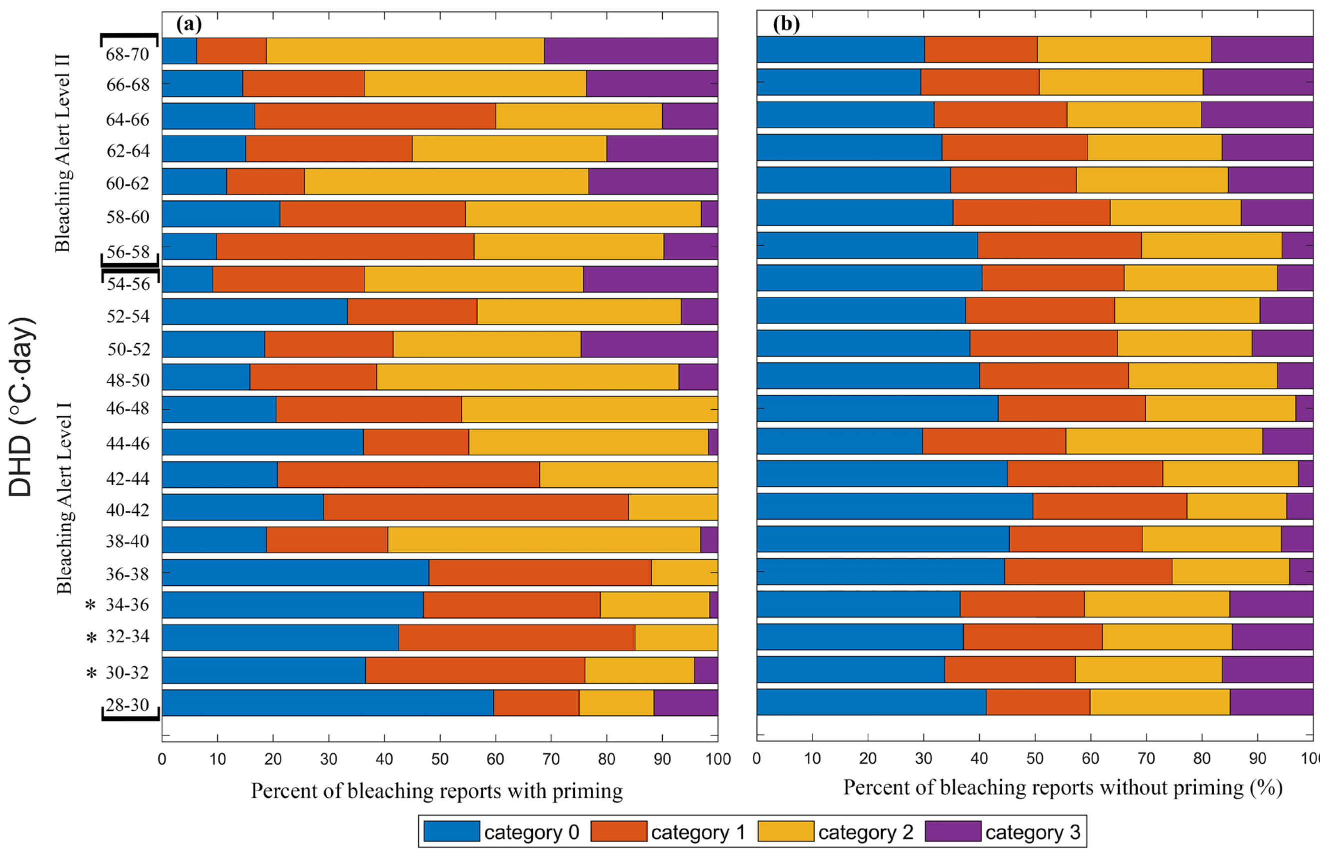

FIGURE 3 | Proportion of bleaching reports in each bleaching severity category for the reports (a) with priming conditions (left) and (b) without priming conditions (right). Data are sorted by marine heatwave (MHW) magnitude from 28°C to 70°C·day, in bins of 2°C·day. Asterisks indicate a significantly ($p<0.05$) larger fraction of Category 0 (no bleaching) and Category 1 (mild bleaching) reports in the priming group (a, left) against the no priming group (b, right). DHD, degree heating day.

$p = 0.963$, 0.402, respectively) that is likely due to the much smaller size of the bleaching reports of Category 3. There was no difference in the priming metrics for reports coinciding with stronger MHW events (DHD ≥56°C·day). These results imply that the occurrence of priming conditions correlates with lower bleaching severity in cases of some moderate MHWs. This finding is consistent with the differences in the bleaching fractions found between reports with and without priming conditions.

The mixed-effects regression analyses further confirm the role of each of the priming characteristics in modulating the sensitivity of coral bleaching to heat stress. The heat stress–only model showed a positive relationship between DHD and bleaching severity for both moderate and severe MHWs (Table 2). When priming metrics were added to the models, the positive relationship with DHD remained, but the priming and recovery period metrics had a negative relationship with bleaching severity, provided the MHW magnitude was moderate or Bleaching Alert Level I (28°C·day ≤ DHD < 56°C·day, Table 2). For example, the priming strength model (DHD and A_p) indicated that given a 34°C·day MHW, increasing the A_p by 18°C·day decreased the bleaching severity by 11.1%. For moderate MHWs, the interaction between DHD and each of the priming metrics on bleaching severity was positive, which indicates that the compensating effects of priming conditions on bleaching severity decreased with greater heat stress.

For models of severe MHWs using individual priming or recovery metrics (Equation 1), only the recovery period metric (D_r) showed a significant relationship (Table 2, right side). In the model including both priming and recovery metrics, the priming period (A_p) was significant and had a positive model coefficient, implying the greater intensity of priming increases bleaching severity, whereas the recovery period (D_r) coefficient was negative, implying longer recovery periods decrease bleaching severity (Table 2). The net effect of these counteracting drivers and the interaction between the variables in the model suggest that contrary to moderate MHWs, priming in advance of severe MHW can lead to an increase, rather than a decrease, in bleaching severity. For example, the model indicates that for a 56°C·day MHW, the priming conditions with the largest values of A_p (22.95°C·day) and D_r (46 days) analyzed in these regressions increase the bleaching severity by 6.3%.

The sensitivity tests applying shorter (7–35 days) and broader (5–49 days) duration limits for the priming and recovery periods showed relatively weak effects of priming on bleaching severity. The mixed-effects regression analyses using different duration limits showed a similar role of each of the priming characteristics in alleviating the sensitivity of coral bleaching to heat stress (Table 2; Tables S1 and S2; Figures S1–S6). The exception is that no significant alleviating effect is found for the priming strength (A_p) in the model with both priming and recovery metrics using the duration limit of 7–35 days (Table 2; Table S1). With both the shorter and broader duration limits, there is a smaller number of DHD bins which experienced a significantly larger fraction of no and mild bleaching reports with priming conditions (Figure 3; Figures S3 and S4). While the D_p values in the reports with priming conditions in the sensitivity analysis are also significantly higher for reports with no bleaching, this difference pattern does not show in the A_p values (Figure 4, Figures S5 and S6). Given the broadly consistent results from the sensitivity tests, the original duration limits of 7–49 days were applied for the remainder of the manuscript.

3.2 | Frequency of the Occurrence of Priming Conditions Over the Past Four Decades

Over three-quarters (79%) of coral reef cells experienced priming conditions prior to a moderate MHW at least once between 1985 and 2020 (Figure 5). A majority of coral reef cells (54.5%) experienced priming conditions less than four times during this period, or roughly less than once per decade on average (Figure S7). Less than 1% (~0.2%) of the cells experienced priming conditions eight or more times, or roughly twice or more per decade (Figure S7). The map indicates that such relatively high frequency of priming conditions occurred mostly in coral reefs in parts of the western to central tropical Pacific, including areas around Fiji, Vanuatu, Solomon Islands, Papua New Guinea, and Indonesia, as well as in southeastern Africa and the Gulf of Mexico (Figure 5).

The fraction of coral reef cells that experienced priming conditions prior to a bleaching-level MHW increased over time, with a greater rate of increase associated with severe MHWs (Figure 6). However, when normalized by the number of bleaching-level MHWs, the fraction of MHWs preceding by priming conditions decreased significantly over time (Figure S8, $p = 0.040$), implying that the rate of increase in bleaching-level MHWs was greater than that of pre-MHW priming conditions. The fraction of moderate MHWs with priming increased from the first to the second half of the study period in 32.5% of reef cells and decreased in 31% of reef cells (Figure 7a). Of the reef cells that experienced an increase in priming frequency in advance of moderate MHWs, 75.4% of the increases were < 0.3 (i.e., 30% of moderate MHWs). There were coral cells (~0.2%) around western Kiribati, the northwest of Palau, east of Papua New Guinea and Honduras, and in the South Pacific Ocean where the ratio of priming frequency to MHW frequency experienced large increases by ≥ 0.9 in the latter half of study period (Figure 7a). Some cells in the central South Pacific experienced an increase in priming occurrence but no change or a decrease in bleaching-level MHW occurrence (Figure S9). For severe MHWs (DHD ≥ 56°C·day), the fraction with priming increased in 11.8% of global coral cells and decreased in 8.3%.

4 | Discussion

Coral bleaching events have increased globally along with more frequent warm-season MHW since the early 1980s (Donner, Rickbeil, and Heron 2017; Hughes, Anderson et al. 2018). In years with strong El Niño events (e.g., 1997–1998 and 2015–2016), widespread thermal stress has led to global-scale bleaching events, in which mass coral bleaching occurred concurrently in multiple ocean regions (Donner, Rickbeil, and Heron 2017; Eakin, Sweatman, and Brainard 2019; Hughes, Kerry et al. 2018; Lough, Anderson, and Hughes 2018). Projected increases in the frequency and

TABLE 2 | Results of mixed-effects models relating bleaching severity to heat stress (DHD), priming metrics (D_p, A_p, and D_r), and the interaction between the heat stress and priming variables (DHD: A_p, DHD: D_p, and DHD: D_r) on bleaching percentage. See Section 2.4 for model descriptions.

		Moderate MHW				Severe MHW			
Model	**Variable**	**Coefficient**	***p***	**Intercept**	**Residual**	**Coefficient**	***p***	**Intercept**	**Residual**
Heat stress only	DHD	0.002	< 0.001	0.037	−0.179	0.007	< 0.001	−0.331	−0.195
Priming Strength	DHD	0.001	0.001	0.068	−0.183	0.007	0.000	−0.334	−0.196
	A_p	−0.053	< 0.001			0.013	0.460		
	DHD: A_p	0.001	< 0.001			< 0.001	0.897		
Priming duration	DHD	0.001	0.002	0.070	−0.184	0.007	< 0.001	−0.332	−0.195
	D_p	−0.017	< 0.001			0.001	0.895		
	DHD: D_p	0.000	< 0.001			< 0.001	0.744		
Recovery duration	DHD	0.001	0.022	0.085	−0.181	0.007	< 0.001	−0.300	−0.192
	D_r	−0.018	< 0.001			−0.012	0.001		
	DHD: D_r	0.000	< 0.001			< 0.001	< 0.001		
Priming strength & recovery period	DHD	0.001	0.099	0.095	−0.187	0.007	< 0.001	0.299	−0.194
	A_p	−0.039	< 0.001			0.042	0.023		
	D_r	−0.013	< 0.001			−0.016	< 0.001		
	DHD: A_p	0.001	< 0.001			−0.001	0.061		
	DHD: D_r	0.000	< 0.001			< 0.001	< 0.001		

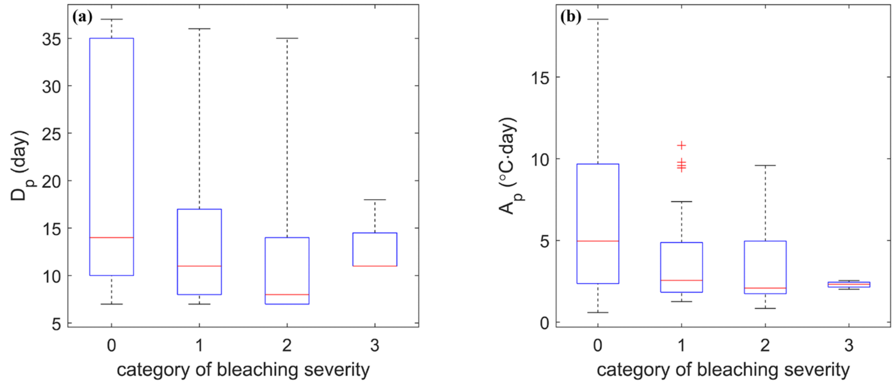

FIGURE 4 | Quartile plots of the values of the priming metrics: (a) duration of priming period (D_p, day), and (b) magnitude of priming heat stress (A_p, °C·day), for bleaching reports corresponding to 30°C–36°C·day marine heatwave (MHW) events. The red plus signs indicate the outliers.

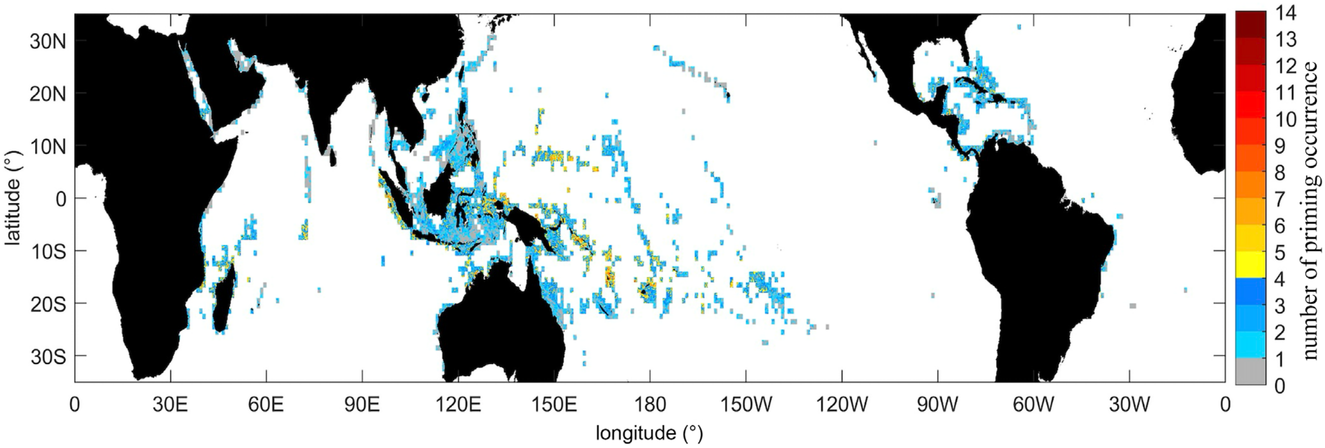

FIGURE 5 | The number of priming occurrences prior to a moderate marine heatwave (MHW) during the 1985–2020 period in all coral reef cells globally. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

severity of bleaching conditions under low emissions scenarios led the IPCC to conclude that warm-water coral reefs are at high risk even with 1.5°C of global average surface warming (Cooley et al. 2022; Fox-Kemper et al. 2021; Hoegh-Guldberg et al. 2018). Given the grave threat to coral reefs, it is critically important to understand what factors might increase coral reef resilience to heat stress in the near term.

Previous studies have examined the effects of past climate experience, clouds, light, and local human disturbances on coral bleaching sensitivity to heat stress (Ban, Graham, and Connolly 2014; Gonzalez-Espinosa and Donner 2021; Maina et al. 2008; McClanahan and Azali 2021; Safaie et al. 2018; Thompson and van Woesik 2009). The heterogeneity of coral reef response to thermal stress has led to research on identifying "super reefs" or climate refugia (Cacciapaglia and van Woesik 2016; DeCarlo et al. 2020; Gonzalez-Espinosa and Donner 2021; Hoegh-Guldberg, Kennedy, Beyer, McClennen, and Possingham 2018; Darling et al. 2019). Priming has been identified as one of the mechanisms that may confer coral resilience (Hackerott, Martell, and Eirin-Lopez 2021) and it has been suggested as an intervention to improve coral resilience (National Academies of Sciences, Engineering, and M 2019). While a few studies have shown that priming reduced bleaching severity in laboratory experiments (e.g., Bellantuono,

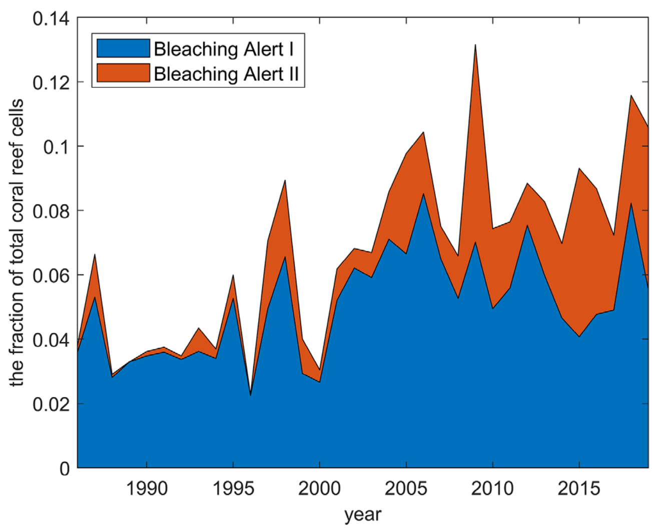

FIGURE 6 | Fraction of primed coral reef cells each year from 1985 to 2020, in advance of moderate versus severe marine heatwaves (MHWs).

Hoegh-Guldberg, and Rodriguez-Lanetty 2012; Middlebrook, Hoegh-Guldberg, and Leggat 2008) and with individual species in some locations (e.g., Florida; DeMerlis et al. 2022), the effectiveness of priming under different levels of heat stress, and

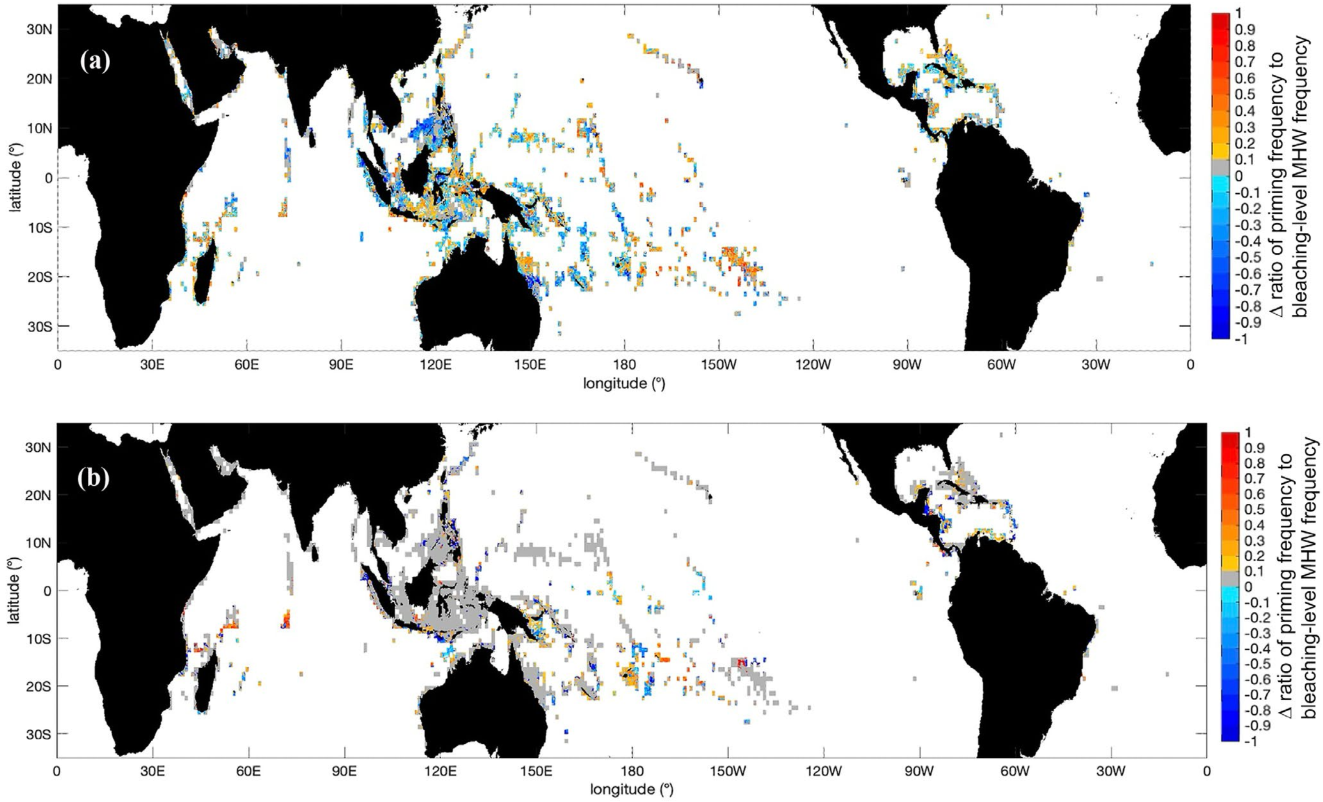

FIGURE 7 | Changes in the fraction of (a) moderate (28 ≤ DHD < 56°C·day) marine heatwave (MHW) and (b) severe (DHD ≥ 56°C·day) MHW preceding by priming between the first half (2003–2020) of the record and the second half (Year 1985–2002). Map lines delineate study areas and do not necessarily depict accepted national boundaries. DHD, degree heating day.

whether priming conditions were common around the world have been largely unknown.

The results of this study suggest that exposure to priming conditions may reduce coral reef susceptibility to bleaching, provided that the subsequent MHW is moderate (28°C ≤ DHD < 56°C·day). The initial exploratory analysis identified that with 30°C–36°C·day MHWs, no and mild bleaching reports were more common in cases with priming conditions, and the value of priming characteristics—magnitude of priming heat stress (A_p) and duration of priming period (D_p)—was higher. Having found initial evidence for an effect of priming conditions on bleaching severity within a range of moderate MHWs, we then conducted the mixed-effects regressions analysis separately for moderate (28°C ≤ DHD < 56°C·day) and severe (DHD ≥ 56°C·day) MHWs, following the categories historically employed by the NOAA CRW program. The mixed-effects linear regression analyses further indicate that priming conditions correlated with lower percent bleaching provided that the priming conditions occurred prior to a less intense MHW. While the mitigating effects of priming conditions implied by the mixed-effects models are not considerable (e.g., < 12%), it may have an important impact on the survival of corals during MHWs and the structure of postbleaching communities, given that priming conditions may be more effective with particular taxa or growth forms.

Considering the protective effects of priming, we evaluated priming frequency and changes in the fraction of priming occurrence relative to MHW occurrence across global coral cells over the past four decades. Some coral cells in the parts of the western to central equatorial and South Pacific had relatively high frequency of priming in advance of moderate MHWs and also increases in the fraction of moderate MHW preceded by priming had a larger likelihood of priming protection. The coral cells in the central South Pacific which experienced increased priming occurrence, but no change or even a decrease in bleaching-level MHW occurrence, could have the potential to become refugia for corals. However, the results also suggest that priming conditions may transition from alleviating to not influencing or even aggravating coral bleaching as the magnitude of MHW increases beyond the moderate range. For the 11.8% of coral reef cells in which the fraction of severe MHWs preceded by priming increased during the study period, the bleaching susceptibility may be increasing faster than implied by the change in MHW magnitude alone.

Although the effect detected in this study is small, and potentially limited in a warmer future, this study provides large-scale confirmation for the effect of priming on coral sensitivity to bleaching, previously observed in laboratory and field studies (reviewed in Hackerott, Martell, and Eirin-Lopez 2021). Reduced coral bleaching severity has been observed in a few species of Acroporids after exposure to elevated temperatures in the laboratory (Bellantuono, Hoegh-Guldberg, and Rodriguez-Lanetty 2012; Bay and Palumbi 2015; Middlebrook, Hoegh-Guldberg, and Leggat 2008). Priming conditions with variable thermal exposures also have resulted in delayed onset of bleaching in the Caribbean staghorn coral, *Acropora* *cervicornis,* in Florida in a 3-month experiment (DeMerlis et al. 2022). Exposure to a heat shock after corals (*A. cervicornis*) were primed with various doses of heat stress for 1–2 days in the laboratory showed lower bleaching severity in corals primed with moderate doses of heat stress but showed higher bleaching severity in the corals exposed to a relatively high dose of heat stress (Martell 2023). On the Great Barrier Reef, the thermal signature of priming conditions has been shown to be protective in advance of bleaching-level heat stress, although this protective effect will likely disappear as the climate continues to change (Ainsworth et al. 2016). These previous results, although limited, are consistent with effects of priming conditions, we detected using real-world bleaching observations, providing strong laboratory-based evidence for environmentally mediated priming (Putnam et al. 2017).

The evidence for coral reef systems from this study points to the value of exploring the effect of priming on the sensitivity of other marine ecosystems threatened by MHWs, like seagrasses and kelp forests. Priming may also play a key protective role for other organisms and ecosystems from environmental stressors. Stress memory has been evoked by priming with sublethal environmental stressors in a variety of taxa including bacteria, yeasts, plants, higher invertebrates, and vertebrates (Guan et al. 2012; Hilker et al. 2016; Hilker and Schmülling 2019; Melillo et al. 2018; Nguyen et al. 2020; Walter et al. 2013). It can result in direct benefits to fitness or survival in organisms, such as microbes (Andrade-Linares, Lehmann, and Rillig 2016; Wesener and Tietjen 2019) and seagrasses (Nguyen et al. 2020).

One limitation of this analysis is the coarse nature of the bleaching reports, which integrates the bleaching response of all taxa present at each location. Taxa-specific responses to priming and to heat stress may potentially explain why the effect of priming identified in mixed-effects models is small, and why previous laboratory experiments find large variances in the effects of priming (Baird and Marshall 2002; Fournie et al. 2012; Putnam et al. 2017). Uncertainties around the duration of the priming and recovery periods and the magnitude of pre-MHW heat stress required to effectively protect organisms and ecosystems from heat stress may also contribute to underrepresented variances in the priming effects (Middlebrook et al. 2012; Bellantuono, Hoegh-Guldberg, and Rodriguez-Lanetty 2012). Future work could focus on taxa-level response to priming conditions using more detailed regional bleaching databases. For example, researchers could compare the response of key taxa locations with and without priming conditions, to assess the influence of environmentally mediated priming (*sensu*, Putnam et al. 2017) on coral thermal tolerance, given there may be physiological benefits to corals in these regions.

As other environmental factors can also influence the sensitivity of coral reefs to heat stress, there might be interactions between priming conditions and other factors. Particularly, changes in low-level cloud cover can contribute to the development of the priming and recovery periods and can also induce changes in irradiance, another stressor to corals that influences bleaching. A period with minimal low-level cloud cover may induce mild heat stress, whereas a subsequent increase in low-level cloudiness would reduce light stress on corals as well as possibly terminate the period of sublethal heat stress. Future research on the effect of priming conditions on coral reefs would benefit from incorporating the interaction effects with other meteorological and environmental variables.

Given the recent and projected increase in the severity of MHWs at the global scale (Li and Donner 2022; Frölicher, Fischer, and Gruber 2018), the detected decrease in effectiveness of priming at higher MHW magnitudes suggests that priming conditions will, in general, become less effective at protecting coral reefs from bleaching over time. While the fraction of priming occurrences has increased relative to moderate MHW occurrences during the study period over roughly one-third of global coral cells, the large increase in the number of MHW events may overwhelm the potential benefits from priming. Furthermore, increases in the accumulated heat stress during MHWs under continued climate change imply that priming conditions are likely to become much less effective at mitigating bleaching and even amplifying bleaching in the future. The priming and postpriming recovery periods are also likely to shrink in the future along with the increasing duration of MHWs under climate change (Ainsworth et al. 2016; Li and Donner 2023). The potential loss of the protective effects, and increase in possibly adverse effects, from priming further confirms the IPCC consensus that achieving the goals of the Paris Climate Agreement and limiting warming to 1.5°C is vital to preserving the condition of many of the world's coral reefs (Cooley et al. 2022; Logan et al. 2021; McManus et al. 2021).

Author Contributions

Xinru Li: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, validation, visualization, writing – original draft, writing – review and editing. **Simon D. Donner:** conceptualization, funding acquisition, methodology, resources, supervision, validation, writing – review and editing. **Harmony A. Martell:** conceptualization, methodology, validation, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Datasets used in this study are all publicly available. The NOAA Coral Reef Watch CoralTemp v3.1 Global Daily 5-km SST dataset is available at https://coralreefwatch.noaa.gov/product/5km/index_5km_sst.php. The global map of warm-water coral reefs is available at https://doi.org/10.34892/t2wk-5t34. The warm-water coral bleaching database is available at https://zenodo.org/records/6780843. The codes used to compute the warm-season MHW metrics and produce the figures in the paper are available at DOI: 10.5281/zenodo.14041857

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.