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ARTICLE

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Increasing disturbance frequency undermines coral reef recovery

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Abstract

Climate-driven alterations to disturbance regimes are increasingly disrupting patterns of recovery in many biomes. Here, we examine the impact of disturbance and subsequent level of recovery in live hard coral cover on the Great Barrier Reef (GBR) across the last three decades. We demonstrate that a preexisting pattern of infrequent disturbances of limited spatial extent has changed to larger and more frequent disturbances, dominated by marine heatwaves and severe tropical cyclones. We detected an increase in the impact (measured as coral loss) across 265 individual disturbance impacts on 131 reefs in a 36-year dataset (1985–2022). Additionally, the number of survey reefs impacted by disturbance has increased each decade from 6% in the 1980s to 44% in the 2010s, as has the frequency of mass coral bleaching across the GBR, which has increased between 19% and 28% per year, and cyclones (3%–5% per year), resulting in less time for recovery. Of the 265 disturbance impacts we recorded, complete recovery to the highest levels of coral cover recorded earlier in this study (the “historical benchmark”) occurred only 62 (23%) times. Of the 23% of disturbance impacts that resulted in complete recovery to historical benchmarks, 34/62 recovered to their benchmark in 2021 or 2022. Complete recovery was more likely when the historical benchmark was <25% live hard coral cover. The lack of recovery was attributed to recovery time windows becoming shorter due to increases in the frequency of cyclones and of thermal stress events that result in mass coral bleaching episodes. These results confirm that climate change is contributing to ecosystem-wide changes in the ability of coral reefs to recover.

KEYWORDS
climate change, coral assemblages, coral bleaching, coral reefs, crown-of-thorns starfish, cyclones, Great Barrier Reef, recovery

INTRODUCTION

Understanding ecosystems' response to and recovery from perturbations is key to predicting ecological, economic, and societal consequences of environmental disturbances. Ecosystems around the world are increasingly being affected by climate change and local human impacts (Bjorkman et al., 2018; Jackson et al., 2001; Johnstone et al., 2016; Walther et al., 2002). However, detecting and measuring the effects of climate change on natural systems and associated societies is complicated by the complexity and natural variability of ecosystems and the interactions between climate change and other drivers of change. Climate change is boosting the frequency and/or intensity of natural disturbances (i.e., storms, bushfires, and droughts) that have always influenced the ecology of ecosystems, including arctic tundra, temperate and tropical forests, freshwater lakes, and grasslands (Bjorkman et al., 2018; Connell, 1978; Johnstone et al., 2016; White & Jentsch, 2001). Three fundamental components determine the consequences of these disturbances: (1) *exposure* of biological elements to disturbance events, (2) *impact* of the disturbance (change in state, dependent on the severity of the event, resistance, and sensitivity), and (3) ability of the system to *recover* from disturbances (Kelly & Harwell, 1990). Characterizing disturbance–recovery cycles is becoming particularly important in ecosystems like tropical shallow water coral reefs, which not only support the livelihoods and food security of half a billion people globally but are also among the most vulnerable to climate change (Hoegh-Guldberg et al., 2018).

While considerable research effort has documented (1) *exposure* to and (2) *impact* of disturbances to coral reefs (e.g., Bruno & Selig, 2007; Emslie et al., 2008; Graham et al., 2008; Hughes, Kerry, et al., 2017, 2018; Ortiz et al., 2018; Osborne et al., 2011), *recovery*—the rate and manner in which an ecosystem recovers toward the predisturbance state—remains surprisingly poorly characterized for this ecosystem. Relatively few studies have attempted to quantify large-scale (hundreds of kilometers) reef recovery of corals beyond the scale of individual reefs (Baker et al., 2008; Connell, 1997; Graham et al., 2011; Halford et al., 2004; Osborne et al., 2017). Of these, few track multi-decadal timescales (but see Connell, 1997), explore recovery beyond increases in live hard coral cover (hereafter "hard coral cover"), especially reassembly of community composition or recovery of different coral taxa (exceptions: Emslie et al., 2008; Johns et al., 2014; McWilliam et al., 2020; Ortiz et al., 2018), or use empirical data-driven assessment rather than modeled estimates (e.g., Bozec et al., 2022). Exposure to acute disturbances such as marine heatwaves, cyclones, or crown-of-thorns starfish (COTS) outbreaks, and chronic pressures like poor water quality, disease, overfishing and their consequences (e.g., reduction in hard coral cover, Bruno & Selig, 2007; Gardner et al., 2003, and associated changes in benthic assemblage, Hughes, Kerry, et al., 2018) are well characterized. However, limited quantification of the level of recovery of hard coral cover compared to historic benchmarks leaves a fundamental gap in our understanding of reef disturbance dynamics, undermining our ability to assess reef futures in a rapidly changing world, and risking a view fueled by shifting baselines. A better understanding of recovery will be critical to designing successful management goals, restoration outcomes, promotion of natural recovery conditions, and nature-based solutions.

The level of recovery at a given coral reef is the product of the predisturbance coral assemblage composition and its response diversity, the type, severity, and scale of disturbances, and the interval between them, as well as the availability of larvae, connectivity to other reefs and colony growth rates (Graham et al., 2011; Hughes & Connell, 1999; Mellin et al., 2019). Under a scenario where reefs have increasingly shorter intervals for recovery between disturbances, it has been assumed that hard coral cover and diversity may "ratchet" down over time (sensu Birkeland, 2004) in a series of declines and recovery cycles, with each recovery reaching lower levels than the last until an alternative state is reached, with subsequent impacts on the ability of reefs to provide ecosystem services that promote biodiversity and associated societal benefits.

Long-term monitoring programs offer critical insights into the decline and recovery of coral reefs (e.g., Gouezo et al., 2019), since disturbance–recovery cycles often extend beyond the careers of individual researchers. Few datasets extend beyond 20 years (but see Connell, 1997; Tanner et al., 1994), and those that do are generally geographically restricted (but see Gardner et al., 2005; Ortiz et al., 2018). The Australian Institute of Marine Science (AIMS) Long-Term Monitoring Program (LTMP) has collected data on coral reef status over 36 years on the Great Barrier Reef (GBR) on the northeast coast of Australia. The large spatial extent (1700 km, 13 degrees of latitude) and temporal coverage (36 years) of the LTMP dataset provides a globally unique opportunity to explore patterns of coral reef recovery (Ortiz et al., 2018) and to ask fundamental questions about how reef recovery on the GBR may be changing as disturbance regimes intensify under climate change (e.g., more frequent and severe marine heatwaves causing mass coral bleaching).

The disturbance regime on the GBR is expected to alter further as climate change accelerates, with consequences for natural recovery trajectories. The expectation is that there will be increases in disturbance frequency, which will result in shorter inter-disturbance intervals (Emanuel, 2013; Hoegh-Guldberg, 1999), creating a complex recovery trajectory where the legacy of one disturbance overlaps with the next. The response of reefs to individual disturbance events, including GBR-wide COTS outbreaks and recent mass coral bleaching events in 2016, 2017, 2020, and 2022, are well documented by short-term studies (e.g., Garpe et al., 2006; Graham et al., 2006; Hughes, Barnes, et al., 2017; Hughes, Kerry, et al., 2017, 2018; Pisapia et al., 2019; Stuart-Smith et al., 2018). However, it is rare to have a study with sufficient spatiotemporal scope to quantify the effects of multiple recurrent disturbances on hard coral cover declines and recovery across ecosystem scales, and more importantly to detect changes to disturbance regimes and recovery potential. Three studies that have looked at multiple disturbances (Adjeroud et al., 2018; MacNeil et al., 2019; Vercelloni et al., 2020) documented altered communities with varying capacities for recovery driven by recruitment and survival, the types of disturbance regimes, and underlying or chronic anthropogenic pressures.

The GBR has experienced six mass coral bleaching events since 1998, of which four have occurred since 2016, representing an increase in the frequency of thermal stress events causing mass coral bleaching (Hughes, Anderson, et al., 2018). However, model predictions for the future patterns of cyclone frequency and strength have a great deal of uncertainty for the GBR (Dixon et al., 2022). COTS outbreaks are also well documented on the GBR, with the first recorded outbreak occurring in the early 1960s (Barnes, 1966; Pearson & Endean, 1969). There have been four distinct episodes of outbreaks starting in approximately 1962, 1979, 1995, and 2010 (Pratchett et al., 2024). While thermal disturbances will likely increase in frequency under climate change, COTS outbreaks do not appear to be strongly influenced by climate drivers, and they represent a chronic pressure once outbreaks become established.

In this study, we use the AIMS LTMP dataset, an extensive single standardized set of coral reef in-water observations, to explore coral reef recovery on the GBR in the context of exposure–response–recovery relationships. The long temporal extent (36 years) of this dataset allowed us to measure the success of recovery compared to predisturbance benchmarks (important to avoid shifting baselines, where recovery is compared to benchmarks that are diminishing through time), across >450 reefs. Here, we first explore *exposure* of each of these coral reefs to disturbances, specifically if and how the disturbance regime—including the (1) spatial extent, (2) severity, and (3) frequency of disturbances—has changed over time. Secondly, we examine the biological *impact* from disturbance using coral cover as a metric to examine the magnitude of response to exposure on the GBR across space and time (on individual reefs, and across three GBR subregions). Finally, quantification of these two elements allows us to examine *recovery* trajectories of reefs, providing an unprecedented insight into the timeframes, rates, and magnitude of coral reef recovery across the GBR.

METHODS

Survey methods: Hard coral cover as a recovery metric

Manta tow surveys were used to assess changes in living hard coral cover as an indicator of patterns of disturbance and recovery across three GBR subregions (northern [11.0–15.4° S], central [15.4–20.7° S], and southern [20.7–23.9° S]), over a 36-year period. A total of 492 reefs were surveyed repeatedly between 1986 and 2022 (numbers of reefs surveyed each year are provided in Appendix S1: Table S1). There has always been a set of "core" reefs that are targeted for surveys every year, plus a set of "cycle" reefs that are targeted every 2–3 years, and another set that are surveyed haphazardly. The core reefs were chosen in advance to capture the main biophysical gradients on the GBR and were never changed in response to disturbances. The sampling design has evolved over time from the 1980s when the program conducted only manta tow surveys to examine the spatial distribution of COTS, to the 1990s and beyond, when detailed surveys were added to manta tow surveys. A further change occurred in 2006 to accommodate the desire of the Great Barrier Reef Marine Park Authority to assess the impact of rezoning the GBR (Fernandes et al., 2005), and some core reefs were added to address this. Sampling became biennial for a decade, alternating between a set of 60 core reefs for the historical long-term monitoring, and another set of 70 core reefs aimed at addressing the issue of rezoning. A final change occurred in 2021 that amalgamated the two sets of reefs back to annual manta tow surveys on 90 core reefs. Hence, reefs were revisited annually, biennially, or haphazardly, and survey frequency and interval varied among reefs (see Appendix S1: Tables S1 and S2). Across the GBR, the average number of years between surveys in each decade was as follows: 1986–1990—2.18 (±0.139) years, 1991–2000—1.9 (±0.081) years, 2001–2010—2.07 (±0.089) years, and 2011–2020—1.84 (±0.044) years (Appendix S1: Table S2).

Trained observers were towed behind a small boat and visually estimated the proportion of living hard coral cover on the reef slope in a 10-m-wide band during a 2-min tow (approximately 200 m). Hard coral cover was recorded on a categorical scale (0%, >0%–5%, >5%–10%, >10%–20%, >20%–30%, >30%–40%, >40%–50%, >50%–62.5%, >62.5%–75%, >75%–87.5%, >87.5%–100%) (Miller et al., 2015). Hard coral cover is a coarse metric of coral reef condition which does not reveal important information such as diversity, coral community composition, or demography and recruitment. However, it is a standard, globally used method for assessing reef condition and is particularly useful for comparisons across large spatial scales, such as the 144,000 km^2 GBR. The number of 2-min tows required to complete an individual reef survey depended on the size of the reef. To examine how hard coral cover on reefs of the GBR has changed through time, annual hard coral cover at each reef was estimated using Bayesian hierarchical linear models (see *Impacts of disturbances on GBR reefs* for model details). All analyses were conducted in R 4.2.2 (R Core Team, 2022).

Exposure of GBR reefs to disturbance

Mass coral bleaching

Six well-documented mass coral bleaching events have occurred during the 36-year survey period in 1998, 2002, 2016, 2017, 2020, and 2022, and LTMP data records for bleaching began in 1995. During each event, comprehensive aerial surveys of the GBR were undertaken at an elevation of approximately 150 m, timed for the March–early April period when bleaching was widespread and particularly conspicuous (Berkelmans et al., 2004; Hughes, Kerry, et al., 2017). The number of reefs surveyed varied in each year—638 (1998), 631 (2002), 1156 (2016), 742 (2017), 1036 (2020), and 719 (2022) individual reefs from the coast to the continental shelf edge were assessed between the latitudes of 8.8° S and 23.85° S. Each reef was visually assessed and ascribed to one of five categories of bleaching severity, using the same protocols in each event: 0 (no bleaching), 0% of corals bleached; 1 (minor bleaching), >0%–10%; 2 (moderate bleaching), 10%–30%; 3 (major bleaching), 30%–60%; and 4 (severe bleaching), >60% of corals bleached. In 2017, 2020, and 2022, a sixth category was added—5 (extreme bleaching), >80% of corals bleached. Aerial scores in 2016 were ground-truthed against underwater assessments (Hughes, Anderson, et al., 2018). For years outside of the five mass coral bleaching events, where only localized bleaching occurred but no aerial surveys were conducted, we estimated the same categories of bleaching severity during underwater surveys of individual reefs (Miller et al., 2018). No bleaching in categories 3, 4, or 5 was recorded in these years. The highest bleaching category recorded in these years was a 2, at one reef in 1999, two reefs in 2004, and one reef in 2019.

Cyclones

We used models of the reconstructed speed and duration of extreme winds generated by each tropical cyclone that crossed the GBR from 1985 to 2021 to map a predicted damage zone within which wind-driven waves of heights sufficient to severely damage most vulnerable coral communities could have developed, noting that actual damage within these zones is likely to be patchy, as per Puotinen et al. (2016). We subdivided this damage zone into four categories based on the predicted height of the top one third of waves (Hs—significant wave height) as follows: level 0 (Hs < 4 m; severe damage unlikely), level 1 (4–6 m; severe damage possible), level 2 (6–8 m; severe damage likely), and level 3 (Hs ≥ 8 m; severe damage very likely). The spatial extent of level 1 or above (Hs ≥ 4 m) reliably detected the extent of severe damage to corals (Puotinen et al., 2016). We used the predicted wave height fields to calculate the number of GBR survey reefs located in each of the four risk-level categories each year from 1985 to 2020.

COTS outbreaks

Densities of *Acanthaster* c.f. *solaris* (COTS) were recorded during manta tow surveys (Miller et al., 2015). The COTS outbreak status of each reef was determined by the average number of individuals per 2-min tow (*Zero* = 0 individuals, *No Outbreak* [NO] = <0.22 individuals, *Incipient Outbreak* [IO] = >0.22 < 1.0 individuals, *Active Outbreak* [AO] = ≥1.0 individuals). The coral cover on *No Outbreak* reefs is not expected to be impacted by COTS numbers, while *Incipient Outbreak* levels may reduce coral cover, and *Active Outbreaks* will decrease coral cover substantially (Miller et al., 2015).

To assess whether the occurrence of severe categories of coral bleaching, cyclones, and COTS have increased through time in the three regions of the GBR, we first assigned individual reefs a binary score (whether or not an active COTS outbreak, a cyclone with Hs category 1, 2, or 3 (Hs > 4 m), or bleaching category 3 or 4 occurred in any 1 year). We then ran a Bernoulli GLMM (Equation 1) with each binary occurrence of the focal disturbance category for each reef/year as the response variable, year as a linear predictor, an interaction term between year and region, and reef as a random effect (sensu Hughes, Anderson, et al., 2018). COTS outbreaks tend to occur in temporal clusters at a given reef; therefore, we included a first-order autocorrelative term in these models. Models were run in the *glmmTMB* package (Brooks et al., 2017) using Laplace approximate differentiation.

$$\begin{aligned} y_{i,r} &\sim B_{\text{in}}(\pi_{i,r}, 1) \\ \ln\left(\frac{\pi_{i,r}}{1-\pi_{i,r}}\right) &= \beta_0 + \gamma_r + \beta_1 Y_i + \sum_{j=2}^{n} \beta_j R_i + \sum_{j=4}^{n} \beta_j Y_i R_i + \epsilon^*_{i,r} \\ \text{Corr}\left(\epsilon_{i,j}, \epsilon_{i',j'}\right) &= \rho^{|t_i - t_{i'}|} \text{for } r = r' \text{ and } |t_i - t_{i'}| = 1 \end{aligned} \tag{1}$$

The i_{th} severe disturbance category count observation (y) from the r_{th} reef is assumed to be drawn from a Bernoulli (B_{in} with $p = 1$) distribution with probability of $\pi_{i,r}$. The (logit) probabilities were described by a linear model that included an intercept (β_0), varying effects of reef (γ_r) as well as the population effects of time (Y), region (R) and their interaction. * A first-order autoregressive (AR1) structure was also incorporated within each reef ($\epsilon^*_{i,r}$) for COTS only.

Impacts of disturbances on GBR reefs

We first modeled temporal trends in hard coral cover on each individual reef employing Bayesian hierarchical models (Equation 2) using the package *INLA* (Rue et al., 2009). Categorical hard coral estimates were converted to mid-points (Appendix S1: Table S3), and these were used as the response variable.

$$y\_ij = \lceil C\_ij \times n\_ij \rceil \tag{2}$$

Models were run separately for each individual reef and had the fixed effect of year, using a beta error distribution, and incorporated varying intercept and slope effects of reef (Equation 3). Year (x_{ij}) was modeled as a fixed categorical effect (β_i) with weakly informative Gaussian priors. Varying intercepts (γ_0) and slopes (γ_j) are assumed to be drawn from a multivariate Gaussian distribution with zero mean and covariance ($\sum$). For ease of prior specification, covariance matrices for each reef were decomposed into respective correlation matrices with LKJ prior (regularization = 1; jointly uniform over all such correlation matrices) and variances (concentration = 1; jointly uniform over variances) and gamma hyperprior (scale of 1 and shape of 1).

$$\begin{gathered} y_{ij} \sim B_{\text{in}}\left(n_{ij}, \pi_{ij}\right) \\ \ln\left(\frac{\pi_{ij}}{1-\pi_{ij}}\right) = \left(\gamma_{0j} + \beta_0\right) + \left(\gamma_j + \beta_i\right) x_{ij} \\ \beta_0 \sim N(0,10) \\ \beta_i \sim N(0,2.5) \\ \gamma_0, \gamma_j \sim \text{MVN}\left(0, \Sigma_j\right) \\ \Sigma_j \sim \text{decov}(1,1,1,1) \end{gathered} \tag{3}$$

These models were also fit separately for each of the northern, central, and southern GBR using STAN (Stan Development Team, 2018) via the *brms* package (Bürkner, 2017) to produce modeled trends in hard coral cover for each of the three regions (Equation 4). Models used three chains of 10,000 iterations with a warmup of 5000 iterations, and a thinning rate of 5.

$$\begin{aligned} y_{i,r} &\sim \text{Beta}\left(\pi_{i,r}, \phi_T^2\right) \\ \ln\left(\frac{\pi_{i,r}}{1-\pi_{i,r}}\right) &= \beta_0 + \gamma_r + \sum_{j=1}^{n} \beta_j T_i \\ \gamma_r &\sim N(0, \sigma_r) \\ \phi_T &\sim \Gamma(0.01, 0.01) \\ \beta_0 &\sim N(0,3) \\ \beta_{[1,n]} &\sim N(0,3) \\ \zeta_r &\sim N(0,1) \\ \sigma_r &\sim \Gamma(2,1) \end{aligned} \tag{4}$$

Live hard coral cover (y) from the i_{th} manta tow from the r_{th} reef is assumed to be drawn from a beta (Beta) distribution parameterized, respectively, by a mean ($\mu_{i,r}$) and separate dispersion (ϕ) per year. The (natural log of the odds of) means were described by a linear model that included varying effects of reef (γ_r) as well as the population effects (β_j) of year (T) modeled as treatment contrasts.

Weakly informative gamma priors were applied to the dispersion parameter, and weakly informative normal priors were applied to the intercept and population (year) effect parameters. The varying effects were further reparameterized into non-centered versions (for computational reasons) with weakly informative priors applied to the variances (σ_r).

Next, we calculated reef-level relative percent coral loss and subsequent recovery as per Figure 1. To assess whether the magnitude of coral loss is increasing through time, we modeled (1) the postdisturbance hard coral cover (year of lowest hard coral cover immediately following a disturbance impact—Equation 5), and

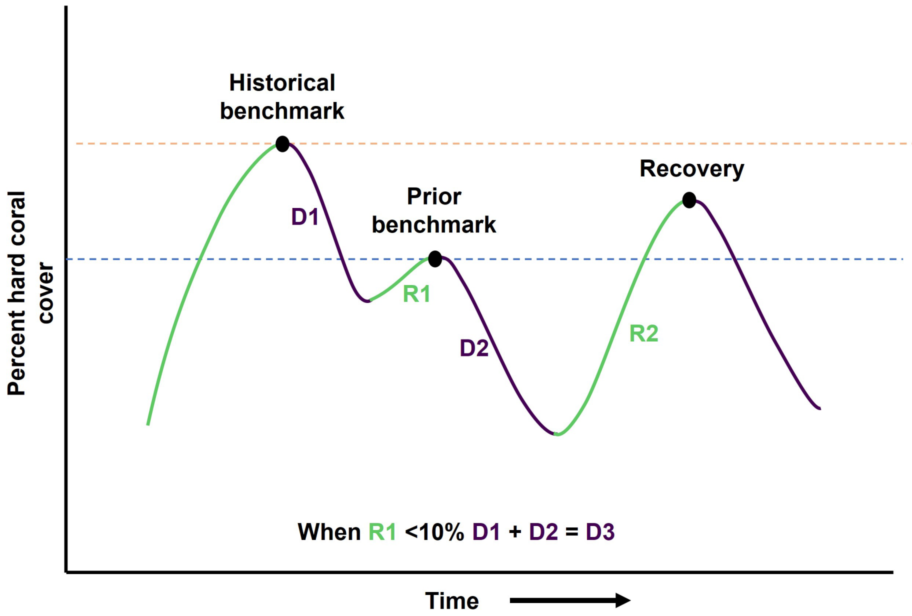

FIGURE 1 Definitions of *disturbance impacts* (D) and *recovery* (R) in this study. D1 and D2 are defined as a *single disturbance* when R1 >10% absolute hard coral cover. If R1 is <10%, D1 and D2 are treated as a *single consecutive disturbance* (D3). R2 is the second recovery period that continues until coral declines again >10% or reaches the end of the temporal series. R dashed horizontal line represents the *historical benchmark* for recovery, Blue dashed horizontal line represents the *prior benchmark* for recovery. In this theoretical example, the point at the end of R1 has achieved complete recovery to the *prior benchmark* (i.e., ≥100% of prior threshold), but has not completely recovered to the *historical benchmark* (i.e., <100% of historical benchmark).

(2) relative hard coral loss against the year of disturbance (Equation 6), with reef and disturbance type included as varying effects using a Gamma distribution with a log-link function. Both models were run using the *brms* package (Bürkner, 2017) and used three chains each with 1500 iterations after a "warmup" of 500 and a thinning rate of 2. The model for level of postdisturbance hard coral cover included default priors for the intercept (student_*t*: df = 3, μ = −2, SD = 2.5), beta (flat), SD (student_*t*: df = 3, μ = 0, SD = 2.5), and shape (gamma: shape 1 = 0.01, shape 2 = 0.01).

1. Postdisturbance hard coral cover

$$\begin{aligned} y_{i,d,r} &\sim \Gamma(\mu_{i,d,r}, \varphi) \\ \ln(\mu_{i,d,r}) &= (\beta_0 + \gamma_d + \gamma_r) + \beta_1 T_i \\ \gamma_d &= \zeta_d \sigma_d \\ \gamma_r &= \zeta_r \sigma_r \\ \varphi &\sim \Gamma(0.01, 0.01) \\ \beta_0 &\sim t(3, -2, 2.5) \\ \beta_{[1,n]} &\sim U(-\infty, \infty) \\ \zeta_{[d,r]} &\sim N(0,1) \\ \sigma_{[d,r]} &\sim t(3, 0, 2.5) \end{aligned} \tag{5}$$

The i_{th} disturbance cover observation (y) from the d_{th} disturbance and r_{th} reef is assumed to be drawn from a gamma (Γ) distribution with shape parameters of $\mu_{i,d,r}$ and φ parameterized to represent the mean and dispersion, respectively. The (natural log) means were described by a linear model that included an intercept (β_0), varying effects of disturbance (γ_d) and reef (γ_r) as well as the population effects (β_1) of disturbance year (T). Weakly informative normal and gamma priors were applied to the intercept and dispersion parameters, respectively. A flat improper prior was applied to the population effect parameter. The varying effects were further reparameterized into non-centered versions (for computational reasons) with weakly informative priors applied to the variances ($\sigma_{[d,r]}$).

2. Relative loss of hard coral cover

$$\begin{aligned} y_{i,d,r} &\sim \Gamma(\mu_{i,d,r}, \varphi) \\ \ln(\mu_{i,d,r}) &= (\beta_0 + \Delta_d + \Delta_r) + \sum_{j=1}^{n} \beta_j T_i \\ \Delta_d &= \zeta_d \sigma_d \\ \Delta_r &= \zeta_r \sigma_r \\ \varphi &\sim \Gamma(0.01, 0.01) \\ \beta_0 &\sim t(3, 4, 2.5) \\ \beta_{[1,n]} &\sim t(-\infty, \infty) \\ \zeta_{[d,r]} &\sim N(0,1) \\ \sigma_{[d,r]} &\sim t(3, 0, 2.5) \end{aligned} \tag{6}$$

The i_{th} relative decline observation (y) from the d_{th} disturbance and r_{th} reef is assumed to be drawn from a gamma (Γ) distribution with shape parameters of $\mu_{i,d,r}$

and φ parameterized to represent the mean and dispersion, respectively. The (natural log) means were described by a linear model that included an intercept (β_0), varying effects of disturbance (γ_d) and reef (γ_r) as well as the population effects (β_1) of disturbance year (T). Weakly informative normal and gamma priors were applied to the intercept and dispersion parameters, respectively. A flat improper prior was applied to the population effect parameter. The varying effects were further reparameterized into non-centered versions (for computational reasons) with weakly informative priors applied to the variances ($\sigma_{[d,r]}$).

The convergence of models was assessed visually using trace and residual plots, and examining r-hat ($\hat{r}$) values to insure they were all <1.01 (Appendix S1: Figures S1–S4, Tables S4 and S5).

To assess whether the disturbance interval has changed per decade for (1) bleaching, (2) cyclones, and (3) COTS, we calculated the interval in years from one occurrence to the next, and assigned the interval to the decade in which the disturbance first occurred. This meant that bleaching had no interval for the period 1986–1990, and COTS returned no interval for the 2011–2020 period. We modeled the number of years between disturbances as the response variable with a negative binomial (NB) error distribution (with a log link function) using decade as a fixed term and reef as a varying effect (Equations 7–9).

1. Bleaching:

$$\begin{aligned}
y_{i,r} &\sim \mathrm{NB}(\mu_{i,r}, \phi) \\
\ln(\mu_{i,r}) &= \left(\beta_0 + \gamma_{r[i],0}\right) + \sum_{j=1}^{2} T_{[i],j} \cdot \left(\beta_j + \gamma_{r[i],[j]}\right) \\
\phi &\sim \Gamma(0.01, 0.01) \\
\beta_0 &\sim N(-1, 1) \\
\beta_{[1,2]} &\sim U(-\infty, \infty) \\
\begin{pmatrix} \gamma_{[r],1} \\ \gamma_{[r],2} \\ \gamma_{[r],3} \end{pmatrix} &\sim N\left(\begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}, \mathbf{\Sigma_r}\right) \\
\mathbf{\Sigma_r} &= \begin{pmatrix} \sigma_{r_1}^2 & \rho_r\sigma_{r_1}\sigma_{r_2} & \rho_r\sigma_{r_1}\sigma_{r_3} \\ \rho_r\sigma_{r_1}\sigma_{r_2} & \sigma_{r_2}^2 & \rho_r\sigma_{r_2}\sigma_{r_3} \\ \rho_r\sigma_{r_1}\sigma_{r_3} & \rho_r\sigma_{r_2}\sigma_{r_3} & \sigma_{r_3}^2 \end{pmatrix} \\
\sigma_{r_{[1,2,3]}} &\sim t(3, 0, 2.5) \\
\rho_r &\sim \mathrm{LKJcorr}(1)
\end{aligned} \tag{7}$$

The i_{th} bleaching interval observation (y) from the r_{th} reef is assumed to be drawn from an NB distribution parameterized by a mean ($\mu_{i,r}$) and dispersion (φ), respectively. The (natural log) means were described by a linear model that included an intercept (β_0), varying effects of reef ($\gamma_{r,0}$) and decade changes per reef ($\gamma_{r,j}$) as well as the population effects (β_1) of decade (T).

Weakly informative priors were applied to the intercept and dispersion parameters. A flat improper prior was applied to the population (decade) effect parameter. The varying effects are assumed to follow a multivariate normal with a reef-specific covariance structure whose variances follow a weakly informative flat t distribution and whose correlation follows a LJK distribution with parameter of 1.

2. Cyclones

$$\begin{aligned}
y_{i,r} &\sim \mathrm{NB}(\mu_{i,r}, \phi) \\
\ln(\mu_{i,r}) &= (0 + \gamma_r) + \sum_{j=1}^{n} \beta_j T_i \\
\gamma_r &= \zeta_r \sigma_r \\
\phi &\sim \Gamma(0.01, 0.01) \\
\beta_{[1,n]} &\sim U(-\infty, \infty) \\
\zeta_{[d,r]} &\sim N(0, 1) \\
\sigma_{[d,r]} &\sim t(3, 0, 2.5)
\end{aligned} \tag{8}$$

The i_{th} cylone interval observation (y) from the r_{th} reef is assumed to be drawn from an NB distribution parameterized by a mean ($\mu_{i,r}$) and dispersion (φ), respectively. The (natural log) means were described by a linear model that included varying effects of reef (γ_r) as well as the population effects (β_j) of decade (T) parameterized as cell means (e.g., no intercept).

Weakly informative priors were applied to the dispersion parameter, and flat improper priors were applied to the population (decade) effect parameter. The varying effects were further reparameterized into non-centered versions (for computational reasons) with weakly informative priors applied to the variances ($\sigma_{[d,r]}$).

3. COTS

$$\begin{aligned}
y_{i,r} &\sim \mathrm{NB}(\mu_{i,r}, \phi) \\
\ln(\mu_{i,r}) &= \left(\beta_0 + \gamma_{r[i],0}\right) + \sum_{j=1}^{2} T_{[i],j} \cdot \left(\beta_j + \gamma_{r[i],[j]}\right) \\
\phi &\sim \Gamma(0.01, 0.01) \\
\beta_0 &\sim N(-1, 1) \\
\beta_{[1,2]} &\sim U(-\infty, \infty) \\
\begin{pmatrix} \gamma_{[r],1} \\ \gamma_{[r],2} \\ \gamma_{[r],3} \end{pmatrix} &\sim N\left(\begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}, \mathbf{\Sigma_r}\right) \\
\mathbf{\Sigma_r} &= \begin{pmatrix} \sigma_{r_1}^2 & \rho_r\sigma_{r_1}\sigma_{r_2} & \rho_r\sigma_{r_1}\sigma_{r_3} \\ \rho_r\sigma_{r_1}\sigma_{r_2} & \sigma_{r_2}^2 & \rho_r\sigma_{r_2}\sigma_{r_3} \\ \rho_r\sigma_{r_1}\sigma_{r_3} & \rho_r\sigma_{r_2}\sigma_{r_3} & \sigma_{r_3}^2 \end{pmatrix} \\
\sigma_{r_{[1,2,3]}} &\sim t(3, 0, 2.5) \\
\rho_r &\sim \mathrm{LKJcorr}(1)
\end{aligned} \tag{9}$$

The i_{th} COTs interval observation (y) from the r_{th} reef is assumed to be drawn from an NB distribution parameterized by a mean ($\mu_{i,r}$) and dispersion (φ), respectively. The (natural log) means were described by a linear model that included an intercept (β_0), varying effects of reef ($\gamma_{r,0}$) and decade changes per reef ($\gamma_{r,j}$) as well as the population effects (β_1) of decade (T).

Weakly informative priors were applied to the intercept and dispersion parameters. A flat improper prior was applied to the population (decade) effect parameter. The varying effects are assumed to follow a multivariate normal distribution with a reef-specific covariance structure whose variances follow a weakly informative flat t distribution and whose correlation follows a LJK distribution with parameter of 1.

All models were fitted using the *brms* package (Bürkner, 2017) and used three chains each with 1500 iterations after a "warmup" of 500 and a thinning rate of 2. The convergence of models was assessed visually using trace and residual plots and examining r-hat ($\hat{r}$) values to insure they were all <1.01 (Appendix S1: Figures S5–S10, Tables S6–S8).

We then used generalized additive models (GAMs) to investigate the effect of postdisturbance cover, benchmark coral cover, and time on the level of hard coral recovery, relative to the prior and historical benchmarks. Models were run separately for each (1) historical benchmark (Equation 10), and (2) prior benchmark (Equation 11) using a scaled t (SCAT) distribution, with smoothing parameters fitted to log postdisturbance coral cover, the benchmark cover, and years taken to recover, while reef was included as a random smooth term.

1. Historical benchmark

$$\begin{aligned} y_{i,r} &\sim \mathrm{SCAT}\left(\mu_{i,r},\sigma^2\right)\\ \mu_{i,r} &= \beta_0+\gamma_r+f(\log(\mathrm{DC}_i))+f(\mathrm{BC}_i)+f(\mathrm{YBR}_i)+\epsilon_{i,r}\\ \gamma_r &\sim N(0,\sigma_r)\\ f(\log(\mathrm{DC}_i)) &= \sum_{j=1}^{K}\beta_j\psi_j(\log(\mathrm{DC}_i))\\ f(\mathrm{BC}_i) &= \sum_{j=K+1}^{M}\beta_j\psi_j(\mathrm{BC}_i)\\ f(\mathrm{YBC}_i) &= \sum_{j=M+1}^{N}\beta_j\psi_j(\mathrm{YBR}_i)\\ \mathrm{Corr}\left(\epsilon_{i,j},\epsilon_{i',j'}\right) &= \rho^{|t_i-t_{i'}|}\text{ for } r=r' \text{ and } |t_i-t_{i'}|=1 \end{aligned} \tag{10}$$

The i_{th} relative benchmark recovery observation (y) from the d_{th} disturbance and r_{th} reef is assumed to be drawn from a scaled t distribution (SCAT) distribution with mean of $\mu_{i,d,r}$ and variance of φ. The means were described by an additive model that included an intercept (β_0), varying effects of reef (γ_r) as well as thin-plate smoothers $f()$ for (natural log) disturbance cover, benchmark cover, and year of recovery to benchmark. A first-order autoregressive (AR1) structure was also incorporated within each reef ($\epsilon_{i,r}$).

2. Prior benchmark

$$\begin{aligned} y_{i,r} &\sim \mathrm{SCAT}\left(\mu_{i,r},\sigma^2\right)\\ \ln\left(\mu_{i,r}\right) &= \beta_0+\gamma_r+f(\log(\mathrm{DC}_i))+f(\mathrm{BC}_i)+f(\mathrm{YBR}_i)+\epsilon_{i,r}\\ \gamma_r &\sim N(0,\sigma_r)\\ f(\log(\mathrm{DC}_i)) &= \sum_{j=1}^{K}\beta_j\psi_j(\log(\mathrm{DC}_i))\\ f(\mathrm{BC}_i) &= \sum_{j=K+1}^{M}\beta_j\psi_j(\mathrm{BC}_i)\\ f(\mathrm{YBC}_i) &= \sum_{j=M+1}^{N}\beta_j\psi_j(\mathrm{YBR}_i)\\ \mathrm{Corr}\left(\epsilon_{i,j},\epsilon_{i',j'}\right) &= \rho^{|t_i-t_{i'}|}\text{ for } r=r' \text{ and } |t_i-t_{i'}|=1 \end{aligned} \tag{11}$$

The i_{th} recovery to prior cover observation (y) from the d_{th} disturbance and r_{th} reef is assumed to be drawn from a scaled t distribution (SCAT) with mean of $\mu_{i,d,r}$ and variance of φ. The means were described by an additive model that included an intercept (β_0), varying effects of reef (γ_r) as well as thin-plate smoothers ($f()$) for (natural log) disturbance cover, benchmark cover, and year of recovery to benchmark. A first-order autoregressive (AR1) structure was also incorporated within each reef ($\epsilon_{i,r}$).

GAMs were fitted using the *mgcv* package (Wood, 2011). GAMs were fitted with an AR1 term to account for spatial autocorrelation. Plots of residuals and autocorrelation were examined for fit of model and evidence of autocorrelation (Appendix S1: Figures S11 and S12).

Recovery from disturbance impacts

Reefs exposed to Disturbance Impacts (D1, D2, D3: Figure 1) were defined as those where reef-wide absolute hard coral loss was greater than 10% between consecutive surveys. The cutoff of 10% change in hard coral cover was deemed appropriate as the data behind the hard coral estimates are categorical and we wanted to insure the classification of a disturbance impact was not simply the result of sampling error. Following each survey, each reef was assigned to one of five categories—either no impact, or, where a >10% decline was observed, the impacts from one of four disturbance types (coral bleaching, COTS, cyclone, multiple—where multiple indicated more than one disturbance type occurring concurrently at the time of survey). The disturbance type was identified by characteristic and recognizable effects on coral communities, for example, the presence of COTS or their feeding scars, dislodged, overturned, and broken colonies with algal growth (e.g., light green turfs) indicative of recent storm damage or percent of corals that had bleached during in-water or aerial surveys. Where there was no evidence for a disturbance but an impact (i.e., >10% decline in hard coral cover) was recorded, the cause of the decline was assigned as unknown. Unknown disturbances were not included in the analysis of disturbance occurrence, which focused on COTS, cyclones, and coral bleaching. Unknown disturbances were included in the analyses of disturbance impacts and recovery.

The impact of single disturbances was defined as just 1 year of decline on a reef, bounded by an increase in absolute coral cover >10% or the end of the data series. Consecutive disturbances were instances of coral decline that continued across multiple surveys until there was an absolute increase of >10% (R1 and R2 in Figure 1), and resulted from where one or more disturbance impacts affected a given reef over several years (e.g., D1, D2, and D3 in Figure 1). For example, coral mortality triggered by an outbreak of COTS, cyclone, or bleaching can unfold over a protracted period of several years, or a cyclone may occur in 1 year and a bleaching event in the next.

We then examined recovery on disturbed reefs, applying the following rules (see Figure 1):

1. Recovery (R) following a disturbance impact was defined as an absolute increase in hard coral cover of >10% (R1 and R2 in Figure 1).
2. Recovery continued until there was another disturbance (i.e., (a) >10% decrease in hard coral cover or (b) the data series ended.) When coral cover was still increasing at the end of the series, the recovery was recorded as incomplete.
3. To examine recovery, we used two benchmarks (1) the *historical benchmark* which was the highest level of hard coral cover recorded prior to 2010 (red dashed line in Figure 1) and (2) the *prior benchmark* which was the highest hard coral cover recorded in the survey prior to an individual disturbance impact (blue dashed line in Figure 1). It was possible for these benchmarks to be the same.
4. Complete recovery occurred when reef-wide average hard coral cover reached ≥100% of prior or historical benchmarks. Complete recovery was defined using modeled annual median hard coral cover rather than 95% credible intervals to remove any ambiguity associated with the use of overlapping errors. Modeled annual hard coral cover is described below (see *Impacts of disturbances on GBR reefs* for model details).

We then calculated the absolute and relative decline of hard coral cover following each disturbance impact in the dataset, and the subsequent level of recovery back to both the prior and historical benchmarks, along with the recovery time (the time in years from the year of disturbance impact (lowest hard coral cover) to the year of recovery), the rate of recovery (annual change in hard coral cover) and the interval between successive disturbance impacts at an individual reef (calculated from the year it occurred until the next occurrence). To determine the extent of recovery of hard coral cover following disturbance, we compared how many disturbance impacts resulted in complete recovery (≥100% of historical and prior benchmark) versus the number of reefs with partial recovery (<100% of benchmarks) up to and including 2022. Recovery of 100% or more means that the median modeled hard coral cover in the year of recovery achieved the same or a higher level than the prior or historical benchmark.

To test whether the recovery rate has changed through time, we used a Bayesian hierarchical model to examine the rate of recovery (change in percent hard coral cover per year) against the year of recovery (Equation 12). The percent of hard coral cover prior to the disturbance was fitted as a covariate, with reef and disturbance type included as varying effects.

$$\begin{aligned}
y_{i,d,r} &\sim \Gamma\left(\mu_{i,d,r},\varphi\right)\\
\ln\left(\mu_{i,d,r}\right) &= (\beta_0+\gamma_d+\gamma_r)+\beta_1 C_i+f_1(T_i)+f_2(T_i,C_i)\\
\gamma_d &= \zeta_d\sigma_d\\
\gamma_r &= \zeta_r\sigma_r\\
f_1(T_i) &= \sum_{j=3}^{5}\beta_j\phi_j(T_i-1980)\\
f_2(C_i,T_i) &= \sum_{j=5}^{8}\beta_k C_i.\phi_j(T_i-1980)\\
\varphi &\sim \Gamma(0.01,0.01)\\
\beta_0 &\sim N(-1,1)\\
\beta_{[1,8]} &\sim N(0,5)\\
\zeta_{[d,r]} &\sim N(0,1)\\
\sigma_{[d,r]} &\sim t(3,0,1)
\end{aligned} \tag{12}$$

The i_{th} recovery rate observation (y) from the d_{th} disturbance and r_{th} reef is assumed to be drawn from a gamma (Γ) distribution with shape parameters of $\mu_{i,d,r}$ and φ parameterized to represent the mean and dispersion, respectively. The (natural log) means were described by a linear model that included an intercept

(β_0), varying effects of disturbance (γ_d) and reef (γ_r) as well as the main and interactive population effects (β_1) of prior cover (C) and the third-order orthogonal effects over decades (ϕ_j) such that $\sum_j^n \phi_j(T_i - 1980) = 0$. Weakly informative normal, normal, and gamma priors were applied to the intercept, population effect and dispersion parameters, respectively. The varying effects were further reparameterized into non-centered versions (for computational reasons) with weakly informative priors applied to the variances ($\sigma_{[d,r]}$).

The model was fitted using the *brms* package (Bürkner, 2017) and used three chains each with 1500 iterations after a "warmup" of 500 and a thinning rate of 2. The convergence of models was assessed visually using trace and residual plots and examining r-hat ($\hat{r}$) values to insure they were all <1.01 (Appendix S1: Figures S13 and S14).

RESULTS

Exposure of GBR reefs to disturbance

The number and frequency of disturbance events varied across the GBR. From 1985 to 2022, the LTMP surveyed 492 reefs in total, recording 265 instances of declines of coral cover of >10% on 131 of those reefs. The central GBR accounted for 49.8% of the 265 disturbance events across 30.5% of the 190 reefs surveyed, while 27.5% of disturbance events were recorded on 25.9% of 143 reefs surveyed in the northern GBR and 22.7% of disturbance events were recorded on 22.6% of the 159 southern GBR survey reefs. Over the 36-year period, only 10% of disturbance events were single disturbances at a reef in 1 year, whereas the vast majority were disturbance events across multiple consecutive surveys on the same reef. The length of time between consecutive disturbances ranged from 2 to 27 years with an average of 6.6 years. Multiple disturbance events occurring concurrently at a single reef in a single year were also common, arising in 35% of cases. Consecutive and multiple disturbance events were composed of varying combinations of different types of individual disturbances, especially in combination with COTS outbreaks, which tended to persist at reefs for several years.

At a GBR-wide scale, disturbance events have become more frequent and severe through time. The frequency and spatial extent of disturbance events escalated considerably between 2011 and 2022, with cumulative impacts from outbreaks of COTS, cyclones, and mass coral bleaching, especially in the northern and central GBR (Figure 2; Appendix S1: Figure S15). During the last decade, multiple mass coral bleaching events have emerged, superimposed on a background of smaller scale disturbance events. There were no recorded severe mass coral bleaching events prior to 1998, then two events in 1998 and 2002, followed by a 14-year gap before the first recorded back-to-back mass bleaching events in 2016 and 2017, and a further two events in 2020 and 2022 (Figure 2). This sequence of mass coral bleaching events, coupled with severe outbreaks of COTS and punctuated by cyclones, represents an escalation from uncommon events of limited spatial extent prior to 2011 to the increasing frequency and larger spatial footprint of disturbance events after 2011 (Figure 2).

Northern GBR

Since large-scale monitoring began, the probability of an individual reef in the northern GBR being impacted by severe coral bleaching (>30% of corals bleached), active outbreaks of COTS, and damaging cyclones Hs > 6 m has increased significantly (Figure 3a–c, Table 1). For example, the 2016 bleaching event was the first time during this study that 100% of surveyed northern GBR reefs were affected by a single disturbance event, and severe levels of bleaching (>30% of colonies affected) were recorded on 92% of surveyed northern reefs (Figure 2). In 1998 and 2002, only low levels of bleaching (<10% of colonies) occurred on a maximum of 26% of surveyed northern reefs, and no occurrences of severe bleaching were recorded (Figure 2). The percent of reefs affected by severe cyclones was greater in 2014 and 2015 on monitored northern GBR reefs than at any time during this study (Figure 2), as was the number of active outbreaks of COTS, which peaked in 2015 (Figure 2—yellow bars). Bernoulli GLMMs revealed an increase in the probability of severe bleaching by 19.2% per year from a very low probability of 0.01 in 1995, while the probability of COTS outbreaks and severe cyclones increased by 1.2% and 4.6% per year, respectively (Table 1). The period between 2011 and 2017 saw significant impacts from back-to-back mass coral bleaching in 2016 and 2017, COTS outbreaks and two severe tropical cyclones, which resulted in coral cover declines on the vast majority (81%) of northern survey reefs (Appendix S1: Figure S16). We measured a 58% decline in region-wide hard coral cover from 25% in 2011 to 11% in 2017, with decreases ranging from 0% to 14% per year on individual reefs (Appendix S1: Figure S16). From 2017 to 2022 was a period free from events causing major coral mortality, and this period has resulted in increases in hard coral cover to the highest levels recorded during the study (Figure 4). However, there was a widespread, severe mass bleaching event in 2022 in the northern GBR and the impact of this event is as yet unmeasured.

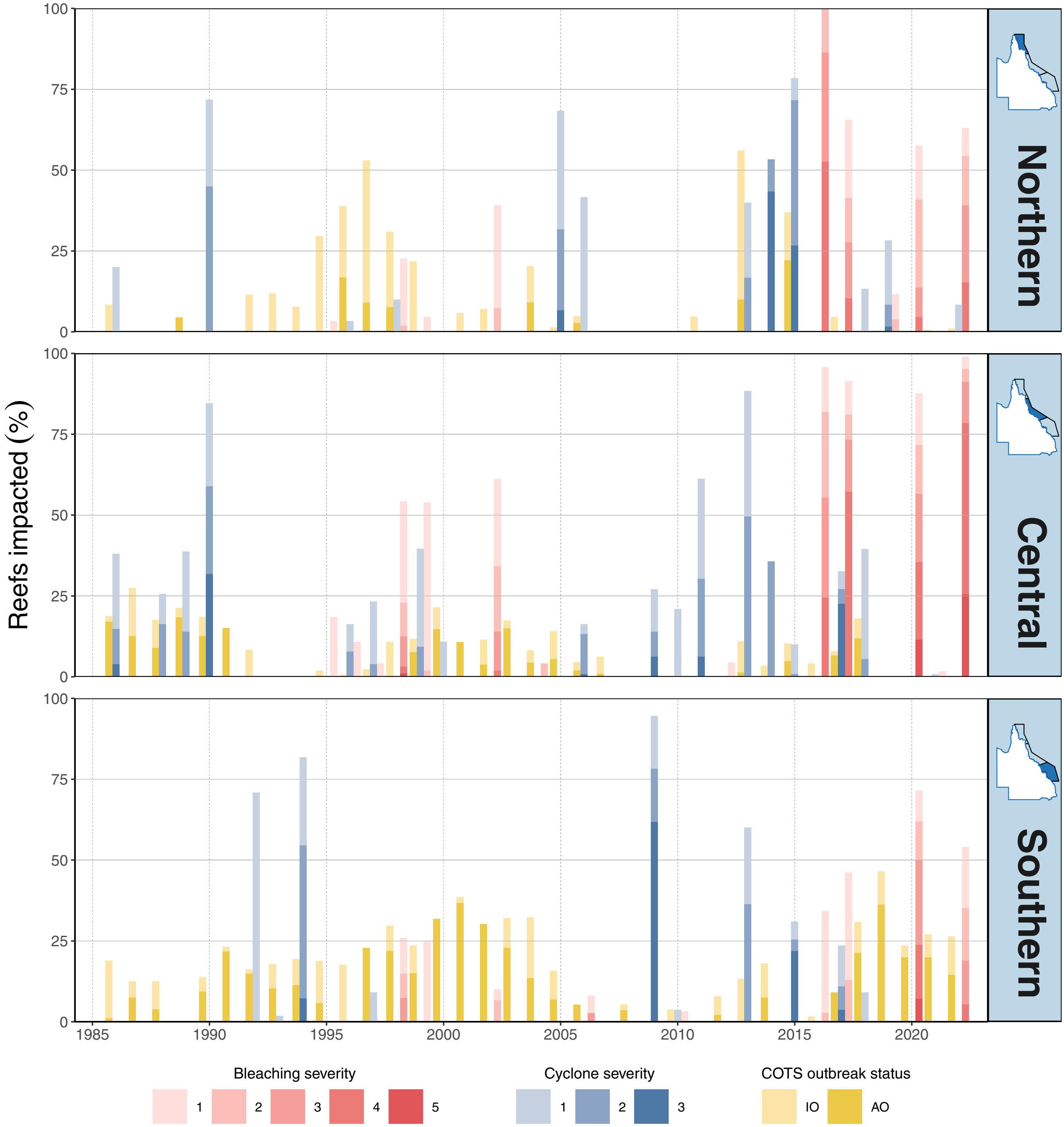

FIGURE 2 The disturbance regime of the Great Barrier Reef (GBR) 1986–2022. Bars represent the percent of survey reefs impacted by disturbances; yellow = crown-of-thorns Starfish (COTS) outbreaks, blue = cyclones and red = bleaching (numbers of reefs surveyed each year Appendix S1: Table S1). Darker shading represents higher severity categories. Red bars display the spatial footprint of bleaching on the GBR, as measured by manta tow surveys from January to April in years with no aerial surveys, and where extensive aerial surveys overlapped with Australian Institute of Marine Science (AIMS) Long-Term Monitoring Program (LTMP) survey reefs in mass bleaching events. Bleaching severity categories are: 0 = 0% of corals bleached, 1 = 1%–10%, 2 = 10%–30%, 3 = 30%–60%, 4 = >60–80%, 5 = > 80%. Yellow bars show the extent and severity of outbreaks of the corallivorous COTS *Acanthaster* c.f. *solaris* (COTS) on reefs surveyed on the GBR. Severity of COTS outbreaks is determined by the average number counted for each 2-min manta tow (~2000 m^2): *Zero* = 0, *No Outbreak* = <0.22 COTS per tow, *Incipient Outbreak* (IO) = >0.22 < 1.0, *Active Outbreak* (AO) = >1.0. Blue bars show the modeled significant wave height (Hs) levels for each tropical cyclone with the potential to impact reefs of the GBR: 0 = Hs ≤ 4 m, 1 = Hs ≥ 4 m < 6 m, 2 = Hs ≥ 6 m < 8 m, 3 = Hs ≥ 8 m.

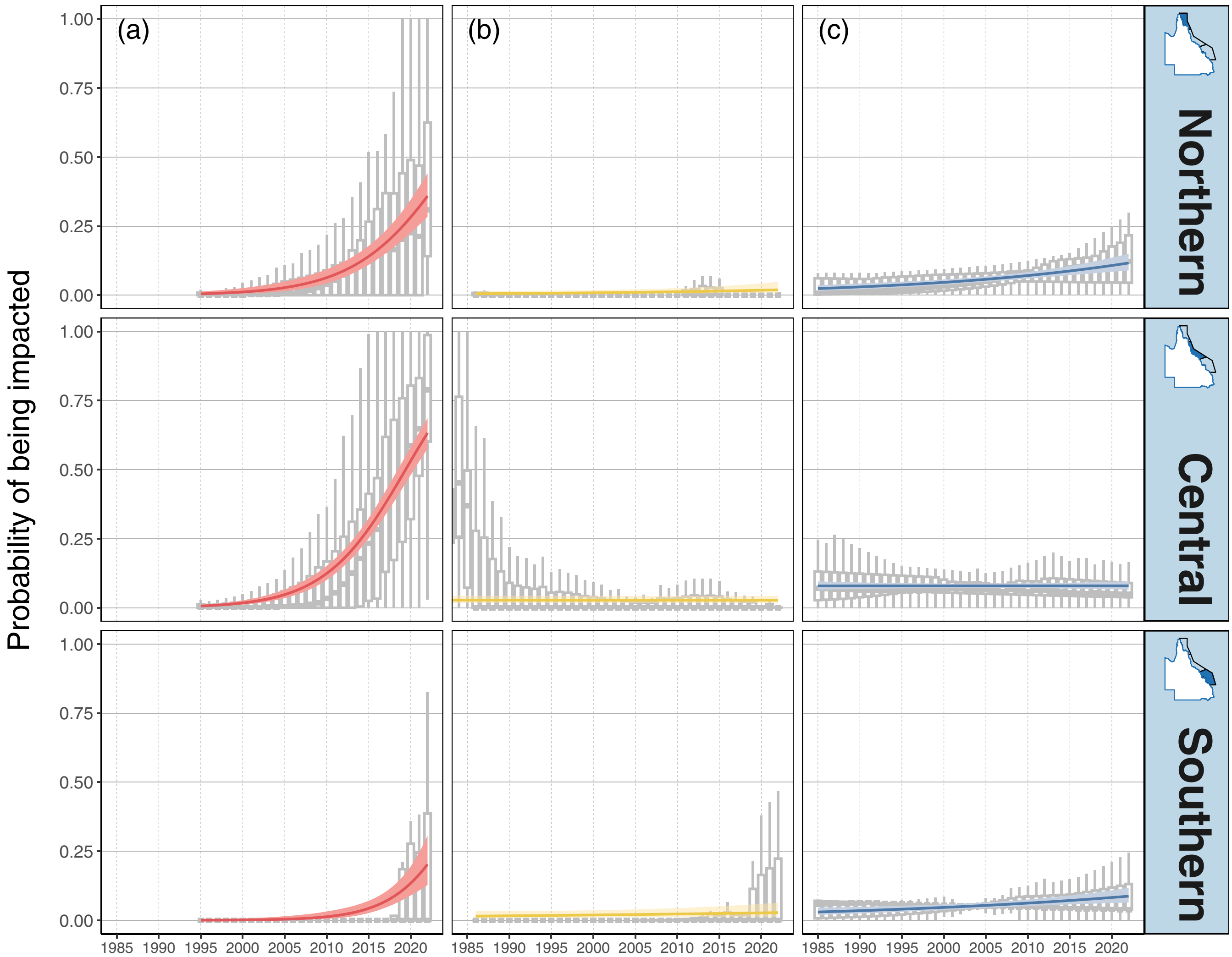

FIGURE 3 The modeled change in probability of all severe disturbances including (a) bleaching category 3 or 4; (b) COTS active outbreaks; and (c) cyclones causing significant wave heights (Hs) >6 m on the northern, central, and southern Great Barrier Reef survey reefs, 1986–2022. Data for bleaching were not collected in the earliest years of the study and so the bleaching analysis is constrained to 1995–2022. The line and shading are the mean probability of impact plus 95% CIs predicted from a Bernoulli generalized linear mixed model run for combined severe disturbances.

Central GBR

The percent of reefs impacted by mass coral bleaching increased since 1998 on the central GBR, where severe bleaching (>30% of colonies affected) was recorded on 96% of monitored reefs in 2016, 89% in 2017, and 55% in 2020 compared to 52% of monitored reefs in 1998 and 45% in 2002 (Figure 2). Since 2009, there were seven cyclones on the central GBR, three of which impacted >25% of survey reefs, one that impacted 60% of reefs, and one that caused damage to an estimated 80% of surveyed reefs. Prior to 2008, cyclones were less frequent and tended to impact fewer reefs than after 2008 (Figure 2). On the central GBR, Bernoulli GLMMs revealed that the odds of severe bleaching impacting individual reefs has increased significantly between 1995 and 2022 at an average of 23.1% per year, while there has been no change in the probability of impacts of severe cyclones, and a decrease in the probability of a COTS outbreak (Figure 3a–c, Table 1). Two mass bleaching events and two cyclones caused a decline in coral cover on the central GBR from 22% in 2016 to 14% in 2018 (Figure 4). From 2018 to 2022 there have been increases in hard coral cover to the highest levels yet recorded, coinciding with a period free from major coral mortality (Figure 4). Similar to the northern GBR, there was a widespread, severe mass bleaching event in 2022 in the central GBR and the impact of this event is yet to be quantified.

TABLE 1 Changes in the probability of impact of severe disturbances on the northern, central, and southern Great Barrier Reef from 1985 to 2022.

Disturbance	Region	Intercept (95% CIs)	Slope (95% CIs)	Annual change in odds (%)	*t* ratio	*p*
Bleaching	Northern	0.005 (0.002, 0.013)	0.11 (0.06, 0.16)	19.2	4.29	<0.001
	Central	0.01 (0.004, 0.01)	0.18 (0.15, 0.20)	23.1	14.01	<0.001
	Southern	0.0003 (<0.0001, 0.003)	0.22 (0.12, 0.32)	28.0	4.4	<0.001
Crown-of-Thorns Starfish	Northern	0.04 (0.02, 0.08)	0.04 (−0.002, 0.08)	1.2	1.86	0.06
	Central	0.12 (0.09, 0.17)	−0.07 (−0.09, −0.04)	−4.7	−5.48	<0.001
	Southern	0.06 (0.04, 0.10)	0.02 (−0.01, 0.05)	0.7	1.17	0.24
Cyclones	Northern	0.02 (0.016, 0.04)	0.05 (0.03, 0.06)	4.6	5.25	<0.001
	Central	0.08 (0.07, 0.1)	<0.0001 (−0.01, 0.01)	0.01	0.02	0.99
	Southern	0.03 (0.02, 0.05)	0.03 (0.01, 0.04)	3.1	3.35	0.001

Note: Data are from generalized linear mixed models fitted separately to each response variable (Disturbance) with time (Year) as the fixed effect and Reef as a random term. Intercept and 95% CIs represent the odds of being impacted by disturbance (e.g., probability of being disturbed divided by probability of not being disturbed) at the start of the time series. Slope (and CI) is the change in odds per year (but on a fold scale rather than on a percentage scale). On a fold scale, a value of 2 indicates a twofold increase (e.g., a doubling, or 100% increase). Annual percent change in odds describes the annual change in probability from Time 0 (Intercept), of a severe disturbance impacting survey reefs, such that a positive response means the probability has increased throughout the time series, while a negative response means the probability has decreased; *t*-ratios and *p*-values associated with tests of change to the slope are also shown.

Southern GBR

There was an increase in the frequency of disturbance events in the southern GBR (Figure 2). There were few instances where greater than 30% of reefs were impacted by a single severe disturbance event prior to Cyclone Hamish in 2009, which affected 95% of survey reefs and caused widespread coral loss. Additionally, while the southern GBR escaped severe mass coral bleaching in both the 2016 and 2017 events (Hughes, Anderson, et al., 2018; Hughes, Kerry, et al., 2017), the 2020 and 2022 events caused bleaching on 71.4% and 54% of monitored reefs respectively, representing a substantial increase in the number of reefs affected by bleaching (Figure 2). In the southern GBR, modeling of the occurrence of disturbances using Bernoulii GLMMs revealed that the probability of reefs being impacted by coral bleaching has increased by 28% per year since 1995, while the probability of being impacted by a cyclone has increased by 3.1% annually since 1985, with no change detected in the probability of COTS outbreaks (Figure 3a–c, Table 1).

Impacts of disturbances on GBR reefs

We used Bayesian hierarchical models to examine whether the amount of hard coral cover left after a disturbance impact or the amount of coral lost due to a disturbance impact has changed through time. Of the 131 reefs impacted by hard coral losses >10%, the amount of hard coral remaining postdisturbance has declined by 1.02% (0.36%–1.7%) per year since the mid-1980s (Figure 5a: Bayesian exceedance probability = 0.998), and the amount of coral cover loss from disturbance impacts has increased each year by 0.56% (0.16–0.93) (Figure 5b: Bayesian exceedance probability = 0.997). We also examined whether the number of reefs being impacted by disturbance or the interval between disturbances has changed through time. The percentage of survey reefs where disturbance events occurred has increased in each decade of the study (Figure 5d) in all three regions (Appendix S1: Figure S15). While over 300 reefs were surveyed in the first two decades of the study, the incidence of disturbance events was relatively low (1986–1990—6.03%, 1991–2000—19.4%; Figure 5d). However, by 2011–2020, during which the lowest number of reefs were surveyed in the entire study, 44% of reefs were impacted by disturbance (Figure 5c). The increasing incidence of disturbance events has meant that the interval between events across the whole GBR has substantially diminished, particularly in the last decade (Figure 5d). For example, the interval between successive mass coral bleaching events was significantly shorter in the decade 2011–2020 (Figure 5d: mean = 2.2 years, 95% CI 1.9–2.4), compared with the period 1995–2000 (mean = 10.3 years, 95% CI 9.01–11.7) and 2001–2010 (mean = 12.9 years, 95% CI 9.1–17.2). Note that LTMP bleaching records began in 1995. Similarly, the interval between severe cyclones across the GBR has decreased in the decade 2011–2020 to a mean of 2.1 years (95% CI 1.9–2.3) from a mean of 9.0 years (95% CI 8.2–9.9) in the decade 1991–2000 (Figure 5d).

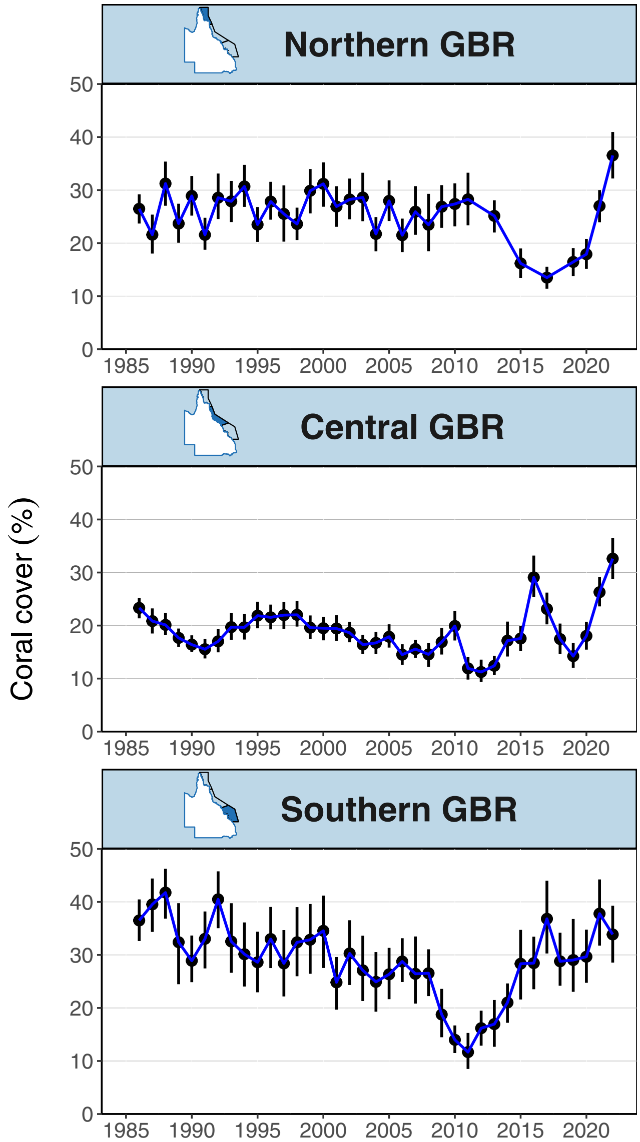

FIGURE 4 Trends in average hard coral cover for the northern, central and southern Great Barrier Reef (GBR) based on Bayesian hierarchical models of manta tow data. Survey data from 492 reefs contributed to the 36-year time series; error bars represent 95% credible intervals.

Recovery from disturbance impacts

We examine how many reefs that were impacted by disturbance had recovered to the prior and historical benchmarks and found complete recovery (100% or more of the benchmark) of GBR reefs was a relatively rare occurrence. Only 116 out of 265 (44%) disturbance impacts were followed by complete recovery to the prior benchmark, and 62 out of 265 (23%) regained the historical benchmark for hard coral cover (Figure 6a,b). Of the 149 instances (out of 265 recorded disturbance impacts) of partial recovery to the prior benchmark, only 7% recovered by less than half, and the vast majority by more than 50% (Figure 6c). Similarly, of the 203 instances of partial recovery to the historical benchmark, 8% recovered by less than 50% of the benchmark, with the vast majority recovering by more than a half (Figure 6d). Despite the general lack of complete recovery during the time series, there was an increase in the number of reefs achieving complete recovery to the historical benchmark in 2021 and 2022 (Figure 6a). Of the 23% of disturbance impacts that completely recovered to the historical benchmark, over half (34/62) recovered in either 2021 or 2022. This, coupled with a large proportion of reefs obtaining 50%–99% recovery, has led to region-wide increases in hard coral cover in the central and northern GBR in 2022, to the highest average levels recorded there in 36 years of monitoring (Figure 4). However, there is a lower proportion of reefs that fully recover historically compared with prior benchmarks, resulting in a ratcheting down of coral cover on 47 out of 131 reefs (36%) on which we detected disturbance impacts with hard coral losses >10% and represents an example of shifting baselines of recovery.

The polynomial model to investigate whether the rate of hard coral recovery has changed through time revealed strong evidence for a positive second-order term (Figure 7: median = 2.41 (−0.4 to 5.4), Bayesian exceedance probability = 0.95). This indicates that the rate of recovery declined from the early years of the study until the middle of the time series but has increased slightly since 2010 (Figure 7). Indeed, the highest recovery rates occurred at the start of the time series (1988, 1989), while the lowest recovery rates occurred in 2013 and 2019 corresponding to a period of intense cumulative disturbances that impacted the GBR between 2012 and 2017. There was also a positive relationship between the recovery rate and the level of hard coral cover remaining after the disturbance (partial median effects = 1.84 [95% CI 0.43–3.22]).

We used GAMs to examine how the amount of postdisturbance hard coral cover, the level of the benchmark, influenced the level of recovery observed. Complete recovery to both the prior and historical benchmarks was more likely when the postdisturbance coral cover remained above 30% (Figure 8a,b), and the prior and historical benchmarks were lower than 20% and 25%, respectively (Figure 8c,d). For example, the highest level of recovery observed was 363% on one reef in the southern GBR (Figure 6c,d), but the historical benchmark was only 15% coral cover. Modeled predictions of time required for complete recovery to the historical benchmark were >30 years, while complete recovery to the prior benchmark was on the order of 15–20 years (Figure 8e,f).

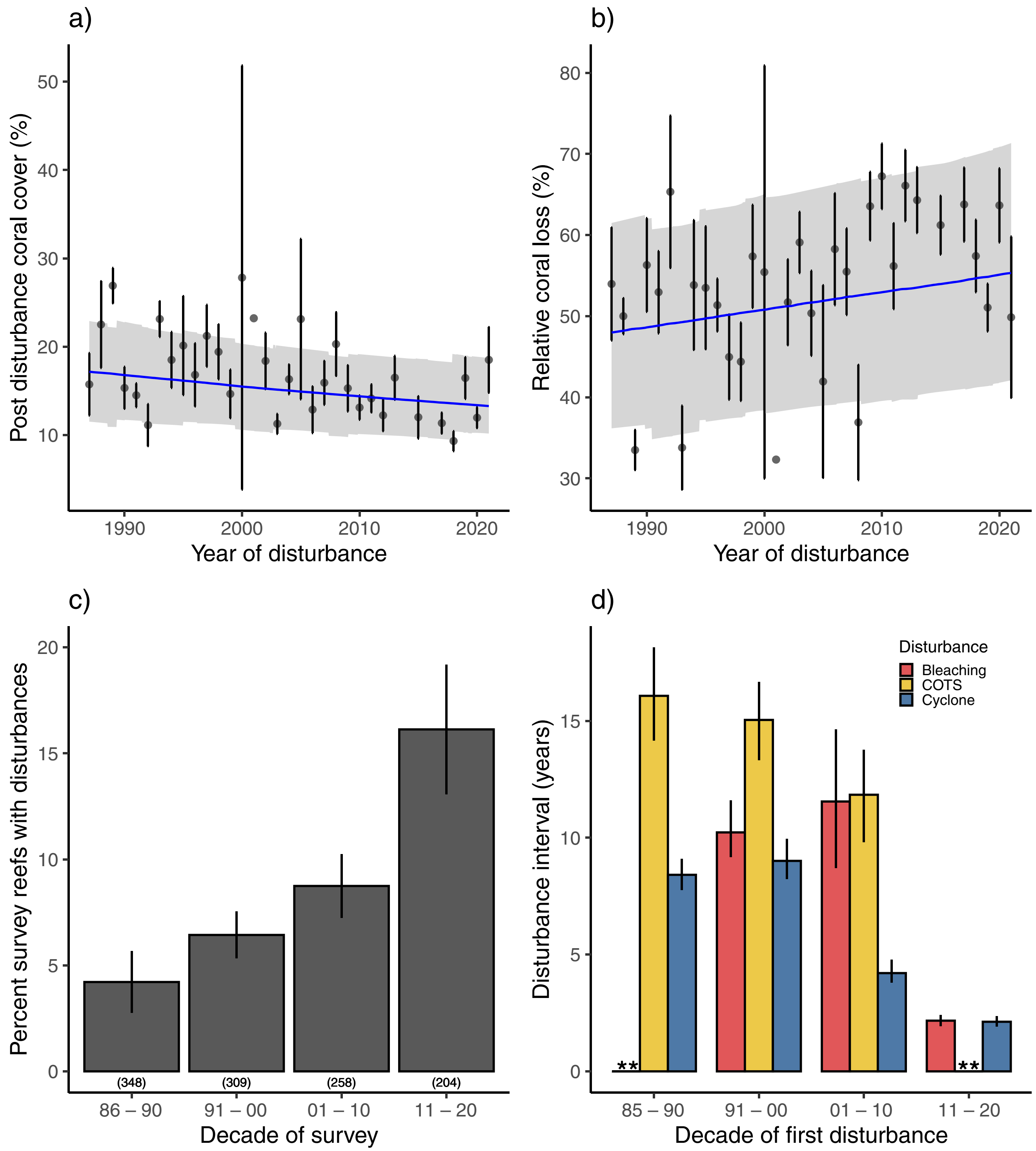

FIGURE 5 Changes in disturbance event impacts through time. (a) The level of postdisturbance hard coral cover. (b) The average magnitude of relative coral loss across all disturbance events by year of disturbance. For panels (a) and (b) data are raw means ± SE, the blue line is the fitted model trend, and the gray ribbon is the highest probability density (HPD) 95% CIs from a Bayesian hierarchical model. (c) The percentage of survey reefs that were impacted by disturbances, and (d) disturbance interval per decade (mean number of years between disturbance events binned by the decade in which the first disturbance occurred). **No coral bleaching occurred from 1985 to 1990, and the current crown-of-thorns starfish (COTS) outbreak wave from 2011 to 2020 was occurring at the time of writing, and hence there are no intervals for these two periods. Data are means with associated Bayesian HPD 95% CI from a Bayesian hierarchical model.

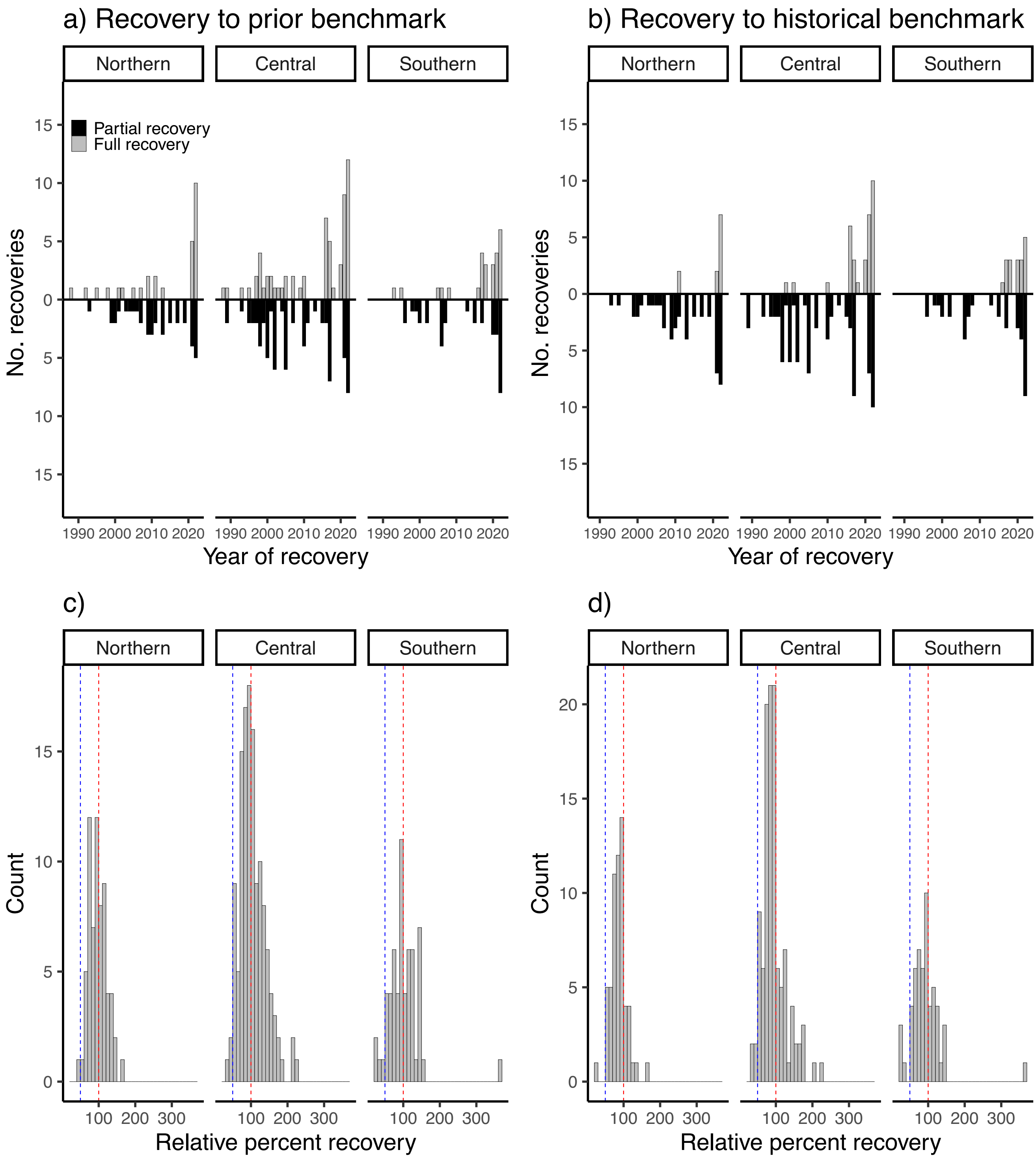

FIGURE 6 The number of reefs recovering to (a) the prior benchmark, and (b) the historic benchmark on the Great Barrier Reef. Frequency distribution of percent recovery to (c) prior benchmark, and (d) historical benchmark. Blue vertical dashed line on the left is 50% recovery to benchmark and red vertical dashed line on the right is complete (100%) recovery.

DISCUSSION

Ecologists have long studied how ecosystems change through time, especially the ways in which they are impacted by and recover from disturbances. However, the magnitude and pace of contemporary disturbance regimes imposed by climate change threatens many ecosystems. Increasing temperatures have directly caused the replacement of temperate kelp forests by less complex turf algae or urchin barrens (Wernberg et al., 2016), increased the

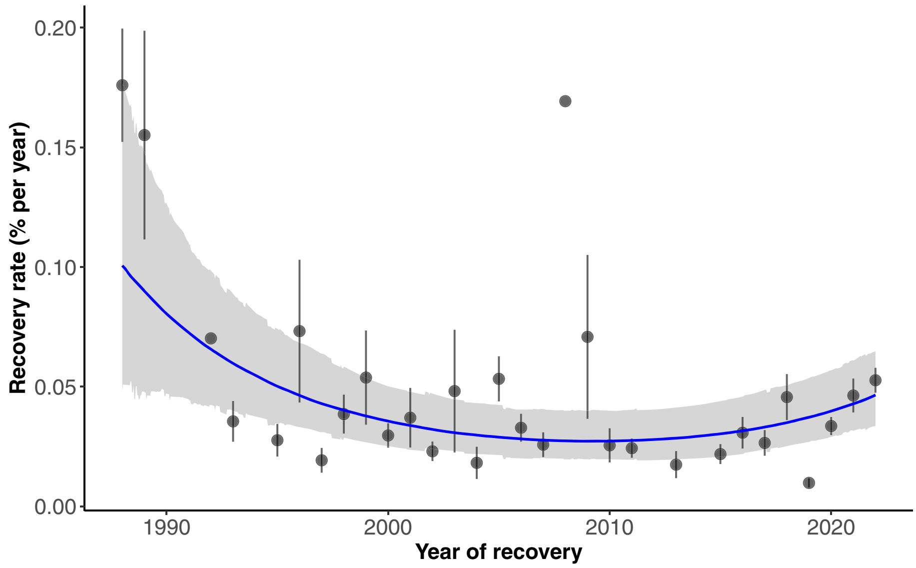

FIGURE 7 Changes in recovery rate (percent hard coral cover per year) on the Great Barrier Reef. Data are raw means ± SE, the blue line is the fitted model trend, and the gray ribbon is the highest probability density (HPD) 95% CIs from a polynomial Bayesian hierarchical model.

frequency and severity of mass coral bleaching (Hughes, Kerry, et al., 2018), reduced the accumulation of ice on northern hemisphere lakes over winter (Sharma et al., 2019), and increased the frequency and severity of fires affecting terrestrial forests (Kasischke et al., 2010; Pritchard et al., 2017). The increased frequency of disturbance events and diminishing recovery observed in the last decade (2010–2020) of this study echo the increasing climate-induced disturbance regimes that are eroding the integrity of many ecosystems around the globe (IPCC, 2021). There is a pressing need to understand how accelerating disturbances are impacting the ability of natural systems to respond, especially when ecosystems (e.g., coral reefs) provide important services to hundreds of millions of people. Here, we present compelling evidence that the disturbance regime of the GBR ecosystem has changed in the last decade (2010–2020). Our results reveal an increase in the spatial extent and frequency of coral bleaching and tropical cyclones, and an increase in the disturbance impact (i.e., coral loss) in the most recent decade of the study. The unprecedented cluster of disturbances in the last decade coincided with the largest spatial extent of reefs affected; the 2016 bleaching event was the first time in this 36-year study that 100% of monitored reefs of a GBR region (the northern GBR) were impacted by a single disturbance. Similarly, 100% of surveyed reefs were impacted by bleaching 6 years later in the central GBR in 2020.

The cluster of impacts on GBR coral reefs in the last decade, unparalleled in the 36 years of this study, is particularly illustrated by the four mass coral bleaching events in 7 years. This unprecedented frequency of widespread mass coral bleaching is set against a routine background of numerous severe tropical cyclones and a fourth wave of COTS outbreaks on the GBR.

Our analyses further revealed that the level of coral cover after disturbance impacts has not only declined through time but also influenced the recovery rate, and that the magnitude of coral loss after each disturbance impact was greater in the last decade than at the beginning of the study. There was also a reduction in the recovery rate in the middle of the time series compared to the start, although the recovery rate increased slightly toward the end. The lowest recovery rates corresponded to a period of intense cumulative disturbances between 2012 and 2017. These trends indicate that, together with the increased intensity and frequency of the disturbance events, the impacts (i.e., loss of coral cover) of disturbances are also increasing. However, it should be noted that these results apply only to reefs that were impacted by disturbances (i.e., had a loss of hard coral cover >10%), and there are likely reefs that exhibited resistance to disturbance events with little impact (i.e., <10% hard coral loss) which were not included in the analyses. Our goal was to investigate whether the observed impact of disturbances on hard coral cover has changed through time, and whether this was linked to changes in disturbance regime. Questions about changes to resistance or resilience to disturbance would need to include reefs that did not suffer coral loss >10% during the same period.

Severe climate-induced disturbance events are predicted to occur more frequently under climate change (Emanuel, 2013; Hoegh-Guldberg, 1999), and our results provide evidence that these changes are already

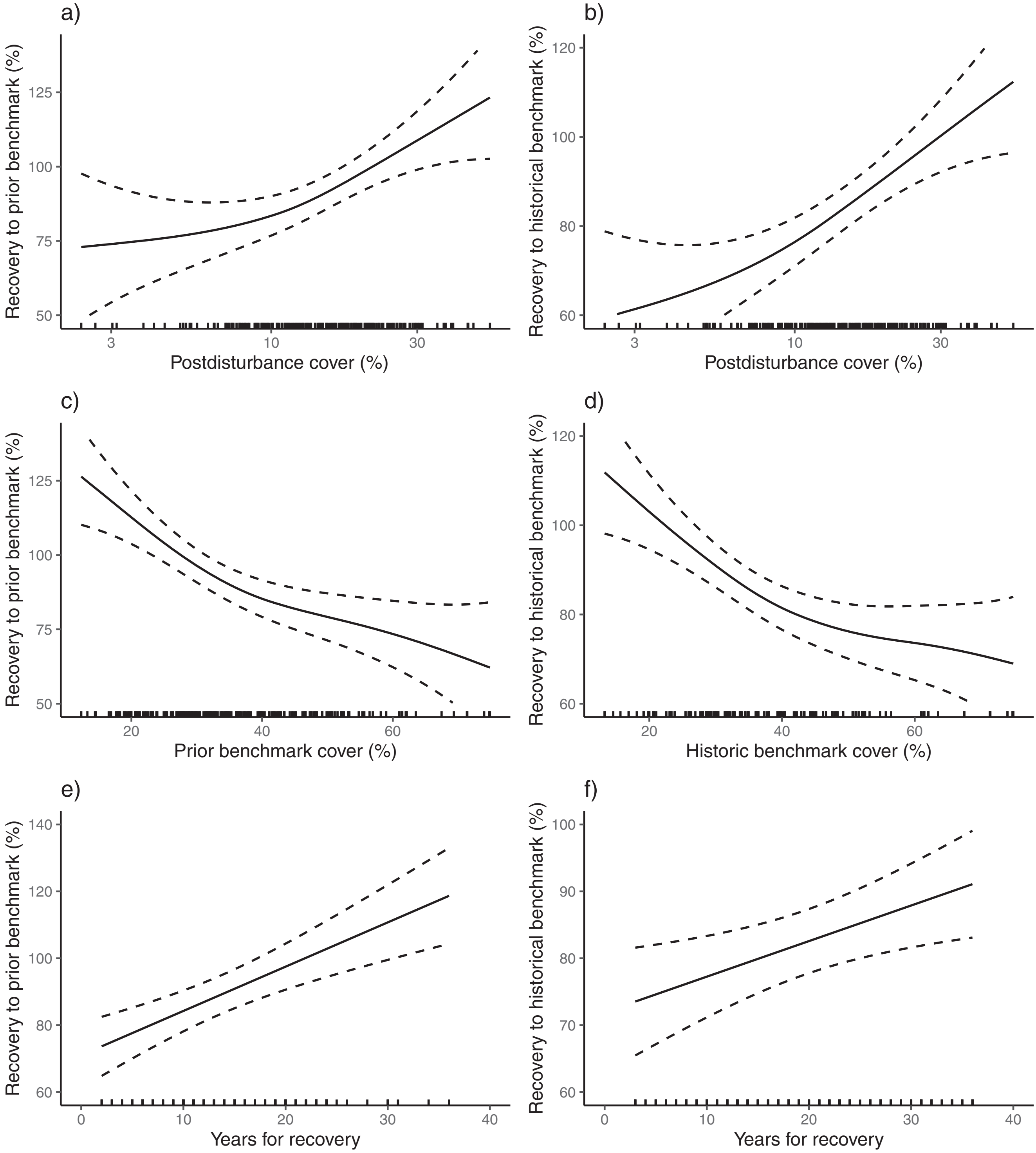

FIGURE 8 The effect of postdisturbance coral cover, benchmark cover, and the number of years on the relative percent hard coral cover recovery to the prior benchmark (a, c, e: left column) and the historical benchmark (b, d, f: right column) on the Great Barrier Reef. Data are partial plots from a generalized additive model.

occurring. There is now less time for recovery compared to the 1980s, with the inter-disturbance interval being reduced by a third in the last decade, exemplified by the back-to-back mass coral bleaching events in 2016 and 2017. Shorter intervals between disturbance events have also been documented in terrestrial ecosystems, especially boreal and neotropical forests where cumulative disturbance events and higher frequencies of human and natural disturbance events have led to a general erosion of resilience and stability (Buma et al., 2013;

Hérault & Piponiot, 2018; Whitman et al., 2019). However, the relationship between disturbance frequency and recovery may not be simple or linear. A study of 283 disturbance and recovery events in tropical forests found that in some cases, increasing frequency of disturbance events at a site through time elevates recovery rates as the system was able to respond dynamically and adapted to increased frequency of disturbance (Cole et al., 2014). Similarly, hardier corals that survived the 2016 heatwave in the northern and central GBR were more resistant to bleaching in 2017, although the second heatwave was hotter and longer in most locations (Hughes, Kerry, Connolly, et al., 2019). The most common scenario we observed for complete recovery to historical benchmarks was when reefs had a low benchmark to begin with, or when coral cover remained relatively high following loss of cover.

In this study, we highlight three important results: (1) that recovery back to a high benchmark was rarely observed, (2) complete recovery was most likely only for already degraded reefs with low historical benchmarks, and (3) reefs were better able to recover from disturbance impacts when coral losses were small, or postdisturbance coral cover was not reduced to below 30%. Complete recovery from disturbance impacts was uncommon during this study; 56% of disturbance impacts did not result in complete recovery to prior benchmarks, and recovery from 77% of impacts failed to reach the historical benchmark. While shorter recovery periods are no doubt important, legacy effects from chronic disturbances such as reduced growth, reproduction, and recruitment will also impair recovery during periods free from disturbances (Ortiz et al., 2018; Osborne et al., 2017).

A notable exception to the diminishing recovery potential in the decade 2010–2020 was the increase in the number of reefs with complete recovery and an elevated rate of recovery in 2021 and 2022. Complete recovery to the prior benchmark jumped markedly in these 2 years with the highest proportion of impact recoveries achieving this benchmark than at any other time during the study; this played a large role in driving regional recovery. The recovery of reefs in these 2 years was due in part to a period free from coral mortality, coupled with a two-phase recovery trajectory apparent on many coral reefs (Warne et al., 2022). Two-phase recovery trajectories occur during the first 2–5 years of recovery and consist of an initial period of slow coral growth per unit cover before an accelerated sigmoidal growth period. We suspect that the recent regional recovery resulted from a conflux of low mortality years coupled with the sigmoidal recovery trajectory across large tracts of the GBR. The third phase of recovery trajectories typical on coral reefs is a logarithmic deceleration phase of decreasing growth caused by environmental limitations, until the system reaches an asymptotic carrying capacity threshold (Vercelloni et al., 2019). The slower first and third phases of recovery relate to our study's estimates of a 15- to 20-year period to reach the prior benchmark, and a 30+ year period to achieve historical benchmarks. The record high coral cover of 2021–2022 was due to the very low coral cover of most of the central and northern reefs after 2017 (a low prior benchmark) was followed by a period without disturbance impacts across the GBR, and all of the survey reefs in the relevant regions encountered the exponential growth curve at the same time, with no small impacts to offset the increases.

These average increases on monitored reefs suggest that although there was a significant reduction in broodstock and recruitment evident following the 2016 and 2017 mortality events (Hughes, Kerry, Baird, et al., 2019), these levels were sufficient to supply enough larvae to recolonize northern and central GBR reefs and to stimulate increases in hard coral cover. Recovery potential depends on a complex interaction between the predisturbance community, the type of disturbance event, traits of the remaining populations (Gouezo et al., 2019), and in marine ecosystems, on connectivity to sources of larvae and spatial variations in recruitment (Holbrook et al., 2018; Hughes et al., 2021). However, the reduction of disturbance intervals in the last decade reflects a trend toward disturbance frequencies that promote fast-recruiting and fast-growing but vulnerable species, such as *Acropora* spp. (Ortiz et al., 2021). These species, particularly those with tabular growth forms, can quickly contribute to two-dimensional increases in percent hard coral cover. The finding of regional increases in 2021 and 2022, despite the number of reefs that failed to recover to historical benchmarks, also highlights that such regional aggregations of data smooth over the complexities of recovery at much finer spatial scales.

The finding that more reefs completed recovery to the prior benchmark than historical benchmark exemplifies the concept of shifting baselines (Bellwood et al., 2004; Bohnsack, 2003; Pauly, 1995) and represents evidence for a degradation and "ratcheting down" of coral reefs through time (Birkeland, 2004). Most reefs underwent partial recovery of coral cover that reached between 50% and 99% of the benchmarks, showing that fundamental processes of coral repair, recruitment, and colony growth continue to underpin the initial stages of hard coral recovery, but they are no longer sufficient to allow complete recovery. These recovery trajectories demonstrate that GBR reefs still maintain the intrinsic ability to begin recovery of hard coral cover back to prior benchmarks, but achieving recovery back to historic highs is increasingly less likely. Ratcheting down of coral cover and evidence for shifting baselines has been observed across the globe (Pandolfi et al., 2003), including the Caribbean (Gardner et al., 2003; Hughes, 1994; Jackson et al., 2014), the Indian Ocean (Sheppard, 1999), and Indo-Pacific (Bruno & Selig, 2007). For many ecosystems, we lack the long-term data to inform an understanding of historical baselines, and the shifting baseline often becomes ingrained in socio-ecological systems (Soga & Gaston, 2018). Evidence for shifted baselines exists for species from plants (Kai et al., 2014) to fur seals (Newsome et al., 2007), ecosystems from forests (Wu et al., 2011) to Arctic marine environments (Wassman et al., 2011), and fields from ethnobotany (Hanazaki et al., 2013) to fisheries (Pinnegar & Engelhard, 2008).

The diminishing interval between disturbance events is particularly important when considering the composition of the coral assemblages prior to disturbances, as this will also determine how long a time is necessary for recovery and constitutes the second, and equally important, element of shifting baselines—the concept of community reassembly (Johns et al., 2014; McWilliam et al., 2020). In ecosystems as complex as coral reefs, recovery and reassembly of hard coral communities takes different lengths of time depending on the biophysical setting and interacting human activities, and the mechanisms of recovery can be specific to individual taxa (Gouezo et al., 2019). The recovery of hard coral cover does not necessarily equate to reassembly of the community structure to predisturbances levels, and full coral community reassembly of shallow-water corals generally requires intervals without severe disturbances that last for one to two decades (Johns et al., 2014; Osborne et al., 2017). Assemblages dominated by fast-growing *Acropora* corals require a shorter recovery and reassembly period than those with a large proportion of slower growing massive corals (Johns et al., 2014). However, the results from the present study indicate that recent disturbance intervals are now too short even for *Acropora*-dominated communities to fully recover. The GBR's intrinsic recovery potential will not be sustained if climate-related disturbances are not addressed, and the interval available for recovery continues to decline.

In the coming decades, warming sea temperatures will inevitably further increase the frequency of thermal stress events that trigger mass coral bleaching. Current models cannot resolve how changes in cyclone severity and frequency at scales relevant to the GBR will affect damage to reefs (Dixon et al., 2022). While the frequency of cyclones globally is declining as the climate warms (Chand et al., 2022), increased thermal energy in ocean basins is expected to favor intensification of the cyclones that do form (Wu et al., 2022). The results presented here show that the time between recurrent disturbances is already too short to allow complete recovery of hard coral cover to historical baselines on many individual reefs of the GBR. Our study reinforces that the impacts of climate change are a contemporary reality that threatens the integrity of many ecosystems across the globe (Duarte et al., 2012; Smale et al., 2019; Solomou et al., 2017), particularly coral reefs (Hughes, Barnes, et al., 2017) and even of vast reef ecosystems such as the GBR (Hughes, Kerry, et al., 2017). Additionally, our results indicate that there have been more disturbances in the latest decade (2010–2020) than in any other recorded decade. The interval between disturbances has decreased decade by decade (Hughes, Anderson, et al., 2018). This suggests that the estimate of disturbance interval is a robust indicator of a changing regime of more frequent disturbances. A long-term dataset collected using consistent methods such as the one used here can contextualize individual events and ecosystem responses and provide a powerful basis for interpreting the observed changes. Unless immediate action is taken to reduce warming, the continued global degradation of coral reefs is inevitable.

AUTHOR CONTRIBUTIONS

The study was conceptualized by Michael J. Emslie, Murray Logan, and Camille Mellin. Michael J. Emslie wrote the first draft of the paper. All authors contributed to writing subsequent drafts. Michael J. Emslie, Murray Logan, Marji Puotinen, and Camille Mellin coordinated data compilation, analysis and graphics. Aerial bleaching surveys in 2016, 2017, and 2020 of the GBR were executed by James T. Kerry and Terry P. Hughes. Underwater visual censuses and manta tows were undertaken on the GBR by Michael J. Emslie, Peran Bray, Alistair J. Cheal, Kerryn A. Johns, Michelle J. Jonker, Ian R. Miller, Kate Osborne, Hugh Sweatman, Daniela M. Ceccarelli and Tane Sinclair-Taylor.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Emslie, 2024a) are available in Zenodo at https://doi.org/10.5281/zenodo.11375985. Code (Emslie, 2024b) is available in Zenodo at https://doi.org/10.5281/zenodo.11495597.

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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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