

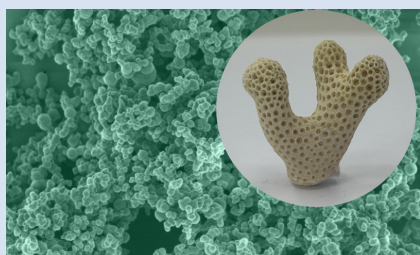
Geochemical constraints on the use of an amorphous precursor phase by corals

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<https://doi.org/10.7185/geochemlet.2623>

Abstract



A growing body of evidence suggests that corals, like many other marine calcifying organisms, may form at least parts of their aragonite skeleton *via* an amorphous calcium carbonate (ACC) or other metastable precursor phase. This is in apparent conflict with our understanding of coral skeletal chemistry, in that most trace element systems can be modelled with just minor modifications to the inorganic aragonite distribution coefficients (*e.g.*, *via* Rayleigh fractionation), whereas ACC, and crystalline CaCO_3 derived from ACC, has a vastly different chemistry. *Via* a simple geochemical model, we show that these observations may be reconciled provided either: i) ACC undergoes near complete dissolution and exchange with the calcifying fluid during crystallisation, and/or ii) skeletogenesis *via* this pathway is of overall minor importance. Comparing the chemical composition of different skeletal components additionally demonstrates that differential degrees of ACC utilisation is unlikely to be the main cause of well documented micro-scale chemical heterogeneity. While important processes remain poorly constrained, in particular the mode and chemical dynamics of ACC crystallisation in biological systems in seawater, our results highlight how biomineral geochemistry can place important constraints on the role of ACC in forming biominerals.

Received 13 March 2026 | Accepted 10 May 2026 | Published 29 June 2026

Introduction

The chemical and isotopic composition of coral aragonite act as important tracers of past environment (*e.g.*, Beck *et al.*, 1992). Many of these proxies have roots in thermodynamics or empirical observations (D'Olive *et al.*, 2019; Gaetani and Cohen, 2006) but their utility is fundamentally limited by 'vital effects' – physiological processes that at least partially decouple skeletal composition from environmental signals and drive species and colony-level variations (Gagnon *et al.*, 2007). While this issue has been known about for as long as biomineral geochemistry has been used in climate reconstruction (Urey *et al.*, 1951), the mechanistic causes remain poorly constrained (Evans *et al.*, 2025).

Skeleton formation in the stony (Scleractinian) corals occurs at the interface between the hard aragonite skeleton and the coral polyp in spaces $\sim 10 \mu\text{m}$ in size, filled with a seawater derived fluid (Ram and Erez, 2025) with a chemistry that is modified to promote CaCO_3 precipitation (Sevilgen *et al.*, 2019). Coral skeletons exhibit considerable μm scale chemical heterogeneity (Standish *et al.*, 2024), and are characterised by two microstructural components: i) rapid accretion deposits known as the centres of calcification (COCs) that are organic-rich, and associated with nucleation of new skeleton and accomplish skeletal extension, and ii) the fibrous aragonite thickening deposits that grow more slowly and are organic-poor (Cuif and Dauphin, 2005).

Recent work has identified a role for amorphous calcium carbonate (ACC) and other metastable precursor phases in the calcification process of corals (*e.g.*, Schmidt *et al.*, 2024), in common with many other marine calcifying organisms

(Gilbert *et al.*, 2022). ACC is broadly characterised by trace element (TE) distribution coefficients (D_X) ~ 1 –2 orders of magnitude higher than aragonite grown by a classical ion-by-ion mechanisms (Fig. 1a; Evans *et al.*, 2020), where:

$$D_X = X/\text{Ca}_{\text{mineral}}/X/\text{Ca}_{\text{seawater}} \quad \text{Eq. 1}$$

and X/Ca is the molar concentration of element X relative to Ca in the mineral or in seawater. As such, the observation of ACC at the growing crystal surface is seemingly at odds with our knowledge of coral skeletal chemistry, because inorganic aragonite precipitated from seawater is compositionally similar to coral aragonite for most trace element systems (Fig. 1b) with only minor modifications to the inorganic partition coefficients. For example, kinetic processes (Gaetani and Cohen, 2006) and Rayleigh fractionation can drive changes in distribution coefficients, in the latter case causing them to trend towards 1 as calcium is utilised in an enclosed reservoir (Fig. 1c; Ram and Erez, 2025). Together, these processes are sufficient to explain the entirety of the offset of most TE systems from the composition of inorganic aragonite, such that the inclusion of ACC – from a geochemical viewpoint alone – at best appears to be an unnecessary complication in modelling coral skeletal chemistry, and may be difficult to align with our understanding of the chemistry of ACC.

A factor that must be considered in reconciling these observations is the way in which the organism produces and utilises the metastable precursor phase. ACC may be produced and stored intracellularly in vacuoles or vesicles before being delivered to the calcification site (as in echinoderms; Vidavsky *et al.*, 2016), or nucleate directly in this enclosed space, either

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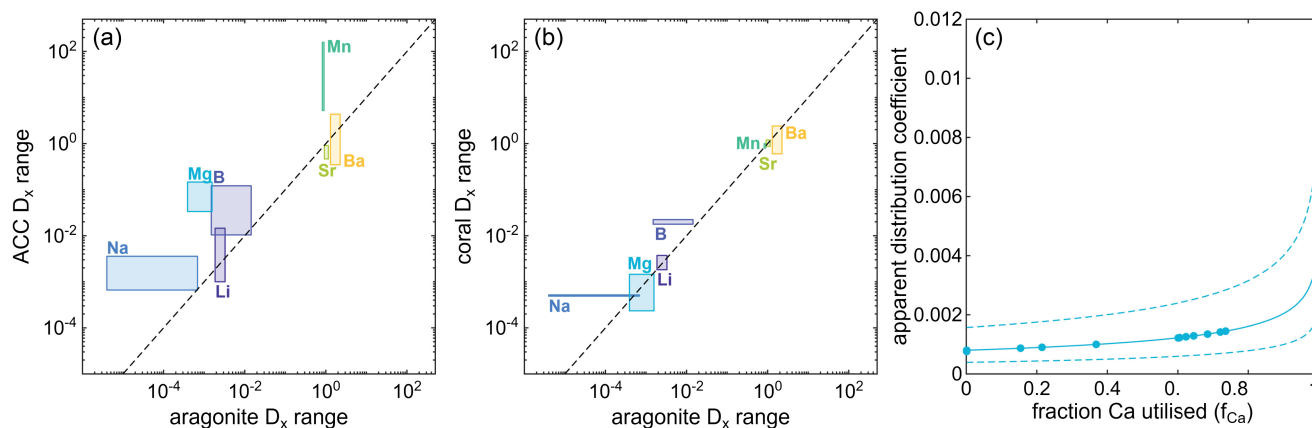


Figure 1 Trace element distribution coefficients in amorphous calcium carbonate (ACC), inorganic aragonite, and coral aragonite, and the impact of Rayleigh fractionation in a closed reservoir on these (see the [Supplementary Information](#) for sources). (a) ACC is characterised by trace element distribution coefficients 1–2 orders of magnitude higher than aragonite in many cases (see [Evans et al., 2020](#) for ACC data and the [Supplementary Information](#) for aragonite data sources). (b) In contrast, inorganic aragonite precipitated from seawater and coral skeletons are characterised by broadly similar distribution coefficient ranges. (c) A Rayleigh fractionation model demonstrates that the composition of many corals (circles) can be reconciled with the inorganic distribution coefficient and moderate degrees of Ca utilisation.

homogeneously or on/in the vicinity of the growing biomineral surface. In both cases, crystallisation may proceed either *via* a dissolution-reprecipitation reaction ([Giuffrè et al., 2015](#)) or solid state transformation ([Jantschke and Scholz, 2025](#)). Where a given biomineral falls between these end member possibilities will strongly impact the chemistry of the resulting crystal, as will the degree to which crystallisation takes place in a localised environment with a chemistry dominated by ACC dissolution rather than that of the average composition of the calcification site ([Branson et al., 2025](#)). In the case that ACC is delivered to and fully dissolved into the fluid at the calcification site, the amorphous phase would drive skeletal composition only *via* the degree to which this process modifies the bulk chemistry of this space. In contrast, if it is formed directly at the crystal surface and transformed without any further exchange, the biomineral would have a composition more similar to ACC.

[Sun et al. \(2020\)](#), principally on the basis of crystallographic observations, proposed that coral biomineralisation could occur *via* both ACC attachment and be ‘space filling’ *via* subsequent ion-by-ion growth. Geochemical data can place some unambiguous constraints on the dynamics of this process. For example, that coral aragonite does not have a composition similar to ACC, even on a micrometre scale ([Standish et al., 2024](#)), suggests that solid state ACC crystallisation cannot be more than a minor process during the formation of any skeletal component. However, this leaves a wide range of possibilities in terms of the extent to which ACC could modulate coral skeletal chemistry.

We assess how aragonite formation *via* an ACC precursor phase might be reconciled with coral skeletal composition by evaluating a simple geochemical model using a compilation of coral trace element data. We focus on the following key questions: 1) Can the compositional similarity between coral and inorganic aragonite be reconciled with precipitation *via* ACC? 2) Does the relative contribution of ACC crystallisation *versus* ion-by-ion growth play a role in driving the observed chemical differences between the COC and fibre regions?

Including an ACC Phase in a Simple Coral Model

We interpret published skeletal trace element data ([Table S-1](#)) within the context of a simple, two stage Rayleigh distillation

model designed to mimic key coral biomineralisation processes (see the [Supplementary Information](#)). We assume that the calcification site (extracellular calcifying fluid; ECF) contains seawater, and that the composition of this fluid is modified only *via* the delivery and (partial) dissolution of ACC, which is formed in a separate, enclosed space. We recognise this is a simplification as ion transport (*e.g.*, *via* Ca^{2+} ATPase) is not included. However, this would have only a minor impact on our findings given that ECF $[\text{Ca}^{2+}]$ measurements are typically close to seawater values ([Al-Horani et al., 2003](#)). The model is centred on the case that ACC is formed in vesicles or vacuoles before delivery to the ECF ([Sun et al., 2020](#)), but our results are insensitive to this assumption (see the [SI](#)). Both the ACC and aragonite precipitation steps incorporate Rayleigh distillation ([Ram and Erez, 2025](#)), and we make the simplifying assumption that the ECF is otherwise fully replenished, *i.e.* this is not a steady state model that considers the effect of the rate of seawater *versus* ACC transport as a variable. The ACC/seawater ratios in the ECF were modelled over wide ranges, with ACC completely dissolving at low ACC/seawater ratios (10^{-2} to 10^0 mg/mL). Beyond this range we assume some portion of the ACC undergoes solid state transformation upon attachment, which is linearly varied from 0 % at 10^0 mg/mL to complete solid state transformation at 10^1 mg/mL. The rationale for these two conditions is that at low ACC/seawater ratios, ACC would readily dissolve as the ECF is characterised by a saturation state lower than the solubility product of ACC ([Purgstaller et al., 2019](#)). At higher ratios, ACC is sufficiently stable that solid state transformation may become important. While we do not know the point at which the crystallisation mechanism may change, our key findings are insensitive to this choice, and we explore alternative models in which ACC undergoes complete dissolution at all ACC/seawater ratios in the [SI](#).

The Impact of ACC on Coral Skeletal Chemistry

Modelled skeletal Sr/Ca is shown as an example in [Figure 2](#), for a wide range of possible degrees of calcium utilisation (*i.e.* Rayleigh distillation) and ECF ACC/seawater ratios. For this system, the model predicts minor changes in Sr/Ca for a wide range of both parameters, which is because aragonite D_{Sr} is close to 1, making the model insensitive to Rayleigh fractionation, and ACC D_{Sr} is sufficiently close to 1 ([Fig. 1a](#)) that moderate degrees

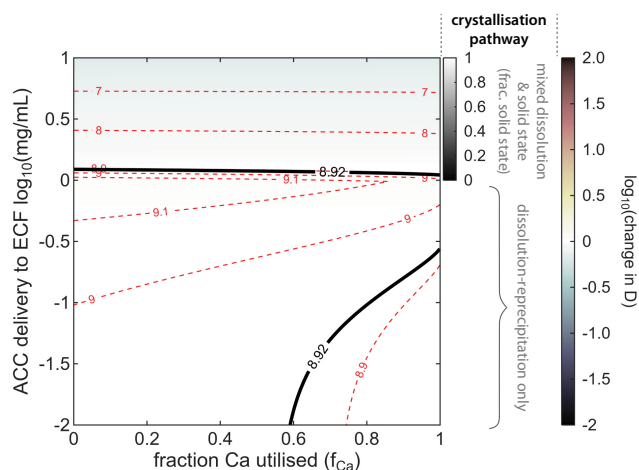


Figure 2 The impact of ACC delivery to the calcification site on coral Sr/Ca. Contours show predicted skeletal Sr/Ca in mmol/mol for a given degree of ACC transport to the calcification site and Rayleigh fractionation (f_{Ca} , the proportion of the Ca in a compartment that is consumed), assuming that the inorganic aragonite distribution coefficient otherwise applies. Panel colour shows the predicted change in the apparent distribution coefficient relative to the case of no ACC delivery (where e.g., a value of -1 would indicate a predicted distribution coefficient 1 order of magnitude lower than that had no ACC been present). The model assumes that ACC is fully dissolved and reprecipitated at low ACC/seawater ratios but undergoes increasing degrees of solid state crystallisation at higher ratios, as the solubility limit of ACC is reached (left hand colour bar). The black line shows the mean symbiotic coral fibre Sr/Ca based on our data compilation (Table S-1), indicating a range of parameter space can explain these data.

of ACC delivery do not substantially alter the ECF Sr/Ca. Only in the region of the model space in which solid state crystallisation dominates (ACC/seawater $> 10^0$) does the predicted Sr/Ca substantially decrease, driven by the lower ACC D_{Sr} . The model therefore demonstrates that the hypothetical average coral in our compilation can be modelled using a wide range of these parameters (black line in Fig. 2).

Figure 3 expands this analysis to include five other commonly analysed or informative trace element systems. Here, the panels are coloured with the change in the ‘apparent’ measured distribution coefficient between the coral skeleton and surrounding seawater compared to the case of no ACC involvement. For example, a change in $\log_{10}D$ of 1 indicates an apparent distribution coefficient 1 order of magnitude higher for a given set of model parameters, relative to the case that no ACC is present. This exercise demonstrates that while skeletal chemistry should be measurably sensitive to these factors, the overall magnitude of change across the parameter range is small in most cases (Li, Na, Sr, Ba). Therefore, dissolution of ACC in the ECF up to ratios of 10^0 mg/mL is readily reconcilable with observed coral skeletal composition (*i.e.* ~ 40 % of the skeleton formed from Ca delivered *via* ACC), and we therefore show that coral chemistry – in broad terms – is not in conflict with a biomineralisation model in which ACC is a key component.

The above result is similarly the case for Mg, up to the point that ACC undergoes solid state transformation or reprecipitation in a highly localised environment. Here, very minor degrees of ACC inclusion (*i.e.* a few percent) drive large changes in the predicted distribution coefficient, because ACC D_{Mg} is 2 orders of magnitude higher than that of aragonite (Evans *et al.*, 2020; Gaetani and Cohen, 2006). As such, while it is possible to reconcile large amounts of dissolved ACC with skeletal

geochemistry, it is not possible to reconcile coral Mg/Ca with substantial degrees of solid state or localised crystallisation. Given that ACC and/or other metastable phases have been observed attached to the growing edge of coral skeletons (Mass *et al.*, 2017; Schmidt *et al.*, 2024), coral Mg/Ca requires either that this process is of minor importance, or that ACC exchange with the ECF during crystallisation is efficient and near complete. In addition, we note that while skeletal chemistry may be reconciled with large degrees of ACC dissolution, direct measurements of ECF carbonate chemistry constrain ACC delivery to the lower part of the range modelled here, *e.g.*, 10^0 mg/mL ACC (~ 35 % of skeletal Ca from ACC) would result in ECF DIC ~ 2 – $3\times$ that of direct observations (Sevilgen *et al.*, 2019).

Can ACC Explain Heterogeneity between Skeletal Components?

The average trace element composition of COCs and fibres in the same specimen is systematically offset across a wide number of species (Fig. 4a,b, Table S-1), with COCs characterised by Mg/Ca and Sr/Ca ~ 30 % and ~ 5 % higher, respectively, albeit with considerable inter-species/sample variability. We explore whether these offsets can be explained by COC formation being characterised by different degrees of calcium utilisation, ACC delivery, or precipitation rate, by extracting 2 D planes from the models shown in Figure 3. For example, the hypothesis that the COC/fibre offset may be explained by a greater degree of calcium utilisation (f_{Ca} , the fraction of the Ca in a compartment that has been consumed) can be tested by extracting and plotting modelled Mg/Ca and Sr/Ca values across the full range of f_{Ca} . In doing so (Fig. 4c, dark blue line) it becomes clear that a change in this process could result in large changes in skeletal Mg/Ca, but cannot explain the observed COC/fibre Sr/Ca differences, because Sr/Ca is very insensitive to Rayleigh distillation (Fig. 2). Assessing the impact of ACC delivery and crystallisation by performing the same exercise in the perpendicular direction in model space (teal line in Fig. 4c) similarly demonstrates that the COC/fibre Mg/Ca offset may be explained by a greater degree of ACC during COC formation, but that differential degrees of solid state ACC crystallisation alone cannot explain the majority of the variance in the Sr/Ca data, as Sr/Ca is an insensitive tracer of ACC as the distribution coefficient is similar in ACC and aragonite.

Moreover, we note that while differential contributions of ACC to the COC and fibre regions could conceivably explain some of the intra-skeletal coral heterogeneity, the predicted direction of this effect is inconsistent between the two elemental systems: an ACC contribution *via* solid state crystallisation, which would be required to explain the observed increase in Mg/Ca, results in a minor Sr/Ca decrease (teal line, Fig. 4c), whereas COCs in fact have higher Sr/Ca in most cases (Fig. 4a,b). Further work is required to resolve this, in particular, better knowledge of the degree to which aragonite crystallised from ACC retains an ACC chemical signature; if ACC can be dissolved and reprecipitated even at very high ACC/seawater ratios, this process could explain much of the Sr/Ca variance (dashed line, Fig. 4c), although this would be at odds with our understanding of ECF chemistry more broadly. While ACC may ultimately represent an important piece of the puzzle (Schmidt *et al.*, 2024), we note that the kinetic rate effect on Mg and Sr incorporation into aragonite (Gaetani and Cohen, 2006; Zhong and Mucci, 1989) acts in both the right direction and is of approximately the right magnitude to explain much of the observed COC/fibre offsets (black arrow, Fig. 4c). Coupled with a moderate degree of ACC delivery and dissolution (< 1 mg/mL, *i.e.* < 40 % of skeletal Ca from ACC dissolution), which additionally acts to

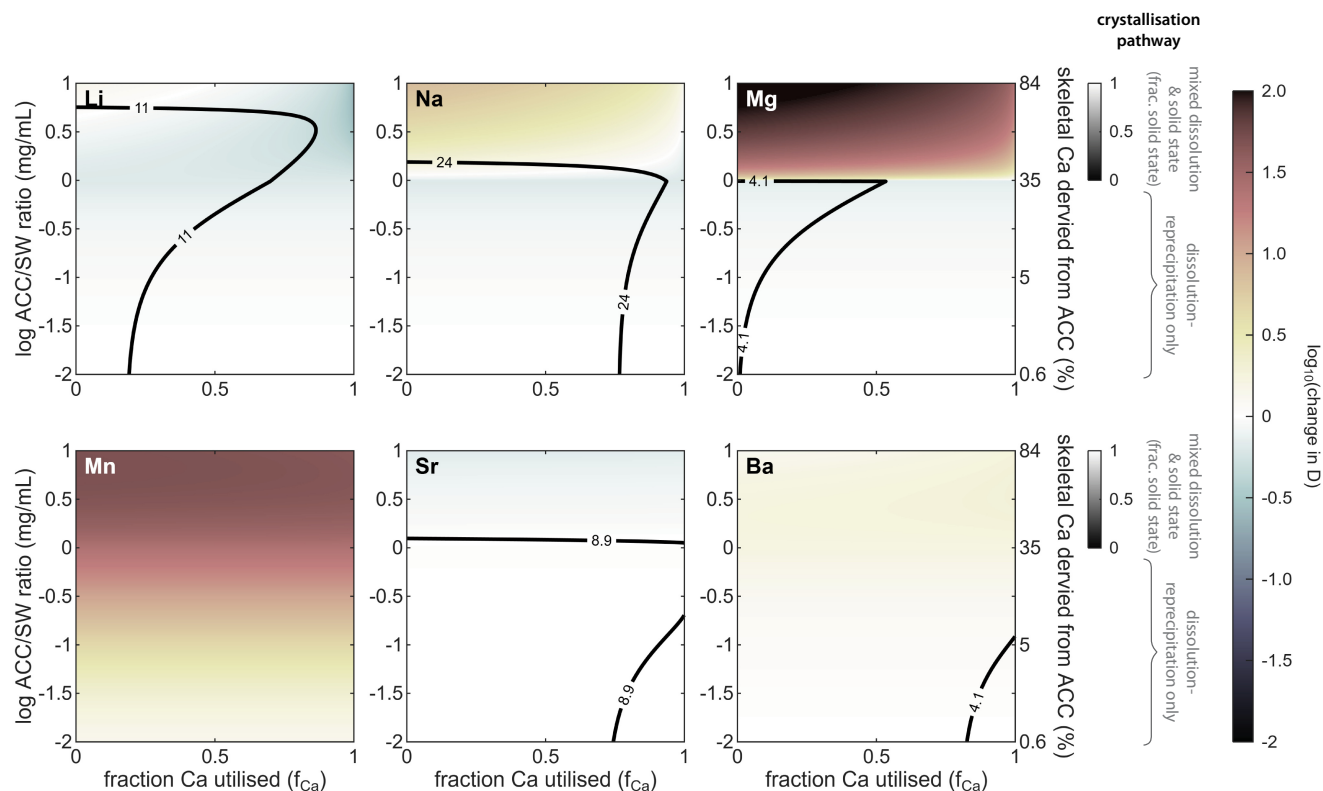


Figure 3 The change in apparent distribution coefficient for a given degree of ACC delivery and Rayleigh fractionation for a suite of commonly analysed trace elements in coral skeletons, relative to the case that no ACC is delivered to the calcification site but an equivalent degree of Rayleigh fractionation. The black lines show the location of the average fibre measurement of all symbiotic corals in our compilation (Table S-1). Most systems (Li, Na, Sr, Ba) have a minor sensitivity to the inclusion of ACC in a trace element model like this, either because the concentration of the element in ACC is very low (Li, Na), or because the ACC and aragonite distribution coefficients are broadly similar (Sr, Ba). In contrast, Mg is a sensitive tracer of the involvement of ACC if crystallisation is a localised or solid state process ($\log_{10}(\text{ACC}/\text{SW}) > 10^0$). Note that for all systems except Mn, no substantial change in the apparent distribution coefficient is expected at low to moderate degrees of ACC delivery. Mn is in contrast a sensitive tracer of ACC, notable because any degree of ACC transport results in a model that predicts higher D_{Mn} than the (sparse) data (see Fig. 1b) under the assumption of the inorganic distribution coefficients used here.

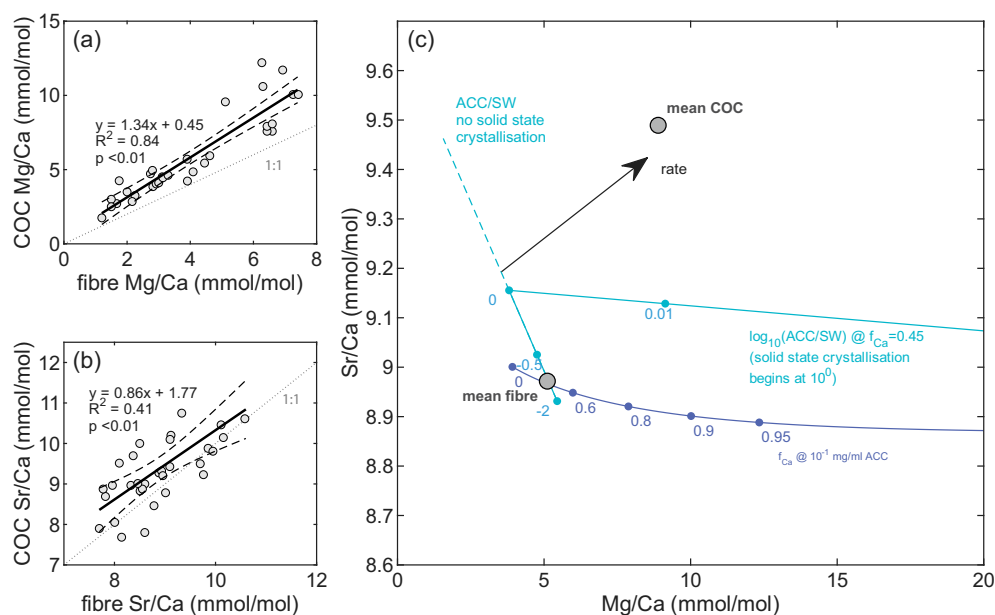


Figure 4 The relationship between COC and fibre Mg/Ca and Sr/Ca, and possible drivers. COC and fibre (a) Mg/Ca and (b) Sr/Ca between samples/species are strongly correlated, with most COC measurements offset to higher values. Least squares linear regressions and 95 % CI are shown in both cases. (c) Mean COC and fibre Mg/Ca and Sr/Ca are offset by ~ 4 and ~ 0.5 mmol/mol, respectively. The trajectories of Rayleigh fractionation and differential degrees of ACC delivery are overlain, to explore whether change in these processes can explain the different compositions of these skeletal components. While both can explain the higher COC Mg/Ca (the length of the trajectories is greater than the COC/fibre difference), neither can explain the Sr/Ca data. Instead, the trajectory of the kinetic rate effect on Mg and Sr incorporation (black arrow; Gaetani and Cohen, 2006; Mavromatis et al., 2022) suggests that this is the principal driver.

increase Sr/Ca but not Mg/Ca, COC chemistry may be overall more parsimoniously ascribed to a faster precipitation rate (Brahmi *et al.*, 2012).

In conclusion, we show that minor to moderate amounts of ACC delivery to the ECF (~0.01–1 mg/mL, equivalent to ~1–40 % of skeletal Ca) can be reconciled with coral skeletal chemistry, despite the very different chemical composition of ACC and aragonite, provided that either the majority of this ACC undergoes complete dissolution and/or exchange with the bulk ECF. In contrast, if solid state transformation or localised reprecipitation of ACC is the main mechanism by which ACC contributes to calcification, then only ~1 % of skeletal Ca derived from ACC can be reconciled with coral aragonite. If correct, this suggests that even if coral skeletogenesis involves ACC, the physiochemical conditions within the ECF remain the key driver of coral skeletal growth, as it is this that controls the dissolution/ reprecipitation process. However, major gaps in our knowledge remain, with resolving the style of ACC crystallisation and the chemistry of intermediate phases key to comprehensively and mechanistically understanding skeletal chemistry.

Acknowledgements

The model code is available in the [Supplementary Information](https://zenodo.org/records/20701444) and at <https://zenodo.org/records/20701444>.

We thank Tom DeCarlo and two anonymous reviewers for their comments and Eric Oelkers for his editorial handling that together greatly improved this manuscript. GLF was supported in this work by Horizon Europe ERC Advanced Grant #884650 (Microns2Reefs). DE acknowledges support from the Royal Society (award reference UFR1\221735) and UKRI (UKRI Frontier Research Guarantee Proposal (Horizon Europe ERC Starting Grants Guarantee), award reference EP/Y034252/1).

Editor: Eric Oelkers

Additional Information

Supplementary Information accompanies this letter at <https://www.geochemicalperspectivesletters.org/article2623>.



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Cite this letter as: Foster, G.L., Evans, D. (2026) Geochemical constraints on the use of an amorphous precursor phase by corals. *Geochem. Persp. Let.* 40, 56–61. <https://doi.org/10.7185/geochemlet.2623>

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Geochemical constraints on the use of an amorphous precursor phase by corals

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Supplementary Information

The Supplementary Information includes:

- Rayleigh Distillation Model Description
- Data Sources Used to Perform the Calculations
- Model Code
- Table S-1
- Figures S-1 and S-2
- Supplementary Information References

Rayleigh Distillation Model Description

The model presented in the main text can be represented algebraically as follows. The Rayleigh distillation equation for the final aragonite precipitation step is written as:

$$D = (1 - f_{Ca}^{\alpha}) / (1 - f_{Ca}) \quad (\text{Eq. S-1})$$

where D is the ‘apparent’ distribution coefficient of the biomineral relative to seawater, f_{Ca} is the fraction Ca utilised, and α is the open system inorganic distribution coefficient. To include an ACC precursor step, the equation must be modified to account for the dissolution-reprecipitation of ACC. This is principally because calcium is greatly concentrated in solid phases, which means that the delivery of minor amounts of ACC to the calcifying space could greatly increase the seawater $[Ca^{2+}]$ once it is dissolved (e.g. 1 mg of ACC dissolved in 1 ml of seawater would result in an approximately doubled $[Ca^{2+}]$). To our knowledge, there are no constraints on the rate at which ACC is delivered to the calcifying space in organisms that utilise this pathway. As such, we modify Eq. S-1 to include the calcification site ACC/seawater ratio as an unknown, which allows the resulting apparent distribution coefficients in biogenic aragonite to be modelled as a function of both this ratio and the fraction Ca utilised in the subsequent calcite precipitation:

$$D = (1 - f_{Ca}^{\alpha}) / (1 - f_{Ca}) \cdot (X/Ca_{ECF}) / (X/Ca_{SW}) \quad (\text{Eq. S-2})$$

where X/Ca_{ECF} and X/Ca_{SW} are the molar trace element/Ca ratios at the calcification site and in seawater respectively. The element/Ca ratio of the calcification site can be calculated by determining the degree to which the trace element concentration is modified by ACC delivery, by multiplying the molar ACC element/Ca ratio by the amount of ACC delivered, and adding this to the existing concentration from seawater transport, by expanding as follows:

$$D = (1 - f_{Ca}^{\alpha}) / (1 - f_{Ca}) \cdot (([TE_{SW}] + r_{ACC-SW} \cdot D_{ACC} \cdot X/Ca_{SW}) / [Ca_{ECF}]) / (X/Ca_{SW}) \quad (\text{Eq. S-3})$$

where $[TE_{SW}]$ is the trace element concentration in seawater, r_{ACC-sw} is the ratio of ACC/seawater in the calcifying space, D_{ACC} are the empirically derived ACC trace element distribution coefficients (derived from inorganic precipitation experiments), X/Ca_{sw} is the molar trace element/Ca ratio in seawater, and $[Ca_{ECF}]$ is the calcification site $[Ca^{2+}]$. Because we model this as a two-stage process, two Rayleigh distillation models must be produced, one for the aragonite precipitation step (Eq. S-1), and one for the ACC precipitation step. As such, D_{ACC} in Eq. S-3 modifies the ACC values given by Evans *et al.* (2020) as follows:

$$D_{ACC} = (1 - f_{Ca}^{\beta}) / (1 - f_{Ca}) \quad (\text{Eq. S-4})$$

where β are the empirical ACC distribution coefficients. We use $f_{Ca} = 0$ for the ACC precipitation step for simplicity in the absence of any information regarding its likely value, and note that this choice has no material impact on our results (see Fig. S-1). Combining Eqs. S-3 and S-4 gives predicted apparent distribution coefficients for biogenic aragonite in three-dimensional $f_{Ca-aragonite}$ - f_{Ca-ACC} - r_{ACC-sw} space where $f_{Ca-aragonite}$ and f_{Ca-ACC} are the fraction Ca utilisation during the aragonite and ACC precipitation step respectively.

ACC dissolution is likely to take place only up to certain ACC/seawater ('water/rock') ratios because beyond a certain point, partial ACC dissolution will result in a calcification site oversaturated with respect to the remaining solid phase, which would then be stabilised. We do not know that solubility of biogenic ACC, but by analogy to inorganically precipitated ACC from seawater, seawater becomes oversaturated with respect to ACC at $[Ca^{2+}][CO_3^{2-}]$ products of $\sim 100 \text{ mM}^2$ (Evans *et al.*, 2019). For this reason, we smoothly transition between complete ACC dissolution-reprecipitation at (and below) $ACC/seawater = 10^0 \text{ mg/ml}$ (equivalent to an ECF $[CO_3^{2-}]$ approaching 10 mM) and complete solid state crystallisation, i.e., no cation exchange with the ECF, at $ACC/seawater = 10^1 \text{ mg/ml}$. While this latter choice is arbitrary, the threshold for the point at which only solid state crystallisation occurs impacts our results only in expanding or shrinking the portion of the parameter space with $ACC/seawater > 10^0 \text{ mg/ml}$.

Data Sources Used to Perform the Calculations

The data reported in the supplementary table and displayed in main text Fig. 4A,B can be found in the following references: (Allison and Finch, 2004, 2007; Allison *et al.*, 2005; Brahmi *et al.*, 2012; Case *et al.*, 2010; Chen *et al.*, 2022; Cohen *et al.*, 2001; Cuif and Dauphin, 1998; Fietzke and Wall, 2022; Gagnon *et al.*, 2007; Jurikova *et al.*, 2019; Meibom *et al.*, 2004, 2006; Rollion-Bard and Blamart, 2015; Schleinkofer *et al.*, 2019; Sinclair and Risk, 2006; Standish *et al.*, 2024).

The model described above uses inorganic aragonite trace element distribution coefficient data from the following references: (Castillo Alvarez *et al.*, 2025; Fuger *et al.*, 2019; Gaetani and Cohen, 2006; Gvirtzman *et al.*, 1973; Holcomb *et al.*, 2016; Okumura and Kitano, 1986; Raiswell and Brimblecombe, 1977).

Model Code

The model code (.mlx) is available for download from the online version of this article at <https://doi.org/10.7185/geochemlet.2623>.

Supplementary Table

Table S-1 A compilation of coral skeletal data used to compare to our model results.

Table S-1 (.xlsx) is available for download from the online version of this article at <https://doi.org/10.7185/geochemlet.2623>.

Supplementary Figures

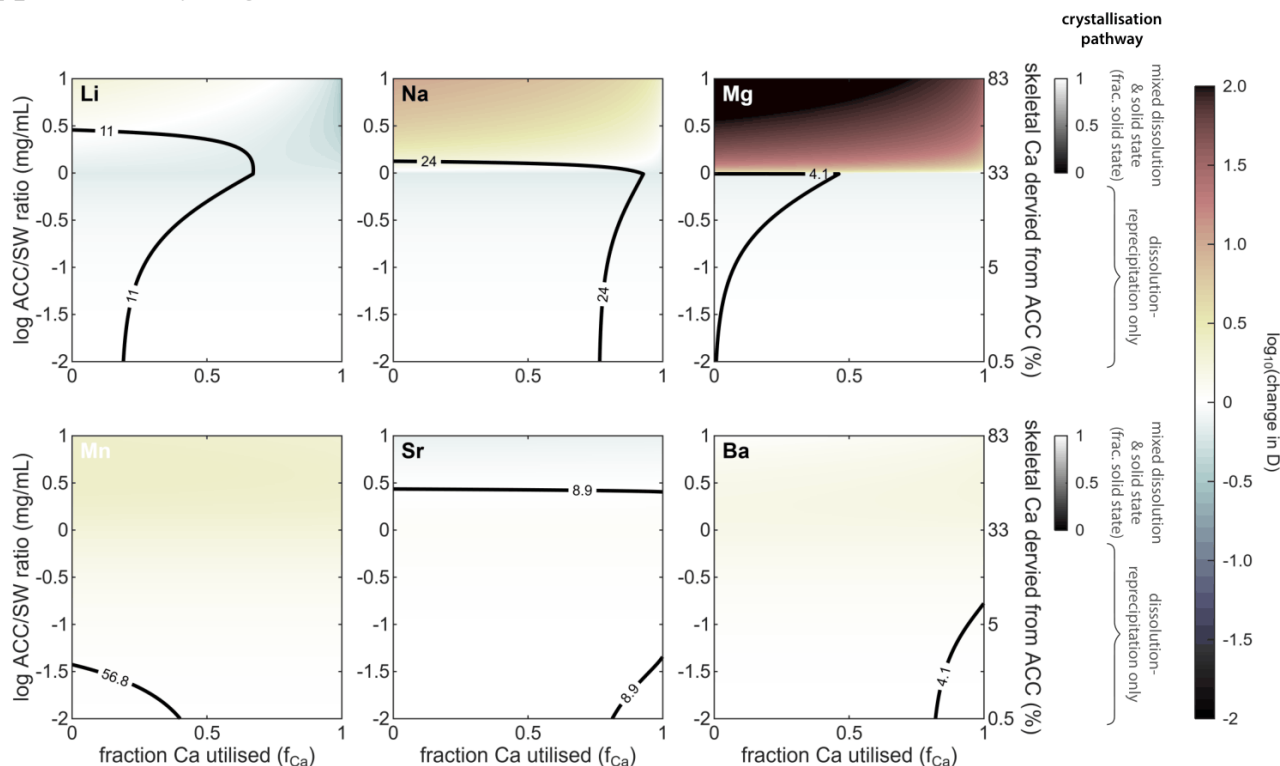


Figure S-1 As main text Fig. 3, except assuming $f_{Ca} = 0.5$ rather than $f_{Ca} = 0$ during the ACC precipitation step.

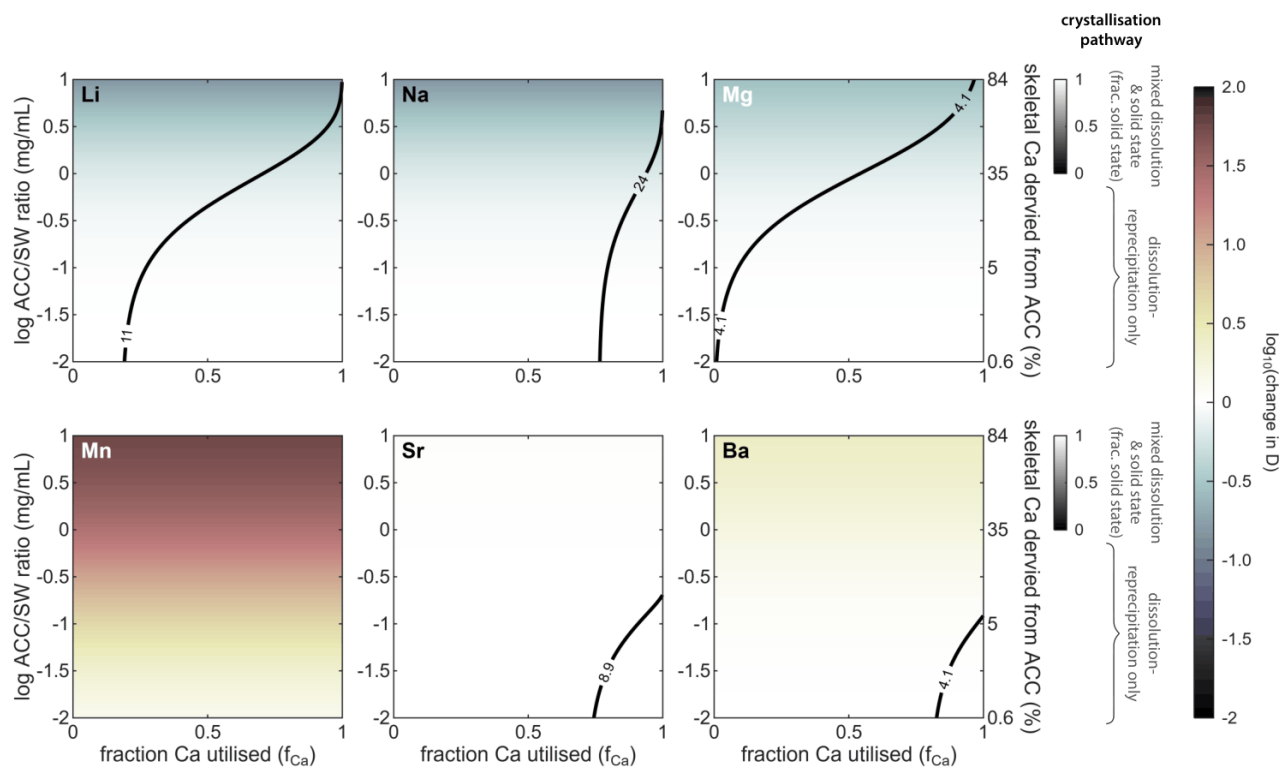


Figure S-2 As main text Fig. 3, except alternatively assuming that ACC undergoes complete dissolution-reprecipitation at all ACC/seawater ratios (our preferred model discussed in the main text switches to solid state transformation above 10^0 mg/ml ACC/seawater). All trace element systems except Mn remain insensitive to ACC delivery up to substantial degrees of ACC transport ($\sim 10^0$ mg/ml).

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