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Water column productivity and temperature predict coral reef regeneration across the Indo-Pacific

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Predicted increases in seawater temperatures accelerate coral reef decline due to mortality by heat-driven coral bleaching. Alteration of the natural nutrient environment of reef corals reduces tolerance of corals to heat and light stress and thus will exacerbate impacts of global warming on reefs. Still, many reefs demonstrate remarkable regeneration from past stress events. This paper investigates the effects of sea surface temperature (SST) and water column productivity on recovery of coral reefs. In 71 Indo-Pacific sites, coral cover changes over the past 1-3 decades correlated negative-exponentially with mean SST, chlorophyll *a*, and SST rise. At six monitoring sites (Persian/Arabian Gulf, Red Sea, northern and southern Galápagos, Easter Island, Panama), over half of all corals were <31 years, implying that measured environmental variables indeed shaped populations and community. An Indo-Pacific-wide model suggests reefs in the northwest and central Indian Ocean, as well as the central west Pacific, are at highest risk of degradation, and those at high latitudes the least. The model pinpoints regions where coral reefs presently have the best chances for survival. However, reefs best buffered against temperature and nutrient effects are those that current studies suggest to be most at peril from future ocean acidification.

Interpreting ecological consequences of increasingly significant and widespread mortality of warm water corals[1] is often confounded by highly variable, sometimes regionally inconsistent, regeneration[2–4]. An increasing number of experimental studies suggests that negative effects of rising SST may be exacerbated by altered nutrient levels in reef waters, which in their own right pose many problems to the habitat-forming species, the scleractinian corals[5–11]. Anthropogenic alteration of the natural nutrient environment can negatively affect coral reefs not only via a range of indirect stressors[6], but also by direct effects on the functioning of the coral-zooxanthellae symbiosis. Specifically, unfavorable nutrient levels can reduce the heat and light stress tolerance of corals, rendering them more susceptible to often fatal coral bleaching[5]. While corals can occur naturally and do well in high-temperature and/or high-nutrient environments, temperature and nutrient stress together are among the most significant threats to many reefs today[6,12]. Additionally, ocean acidification represents a significant near-future challenge[13]. Since the increasing anthropogenic nutrification of coastal waters and climate change will affect the availability of nutrients in reefal waters[14–16], interactions of temperature and nutrient effects merit attention and are the subject of this paper.

Phytoplankton growth is directly dependent on nutrient availability and newly introduced dissolved inorganic nutrients are often taken up rapidly and regenerated by planktonic algae in oligotrophic reef waters[17]. Therefore, the phytoplankton density, usually measured as chlorophyll-*a* (chl-*a*) concentration, represents a robust indicator of nutrification[17,18]. Elevated phytoplankton loads have been suggested to affect corals by, for instance, altering their natural nutrient environment[6] or by promoting outbreaks of coral predators[11]. Thus water column chl-*a* levels can be indicators for both direct[5–8] and indirect[6,11] negative nutrient effects on coral reefs, especially where high chl-*a* levels have not previously been the norm. Since the link between nutrient-levels and bleaching (i.e. coral degradation) is now well-established, it is of increasing interest to evaluate the relationship between coral regeneration and nutrient/temperature interactions, whether or not levels are natural or anthropogenically altered.

Using our own and published data, coral cover trajectories up to three decades (regeneration=ratio of 1980s or 1990s to 2010s coral cover) in 71 Indo-Pacific reef sites were evaluated in relation to SST and chl-*a* as a proxy for nutrient levels. Sites encompassed high variability in nutrient and temperature regime, covering presumed
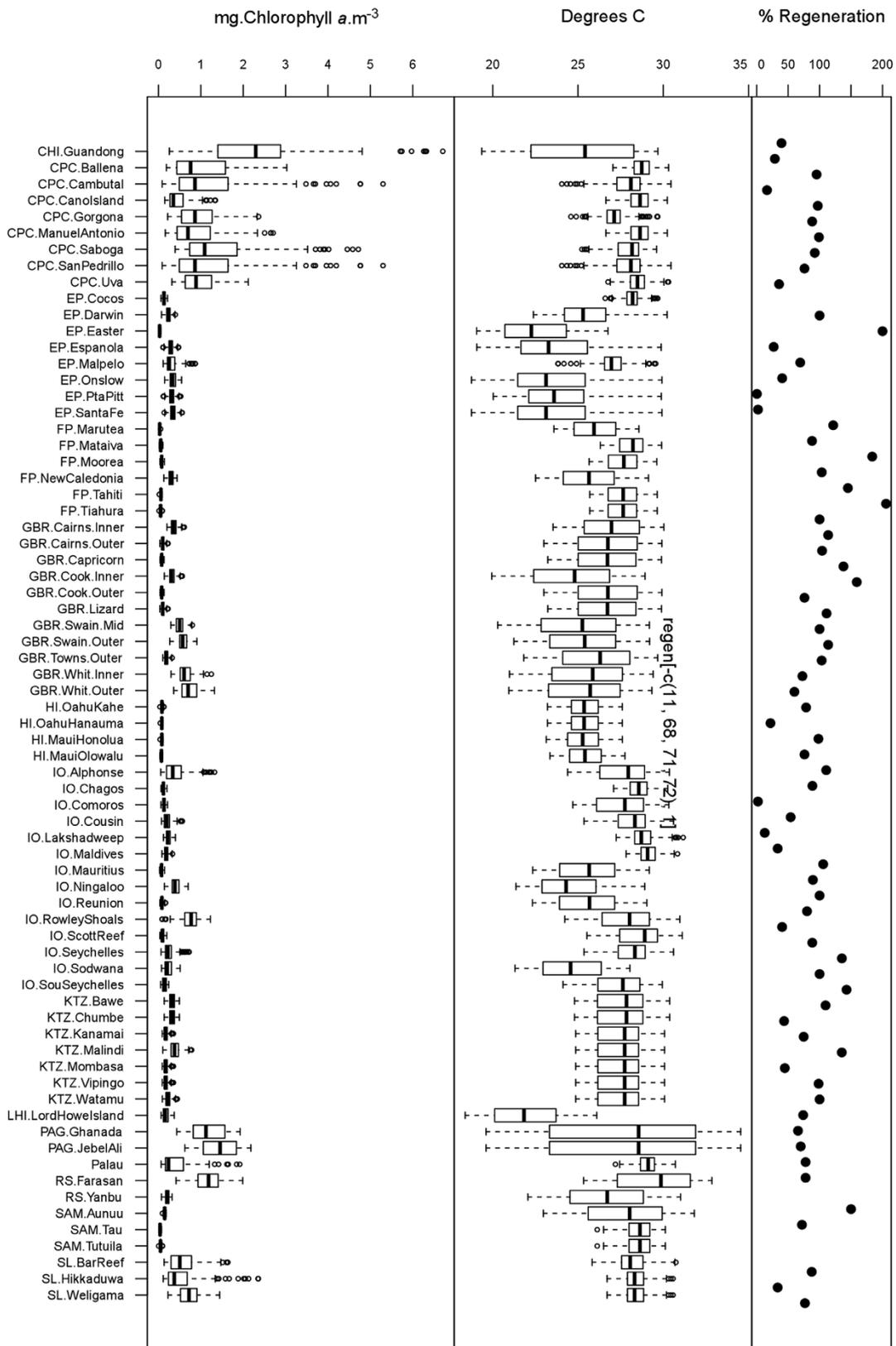
extreme and benign situations. General changes in coral cover deduced from meta-analysis were verified with detailed *in-situ* monitoring data at the population-level. The coral monitoring period coincided with the global availability of remotely-sensed SST and chl-*a* data, allowing cross-checks. Sites used for meta-analysis were from all regions of the Indo-Pacific, but long-term monitoring sites encompass the warmest (Southern Red Sea=SRS, Persian/Arabian Gulf=PAG), some of the highest chl-*a* sites (Panama=CPC, southern Galápagos=EP-sGAL, PAG) to the coolest and lowest chl-*a* sites (Easter Island in the Eastern Pacific=EP; Fig. 1; Fig. 2).

Results

We ensured that the environmental data available for meta-analysis were relevant for coral population dynamics by evaluating coral age-structure at the six monitoring sites (see supplemental information). Corals are long-lived but across the Indo-Pacific, heat stress-induced mass mortalities have caused significant die-back, especially of large old corals, since the early 1980s (Supplementary information; Table S.1, S.2). Coral size-distributions in monitoring sites suggest that most (>50%) are younger than 31 years (Fig. S.1). Thus, the 31year Optimum Interpolation SST (OISST, ref. 19) time-series covered the lifetime of most corals and was adequate to describe the thermal environment shaping the present coral populations/coral community. The 13-year chl-*a* time-series (1997–2010) covered the major die-back events and the most important period of regeneration (size classes 1 and 2 for all species, size class 3 for most; Fig. S.1).

SST, chl-*a* and coral trajectory varied widely across the sampling region (Fig. 1, Fig. 2). Highest SST medians (SRS=Southern Red Sea), and highest SST maxima (PAG= Persian/Arabian Gulf) existed in the NW Indian Ocean, lowest SST medians (LHI= Lord Howe Island, and EP-Easter Island) and lowest SST minima (LHI; EP-sGAL=southern Galápagos) in the South and Eastern Pacific. Greatest range of SST existed in PAG, sGAL, and CHI (China). Highest chl-*a* values were in CHI and CPC (Costa Rica/Panama/Colombia; Fig. 1, Fig. 2). The high chl-*a* values and their spread in

CPC can be attributed to upwelling and coastal runoff during the wet season. PAG and SRS, situated in arid regions, had higher median chl-*a* than CPC, but lower extreme values and spread. Seasonal upwelling exists in SRS, but not PAG.

Exploratory data analysis (Regression Tree) showed mean chl-*a*, then mean SST and its slope (of a linear model over the entire period) to best group sites based on coral regeneration (Fig. 3). Model selection (Linear Model, Generalized Mean Squares, General Additive Model, see methods) by optimization of Information Criteria (AIC, BIC, GCV) suggested negative relationship of regeneration with mean chl-*a* and SST variables.

An Indo-Pacific model of coral regeneration likelihood (% regeneration as dependent variable vs. SST and chl *a*) was developed as a linear mixed-effect model in the form "log(Regeneration)=i + r(mean chl-*a*) + r(mean SST) + r(mean SST slope) + r(mean SST slope)^2 + ε" (Fig. 3) which reproduced observed patterns from monitoring and meta-analysis (Fig. 4).

Discussion

Both elevated SST and nutrients, especially if representing a disturbance of the natural nutrient regime, can harm reef corals at the individual and the ecosystem level[3,5,6,11,12,20]. Since chl-*a* concentrations are a reliable indicator of the latter stressor, the link of ocean-wide coral reef recovery trajectories to chl-*a* and the interaction of chl-*a* with SST in the statistical model is supported by coral physiology and ecosystem responses.

The relationship between regeneration and SST/chl-*a* is negatively exponential and effects are multiplicative/divisive (after taking the anti-log of an originally linear, but logarithmically-scaled model). This helps explain why damage patterns on reefs are frequently observed as a slow progression within a realm of rather low degradation that may not be easily discernible, until a point is reached from which fast degradation results in rapid ecosystem collapse[21]. Interestingly, an exponential increase in number of coral bleaching reports since the 1980s, when warming and anthropogenic nutrifica-

Figure 1 | Location of 71 sites used in this study. Site codes from NW to SE: PAG=Persian/Arabian Gulf, NRS=Northern Red Sea (Yanbu, Wajh), SRS=Southern Red Sea (Farasan), IO=Indian Ocean, KTZ=Kenya/Tanzania, SL=Sri Lanka, CHI=China, GBR=Great Barrier Reef, HI-Hawaii, LHI=Lord Howe Island, FP=French Polynesia (including New Caledonia), SAM=Samoa, EP=Eastern Pacific, EP-Coc=Cocos; CPC=Costa Rica/Panama/Colombia, EP-nGAL=northern Galápagos, EP-sGAL=southern Galápagos, EP-Easter=Easter Island (Rapa Nui). In many instances, more than one site is included under the location acronym but could not be shown on this map. Details for each site and pertinent literature can be found in tables S.1 and S.2. Outline of continents produced using the open-source software R library "mapdata".

Figure 2 | Boxplots of SST and Chlorophyll *a* (chl-*a*) data for each sampling site over the entire sampling period (1983–2012 for SST and 1997–2010 for chl-*a*). Third column is regeneration from earliest to latest known survey date at the given site (Supplement Table S.3).

tion trends began to manifest themselves clearly through damage on coral reefs[21], mirrors the exponential decrease of regeneration potential.

Across the Indo-Pacific, the link between low regeneration capacity (Fig. 3 and 4a) and coral bleaching susceptibility[6] with a combination

of high SST and chl-*a* levels suggests that SRS and, to a lesser extent, PAG are most prone to severe degradation (Fig. 4a), as is the area of the central Indian Ocean and the Western Pacific Warm Pool. In the Eastern Pacific and Meso-America, upwelling cells influence coral trajectory potential positively, apparently due to cooling. In Colombia,
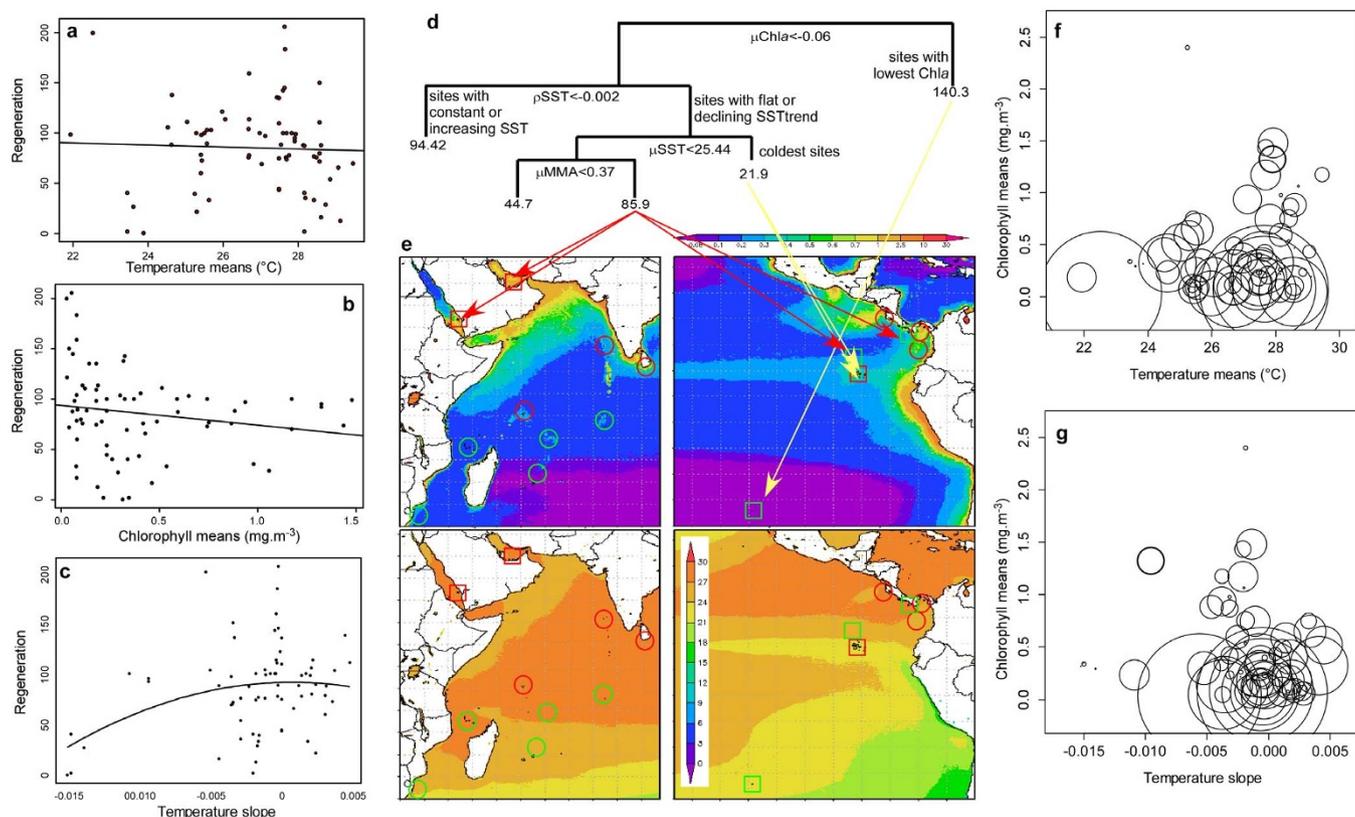
Figure 3 | Relationships of chl-*a*, SST and coral regeneration. (a,b) Linear relationships of regeneration with SST and chl-*a* means (c) quadratic relationship with the slope of a linear model of SST against time (~SST change 1981–2013). (d) Regression tree. Values at each branch are mean coral regeneration percentages in the group; µchla=mean chl-*a*, ρSST=slope of SST over entire dataset, µSST=mean SST over entire dataset, µMMA=mean of monthly anomaly. Groups are indicated on (e) which are mean chl-*a* (1997–2010; in mg.m^{-3}) and mean SST (2002–2010; in °C) from MODIS Aqua (Circles=meta-analysis, squares=monitored sites, red=declining regeneration, green=steady/increasing regeneration.). (f) Bubble plots provide another view at SST, chl-*a* and regeneration. Coral regeneration as relative bubble size. Despite much scatter, regeneration decreases with increased chl-*a* levels (decreasing size of bubbles along y-axis).

Panama (Gulfs of Panama and parts of Chiriqui), and cooler parts of Costa Rica and Mexico, corals are more likely to be resilient (Fig. 4; ref. 22). This dynamic is primarily correlated with mean SST, rather than with water column productivity (Fig. 3e and 4a). The potentially most resilient reefs, according to this model, are expected in high-latitude areas (Cabo Pulmo in Mexico, Lord Howe and Easter Islands, SE Africa, northernmost Red Sea).

Coral monitoring supports the regeneration pattern obtained by statistical analysis. PAG, CPC and the Eastern Pacific experienced episodes of coral mass mortality since the 1980s[23–26]. Upward trends in coral recovery were observed outside the upwelling areas in the Eastern Pacific and CPC (Fig. 4b). EP-Easter bleached in 1980[26] and macroalgae dominated over low coral cover[27] but since then a continuing upward trend in coral cover, like in EP-nGAL (die-back in 1983), has been observed, even despite bleaching and mortality in 2000. Little coral regeneration occurred in EP-sGAL, where mean chl-*a* is >20% higher than EP-nGAL and EP-Easter. However, the model suggests a potentially overall resilient area in all of the Galápagos (Fig. 4a), which monitoring contradicts. The meager recovery in the southern islands might be due to low availability of recruits after almost complete elimination of corals in 1983, and a low-pH environment[13]. Certainly a multitude of factors, including others than those captured in our model, are at play in this oceanographically and biologically highly complex area. Also parts of CPC (Gulf of Panama, Chiriqui) regenerated since mass-mortality in the 1980s, but high-SST and -chl-*a* sites in Costa Rica did not (Fig. 4b). After the 1960s and 1980s mortality in PAG, corals regenerated until 1996/8 and from then on cover and size declined. SRS bleached in

1998 and has only recovered in deeper sites with significant declines on shallow reefs (Table S.2). PAG, SRS had the highest combination of SST and chl-*a* values of all 71 sites (with exception of CHI). Our model suggests that NRS (low chl-*a*, low mean SST) has higher regeneration potential than SRS, which supports findings by others[28]. In conclusion, coral reefs in regions with high chl-*a* and/or high SST generally show lower regeneration potential/capacity (CRC, PAG, SRS). This correlation suggests that the higher level primary production in these areas is associated with nutrient conditions that are, at least when combined with SST anomalies, unfavorable for corals[6]. A strong warming trend in the central Indian Ocean and Western Pacific Warm Pool also contribute to expected low resilience while a tempered thermal regime and low chl-*a* levels correlate with the upward trajectory of coral recovery in the Eastern Pacific and at some higher latitude settings.

This study highlights a double-threat to coral reefs today: changes in nutrient and thermal environment interact to the detriment of coral regeneration. These stressors will combine with increasing intensity with ocean acidification effects, specifically due to the consequences of elevated pCO_2 and low pH[12,29]. Future productivity of coral reef waters will be influenced either by nutrient enrichment of coastal waters due to the intensified use of coastal areas by a growing human population and increased coastal upwelling[14,15] or nutrient impoverishment of oceanic waters due to stronger stratification of the water column promoted by warming surface waters[16]. The cooler, nutrient-rich upwelled water might mitigate heat-induced bleaching and stimulate coral growth[6]. The results of this study suggest however, that the suite of negative effects on coral reef ecosystem
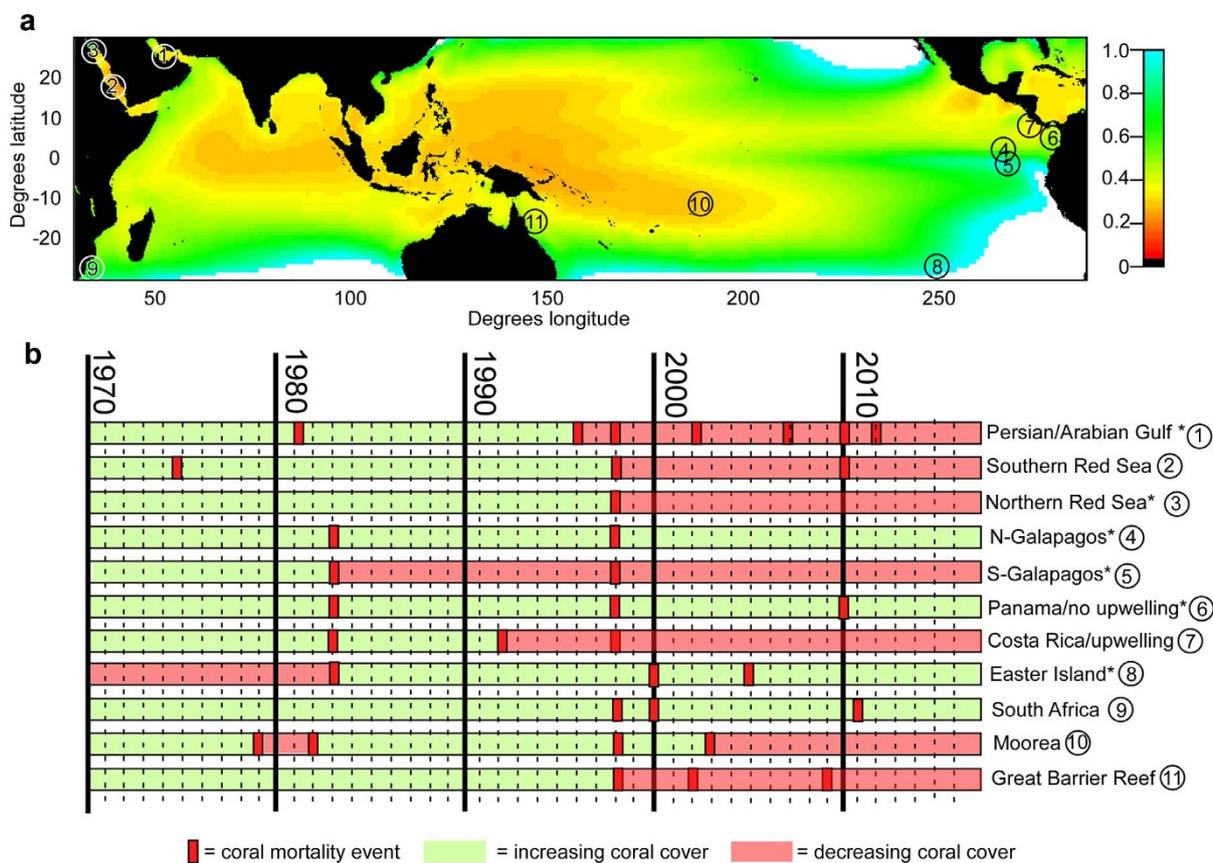
Figure 4 | (a) Indo-Pacific model of present coral regeneration potential. The index is based on the model log(Regeneration)=i + r_1(mean chl-a) + r_2(mean STT) + r_3(SST slope) + r_4(SST slope)^2 + ε over 31 yr. Warmer colors (lower index value) relate to increased mortality/decreased regeneration likelihood. This model was built on Indo-Pacific data and should not be considered valid for the Caribbean. (b) measured trajectories (*=our long-term monitoring sites, others represent literature data; see Tables S.1 and S.2).

functioning[6] plays an important role in the response of coastal reefs to nutrient enrichment. The expected impoverishment of oceanic waters might benefit some reefs by reducing the pressure from indirect effects of elevated nutrient concentrations. However, the combination of low nutrient stress on zooxanthellae and increased temperatures also can promote coral bleaching and mortality[5,6]. In fact, during the 1997/98 coral die-off at s-GAL, reefs were not only exposed to exceptionally high temperatures but also to a sharp drop of surface water chlorophyll a and nutrient levels due to an El Niño Southern Oscillation (ENSO)-mediated reduction of major upwellings (Fig. S.2)[30]. Thus, the potential future reduction of water productivity alone might not necessarily bring the needed relief to coral reefs but could possibly act in combination with increased heat stress levels to accelerate reef decline. Hence, predictions of the fate of coral reefs should consider that reef survival will depend on the interaction of multiple stressors which might result in pronounced regional differences.

Our model nonetheless shows that wide areas of the ocean are presently suitable for maintenance of reasonable conditions for reef regeneration (Fig. 4a). At the same time, our model identifies that the reefs spared from the negative effects of elevated SST and chl-a levels are those expected to suffer the strongest impacts of ocean acidification[13]. Under strict local environmental management, currently the most powerful mitigation tool for climate change stresses on coral reefs, there may still persist hope for the future of at least some coral reefs.

Methods
The flow of statistical and numerical analyses was as follows:

1) Obtain trajectory of coral cover by monitoring and/or meta-analysis and acquire environmental data (SST, chl-a) for the same geographic area.
2) Check validity of environmental data against coral population structure at monitoring sites.
3) Calculate statistics for SST and chl-a data.
4) Perform thorough data exploration[31].
5) Use exploratory data analysis due to large number of possible explanatory variables. Here, unvariate regression tree analysis was used[32,33,38,39]. Find the best-splitting variables, in this case the variables that caused the first four dichotomies.
6) Explore data structure of response variable (regeneration) w.r.t. chosen best-splitting control variables.
7) Fit model of increasing complexity (if needed), perform model selection and validation[33] and evaluate fit.
8) Grid SST data across the tropical Indo-Pacific (1 $\times$ 1 geographic degrees. 1981–2013), grid chl-a across the tropical Indo-Pacific and regrid SST to same pixel-resolution as chl-a.
9) Apply model equation obtained under 7 to every grid-point.

We used our own monitoring data and that from the published literature to obtain values of coral cover from sites across the Indo-Pacific dating as far back in time as possible. Many datasets (N=75) were found from the 1980s and early 1990s, thus pre-dating the marked and well-known mass mortalities of 1998. Percent-increase (or decrease) of coral cover between the 1970/80/90s and the mid 2000–2010s or later was calculated and called the "regeneration" (Tables S.1, S.2). Some datasets were excluded from analysis. For example, Cocos Island[34] and some sites in American Samoa[35] showed strong regeneration from very low coral cover in the 1980s that resulted from predation. In these sites, increases of several hundred percent in cover values (Table S.2) were observed. Besides generating statistically problematic outliers, these data points were also unusual since the mortality from which regeneration was observed, was not due to bleaching or any climatic factor but predator outbreaks. Also, at least in Samoa, that high regeneration trend was interrupted by later mortality events[36]. Final analyses shown in this paper utilize 71 of the 75 potentially available sites.

Additionally, detailed monitoring information exists for sites on the western (SRS, PAG) and eastern (EP-sGAL, EP-nGAL, EP-Easter, CPC) sides of the tropical Pacific, with data stretching back to the 1980s (Table S.1). *In-situ* environmental and

Table 1 | Statistics derived from SST and chl-*a* data

DATA	STATISTICS
raw = mean monthly SST (372 months)	**mean** of 372 mean monthly SST **variance** of 372 mean monthly SST **y-intercept** of linear model fit to 372 mean monthly SST **slope** of linear model fit to 372 mean monthly SST **change** of mean monthly SST over 372 months (last minus first projected values of linear model fit) **monthly anomaly** (annual mean of mean monthly SST minus each mean monthly SST) **annual mean monthly anomaly** (per-year mean of 12 monthly anomalies **mean of all annual mean monthly anomalies** (mean of above across all years) **mean of monthly anomaly** (per-month mean of all monthly anomalies over all years) **y-intercept** of linear model fit to 33 annual mean monthly anomalies **slope** of linear model fit to 33 annual mean monthly anomalies
raw = mean monthly chl-*a* (160 months)	**mean** of 160 mean monthly chl-*a* **variance** of 160 mean monthly chl-*a* **y-intercept** of linear model fit to 160 mean monthly chl-*a* **slope** of linear model fit to 160 mean monthly chl-*a* **change** of mean monthly chl-*a* over 160 months (last minus first projected values of linear model fit)

population-level coral data exist. Coral cover data are from fixed transects that have been repeatedly visited over the monitoring period. Size-class information was derived from phototransect analyses conducted at least once at the end of the monitoring period. At all sites, the monitoring period coincides with the global availability of remotely-sensed SST and chl-*a* data, allowing cross-checks with *in-situ* data and evaluation of coral trajectories against uniformly measured environmental variables.

While *in-situ* thermal data exist at all monitoring sites, time-series were too short (mostly <10 yr) to allow a meaningful evaluation of trends. The exception was a 48-year temperature dataset from Puerto Ayora (St. Cruz, EP-sGAL; courtesy CDRS; ref. 40). Therefore, we used synthetic temperature datasets, the Reynolds OISST and the HadISST[19,37]. We checked the correlation of mean monthly SST in the time-window 1981-2012 of the synthetic datasets against that of the Puerto Ayora data. OISST correlated (Fig. S.3) better (R^2=0.92) than HadISST (R^2=0.88). Remotely-sensed data reproduced locally observed temperature dynamics, however, *in-situ* data were shifted downward by ~ 1°C, a result of the *in situ* thermosensor situated in deeper water than what SST temperature models consider the ocean's surface skin. Extremes in OISST were of smaller magnitude than *in situ*. Also for PAG, *in situ* variability of 14.2–36.2°C[25] is higher than in OISST. Despite inconsistencies relating to extremes due to synthetic data representing 1 × 1° boxes, overall regional differences in temperature regimes and temperature anomalies known to be important for coral dynamics were faithfully reproduced in the synthetic datasets. Thus, OISST data were considered adequate for the current analysis.

Chl- *a* levels are a good proxy for nutrient levels in coastal waters[17,18]. Therefore, Chl-*a* data from the MODIS sensor were extracted for the monitoring sites as 0.1 degree boxes from NASA Giovanni[41] from September 1997 to December 2012. A coherent series of 160 months was obtained over all sites. Remotely-sensed monthly mean chl-*a* data were compared to a monitoring time series (one sample per month) from the Florida Keys from 1997–2010[42]. The two datasets showed similar trends, but the correlation was not significant, as could be expected due to the different data structure (irregular daily measurements against monthly means).

We calculated several indices that we plotted against the percent-change in coral cover over the period for which SST and chl-*a* data were available (Table 1).

Statistical considerations: Data consisted of several different measures obtained from two time-series (SST and chl-*a* statistics) per site. The response variable was coral regeneration (over all sites, thus a continuous variable) against the explanatory variables that were indices derived from the SST and chl-*a* time-series. Because time-series were collapsed into single indices, the data needed not be considered nested in time. Therefore, data were checked for spatial, but not temporal, autocorrelation. Pair-wise correlations suggested co-linearity among 1/3 of variables which could then be neglected. Pair-plots also gave no *a priori* indication that the relationships of explanatory variables (temperature and chl-*a*) with the response variable (regeneration) should not be linear, thus permitting the exploration of linear models. We first employed univariate regression tree analysis[31,32,38,39] to reduce the high number of possible explanatory variables for inclusion in further statistical modeling. This suggested chl-*a* means, the slope of SST increase over the entire dataset, and SST means to be the key variables.

We then fitted a linear model that assumed no interactions and included first all available response variables, then reduced progressively to the three suggested by regression tree (Fig. S.4). Homogeneity of variances was explored by plotting and testing residuals. Some variance structure was found (non-normal variance decreasing with the square of the mean). Potential violation of spatial independence (indices between closer sites should vary less than between remote sites) was examined as a source for variance structure by plotting residuals against geographical position in bubble plots and by variograms. This analysis did not suggest strong spatial structure in the data (Fig. S.5). Similar to 43, some relationship of regeneration

with latitude and longitude was found, and therefore shape of variogram and min-imization of AIC and BIC were used to evaluate the spatial correlation structure for the model. Potential heterogeneity in the random part of the model suggested further exploration of data structure by a general least squares model first with constant power variance structure[31]. However, introduction of spatial correlation structure did not significantly improve the linear model (higher df, slightly lower AIC but no significant improvement by ANOVA) and was therefore rejected in favor of a more simple explanatory model.

Optimization of the linear model by AIC suggested a structure without interaction terms of chl-*a* means with temperature slope and mean temperature respectively. This suggests that SST and chl-*a* levels, as proxy for nutrification, each independently act linearly on the log of regeneration. While chl-*a* and SST means showed linear responses to log(regeneration), that of SST increase was best modelled as quadratic with the lowest values at the sites that showed the strongest declines and a regen-eration maximum near zero change. This suggests that excursion to either side, increase as well as decrease in SST, negatively affects regeneration. Since some het-erogeneity of variances was not overcome by transformation, this variance structure was considered potentially biologically meaningful and no further efforts to eliminate it were made. Therefore also a general additive model (GAM) with Gaussian distri-bution of regeneration against the three key variables was investigated that allowed for nonlinear relationships. The model was significant with the two temperature indices as suggested by regression tree analysis, but not with the chl-*a* means (F=2.3, p=0.06). However, deletion of chl-*a* means from the model significantly increased deviance (F=3.1, p=0.001), so they needed to be retained. Model optimization by AIC suggested the strongest interaction between chl-*a* means and SST Slope, as also suggested by the regression tree. This again suggests that the effects of nutrients vary with temperature change – a key interaction under climate change scenarios.

The GAM, allowing interactions of the modeled variables, however still suggested an almost linear relationship between regeneration, chl-*a* means and temperature means and a relationship between regeneration and temperature slope that did not add much information to that obtained by the linear model. Clearly, despite some variance structure, it was sufficient to accept linear relationships between chl-*a* and SST means with regeneration, and a quadratic relationship with SST slope (Fig. S.6). Thus, when acting alone, mean chl-*a* and temperature levels have simple and negative relationship with coral regeneration. It is from their interaction, that nonlinearities arise. Other measured variables were less important, but also less linear in their relationships.

The model. From above analyses, the final model to be extrapolated across the Indo-Pacific took the shape:

logRegeneration=8.1356-0.0528*mean_chl-*a* + (-4.0427*mean_SST) + (-0.2421*SST_slope) + (-0.3301*(SST_slope)²).

This model was calculated over all cells extracted for the tropical Indo-Pacific as shown in Fig. 4a and supplement Fig. s.7. Cooler oceanic regions off Peru and California with lower SST and low mean chl-*a* concentrations calculated as having high regeneration likelihood (supplement Fig. s.7). These areas were set to zero (white regions in Fig. 4a), since they are not relevant for coral reefs. Over the reef belt, calculated values of the regeneration index spanned the domain 0.2–0.9.

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Acknowledgments

Author contributions

B.R. and J.W. conceived the study. S.P., B.R. and J.W. monitored sites in Persian Gulf and Red Sea, P.G., E.W. and B.R. monitored sites in Panama, Galápagos and Easter Island. B.R., J.W. and C.D.A. assessed remote sensing data. All authors wrote, corrected and read the paper, critiqued statistics and model.

Additional information