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Temperature-driven coral decline: the role of marine protected areas

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Abstract

Warming ocean temperatures are considered to be an important cause of the degradation of the world's coral reefs. Marine protected areas (MPAs) have been proposed as one tool to increase coral reef ecosystem resistance and resilience (i.e. recovery) to the negative effects of climate change, yet few studies have evaluated their efficacy in achieving these goals. We used a high resolution 4 km global temperature anomaly database from 1985–2005 and 8040 live coral cover surveys on protected and unprotected reefs to determine whether or not MPAs have been effective in mitigating temperature-driven coral loss. Generally, protection in MPAs did not reduce the effect of warm temperature anomalies on coral cover declines. Shortcomings in MPA design, including size and placement, may have contributed to the lack of an MPA effect. Empirical studies suggest that corals that have been previously exposed to moderate levels of thermal stress have greater adaptive capacity and resistance to future thermal stress events. Existing MPAs protect relatively fewer reefs with moderate anomaly frequencies, potentially reducing their effectiveness. However, our results also suggest that the benefits from MPAs may not be great enough to offset the magnitude of losses from acute thermal stress events. Although MPAs are important conservation tools, their limitations in mitigating coral loss from acute thermal stress events suggest that they need to be complemented with policies aimed at reducing the activities responsible for climate change.

Keywords: acclimation, climate change, conservation, coral, marine protected areas, resilience, resistance

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Introduction

Warming ocean temperatures are one of the most pervasive threats to marine ecosystems (Halpern *et al.*, 2008) and are predicted to have wide-ranging ecological consequences, particularly for thermally sensitive ecosystems like coral reefs. Increased temperatures can have several negative consequences for corals including mortality from coral bleaching (Glynn, 1993), slowed growth (Cantin *et al.*, 2010) and increased disease prevalence (Bruno *et al.*, 2007). In spite of these challenges, there is still optimism that protected areas can be useful for conservation in the face of climate change (Grimsditch & Salm, 2005; Hughes *et al.*, 2005) if they can increase ecosystem resilience (sensu Holling, 1973). Protected areas may be able to moderate climate change effects by promoting the conditions necessary for recovery from disturbances (Heller & Zavaleta, 2009), yet there remain questions about whether or not reducing local stressors will promote ecosystem resilience (Côté & Darling, 2010). To determine whether or not protected areas can be effective in mitigating climate change impacts on coral reefs, we need to understand whether or not current protection is conferring positive benefits and possible limitations to this approach.

Coral reefs are widely recognized to be particularly vulnerable to climate change because reef-building corals already live near their upper thermal limits (Glynn, 1993). If warming continues at a similar rate, current thermal limits for most corals will be exceeded in the next 100 years without rapid acclimation or adaptation (Donner *et al.*, 2005; Hoegh-Guldberg *et al.*, 2007). Even rises of 0.1 °C could increase the geographic extent of bleaching in the Caribbean by 42% (McWilliams *et al.*, 2005). When corals experience temperatures more than 1 °C beyond typical maximum summertime averages, they can lose their symbiotic algae or zooxanthellae in a process known as coral bleaching, which can cause extensive mortality at regional scales (Glynn, 1993).

Marine protected areas (MPAs) are thought to be able to increase resilience to climate change by directly mitigating other stressors like overfishing and land-based sediment and nutrient inputs (Grimsditch & Salm, 2005) or by protecting populations that may promote

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overall ecosystem resilience through connectivity with degraded populations (Mumby *et al*., 2011). Overfishing of predators has had far-reaching effects on marine ecosystems (Estes *et al*., 2011) initiating major changes in species abundances as well as ecosystem structure and function. MPAs have been shown to be effective in restoring food webs (Mumby & Harborne, 2010; Edgar *et al*., 2011), with demonstrated increases in ecosystem resilience to climate-driven impacts in temperate marine ecosystems (Ling *et al*., 2009). By reducing additional stressors like sediment or nutrient input, MPAs may also be able to reduce physiological stress on corals, making them more resilient or resistant to climate-related disturbances (Grimsditch & Salm, 2005; Baskett *et al*., 2010). In addition, effective design of MPA networks may be able to spread the risk of climate-related disturbances and protect key source populations that may be more resistant or resilient to climate impacts (Mumby *et al*., 2011).

MPAs have been shown to help maintain dominance by reef-building corals (Mumby *et al*., 2007; Selig & Bruno, 2010). Individual MPAs have positive effects on coral cover by limiting algal growth and facilitating coral recruitment (Mumby *et al*., 2007). Global-scale analyses have also found that MPAs have helped to maintain coral cover levels over time, while unprotected reefs continued to decline (Selig & Bruno, 2010). However, evidence that MPAs can mitigate acute thermal stress impacts on coral cover is equivocal (Côté & Darling, 2010). Most MPAs do not include a terrestrial component so the primary mechanism by which they can affect coral reefs is through fisheries management. By controlling fishing, protection could result in a more complete suite of herbivorous fish, which may suppress macroalgal growth following bleaching events. Nonetheless, local studies of MPAs have not always found that protection enabled recovery from acute thermal stress events (Jones *et al*., 2004; Ledlie *et al*., 2007; McClanahan, 2008). In the Seychelles, there has been little recovery from major coral mortality following the 1998 El Niño event in spite of unchanging high herbivore abundance over the study period (Ledlie *et al*., 2007). Analyses from several sites across the Indian Ocean have also not found differences in coral declines between MPAs and fished areas following the 1998 El Niño event (Graham *et al*., 2008). From these studies, it remains unclear whether or not the reduction in fishing within MPAs can reduce impacts on corals from acute thermal stress.

Therefore, testing whether or not MPAs can be useful in mitigating temperature-associated coral loss is critical so that we can determine which management interventions may be useful. Several MPA design factors may promote thermal stress resistance or resilience. One strategy assumes that placing MPAs in locations with specific temperature profiles will increase overall reef resilience (West & Salm, 2003; Grimsditch & Salm, 2005). There is a tremendous amount of spatial and temporal variability in temperature anomaly frequency and magnitude on coral reefs (Selig *et al*., 2010). This variability can be exploited to identify reefs with greater potential resistance to both chronic and acute thermal stress (Maina *et al*., 2008; Mumby *et al*., 2011). Ideally, reefs that are more acclimated must be adequately protected and connectivity between these populations and less resistant populations must be maintained to facilitate overall coral reef resilience.

We combined spatial databases of temperature anomalies (Selig *et al*., 2010), MPAs, and live coral cover (Bruno & Selig, 2007; Schutte *et al*., 2010) to test the hypothesis that MPAs mitigate coral cover loss caused by ocean warming and coral bleaching. We compared the effect of temperature on coral cover within 298 tropical MPAs to those in adjacent unprotected areas. Coral cover is an important metric of coral reef “health” because live coral provides the foundation for the entire reef ecosystem and many reef taxa are dependent on its physical structure (Jones *et al*., 2004; Graham *et al*., 2006). However, other metrics of resilience may also be indicative of reef health including coral size, coral and fish diversity, fish abundance, macroalgal cover, and connectivity to other reef communities (Grimsditch & Salm, 2005; Graham *et al*., 2011; Mumby *et al*., 2011).

If MPAs are not currently mitigating the impacts of acute thermal stress events, there are several design factors that could contribute to their ineffectiveness including placement, size, time since establishment, degree of protection, degree of enforcement, connectivity to other reefs, and other socioeconomic factors (McClanahan, 1999; Maina *et al*., 2008; Mora & Sale, 2011). We analyzed how two design factors – MPA size and thermal stress regime – could influence the likelihood that the current set of MPAs can mitigate the impacts of warm temperature anomalies on coral cover. If MPAs are too small, they may be susceptible to widespread mortality from a single anomaly event. In this case, there may not be enough larval supply originating from within the MPA to restore degraded areas. Therefore, we analyzed patterns in temperature anomaly size to compare them with the current distribution of MPA sizes.

In addition, if MPAs are not protecting areas characterized by natural temperature fluctuations on reefs, they may have populations that are less thermally tolerant to acute thermal stress events. Populations that have experienced previous temperature variability are more likely to be acclimated or adapted to temperature stress and resistant to future events (McClanahan *et al.*, 2007; Thompson & van Woesik, 2009; Ateweberhan & McClanahan, 2010) and may also be critical source populations for reefs that are degraded by acute temperature stress events or other human disturbances. If these more resistant populations are not adequately protected, MPAs may be less effective in mitigating temperature-driven coral losses. In a separate analysis, we quantified the mean temperature anomaly frequency and variability on reefs within all MPAs and then assessed whether or not these patterns were similar to those of all reefs worldwide. With this approach, we were able to determine if MPAs are currently protecting reefs that we would expect to be more acclimated to acute temperature stress. Together, these analyses enabled us to evaluate whether or not MPAs can mitigate the effects of recent thermal stress on coral cover loss and to identify possible shortcomings in their current design.

Materials and methods

Global databases of thermal stress, coral cover, and coral reef marine protected areas

We created a 21-year dataset of weekly temperature anomalies covering the entire range of tropical reef-building corals (37°N –37°S) using the National Oceanic and Atmospheric Administration's (NOAA) National Oceanographic Data Center (NODC) Coral Reef Temperature Anomaly Database (CoRTAD) Version 1.0 (available at http://www.nodc.noaa.gov/SatelliteData/Cortad). The CoRTAD was developed from the NODC and University of Miami's Rosenstiel School of Marine and Atmospheric Science Pathfinder Version 5.0 temperature data (Casey *et al.*, 2010; Selig *et al.*, 2010). These data have the highest spatial resolution (~4 km) for the longest time period of any publicly available satellite temperature data. We used data with a quality flag of four or better (Kilpatrick *et al.*, 2001). We initially filled the remaining data gaps (21.2% of the data) using a 3 × 3 pixel median spatial fill; remaining gaps were filled temporally using the Piecewise Cubic Hermite Interpolating Polynomial (PCHIP) function in Matlab (The Mathworks Inc, 2006). Climatologies were created using a harmonic analysis procedure to fit the annual and semi-annual signals to the time series at each grid cell location (Selig *et al.*, 2010). We defined thermal stress anomalies (TSA) as deviations of 1 week where the temperature was 1 °C or greater than the mean maximum climatological week or the long-term average warmest week from 1985 to 2005. Although the specific temperatures that cause coral bleaching and mortality are highly species-specific, this is a generally accepted threshold for conditions that may result in bleaching (Glynn, 1993).

We also developed a live coral cover database from several publicly available databases from the peer-reviewed and gray literature (Bruno & Selig, 2007; Schutte *et al.*, 2010). In general, the surveys used some variant of the point intersect or line transect technique. We only used data from 15 m depth or above to avoid depth biases in coral cover. Our final global database contained 8040 surveys from more than 4260 reefs from 1987 to 2005.

Our spatial database of MPAs was built primarily using data from the publicly available World Database on Protected Areas. These data were then supplemented and updated with MPA data from The Great Barrier Reef Marine Park Authority, The Nature Conservancy, NOAA, the US Geological Survey and the US Department of Interior. Most of the MPA data had exact boundaries, but some locations had only information about the center latitude and longitude point of the MPA location. Of the 298 MPAs used in this analysis, approximately 25 had information on total area but not actual boundaries. The extent of these MPAs had to be approximated and area calculations represent estimates based on the best available data. For areas in which we only had point data, we created artificial circular boundaries based on the total known area of the MPA (Mora *et al.*, 2006). Because we were interested only in coral reef MPAs, we selected only parks that fell within 50 km of a known coral reef location (Selig & Bruno, 2010).

Statistical analyses

Effect of protection and temperature anomalies on coral cover. We used a multilevel model to evaluate whether or not protection in MPAs changed coral cover responses to thermal stress from 1987 to 2005 compared to unprotected corals (McMahon & Diez, 2007). By using a multilevel model, we were able to estimate how protection and thermal stress affected variability in coral cover over time on each reef as well as a population average for all reefs. The multilevel modeling approach also allowed us to account for the temporal and spatial correlation in the data (McMahon & Diez, 2007). At each level we assigned different random effects to account for spatial and temporal correlation. For example, at level 1, individual observations on a reef were assigned a unique random effect. At level 2, the random effect accounted for repeated surveys on the same reef over time. Level 3 accounted for spatial correlation within the spatial grouping unit where protected and unprotected reefs were paired. Surveys on unprotected reefs were paired with surveys from the nearest MPA up to a distance of 200 km. This distance threshold was determined through log-likelihood analysis (Selig & Bruno, 2010). We applied a logit transformation to the percent coral cover data and treated the logit as normally distributed (Lesaffre *et al.*, 2007). We also centered our time regressor at 1996 to facilitate model convergence, provide an interpretable intercept, and to minimize correlation among random effects (Singer & Willet, 2003). Centering the time regressor on the year 1996 was found to produce the least degree of correlation between the random effects. We used the nlme library in R 2.5.1 (R Development Core Team, 2007) and WinBUGS 1.4.3 (Lunn *et al.*, 2000) to analyze our models.

After determining the basic model structure, we explored how to incorporate temperature into the model. We examined models with no lag in temperature anomalies and variations of 1, 2, and 3 year lags. Using Akaike Information Criterion

(AIC), we found that a variable that contained the frequency of weekly anomalies in the two calendar years preceding the year of each coral cover survey (*lag TSA*) best explained variation in coral cover (see Supporting Information; Akaike, 1973).

The basic trend model Eqn (1) we fit to each reef described logit coral cover (Y) in terms of year (T) and its centering constant ($T_c = 1996$), the frequency of anomalies in the 2 years preceding the coral cover survey (*lag TSA*) and the random error (ε). The subscripts i, j, and k designate the spatial unit for pairing MPA and non-MPA reefs, the reefs within that unit, and the individual survey measurement for that reef, respectively.

$$\begin{aligned} &\textit{Level } 1\text{: } Y_{ijk} = \beta_{0ij} + \beta_{1ij}(T_{ijk} - T_c) + \beta_{2ij} \textit{lag TSA}_{ijk} + \varepsilon_{ijk}, \\ &\qquad \varepsilon_{ijk} \sim N(0, \sigma^2) \end{aligned} \tag{1}$$

The subscript j appearing in the parameters β_{0ij} (intercept), β_{1ij} (trend), β_{2ij} (*lag TSA*) signifies that these parameters are allowed to vary from reef to reef. Their variability is described in Eqn (2):

$$\begin{aligned} &\beta_{0ij} = \beta_{0i} + \beta_{3i}\textit{Protection status}_{ij} + u_{0ij} \\ \textit{Level } 2\text{: } &\beta_{1ij} = \beta_{1i} + \beta_{4i}\textit{Protection status}_{ij} + u_{1ij} \\ &\beta_{2ij} = \beta_{2i}, \\ &\begin{bmatrix} u_{0ij} \\ u_{1ij} \end{bmatrix} \sim N\left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \tau_0^2 & \tau_{01} \\ \tau_{01} & \tau_1^2 \end{bmatrix} \right) \end{aligned} \tag{2}$$

Here, *Protection status* is a reef level predictor that varies among reefs (protected vs. unprotected) but is constant for observations taken on the same reef. Random effects for reef j in spatial unit i (u_{0ij}, u_{1ij}, and u_{2ij}) are assumed to have a joint normal distribution as shown. *Protection status* is a dummy variable where 1 = protected and 0 = unprotected. Random effects from different reefs are assumed to be independent and also independent of the level 1 error terms. The subscript i on the trend, *lag TSA*, and intercept parameters, as well as the coefficients of the level 2 predictor *Protection status*$_{ij}$ in Eqn (2) indicates that these parameters can vary across spatial units as described by Eqn (3):

$$\begin{aligned} &\beta_{0i} = \beta_0 + \beta_5\, \textit{Indian}_i + \beta_6 \textit{Pacific}_i + v_{0i} \\ &\beta_{1i} = \beta_1 + v_{1i} \\ \textit{Level } 3\text{: } &\beta_{2i} = \beta_2 \\ &\beta_{3i} = \beta_3 \\ &\beta_{4i} = \beta_4, \\ &\begin{bmatrix} v_{0i} \\ v_{1i} \end{bmatrix} \sim N\left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \omega_0^2 & \omega_{01} \\ \omega_{01} & \omega_1^2 \end{bmatrix} \right) \end{aligned} \tag{3}$$

In Eqn (3), we included ocean basin as a level 3 predictor because earlier modeling efforts (Selig & Bruno, 2010) and different temperature patterns in the different basins indicated that coral cover may be modified by ocean basin. The Caribbean serves as the baseline level in this model and corresponds to Pacific = Indian = 0. Random effects for level 3 are designated by v_{0i} and v_{1i}.

To develop a final model, we determined the basic level-1 model and included random effects where statistically necessary (Table S1). We tried several variations on the basic level-1 model shown in Eqn (1) including the interaction of time (coral cover trend) and *lag TSA*, but rejected them using AIC (Table S1). By fitting models to individual reefs, we observed that intercepts (logit coral cover in 1996) varied widely across reefs and spatial grouping units, whereas coral cover trend coefficients were less variable and *lag TSA* coefficients had almost no variability. Random effects account for unobserved heterogeneity in the model so we included random effects only for the intercept and trend. Then we determined how to add *Protection Status* and ocean as predictors, using AIC to identify which model was the best fit model (Table S1; Akaike, 1973). To obtain more realistic estimates of parameter precision and credible intervals, we refit the final model as a Bayesian model with uninformative priors in WinBUGS 1.4.3. (MRC Biostatistics Unit, Cambridge, UK).

Marine protected areas vs. temperature anomaly size. We analyzed patterns in anomaly area throughout the tropics and by region to determine anomaly area statistics for geographic areas with similar diversity or management (Fig. 1). Analyses were done by region because different oceanographic patterns may lead to natural differences in average anomaly size. Knowing how anomaly areas vary by region can give managers and policymakers more precise data for optimal MPA design. For each 4 × 4 km pixel, we created a time series of anomaly presence/absence for each of the 1096 weeks in our 21-year temperature anomaly database. Only anomalies which contained at least one pixel that overlapped a known coral reef location were included. We used the Image Processing Toolbox in Matlab 7.3 (The Mathworks, Natick, MA, USA) (bwlabel function) to identify each anomaly and determine whether or not it was connected to a neighboring thermal stress event in any of the eight adjacent pixels. Each contiguous temperature anomaly cluster grouping was assigned a unique number and represented a single data point, whose time and location were recorded. We then generated a frequency distribution of the size (spatial extent) of these clusters, as well as the mean, maximum, and variance for each region and for each week.

Temperature anomaly patterns of coral reef Marine protected areas vs. all reefs. We used Monte Carlo simulations to test whether or not temperature anomaly patterns varied significantly between reefs in MPAs and all reefs. Although 21 years is relatively short on a climatological time-scale, the spatial scale of the data provides a high level of sampling. For this analysis, we focused on 7 years of interest instead of the whole time series for ease of interpretation: 1985, 1988, 1995, 1998, 2000, 2002, and 2005. The years 1988, 1998, 2002, and 2005 were selected because they were El Niño years or years with documented major thermal stress. We included 1985 and 2000 as reference years. To assess whether or not the temperature anomaly patterns exhibited at reef locations in MPAs are typical of all reefs, we extracted temperature anomaly frequency values across all reef locations (55 626 4 km reef pixels as defined by reef locations from the database described above) including those to generate an ‘all reefs’ population. Of the 55 626 reefs pixels, 10 555 of them were in MPAs. We then

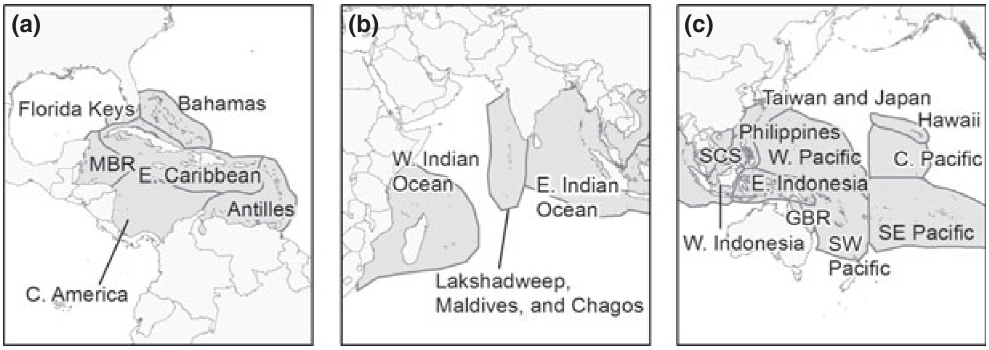

Fig. 1 Region delineations for the analysis. Boundaries for regions are based on biogeographic patterns in diversity and similar management in the (a) Caribbean (MBR = Mesoamerican Barrier Reef), (b) Indian Ocean, and (c) Pacific Ocean (SCS = South China Sea; GBR = Great Barrier Reef; E. Indonesia and PNG = East Indonesia and Papua New Guinea).

drew temperature anomaly values from a random set of 10 555 reefs from the overall population of 55 626 and iterated this step 10 000 times. For each sample, we calculated the variance, interquartile range, median absolute deviation, mean and median for temperature anomalies within that calendar year. The frequency distribution of each summary statistic calculated from the random samples was then used to estimate the sampling distribution of that statistic. The observed value of the statistic for MPAs was compared to the theoretical population distribution of that statistic to determine if the MPA value was typical. We then used Pearson's X^2 Goodness of fit test to get more specific information about how the distributions between all reefs and MPAs varied. Because of our large sample size, formal significance testing would virtually guarantee finding a significant lack of fit. However, we were able to use the Pearson residuals to determine which temperature anomaly categories were driving the lack of fit.

Results

Effect of protection and temperature anomalies on coral cover

The best model described coral cover as a function of time, thermal stress, protection, and ocean. *Protection status* (a level-2 predictor) modified both the change in coral cover and intercept (coral cover in 1996, the centering year), whereas ocean basin affected only the intercept (level-3 predictor). Random effects were necessary for both reefs and spatial grouping units. Using an AIC framework, we found the best model to explain the logit transformation of percentage coral cover to be given by Eqn (4):

$$\begin{aligned} logit\left(p_{ijk}\right) = {} & \beta_0 + v_{0i} + v_{2i} + \beta_{2ij} lagTSA_{ijk} \\ & + \beta_{3ij} MPA_{ijk} + \beta_7 Indian_i \\ & + \beta_8 Pacific_i + u_{0ij} + u_{2ij} \\ & + \left(\beta_1 + v_{1i} + \beta_{4i} MPA_{ij} + u_{1ij}\right) \\ & \left(T_{ijk} - \mathrm{T_c}\right) + \varepsilon_{ijk}. \end{aligned} \tag{4}$$

We found that protection in MPAs did not mitigate the effect of temperature anomalies on coral cover (Figs 2 and 3). As with previous work, protection had a significant effect on the direction and magnitude of coral cover trend (Selig & Bruno, 2010). The trend outside MPAs was negative, indicating a decline in coral cover over time. Within MPAs, though, the coral cover trend was weakly positive, although not significantly different from zero (Fig. 2). However, when we fit a model that allowed presence of an MPA to modify the effect of temperature anomalies on coral cover, the interaction term was not significant ($P > 0.1$) and the model was not a better fit. Therefore, MPAs did not modify the effect of acute thermal stress on coral cover (Fig. 3). These results were consistent for both a 1-year and 2-year lag for temperature anomalies. In other words, MPAs may benefit corals through the mitigation of other stressors (i.e. overfishing and terrestrial inputs), but they are not explicitly altering the effect of recent temperature anomalies on coral cover.

Temperature anomalies had a significant negative effect on coral cover ($P < 0.0001$). Although this finding is consistent with a general understanding that temperature anomalies have a negative impact on coral cover (Glynn, 1993), our model quantifies the general magnitude and rate of coral cover loss as a function of temperature anomaly frequency (Fig. 4; Table S2).

Marine protected areas vs. temperature anomaly size

The overall anomaly size distribution illustrates that 70% of temperature anomalies are less than 75 km^2, but that a few anomalies are over 1 000 000 km^2. Temperature anomaly sizes varied annually and regionally (Figs 1 and 5). At a regional scale, variability in the size of smaller temperature anomalies was generally low (under 100 km^2). Most of the variability occurred in the tail of the distribution where there were few large

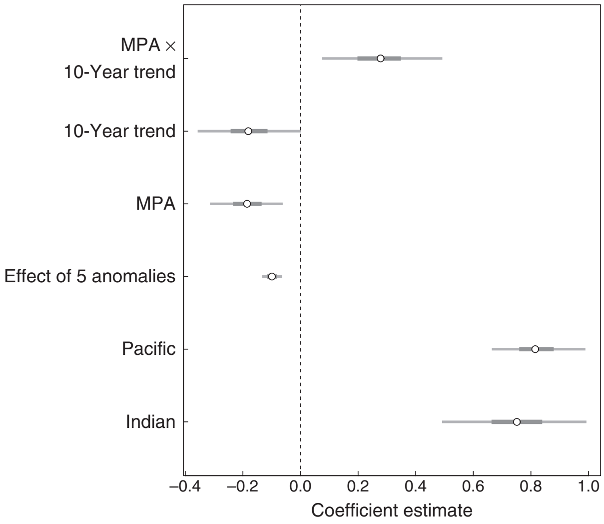

Fig. 2 Coefficient estimates for the multilevel model. The 95% credible intervals (thin gray line) and the 50% credible intervals (thick gray line) as well as point estimates (median) of the posterior distributions for all parameters using a Bayesian approach to fit the model in Eqn (4). There is a 95% probability that the true value lies within the 95% credible interval. The MPA × 10-Year Trend term should be contrasted with the 10-Year Trend term, which is the trend for controls. The MPA × 10-Year Trend term is an effect and gets added to the 10-Year Trend term when MPA = 1 to obtain the trend for MPAs. The magnitude of the anomaly effect varies according to the number of anomalies in the 2 years preceding the live coral cover survey. The effect of five total anomalies is displayed.

temperature anomalies (Fig. 5). Contrary to expectations, the size of the region seemingly did not affect the pattern of temperature anomaly sizes. The smallest region in the analysis, the Florida Keys, also had some of the largest temperature anomaly sizes. More size variability was present in Pacific regions that are affected by El Niño events (Fig. 5).

Temperature anomaly patterns of coral reef marine protected areas vs. all reefs

Protected reefs experienced fewer total anomalies during the calendar years that we analyzed than the general population of reefs (Fig. 6). For the years studied, MPAs generally had more reefs with low frequencies of anomalies (0–1) than the general population of reefs. MPAs also included fewer reefs with moderate anomaly frequencies (2–6) except during 1998 and 2002. During the 1998 El Niño, more reefs with low anomaly frequencies were protected in MPAs, and fewer reefs with higher anomaly frequencies (6–12) were protected. In addition, the 1998 event was the most deviant from a random sample of temperature anomalies with nearly every anomaly category exceeding the Pearson critical value.

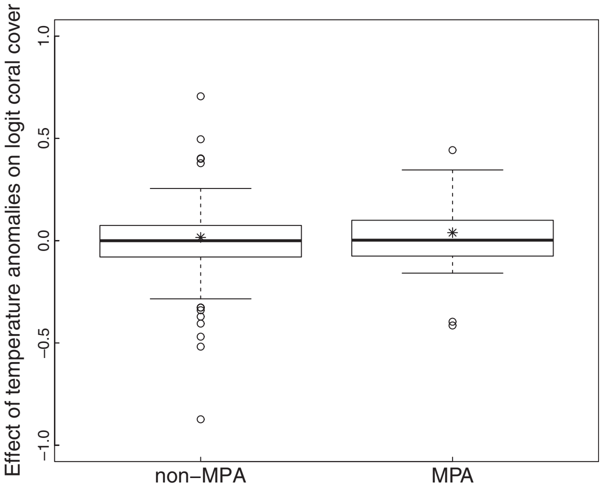

Fig. 3 The effect of thermal stress anomalies (TSA) on logit coral cover for each spatial grouping unit split by MPA and non-MPA. The bottom edge of the box denotes the first quartile of the data, the top edge locates the third quartile, and the horizontal line inside the box corresponds to the median. The mean values are represented by the black stars. Both unweighted and weighted (inverse of the standard error of the mean) t-tests based on the observations of the coefficients for MPAs vs. non-MPAs in the figure were non-significant ($P > 0.65$). These results are consistent with the more accurate estimates from the multilevel model ($P > 0.15$; see text).

For each year, we took the 95% percentile-based confidence intervals from the Monte Carlo simulations and compared them to MPA anomaly patterns. From these analyses, we determined that MPAs generally had lower mean frequency of anomalies (Fig. 6a) and lower standard deviations (Fig. 6b) than all reefs. Our results suggest that locations protected within MPAs experience different temperature patterns than all reefs and do not contain similar frequencies of temperature anomalies.

Discussion

The success of MPAs in restoring fisheries and trophic structure on coral reefs (Alcala *et al.*, 2005; Edgar *et al.*, 2011) has led to increased optimism that they may also be useful for mitigating temperature stress associated with climate change (Sandin *et al.*, 2008). However, our global analysis found that MPAs are not reducing the negative effects of temperature anomalies on coral cover over time (Fig. 3). Our analyses also suggest that the lack of an MPA effect may be partially due to the current design of many MPAs.

We found a clear negative relationship between temperature anomaly frequency and change in coral cover

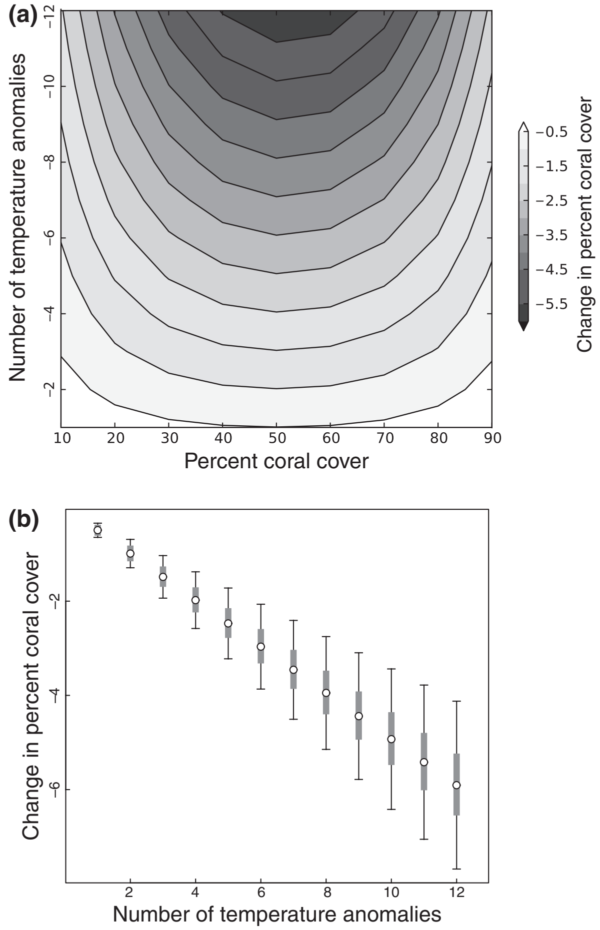

Fig. 4 Multilevel model predictions of the annual effect of thermal stress anomalies (TSA) on the change in coral cover at (a) different levels of coral cover and anomaly frequencies and (b) when coral cover is 50%. The 95% credible intervals (thin black line), 50% credible intervals (thick gray line), and point estimates (median) of the posterior distributions are shown.

(Fig. 4a). The degree of coral loss depended both on anomaly frequency and the starting coral cover (Graham *et al.*, 2011; Fig. 4a; Table S2). For example, at 10% coral cover, four anomalies resulted in coral cover losses of 0.9% whereas at 50% coral cover, losses were 2.4% (Fig. 4a and b; Table S2). Several biological factors could be driving the unimodal relationship between percent cover and annual change in coral cover (Fig 4a). Recovery dynamics are likely to be nonlinear and sites with lower post disturbance coral cover levels had been shown to have faster recovery rates than sites with higher coral cover levels (Graham *et al.*, 2011). At relatively low coral cover levels, the lower loss rates could be reflective of the presence of weedier species that are less vulnerable to additional acute thermal stress. Bleaching rates on individual reefs can be highly idiosyncratic (Berkelmans & Willis, 1999), but our results suggest that there was a general relationship between the number of recent temperature anomalies, coral cover at the time of surveying, and rate of coral cover loss.

In addition, when the magnitude of coral loss as a result of temperature anomalies was compared to the magnitude of positive MPA effects, our results indicated that MPAs alone may not be sufficient to mitigate temperature anomaly effects on coral reefs. Under optimal conditions, MPAs generally resulted in average increases in coral cover of 1–2% per year (Selig & Bruno, 2010). At 50% coral cover, 8 weekly anomalies of more than 1 °C above summertime averages were correlated with an annual 3.9% loss in coral cover. Eight weekly anomalies is a threshold that generally results in widespread bleaching and significant mortality (Eakin *et al.*, 2010). In a relatively normal year like 2000, 48% of reefs had no anomalies and only 4% of

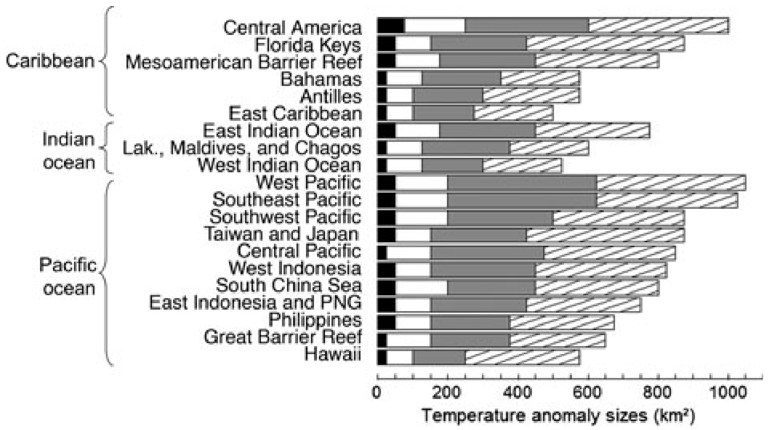

Fig. 5 Anomaly sizes for different regions (as specified in Fig. 1). Bars represent the anomaly size at which 50% (black), 75% (white), 90% (gray), and 95% (hashed) of the sizes are included (Lak., Maldives, and Chagos = Lakshadweep, Maldives and Chagos; E Indonesia and PNG = East Indonesia and Papua New Guinea).

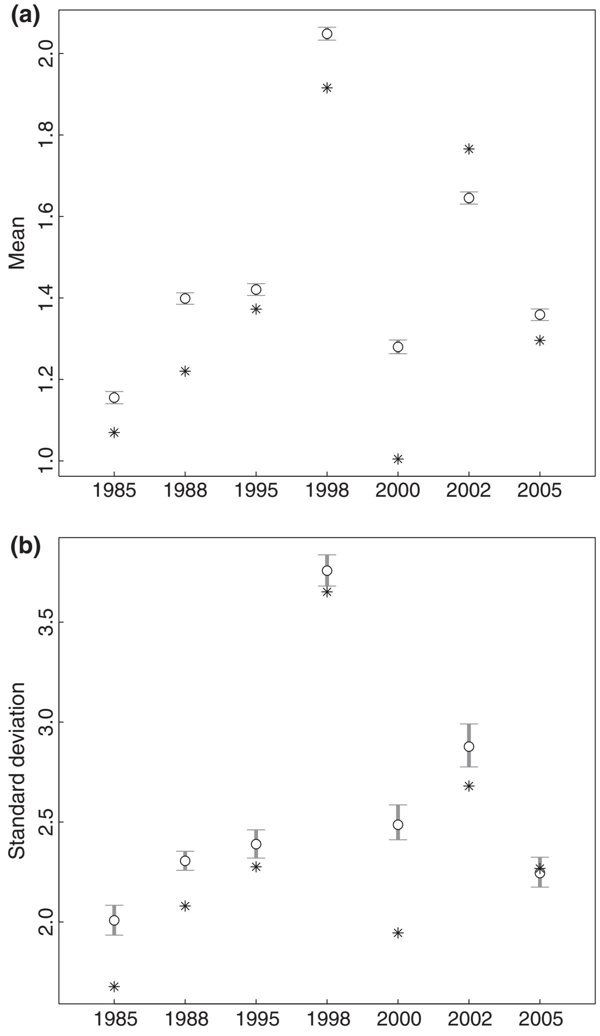

Fig. 6 Comparison of anomaly frequency within MPAs to anomaly frequency of all reefs. Variability for selected years in (a) mean anomaly frequency of all reefs and 95% confidence intervals (open circles and error bars) compared to reefs within MPAs (stars) and (b) standard deviation in anomaly frequency for all reefs and 95% confidence intervals (open circles and error bars) compared to reefs within MPAs (stars). The mean anomaly frequency and standard deviation within MPAs are generally lower than anomalies on all reefs.

reefs experienced eight or more temperature anomalies. However, during the 1998 El Niño nearly 17% of reefs experienced eight or more temperature anomalies. If the frequency of thermal stress events increases, the balance between coral loss from temperature anomalies and the benefits from MPAs may become even less likely to produce a net gain in coral cover over time on affected reefs.

Several factors could explain the failure of MPAs to protect against thermal stress. Reducing local stressors may not increase resilience to thermal stress because stress-tolerant species may be less abundant or populations may not have become acclimated to stress (Côté & Darling, 2010). In addition, MPA benefits appear to be realized only after 4–14 years of protection, depending on the location (Selig & Bruno, 2010) and the period of study may not have included enough time to identify the positive effects of protection after acute thermal stress events, i.e. the study could have underestimated the effects of MPAs on coral recovery. Another possibility is that MPAs are not currently optimally designed because of their placement or size. In the Western Indian Ocean, nearly half of no-take MPAs are located in regions identified as being of medium to high susceptibility (Maina *et al.*, 2008). Although our model accounted for the differences in temperature anomaly frequencies between MPAs and non-MPAs, these underlying patterns may affect the susceptibility of protected reefs. If MPAs are located in places that do not promote acclimation or resistance, they may be less likely to be able to provide benefits during future thermal stress events.

Focusing conservation efforts on protecting reefs with a history of more moderate temperature anomaly frequencies and variability may be necessary for developing a set of MPAs capable of slowing or reversing coral decline. Field research suggests that previous exposure to moderate levels of temperature variability results in less future mortality (McClanahan *et al.*, 2007; Thompson & van Woesik, 2009; Ateweberhan & McClanahan, 2010). Corals experiencing moderate anomaly frequencies may also have higher adaptive capacity because they are more acclimated to thermal stress (Thompson & van Woesik, 2009; Mumby *et al.*, 2011; Oliver & Palumbi, 2011). Locations with low anomaly frequencies may actually be more vulnerable when they do experience an acute thermal stress event (McClanahan *et al.*, 2007; Côté & Darling, 2010). For several years during our study period, MPAs had substantially lower anomaly frequencies and less variability in temperature anomaly frequency than all reefs (Fig. 6). Protecting reefs with more historic temperature variability may increase the efficacy of MPAs in mitigating coral decline.

In addition, our analysis of anomaly sizes suggests that MPAs may be too small to adequately protect against thermal stress. One tenet of protected area design has been to create protected areas or networks that are larger than the typical natural disturbance regime so that enough species and ecosystem function remain to recover from disturbance events (Pickett & Thompson, 1978). We found that anomalies varied considerably in size based on region and year (Fig. 5). Most thermal stress events are relatively small, but the overall distribution includes a small number of large anomalies, particularly during major events like the strong El Niño in 1998 when anomaly sizes exceeded 1 million km^2 during a few weeks. Because no MPA can encompass such a large contiguous area, managers may need to design MPAs to insure against a reasonable degree of thermal stress by constructing MPAs to be larger than an acceptable percentage of anomaly events (Fig. 5). For example, in the Western Indonesia region, an MPA greater than 50 km^2 would be larger than 50% of anomaly events and at 150 km^2, it would be larger than 75% of anomaly events. Currently, about 40% of coral MPAs are 1–2 km^2 (Mora *et al*., 2006), considerably smaller than a typical anomaly. Therefore, most MPAs are likely to be wholly affected by a single anomaly event. Larger MPAs could increase resilience from acute thermal stress events because they would be more likely to contain unaffected populations within their boundaries. These populations might then be able to provide new recruits to locations that had experienced mortality during the event.

The positive effects of MPAs on coral resilience can only be mediated indirectly through the two stressors that MPAs can directly affect – overfishing (Russ *et al*., 2004; Edgar *et al*., 2011) and nutrient and sediment pollution if they include a terrestrial component (Wolanski & De'ath, 2005). Through the mitigation of these stressors, MPAs could potentially provide a mechanistic indirect benefit to corals (Mumby *et al*., 2007; Baskett *et al*., 2010; Selig & Bruno, 2010). In several cases, though, local protection has not mitigated these stressors due to poor enforcement (Huntington *et al*., 2011) or design flaws (i.e. placement or lack of a terrestrial component) (McClanahan, 1999; Jones *et al*., 2004; Kramer & Heck, 2007). The failure of many MPAs to measurably mitigate these and other impacts could explain why they have no apparent effect on reef resilience to thermal stress.

It has been estimated that the thermal limits of corals will need to increase at rates of 0.2–1.0 °C per decade to avoid future mass bleaching and mortality (Donner *et al*., 2005), a rate that may be difficult to achieve (Hoegh-Guldberg *et al*., 2007). Although MPAs and other forms of local fisheries management are important tools for reef preservation and restoration, our results caution against relying on MPAs to substantially alter the course of climate change-induced coral degradation. MPAs are clearly an important tool in managing coral reef ecosystems, but they must be complemented with direct measures aimed at reducing the anthropogenic activities responsible for climate change.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. AIC values for different multi-level model forms. The number of temperature anomalies must be a level-1 variable because it varies at the reef level. In each group of models, we selected the model with the lowest AIC (bold). Models are listed in order of increasing complexity. In cases where the difference between two models was less than 2, which indicates that both models have support in an AIC context (Burnham & Anderson, 2002), we selected the most parsimonious model. Models that did not converge have no AIC value and are indicated with a dash.
Table S2. Multilevel model predictions of the mean annual effect of thermal stress anomalies (TSA) on the change in coral cover at (a) 10%, (b) 20%, (c) 50%, and (d) 80% coral cover and 95% credible intervals.