## A crystal structure perspective on coral skeleton trace element environmental proxies and their reliability under stress conditions

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Scleractinian coral skeletons have long served climate scientists as reliable recorders of past environments due to their longevity and layered nature. Empirical proxies based on trace element (TE) incorporations into coral skeletal aragonite are used to track changes in environmental parameters such as sea surface temperature, aragonite saturation state, wind, and more. However, we still know relatively little about why these environmental proxies work, how these TE signals are trapped in coral aragonite, and whether they may be affected by physiological stress. Here, we present a combined mineralogical and trace element geochemistry approach to understand how TEs are incorporated into coral aragonite skeletons on an atomic scale. We observed that changes in TE:Ca ratios across a multiyear coral skeleton transect from Butaritari Atoll from the central equatorial Pacific are often correlated with measurable shifts in aragonite unit cell parameters-indicating that TEs and crystal structures are linked. We also observe that Raman-based carbonate bonding disorder, measured as the full width at half maximum of the  $v_1$  mode (a proxy for calcifying fluid aragonite saturation states), is positively correlated with increasing skeleton calcification rates, and negatively correlated with increasing sea surface temperatures (thermal stress). Beyond general correlations between crystal structures and specific trace elements, we also find that correlations between these many variables are subject to change when the coral experiences events of thermal stress. This calls into question the reliability of some trace element proxies when an organism is undergoing stress. By assessing a range of TEs and mineralogical parameters at once, we suggest that TEs such as Sr that have consistent relationships with unit cell parameters, even during periods of thermal stress, provide the most reliable and straightforward paleoclimate proxies from this mechanistic perspective. Future studies would benefit from a targeted approach to separating the effects of specific variables and TEs on crystal structure parameters.