Understanding cold bias: Variable response of skeletal Sr/Ca to seawater $pCO_2$ in acclimated massive Porites corals

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Coral skeletal Sr/Ca is a palaeothermometer commonly used to produce high resolution seasonal sea surface temperature (SST) records and to investigate the amplitude and frequency of ENSO and interdecadal climate events. The proxy relationship is typically calibrated by matching seasonal SST and skeletal Sr/Ca maxima and minima in modern corals. Applying these calibrations to fossil corals assumes that the temperature sensitivity of skeletal Sr/Ca is conserved, despite substantial changes in seawater carbonate chemistry between the modern and glacial ocean. We present Sr/Ca analyses of 3 genotypes of massive Porites spp. corals (the genus most commonly used for palaeoclimate reconstruction), cultured under seawater $pCO_2$ reflecting modern, future (year 2100) and last glacial maximum (LGM) conditions. Skeletal Sr/Ca is indistinguishable between duplicate colonies of the same genotype cultured under the same conditions, but varies significantly in response to seawater $pCO_2$ in two genotypes of Porites lutea, whilst Porites murrayensis is unaffected. Within P. lutea, the response is not systematic: skeletal Sr/Ca increases significantly (by 2–4%) at high seawater $pCO_2$ relative to modern in both genotypes, and also increases significantly (by 4%) at low seawater $pCO_2$ in one genotype. This magnitude of variation equates to errors in reconstructed SST of up to $−5°C$.

Coral skeletal Sr/Ca is influenced by sea surface temperature (SST) and is a widely used palaeothermometer. Strong correlations have been observed between instrumental SST records and skeletal Sr/Ca in modern corals over seasonal to decadal timescales, providing a reliable proxy for the reconstruction of multi-centennial SST variations and valuably extending the record of many natural climate oscillations back to the 16th Century. Over millennial timescales, the accuracy of SST estimates from Sr/Ca ratios in fossil corals has been questioned as they frequently yield improbably cool or spatially inconsistent values. Whilst some of these inconsistencies have been explained by regional oceanographic dynamics, a number of possible influences on skeletal Sr/Ca in coral remain unresolved. Skeletal Sr/Ca is correlated with skeletal growth rate in some but not all corals and may be influenced by diagenesis, skeletal ultrastructure, metabolic cycles, and potential variations in seawater Sr/Ca. Calibration equations describing the temperature dependence of coral Sr/Ca also vary significantly, both between species and within a single species sampled from different reef locations. However these factors appear insufficient to explain cold bias e.g. in an early Holocene Tahitian fossil coral. Understanding the origin of sensitivity variations within the Sr/Ca-SST relationship is essential if we are to interpret accurately the high resolution climate records encoded in coral skeletons and benefit from their application in resolving the controls on past climates and predicting future change. Coral palaeoproxy relationships are derived by correlating annual SST variations with skeletal Sr/Ca in modern specimens. In applying these empirical relationships to fossil specimens, it is implicitly assumed that the processes affecting skeletal geochemistry have not changed between the present and past. It is unlikely that this is the case: in particular, atmospheric CO2 has varied significantly over glacial-interglacial time scales affecting both seawater pH and dissolved inorganic carbon (DIC) chemistry, factors which influence skeletal trace element incorporation in some calcitic marine organisms.

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The influence of pH and DIC on coral skeletal Sr/Ca is poorly constrained. Culture studies investigating the effect of reduced seawater pH across a range of ocean acidification scenarios yielded mixed results: seawater pH and Sr/Ca were negatively correlated in Acropora digitifera28 and newly settled recruits of Favia fragum27 but were unrelated in Montipora capitata31. No systematic variation in skeletal Sr/Ca was found over a wider pH range (both lower and higher than present day) in Stylphora pistillata28. With the exception of A. digitifera29, these studies used addition of HCl or NaOH to manipulate seawater pH at constant seawater pCO2, consequently shifting other carbonate system parameters to unrealistic values29. Additionally, the short acclimation times (5–35 days) of three26–28 of the four studies are probably insufficient to enable coral physiological responses e.g. changes in zooxanthellae density, to adapt to changes in environment.

We test the direct impact of variations in seawater pCO2 on skeletal Sr/Ca in massive Porites spp. corals, the coral genus most commonly used for palaeoclimate reconstruction. Heads from 3 genetically distinct corals (2 × Porites lutea and 1 × Porites murrayensis; Fig. 1) were divided into smaller sub-colonies (each >8 cm diameter) and cultured in a mixture of natural and synthetic seawater. Corals were housed in a purpose-built large-volume aquarium system constructed of low CO2 permeability materials. The seawater in each treatment was bubbled with gas mixes set to reach the target seawater pCO2 compositions. Corals were maintained at ambient pCO2 conditions for 2 months, adjusted to pCO2 treatment conditions over another 2 months and then acclimated at the final treatment pCO2 for 5 months. Final seawater pCO2 target levels ranged from the last glacial maximum (LGM; ~180 μatm), through present day (~400 μatm) to levels projected by the year 2100 (~750 μatm). Actual seawater pCO2 levels (198, 416 and 750 μatm) in the reservoirs were calculated from total alkalinity and DIC using the CO2SYS program30. Seawater Sr/Ca, temperature, salinity and DIC system parameters were maintained within narrow limits throughout the study (Table 1).

The skeleton deposited in the 5-week period, following the acclimation, was identified by alizarin red staining (Fig. 1), and skeletal Sr/Ca of this region was analysed by secondary ion mass spectrometry (SIMS). Skeletal deposition is concentrated at the skeleton surface in massive Porites corals, although subtle thickening of the trabeculae may occur over a period of weeks31. The high spatial resolution of SIMS allows the selective analysis of deposition is concentrated at the skeleton surface, avoiding the centres of calcification where Sr/Ca is anomalously high, and any material which thickens the trabecula and may be deposited a considerable time later32. The accuracy of our SIMS estimates is hindered by uncertainty in the elemental composition of the NaHaxby2 standard, but our analytical precision, which is critical to palaeothermometry, is good (within 0.6%, or 0.018 mmol mol−1, (2σ), equivalent to ±0.4°C).

**Results and Discussion**

**Skeletal Sr/Ca varies with seawater pCO2 in some genotypes.** Coral aragonite Sr/Ca partition coefficients (Kp Sr/Ca = skeletal Sr/Ca/seawater Sr/Ca) are estimated for each coral (Supplementary Table S1). Kp Sr/Ca varies significantly in response to perturbations in seawater pCO2 in both genotypes of P. lutea but is unaffected in P. murrayensis (Fig. 2). Seawater temperatures do not vary significantly between the treatments (Table 1) and we observe excellent agreement (within 0.3%) in the KD Sr/Ca of duplicate sub colonies of the same coral genotype within each treatment (Fig. 2), indicating that minor differences in coral positioning and lighting in each tank do not affect skeletal Sr incorporation. Kp Sr/Ca is significantly increased at high seawater pCO2 compared to ambient in both genotypes of P. lutea (by 4% in genotype 1, and 2% in genotype 2; p < 0.05, ANOVA and Tukey post-hoc). Kp Sr/Ca is also significantly increased (by 4%; p < 0.05) in P. murrayensis genotype 2 at low pCO2 compared to ambient. In contrast, Kp Sr/Ca does not vary significantly between the P. murrayensis sub-colonies cultured over the full seawater pCO2 range.

Two hypotheses have been proposed to explain the impact of seawater pCO2 on coral skeletal Sr/Ca26. Coral aragonite precipitates from an extracellular calcifying fluid enclosed in a semi-isolated space between the coral tissue and underlying skeleton, and corals increase the pH of this fluid (upregulate pH) above that of ambient seawater to promote high fluid aragonite saturation states favourable for skeletal precipitation. The coral calcification fluid is derived from seawater which is transported paracelularly (between cells) to the calcification site and from additional Ca transported transcellularly (across cells) via L-type Ca channels31,34 and the enzyme Ca-ATPase35,36. Enhancing transcellular Ca transport could decrease the Sr/Ca of the calcification fluid. This hypothesis is appealing as corals maintained at high seawater pCO2 are able to upregulate calcification fluid pH more to partially offset the effect of lowered seawater pH36. Ca-ATPase is a Ca2+:H+ antiport which increases the pH of the calcification fluid37 and may be expected to have a higher activity under high seawater pCO2. This hypothesis suggests that coral skeletal Sr/Ca is decreased at high seawater pCO2. However, Sr2+ has a similar ionic radius to Ca2+ and inhibition of Ca channels and Ca-ATPase in the branching coral, Pocillopora damicornis, did not affect skeletal Sr/Ca, suggesting that transmembrane Ca transport does not fractionate Sr/Ca in the calcification fluid38.

Alternatively, skeletal Sr/Ca variations may reflect elemental partitioning during aragonite precipitation (Rayleigh fractionation). Rayleigh fractionation occurs when variable volumes of an isolated fluid reservoir are used for solid precipitation, and a trace element ion (in this case Sr) is either discriminated against or preferentially incorporated compared to the major precipitating ion (in this case Ca). The Sr/Ca partition coefficient in aragonite is ~1.09, so Sr is preferentially incorporated into the growing crystals over Ca40. As precipitation proceeds, the Sr/Ca of the fluid remaining in the reservoir, and of the carbonate subsequently precipitated in it, decreases. The final Sr/Ca of the aragonite reflects the proportion of the reservoir used in precipitation40. The deposition rate of coral aragonite is strongly dependent on the saturation state of the calcifying fluid41,42. At high calcification fluid saturation states, a higher proportion of the fluid reservoir may be used for calcification resulting in a low skeletal Sr/Ca. Although corals at high seawater pCO2 increase the pH of the calcification fluid more than their counterparts cultured at ambient pCO2, they do not ultimately attain such a high fluid pH36 and calcification rates in these corals are usually reduced43. This hypothesis suggests that coral skeletal Sr/Ca will be increased at high seawater pCO2. Neither hypothesis immediately explains our observed pattern of skeletal Sr/Ca...
variations where skeletal Sr/Ca is increased in some corals at both low and high seawater pCO2. However it is unlikely that the two hypotheses operate independently as the saturation state of the calcification fluid is probably highly responsive to Ca-ATPase activity.

Growth rate and skeletal Sr/Ca. We explored the relationship between coral aragonite:seawater Kd Sr/Ca and skeletal growth rate, inferring that Rayleigh fractionation is linked to skeletal precipitation rate. We observe significant differences in both the skeletal extension and calcification rate of some genotypes between treatments (Supplementary Table S2). However, correlation between Kd Sr/Ca and either skeletal linear extension or calcification rate (Supplementary Fig. S1) are insignificant in all coral genotypes (p > 0.3; Pearson's correlation). Our data suggest that variations in Sr incorporation between corals do not reflect Rayleigh fractionation.

Alternative controls on skeletal Sr/Ca. We observe significant variation in skeletal Sr/Ca between different coral genotypes cultured at the same seawater pCO2 (Fig. 3) demonstrating that other factors also influence Sr incorporation. The origin of this is currently unknown. The mucus layer at the coral surface behaves as a Donnan matrix, concentrating Ca2+ from seawater prior to transport across the coral ectoderm tissue44 and matrix variations between corals could conceivably subtly influence the Sr/Ca of seawater transported to the calcification fluid. Organic molecules at the calcification site also play a major role in regulating aragonite nucleation and growth45. Skeletal organic materials differ between coral species46, and may influence skeletal trace element content either because biomolecules impact the incorporation of trace elements in the crystal lattice, or due to direct organic-metal complexing. Understanding the role of these organic templates in fractionating Sr/Ca during calcification, and quantifying differences between coral genotypes even within an individual species, will be a critical step forward in resolving biological influences on skeletal Sr/Ca from the thermal signature.

Implications for SST reconstructions. Our data show that seawater pCO2 can be a significant factor affecting the Sr/Ca of massive tropical coral skeletons frequently used for palaeotemperature reconstruction. Decreasing seawater pCO2 from ambient (416 μatm) to values consistent with the LGM (198 μatm) increases skeletal Sr/Ca by 4% in one of the three coral genotypes. The sensitivity of coral skeletal Sr/Ca to temperature is typically ~0.8–1% °C⁻¹ and the effect of the decrease in seawater pCO2 implies a cooling of 4–5 °C in this single genotype, although all colonies were cultured at the same temperature. The influence of seawater pCO2 on skeletal

Figure 1. Multiple genotypes of massive Porites spp. stained with alizarin. Representative colonies of (a) Porites lutea genotype 1; (b) Porites lutea genotype 2; (c) Porites murrayensis, cultured at ambient pCO2 within our aquarium system. (d) Alizarin stain lines mark skeletal extension during the 5-week experimental period. Scale bars are 1 mm.
Table 1. Summary of the physical and chemical composition of seawater in each culture treatment, measured over the 5-week experimental period. Values are the mean ± 1σ. Dissolved inorganic carbon (DIC) and Total Alkalinity (TA) were used to calculate seawater carbonate system components (pH, pCO2, HCO3−, CO32− and ΩAr) using CO2SYS (Pierrot et al.30), whereby pH is Total scale; K1 and K2 are from Mehrbach et al.61 refit by Dickson and Millero; KSO4 as determined by Dickson.

| Treatment                | Sr/Ca (μmol/ mol) | Temperature (°C) | Salinity | DIC (μmol/kg) | pH | pCO2 (μatm) | HCO3− (μmol/kg) | CO32− (μmol/kg) | ΩAr |
|--------------------------|-------------------|------------------|----------|---------------|----|-------------|----------------|-----------------|-----|
| Last Glacial Maximum     | 12.27 ± 0.09      | 25.3 ± 0.1       | 35.1 ± 0.04 | 2289 ± 14    | 1831 ± 11 | 8.28      | 198            | 1511            | 315     | 5.01 |
| Modern Day               | 12.07 ± 0.03      | 25.2 ± 0.2       | 35.2 ± 0.08 | 2290 ± 8     | 1999 ± 8  | 8.03      | 416            | 1780            | 207     | 3.29 |
| Future (~ Year 2100)     | 11.85 ± 0.03      | 25.1 ± 0.2       | 35.2 ± 0.05 | 2293 ± 5     | 2113 ± 11 | 7.81      | 750            | 1954            | 138     | 2.19 |

Sr/Ca may explain the ‘cold bias’ observed in some fossil corals, which suggest that tropical SSTs at the last or penultimate deglaciations in the Atlantic47 and Pacific48 Oceans were ~6 °C cooler than at present. These estimates contrast with other marine proxies which indicate that SSTs typically cooled by 2–3 °C at most at this time49,50. Proposed variations in seawater Sr/Ca over glacial-interglacial periods are insufficient to explain the ‘cold bias’ observed in coral SST reconstruction20.

We find that the influence of seawater pCO2 on skeletal Sr/Ca is inconsistent between corals, even of the same species, and this prevents the calculation of a correction factor to compensate for past variations in seawater pCO2. Skeletal Sr/Ca is unaffected by pCO2 over the modern-LGM range relevant to paleotemperature reconstruction in two of our cultured genotypes, yet one genotype shows a substantial, and significant response that is observed across duplicate sub-colonies. We are unable to relate the seawater pCO2 effect to coral growth rate indicating that coral extension cannot be used to correct skeletal Sr/Ca for an indirect influence of pCO2 in Porites spp., despite successful application of a growth correction in other coral genera51. Further culture work is required to resolve the relationship between skeletal Sr/Ca and seawater pCO2 across a wider range of coral genotypes, and to identify how seawater pCO2 contributes to ‘cold bias’. At present, the accuracy of absolute tropical past SST estimates from skeletal Sr/Ca of fossil corals is limited by this uncertainty. In contrast, relative changes in annual seawater temperature are usually well preserved in coral skeletal Sr/Ca52 and fossil specimens may yet provide good records of Sr/Ca derived seasonal SST variations which can be used to infer the amplitude of future ENSO53 and interdecadal climate events54. However, it will also be important to quantify in further studies whether skeletal Sr/Ca temperature sensitivity varies between different coral genotypes, and is affected by seawater pCO2.

In this study we hypothesise that inconsistencies in SST reconstructions of the LGM from coral Sr/Ca may be explained by a change in seawater pCO2 between the modern and glacial ocean, equivalent to ~220 μatm. Approximately 50% of this increase in pCO2 towards present day has occurred in the last 150 years as a result of rising greenhouse gas emissions, overlapping with multi-centennial coral Sr/Ca records. Anthropogenic CO2 emissions are isotopically depleted in 13C, and a centennial-scale decrease in the δ13C of surface ocean DIC attributable to rising atmospheric CO2 concentrations is also observed in the skeletal aragonite of >200 year-old corals collected at the end of the 20th century56,57. Between 1850 and 2000, the ~85 μatm increase in atmospheric CO2 is clearly preserved in the carbon isotope ratios of these corals, yet there is no discernible influence on skeletal Sr/Ca5,6. In our culture study, a significant increase in skeletal Sr/Ca was observed at low pCO2 compared to ambient in one of three genotypes, and we may therefore expect some corals to show a decrease in Sr/Ca with rising CO2 over the 20th century. In practice, any CO2 forcing on coral Sr/Ca is likely to be obscured by significant interannual variations in SST caused by ENSO against a global trend of increasing SST56,58. It is also important to

![Figure 2. Influence of seawater pCO2 on coral aragonite:seawater Sr/Ca partition coefficients (Kp Sr/Ca) for 3 genotypes of Porites spp. following acclimation to 198, 416 and 750 μatm pCO2 at 25 °C. Bars represent the mean Kp Sr/Ca of multiple analyses (n = 12–41; see Table S1) across 2 or more skeletal units within individual colonies. Within each species/genotype, different letters indicate significant differences between treatments (p < 0.05; ANOVA and Tukey post-hoc). Error bars represent the combined 95% confidence limits of seawater and skeletal Sr/Ca measurements.](image-url)
bear in mind that 70% of the increase in atmospheric CO2 between 1850 and 2000 occurred in the second half of the twentieth century, so the majority of these multi-centennial coral Sr/Ca records span very small (10–20μatm) changes in pCO2. Longer coral Sr/Ca datasets extending into the 21st century are required to investigate the effect of >100μatm changes in CO2 on in situ skeletal Sr/Ca.

Our study demonstrates that the variations in published skeletal Sr/Ca-SST calibrations between corals of the same species do not necessarily reflect differences in physical (e.g. temperature, light levels and ocean currents) and chemical (e.g. nutrient levels and composition) conditions2. Rather skeletal Sr/Ca varies significantly between coral genotypes even of the same species cultured under the same conditions. Resolving how genotypic variations affect coral biomineralisation and impact skeletal geochemistry is a key target for future research.

Methods

Aquarium System. Culturing experiments were carried out in the marine culturing facility at the Department of Earth & Environmental Sciences, University of St Andrews, UK. Corals were maintained in 21 litre cast acrylic tanks, recirculated from high density polyethylene reservoirs containing ~900 litres of seawater. The reservoirs were bubbled (at 10 L min⁻¹) with gas mixes set to reach the target seawater pCO2 compositions. The modern day treatment was aerated with untreated ambient air. The high and low CO2 treatments were aerated with ambient or low-CO2 air, respectively, combined with high purity CO2 (Foodfresh, BOC, UK). Flow rates of air and CO2 were regulated by high-precision mass flow controllers (SmartTrak 50 Series, Sierra USA) controlled with ambient or low-CO2 air, respectively, combined with high purity CO2 (Foodfresh, BOC, UK). Flow rates of air and CO2 were regulated by high-precision mass flow controllers (SmartTrak 50 Series, Sierra USA) controlled by purpose-written MATLAB® programs. Low-CO2 air was produced by bubbling ambient air through a caustic solution (0.9 M NaOH and 0.1 M Ca(OH)₂) and rinsing it by bubbling through deionised water.59 The [CO2] of the low-CO2 air (before mixing with CO2) was monitored every 2 hours by automated non-dispersive infra-red CO2 analysers (WMA04, PP systems, USA) and ranged from 20–100 μatm depending on the age of the caustic solution. The [CO2] of the low, ambient and high CO2 gas streams (after addition of any CO2) was monitored automatically 3–4 times per day and were 180 ± 3, 400 ± 5 and 761 ± 6 μatm (mean ± 1σ) over the experimental period. Corals were maintained under LED lighting (Maxspect R420R 160w–10000k) on a 12 h light: 12 h dark automatically 3–4 times per day and were 180 ± 3, 400 ± 5 and 761 ± 6 μatm (mean ± 1σ) over the experimental period. Corals were fed weekly with rotifers.

Monitoring Seawater Composition. Dissolved inorganic carbon (DIC) was measured weekly in each reservoir by LI-7000 CO2 differential, non-dispersive, infrared gas analyser (Apollo SciTech; AS-C3). Samples were calibrated against a natural seawater certified reference material (CRM; A. Dickson, Scripps Institution of Oceanography). Internal reproducibility was calculated from the standard deviation of 8 replicate measurements of a single sample (σ/√n), and was always <0.1%. Multiple measurements of the CRM were analysed as unknown samples over the 4 week period to check the calibration, and these were in good agreement with the certified value (unknown = 209 ± 6 (1σ) μmol kg⁻¹, n = 4; CRM = 204 μmol kg⁻¹).

Total alkalinity (TA) was measured twice daily by automated Gran titration (Metrohm, 888 Titrand). Precision of duplicate ~30 ml TA analyses was typically ±2 μequ kg⁻¹. Between days, the precision of multiple measurements of synthetic Na2CO3 standards (1015, 1190, and 1379 μmol kg⁻¹) was consistently ±3 μequ kg⁻¹ (1σ, n = 14, 10 and 8, respectively). The total alkalinity, [Ca] and [Sr] of the culture seawater was maintained by additions of 0.6 M Na2CO3 and a mixture of 0.58 M CaCl₂ + 0.02 M SrCl₂ by 200 μl volume solenoid diaphragm pumps, evenly spaced over a 24 hour period, controlled by a custom-written MATLAB® dosing control program. We adjusted addition rates to maintain total alkalinity within narrow limits (±14 μmol kg⁻¹). Total alkalinity variations of this magnitude have little effect on seawater carbonate chemistry (~0.002 pH units, ~0.6% [DIC]) at constant seawater pCO2.

Seawater samples were collected weekly during the experimental period for Sr and Ca analysis by quadrupole ICP-MS (Thermo Scientific X Series) at the National Oceanography Centre, Southampton. Samples were diluted 1000-fold in 5% HNO₃ (with 5 ppb In as an internal standard) and calibrated against matrix-matched synthetic
standards prepared from 1000 μg ml$^{-1}$ single-element stock solutions (Inorganic Ventures) in 5% HNO$_3$. Based on replicate analyses ($n=4$) of IAPSO standard seawater, external reproducibility ($s/n$) was 0.6% for Sr/Ca. Measured values of Sr/Ca in IAPSO (8.78 ± 0.05 (1σ) mmol mol$^{-1}$) were in excellent agreement with certified values (8.77 mmol mol$^{-1}$).

Nutrients were measured in filtered (Whatman GF/F, ~0.7 μm) seawater samples from each reservoir by flow cell spectrophotometry (Lachat 8000; Scottish Association of Marine Science). Concentrations of NH$_4^+$ (<0.19 ± 0.01 μmol L$^{-1}$, mean ± 1σ), PO$_4^{3-}$ (<0.06 ± 0.00 μmol L$^{-1}$), SO$_4^{2-}$ (<1.3 ± 0.03 μmol L$^{-1}$) and NO$_3^-$ (<0.95 ± 0.02 μmol L$^{-1}$) were within the range reported for pristine reef waters$^{60}$.

**Coral sample processing and SIMS.** Skeletal samples were prepared from the maximum growth axis and fixed in epoxy resin (Epo thin, Struers UK) in 2.5 cm diameter circular moulds, under vacuum. Polished, gold coated sections were analysed using a Cameca imf-4f ion microprobe in the School of Geosciences at the University of Edinburgh ($^{18}$O ion beam accelerated at 10.8 kV; primary beam current = 8 nA; energy off-set = 75 eV; field aperture 1; contrast aperture 2). Trace element data were collected over 8 days, and multiple analyses of a fossil coral aragonite standard, NaHaxby2 (Sr/Ca = 2.87 mmol mol$^{-1}$), were made each day. Calculation of relative ion yields (RIYs) and standardisation of data was performed as in Allison $^{16}$. Internal reproducibility was calculated from ten cycles of a single SIMS analysis (2σ/√10) and was ~0.4% for Sr/Ca. External reproducibility (the precision of ~15 daily analyses on the standard) was 0.6%, or 0.018 mmol mol$^{-1}$ for Sr/Ca. Where significant variations in the RIY for NaHaxby2 were observed between days, instrument drift was distinguished from heterogeneity in the composition of the standard through additional analyses of the same area on a subsequent day. Samples were calibrated against mean standard RIYs, either from daily or weekly analyses depending on this assessment of instrument performance. See Allison et al.$^{16}$ for representative images of skeletal ultrastructure and SIMS analyses pits$^{32}$.

Daily calcification rates (μmol CaCO$_3$ cm$^{-2}$ day$^{-1}$) were estimated for each sub colony from the measured change in seawater TA over an isolation period in the light (5 hours), and the dark (7 hours), on three separate occasions over the experimental period. Linear extension (μm) was measured as the distance between the alizarin stain lines in each analysed trabecula.

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Author Contributions
N.A., A.F. and C.H. designed the study and built the culturing system with K.H. Coral culturing was performed by C.C. and N.A. SIMS was performed by C.C. and N.A. All authors contributed to the analysis of the results and to the writing of the paper.

Additional Information
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