

RESEARCH ARTICLE

Past disturbances and local conditions influence the recovery rates of coral reefs

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Abstract

Corals are being increasingly subjected to marine heatwaves. Theory suggests that increasing the intensity of disturbances reduces recovery rates, which inspired us to examine the recovery rates of coral cover following marine heatwaves, cyclones, and other disturbances at 1921 study sites, in 58 countries and three oceans, from 1977 to 2020. In the Atlantic Ocean, coral cover has decreased fourfold since the 1970s, and recovery rates following disturbances have been relatively slow, except in the Antilles. By contrast, reefs in the Pacific and Indian Oceans have maintained coral cover and recovery rates over time. There were positive relationships between rates of coral recovery and prior cyclone and heatwave frequency, and negative relationships between rates of coral recovery and macroalgae cover and distance to shore. A recent increase in the variance in recovery rates in some ecoregions of the Pacific and Indian Oceans suggests that some reefs in those ecoregions may be approaching a phase shift. While marine heatwaves are increasing in intensity and frequency, our results suggest that regional and local conditions influence coral recovery rates, and therefore, effective local management efforts can help reefs recover from disturbances.

KEYWORDS

climate change, corals, cyclones, marine heatwaves, recovery

1 | INTRODUCTION

Increasing the intensity and frequency of disturbances in natural systems theoretically reduces the recovery rate (Dakos et al., 2012; Veraart et al., 2011). Yet some studies indicate that if a system is to persist, recovery rates must rise in tandem with environmental stress (Pianka, 1970). Indeed, a paleontological study examining recovery rates in tropical rainforests over the past 20,000 years found that recovery rates increased with an increase in disturbance frequency (Cole et al., 2014). Similarly, the recovery rates of several fish populations increased following several decades of heightened fishing pressure but decreased following intensive overexploitation (Neubauer et al., 2013). Such a decoupling between theory and field

estimates led us to examine the recovery rates of corals across the Pacific, Indian, and Atlantic Oceans and to determine the impact of disturbance frequency and intensity since the 1970s.

Historically, cyclones, diseases, and Crown-of-thorns sea stars have been the predominant disturbances on coral reefs (Colgan, 1987; Connell, 1978; Gardner et al., 2005). However, marine heatwaves are increasing in frequency, intensity, and duration across the oceans (Oliver et al., 2021; van Hooidonk et al., 2013). Marine heatwaves impact reefs on larger spatial scales than cyclones (Dietzel et al., 2021) and cause coral bleaching (Glynn, 1993; Hoegh-Guldberg et al., 2007), frequently leading to coral mortality and changes in species composition (Loya et al., 2001; Pandolfi et al., 2011; van Woesik et al., 2022). Some coral populations

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recover from bleaching and mortality events whereas other coral populations do not (Graham et al., 2011; van Woerik et al., 2011). Although there has been a dedicated effort to examine the geographical response of corals to thermal stress events (McClanahan et al., 2020; Safaie et al., 2018; Sully et al., 2019), few studies have reported responses in coral recovery following bleaching events (Connell, 1997; Gilmour et al., 2013; Graham et al., 2011, 2015). Therefore, there is a need to quantify coral recovery under these novel disturbance regimes and to determine recovery expectations at local, regional, and global scales, particularly given the accelerating rate of ocean warming.

There are potentially many reasons why corals at some localities recover more quickly than corals at other localities (González-Barrios et al., 2023; Graham et al., 2011). Differences in recovery may depend on the intensity, scale, and frequency of past disturbances (Dietzel et al., 2021; González-Barrios et al., 2023; Hughes et al., 2019; Thompson & van Woerik, 2009). Reefs that experience mild disturbances may continue to support remnant corals, from which recovery can be rapid (Brown & Suharsono, 1990; Schoepf et al., 2020b), whereas reefs that experience intense disturbances will support low coral cover immediately following the disturbances, and recovery will primarily depend on recruitment from other reefs (Gilmour et al., 2013; Golbuu et al., 2007). Recovery from such intense disturbances may take decades on regionally isolated reefs (Gilmour et al., 2013), particularly when recovery depends on recruitment from distant reefs. Even on aggregated reefs, such as the Great Barrier Reef, large-scale disturbances can isolate disturbed reefs, slowing recruitment and recovery (Dietzel et al., 2021). By contrast, highly aggregated reefs that are mildly disturbed can recover rapidly (Golbuu et al., 2012).

Rates of recovery also depend on environmental circumstances, both regionally (González-Barrios et al., 2023; Graham et al., 2011; Houk et al., 2020; Souter et al., 2021) and locally (Golbuu et al., 2007; Graham et al., 2015). For example, coral recovery is highly dependent on habitat type (Gouezo et al., 2019) and the structural complexity of the reef (Graham et al., 2015). In addition, high nutrient loads (Graham et al., 2015) and the direct influence of rivers (Golbuu et al., 2011) can deter coral recovery. Biological circumstances can also play a role in coral recovery, such as the density of herbivorous fishes (Graham et al., 2015), the presence of macroalgae (Fabricius et al., 2023; Smith et al., 2023), and community composition (Darling

et al., 2019; McWilliam et al., 2020). To date, most coral reef recovery studies have been localized (Gilmour et al., 2013; Golbuu et al., 2007; Gouezo et al., 2019; Schoepf et al., 2020a; but see González-Barrios et al., 2023; Tebbett et al., 2023). There is, therefore, a need to quantify coral recovery at local, regional, and global scales, particularly given the accelerating rates of ocean warming. Here, we examine coral recovery rates in the Pacific, Indian, and Atlantic Oceans from 1977 to 2020 and seek to determine whether the rates of recovery are geographically predictable.

2 | METHODS

2.1 | Collection of coral cover data

The recovery data used in this study were field measurements of two-dimensional estimates of coral coverage expressed as a percentage at each study site. A study site is defined as a unique latitude–longitude coordinate point. We compiled 24,992 data records on coral cover for 12,266 sites in three oceans from 1977 to 2020 (see Supplementary Information for details) (Figure 1). Rates of recovery were derived from 1921 study sites with two or more time steps. There were two main data sources for this project. The first data source was a compilation of data from established monitoring programs (Table S4). The second data source was data extracted from the published scientific literature, which was currently unavailable in any database (Table S5). Data were collected from 154 primary sources and five databases (Tables S4 and S5). Data were collected from the primary literature, from (i) published figures, using WebPlotDigitizer Version 4.6 (Rohatgi, 2022), (ii) tables, and (iii) the main text when provided. We collected information on a site's latitude and longitude coordinates, sampling date and depth, and coral cover information. Latitude and longitude coordinates were converted to decimal degrees and when not explicitly provided the coordinates were added using Google Earth using the figures provided in the article as a guide. Any coordinates that fell on land or were >1 km from a reef were removed. Depth values (m) that were given as a range in the published article were averaged. A midpoint was selected for date ranges. All of the primary literature resources that were used to derive data are provided in Table S5, in the supplementary document.

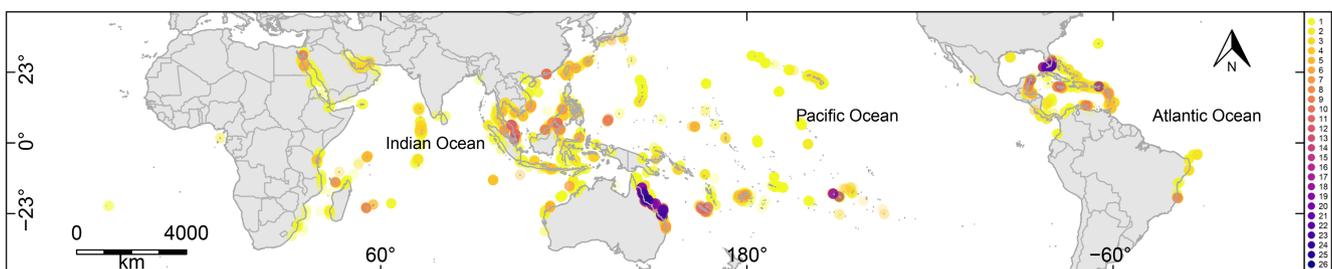


FIGURE 1 The study sites ($n = 12,266$). The colors signify the number of repeated surveys (from 1 to 26) at each study site from 1977 to 2020. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

2.2 | Determining recovery periods

The data on coral cover at each study site were considered as time series. To detect recovery periods and disturbances, the coral cover of each time series was converted to relative coral cover (i.e., relative to the maximum cover in the time series), and the dates (i.e., month and year) were identified when the coral cover was at local minimum and maximum values. The “expand. Grid” function was used in R (R Core Team, 2022) to create all possible combinations of the local minimum and maximum values, which includes illogical instances where the start date would occur after the end date. To avoid this illogical problem, we removed any instances where the end date occurred at the same time or before the start date so that only instances where the start date occurred before the end date remained in the dataset. The cumulative change in coral cover (Δ) was calculated using the following equation:

$$\text{Change in coral cover } (\Delta) = \frac{\text{Sum } (Y_2 - Y_1) + \varepsilon}{t_2 - t_1}, \quad (1)$$

where Y_1 is a list containing all time-series data between the start value and the end value -1 . Y_2 is a list containing all time-series data between the start value $+1$ and the end value, t_1 is the time-stamp of the start value, t_2 is the time-stamp of the end value, and ε is the relative coral cover error value used to account for noise and sampling error. When evaluating recovery, ε was set to 10% relative cover, and for disturbances, ε was set to -10% relative cover. After Δ was calculated for every combination of values in the expanded grid, Δ values were compared to determine where recovery periods or disturbances were occurring. Recovery periods were identified as sections of the time series where Δ values were positive and disturbances were identified as sections where Δ values were negative. We wrote an algorithm to categorize recovery periods and duration.

Once a recovery period or a disturbance was identified, the algorithm was programmed to move to the endpoint of that period and continue to evaluate the time series for further events. To check for any potential biases, the algorithm was programmed to determine whether the magnitude of change was greater than or less than the change without the first data point. If the magnitude of change was greater without the first data point, then the first data point was removed from the set and marked as a separate event. Next, the recovery periods and disturbances were run through separate combining functions to examine whether they were chronologically adjacent. If two or more identified periods were chronologically adjacent and similar, then the algorithm was programmed to check whether the difference in relative coral cover between the end of the first period and the beginning of the second period was greater than -10% change for recovery periods and less than 10% change for disturbances. If the difference was within 10%, then the periods were combined. All overlapping recovery periods were combined. Recovery periods that occurred within a disturbance or had less than a 10% change in relative coral cover were removed (the algorithms and associated functions are all available on <https://zenodo.org/records/10366199>).

2.3 | Calculating rate coefficient

To calculate the recovery rate, an exponential growth equation and a modified Gompertz equation were utilized. Recovery periods with three or more time steps that exhibited exponential growth were calculated using an exponential growth equation (Equation 2) defined as

$$\text{Coral cover}_t = \text{Coral cover}_{t_0} e^{r\Delta t}, \quad (2)$$

where Coral cover_{t_0} is the coral cover at time 0, Coral cover_t is the coral cover at time t , r is the rate of recovery coefficient, and Δt is the difference in time in years over which coral cover was estimated in the field studies. The r coefficients were estimated using the *nlsLM* function in the “*minpack.lm*” package (Elzhov et al., 2022). Note that a nonlinear least squares approach requires more than two data points to calculate exponential growth and exponential growth cannot be estimated when coral cover exhibits sigmoidal growth. Recovery periods with four or more time steps that exhibited sigmoidal growth were calculated using a modified Gompertz equation (Equation 3) defined as

$$\text{Coral cover} = (a - d)e^{-e^{-(t-f)}} + d, \quad (3)$$

where a is an estimate of the maximum potential coral cover for a given site, d is the minimum coral cover of the time series, f is the inflection point marking the maximum increase, c is the sigmoidal growth rate, and t is time in years. The coefficients of Equation 3 were estimated using the field data and the package “*drc*” (Ritz et al., 2015). Note that the nonlinear least squares approach requires more than three data points to estimate the coefficients of the Gompertz equation. Coral cover values from time 0 and f (the inflection point) were then used to solve for r in Equation 2. Recovery rates for time series with only two time steps, or sigmoidal growth with three time steps were calculated by solving Equation 2 for r using the first and last values in the time series.

2.4 | Deriving environmental variables

To examine the relationship between coral recovery and 14 environmental variables and habitat type, we collated data at each site for (i) frequency of heatwaves before recovery, (ii) maximum Degree Heating Weeks (DHW) during recovery, (iii) water clarity which is herein referred to as turbidity (K_d490) (note that while turbidity specifically describes suspended particles, K_d represents changes in water clarity from both particles, dissolved materials, and the water itself; in previous publications, we used the term turbidity, and therefore to be consistent, we will use turbidity in the present study), (iv) depth (m), (v) total gravity (Cinner et al., 2018), (vi) distance to shore (m), (vii) sea surface temperature (SST) kurtosis, (viii) SST skewness, (ix) climate velocity ($^{\circ}\text{C year}^{-1}$), (x) reef density (i.e., the percentage of reef area per 100km^2), (xi) initial coral cover, (xii) macroalgae cover at the beginning of the recovery period, (xiii) cyclone frequency before recovery, (xiv) maximum cyclone windspeed during recovery, and (xv) habitat type.

To examine the historical frequency and intensity of marine heatwaves, DHW values were compiled for all sites from 1985 to 2020 using the National Oceanic and Atmospheric Administration Coral

Reef Watch Database and DHW ("NOAA Coral Reef Watch," 2018). While marine heatwaves in the eastern Pacific extend back to the early 1980s, the availability of NOAA heatwave data started in March 1985. The percentage of time that a site experienced a DHW of eight or more across a time period was used to identify the intensity of marine heatwaves in an ocean basin. DHW values from 1985 to 2020 were extracted for all sites using 5-km daily resolution DHW data, using the nearest 5 adjacent cells, from NOAA's Coral Reef Watch ("NOAA Coral Reef Watch," 2018). To provide a metric for the change in frequency and intensity of heatwaves on an ocean-basin scale, the percentage of sites that experienced a DHW event of 8 or greater was calculated for all years from 1985 to 2020 for each ocean. To determine the frequency of heatwaves at a site before a recovery event, the number of heatwaves ($DHW \geq 4$) from March 1985 to the start of the recovery period was divided by the difference in years from 1985 to the start of the recovery period. The maximum DHW during recovery was extracted as the maximum value that occurred between the first and last time steps during the recovery period.

Turbidity was derived from the National Aeronautics and Space Administration's (NASA) Earth Observing System Data and Information System (EOSDIS) Modis-Aqua satellite database, which measured turbidity as the diffuse attenuation coefficient of light at 490nm wavelength (K_d490) at a 4-km monthly resolution beginning in mid-2002 to March 2020 (<https://oceancolor.gsfc.nasa.gov/l3/>). These data were used to calculate the mean turbidity at each site. Depth was reported during field sampling and is the mean depth of the site in meters. Total gravity is a measure of local human pressure on a reef, calculated as a function of human population size and travel distance to the reef at a resolution of 10km, globally (Cinner et al., 2018). Distance to shore was measured using Google Earth as the distance of each site to the nearest landmass in meters. SST kurtosis is the sharpness of shape-related SST distribution at each study site. SST skewness is the degree of asymmetry of the shape-related SST distribution at each study site. The kurtosis and skewness measurements were derived from NOAA's Optimum Interpolation SST V2 (Reynolds et al., 2002) (<https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.html>) data at $1^\circ \times 1^\circ$ weekly resolution from 1990 to 2022 and calculated using the package "e1071" (Meyer et al., 2023). Climate velocity ($^\circ\text{C year}^{-1}$) is the change in mean monthly SST at a resolution of $1^\circ \times 1^\circ$ from 1960 to 2009 calculated using the package "VoCC" (García Molinos et al., 2019). Habitat type was derived from Allen Coral Atlas ("Allen Coral Atlas," 2022). Reef density was calculated from Allen Coral Atlas ("Allen Coral Atlas," 2022) (see Figures S2 and S3) and represents the percent coral-reef area within 10km^2 . Initial coral cover and initial macroalgae cover were derived from the first point in the recovery period. Coral cover before the recovery period was also derived but was not used in the model as it was highly correlated (>0.7) with initial coral cover. Prior cyclone frequency is the number of cyclones that occurred within 1 arc degree ($\sim 111\text{km}$) of a site from 1970 to the start date of the recovery period divided by the number of years from 1970 to the start date. The maximum cyclone windspeed was calculated from NOAA's International Best Track Archive for Climate Stewardship (IBTrACS)

data, v. 04 (Knapp et al., 2010, 2018) and is the maximum windspeed of cyclones that occurred within 1 arc degree ($\sim 111\text{km}$) of a site during a recovery period. If no cyclones occurred within 1 arc degree ($\sim 111\text{km}$) of a site during the recovery period, the value was set to 0.

2.5 | Data analysis

The Dunn's test with Holm corrections (Dunn, 1964) using the R package "FSA" (Ogle et al., 2023) was run following a Kruskal–Wallis test to determine whether the distributions of the r -coefficients were statistically different across ocean basins. The Anderson–Darling test (Scholz & Stephens, 1987) using "kSamples" (Scholz & Zhu, 2019) was used to determine whether the r -coefficients for each of the four time steps, for each subregion, were likely to stem from the same distribution. We also examined whether the variance of the rates of recovery varied over time using a nonparametric Fligner–Killeen test on both the ecoregion and basin scale. In addition, we constructed a Bayesian mixed effects model that considered the coral reef environment as a Gaussian random field in which the coral recovery observations (r) at a specific study site (i) were recorded over time, represented as

$$\log(r_i) = \alpha + \sum_{j=1}^{n_\beta} \beta_j z_{ji} + \sum_{k=1}^{n_r} f^{(k)}(u_{ki}) + v_{i,t} + \varepsilon_i, \quad (4)$$

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 ($k = 1$ to n_r), v is the resurveyed site through time t considered as a first-order random walk to avoid temporal autocorrelation, and ε_i is the measurement error defined by a Gaussian white-noise process ($\sim N(0, \sigma^2)$). The posterior distributions were estimated using an Integrated Nested Laplace Approximation using the R packages "INLA" and "INLAutils" (Lindgren & Rue, 2015; Redding et al., 2017; Rue et al., 2009). The spatial domain represents all spatial processes, including observed and unobserved spatial latent effects that can affect variation in coral recovery. We developed a spatial projection mesh by defining the Matérn field using triangulation to partition out the spatial effects of the measured covariates on coral recovery (Blangiardo & Cameletti, 2015; Lindgren et al., 2011). The spatial effects were determined using stochastic partial differential equations (Lindgren et al., 2011).

Using "corrplot" (Wei & Simko, 2021), we tested all environmental variables for collinearity and removed any positive or negative collinear variables >0.7 . We used 14 uncorrelated, continuous environmental variables and habitat type as fixed effects. We defined sites, oceans, and year as random effects to partition any spatial or temporal autocorrelation. Additionally, the number of samples in the recovery period and the derivation method of recovery rate were defined as random effects to remove potential artifacts from the methodology. All covariates used in the analysis were standardized by subtracting the mean and dividing by the standard deviation. We were mainly interested in the β coefficients in Equation 4 to determine the relationships between the fixed-effect covariates

and coral recovery. We used penalized complexity priors throughout the analyses (Simpson et al., 2017; Zuur et al., 2017). To validate the 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. Model selection was based on the lowest Watanabe–Akaike information criterion. All R code scripts and datasets will be available when the manuscript is accepted for publication at <https://zenodo.org/records/10366199>.

3 | RESULTS

In all oceans, the percentage of sites that experienced moderate (DHW ≥ 4 and < 8) and severe marine heatwaves (DHW ≥ 8) has increased sevenfold since 1998, with the highest percentage occurring in the Pacific and Indian Oceans, whereas the percentage of sites that experienced cyclones remained consistent throughout the sampling period (Figure 2). Overall, coral cover has remained relatively stable in the Pacific since the 1970s and in the Indian Oceans since the 1990s. By contrast, coral cover has declined fourfold in the Atlantic Ocean since the 1970s (Figure 3).

The overall recovery rates following disturbances in the Pacific Ocean have been significantly higher than the recovery rates in the Atlantic Ocean, but with no statistical difference between the Pacific and Indian Oceans or the Indian and Atlantic Oceans (Table S1). At low latitudes in the western Pacific, recovery rates have remained relatively high, particularly in the Coral Triangle

(which includes reefs of Indonesia, Malaysia, the Philippines, Papua New Guinea, the Democratic Republic of Timor-Leste, and the Solomon Islands) (Figure 4; Table S2). Overall, we did not detect a slowing of recovery rates in the Pacific and Indian Oceans. In the Pacific Ocean, recovery rates were similar from 1988 to 2020 on the reefs of Taiwan, Palau, the Banda Sea, south Vietnam, New Caledonia, the Society Islands, the southern Great Barrier Reef, and Moreton Bay. The recovery rates significantly increased over time (Anderson–Darling test, $p < .05$) in the Gulf of Thailand, the Sulu Sea, the Savu Sea, and the northern and southeastern Great Barrier Reef, but significantly decreased in the Java Sea and Fiji (Anderson–Darling test, $p < .05$). The variance in recovery rates significantly increased (Fligner–Killeen test, $p < .05$) on the reefs in the Sulu Sea, Savu Sea, southeastern Great Barrier Reef, and Moreton Bay, and peaked on the northern Great Barrier Reef in 1999–2009. The variance in recovery rates significantly decreased in the Java Sea (Fligner–Killeen test, $p < .05$) (Figure 4; Table S3). In the Indian Ocean, recovery rates did not change over time in the Persian Gulf, the Red Sea, the Maldives, Comoros, and in Mascarene. The recovery rates significantly increased between 1988 and 2009 (Anderson–Darling test, $p < .05$) in the Strait of Malacca and on Scott Reef. In the Atlantic Ocean, neither the recovery rates nor variance in recovery rate changed significantly in Jamaica, the southern Caribbean, or Brazil. Coral recovery rates were highest in the Antilles, from the Dominican Republic in the north to Trinidad and Tobago in the south, and recovery rates have increased since 2010 (Anderson–Darling, $p < .05$) (Figure 4;

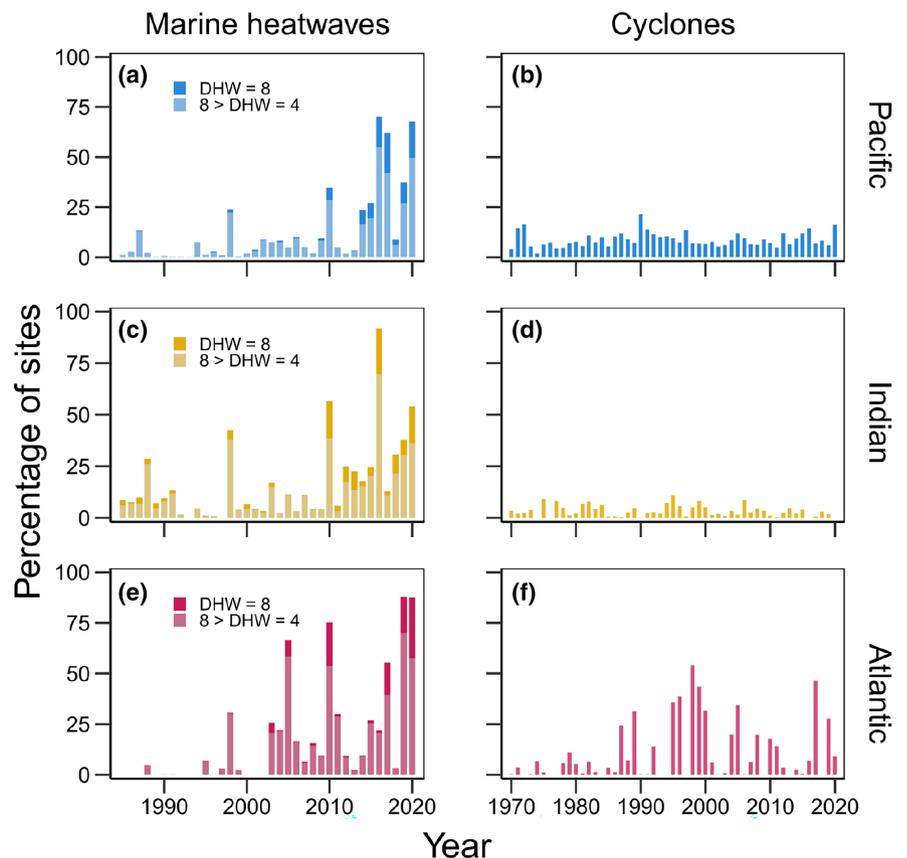


FIGURE 2 Percentage of sites that have experienced (a) marine heatwaves and (b) cyclones in the Pacific Ocean (sites, $n = 7150$), (c) marine heatwaves and (d) cyclones in the Indian Ocean (sites, $n = 1548$), and (e) marine heatwaves and (f) cyclones in the Atlantic Ocean (sites, $n = 3520$). The time periods include 1985–2020 for heatwaves and 1970–2020 for cyclones. Light tones represent moderate marine heatwave events (DHW ≥ 4 and < 8) whereas dark tones represent severe marine heatwave events (DHW ≥ 8) within the marine heatwave column.

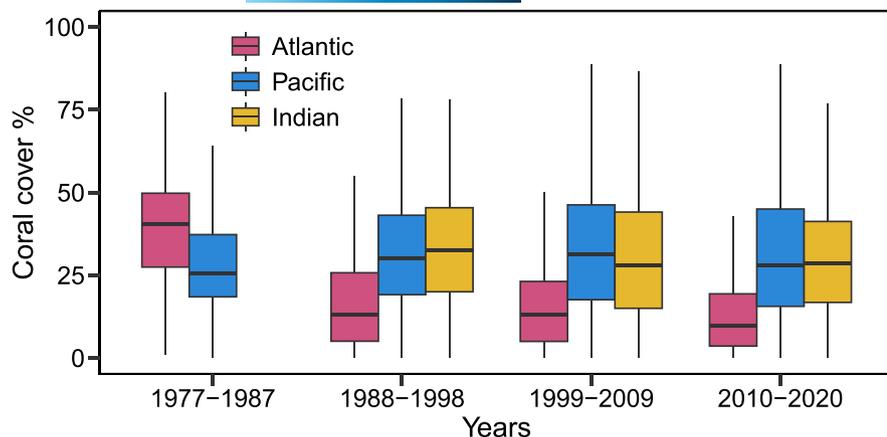


FIGURE 3 Percentage of coral cover in the Pacific, Indian, and Atlantic Oceans from 1977 to 2020 ($n=24,992$). Each ocean has a different fill color, the black horizontal lines represent median values for each decade, the boxes represent the upper and lower quartiles (i.e., 50% of the data), and the black vertical bars represent the minimum and maximum values of the data (excluding outliers).

Table S2). By contrast, coral recovery rates in Jamaica have remained relatively low over the past several decades. The average recovery rates decreased in the western Caribbean and Florida since 2009 (Anderson–Darling test, $p < .05$) (Figure 4; Table S2). The variance in the recovery rates decreased in the western Caribbean, Antilles, and Florida since 2009 (Fligner–Killeen test, $p < .05$) (Figure 4; Table S3).

The results of the best model with the lowest Watanabe–Akaike information criterion are presented in Figure 5. There were positive relationships between rates of coral recovery at each site and kurtosis of sea surface temperature, prior cyclone frequency, and prior heatwave frequency (Figure 5). There were negative relationships between rates of coral recovery at a site and (i) maximum windspeed during recovery (i.e., cyclone intensity during recovery), (ii) macroalgae cover at the beginning of the recovery period, (iii) distance to shore, (iv) maximum DHW during the recovery period (i.e., heatwave intensity during recovery), (v) coral cover at the beginning of the recovery period, (vi) the interaction between coral cover and macroalgae at the beginning of the recovery period, and (vii) all habitat types (Figure S7). Depth and turbidity showed negative relationships with rates of coral recovery, but only at the 80% level (Figure 5). We found no relationships between rates of coral recovery and the velocity of sea surface temperature, fishing pressure (i.e., total gravity in Figure 5), sea surface temperature skewness, and reef density.

4 | DISCUSSION

Since the 1970s, coral cover in the Atlantic Ocean has decreased fourfold, and recovery rates following disturbances have been relatively low, except in the Antilles where recovery rates have recently increased. By contrast, coral cover and recovery rates in the Pacific and Indian Oceans have remained moderate over time, and recovery rates have even increased in some ecoregions such as in the Coral Triangle region. The Coral Triangle region, which includes reefs of Indonesia, Malaysia, the Philippines, Papua New Guinea, the Democratic Republic of Timor-Leste, and the Solomon Islands, has also experienced relatively low coral bleaching over the past three decades (Shlesinger & van Woesik, 2023; Sully et al., 2022) and has

been identified as a region with high-recovery potential (Novi & Bracco, 2022). Similarly, our study found that recovery rates have increased along the northern Great Barrier Reef, between 1998 and 2020, and on reefs in the Strait of Malacca, between 1988 and 2009. This increase in the northern Great Barrier Reef agrees with a recent study that showed rapid coral recovery in the northern Great Barrier Reef following 2020, 3 years after the 2015–2017 marine heatwave (AIMS, 2021). Therefore, contrary to theoretical expectations (Dakos et al., 2012; Livina et al., 2010; Scheffer et al., 2012; Scheffer & van Nes, 2006; Veraart et al., 2011), our study did not find an overall slowing of recovery rates with increased marine heatwaves in the Pacific Ocean.

There were several interesting relationships between coral recovery and contemporary environmental conditions. There was a positive relationship between the rates of coral recovery and shape-based geographical patterns of sea surface temperature kurtosis (Figure 5)—extremes in kurtosis were most prominent in the Indian Ocean (Figure S5). This relationship suggests that corals in localities with narrow temperature ranges recover faster from disturbances than corals in localities with wide temperature ranges. There were also positive relationships between the rate of coral recovery and both prior cyclone frequency and prior heatwave frequency (Figure 5). As cyclone frequency did not change throughout the study (Figure 2), or even longer (Webster et al., 2005), the positive relationship between recovery rates and cyclone frequency suggests that reefs in regions with high cyclone activity have long adjusted to these physical disturbances. In addition, cyclones (Webster et al., 2005) and recent marine heatwaves (Sully et al., 2019) have been recently co-occurring in subtropical regions, and the cooling effect of cyclones may buffer reefs from thermal stress, potentially facilitating recovery (Carrigan & Puotinen, 2014; Manzello et al., 2007). Unlike cyclones, the frequency of marine heatwaves has recently increased (Figure 2), indicating that the positive relationship between heatwave frequency and recovery rates stems from a more recent adjustment to increased marine heatwave disturbance (González-Barrios et al., 2023; Maynard et al., 2008; Thompson & van Woesik, 2009).

There were negative relationships between the rates of coral recovery and both the maximum cyclone windspeed and the maximum DHW during recovery (Figure 5). These relationships indicate that

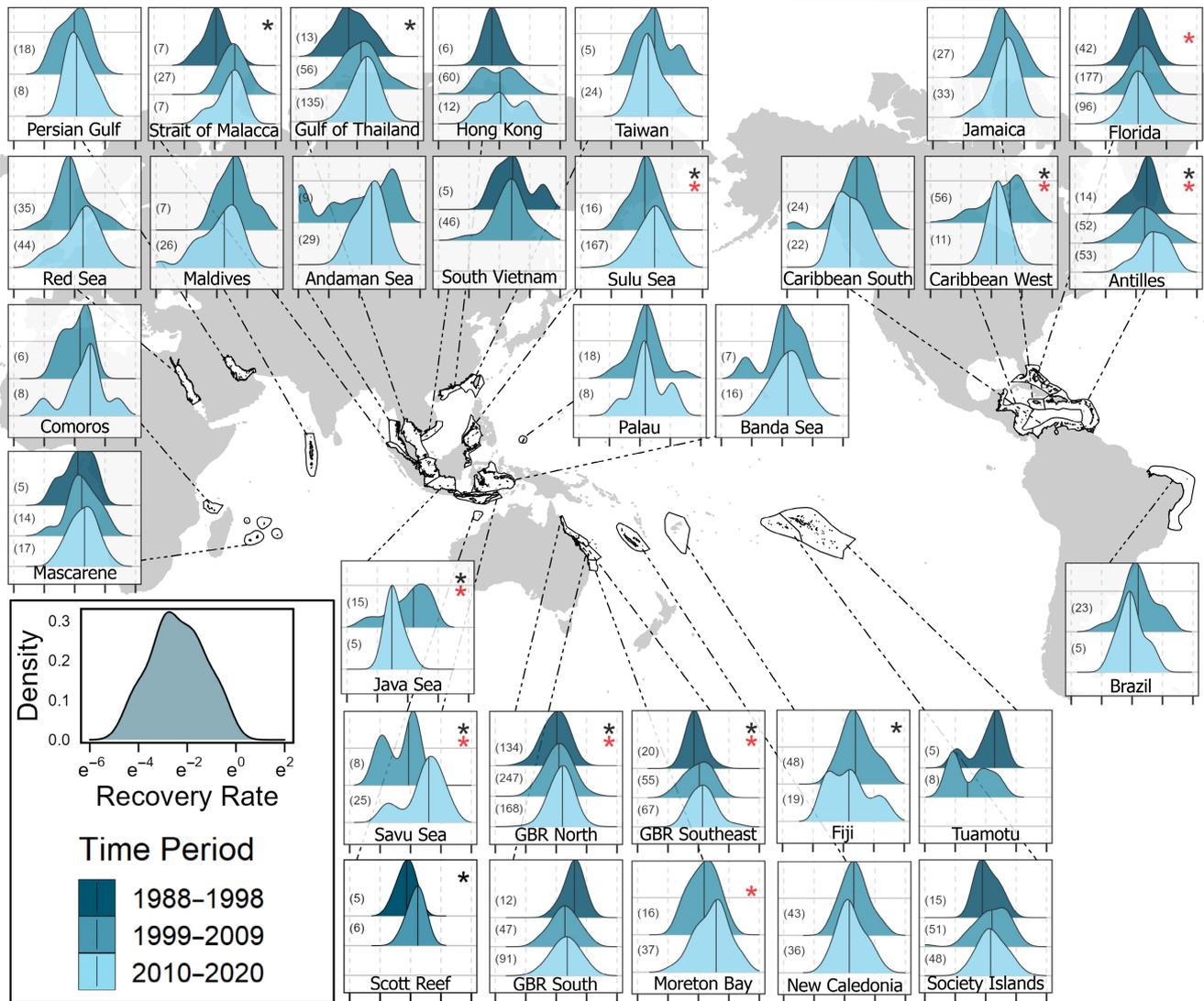


FIGURE 4 Density plots of recovery rates of coral cover in the Pacific, Indian, and Atlantic Oceans from 1988 to 2020. Map displaying the probability density functions of recovery rates of corals on a log-scale x-axis within ecoregions in the Pacific, Indian, and Atlantic Oceans. Recovery rates are grouped evenly by year with recovery rates from 1977 to 1987 not shown because of insufficient samples but these data were considered in the statistical analysis. The fill colors of probability density plots correspond to the time period, and the black vertical lines represent the medians. The sample size for each time period within an ecoregion is displayed in parentheses on the left side of each subplot. Black asterisks denote statistical significance in the change in the distributions over time (using an Anderson–Darling test), whereas red asterisks denote statistical significance in the change in the variance over time (using a Fligner–Killeen test). Black outlines on the map represent ecoregions.

additional disturbances during recovery periods impede recovery rates (Figure 5). Additionally, intense heatwaves appear to be more detrimental to recovery than cyclones (Figure 5), which agrees with an analysis in the Great Barrier Reef that compared cyclone Yasi with heatwave impact (Dietzel et al., 2021). While the trend was not strong (80% credible intervals, Figure 5), there was a negative relationship between the rates of coral recovery and depth. In the Seychelles, Graham et al. (2015) also found the highest rates of recovery on shallow reefs. As light diminishes with depth, the rates of photosynthesis, calcification (Chalker, 1981; Mass et al., 2007), and coral recruitment also decline, particularly acroporid recruitment (Golbuu et al., 2007). Consistent with the depth trends, although not strong (80% credible intervals, Figure 5), turbidity had a negative relationship with the rates

of coral recovery. Even though previous studies have shown that corals in turbid waters are generally more resistant to thermal stress than corals in clear waters (Barnes et al., 2015; Sully & van Woesik, 2020), here we show that, in general, when disturbed, corals in turbid water reefs recovered more slowly than corals in clearwater reefs. These results agree with the study by MacNeil et al. (2019), who showed that poor water quality impaired coral reef recovery on the Great Barrier Reef following bleaching.

Our results show a strong negative relationship between coral recovery and the percentage of macroalgae present at the beginning of a recovery period (Figure 5). The presence of macroalgae can damage coral tissue through allelopathy (Rasher & Hay, 2010) and slow coral recovery by releasing waterborne chemicals that repel potential

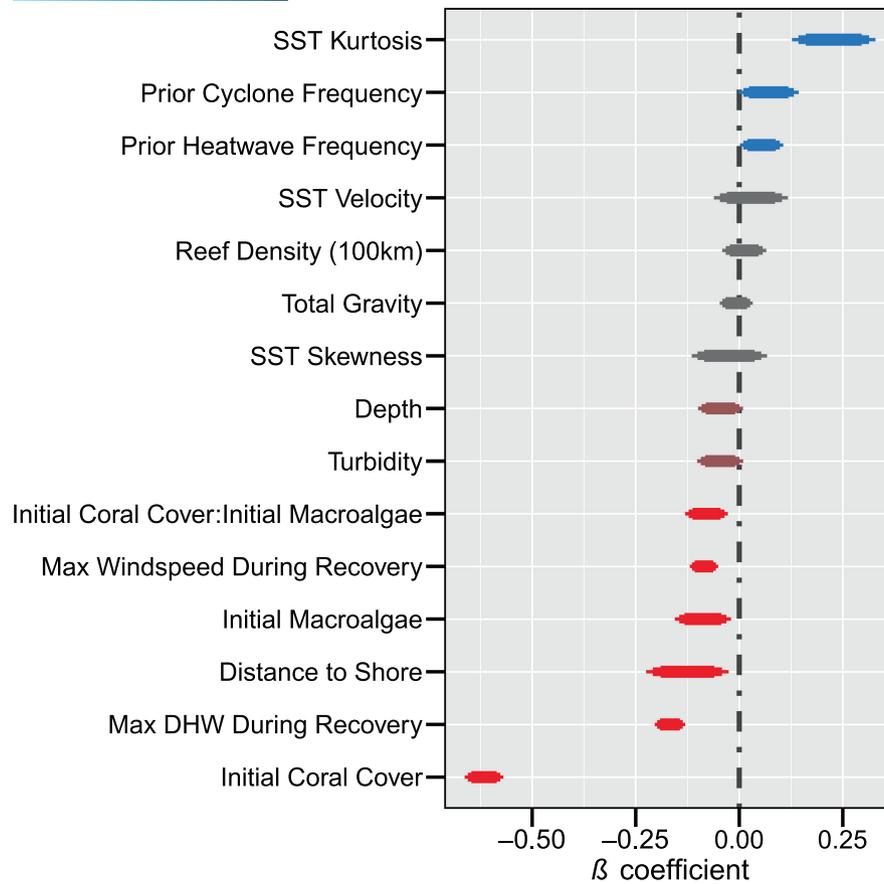


FIGURE 5 Relationships between the recovery rates of coral cover following disturbances and 15 variables from 1977 to 2020. There were 3120 unique recovery events representing 1921 sites in 58 countries in the Pacific, Indian, and Atlantic Oceans. Thin, medium, and thick horizontal bars represent credibility intervals at 95%, 90%, and 80%, respectively. Coefficients are blue when 90% credibility intervals are positive and do not overlap with zero, and coefficients are red when 90% credibility intervals are negative and do not overlap with zero. Coefficients are dark red when 80% credibility intervals are negative and do not overlap with zero. Where SST is the sea surface temperature ($^{\circ}\text{C}$), SST Kurtosis is the sharpness of the peak of the SST distribution, SST Velocity is the change in the mean monthly SST from 1960 to 2009, SST Skewness is the degree of asymmetry of the SST distribution, Total gravity is a measure of local human pressure on a reef, calculated as a function of human population size and travel distance to the reef at a global resolution of 10 km, Reef Density (100 km) is the percentage of reef area within a global 100 km² grid space, Turbidity is measured as K_d 490 values, Depth is the depth (m) of the site, Initial Coral Cover is the coral cover at a site at the beginning of the recovery period, Initial Macroalgae is the macroalgae cover at a site at the beginning of a recovery period, Max Windspeed During Recovery is the maximum cyclone windspeed during the recovery period, Distance to shore (m) is the distance from the site to the nearest landmass, Max DHW During Recovery is the maximum Degree Heating Week (DHW) value during the recovery period, Prior Cyclone Frequency is the frequency of cyclones within 1 arc degree of the site between 1970 and the start of the recovery period, and Prior Heatwave Frequency is the frequency of heatwaves (DHW ≥ 4) at a site, from 1985 to the start of the recovery period.

larval settlers (Doropoulos et al., 2014; Vermeij et al., 2009). Physical and chemical interference by macroalgae can also increase post-settlement mortality (Arnold et al., 2010; Box & Mumby, 2007; Kuffner et al., 2006). Coral-algal interactions can be energetically demanding, leading to reduced coral growth rates (Lirman, 2001) and reduced fecundity (Tanner, 1995). Additionally, the presence of macroalgae can coincide with an increase in pathogenic bacteria that can contribute to the rise in coral disease that causes mortality (Zaneveld et al., 2016). Macroalgae can also sensitize corals to heat stress events, exacerbating coral mortality through marine heatwaves (Donovan et al., 2021; Zaneveld et al., 2016). Although macroalgae is a natural component of coral reefs (Vroom et al., 2006), nutrient pollution and the overfishing of herbivores are among the primary drivers of increases in macroalgal

abundance (Fabricius, 2005; Mumby et al., 2007). Both stressors occur at the local scale and are subject to local management decisions. Effective management decisions to reduce nutrients (e.g., improved sewage treatment, controlling watershed discharge) (Fabricius, 2005), and protect areas for herbivorous fishes, can facilitate the reduction of abundant macroalgae (Bruno et al., 2019; Mumby et al., 2007).

There were also a few surprising relationships in our global study. For example, the initial coral cover following disturbances had a negative relationship with recovery rates (Figure 5). These results imply that as disturbances make space available, and given a sufficient larval supply, early-successional fast-growing species can rapidly take over that space. Alternatively, recovery is suppressed at sites that supported macroalgae and had low coral cover following

disturbances (Figure 5). The results also show a negative relationship between coral recovery rates and distance to shore, indicating that, on average, reefs at an extensive distance from land recover more slowly than other reefs, potentially because of reef isolation. Interestingly, we found no relationships between rates of coral recovery and the local human population size and their travel distance to the reef (i.e., total gravity), sea surface temperature skewness, the velocity of sea surface temperature, and reef density at the 100-km scale. The lack of a relationship between coral recovery rates and total gravity agrees with prior literature (Baumann et al., 2022; Bruno & Valdivia, 2016).

While the reefs in the Indian and Pacific Oceans have shown recent resilience to disturbances, the recent increase in the variance of the recovery rates of corals in some ecoregions suggests that reefs in the Indo-Pacific are not immune to deterioration. An increase in the variance of recovery rates following disturbances is a useful precursor of a pending regime shift (Perretti & Munch, 2012). Although an increase in the variance in recovery was not evident in all ecoregions that were examined, our results do suggest that some reefs in the Indo-Pacific reef system may be getting closer to a tipping point (Guttal & Jayaprakash, 2008, 2009), and further disturbances may force a phase shift. The literature suggests that when phase shifts occur, they occur rapidly (Scheffer et al., 2012). While change on any given reef can occur rapidly, change in an ecoregion or across an ocean basin can be gradual (Budd & Johnson, 1999). For example, through the Plio-Pleistocene cooling period, there was a progressive decline in corals followed by the extinction of 12 coral genera in the Atlantic Ocean (Budd & Johnson, 1999), even though these same coral genera remained common in the Pacific and Indian Oceans (van Woesik et al., 2012). Such gradual changes involving metapopulations locally flickering on and off and gradually diminishing regionally appear to be occurring on some contemporary reefs in the Pacific (Zhang et al., 2023) and Indian Oceans (Graham et al., 2011), and can be seen in modern-day acroporid populations in the Caribbean (Aronson & Precht, 2001; Gardner et al., 2003). When and whether the reef systems in the Indo-Pacific lose their resilience will depend on the rate of ocean warming, the degradation of regional and local conditions, the size of the metapopulations (Holling, 1973; Mumby et al., 2007), the variability of habitats in the subregions (Woesik et al., 2012), and the extent of reef connectivity (Wood et al., 2014).

The geographical and temporal trends observed in this study are useful, although there are some limitations to the study, including detectability issues. For example, because the study used sites of opportunity, no sites were surveyed consistently for the entire study period, and sampling was relatively sparse at the beginning of the study period. This limitation is most evident in the Java Sea, where two separate studies focused on different reef habitats in different time periods, resulting in a significant decrease in both recovery rates and variance in recovery rates across time periods (Figure 4; Tables S2 and S3). Moreover, some ocean regions have been sparsely surveyed, or at least we have few data for some ecoregions, for example, the reefs around India and Sri Lanka. There were also minimal data on coral recovery for the 1970s in the Pacific Ocean and for the

1970s and 1980s in the Indian Ocean. This uncertainty is amplified by an inherent sampling bias towards locations with relatively high coral cover, which ignores reef locations that historically may have been healthy but have recently deteriorated. Additionally, we have only examined sites that have recovered and have not considered sites that did not recover. Moreover, we only tested coral recovery against 14 environmental variables and have insufficient data on a global scale on other key drivers that influence coral recovery, such as rates of herbivory (Bellwood et al., 2006), water quality (MacNeil et al., 2019; Thompson et al., 2014) and coral species composition (Done, 1992; Johns et al., 2014), which prevents us from understanding the relationship between biodiversity and the recovery rate of a reef. Yet, we bring to the literature the most comprehensive study to date on coral recovery following disturbances, presenting a global perspective on the dynamics of coral reefs through ongoing climate change.

In conclusion, our study shows major differences in recovery rates of coral cover within and across the oceans. Coral cover has declined fourfold in the Atlantic Ocean since the 1970s, and although coral cover has fluctuated following disturbances since the late 1990s, it has remained stable across decadal timescales in the Pacific and Indian Oceans. The overall recovery rates following disturbances in the Pacific and Indian Oceans have been considerably higher than in the Atlantic Ocean, particularly in the Coral Triangle. There were positive relationships between rates of coral recovery and prior cyclone and heatwave frequency, and negative relationships between rates of coral recovery and macroalgae cover and distance to shore. While it is still uncertain why some ecoregions, such as the Savu Sea, show a large variation in coral recovery, whereas other regions, such as New Caledonia, show more homogeneous recovery rates, coral reefs in the Pacific and Indian Oceans have shown considerable resilience to the increasing intensity and frequency of marine heatwaves. The recent increase in the variance in coral recovery rates over the past three decades in the Pacific and Indian Oceans suggests that some reefs in specific ecoregions may be getting closer to a tipping point, and further marine heatwaves may cause a phase shift, beyond which recovery is less likely. Previous studies have shown that local conservation action can help reef corals resist heat-stress events associated with climate change (Donovan et al., 2021). The present study also shows that local conservation to prevent macroalgal overgrowth may also help reef recovery from disturbances. Therefore, both local management decisions and global action to slow and reverse greenhouse emissions are necessary to preserve reefs in the future.

AUTHOR CONTRIBUTIONS

Andrew S. Walker: Formal analysis; investigation; methodology; software; visualization; writing – original draft; writing – review and editing. **Chelsey A. Kratochwill:** Data curation; software; visualization; writing – original draft; writing – review and editing. **Robert van Woesik:** Conceptualization; funding acquisition; project administration; resources; supervision; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at <https://zenodo.org/records/10366199>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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