The long-term impact of magnesium in seawater on foraminiferal mineralogy: Mechanism and consequences

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Abstract Foraminifera are unicellular protists, primarily known for their calcium carbonate shells that provide an extensive fossil record. This record, ranging from Cambrian to present shows both major shifts and gradual changes in the relative occurrence of taxa producing different polymorphs of carbonate. Here we present evidence for coupling between shifts in calcite- versus aragonite-producing species and periods with, respectively, low and high seawater Mg/Ca throughout the Phanerozoic. During periods when seawater Mg/Ca is <2 mol/mol, low-Mg calcite-producing species dominate the foraminiferal community. Vice versa, high-Mg calcite- and aragonite-producing species are more abundant during periods with relatively high seawater Mg/Ca. This alteration in dominance of the phase precipitated is due to selective recovery of groups producing the favorable polymorph after shifts from calcite to aragonite seas. In addition, relatively high extinction rates of species producing the mineral phase not favored by the seawater Mg/Ca of that time may be responsible for this alteration. These results imply that the current high seawater Mg/Ca will, in the long term, favor prevalence of high-Mg and aragonite-producing foraminifera over calcite-producing taxa, possibly shifting the balance toward a community in which calcite production is less dominant.

1. Introduction

In 1983, Sandberg proposed that the mineral phase of inorganic carbonates that precipitated from seawater reflects Phanerozoic seawater chemistry [*Sandberg*, 1983]. Shifts between so-called aragonite and calcite seas are primarily caused by long-term changes in the ratio of [Mg^{2+}] over [Ca^{2+}] in seawater [*Dickson*, 2002; *Hardie*, 1996; *Lowenstein et al.*, 2001] (i.e., Mg/Ca$_{sw}$). This ratio varies over geological timescales due to changes in the balance between weathering, oceanic crust production, dolomite formation, and rate of carbonate burial [*Arvidson et al.*, 2006, 2011; *Berner*, 2004; *Farkaš et al.*, 2007; *Hardie*, 1996; *Holland*, 2005; *Wilkinson and Algeo*, 1989]. Dominance of organisms producing calcite (e.g., rugose and tabulate corals) or aragonite (e.g., corals and dasycladacean algae) as well as abiotically precipitated calcite and aragonite follows trends in Mg/Ca$_{sw}$ [*Stanley*, 2006; *Stanley and Hardie*, 1998]. The impact of Mg/Ca$_{sw}$ on biogenic mineralogy can be explained by differences in affinity of Mg ions for calcite versus aragonite crystal surfaces [*De Choudens-Sánchez and González*, 2009; *Fallini et al.*, 1994; *Fernández-Díaz et al.*, 1996; *Nancollas and Sawada*, 1982; *Reddy and Wang*, 1980]. Magnesium ions adsorb relatively well to calcite surfaces compared to those of aragonite [*Mucci and Morse*, 1985], resulting in a relative decrease in calcite growth rate at high seawater [Mg^{2+}] [*Berner*, 1975]. The boundary between nucleation fields for inorganic aragonite and calcite lies at a Mg/Ca$_{sw}$ of 2 mol/mol [*Sun et al.*, 2015] and depends on temperature and pressure [*Berner*, 1975]. Recently, it is shown that seawater sulfate concentrations have an (additional) effect on the seawater Mg/Ca threshold [*Bots et al.*, 2011]. Periods with Mg/Ca$_{sw} < 2$ (e.g., Devonian and Silurian) are associated with calcite-producing organisms and are therefore termed "calcite seas," whereas "aragonite seas" are defined by periods with Mg/Ca$_{sw} > 2$ and are characterized by dominance of aragonite and/or high-magnesium calcite producers [*Dickson*, 2004; *Stanley*, 2008] (e.g., Permian and Triassic). The biological mechanisms affected by changes in Mg/Ca$_{sw}$ may include decreasing growth rates and increased energy costs for calcification by organisms producing an unfavored $CaCO_3$ crystal phase [*Ries*, 2010]. Both of these biological impediments result in a dominance of calcite-producing organisms during periods with low Mg/Ca$_{sw}$, while favoring those precipitating aragonite when Mg/Ca$_{sw}$ is high.

Although the relationship between Phanerozoic changes in seawater Mg/Ca and the evolutionary history of many marine calcifiers has been analyzed [*Kiessling et al.*, 2008; *Porter*, 2010; *Stanley*, 2008], the response of

foraminifera to changes in Mg/Ca$_{sw}$ is only sparsely investigated [*Martin*, 1995]. Most low-Mg calcite-producing or hyaline taxa are known to actively control the amount of magnesium incorporated [*Bentov and Erez*, 2006; *De Nooijer et al.*, 2014]. Since the Mg/Ca of the calcifying fluid is, in this case, dissimilar from that of ambient seawater, foraminifera might potentially be unaffected by changes in Mg/Ca$_{sw}$. High concentrations of seawater Mg^{2+}, however, may require allocation of more energy to maintain biomineralization and thereby link long-term changes in Mg/Ca$_{sw}$ to the success of aragonite- versus calcite-producing foraminifera. Geological longevity, areal and depth distribution, composition of the tests (aragonite or calcite), and importance in the global carbon cycle, however, make foraminifera particularly suitable to study the interplay between seawater chemistry and biogenic mineralogy. Here we present an analysis of foraminiferal abundances through the Phanerozoic and relate their mineralogy to changes in Mg/Ca$_{sw}$ and mass extinction events. Past shifts in dominance of calcite- versus aragonite-producing foraminifera serve as an analogue to evaluate future foraminiferal success under ongoing climate and environmental stress.

2. Methods

2.1. Foraminiferal Occurrences Over Geological Timescales

In order to investigate major trends in foraminiferal distribution, we analyzed foraminiferal occurrences in the Paleobiology database of Fossilworks (http://fossilworks.org). In general, we used the database in default mode, with some small exceptions, and this input data are listed in the supporting information. In short, we extracted 6270 collections with 37,586 species occurrences covering the last 500 Ma [*Kiessling et al.*, 2015], when queried the database for *Foraminferea*, *Foraminiferida*, and *Foraminifera* (genus level or above). All foraminiferal species occurrences were grouped into ~5 Myr time bins ("Fossil Record 2 bin"). Occurrences were extracted from the database on a species level, excluding contributions with open nomenclature (aff., cf., "…," and "?") [*Bengston*, 1988] which take into account different levels of uncertainty during the determination on species level. To estimate global foraminiferal abundances, the full geographical range was used. By enabling the database's "scale option" we also extracted composition and life habitat information of every species. The assignments of these mineralogical and ecological attributes were based on a number of sources reporting mineralogy and habitat preferences for the different foraminiferal (sub)orders [*Loeblich and Tappan*, 1984, 1988]. The composition of the tests was aragonite or calcite with low (LMC; <8%wt MgCO$_3$) and high magnesium content (HMC; >8%wt MgCO3). So-called intermediate-Mg calcite (4–8%wt MgCO$_3$) was already labeled LMC by the authors of the database. This distinction coincides with known differences in biomineralization strategies (e.g., hyaline versus porcelaneous foraminifera, respectively [*De Nooijer et al.*, 2009; *Hemleben et al.*, 1986]). Life habitat information was either planktonic or benthic (infaunal, semi-infaunal, and epifaunal). For 10.5% of all species present in the database, the CaCO$_3$ mineralogy is unknown or not recorded and was therefore excluded from further statistical analysis. Also, species which do not (actively) calcify, like agglutinated and naked foraminifera, or precipitate carbonate but opaline silica [*Gupta*, 2002] (order Silicolocilinida), for example, were not used for this analysis. Occurrences of species from collections older than 320 Ma were excluded from analysis due to scarcity of collections and consequently very low foraminiferal species occurrences (<25) per time bin. Expression of Fossilworks-derived abundances as proportional occurrences circumvents potential biases introduced when using absolute abundances [*Valentine et al.*, 2013]. The resulting four groups (HMC, aragonite, LMC benthic, and LMC planktonic) generally follow the "classic" orders [*Loeblich and Tappan*, 1988]. However, there are some exceptions. For instance, the "aragonite" group comprises the orders Involutinida and Robertinida and also includes the aragonitic taxon Favusellacea, which is actually part of the calcite-producing order Globigerinida, according to *Loeblich and Tappan* [1988]. Another example is the aragonite precipitating *Hoegludina elegans* from the low-Mg calcite-producing order Rotaliina, which is also placed in the aragonite group in our study. Because of such exceptions, we decided not to generalize Fossilworks to solely looking at the species occurrence of different orders. However, our assigned groups still overlap strongly with the orders. Diversity graphs were created for these four compiled groups by using the diversity graph function of FW. As a result, the compiled data provide an assessment of rational occurrences at species level and thereby indicate the dominance or rareness of the four groups relative to each other. In some time bins (e.g., around ~70 and 100 Ma), planktonic foraminifera make up > 90% of the total occurrences. This could be due to a possible bias of Fossilworks toward planktonic foraminifera. However, when performing the analysis without the planktonic LMC group, we still observe the same general pattern for all the other groups (see supporting information).

2.2. Aragonite Versus Calcite Sea Events

Since different Mg/Ca$_{sw}$ reconstructions yield slightly different timings of calcite-aragonite sea events [*Evans and Müller*, 2012], we choose to define periods in which reconstructions [*Farkaš et al.*, 2007; *Stanley and Hardie*, 1998] agree as the "true" calcite and aragonite sea events. To test whether occurrences of LMC versus aragonite/HMC producers are significantly different in these calcite and aragonite seas or before/after mass extinction events [*Raup and Sepkoski*, 1982], two-way Student's *t* tests assuming equal variances were performed. We compared the average *p*(aragonite + HMC) between adjacent calcite and aragonite seas, as well as between all calcite and aragonite sea intervals combined. Finally, the three bins before and after three mass extinction events with student's *t* tests to determine whether these average occurrences were different. Our analyses include the end-Permian (252 Ma), end-Triassic (200 Ma), end-Cretaceous (65 Ma), and Paleocene Eocene Thermal Maximum (PETM; ~55 Ma) mass extinctions. Due to the resolution of our database, the end Cretaceous and PETM were regarded as one event, despite known differences in their causes and consequences. We in this case compared *p*(aragonite + HMC) of the three time bins before the end Cretaceous (65 Ma) with the three time bins after the PETM (55 Ma). All of the aforementioned events are associated with minor or major perturbations in marine inorganic chemistry [*Hart et al.*, 2014; *Hönisch et al.*, 2012] and are characterized by a decrease in biodiversity, including that of foraminifera.

3. Results

3.1. Seawater Mg/Ca Reconstruction

Long-term patterns in Mg/Ca$_{sw}$ can be reconstructed from model studies taking into account mid-ocean ridge spreading rates, weathering, and dolomite formation [*Hardie*, 1996; *Wilkinson and Algeo*, 1989]. Over the last few decades, these reconstructions have been improved by, e.g., new insights in biochemical cycles. One of the most recent reconstructions [*Farkaš et al.*, 2007] (Figure 1) combines a model of coupled calcium, carbon, and magnesium global cycles [*Hansen and Wallmann*, 2003; *Heuser et al.*, 2005; *Wallmann*, 2001, 2004] with reconstructed seafloor spreading rates based on [87]Sr/[86]Sr [*Veizer et al.*, 1999; *Wallmann*, 2004]. The resulting reconstruction is in close agreement with a number of independent proxies for Mg/Ca$_{sw}$, including Mg/Ca of fluid inclusions [*Horita et al.*, 2002; *Lowenstein et al.*, 2001] and that of rudists [*Steuber and Rauch*, 2005] and echinoderms [*Dickson*, 2002] . This relatively recent Mg/Ca$_{sw}$ reconstruction is largely in agreement with those from earlier studies [*Hardie*, 1996], whereas deviations between models is likely caused by recent updates in the assumptions for the earlier models [*Holland et al.*, 1996; *Holland and Zimmermann*, 2000; *Horita et al.*, 2002]. The model by *Farkaš et al.* [2007] also includes more recent data on global major elements cycling and refined estimates of seafloor spreading rates, resulting in slightly different [Ca^{2+}] and [Mg^{2+}] trends. The transitions between these calcite and aragonite seas deviate somewhat from those of the often-used reconstruction [*Stanley and Hardie*, 1998], which is therefore included in our discussion. This divided the past 500 Ma into two periods with a relatively low Mg/Ca$_{sw}$ (end Cambrian to Devonian and end Triassic to mid-Cretaceous, CI and CII, respectively) and two with a relatively high Mg/Ca$_{sw}$ (Carboniferous to end Triassic and mid-Cretaceous to recent, AII and AIII, respectively).

3.2. The Response of Foraminifera to Changes in Mg/Ca$_{sw}$

Although it has been suggested that foraminifera are "sophisticated biomineralizers" and are, therefore, able to cope with relatively variable Mg concentrations in seawater [*Stanley*, 2008], there is a significant ($p < 0.01$) correlation between average seawater Mg/Ca of combined aragonite versus calcite sea events (CII versus AII + AIII) and the ratio between calcite- versus aragonite-producing foraminifera (Figure 2). Aragonite sea species (taxa-producing aragonite or HMC) are more abundant during periods with high seawater Mg/Ca values. In periods with low Mg/Ca$_{sw}$ values, there is an increase in abundance of LMC-producing taxa. However, after the shift from CII to AIII, there appears to be a lag in the response of the foraminiferal community. Aragonite sea species only start to increase after the end Cretaceous and PETM, not directly when Mg/Ca$_{sw}$ increases. Nevertheless, the effect of mass extinction events on the dominating foraminiferal mineralogy is less clear (Table 1).

Only the end-Triassic extinction, coinciding with a transition from aragonite to calcite sea interval (AII/CII), correlates to a significant ($p < 0.05$) shift in abundance from aragonite to calcite sea species. Furthermore, first appearance of aragonite precipitating foraminifera, i.e., the orders Involutinida and Robertinida, occurs
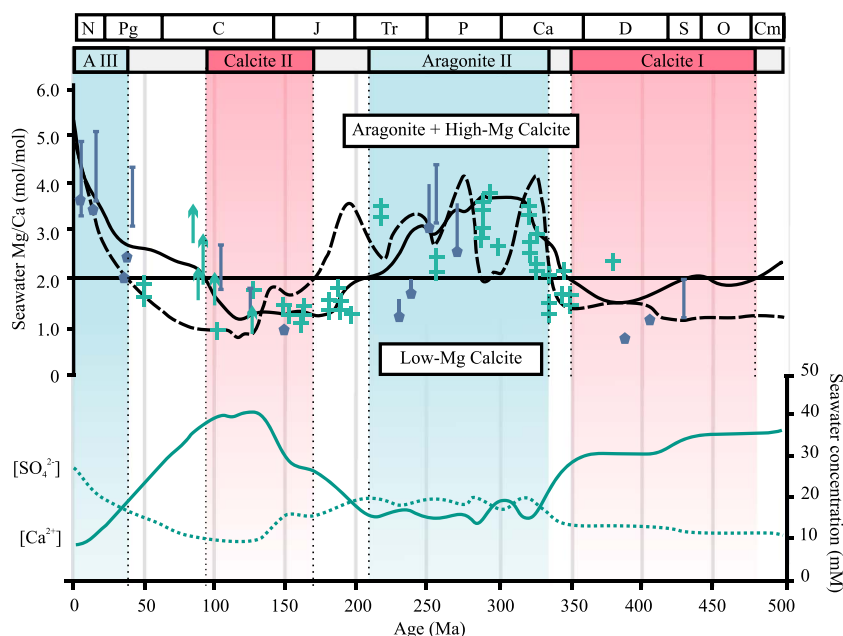
Figure 1. (top) Reconstruction of calcite (CI and CII) and aragonite sea (AII and AIII) intervals based on modeled seawater Mg/Ca reconstructions (solid line [*Stanley and Hardie*, 1998] and dashed line [*Farkaš et al.*, 2007]), supported by Mg/Ca from fluid inclusions (bars [*Lowenstein et al.*, 2001] and pentagons [*Horita et al.*, 2002]) and that of echinoderm ossicles and rudists (arrows [*Steuber and Rauch*, 2005] and crosses [*Dickson*, 2002]). The horizontal line divides calcite sea (Mg/Ca < 2) and aragonite sea (Mg/Ca > 2) intervals [*Berner*, 2004; *Stanley*, 2008]. Accordingly, aragonite sea intervals are indicated by blue panels and calcite sea events with red panels. The grey panels indicate periods where the two models deviate in the timing of the division between calcite and aragonite seas. (bottom) Phanerozoic reconstruction of SO_4^{2-} (dotted line) and Ca^{2+} (solid line) concentrations over geological time [after *Demicco et al.*, 2005]. Cm = Cambrian, O = Ordovician, S = Silurian, D = Devonian, Ca = Carboniferous, P = Permian; Tr = Triassic, J = Jurassic, C = Cretaceous, Pg = Palaeogene, and N = Neogene.
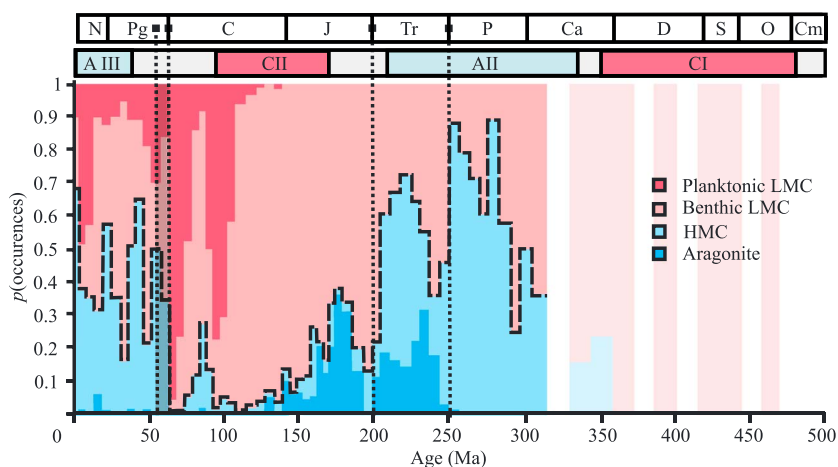

Figure 2. Proportional foraminiferal species occurrences through the Phanerozoic Era. The *p*(occurrences) is the number of times that a species of one of the four groups is present per time bin, relative to the other three groups. Low-Mg calcite-producing (LMC) benthic and planktonic foraminifera (light and dark red areas, respectively) and of high-Mg calcite (HMC) and aragonite foraminifera (light and dark blue areas, respectively) are divided by a dashed black line. The three mass extinction events (P-Tr, Tr-J, PETM, and C-Pg) are indicated by vertical dotted lines. Light shaded data before 320 Ma are not statistically supported due to a limited amount of foraminiferal occurrences in this part of the fossil record. Abbreviations as in Figure 1.

Table 1. Changes in Aragonite Versus Calcite Sea Species Over Mass Extinction Events and Aragonite/Calcite Sea Intervals[a]

Transition or Event	Δmean	t Value	d.f.	p
C/A[b]	0.394	9.85	20	<**0.00**
CII/AIII	0.306	4.91	10	<**0.00**
AII/CII	0.483	7.39	10	<**0.00**
End Permian (252 Ma)	0.310	3.39	2	0.08
End Triassic (200 Ma)	0.444	7.63	2	**0.02**
End Cretaceous (65 Ma) and PETM (55)	0.411	3.07	2	0.09

[a]Bold values are significant. Aragonite (AII and AIII) and calcite (CII) sea intervals. Δmean is the difference between the means of the compared groups.
[b]All Calcite sea periods versus all aragonite sea periods = CII/(AII + AIII).

during aragonite sea II (approximately 250 Ma ago), while planktonic calcite precipitating foraminifera evolve during calcite sea II.

4. Discussion and Conclusion

4.1. Foraminiferal Trends Are Controlled by Seawater Mg/Ca

Long-term trends in fossil foraminiferal occurrences are in line with fluctuations in Mg/Ca$_{sw}$ and community changes of other marine calcifiers [*Stanley*, 2008; *Stanley and Hardie*, 1998; *Porter*, 2010]. However, [SO$_4^{2-}$] has an additional effect on preferential CaCO$_3$ polymorph formation due to its effect on the Mg/Ca threshold separating the nucleation fields for aragonite and calcite. Especially when [SO$_4^{2-}$] decreases below <10 mM [*Bots et al.*, 2011], the Mg/Ca threshold for preferential aragonite increases, resulting in an overall increase of calcite precipitated. Hence, high [SO$_4^{2-}$] promotes the precipitation of aragonite, similar to high seawater Mg/Ca. Since Phanerozoic [SO$_4^{2-}$] reconstructions [*Demicco et al.*, 2005] show a covariation of [SO$_4^{2-}$] with seawater Mg/Ca, it is difficult to disentangle the contribution of these two controls. During biomineralization, however, the [SO$_4^{2-}$] of the calcifying fluid of a foraminifera is much lower than that of the surrounding seawater, as indicated by the low partition coefficient for sulfur [*Berry*, 1998; I. van Dijk et al., manuscript in preparation, 2016]. This implies that despite geological fluctuations in [SO$_4^{2-}$], its effect on the boundary between nucleation fields for calcite versus aragonite precipitation is similar through time.

Nevertheless, periods with relatively low Mg/Ca$_{sw}$ are dominated by calcite-producing foraminifera, whereas aragonite producers are found predominantly during periods with high Mg/Ca$_{sw}$. For other organisms, shifts in dominance of marine calcite and aragonite producers are explained by increased extinction and speciation rates after transitions of Mg/Ca$_{sw}$, or by adaptation to preferred mineralogy by switching from calcite to aragonite precipitation or vice versa [*Ries*, 2004, 2010; *Stanley et al.*, 2002]. For foraminifera, extinction and radiation seem more likely since there are significant differences in community composition before and after mass extinction events. Moreover, no foraminiferal species has yet been found to produce both calcium carbonate phases, nor have culturing experiments with varying Mg/Ca$_{sw}$ [*Evans et al.*, 2015; *Mewes et al.*, 2014; *Segev and Erez*, 2006] suggested that foraminifera can change or adapt to another CaCO$_3$ phase, kinetically favored, e.g., coralline algae [*Stanley et al.*, 2002] and echinoids, crabs, shrimps, and calcareous serpulid worms [*Ries*, 2004]. Since foraminifera do not switch from calcite to aragonite production (or vice versa) as a response to changes in Mg/Ca$_{sw}$, they will eventually be calcifying at unfavorable Mg/Ca$_{sw}$ conditions as a consequence of changing ocean chemistry. For other organisms, this is shown to negatively impact calcification through decreased growth rates and/or increased energy spent on calcification [*Ries*, 2010]. Hyaline and porcelaneous foraminifera have different calcification strategies to produce their shells [*De Nooijer et al.*, 2009, 2014; *Hemleben et al.*, 1986]. The costs involved in calcification are poorly constrained but will depend on biomineralization strategy [*Zeebe and Sanyal*, 2002]. In case Mg^{2+} is selectively removed from the calcifying fluid [*Bentov and Erez*, 2006], increased seawater [Mg^{2+}] will likely increase energy requirements for calcification due to increased pumping rates. When calcification is driven by active, transmembrane transport of Ca^{2+} [*Nehrke et al.*, 2013; *De Nooijer et al.*, 2014], the involved energy may also increase by Mg ions blocking selective Ca transporters. The latter may be overcome by, e.g., increasing the Ca transporter density, which will also increase the energy requirements when calcifying under high [Mg^{2+}].

4.2. Preferential Dissolution

Geological trends in fossil foraminiferal shells are potentially biased by preferential dissolution as a result of changes in seawater saturation state with respect to calcium carbonate. Saturation state (Ω) is the product of seawater carbonate and calcium concentrations ([Ca^{2+}] × [CO$_3^{2-}$]), divided by the solubility product K_{sp}. This solubility product differs between aragonite ($-\log K_{sp} = 6.19$) and low-Mg calcite ($-\log K_{sp} = 6.37$) and therefore results in relatively poor preservation of aragonite shells compared to calcite ones. Such a preservation bias could have affected fossil occurrences of the different foraminiferal groups, thereby compromising our

results, discussion, and conclusions. Although preferential dissolution may have affected foraminiferal taphonomy, it is unlikely to impact overall shifts in dominance of calcite versus aragonite producers since reconstructed seawater saturation states [*Riding and Liang*, 2005] are anticorrelated to changes in Mg/Ca_{sw}. Low Ω states co-occur with high Mg/Ca_{sw} on global and geological scales and vice versa. Even though periods with a low Ω may be reflected by increased aragonite dissolution and therefore decreased preservation, the opposite is found (Figure 2). Hence, the effect of elevated Mg/Ca_{sw} on aragonite production apparently outweighs any potential bias due to preferential dissolution. Depending on the magnitude of increased aragonite dissolution during periods with a low Ω, the observed correlation between Mg/Ca_{sw} and calcite versus aragonite foraminiferal species abundances might be stronger than reported here. However, we cannot account for postburial diagenetic change, which may also cause the preferential dissolution of aragonite and/or replacement by calcite.

4.3. The Effect of Mass Extinction Events

The importance of mass extinction events on the balance between calcite and aragonite producers, in general, has been analyzed by *Kiessling et al.* [2008], who proposed that major environmental perturbations rather than changes in ocean chemistry determine the dominance of calcite versus aragonite producers. This conclusion is based on a study also relying on fossil abundances and included a group "foraminifera + algae," representing a minor portion of the total species occurrences. In Kiessling et al.'s analysis, trends in the combination of all marine-calcifying organisms are mainly driven by mass extinction events, while Mg/Ca_{sw} seems to have a minor impact. This is seemingly in contrast with our results, which suggest the relation between long-term seawater chemical changes and evolution of calcifying organisms is not always straightforward. An explanation for these contrasting results may point to the fact that different controls shape the evolution of marine calcifiers on different levels and/or that each group (e.g., corals, bivalves, and foraminifera) responds differently to changes in Mg/Ca_{sw}. It is therefore crucial to analyze the evolution of (and within) marine-calcifying groups in relation to seawater chemistry separately. It is likely that mass extinction events impact the mineralogy of marine calcifiers, in general, while within these orders, changes in seawater chemistry influence evolutionary success and extinction rates.

When analyzing foraminiferal community shifts as a function of mass extinction events, only the end-Triassic event shows a significant shift from a high-Mg and aragonite-dominated community to one with more low-Mg calcite-producing species. Due to differences in the causes, duration, and magnitude of all events analyzed, in combination with the resolution of our data, the impact of mass extinctions on overall foraminiferal community cannot be unambiguously assessed based on this data set. Nevertheless, for other major groups of calcifying organisms, mass extinction events play an important role in aragonite versus calcite dominance [*Kiessling et al.*, 2008] mainly due to selective recovery of the organisms which precipitated the favored polymorph, which may also be the case for foraminifera.

4.4. First Occurrence, Extinction, and Recovery of Foraminiferal Taxa

The effect of ocean chemistry on foraminiferal evolution is likely caused by (1) timing of the first occurrences of newly formed taxa and (2) selective recoveries and extinctions of taxa before and after Mg/Ca_{sw} transitions and/or major carbon perturbations. This would explain, for instance, the observed lag of dominance by HMC and aragonite producers after the CII/AIII transition.

The importance of Mg/Ca_{sw} on foraminiferal mineralogy is reflected by the first occurrences of newly evolved taxa, generally exhibiting the mineralogy which is favored by the seawater Mg/Ca of that time. For example, all taxa from the orders Involutinida and Robertinida produce aragonite shells and both orders originated in Aragonite sea II (at 303 and 250 Ma, respectively). After establishing their mineralogy, these taxa did not change their mineralogical preference within their calcification mechanism and continued producing aragonite, even during periods of lower Mg/Ca_{sw}. This was already suggested by *Martin* [1995] that Mg/Ca_{sw} plays a key role in determining the mineralogy of clades at their moment of origination [*Porter*, 2007, 2010].

There might be an increased recovery or diversification of taxa producing the polymorph which is supported by seawater Mg/Ca. For instance, high Mg/Ca_{sw} could have played a part in the postextinction recovery by aragonitic trochospiral Robertinida (genera *Oberhauserella* and *Reinholdella*) following the end-Triassic extinction [*Clémence and Hart*, 2013; *Fuchs*, 1967, 1970], which occurred during relatively high Mg/Ca_{sw}. In the Lower Jurassic, calcitic taxa (*Lenticulina*, *Lingulina*, *Paralingulina*, *Nodosaria*, *Pseudonodosaria*, etc.)

gradually began to dominate the assemblage in the developing calcite II ocean [*Copestake and Johnson*, 2014], with the aragonitic taxa (especially *Reinholdella* and *Epistomina*) reduced to a low-diversity lineage throughout the mid–Late Jurassic and Early Cretaceous [*Hart*, 1984; *Hart et al.*, 2009; *Oxford et al.*, 2004].

After the end-Cretaceous extinction event, occurrences of high-Mg foraminiferal taxa increased (Figure 2) and aragonitic pteropods and heteropods became a significant part of the oceanic plankton [*Wall-Palmer et al.*, 2012] while seawater Mg/Ca rose to its current value.

An example of the interplay between the mineralogy of newly originated taxa and selective recovery by subsequent changes in oceanic state can be found in the evolution of planktonic foraminifera. The early planktonic foraminifera, *Conoglobigerina*, were aragonite producers and evolved from aragonitic benthic ancestors in the high Mg/Ca$_{sw}$ ocean of the Early Jurassic [*Hart et al.*, 2003, 2012; *Wernli*, 1988, 1995]. This *Conoglobigerina-Globuligerina-Favusella* lineage appeared to be unsuccessful and did not diversify in the developing calcite II ocean and then became extinct in the mid-Cretaceous, after which the new calcite-producing taxa became highly diverse and successful. These new calcite-producing planktonic foraminifera emerged in the Early Cretaceous, and their evolution can be traced throughout the Cretaceous, despite a number of significant changes in the foraminiferal community at oceanic anoxic events [*BouDagher-Fadel et al.*, 1997; *Hart*, 1999; *Hart et al.*, 2002; *Premoli Silva and Sliter*, 1999].

4.5. Consequences for (Future) Foraminifera

Currently, high seawater Mg/Ca favors occurrence of organisms producing aragonite and high-Mg calcite [e.g., *Stanley*, 2006; *Stanley and Hardie*, 1998]. Following fossil alterations in dominant foraminiferal mineral phases, all extant low-Mg calcite-producing foraminifera, including all planktonic species, are currently living in an ocean that is not favorable to the mineral phase of their shells. Ongoing anthropogenic CO_2 emissions and subsequent ocean acidification are currently resulting in a major marine carbon perturbation by decreasing seawater pH and Ω, which will likewise hamper marine calcification [*Van de Waal et al.*, 2013; *Ilyina and Zeebe*, 2012] as it did in the geological past [e.g., *Hönisch et al.*, 2012]. Since ongoing oceanic CO_2 uptake will cause seawater to become undersaturated with respect to aragonite sooner than it will be for calcite, organisms producing aragonite and high-Mg calcite (scleractinian corals, echinoderms, and some foraminiferal taxa) are generally thought to be most vulnerable to ocean acidification [*Orr et al.*, 2005]. However, foraminiferal species producing this polymorph of carbonate (i.e., aragonite or HMC) are supported by the current high seawater Mg/Ca. Even though they may be relatively vulnerable to ongoing ocean acidification, subsequent recovery and diversification may favor their long-term success. Our results highlight the potential role of seawater Mg/Ca as a possible controller on the success of calcite versus aragonite producers in a changing ocean. We suggest that on longer timescales, high-Mg calcite- and aragonite-producing foraminifera dominance will not be negatively impacted by ongoing ocean acidification due to rapid recovery and diversification after the event, which will be perhaps even at the expense of low-Mg calcite-producing foraminifera.

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