Scleractinian corals produce calcite, and grow more slowly, in artificial Cretaceous seawater

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ABSTRACT

The mineralogies of most biotic and abiotic carbonates have alternated in synchroneity between the calcite (hexagonal) and aragonite (orthorhombic) polymorphs of $CaCO_3$ throughout the Phanerozoic Eon. These intervals of calcite and aragonite production, or calcite seas and aragonite seas, are thought to be caused primarily by secular variation in the molar magnesium/calcium ratio of seawater (mMg/Ca > 2 = aragonite + high-Mg calcite; mMg/Ca < 2 = low-Mg calcite), a ratio that has oscillated between 1.0 and 5.2 throughout the Phanerozoic. In laboratory experiments, we show that three species of scleractinian corals, which produce aragonite in modern seawater and which have flourished as important reef builders primarily during aragonite seas of the past, began producing calcite in artificial seawater with an ambient mMg/Ca ratio below that of modern seawater (5.2). The corals produced progressively higher percentages of calcite and calcified at lower rates with further reduction of the ambient mMg/Ca ratio. In artificial seawater of imputed Late Cretaceous composition (mMg/Ca = 1.0), which favors the precipitation of the calcite polymorph, scleractinian corals produced skeletons containing $>30\%$ low-Mg calcite (skeletal mMg/Ca < 0.04). These results indicate that the skeletal mineral used by scleractinian corals is partially determined by seawater chemistry. Furthermore, slow calcification rates, resulting from the production of largely aragonitic skeletons in chemically unfavorable seawater (mMg/Ca < 2), probably contributed to the scleractinians' diminished reef-building role in the calcite seas of Late Cretaceous and early Cenozoic time.

Keywords: scleractinian corals, calcification, calcite seas, aragonite seas, biomineralization, seawater Mg/Ca, reef building.

INTRODUCTION

Modern scleractinian corals produce skeletons exclusively from the orthorhombic polymorph of calcium carbonate ($CaCO_3$) known as aragonite (Cuif et al., 1999; Cohen and McConnaughey, 2003). Scleractinians have functioned as major reef builders since the beginning of the Oligocene epoch (Frost, 1981), the approximate time when the mMg/Ca ratio of seawater rose above 2 (Hardie, 1996; Lowenstein et al., 2003), into the domain that favors nonskeletal precipitation of aragonite and high-Mg calcite (Fig. 1). Scleractinians arose and assumed a major reef-building role during the Triassic Period, which occupied an earlier aragonite sea interval that lasted until Middle Jurassic time (Stanley, 1988). They flourished despite elevated atmospheric CO_2, which is estimated to have been as much as an order of magnitude higher than that of the present for Late Triassic through Early Cretaceous time (Royer et al., 2001).

Scleractinians persisted as dominant reef builders into the Cretaceous (Stanton and Flü-gel, 1987; Höfling and Scott, 2002). However, in mid-Cretaceous time, after the mMg/Ca of seawater had descended into the calcite domain and approached its lowest Phanerozoic level ($\sim$1) (Fig. 1), scleractinians relinquished their role as major carbonate producers to taxa of rudist bivalves, whose shells consisted largely of calcite at that time (Kauffman and Johnson, 1988; Scott et al., 1990; Steuber, 2002). Thus, scleractinians have conformed to the generalization that throughout Phanerozoic time, hermatypic organisms with $CaCO_3$ skeletons have tended to be most successful in reef building when the Mg/Ca ratio of seawater has favored their predominant skeletal mineral polymorph (Stanley and Hardie, 1999).

To explore the effect of ambient seawater Mg/Ca on coral biomineralization, we grew colonies of three scleractinian coral species representing two families (*Acropora cervicornis* and *Montipora digitata* [Acroporidae]; *Porites cylindrica* [Poritidae]) in artificial seawaters formulated over the range of mMg/Ca

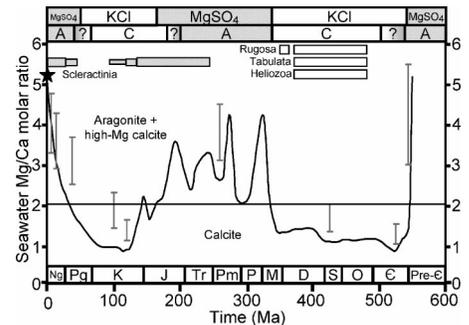**Figure 1. Secular variation in Mg/Ca ratio of seawater and mineralogy of major reef-building corals throughout Phanerozoic. Vertical bars are mMg/Ca ranges estimated from fluid inclusions in marine halites (Lowenstein et al., 2003). Curve is mMg/Ca calculated from brine–magma–river water flux model (Hardie, 1996) and is generally consistent with alternative models that incorporate dolomitization (Holland, 2005). Star represents modern seawater chemistry (mMg/Ca = 5.2). Distribution and polymorph mineralogy of major reef-building corals are represented by horizontal bars (gray = aragonite, white = calcite) (Stanley and Hardie, 1999). Aragonitic scleractinian corals were important reef builders during aragonite seas. Calcitic rugosan, tabulate, and heliozoan corals were important reef builders during Paleozoic calcite seas. Horizontal line is divide between calcite (mMg/Ca <2) and aragonite + high-Mg calcite (mMg/Ca >2) nucleation fields in seawater at 25 °C (Given and Wilkinson, 1985). Temporal distributions of nonskeletal aragonite ("A") and calcite ("C") marine precipitates (Sandberg, 1983) and KCl and $MgSO_4$ marine evaporites (Hardie, 1996) are plotted along top of figure; high Mg/Ca ratios and low concentrations of Ca relative to SO_4 at point of gypsum saturation result in coupling of aragonite precipitates and $MgSO_4$ evaporites, respectively.**

ratios to which the Scleractinia were subjected since their origin in the Triassic (1.0–5.2; Hardie, 1996; Lowenstein et al., 2003). The results indicate that scleractinian coral calcification is significantly affected by ambient seawater chemistry, suggesting that the role of the Scleractinia as major reef builders at various times in the Mesozoic and Cenozoic may have been determined, in part, by secular variation in the Mg/Ca ratio of seawater.
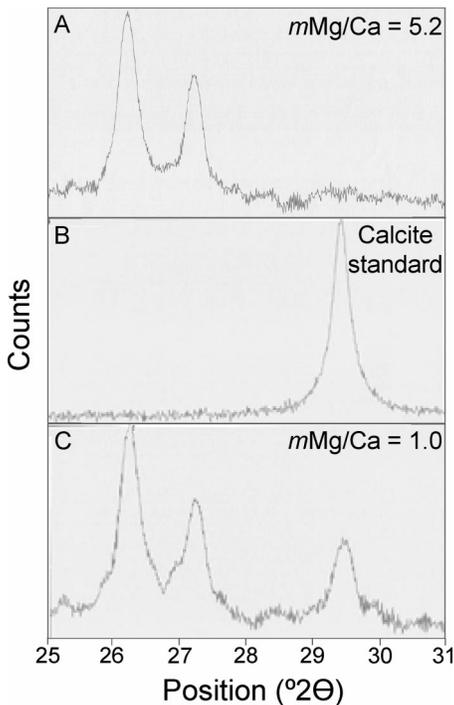
Figure 2. A: X-ray diffraction (XRD) pattern for *Porites cylindrica* coral that produced exclusively aragonite when grown in artificial seawater favoring nucleation of aragonite polymorph (mMg/Ca = 5.2). Primary aragonite peak occurs at $2\theta = 26.2°$ [d(111); 3.40 Å]. **B:** XRD pattern for pure calcite, revealing primary calcite peak at $2\theta = 29.4°–29.5°$ [d(104); 3.03–3.04 Å]. **C:** XRD pattern for *P. cylindrica* coral that produced 33% ± 3% calcite and 67% ± 3% aragonite when grown in artificial seawater favoring nucleation of calcite polymorph (mMg/Ca = 1.0). Proportion of calcite to aragonite was calculated as ratio of areas beneath primary calcite and aragonite peaks.

Figure 3. Backscattered electron (BSE) images (A, D: JEOL 8600 Superprobe), Sr maps (B, E: wavelength-dispersive spectrometry), and Mg maps (C, F: energy-dispersive spectrometry) showing, respectively, skeletal microstructure, aragonite, and calcite in portions of two specimens of *Porites cylindrica* that were grown in artificial seawater favoring abiotic precipitation of calcite over aragonite (mMg/Ca = 1.0). Light areas (mSr/Ca = 0.011–0.016) of Sr maps (B, E) and dark areas (mMg/Ca = 0.003–0.007) of Mg maps (C, F) correspond to aragonite, while dark areas (mSr/Ca = 0.001–0.005) of Sr maps (B, E) and light areas (mMg/Ca = 0.019–0.033) of Mg maps (C, F) correspond to calcite. Calcite is located on outermost portion of coral skeleton, directly beneath coral ectoderm and, therefore, in contact with coral's mechanism of calcification. Scale bars are 100 μm.

METHODS

We grew 70 comparably sized individuals (50 living + 20 dead controls) of each of the 3 species for 60 days in 5 10 gal aquaria containing artificial seawaters that were identically formulated (at modern values) except for their mMg/Ca ratios, which were fixed at 1.0, 1.5, 2.5, 3.5, and 5.2 (Ries, 2004). Coral specimens were acclimated to the artificial seawater treatments over a 30 day period in stages, to minimize any chemical shock from exposure to the modified seawater. Water was maintained at 25 ± 1 °C using a 50 W heater, circulated with two motor-driven pumps, and continuously filtered at a rate of 600 L/h. Coral lights that emit wavelengths commensurate with midday and dawn or twilight natural light provided 8 h/day of irradiation. Corals were fed 1.8 mL of Red Sea CoralGro plankton suspension daily. Red Sea Vitamin (0.75 mL), Coral Trace Element (1.5 mL), and iodine (0.75 mL) supplements were added to the aquaria weekly.
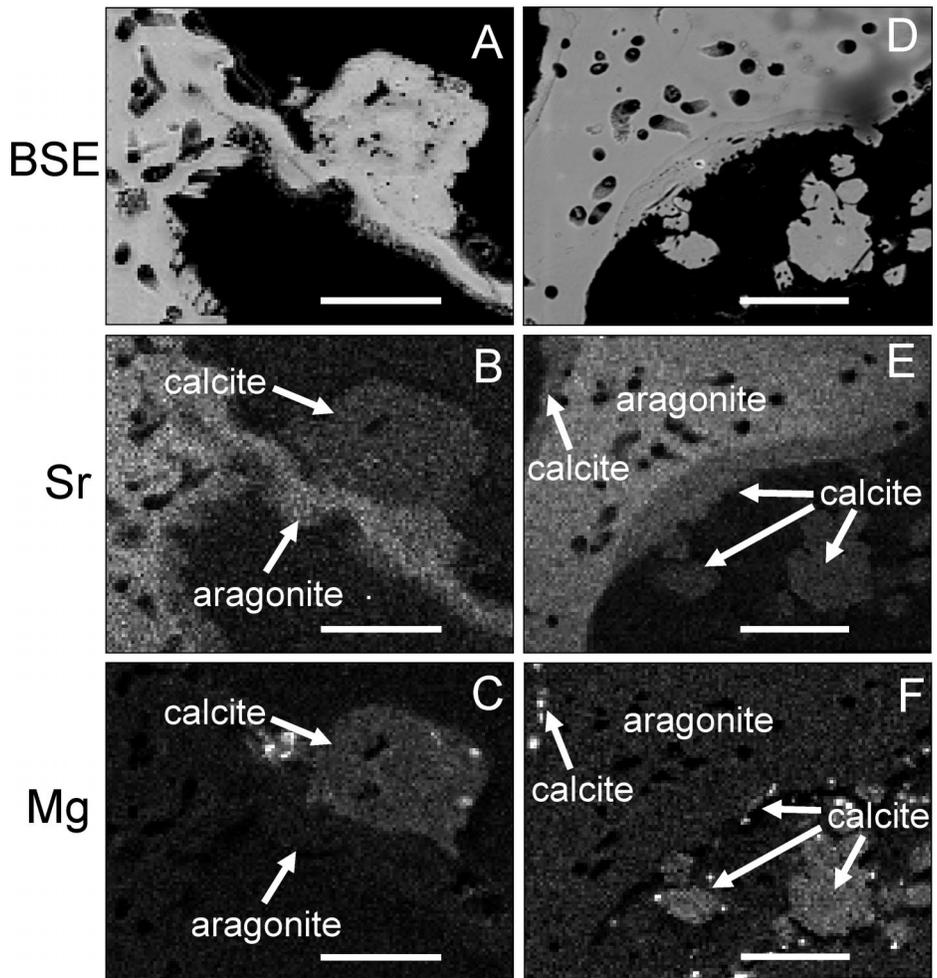
RESULTS AND DISCUSSION

Scleractinian Corals Produce Calcite in Artificial Cretaceous Seawater

X-ray diffraction analysis of new skeletal growth (Fig. 2) revealed that corals grown in artificial seawaters formulated with lower than normal Mg/Ca ratios (mMg/Ca < 5.2) began incorporating the hexagonal calcite polymorph of $CaCO_3$ into their skeleton. Dead corals (n = 60) placed alongside the live corals as controls to monitor the formation of abiotic calcite cements within the coral skeletons failed to incorporate any calcite. The proportion of skeletal calcite in the living corals (Fig. 3) increased with reduction of the ambient Mg/Ca ratio (Fig. 4A). All three species of corals accreted about one-third of their skeletal material as low-Mg calcite when grown in the lowest Mg/Ca artificial calcite seawater (mMg/Ca = 1.0). This suggests that scleractinian corals accreted at least part of their skeleton as low-Mg calcite in the calcite seas of Late Cretaceous and early Cenozoic time (Floris, 1972; Fig. 1).

Mg Fractionation in Corals

The Mg/Ca ratio of the calcitic portions of the corals' skeletons increased proportionally with the Mg/Ca ratio of the ambient seawater (Fig. 4B). Low-Mg calcite was produced with ambient mMg/Ca < 2 and high-Mg calcite (mMg/Ca > 0.04) was produced with ambient mMg/Ca > 2. This relationship is consistent with that observed for Mg incorporation in calcareous animals (echinoids, crabs, shrimp, serpulid worms) (Ries, 2004), coralline algae (Stanley et al., 2002), and some species of coccolithophores (Stanley et al., 2005). The Mg/Ca ratios of the aragonite accreted by the corals also increased with the ambient Mg/Ca
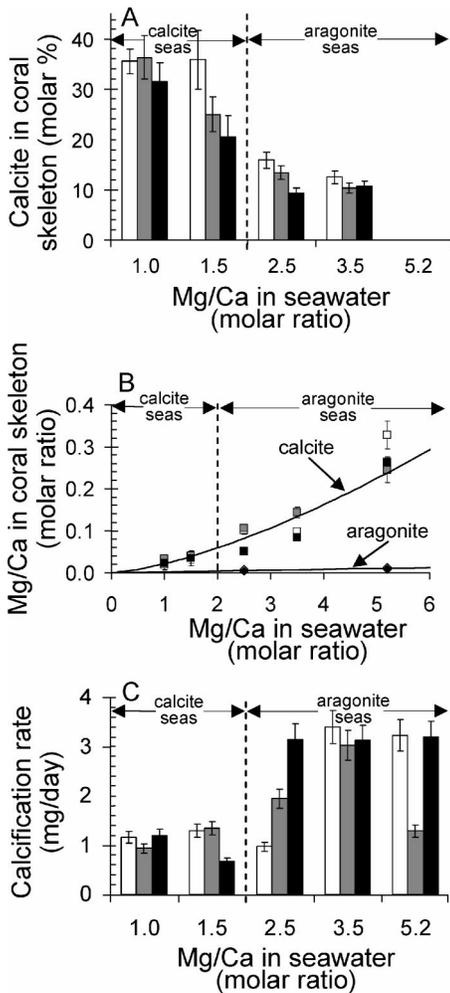
Figure 4. Mineralogy, geochemistry, and calcification rates of *Acropora cervicornis* (white symbols), *Montipora digitata* (gray symbols), and *Porites cylindrica* (black symbols) grown in artificial seawater treatments. A: Molar % calcite in coral skeletons ($n = 15$ for each species). B: *m*Mg/Ca ratio of calcitic (squares) and aragonitic (diamonds) portions of coral skeleton, determined by microprobe (energy-dispersive spectrometry). Solid black lines represent Mg-fractionation curves for coral calcite ($y = 0.0213x^{1.46}$, $R^2 = 0.95$, $n = 45$) and coral aragonite ($y = 0.0020x$, $R^2 = 0.75$, $n = 35$), calculated using least squares regression. C: Calcification rate of corals ($n = 50$ for each species) determined by buoyant weighing at beginning and end of experiment. Ca concentration of seawater decreases as Mg/Ca increases. Error bars indicate instrument error and specimen variation.

ratio (Fig. 4B). Therefore, paleotemperature reconstructions based on the Mg/Ca ratio of fossil coral skeletons require correction for the effect of secular variation in seawater Mg/Ca (Mitsuguchi et al., 1996).

Calcification Rates

Each of the three species of scleractinian corals calcified most rapidly in the aragonite seawater treatments (Fig. 4C). A significant

decrease in the rate of calcification occurred when seawater crossed into the calcite nucleation field at *m*Mg/Ca < 2, most likely due to the difficulty of precipitating aragonite—the corals' predominant skeletal mineral—in this medium.

In pioneering experiments on the influence of Mg and Ca concentrations on coral biomineralization, Swart (1980) grew specimens of *Acropora aquamosa*, *Pocillopora damicornis*, *Acropora cuneata*, and *Porites lutea* for 10 days in seawater with Mg concentrations 100 and 200 mg/L higher than modern values and Ca concentrations 100, 200, and 400 mg/L higher than modern values. Ambient Mg concentrations significantly higher than that of modern seawater prevented new skeletal growth, while Ca concentrations twice those of modern seawater resulted in reduced rates of calcification. The effect of elevated Ca is consistent with our findings that coral calcification rates decreased significantly in artificial seawaters with *m*Mg/Ca ratios that were low (1.0, 1.5) relative to modern values. The short duration of these experiments and the employment of higher concentrations of Mg and Ca than have ever characterized Phanerozoic seawater preclude interpretation of the results in the context of actual past marine conditions.

Other experiments on specimens of *Acropora* sp., *Stylophora pistillata*, *A. cervicornis*, and *A. formosa* showed that calcification rates increase as Ca concentrations are elevated from ~20% to 80% of normal marine values (Chalker, 1976; Gattuso et al., 1998). At Ca concentrations >80%, calcification rates leveled out and, in some cases, declined. However, these experiments did not adjust Mg concomitantly with Ca, and therefore failed to control for the effects of changes in the Mg/Ca ratio of the artificial seawater. When the observed variation in calcification rate is correlated with the implicit variation in Mg/Ca ratio of the artificial seawaters, the results conform to those observed in our study. In addition, the short durations (2–2.5 h) of the experiments may not have allowed sufficient time for the corals to fully equilibrate to the modified ambient conditions.

Modes of Coral Calcification and CaCO₃ Polymorph Control

It has been proposed that organic matter within centers of calcification of scleractinian corals (as much as 1% by volume) is a vestige of organic matrices and templates that specify nucleation of aragonite (Cuif et al., 1999). The fact that corals transferred to artificial calcite seawater still precipitated two-thirds of their skeletal material as aragonite supports the hypothesis that corals exert significant control over their skeletal mineralogy. However, our discovery that corals precipitate approximately one-third of their skeleton as low-Mg cal-

cite in the artificial calcite seawater indicates that their biomineralogical control can be partially overridden by ambient seawater chemistry. The tendency of corals to incorporate Mg (this study) and other trace elements (Cohen and McConnaughey, 2003) into their skeletons in proportions reflecting their abundance in seawater is additional evidence of their limited biomineralogical control. Furthermore, the acicular morphology and spherulitic organization of aragonitic crystals in the sclerodermites of coral skeletons closely resemble the aragonite of marine cements, suggesting that coral aragonite could be deposited in a way similar to abiotic precipitation (Cohen and McConnaughey, 2003).

Seawater reaches the coral's region of calcification, beneath the calicoblastic ectoderm, by moving through and between cells and by diffusion through the porous skeleton (Cohen and McConnaughey, 2003). An ATPase pump elevates Ca in the region of calcification only slightly above the level of ambient seawater (Al-Horani et al., 2003), thereby suggesting that corals precipitate their skeletons from only slightly modified seawater. The high precipitation rate of the coral skeleton, nearly 100 times that of inorganic CaCO₃ precipitation (Cohen and McConnaughey, 2003), has instead been attributed to the pumping of protons from the calcification medium (Al-Horani et al., 2003). It is therefore not surprising that the Mg/Ca ratio of seawater has a significant effect on the chemistry of a coral's calcification medium and, therefore, on its skeletal mineralogy.

While a secondary, abiogenic mode of calcification in scleractinian corals is known to occur beneath the ectodermal calcification space, filling pore spaces no longer occupied by living tissue (Enmar et al., 2000), the calcite observed in our experimental corals actually appears to be primary skeletal material. The biogenic nature of this coral calcite is evident in that: (1) the calcite occurs on the outermost portion of the skeleton (Fig. 3), immediately beneath the corals' ectodermal tissue and, thus, in direct contact with the corals' mechanism of calcification; (2) the fine-scale integration of the calcite crystals with the skeletal aragonite of the experimental corals (Fig. 3) generally preserves the morphology and integrity of the corals' skeletons; and (3) dead corals placed alongside the live corals to monitor the formation of abiogenic calcite cements within the coral skeletons failed to incorporate any calcite.

Implications for the Geologic History of Scleractinian Reef Construction

Our results suggest that scleractinian corals' diminished reef-building role from mid-Cretaceous through Eocene time (Frost, 1981; Stanton and Flügel, 1987; Höfling and Scott,

2002) was caused, at least in part, by a drop in oceanic Mg/Ca over this interval (Fig. 1) to the degree that seawater no longer favored the precipitation of the Scleractinia's predominantly aragonitic mineralogy (Stanley and Hardie, 1999). Depressed calcification rates over this interval may have opened the reef-building environments to the rudist bivalves (Stanley and Hardie, 1999), which were primarily calcitic after the Cenomanian (Steuber, 2002) and became important constituents of carbonate reef facies during the mid-Cretaceous (Kauffman and Johnson, 1988; Scott et al., 1990; Moussavian, 1992; Gili et al., 1995).

The Scleractinia failed to resume their role as major reef builders until well after the extinction of the rudists. They began to form massive widespread reefs again early in the Oligocene (Frost, 1981), shortly after ambient mMg/Ca ratios had risen above two (Fig. 1) into the aragonite stability field (Stanley and Hardie, 1999). A progressive decline in the concentration of atmospheric CO_2 over the Oligocene Epoch (Pagani et al., 2005), which would have increased the $CaCO_3$ saturation state of seawater, may have also contributed to the Scleractinia's resurgence over this interval. The highest calcification rates for the three scleractinian species in this experiment occurred both in modern seawater (mMg/Ca = 5.2) and in seawater with mMg/Ca = 3.5 (Fig. 4C). We hypothesize that the corals' elevated calcification rates in seawater with mMg/Ca = 3.5, a level approached in Oligocene time, resulted from the combined effect of a favorable ambient Mg/Ca ratio (mMg/Ca > 2) and a high concentration of Ca relative to that of modern seawater (Stanley et al., 2005).

CONCLUSIONS

We grew colonies of three species of scleractinian corals representing two families in five artificial seawaters that differed only in their mMg/Ca ratios, which ranged from 5.2 (that of the modern ocean) to 1.0 (a Late Cretaceous level) (Hardie, 1996; Lowenstein et al., 2003). For all three species, stepwise reduction of the ambient Mg/Ca ratio resulted in a progressive decrease in the rate of skeletal calcification and an increase in the proportion of skeletal calcite. We conclude that scleractinians exert only partial control over their skeletal mineralogy, but we suggest that the predominance of the aragonite polymorph in some, if not all, of their species played a role in their mid-Cretaceous decline and their Oligocene resurgence as major reef builders. These experimental results support the broader fossil and geochemical evidence that secular variation in seawater Mg/Ca has influenced the reef-building and sediment-producing roles of many hypercalcifying marine taxa throughout the Phanerozoic (Stanley and Hardie, 1999; Ries, 2004, 2006; Stanley et al., 2002, 2005).

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