JGR Biogeosciences

RESEARCH ARTICLE
10.1029/2021JG006574

Mineral Components of Scleractinian Coral Skeletons Cultured Without Symbionts

S. Motai[1,2], J. Kawano[3], S. Harii[4], Y. Seto[5], T. Watanabe[3], and T. Nagai[3]

[1]Kochi Institute for Core Sample Research, Japan Agency for Marine-Earth Science and Technology, Kochi, Japan, [2]Now at Faculty of Science, Yamagata University, Yamagata, Japan, [3]Department of Earth and Planetary Sciences, Faculty of Science, Hokkaido University, Sapporo, Japan, [4]Sesoko Station, Tropical Biosphere Research Center, University of the Ryukyus, Okinawa, Japan, [5]Department of Planetology, Graduate School of Science, Kobe University, Kobe, Japan

Abstract Skeletons of contemporary reef-building scleractinian corals are formed of aragonite, a polymorph of the calcium carbonate ($CaCO_3$), notwithstanding calcite being a more stable phase under the condition of coral habitats. Circumstances developing aragonite in coral calcification have been addressed currently. Considering that the symbiotic relationship between the coral host and dinoflagellate algae (zooxanthellae) is perhaps relevant to coral calcification, we studied the impact of these symbiotic relationships on $CaCO_3$ polymorph selection. Juvenile scleractinian corals (*Acropora tenuis* and *Acropora digitifera*) absent symbionts were cultured in seawaters with varied Mg/Ca molar ratios (*m*Mg/Ca), and the mineral phases of the skeletons were detected employing X-ray diffraction. The findings revealed that diminutive quantities of calcite precipitated as coral skeleton in *Acropora digitifera* surprisingly in pseudo-present seawater (*m*Mg/Ca∼5). Additionally, coral developed skeletons from only calcite in seawater with an *m*Mg/Ca < 1. The evidence gathered in this investigation suggests that the symbiotic relationship affects the establishment of aragonite skeletons in the course of coral calcification.

Plain Language Summary Skeletons of contemporary reef-building corals are made of calcium carbonate. The calcium carbonates have polymorphs: calcite, aragonite, and vaterite. Aragonite is a component of coral skeletons, but calcite can thermodynamically precipitate more easily than aragonite in the living conditions of corals. Circumstances resulting in aragonite precipitation in coral calcification have been addressed recently. Considering that the symbiotic relationship between the coral host and dinoflagellate algae is perhaps relevant to coral calcification, we studied the impact of these symbiotic relationships on aragonite precipitation. Juvenile scleractinian corals without symbionts were cultured in seawater with varied Mg/Ca molar ratios to evaluate the effects of mineral component differences resulting from Mg/Ca molar ratio on calcium carbonate polymorphs. The mineral phases of the skeletons were identified using an X-ray diffraction. The findings revealed that small quantities of calcite precipitated as coral skeleton in pseudo-present seawater (Mg/Ca molar ratio of ∼5). Additionally, coral developed skeletons from only calcite in seawater with an Mg/Ca molar ratio of <1. The evidence gathered in this investigation suggests that the symbiotic relationship affects the establishment of aragonite skeletons in the course of coral calcification.

Key Points:

- Reef-building corals build their skeletons using calcium carbonate in aragonite form, which is thermodynamically less stable than calcite
- Corals build entirely calcitc skeletons in artificial seawater with low Mg/Ca ratio without a symbiotic relationship with zooxthantellae
- A symbiotic relationship involves $CaCO_3$ polymorph selection in coral calcification

Supporting Information:

Supporting Information may be found in the online version of this article.

Correspondence to:

S. Motai,
motai@sci.kj.yamagata-u.ac.jp

Citation:

Motai, S., Kawano, J., Harii, S., Seto, Y., Watanabe, T., & Nagai, T. (2022). Mineral components of scleractinian coral skeletons cultured without symbionts. *Journal of Geophysical Research: Biogeosciences*, *127*, e2021JG006574. https://doi.org/10.1029/2021JG006574

Received 13 AUG 2021
Accepted 2 FEB 2022

Author Contributions:

Conceptualization: S. Motai
Data curation: J. Kawano, T. Nagai
Funding acquisition: S. Motai
Investigation: S. Motai
Methodology: S. Motai, J. Kawano, S. Harii, Y. Seto, T. Watanabe, T. Nagai
Resources: S. Harii
Software: Y. Seto
Supervision: T. Nagai
Writing – original draft: S. Motai
Writing – review & editing: J. Kawano, S. Harii, T. Watanabe, T. Nagai

1. Introduction

The exoskeletons of modern scleractinian corals consist of aragonite, despite the fact that among $CaCO_3$ polymorphs, aragonite is not as thermodynamically stable as calcite in environments of coral habitats. Some conditions are proposed to be influencing polymorph selection in coral calcification. Among them is the Mg/Ca molar ratio (*m*Mg/Ca) in seawater. When $CaCO_3$ precipitates abiotically from an aqueous solution, the *m*Mg/Ca impacts polymorph selection; aragonite (calcite) precipitates from solutions with high (low) *m*Mg/Ca (Davis et al., 2000; Kitano, 1962). Biotic precipitation exhibits a comparable trend; fluctuation of the *m*Mg/Ca (0.5–5.2) of seawater throughout the Phanerozoic has been involved with aragonite and calcite biotic precipitation transition (Horita et al., 2002; Lowenstein et al., 2001; Stanley & Hardie, 1998; Timofeeff et al., 2006). In the current seawater with the *m*Mg/Ca = 5.2, scleractinian corals develop aragonite skeletons. Conversely, it was noted that several Late Cretaceous (∼70 Ma) corals formed calcite skeletons in the seawater with the low *m*Mg/Ca of ∼1 (Stolarski et al., 2007). Yet in such seawater with the *m*Mg/Ca of ∼1, other corals established aragonite skeletons (Janiszewska et al., 2017; Sorauf, 1999). Likewise, research endeavoring to construct symbiotic coral skeletons in synthetic seawater have demonstrated that aragonite is continuously a significant phase in coral skeletons

in *m*Mg/Ca ranges of 0.5–5.2 (Higuchi et al., 2014; Ries, 2010; Ries et al., 2006). To explicate the presence of calcite skeletons grown in seawater with an *m*Mg/Ca of ∼1, there needs to be some components besides the *m*Mg/Ca to influence $CaCO_3$ polymorph selection.

Temperature potentially modifies the abiotic precipitation of $CaCO_3$ polymorphs from a liquid (Balthasar & Cusack, 2015); culture tests of corals have illustrated that calcite is a major phase when symbiotic corals reared in seawater at *m*Mg/Ca ≤ 1.0 and 19°C (Higuchi et al., 2017). However, environmental conditions with low *m*Mg/Ca and temperatures for calcitic skeleton construction would be difficult habitats of symbiotic corals in natural environment, even during the Cretaceous period, because symbiotic corals favor tropical and subtropical regions, with temperatures ranging from 23°C to 29°C (NOAA, 2021).

$CaCO_3$ polymorph selection governed by taxa-specific biomineralization was proposed as a different mechanism for varying skeletal mineralogy because fossil calcitic and aragonitic corals delineated separate taxa (traditional caryophyllid coral *Coelosmilia* and basal-scleractinian *Micrabacia*, Janiszewska et al., 2017; Stolarski et al., 2007). To determine this prospect, research is needed, such as whether the coral in the identical taxa forms both aragonite and calcite.

Symbiotic relationships of corals with dinoflagellate algae called zooxanthellae (*Symbiodinium* spp.), which substantially transform coral metabolism, additionally impact biomineralization proceedings (e.g., Frankowiak et al., 2016). Thus, we insinuate that algae-coral symbiosis may additionaly persuade $CaCO_3$ polymorph selection. To examine this hypothesis, we cultured aposymbiotic scleractinian juveniles (*Acropora* spp.) in seawater with different *m*Mg/Ca at room temperature. *Acropora tenuis and Acropora digitifera* were the same species employed in earlier investigations culturing symbiotic corals with zooxanthellae (Higuchi et al., 2014; Ries et al., 2006) and now utilized further in this inspection to evade potential taxon-specific consequences. Skeletal mineralogical characteristics of the cultured aposymbiotic corals were defined using X-ray diffraction (XRD) to scrutinize the task of symbiotic relationships at the time of calcification.

2. Materials and Methods

Acropora tenuis and *Acropora digitifera* corals were collected prior to the expected spawning date from the north of Sesoko Island, Okinawa, in 2014. These species were selected because they produce eggs without symbionts (horizontal transmitters), and it is easy to manipulate their juveniles without symbionts (Baird et al., 2009; Harii et al., 2009). The samples were kept in outdoor tanks at the Sesoko Station, Tropical Biosphere Research Center, University of the Ryukyus. After spawning, the gametes of each species were collected and mixed for indoor fertilization and the fertilized eggs of each species were placed in separate containers filled with filtered seawater (0.22 μm) from the Sesoko reef until the planula larval stage. Seawater of the containers was replaced daily.

The planulae larvae were placed in filtered seawater to isolate them from symbionts for 4 days. These planulae larvae were gradually acclimated to seawater with various *m*Mg/Ca ranging from 0.6 to 5.2 (Table 1), for another 4 days. Details about the seawater are provided in Text S1 and Table S1 in the Supporting Information S1.

The artificial peptides (Hym-248) were added to each seawater type, and the final peptide concentration in the seawater treatment was approximately 1×10^{-6} M (Iwao et al., 2002) for larval metamorphosis and settlement on plastic containers. The larvae settled within 12 hr of the addition of Hym-248, and they were then maintained at 24°C–26°C for 8 days. Seawater treatments were replaced daily during culture. The containers with polyps were kept indoors with indirect sunlight and a fluorescent lamp which would be turned off at night. No food was supplied to the polyps due to the short experiment period, because their larvae can settle almost 2 months without foods (Nishikawa et al., 2003).

After primary polyp culture, samples were soaked in tap water and then in liquid sodium hypochlorite for more than 1 hr to remove organic materials from the surface of the coral skeleton. Samples were then cleaned several times using distilled water, dried at ∼25°C, and collected from the plastic containers using a brush tip. Skeletal frameworks were first viewed beneath an optical microscope, and then the most structurally undamaged skeleton from each group in a given *m*Mg/Ca seawater treatment was selected for establishing the $CaCO_3$ polymorph utilizing an X-ray diffractometer (MicroMax-007 HF; Rigaku Co., Ltd.; MoKα; $\lambda = 0.7107$ Å). To produce a sample reflection against the incident X-ray beam collimated to <100 μm, the stage was rotated around the vertical axis. The rotation angle was adjusted for each sample. The two-dimensional diffraction intensity data were

Table 1
Concentrations of Ca and Mg, mMg/Ca in Seawater, and Features of Coral Skeletons

			Acropora tenuis		*Acropora digitifera*	
Ca (mmol/l)	Mg (mmol/l)	*m*Mg/Ca	Calcite wt ratio	Average skeletal weight (μg)	Calcite wt ratio	Average skeletal weight (μg)
21.33 (26)	13.41 (16)	0.63 (1)	1.00	35.71 (n = 16)	1.00	34.43 (n = 9)
19.81 (33)	17.33 (30)	0.87 (2)	1.00	35.96 (n = 18)	0.51	40.17 (n = 11)
9.42 (4)	13.96 (13)	1.52 (2)	0.04	34.48 (n = 18)	0.56	48.54 (n = 21)
10.82 (16)	21.95 (11)	2.03 (3)	0.21	54.55 (n = 2)	0.03	41.38 (n = 15)
14.87 (38)	35.27 (99)	2.37 (9)	0.04	41.82 (n = 20)	0.08	52.43 (n = 21)
10.20 (30)	27.64 (108)	2.71 (13)	0.00	40.09 (n = 7)[a]	0.07	49.86 (n = 19)[a]
13.08 (31)	41.51 (115)	3.17 (12)	0.00	51.64 (n = 16)	0.01	68.83 (n = 23)[a]
9.82 (16)	34.44 (95)	3.51 (11)	0.00	32.50 (n = 1)	0.07	50.51 (n = 18)
10.37 (5)	51.68 (107)	4.98 (11)	0.00	52.72 (n = 12)	0.02	54.91 (n = 37)

Note. The numbers in parentheses for Ca, Mg, and *m*Mg/Ca are standard deviations.
[a]Skeletal weights between values with superscript character "a" and the values of groups with less *m*Mg/Ca are significantly different on the basis of Tukey–Kramer honestly significant difference test ($P < 0.05$).

integrated along Debye–Sherrer rings and converted to conventional one-dimensional intensity data using IPAnalyzer software (Seto et al., 2010). The XRD data was examined by the Rietveld method to approximately suggest the proportionate weight ratios of aragonite and calcite in the skeletons, using the GSAS-II program (Toby & Von Dreele, 2013). The values of ratio were rouded to the nearest hundredth, because XRD has a detection limit of ∼1% by volume in general and standard deviation of these analysis were less the third decimal places. Details about the quantitative phase analysis are provided in Text S2 and Figure S1 in the Supporting Information S1. Each skeleton was weighed employing an electronic microscale (Mettler UMT2, 0.001 mg accuracy, Mettler-Toledo) to compare them with the calcite appearance (Table 1). The Tukey–Kramer test was conducted to compare the differences in growth rates among treatments.

3. Results

The skeletons of juvenile corals lacking symbiotic algae cultured under different *m*Mg/Ca are displayed in Figure 1. All aposymbiotic corals developed a standard skeletal composition including a basal plate, skeletal branches, and six-fold symmetry (i.e., common characteristics connected with those symbiotic corals). They also preserved their skeletal structures throughout growth in seawater with *m*Mg/Ca ranging from 0.6 to 5.0.

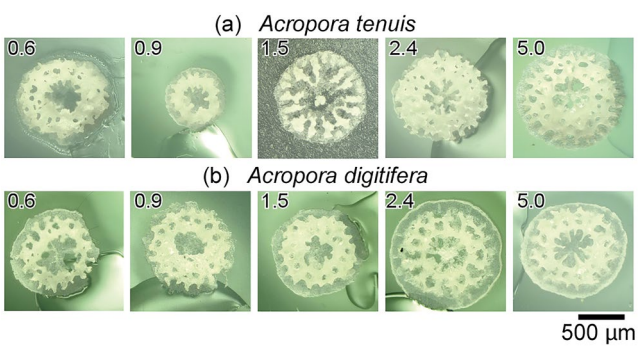

Figure 1. Optical microscope images of (a) *Acropora tenuis* and (b) *Acropora digitifera*. The values displayed at the top left corner of each image are the *m*Mg/Ca of the treatment seawater.

XRD patterns suggested that the skeletons were comprised of aragonite and/or calcite (Figure 2). Generally, a $CaCO_3$ polymorph can be identified by employing two aragonite peaks that appear at 2θ of ∼12.0° and a calcite peak at 2θ of ∼13.5°. Aragonite peaks were evident in the XRD spectra of the skeletons of *Acropora tenuis* and *Acropora digitifera* when *m*Mg/Ca were in the ranges of 1.5–5.0 and 0.9–5.0, respectively (Figures 2a and 2b). However, calcite peaks emerged in *Acropora tenuis* at *m*Mg/Ca < 2.4 and in *Acropora digitifera* at *m*Mg/Ca ranging from 0.6 to 5.0. It is recognized that the aposymbiotic corals formed completely calcitic skeletons at *m*Mg/Ca < 1.0 in *Acropora tenuis* and <0.6 in *Acropora digitifera*. Quantitative analysis of a $CaCO_3$ polymorph by XRD indicated that the calcite ratios rose with diminishing *m*Mg/Ca below 2. The skeletal weight seemed to steadily decrease as the *m*Mg/Ca decreased regardless of the calcite emergence, and the significant decrease of skeletal weight exactly respond to increase ratio of calcite was not detected using Tukey–Kramer test (Table 1), although the presence of calcite might provoke the loss of the skeletal weight (Higuchi et al., 2014).

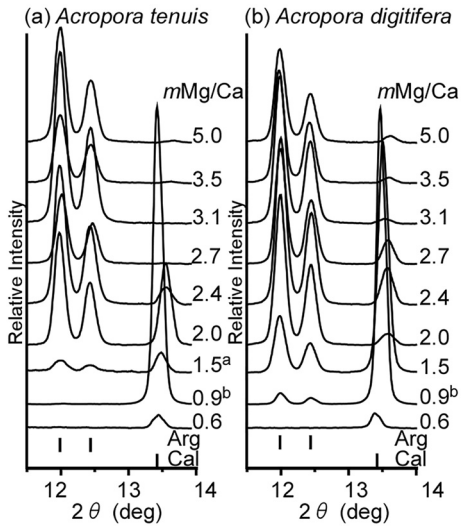

Figure 2. X-ray diffraction (XRD) patterns for coral skeletons cultured in various *m*Mg/Ca seawaters. (a and b) are one-dimensional XRD patterns for *Acropora tenuis* and *Acropora digitifera*, respectively. Intensities of the patterns with (a and b) are scaled at ×2 and ×0.5, respectively, for easier visibility. Positions pointed out by the short, vertical lines below the XRD profiles show where peaks would usually appear for aragonite and calcite. Arg: aragonite, Cal: calcite.

4. Discussion

Juvenile aposymbiotic corals created aragonite skeletons at elevated *m*Mg/Ca ($\gtrsim$3), calcite skeletons at *m*Mg/Ca $\lesssim$ 1, and blended aragonite and calcite skeletons at *m*Mg/Ca > 1 and $\lesssim$3. The culture examination of a symbiotic coral illustrated that calcite, in addition to aragonite, occurs at *m*Mg/Ca $\lesssim$ 2 and their skeletons are comprised of more than half weight aragonite at *m*Mg/Ca between 0.5 and 5.2 (*Acropora tenuis*; Higuchi et al., 2014). Additionally, abiotic $CaCO_3$ chemical deposition from $CaCl_2$-$MgCl_2$-NaCl-$NaCO_3$aq in imitation seawater at 25°C displayed solely aragonite precipitated at *m*Mg/Ca > 2.2, just calcite precipitated at an *m*Mg/Ca < 0.5, and aragonite and calcite co-precipitated at *m*Mg/Ca ranging from 0.5 to 2.2 at 25°C (Balthasar & Cusack, 2015). In contrast with these conclusions, the relationship between the mineral assembly of aposymbiotic coral skeletons and *m*Mg/Ca, which was established in this research, was more comparable to that of abiotic chemical depositions than that of the symbiotic corals. This indicates that the *m*Mg/Ca of seawater more heavily impacts polymorph selection in aposymbiotic corals than symbiotic corals. A discrepancy is anticipated in the *m*Mg/Ca between ambient seawater and the coral calcification space because coral calcification occurs in tiny calcification spaces filled with the so-called "calcification medium", which are separated from seawater by coral tissue itself and their action of modifing the calcification medium (Clode & Marshall, 2003; Johnston, 1980; Tambutté et al., 2007); therefore, minor variations in the *m*Mg/Ca range at which aragonite and calcite appear as abiotic chemical deposits and aposymbiotic coral skeletons are conceivable.

Aposymbiotic coral formed complete calcitic skeletons at *m*Mg/Ca $\lesssim$ 1.0 in this investigation, while symbiotic corals shaped primarily aragonitic skeletons at the equivalent *m*Mg/Ca (Higuchi et al., 2014), in juvenile *Acropora* spp. Such various mineral assembly of the skeletons at the equal *m*Mg/Ca implies some element impacted polymorph selection apart from the *m*Mg/Ca and the taxa-specific consequence, as formerly announced (Higuchi et al., 2014; Janiszewska et al., 2017). The main difference in these studies is the existence or nonexistence of symbiotic relationship. Although further experiments comparing skeletons of primary polyps which grow with symbiotic or aposymbiotic under the same conditions are needed to make a more precise conclusion, a possible interpretation is that the symbiotic relationship between corals and zooxanthellae likely promotes the physiological biomineralization of corals and encourages the structure of aragonite skeletons. One achievement of this may be allowing the coral to be tolerant to changes in its encompassing habitats, such as through the symbiotic relationship (Ohki et al., 2013). Ries et al. (2006) and Higuchi et al. (2014) proposed that aragonite-forced organic matrices create the potential for symbiotic corals to form aragonitic skeletons in calcitic sea conditions (*m*Mg/Ca < 2.0). Organic matrices heterogeneously implanted in coral skeletons may be practicable templates for aragonite nucleation (Cuif et al., 2003). On the other hand, soluble organic matrices extracted from coral skeletons of *Acropora digitifera* may inhibit aragonite growth (Falini et al., 2013). Symbiotic algae might contribute to the production of organic matrices that shape aragonitic polymorphic $CaCO_3$ phase selection and/or counteract the effects of inhibiting aragonite growth, though further experiments considering both of the function of organic matrix and presence or absence symbiont in coral calcification are needed for revealing the detail function of symbionts.

The length of culturing should be also be taken into consideration as a factor affecting polymorph selection of $CaCO_3$. In this research, we cultured aposymbiotic corals for 8 days, conversely, Higuchi et al. (2014) cultured symbiotic corals with aragonitic skeleton for 2 months; moreover, Vandermeulen and Watabe (1973) and Gilis et al. (2014) recorded trace amounts of calcite in the skeletons of *Pocillopora damicornis* grown with zooxanthellae over 3 days. Calcite seems to possibly precipitate at the earliest coral calcification stage rather than during the adult stage. This might be related to the amount of calicoblasts, which are cells involved in the production of skeletons and are abundance in primary polyps as compared to adults (Levy et al., 2021). On the other hand, the modern aposymbiotic screractinian coral *Paraconotrochus antarcticus* forms a matured skeleton comprising

calcite and aragonite in the Southern ocean (Stolarski et al., 2021). The absence of a symbiotic relationship may assist in the precipitation of calcite in mature coral, in addition to the taxa-specific affecting polymorph selection in calcification and the unexpected influence of its temperature (0.5°C–3°C in the Southern ocean) exceeding the range observed in previous studies discussing the influence of temperature on polymorph selection (Balthasar & Cusack, 2015; Higuchi et al., 2014). These might insinuate immature symbiotic relationships in the course of the beginning calcification stage. Thus, this investigation proffered that the symbiotic relationship is a prospective feature affecting polymorph selection in coral skeletons.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

Data sets for this research are included in this paper and its Supporting Information S1 (Table 1, Figure 1, Table S1 in the Supporting Information S1). Data associated with skeletal weight and micro-XRD (Table 1, Figure 2, Figure S1 in the Supporting Information S1) are available open access via the figshare repository at https://doi.org/10.6084/m9.figshare.15140904.

Acknowledgments
We thank K. Ohmori for assisting with ICP-AES measurements, K. Sowa for help in caring for the cultured corals, K. Nagao for access to the electronic microscale and K. Komatsu and H. Kagi for assistance with micro-XRD and measurements. This work was supported by JSPS KAKENHI (Grant Nos. 17K17671, 17J07874).

References

Baird, A. H., Guest, J. R., & Willis, B. L. (2009). Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 551–571. https://doi.org/10.1146/annurev.ecolsys.110308.120220

Balthasar, U., & Cusack, M. (2015). Aragonite-calcite seas—Quantifying the gray area. *Geology*, *43*(2), 99–102. https://doi.org/10.1130/G36293.1

Clode, P. L., & Marshall, A. T. (2003). Skeletal microstructure of galaxea fascicularis exsert septa: A high-resolution SEM study. *Biological Bulletin*, *204*(2), 146–154. https://doi.org/10.2307/1543550

Cuif, J. P., Dauphin, Y., Doucet, J., Salome, M., & Susini, J. (2003). XANES mapping of organic sulfate in three scleractinian coral skeletons. *Geochimca et Cosmochimica Acta*, *67*(1), 75–83. https://doi.org/10.1016/S0016-7037(02)01041-4

Davis, K. J., Dove, P. M., & De Yoreo, J. J. (2000). The role of Mg^{2+} as an impurity in calcite growth. *Science*, *290*(5494), 1134–1137. https://doi.org/10.1126/science.290.5494.1134

Falini, G., Reggi, M., Fermani, S., Sparla, F., Goffredo, S., Dubinsky, Z., et al. (2013). Control of aragonite deposition in colonial corals by intra-skeletal macromolecules. *Journal of Structural Biology*, *183*(2), 226–238. https://doi.org/10.1016/j.jsb.2013.05.001

Frankowiak, K., Kret, S., Mazur, M., Meibom, A., Kitahara, M. V., & Stolarski, J. (2016). Fine-scale skeletal banding can distinguish symbiotic from asymbiotic species among modern and fossil scleractinian corals. *PLoS ONE, Advance online publication*, *11*(1), e0147066. https://doi.org/10.1371/journal.pone.0147066

Gilis, M., Meibom, A., Domart-Coulon, I., Grauby, O., Stolarski, J., & Baronnet, A. (2014). Biomineralization in newly settled recruits of the scleractinian coral *Pocillopora damicornis*. *Journal of Morphology*, *275*(12), 1349–1365. https://doi.org/10.1002/jmor.20307

Harii, S., Yasuda, N., Rodriguez-Lanetty, M., Irie, T., & Hidaka, M. (2009). Onset of symbiosis and distribution patterns of symbiotic dinoflagellates in the larvae of scleractinian corals. *Marine Biology*, *156*(6), 1203–1212. https://doi.org/10.1007/s00227-009-1162-9

Higuchi, T., Fujimura, H., Yuyama, I., Harii, S., Agostini, S., & Oomori, T. (2014). Biotic control of skeletal growth by scleractinian corals in aragonite–calcite seas. *PLoS ONE, Advance online publication*, *9*(3), e91021. https://doi.org/10.1371/journal.pone.0091021

Higuchi, T., Shirai, K., Mezaki, T., & Yuyama, I. (2017). Temperature dependence of aragonite and calcite skeleton formation by a scleractinian coral in low mMg/Ca seawater. *Geology*, *45*(12), 1087–1090. https://doi.org/10.1130/G39516.1

Horita, J., Zimmermann, H., & Holland, H. D. (2002). Chemical evolution of seawater during the Phanerozoic: Implications from the record of marine evaporites. *Geochimica et Cosmochimica Acta*, *66*(21), 3733–3756. https://doi.org/10.1016/S0016-7037(01)00884-5

Iwao, K., Fujisawa, T., & Hatta, M. (2002). A cnidarian neuropeptide of the GLWamide family induces metamorphosis of reef-building corals in the genus Acropora. *Coral Reefs*, *21*(2), 127–129. https://doi.org/10.1007/s00338-002-0219-8

Janiszewska, K., Mazur, M., Escrig, S., Meibom, A., & Stolarski, J. (2017). Aragonitic scleractinian corals in the Cretaceous calcitic sea. *Geology*, *45*(4), 319–322. https://doi.org/10.1130/G38593.1

Johnston, I. S. (1980). The ultrastructure of skeletogenesis in hermatypic corals. *International Review of Cytology*, *67*, 171–214. https://doi.org/10.1016/S0074-7696(08)62429-8

Kitano, Y. (1962). The behavior of various inorganic ions in the separation of calcium carbonate from a bicarbonate solution. *Bulletin of the Chemical Society of Japan*, *35*(12), 1973–1980. https://doi.org/10.1246/bcsj.35.1973

Levy, S., Elek, A., Grau-Bové, X., Menéndez-Bravo, S., Iglesias, M., Tanay, A., et al. (2021). A stony coral cell atlas illuminates the molecular and cellular basis of coral symbiosis, calcification, and immunity. *Cell*, *184*(11), 2973–2987. e18. https://doi.org/10.1016/j.cell.2021.04.005

Lowenstein, T. K., Timofeeff, M. N., Brennan, S. T., Hardie, L. A., & Demicco, R. V. (2001). Oscillations in Phanerozoic seawater chemistry: Evidence from fluid inclusions. *Science*, *294*(5544), 1086–1088. https://doi.org/10.1126/science.1064280

Nishikawa, A., Katoh, M., & Sakai, K. (2003). Larval settlement rates and gene flow of broadcast-spawning (*Acropora tenuis*) and planula-brooding (*Stylophora pistillata*) corals. *Marine Ecology Progress Series*, *256*, 87–97. https://doi.org/10.3354/meps256087

NOAA (National Oceanic and Atmospheric Administration) (2021). National Ocean Service website: In what types of water do corals live? Retrieved from https://oceanservice.noaa.gov/facts/coralwaters.html

Ohki, S., Irie, T., Inoue, M., Shinmen, K., Kawahata, H., Nakamura, T., et al. (2013). Calcification responses of symbiotic and aposymbiotic corals tonear-future levels of ocean acidification. *Biogeosciences*, *10*(11), 6807–6814. https://doi.org/10.5194/bg-10-6807-2013

Ries, J. B. (2010). Review: Geological and experimental evidence for secular variation in seawater Mg/Ca (calcite-aragonite seas) and its effects on marine biological calcification. *Biogeosciences*, *7*(9), 2795–2849. https://doi.org/10.5194/bg-7-2795-2010

Ries, J. B., Stanley, S. M., & Hardie, L. A. (2006). Scleractinian corals produce calcite, and grow more slowly, in artificial Cretaceous seawater. *Geology*, *34*(7), 525–528. https://doi.org/10.1130/G22600.1

Seto, Y., Nishio-Hamane, D., Nagai, T., & Sata, N. (2010). Development of a software suite on X-ray diffraction experiments. *The Review of High Pressure Science and Technology*, *20*(3), 269–276. https://doi.org/10.4131/jshpreview.20.269

Sorauf, J. E. (1999). Skeletal microstructure, geochemistry, and organic remnants in Cretaceous scleractinian corals: Santonian Gosau Beds of Gosau, Austria. *Journal of Paleontology*, *73*(6), 1029–1041. https://doi.org/10.1017/S0022336000030961

Stanley, S. M., & Hardie, L. A. (1998). Secular oscillations in the carbonate mineralogy of reef-building and sediment-producing organisms driven by tectonically forced shifts in seawater chemistry. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *144*(1–2), 3–19. https://doi.org/10.1016/S0031-0182(98)00109-6

Stolarski, J., Coronado, I., Murphy, J. G., Kitahara, M. V., Janiszewska, K., Mazur, M., et al. (2021). A modern scleractinian coral with a two-component calcite–aragonite skeleton. *Proceedings of the National Academy of Sciences*, *118*(3). https://doi.org/10.1073/pnas.2013316117

Stolarski, J., Meibom, A., Przenioslo, R., & Mazur, M. (2007). A Cretaceous scleractinian coral with a calcitic skeleton. *Science*, *318*(5847), 92–94. https://doi.org/10.1126/science.1149237

Tambutté, E., Allemand, D., Zoccola, D., Meibom, A., Lotto, S., Caminiti, N., & Tambutté, S. (2007). Observations of the tissue-skeleton interface in the scleractinian coral *Stylophora pistillata*. *Coral Reefs*, *26*(3), 517–529. https://doi.org/10.1007/s00338-007-0263-5

Timofeeff, M. N., Lowenstein, T. K., da Silva, M. A. M., & Harris, N. B. (2006). Secular variation in the major-ion chemistry of seawater: Evidence from fluid inclusions in Cretaceous halites. *Geochimica et Cosmochimica Acta*, *70*(8), 1977–1994. https://doi.org/10.1016/j.gca.2006.01.020

Toby, B. H., & Von Dreele, R. B. (2013). GSAS-II: The genesis of a modern open-source all purpose crystallography software package. *Journal of Applied Crystallography*, *46*(2), 544–549. https://doi.org/10.1107/S0021889813003531

Vandermeulen, J. H., & Watabe, N. (1973). Studies on reef corals. I. Skeleton formation by newly settled planula larva of *Pocillopora damicornis*. *Marine Biology*, *23*, 47–57. https://doi.org/10.1007/BF00394111

References From the Supporting Information

Markgraf, S. A., & Reeder, R. J. (1985). High-temperature structure refinements of calcite and magnesite Sample. *American Mineralogist*, *70*(5–6), 590–600.

Negro, A. D., & Ungaretti, L. (1971). Refinement of the crystal structure of aragonite. *American Mineralogist*, *56*(5–6), 768–772.