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Beyond Linearity: Reconciling Conflicting Evidence on Sea Surface Temperature Variability and Coral Reef Stability

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Abstract. Coral reefs are one of the most biologically diverse ecosystems in the ocean, but are now under increasing threat from climate related ocean warming. While numerous studies have focused on the impact of sea surface temperature (SST) on coral reef condition, those that specifically looked into whether long-term background SST variability had an impact on reef stability have had conflicting results, with some analyses showing negligible association and others showing significant associations. This paper explores the reasons behind this contradiction, using the findings of new research and reanalysis of the Heatwaves and Coral-Recovery Database, a 44-year global monitoring dataset of over 12,000 reef sites. The standard linear correlation methods used to reanalyze SST variability over the long term revealed only a weak relationship between the SST variability and the two independently derived stability indices. For the coral cover data, however, acute peak thermal stress was a stronger predictor than background variability, site identity explained ~2/3 of the variance and nonlinear modelling revealed a strong U-shaped relationship, undetectable under the linear stress assumption; the same pattern was found for both measures of stability. A weak global effect also masked some strong ocean basin variation in the regional analysis, with even point estimates of opposite sign in certain regions. When combined with other parallel results reported elsewhere, these data suggest that the linkage between long-term SST variability and coral reef stability exists, but it is nonlinear, site-specific and regionally variable – not captured by a simple linear global analysis.

Keywords: Sea surface temperature variability, coral reef stability, nonlinear response, site heterogeneity, regional variability

1. Introduction

Coral reefs are one of the most biologically diverse marine ecosystems on Earth, but are also under threat from ongoing ocean warming and an increase in the frequency of marine heatwaves. Yet, there has been a striking variation in the results of studies looking at the effect of long-term background sea surface temperature (SST) variability on coral reef stability. Some analyses show either the effect is too weak to be measurable or is statistically weak, and others show effects that are substantial and ecologically relevant. This inconsistence might be due to varying geographical areas, different species or varying data quality, but it might also indicate something more fundamental about how the relationship has been analyzed in the first place.

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A comprehensive systematic review of almost three decades of climate change effects on coral reefs was recently undertaken, which produced a synthesis of the overall picture [1]. Instead of summarizing the breadth of this literature, this paper focuses on a more specific, method-oriented question that crosses many of the studies summarized in such a review: why is it that so many analyses find no significant association between long-term SST variability and coral reef stability while others do? Does the relationship actually not exist or is it hidden by assumptions in the analytical framework, most importantly, in the assumption of a linear and global uniform relationship?

To answer this question, this paper brings together the results of recent published works, and reanalyses the Heatwaves and Coral-Recovery Database which is a global monitoring database that includes over 12,000 reef sites spanning 44 years of data [2]. The discussion is presented in the following five steps: Apparent absence of linear association at the global scale, stronger predictive power of acute peak thermal stress as compared to background variability, dominance of site identity compared to any single SST metric, a nonlinear, U-shaped relationship once linear assumptions are relaxed, and significant regional heterogeneity that is hidden by global-average effects. All these together indicate that the link between the long-term SST variability and the stability of the coral reefs is not non-existent, but rather influenced by parameters which simple linear global analysis cannot measure.

2. Five layers of evidence behind an apparent null result

2.1. Weak linear relationship between reef stability and SST variability

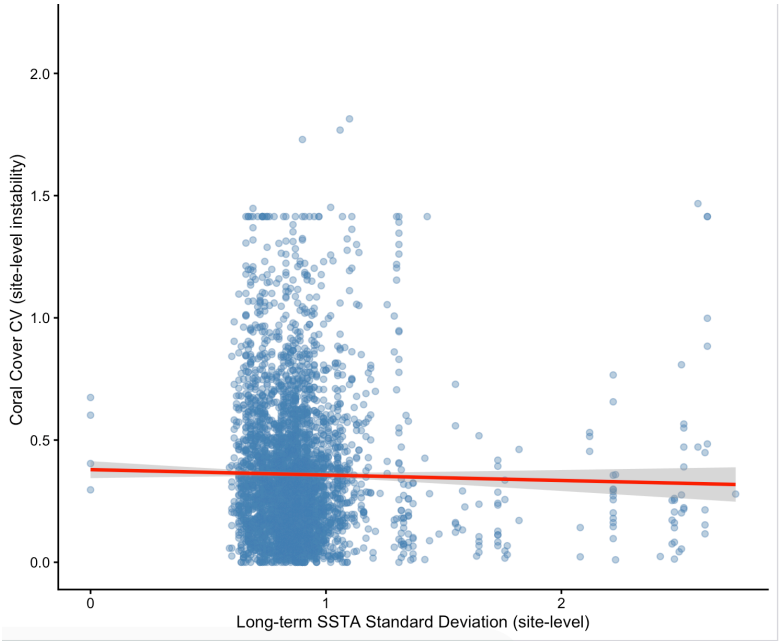

Figure 1. Long-term SSTA standard deviation versus coral cover CV, with linear fit

This dataset contains 12,218 reef sites, of which only 4,167 sites (sample sizes vary slightly depending on data completeness requirements detailed below) had data from at least two observations that could be used to calculate stability metrics. A correlation analysis of the long-term standard deviation of the SST anomalies compared to the coral cover instability (CV) based on n = 3,754 sites with complete data yielded a Spearman coefficient of $\rho = -0.05$ ($p = 0.0013$) but the

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corresponding Pearson correlation was not significant ($p = 0.247$) (Figure 1). This difference is in line with the right-skewed distribution of CV: Pearson correlation is sensitive to skew and extreme values, Spearman correlation, which is based on ranks, is more robust. The effect of this "significant" p-value is small and, in isolation, should not be interpreted as evidence of ecological significance, in a sample of this size. It is also important to note that CV, as with all instability measures based on ratios, is mathematically susceptible to inflation at low mean coral cover; this was not carefully controlled for in the analyses presented here, but is discussed in the Limitations.

If taken alone, this trend would indicate that the background thermal fluctuation is not a very strong predictor of reef stability. However, regional (and even aggregate) apparent stability does not necessarily mean that there is no underlying signal; in the East Asian Seas, a recent large-scale survey of 24,365 surveys, covering nearly 2,000 sites, showed that SST was not associated with coral cover in the aggregate, but models incorporating other environmental covariates were [3]. This suggests that the lack of linear signal found here may be an artifact of the analysis and not necessarily the lack of any relationship — a test of which is performed directly in Section 2.4.

Four alternative explanations are explored in turn in the four sections that follow: measurement choice, site-level confounding, functional form, and spatial aggregation. This series of follow-up analyses was not prespecified but rather represents a post hoc set of analyses; no formal correction was applied to this series of comparisons; therefore, readers should consider this series in conjunction with the supporting evidence from independently published studies summarized at each step.

2.2. An acute peak thermal stress

It is important to first consider the possibility that background variability is not the most appropriate thermal metric to consider, before moving in to the issue of functional form. Using a site-level measure of the highest historical single thermal stress event in each site, expressed as the peak degree heating weeks value recorded at that site (denoted dhw_max), the association with reef instability ($\rho = 0.075$, $p < 0.0001$) is greater than association with long-term background variability alone, and the model based on the former has a lower Akaike Information Criterion (AIC = 1190.6) than the model based on the latter (AIC = 1203.4) (Table 1), with a combined model providing no meaningful improvement. This pattern has remained strong when subject to a log transformation sensitivity test and is consistent with a threshold mode of thermal damage, in which the event of an extreme exposure is of greater importance than the average intensity of the exposure. However, each of the models examined accounted for less than 2% of the variance in reef instability, suggesting that variables related to SST, in any form, do not account for much of the observed variation, and thus have limited explanatory power.

Table 1. AIC comparison of site-level models

Model	df	AIC
M0: Long-term SD only	7	1203.4
M1: dhw_max only	7	1190.6
M2: Both	8	1191.2

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2.3. None of the SST metrics can offer a comprehensive explanation of site identity

A linear mixed-effects model with a random intercept for site (REML) revealed that 65% of the total variation in coral cover was due to differences among sites and 35% of the total variation in coral cover was due to differences within site over time (intraclass correlation coefficient = 0.648). However, when between-site confounding was controlled for by comparing only within-site change across time (a site fixed-effects specification, in which by construction all time-invariant site characteristics, including long-term SST variability itself, are removed), the explanatory power of short-term SST variability dropped to near zero (within site $R^2 = 0.0005$). This is not the only data set to show this pattern, as an independent analysis of Indo-Pacific and Caribbean reefs also showed that SST anomalies did not significantly explain variation in benthic composition, and that variance within reefs was the greatest [4]. These results collectively suggest that the position of a reef, not any specific thermal exposure index, is most important in determining coral cover. It is not, however, to say that SST variability is unimportant — just that its influences can manifest themselves in ways not previously considered with linear models.

2.4. Uncovers a U-shaped relationship

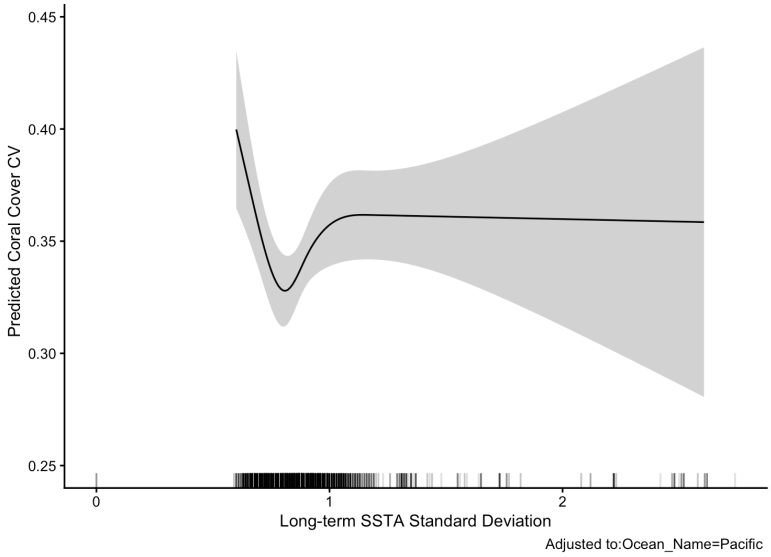

Figure 2. Restricted cubic spline curve for long-term SSTA standard deviation and coral cover CV

If linearity is removed from the equation, things look very different. A restricted cubic spline regression, with four knots (following standard convention) was performed on the long-term SST variability with reef instability, the nonlinear relationship was highly significant (Nonlinear P = 0.0007) and the trend was U-shaped, with instability decreasing as the SST variability increased from low to moderate, reaching a minimum and then increasing again at higher variability (Figure 2). There is no claim of lack of sensitivity of this pattern to alternative placements of the knots, this being a limitation of the current analysis. This pattern was also independently reproduced with the other stability metric (long-term trend in coral cover; Nonlinear P = 0.0161), and thus the shape is not a result of any one metric.

The absolute explanatory power of the nonlinear term was limited (1.7% and 0.8% for the two measures, respectively). This is a small effect on any measure, and should not be interpreted as suggesting that long term SST variation is a significant source of reef stability — note that by far the

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largest source of explained variance is site identity (Section 2.3). The low R2 value does not reflect, however, the spread of the predicted outcomes along the range of the observed outcomes—that is, the fitted curves ranged over about one-fourth of the standard deviation of each outcome. This measure is reported in conjunction with R^2 in particular to avoid mixing up "explains little variance" with "no meaningful pattern" (which are not the same), and to make it clear that both claims are compatible with a relationship that is minor, not dominant, in magnitude.

This U-shape is in general agreement with multiple independent lines of evidence regarding responses of coral thermal tolerances to different thermal histories. A global-scale analysis based on the same lineage of underlying datasets revealed that reefs with a higher historical interannual SST anomaly variance had much lower bleaching prevalence [5] and corals with a higher interannual SST variability had a higher bleaching resistance [6]. Some experiments have also demonstrated that intermediate levels of habitat thermal variability – not extreme levels – are linked to the highest coral thermal tolerances, thought to be a "priming" effect [7]; long-term field monitoring shows that coral thermal tolerances have been changing over time, with increasing tolerance likely a cumulative effect of historical thermal exposure [8]. Evidence that marine heatwaves can lead to a lasting change in coral symbiont community towards more thermally tolerant symbionts over many years provides a plausible underlying mechanism [9]. None of these studies directly mimics the U-shaped statistical relationship exhibited here, but overall, they offer a biologically plausible explanation as to why moderate long-term thermal variability may result in more stable reefs.

2.5. Considerable regional heterogeneity

Adding a layer of complexity is the exposure to acute thermal stress and its impact on reef instability on a basin-by-basin basis. Significant positive effects were detected in the Pacific (0.0038, $p < 0.001$) and more strongly in the Indian Ocean (0.0123, $p = 0.001$); although the point estimates in the Atlantic (−0.0033) and Red Sea (−0.0031) were in the opposite direction, the wider confidence intervals of these smaller sample sizes encompassed zero, which indicates that any apparent regional divergence should be viewed as a tentative signal. The globally averaged effect reported above is thus a patchwork of regionally very different (and perhaps at some locations even opposite) relationships. This finding is consistent with the geographically weighted regression analysis results, which indicate a significant spatial variation in the SST relationship with coral bleaching; a global coefficient might mask important local variation [10]. This regional heterogeneity, taken with the previous four findings, indicates that there are no linear or otherwise one-size-fits-all relationships between long-term SST variations and coral reef stability.

These regional estimates assume independence among sites within the same ocean basin, an assumption in tension with the strong hierarchical clustering documented in Section 2.3 (intraclass correlation coefficient = 0.648). A cluster-robust re-estimation clustering standard errors by biogeographic realm was attempted to address this concern, but could not be performed reliably for most basins because too few distinguishable realms were available (as few as two to three in the Atlantic and Indian Ocean) to support the correction. The regional point estimates above should accordingly be read as suggestive rather than confirmatory.

3. Conclusion

This correlation between long-term SST changes and coral reef stability is not null, but it is nonlinear, site-specific and regionally variable, and it is masked by the linear, global, and aggregated approaches used in much of the current literature. A simple correlation analysis indicated a weak

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relationship between the background variability over the long-term and reef instability, which was actually a result of the metric and the model. However, acute peak thermal stress was the better predictor and hence a threshold mode of damage was suggested. When the SST metrics were analyzed separately, site identity explained about two thirds of the total variation in coral cover, suggesting that location of the reef is more important than changes in the thermal environment of the reef. After relaxing the assumption of linearity, a strong U-shaped relationship was identified between long-term variability and reef stability, replicated independently across two different measures of reef stability, which implies that moderate historical thermal variability might be related to higher reef stability than either low or high variability. Finally, this was not a uniform effect, with a weak global effect masking regionally divergent patterns, with significant positive associations in the Pacific and Indian Ocean, while the point estimates in the Atlantic and Red Sea showed the opposite behaviour, but these apparently reversed trends should still be considered tentative due to the smaller regional sample sizes.

Even more than the particular question of SST and coral reef stability, this has a more general methodological significance, in that the global linear analyses may systematically give a false conclusion of "no relationship," not because there is no signal, but because the form that the signal takes is not the one that the analytical framework is designed to identify. There are a few caveats to all these findings. Stability measures could only be used for reefs with repeated visits, and these reefs had significantly higher coral cover and were at lower latitudes than those visited only once. The nonlinear relationship is also less certain at the highest levels of variability, where there was limited data, the Atlantic and Red Sea were limited by small sample sizes with the coefficient of variance used as one measure of stability is mathematically prone to inflation at low mean coral cover, which was not explicitly controlled for here. As in all observational analyses, none of the relationships reported are necessarily causal, and the order of the analyses is a series of serial follow-up investigations and not a pre-registered analysis plan. The site-level effect should be broken down into individual covariates (e.g. depth, protection, community composition) and the regional heterogeneity should be examined to assess whether it is driven by consistent factors or idiosyncratic to each reef.

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