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Oceanic differences in coral-bleaching responses to marine heatwaves

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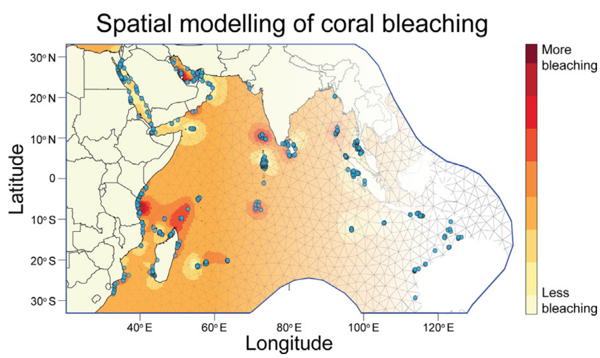
HIGHLIGHTS

- Mass coral bleaching events are a ubiquitous response to marine heatwaves.
- Differences in scope and extent of coral bleaching occur through space and time.
- Spatially explicit Bayesian model was used to examine geographic variation of bleaching.
- Several major differences in bleaching were found among and within oceanic basins.
- Bleaching has tended to occur at increasing temperatures in the last four decades.

GRAPHICAL ABSTRACT



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ABSTRACT

Anomalously high ocean temperatures have increased in frequency, intensity, and duration over the last several decades because of greenhouse gas emissions that cause global warming and marine heatwaves. Reef-building corals are sensitive to such temperature anomalies that commonly lead to coral bleaching, mortality, and changes in community structure. Yet, despite these overarching effects, there are geographical differences in thermal regimes, evolutionary histories, and past disturbances that may lead to different bleaching responses of corals within and among oceans. Here we examined the overall bleaching responses of corals in the Atlantic, Indian, and Pacific Oceans, using both a spatially explicit Bayesian mixed-effects model and a deep-learning neural-network model. We used a 40-year global dataset encompassing 23,288 coral-reef surveys at 11,058 sites in 88 countries, from 1980 to 2020. Focusing on ocean-wide differences we assessed the relationships between the percentage of bleached corals and different temperature-related metrics alongside a suite of environmental variables. We found that while high sea-surface temperatures were consistently, and strongly, related to coral bleaching within all oceans, there were clear geographical differences in the relationships between coral bleaching and most environmental variables. For instance, there was an increase in coral bleaching with depth in the Atlantic Ocean whereas the opposite was observed in the Indian Ocean, and no clear trend could be seen in the Pacific Ocean. The standard deviation of thermal-stress anomalies was negatively related to coral bleaching in the Atlantic and Pacific Oceans, but not in the Indian Ocean. Globally, coral bleaching has progressively occurred at higher temperatures over the last four decades within the Atlantic, Indian, and Pacific Oceans, although, again, there were differences among the three oceans. Together, such patterns highlight that historical circumstances and geographical differences in oceanographic conditions play a central role in contemporary coral-bleaching responses.

1. Introduction

The intensity, frequency, and duration of marine heatwaves are increasing as the planet continues to warm (Bove et al., 2022; Hoegh-Guldberg et al., 2019; Laufkötter et al., 2020). These climate-change-associated

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heatwaves are causing unprecedented, large-scale coral-bleaching events, which often lead to mass coral mortality (Glynn, 1996; Hughes et al., 2018; Leggat et al., 2019; Sully et al., 2019). Bleaching and mortality events lead not only to the decline of coral populations but also to cascading negative effects on the many species that depend on reef corals for shelter and sustenance (Pratchett et al., 2011; Richardson et al., 2018; Stuart-Smith et al., 2018). Yet, oceanic regions vary considerably in past thermal disturbances (Heron et al., 2016; Thompson and van Woesik, 2009), evolutionary histories (Budd and Pandolfi, 2010; Huang and Roy, 2015; Roff, 2021), and both biological and environmental characteristics (Bachman et al., 2022; Roff and Mumby, 2012; Zinke et al., 2018). Therefore, while the biological processes underlying the bleaching responses of corals are seemingly ubiquitous (Baker et al., 2008; Suggett and Smith, 2020; van Woesik et al., 2022), corals respond differently to thermal-stress events depending on history, geography, life histories, and local conditions (Cornwell et al., 2021; Donovan et al., 2021; Gilmour et al., 2022; McClanahan et al., 2020).

Historical events that previously altered coral-community composition and removed thermally vulnerable species can influence the bleaching responses to thermal stress on contemporary coral reefs. Prominent examples of such historical purging occurred in the Atlantic Ocean during the late Plio-Pleistocene, when the Caribbean lost many genera that are still extant throughout the Indo-Pacific, such as *Isopora*, *Galaxea*, *Goniopora*, *Pavona*, *Pocillopora*, and *Stylophora* (Budd et al., 1994; Budd and Wallace, 2008; Pandolfi and Jackson, 2007). Similarly, but in finer taxonomic resolution, the Caribbean has lost a large proportion of the two main *Acropora* species in the past four decades (Aronson and Precht, 2001; González-Barrios et al., 2020). By contrast, the larger and more heterogeneous Pacific and Indian Oceans still support pockets of large populations of corals generally considered thermally vulnerable, such as *Pocillopora* and *Acropora* species (Dietzel et al., 2021; Roff, 2021) — even though reefs in these oceans have experienced substantial population reductions through thermal stresses (Guest et al., 2012; Hughes et al., 2018; McClanahan et al., 2020; Riegl et al., 2017). The Pacific and Indian Oceans also host many more coral species than the Atlantic Ocean and this higher genetic diversity may provide increased capacity for adaptive responses. Therefore, we hypothesize that the broad bleaching responses of coral communities to marine heatwaves in the Pacific and Indian Oceans could be potentially different from the bleaching responses of coral communities in the Atlantic Ocean, which has already lost many of its once-dominant thermally-sensitive species.

The bleaching responses of corals can also vary among regions or habitats within each ocean. Past regional temperatures and habitat-dependent temperature fluctuations have influenced the evolutionary legacies of corals, which may also have repercussions on contemporary coral-bleaching responses to thermal stress (Guest et al., 2012; Howells et al., 2013; Kenkel et al., 2015a; Safaie et al., 2018; Thomas et al., 2022). For example, corals in the Persian-Arabian Gulf have adapted to temperatures that are consistently higher than any other oceanic region worldwide (Howells et al., 2016; Smith et al., 2022). These adaptations to thermal environments may be heritable (Kenkel et al., 2015b; Liew et al., 2020), as recent selective-breeding experiments of corals seemingly transfer enhanced thermal tolerance from parent colonies to offspring (Howells et al., 2021; Quigley et al., 2020). Together, past disturbances, emergent assemblages, and thermal histories all influence the bleaching responses of corals to contemporary thermal stress (Berkelmans, 2002; Donner et al., 2005; Fox et al., 2021; Logan et al., 2014). Yet, a suite of environmental variables also influences thermal stress and the bleaching responses of corals on finer geographic spatial scales (Bachman et al., 2022; McClanahan, 2022; McWhorter et al., 2022), for example, light (Falkowski et al., 1990; Gonzalez-Espinosa and Donner, 2021), depth (Muir et al., 2017; Pérez-Rosales et al., 2021; Smith et al., 2014), flow regimes (Nakamura et al., 2003; Page et al., 2021; Wyatt et al., 2020), and turbidity (Morgan et al., 2017; Sully and van Woesik, 2020; Teixeira et al., 2019).

Over the past four decades, coral-bleaching studies have most commonly occurred at the local scale (Brown et al., 2002; Burgess et al., 2021; Fox et al., 2021; Gilmour et al., 2022; Loya et al., 2001; Maynard et al., 2008; Teixeira et al., 2019), and more recently at regional (Ainsworth et al., 2016; Hughes et al., 2018; Moore et al., 2012; Osman et al., 2018; Stuart-Smith et al., 2018) or global scales (Donner et al., 2005; McClanahan et al., 2019; Safaie et al., 2018; Sully et al., 2019). Nonetheless, broad oceanic differences have rarely been examined and we hypothesize that corals in the major ocean basins will respond differently to thermal stress. Here we use the largest database of global coral bleaching compiled to date (van Woesik and Kratochwill, 2022) to examine the strength, direction, and consistency of the relationships between bleaching responses of corals and a variety of temperature-related metrics in the Atlantic, Indian, and Pacific Oceans. Additional environmental factors that are either suspected or that have been shown in previous studies to influence bleaching responses were also incorporated as potential bleaching predictors (e.g., depth, turbidity, latitude, longitude, and distance to shore). We also examined the influence of coral cover on the bleaching responses of corals to assess the relationship between coral bleaching and coral coverage—to determine whether coral bleaching is positively related to coral cover.

The bleaching responses of corals within and among the Atlantic, Indian, and Pacific Oceans were analyzed using two independent modeling frameworks: (1) a spatially explicit Bayesian mixed-effects model, based on Integrated Nested Laplace Approximation (INLA); and (2) a deep-learning neural-network model. The INLA model was used to determine the influence of fixed, random, and spatial-latent effects. While fixed and random effects are commonly modeled, recent advances in spatially-explicit models capture geographical patterns that are not captured by the environmental variables examined (i.e., spatial-latent effects) (Lindgren and Rue, 2015; Rue et al., 2009). The deep-learning model provided further insight into the nuanced relationships between coral bleaching and environmental variables. Specifically, our objectives were to (i) examine geographical and temporal patterns of coral bleaching, at a broad oceanic scale, within and among the Atlantic, Indian, and Pacific Oceans, (ii) quantify which environmental variables in each of the three oceans were most strongly related to the bleaching responses of corals, and (iii) provide spatial predictions of coral bleaching and coral cover.

2. Methods

We used coral-bleaching data from in situ field surveys compiled in the recent Global Coral Bleaching Database (van Woesik and Kratochwill, 2022). Although the data combined seven different data sources, some of which estimated the bleaching severity of individual coral colonies, we only used site-wide bleaching estimates as our response variable. In this context, for the current study, coral bleaching was defined as the percentage of coral colonies that were recorded as bleached of the total coral colonies recorded per survey. If field surveys characterized bleaching in categories, then the median values of each category were used and expressed as percentages (for further details see van Woesik and Kratochwill (2022). While there were few data on bleaching before the global 1998 bleaching event, the database includes a wide spatial and temporal coverage from 23,288 coral-reef surveys at 11,058 sites in 88 countries, and three oceans, from 1980 to 2020 (Figs. 1, S1-S3).

The 11 environmental variables that were examined to determine whether there were potential relationships with coral bleaching were: (i) coral cover (%); (ii) depth (m), with surveys encompassing shallow to upper mesophotic depth range (i.e., 0–50 m). However, most of the data stem from shallow reefs. In the Atlantic Ocean, surveys ranged from 0 to 43 m with 2 % of the surveys at depths $\geq$ 20 m. In the Indian Ocean, the depth range was 0.65–42 m, with only 0.02 % of surveys at depths $\geq$ 20 m. In the Pacific Ocean, the depth range was 0–50 m, with 0.04 % of surveys at depths $\geq$ 20; (iii) turbidity (K_d490); (iv) latitude; (v) longitude; (vi) distance to shore (km); (vii) mean Sea Surface Temperature (SST) (°C) for the week of the survey; (viii) standard deviation of SST for the week of survey; (ix) the standard deviation of the frequency of Sea Surface Temperature Anomaly (SSTA) over the study period, where the frequency is the number of times over the previous 52 weeks that SSTA $\geq$ 1 °C, and SSTA is the weekly SST minus weekly climatological SST; (x) SSTA Degree

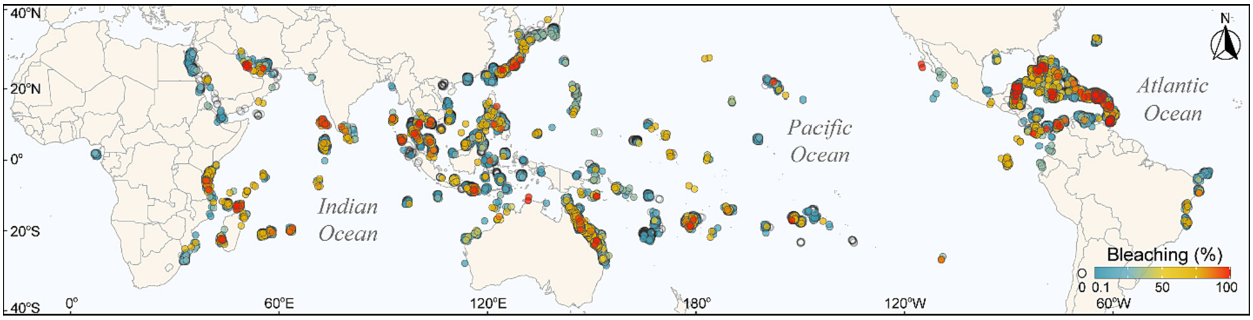

Fig. 1. Prevalence of coral bleaching. Coral bleaching is presented as a percentage of bleached corals at the time of the survey (n = 23,288), measured at 11,058 sites in 88 countries, and three oceans, from 1980 to 2020, based on data compiled by van Woesik and Kratochwill (2022). Colored circles indicate >0 % bleaching (blue) through 100 % bleaching (red), and empty circles indicate no bleaching.

Heating Weeks (DHW), which is the sum of previous 12 weeks when SSTA ≥ 1 °C; and (xi) the standard deviation over the study period of Thermal-Stress Anomaly (TSA) DHW, which is the sum of previous 12 weeks when TSA ≥ 1 °C. For a detailed description of the environmental data sources see the original descriptions of the database by van Woesik and Kratochwill (2022). We initially assessed additional temperature-related metrics and removed metrics with high collinearity. None of the resulting environmental variables used in this study showed high collinearity (Fig. S4).

Two independent-modeling frameworks were used to analyze the bleaching responses of corals within and among the Atlantic, Indian, and Pacific Oceans: 1) a spatially explicit Bayesian mixed-effects model, based on Integrated Nested Laplace Approximation (INLA); and 2) a deep-learning neural-network model. Firstly, we constructed a spatially explicit INLA model that considered the coral-reef environment as a Gaussian random field in which coral bleaching observations (y) at a specific study site (i) were recorded as a percentage of the total coral community that was bleached at the time of the survey. Since coral bleaching was recorded as a percentage, we used a Beta distribution with a logit-link function expressed as:

$$y_i \sim Beta(p_i, \tau) \quad (1)$$

where y_i represents a vector of coral bleaching among sites, p represents the shape parameters of the Beta distribution, and τ qualifies the amount of dispersion. The expected values are represented as:

$$\text{logit}(p_i) = \alpha + \Sigma_{j=1}^{n_\beta} \beta_j z_{ji} + \Sigma_{k=1}^{n_f} f^{(k)}(u_{ki}) + v_{i,t} + \varepsilon_i \quad (2)$$

where α is an intercept coefficient, β_j are coefficients of fixed-effect covariates z_j, (where $j = 1$ to n_β), $f^{(k)}$ is the random effects on covariates u_k (where $k = 1$ to n_f), v is the resurveyed site i through time t considered as a first-order random walk to avoid temporal autocorrelation (i.e., sampling time was considered as a random effect), and ε_i is the measurement error defined by a Gaussian white-noise process ($\sim N(0, \sigma^2_\varepsilon)$). For this analysis, since the environmental variables represent different types of data, each variable was standardized to represent the distance from the variable's mean relative to the standard deviation. This was achieved by subtracting the mean of each environmental variable from each data value and dividing it by the variable's standard deviation. We examined several different model constructs and the results presented in this study are from a model that was selected based on the lowest Watanabe-Akaike Information Criterion.

We performed the INLA analyses initially as a global model (Figs. S5-S7), with the three oceans nested within the global model (i.e., defined hierarchically as a random effect). Additionally, the three oceans were further divided based on their geography into ten ocean realms (Fig. S1), which were also defined hierarchically as a random effect within each ocean. Then, we constructed separate models for each of the Atlantic, Indian, and Pacific Oceans, with the ocean realms nested within each ocean. We used coral cover (%), depth (m), turbidity (K_d490), distance to shore (km), latitude, longitude, and a suite of temperature metrics as fixed effects, and sites, ocean realms, oceans, and time (as the year of the survey) as random effects. The INLA model parameters were estimated using the R packages 'INLA' and 'INLAutils' (Lindgren and Rue, 2015; Redding et al., 2017; Rue et al., 2009). The spatial domain is considered a Gaussian random field, which is indexed in space and represents all spatial processes that can affect variation in coral bleaching (i.e., observed variables and unobserved, spatial-latent effects). To partition out the spatial effects of the measured covariates on coral bleaching, we first developed a spatial projection mesh (i.e., a Delaunay triangulation mesh) that was characterized by the geographic location of the sites (Figs. S5, S8, S11, S14). This mesh allowed an analysis of spatial effects using stochastic partial differential equations (Blangiardo and Cameletti, 2015; Lindgren et al., 2011). We used penalized complexity priors for all INLA analyses (Simpson et al., 2017; Zuur et al., 2017). We were interested in: (i) how much coral bleaching was explained by the β coefficients (Eq. (2)) of the fixed-effect covariates, (ii) the spatial predictions of coral bleaching and coral cover, and (iii) evaluating the unobserved spatial latent effects for the three different oceans. To validate the INLA models we used leave-one-out cross-validation model checking using probability integral transform statistics (Held et al., 2010), and examined the observed against model-fitted plots (Figs. S6, S9, S12, S15).

Secondly, we constructed a deep-learning neural-network model to further characterize the bleaching responses of corals along with each environmental variable and to provide detailed partial-dependency plots by supervised deep-learning, multi-layer feedforward neural network analysis using 'h2o' (Candel and LeDell, 2022) and the associated R package (LeDell et al., 2022). All the data used in the deep-learning model (n = 23,288) were split by 75 %, 15 %, and 15 % to train, validate, and test the model. We evaluated a series of models and selected the model with the lowest deviance as the 'best' model using a random grid algorithm to refine the optimal model characteristics. The 'best' deep-learning model had 10, 10 hidden layers, used model deviance as the stopping metric with three stopping rounds, and used adaptive learning. We used n-fold cross-validation for model validation and partial dependency plots to examine the relationship of coral bleaching with each environmental variable, in each of the three oceans. All models in this study were coded in R v4.1.0 (R Core Team, 2020) and all code and data are available at: https://github.com/rvanwoesik/Oceanic_differences_in_coral_bleaching.

In addition to the INLA and deep-learning models, we used linear mixed-effects models to analyze the 40-year dataset and identify possible long-term trends in the temperature (°C) at which coral bleaching occurred and to determine whether such changes might differ within and among the Atlantic, Indian, and Pacific Oceans. Changes in coral-bleaching temperatures over time were assessed for: (i) all bleaching records (n = 14,057), and (ii) severe-bleaching records, where the percentage of bleaching was >50 % (n = 2251). To account for repeated measures on the same reef, the site was added as a random effect.

3. Results

Sea-surface temperature (SST) (°C) and temperature anomalies measured in degree heating weeks (SSTA DHW) were consistently positively related to coral bleaching in all three oceans (Figs. 2, 3). Yet, there was considerable geographic variation in the relationships between coral bleaching and environmental variables (Figs. 2, 3). For example, coral bleaching was positively related to depth in both the global assessment and in the Atlantic Ocean but was negatively related to depth in the Indian Ocean, whereas depth had no detectable effect on coral bleaching in the Pacific Ocean (Fig. 2). These results suggest that corals in deep habitats were more likely to bleach in the Atlantic Ocean, but depth had less of a consistent effect in the Pacific Ocean, and shallow sites were more likely to bleach in the Indian Ocean (Figs. 2, 3). Coral cover was found to be positively related to coral bleaching in the global assessment and in both the Atlantic and Indian Oceans but had no detectable effect in the Pacific Ocean (Fig. 2).

There was considerable variability in the estimated coefficient for the temperature variable standard deviation of SST in all three oceans (Fig. 2). Nonetheless, the standard deviation of SST was positively related to bleaching in both the global assessment and in the Pacific Ocean (Fig. 2), whereas the same temperature metric had no detectable effect in either the Atlantic or Indian Oceans. By contrast, the standard deviation of Thermal-Stress Anomaly (TSA) measured in Degree Heating Weeks (DHW) was negatively related to coral bleaching in the global assessment, and likewise in the Atlantic and Pacific Oceans (Figs. 2, 3), whereas it had no clear effect in the Indian Ocean, where variability was much larger than in the Atlantic and Pacific Oceans (Fig. 2). Overall, the INLA analyses showed no clear relationships between coral bleaching and turbidity, longitude, and distance to shore (i.e., three of the 11 environmental variables examined) among the three oceans (Fig. 2).

The results of the deep-learning model showed some nuanced relationships that were not apparent using the INLA models. Whereas the INLA analyses incorporated spatial effects and identified the magnitude and direction of the relationships between coral bleaching and the environmental variables, the deep-learning analyses identified further details of these relationships along each environmental gradient (Fig. 3). In this manner, the resulting partial-dependency plots are similar to nonlinear regressions, displaying the response variable (i.e., coral-bleaching percentage) and the standard errors of the coefficients on the y-axis, and displaying the predictor variables on the x-axis. For example, coral bleaching was more likely to be higher at sites with a low coral cover than at sites with a high coral cover in the Atlantic Ocean, whereas coral bleaching seemed to peak at sites with moderate coral cover in the Pacific Ocean, and no clear trend was seen in the Indian Ocean (Fig. 3f). For most variables, the INLA and deep-learning results on the bleaching responses of corals within the Atlantic,

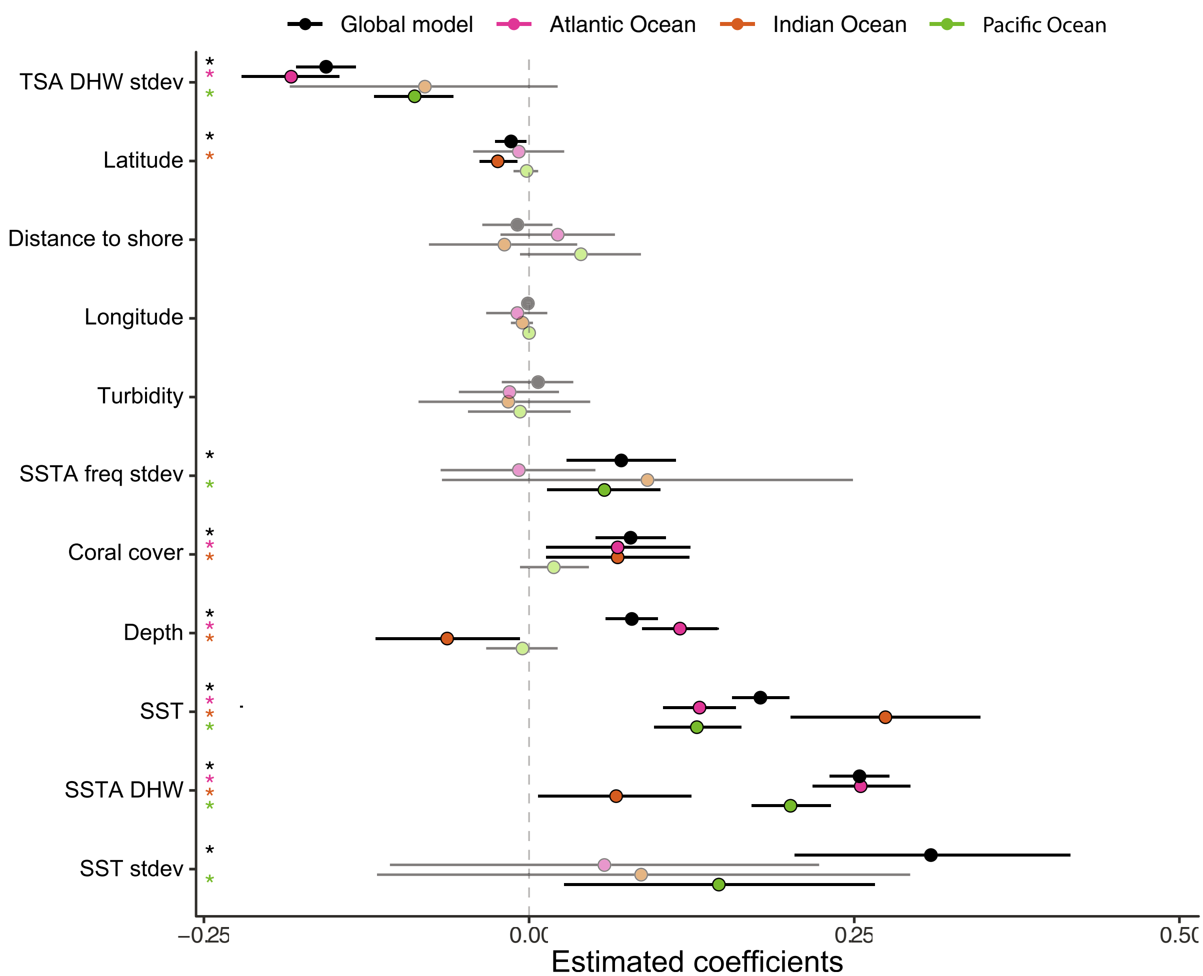

Fig. 2. Relationships between the bleaching responses of corals and the 11 environmental variables. Points represent standardized coefficients of the effect of each environmental variable on the bleaching responses of corals that were estimated using a spatially explicit Bayesian mixed-effects model based on Integrated Nested Laplace Approximation (INLA) with data from 23,288 coral-reef surveys at 11,058 sites in 88 countries, and three oceans, from 1980 to 2020. Lines depict the 95 % credible intervals. The different colors depict the coefficients for the Atlantic, Indian, and Pacific Oceans, whereas the black points portray the coefficients for the global model. TSA is Thermal-Stress Anomaly, DHW is Degree Heating Weeks, stdev is standard deviation, SST is Sea Surface Temperature (°C), SSTA is Sea Surface Temperature Anomaly, and SSTA freq stdev is the standard deviation of the frequency of SSTA. Asterisks indicate where the 95 % credible intervals do not cross zero (dashed line) and therefore suggest that the environmental variable has a clear effect on coral bleaching.

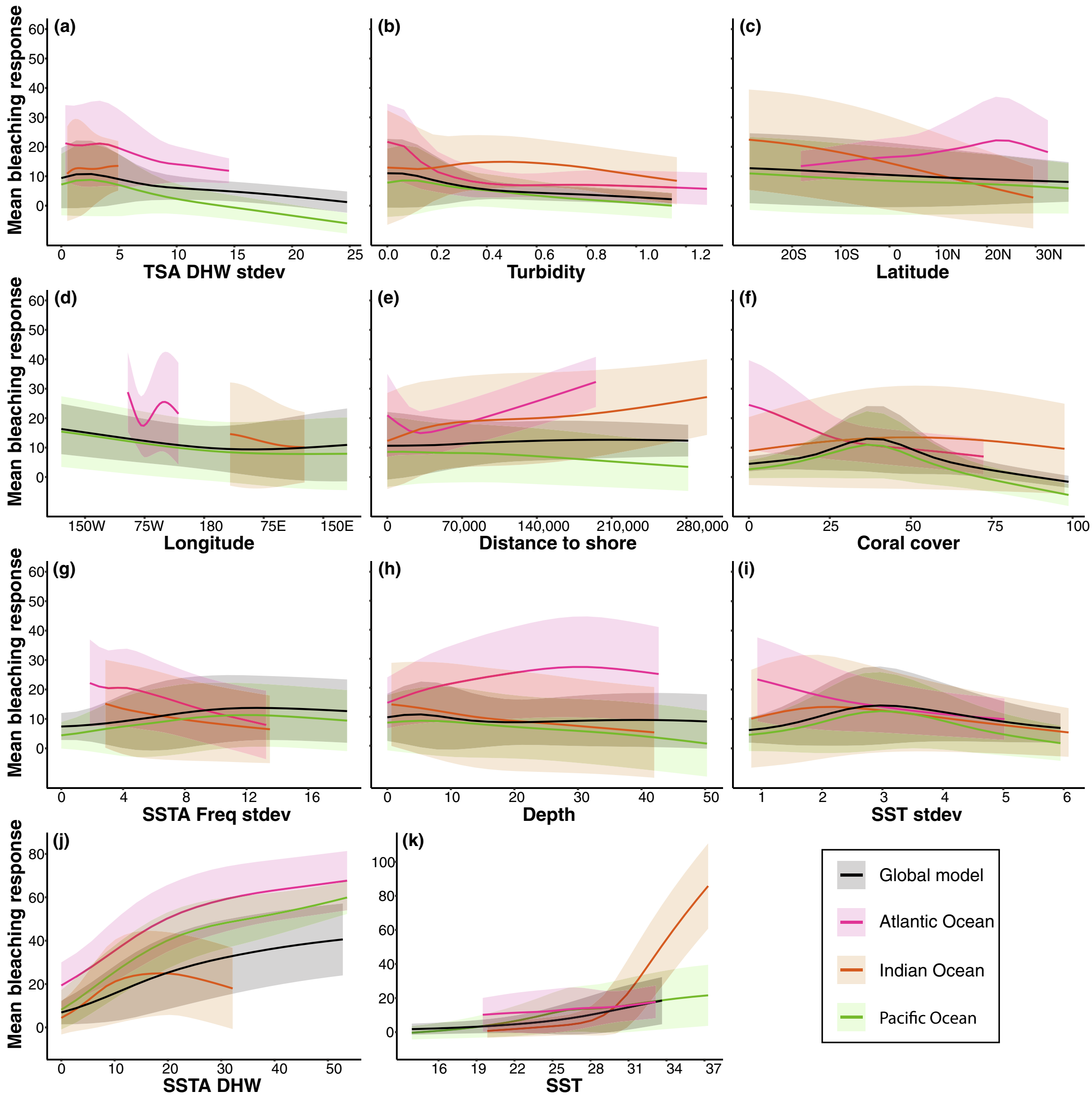

Fig. 3. Partial dependency plots illustrate the effect of each environmental variable on the bleaching responses of corals. Relationships between the bleaching responses of corals and the 11 environmental variables were estimated using a deep-learning model — a neural-network analysis with data from 23,288 coral-reef surveys at 11,058 sites in 88 countries, and three oceans, from 1980 to 2020. The different colors depict the effects, and their standard errors, for the Atlantic, Indian, and Pacific Oceans together with the global model in black. TSA is Thermal-Stress Anomaly, DHW is Degree Heating Weeks, stdev is standard deviation, SST is Sea Surface Temperature (°C), SSTA is Sea Surface Temperature Anomaly, and SSTA freq stdev is the standard deviation of the frequency of SSTA.

Indian, and Pacific Oceans aligned well, although several relationships that were obscured by the large credible intervals using the INLA protocol were unveiled using the deep-learning protocol. For example, the INLA model showed no effect of turbidity within any of the three oceans, whereas the deep-learning model showed that coral bleaching was higher in low-turbidity environments within the Atlantic and Pacific Oceans, but no detectable effect was found in the Indian Ocean (Fig. 3b). Similarly, while the INLA model showed no detectable effect of distance to shore, the deep-learning model showed that in the Atlantic and Indian Oceans coral bleaching was more pronounced on outer reefs (Fig. 3e). The INLA model also showed no detectable effect of the standard deviation of SST on coral beaching in the Atlantic Ocean, whereas the deep-learning model showed a negative tendency in the Atlantic Ocean, with less bleaching at higher standard deviations of SST (Fig. 3i). Similarly, the INLA model did not reveal clear effects of the standard deviation of the frequency of temperature anomalies on coral bleaching in the Indian and Atlantic Oceans, whereas the deep-learning model showed negative tendencies in both oceans (Fig. 3j).

After accounting for all the covariates in the INLA models, the remaining spatial variation in the data represents spatial-latent effects within each ocean that were not explained by the observed environmental variables. In the Atlantic Ocean, such prominent spatial effects were apparent in the vicinity of Trinidad and Tobago, the Virgin Islands, the Dominican Republic, and eastern and western Cuba (Fig. S8c). In the Indian Ocean, latent effects were apparent in southwestern and northern Madagascar, Tanzania, the Lakshadweep Islands, the southern Chagos Archipelago, and the Andaman Islands (Fig. S11c). In the Pacific Ocean, unexplained spatial latent effects of coral bleaching were apparent in the Philippines, southern Japan, the Bonaparte Archipelago, the Marshall Islands, Tuvalu, and Panama (Fig. S14c).

Using the spatial INLA framework, we created prediction maps of coral bleaching and coral cover (Figs. 4, S7, S10, S13, S16). In the four decades

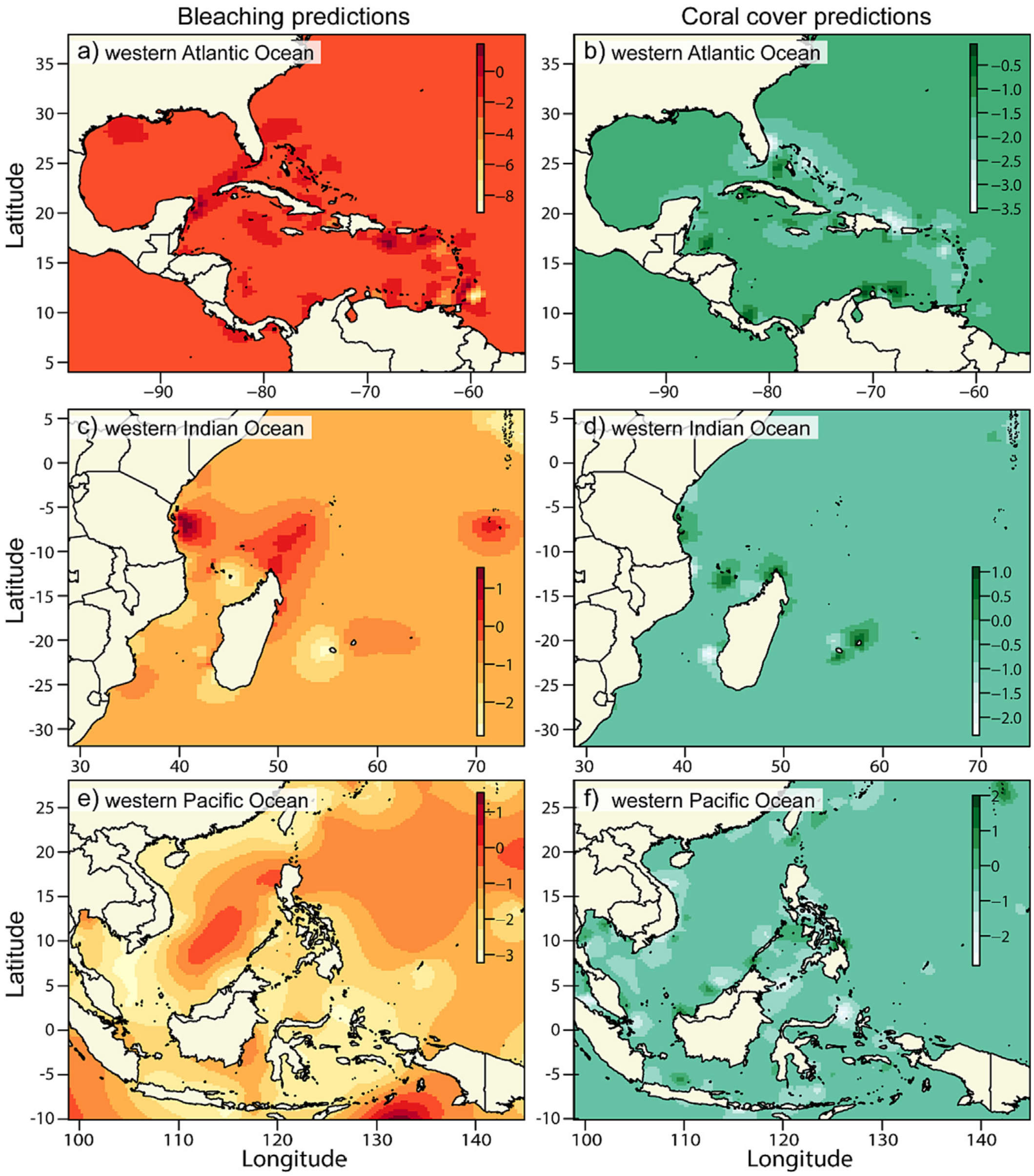

Fig. 4. Spatial predictions of the posterior means, derived from the Integrated Nested Laplace Approximation (INLA) analyses, of coral bleaching (left) and coral cover (right). Predictions for the western Atlantic Ocean (a-b), the western Indian Ocean (c-d), and the western Pacific Ocean (e-f). Note that the values are not absolute values of coral bleaching and coral cover but rather represent relative scales for each geographical area of interest denoting higher and lower values compared with the ocean-wide mean. The broader ocean-scale predictions and their standard deviations are given in the supplementary materials.

between 1980 and 2020 in the Atlantic Ocean, coral bleaching was most prevalent in the Virgin Islands, Puerto Rico, the southern Dominican Republic, the Bahamas, northwestern Cuba, southeastern Mexico (Fig. 4a), and central Brazil (Fig. S10a). By contrast, during the same period, coral bleaching was lower, and the coral cover remained relatively high in some sites off the coasts of Venezuela, Panama, Honduras, Haiti, southwestern Cuba (Fig. 4b), and Brazil (Fig. S10c). In the western Indian Ocean, coral bleaching was particularly high in Seychelles, Tanzania, northern Madagascar, and the southern Chagos Archipelago (Fig. 4c). In the broader Indian Ocean, coral bleaching was also prevalent in the southern Persian-Arabian Gulf, Lakshadweep Islands, the central Andaman and Nicobar Islands, southwestern Sri Lanka, and northwestern Australia (Fig. S13a). Less severe bleaching was recorded in Mozambique, southern Madagascar, Red Sea, central Maldives, Indonesia, and Cocos Islands, whereas relatively less coral bleaching together with a high coral cover were recorded in Mayotte, Reunion, Mauritius (Fig. 4d), southwestern Thailand, northern Malaysia, and Christmas Island (Fig. S13c). In the Pacific Ocean, coral bleaching was relatively high in the northern Philippines, the Spratly Islands, the South China Sea (Fig. 4e), the Marshall Islands, northern Australia, the Great Barrier Reef, and the Galapagos Islands (Fig. S16a), and relatively low coral bleaching was recorded in Taiwan, South China, and Vietnam. Relatively less coral bleaching together with a high coral cover were recorded in the central Philippines, central Indonesia, Malaysia, southern Taiwan (Fig. 4f), Micronesia, Vanuatu, New Caledonia, and French Polynesia (Fig. S16c).

The global trend of coral-bleaching temperature indicates a gradual increase during the last four decades (Fig. 5). The increase in coral-bleaching temperatures is most prominent when looking at severe-bleaching events (i.e., when the percentage of bleaching in a survey was >50 %), which occurred at an increasing temperature with a rate of ca. 0.5 °C per decade for both the Atlantic and Pacific oceans whereas the Indian Ocean showed no detectable trend (Fig. 5b). Globally, the median coral-bleaching temperature has increased from 28.2 °C during 1980–1999 to 28.6 °C during 2000–2009, and to 29.2 °C during 2010–2020 (Fig. 5c).

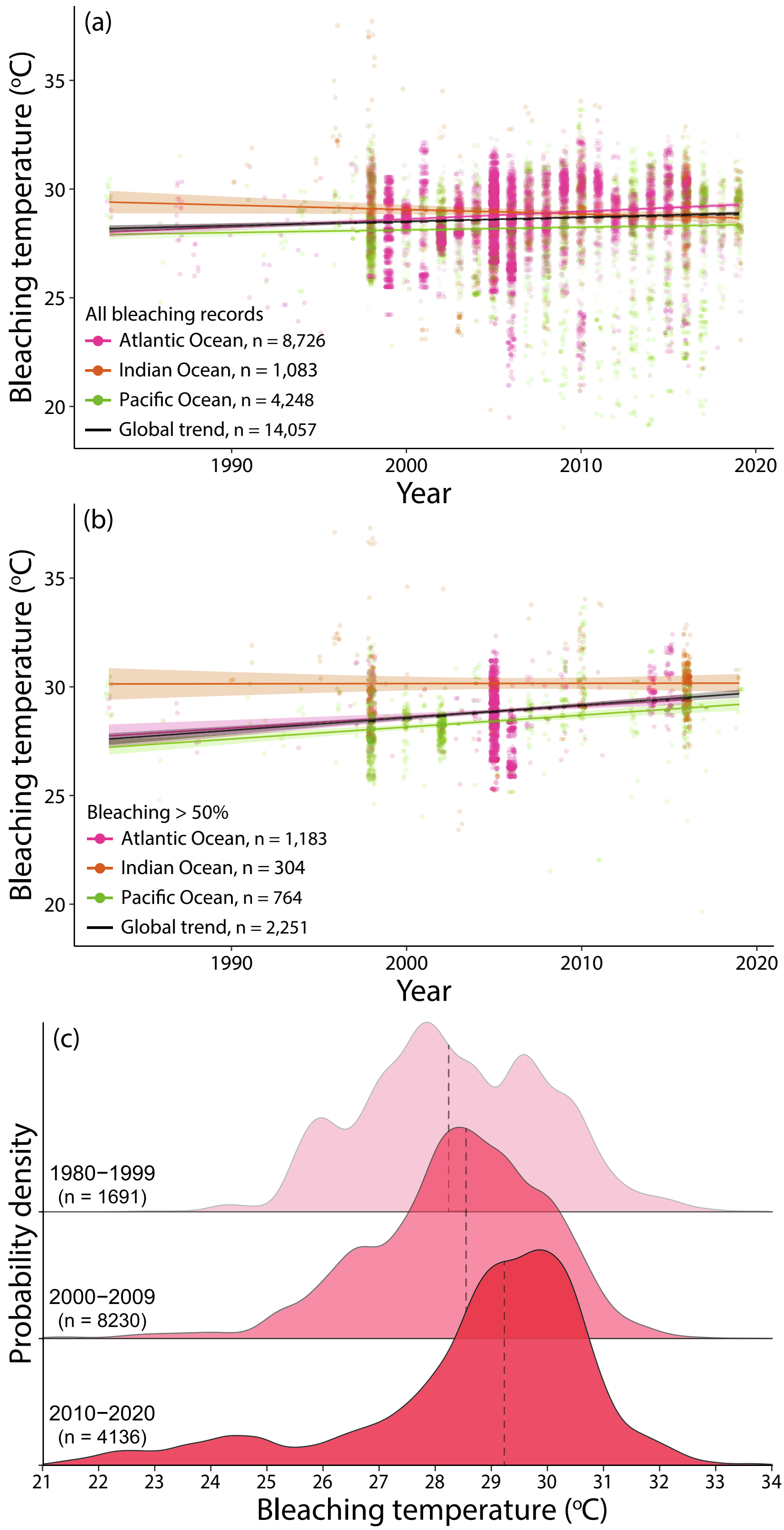

Fig. 5. Increasing trends of coral-bleaching temperatures from 1980 to 2020. (a) All coral- bleaching temperatures (°C) (points) and trends (lines with 95 % confidence intervals). (b) Temperatures (°C) (points) and trends (lines with 95 % confidence intervals) of severe coral bleaching (i.e., when >50 % bleaching was recorded). (c) Probability density distributions of temperatures (°C) at which coral bleaching occurred with dashed lines representing the median coral-bleaching temperature of each period. Data for the earliest decade (i.e., 1980–1989) was limited to only 41 records and therefore the data were pooled with the data from the next decade.

4. Discussion

Our study highlights the extent of spatial and temporal variation in the bleaching responses of corals throughout the world's oceans. The results show several major differences within and among the Atlantic, Indian, and Pacific Oceans. While it was not surprising that coral bleaching varied geographically, our results show a dependency on scale (Elahi et al., 2022; Levin, 1992; Pandolfi, 2002). Trends that were apparent on a global scale were frequently less evident on finer regional scales and vice versa. In most cases, the two modeling frameworks (i.e., an INLA model alongside a deep-learning model) complemented each other in assessing the bleaching responses of corals. The spatially explicit Bayesian mixed-effects model (i.e., the INLA model) provided a spatial component to the coral-bleaching predictions, whereas the deep-learning neural-network model provided further insight into the generalized bleaching responses of corals to environmental variables.

Elevated temperature and high-temperature anomalies were, as expected, consistently positively related to coral bleaching among all three oceans, yet the magnitude of the effects differed, and some temperature metrics were geographically inconsistent. For example, the deep-learning model showed a negative relationship between coral bleaching and the standard deviation of sea-surface temperature in the Atlantic Ocean, but there were non-linear trends in the Indian and Pacific Oceans (Fig. 3). By contrast, the INLA model showed a positive relationship between coral bleaching and the standard deviation of sea-surface temperature in the Pacific Ocean. Similarly, coral bleaching in the Atlantic and the Pacific Oceans appeared to be lower in localities with a high standard deviation in thermal-stress anomalies, whereas in the Indian Ocean there was no clear relationship, likely because of high variation in the data of the Indian Ocean (Fig. 2). By contrast, reefs in the Atlantic Ocean showed a positive relationship between coral bleaching and depth but a negative relationship in the Indian Ocean and no effect of depth on bleaching for the Pacific Ocean. While it seems that corals on deep reefs were more likely to bleach in the Atlantic Ocean, corals on deep reefs in the Indian Ocean were less likely to bleach. This contrast might be because our dataset included more survey data at sites deeper than 20 m (including data from upper mesophotic depths) in the Atlantic Ocean than in the two other oceans.

There are several potential reasons for the overall differences in the bleaching responses of corals among the three oceans, including being conditional on historical events, geographical circumstances, and contemporary thermal regimes. On the one hand, historical seawater temperatures may create certain evolutionary legacies, influencing contemporary coral distributions and thermal tolerances (Fine et al., 2013; Howells et al., 2013; McClanahan et al., 2020; Smith et al., 2022; Thompson and van Woesik, 2009; Voolstra et al., 2021). On the other hand, more recent temperature fluctuations may predispose contemporary corals to increased thermal tolerance through rapid acclimatization, epigenetic modifications, or adaptation (Barshis et al., 2013; Brown et al., 2002; Guest et al., 2012; Hackerott et al., 2021; Matz et al., 2020; Maynard et al., 2008; Oliver and Palumbi, 2011; Schoepf et al., 2022; Thomas et al., 2022). Another plausible explanation for the oceanic differences in the bleaching responses of corals might be related to the species composition. For example, there are major oceanic differences in the abundance of fast-growing, branching coral species (e.g., *Acropora*, *Isopora*, *Pocillopora*, *Stylophora*), which are frequently among the most sensitive species to thermal stress (Frade et al., 2018; Gilmour et al., 2022; Loya et al., 2001; Riegl et al., 2017). While there are well over 100 species of *Acropora* in the Indo-Pacific (Cowman et al., 2020; Wallace et al., 2012), there are only three nominal *Acropora* species in the Atlantic Ocean (van Oppen et al., 2000; Vollmer and Palumbi, 2002). Moreover, compared with historical records, contemporary Atlantic coral reefs support a low abundance of *Acropora* colonies (Pandolfi and Jackson, 2007; Precht and Miller, 2007), and their decline has accelerated in recent decades because of disease and thermal stress (Aronson and Precht, 2001; Pandolfi, 2002; Randall and van Woesik, 2015).

At the global scale, and in both the Atlantic and Indian Oceans, coral bleaching appeared more prevalent where the coral coverage was high, but that pattern was less evident in the Pacific Ocean (Fig. 2). This result may be a consequence of reefs with low coral cover having been already subjected to strong environmental filtering and the purging of the more thermally sensitive corals. As coral species naturally differ in both their short- and long-term thermal tolerances (Burgess et al., 2021; Grottoli et al., 2014; Loya et al., 2001; van Woesik et al., 2011; Voolstra et al., 2020), some of the oceanic differences we found are likely a consequence of major differences in the composition of coral-species assemblages, along with their genotypic diversity, adaptive capacity, and the environmental conditions to which the corals are subjected.

Our results further show that on the broad-community level, coral bleaching has occurred globally at progressively higher temperatures through the last four decades. These results agree with earlier findings based on a smaller dataset (Sully et al., 2019). Yet, the underlying mechanisms as to why corals have shown a general trend to bleach at higher temperatures and why it is not apparent in the Indian Ocean remain unclear. Several different processes, however, can show the same convergent response pattern. Such processes range from the acclimatization of individual coral colonies, such as shifts in endosymbionts (e.g., microalgal or microbial symbionts), epigenetic modifications, and differential bleaching and mortality of certain phenotypes or genotypes, to environmental filtering of more thermally-sensitive species, leading to wide changes in species composition (van Woesik et al., 2022). Resolving the fundamental question of whether the higher temperatures at which corals bleach represents relatively rapid levels of coral acclimatization, adaptation, or shifts in community structure is critical. Such research will also necessitate efforts to increase the taxonomic resolution in many coral bleaching and recovery surveys to identify the corals at a species level. Nonetheless, even for coral species or locations in which acclimatization and adaptation may occur, such adjustment processes are likely to be non-linear and finite, reaching thresholds beyond which further adjustments are unlikely (Ainsworth et al., 2016; Frieler et al., 2013).

While our results largely agree with earlier global assessments of the effects of environmental variables on coral bleaching (Donner et al., 2017; McClanahan et al., 2020; Safaie et al., 2018; Sully et al., 2019), there were however a few disparities between our study and previous studies. Notably, previous studies found that temperature variability may mitigate coral bleaching (Safaie et al., 2018; Sully et al., 2019). We found that the standard deviation of Thermal-Stress Anomaly (TSA; measured in degree heating weeks) was negatively related to coral bleaching, however, we did not find a consistent negative relationship between the standard deviation of Sea-Surface Temperature (SST) and coral bleaching across all oceans, as shown, for example, by Sully et al. (2019), except for such a tendency in the Atlantic Ocean. One reason for the differences among studies may be related to the amount, and spatial and temporal extent of the data. For instance, Safaie et al. (2018) used data from 118 sites, while Sully et al. (2019) compiled data from 3351 sites, whereas in the present study, we obtained data from 11,058 sites. Another reason for the differences among studies may be related to the modeling framework involved in each analysis. The spatially-explicit INLA modeling framework in this study allowed us to explicitly account for spatial autocorrelation in the data and not over-inflate our degrees of freedom. Further exploration of modeling frameworks is necessary to optimize the approach and bridge biological scales so that future predictions of coral bleaching will continue to improve (van Woesik et al., 2022). Moreover, it will be valuable to continue exploring more environmental predictors, including non-temperature-related variables that may be related to site-specific responses. For example, flow regimes (e.g., ocean currents, upwelling, internal waves, etc.) can substantially influence the amount of thermal stress and bleaching of corals (Nakamura et al., 2003; Page et al., 2021; Wyatt et al., 2020). Similarly, local nutrient fluxes are also known to influence coral-bleaching responses (DeCarlo et al., 2020; Donovan et al., 2020; Morris et al., 2019; Wiedenmann et al., 2013). Therefore, it will be beneficial to incorporate such local factors into future predictive models.

Although our study provides a useful step toward understanding the differences in the bleaching responses of corals to thermal stresses within and among the Atlantic, Indian, and Pacific Oceans, some limitations to this approach warrant further consideration. Large-scale studies of this type make the implicit assumption that the environmental variables used in the study accurately reflect the conditions at which corals bleach, and similarly that the response variable accurately reflects the bleaching response of corals on a reef during thermal stress. While there are numerous temperature metrics and products used in coral-bleaching studies (McClanahan, 2022; McClanahan et al., 2019; Safaie et al., 2018; Sully et al., 2019), which continue to improve (DeCarlo, 2020; Skirving et al., 2020), most large-scale temperature metrics, and many other environmental data products, are composite images of remotely-sensed data (which may or not be adequately ground-truthed) that have been integrated to form maps. The integration process is receiving more attention as spatial error can be propagated across space and is proportional to data availability (Meyer and Pebesma, 2022). Other additional sources of data uncertainty include the potential decoupling between a peak in thermal stress and the time of survey. Surveys conducted before or after a peak in thermal stress may report different levels of bleaching than surveys conducted during a peak in thermal stress. Likewise, inconsistencies in temporal sampling can introduce additional bias. For example, sites, with or without bleaching, that were surveyed in the early years of this study and not surveyed through the latter years of the study may bias temporal interpretation. In addition, while our dataset has extensive geographical coverage, repeated sampling at remote localities is still limited. Another caveat is the nature of the compiled database that includes survey results using different field methodologies — coral bleaching may be over- or under-estimated depending on the methodology deployed. Still, the potential issues using data from different assessment protocols may be relatively negligible, compared with the geographical and temporal benefit that is gained by examining a global dataset at tens of thousands of survey sites. Such large-scale studies are likely to capture the broad regional and oceanic trends in bleaching responses, although they might miss nuances at local scales.

Much attention is increasingly being given to conservation research and management needs on local, regional, national, and international levels, especially considering global warming as the single largest threat to coral reefs (Beyer et al., 2018; Hoegh-Guldberg et al., 2018; Hughes et al., 2017; Kleinhaus et al., 2020; Mumby et al., 2011). Only directing efforts to protect areas that might be regarded as climate refugia, based on their current and projected temperature regimes, does not seem enough to preserve reefs into the future (Dixon et al., 2022) and a more holistic approach to preservation is warranted (Beger et al., 2015; Gajdzik et al., 2021; van Woesik et al., 2022). To that end, our maps of the geographic variation in the bleaching responses of corals to thermal stress are valuable and can be used alongside other spatial studies that assess the thermal tolerance of corals (Cornwell et al., 2021; Dixon et al., 2015; Drury et al., 2022) and highlight localities with high adaptive potential to thermal stress (Matz et al., 2020; Selmoni et al., 2020a; Walsworth et al., 2019). Such work can be combined with studies on the magnitude of human impacts (Andrello et al., 2022; Elahi et al., 2022), studies on reefs with high species and genetic diversity (Beger et al., 2014; Selmoni et al., 2020b), and studies on locations that may still currently support high coral coverage (Elahi et al., 2022; Sully et al., 2022). Together, such spatially-explicit approaches are essential for designing conservation networks of prioritized interconnected reefs (Beger et al., 2015; Cheung et al., 2021; Chollett et al., 2022; Gajdzik et al., 2021; van Woesik et al., 2022; Vercammen et al., 2019) and are key to supporting policies and providing decision-support tools for the management and spatial planning of coral-reef conservation efforts.

CRediT authorship contribution statement

Tom Shlesinger: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Writing – original draft, Visualization. **Robert van Woesik:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Writing – original draft, Visualization, Funding acquisition.

Data availability

The data used in this study were sourced from the Global Coral-Bleaching Database compiled by van Woesik and Kratochwill (2022). All code and data used in this study will be available upon publication at: https://github.com/rvanwoesik/Oceanic_differences_in_coral_bleaching.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.162113.

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