Biogeosciences Discussions

Impact of seawater pCO$_2$ changes on calcification and on mG/cA and sR/cA in benthic foraminifera calcite (*Ammonia tepida*): results from culturing experiments

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Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

◄◄ | ►►

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Abstract

Evidence is accumulating of increasing concentrations of dissolved carbon dioxide in the ocean and associated acidification impacts on calcifying organisms. Among these organisms, benthic and planktonic foraminifera are responsible for a large amount of the globally precipitated calcium carbonate. Therefore, their response to an acidifying ocean may have important consequences for future inorganic carbon cycling. To assess the sensitivity of benthic foraminifera to changing carbon dioxide levels and subsequent alteration in seawater carbonate chemistry, we cultured specimens of the shallow water species *Ammonia tepida* at two concentrations of atmospheric CO_2 (120 and 2000 ppm) and two temperatures (10°C and 15°C). Shell weights and elemental compositions were determined. Results indicate that shell weights decrease with decreasing $[CO_3^{2-}]$, and increase with decreasing temperature. Changes in $[CO_3^{2-}]$ or total dissolved inorganic carbon do not affect the Mg partition coefficient. On the contrary, Sr incorporation is enhanced under increasing $[CO_3^{2-}]$. Implications of these results for the paleoceanographic application of foraminifera are also discussed.

1 Introduction

Since the mid 19th century, utilization of fossil fuels and land use change impacted biogeochemical carbon cycling, leading to global environmental perturbations (see e.g. IPCC report, 2001, 2007). Increased levels of atmospheric CO_2 resulted in increased concentrations of dissolved CO_2 ($CO_{2(aq)}$) especially in the surface ocean (Caldeira and Wickett, 2003). It has been estimated that the oceans have taken up approximately 30% of the CO_2 emitted (Sabine et al., 2004) and thereby mitigated human induced global warming. In addition, this also resulted in surface ocean acidification. Increasing atmospheric CO_2 concentrations from 280 (pre-industrial value) to 380 ppmv (actual value) decreased oceanic pH by approximately 0.1 unit (Orr et al., 2005). Estimates of future atmospheric pCO_2 suggest values reaching 800–1000 ppmv

Full Screen / Esc

by the end of this century (IPCC, 2001), equivalent to another 0.3 unit decrease in ocean pH (Caldeira and Wickett, 2005).

Since marine calcifying organisms build their calcareous skeletons according to the simplified reaction $Ca^{2+}+2HCO_3^- -> CaCO_3+CO_2+H_2O$, an impact of CO_2 on biocalcification is expected. Indeed, an increasing number of field and laboratory studies demonstrate the impact of increased seawater $[CO_{2(aq)}]$ and related changes in carbonate chemistry on both planktonic and benthic marine calcifying organisms, such as coccolithophores, corals, shellfish and foraminifera (e.g. Bijma et al., 1999; Kleypas et al., 1999; Leclercq et al., 2000; Riebesell et al., 2000; Zondervan et al., 2001; Delille et al., 2005; Gazeau et al., 2007). In turn, a decrease in calcification of marine calcifiers may act as a negative feedback on atmospheric CO_2 levels (assuming the organic pump remains constant) (Riebesell et al., 2000; Zondervan et al., 2001; Ridgwell, 2007). Establishing an accurate relationship between pCO2 and calcification is crucial for assessing the impact of such a feedback in the future.

During calcification, elements such as Sr and Mg are incorporated into biogenic calcium carbonate. The ratio of these elements to Ca depends on the physical and chemical conditions in the calcification environment. Therefore, elemental compositions of foraminiferal tests have become an important tool to estimate past oceanic conditions (e.g.: Boyle 1981; Marchitto et al., 1998; Martin et al., 1999; Rickaby and Elderfield, 1999; Russell et al. 2004; Hall and Chan, 2004, 2005). Magnesium occurred in seawater with nearly constant ratios to calcium (for the last 1 Myr, Broecker and Peng, 1982), and variations in Mg/Ca in benthic foraminiferal tests on shorter timescale are shown to be mainly related to changes in temperature. (Nürnberg et al., 1996; Rathburn and DeDeckker, 1997; Rosenthal et al., 1997; Hastings at al., 1998; Lea et al., 1999; Toyofuku and al., 2000; Lear and al., 2002; Reichart et al., 2003; Anand et al., 2003; Barker et al., 2004). However, other environmental parameters like salinity, and pH or $[CO_3^{-2}]$, may influence Mg incorporation as well. An abrupt change in the elemental compositions of benthic foraminiferal tests with water depth have been related to changes in the local carbonate ion concentration (McCorkle et al., 1995; Elderfield

et al., 1996; Marchitto et al., 2000). However, contradictory responses to variations in pH or [CO_3^{-2}], on Mg incorporation into foraminiferal calcite, have been observed in recent field and culture studies (Lea et al., 1999; Russell et al., 2004; Elderfield et al., 2006; Rosenthal et al., 2006; Rathmann and Kuhnert, 2008). The application of calcitic Sr/Ca ratios in paleoceanography is less straightforward, although it appears to be marginally influenced by temperature (Rathburn and DeDeckker, 1997; Mortyn et al., 2005). Recent studies have shown that variations in [CO_3^{2-}] and consequently in the calcite saturation state (Ω) may determine Sr incorporation (Lea et al., 1999; Russell et al., 2004; Mortyn et al., 2005; Rosenthal et al., 2006; Rathmann and Kuhnert, 2008).

In order to quantify the effect of ocean acidification on foraminiferal calcification and to improve the robustness of proxy based reconstructions, we cultured foraminifera under controlled physico-chemically conditions. We combined test weight and size measurements with Mg/Ca and Sr/Ca analyses of specimens of the symbiont barren, shallow water species Ammonia tepida, grown under different pCO$_2$ conditions (120 and 2000 ppm) two temperatures (10 and 15°C) and two salinities (24 and 33).

2 Material and methods

2.1 Collecting and culturing foraminifera

In spring 2006, live specimens of the symbiont-barren species *A. tepida* (molecular type T6E, Hayward et al., 2004) were collected at an intertidal flat in the German Wadden Sea (near Dorum). Sediments were sieved over a 630 μm mesh to remove larger meiofauna, keeping the finer fraction with the foraminifera in stock-cultures. Within two weeks after collecting, living specimens were picked from these stock-cultures, using an inverted microscope (Zeiss Axiovert 200M) pseudopodial activity (a sign of vitality). Living specimens were subsequently transferred to one of eight semi-closed aquaria. Aquaria contained filtered seawater (0, 2 μm) of salinity 33 (natural seawater from the North Sea, near Helgoland) or salinity 24 (natural seawater diluted with

deionised water, to mimic salinity near the collection site) (Table 1). Two gas mixing pumps (DIGAMIX, H Wösthoff Meßtechnik GmbH) were used to adjust the pCO_2 of the culture water. To prevent evaporation, the water was bubbled with air pre-saturated with water. The pCO_2 of the water was adjusted to 120 ppm (pH=8.4) and 2000 ppm (pH=7.5), respectively. The duration of the experiment was one and a half months. Salinity and pH levels were verified every second day (WTW conductivity meter 330i with TetraCon 325 electrode; WTW pH 3000 with Schott BlueLine Electrodes calibrated with NIST buffers) (Table 1). To minimize bacterial growth and changes in salinity (due to evaporation), growth media were replaced every two weeks. Samples were taken at the start and end of each replacement for dissolved inorganic carbon (DIC), total alkalinity (TA), and elemental composition (ICP-OES) measurements. Dissolved inorganic carbon samples were sterile-filtered (0.2 μm) and stored in 13 mL-borosilicate flasks free of air-bubbles at 4°C until they were measured photometrically with an auto-analyzer (Technicon TRAACS 800, Bran&Lübbe, Norderstedt, Germany) with an average precision of 10 μmol kg^{-1} based on triplicate analyses. Alkalinity samples were stored in 300-mL borosilicate flasks at 4°C and measured in triplicate by potentiometric titration with an average precision of 8 μEq kg^{-1} (Brewer et al., 1986). Total alkalinity was calculated from linear Gran Plots (Gran, 1952). The carbonate chemistry was kept constant during the experiments (Table 1). Foraminifera were fed with a mixture of dried algae (*Phaeodactylum triconortum, Dunaliella salina* and *Isochrisis galbana*) at the beginning of the experiment and every second week when growth media were changed. To each growth medium, 5 mg/L of the fluorescent compound calcein was added. This fluorescent-labelling technique was used as a means to distinguish newly grown calcite (fluorescent) from pre-existing calcite (non fluorescent) after termination of the experiments (Bernhardt et al., 2004) (Fig. 1). Only chambers labelled with calcein were measured by LA-ICP-MS. The Mg and Sr partition coefficients D(Me)=(Me/Ca)ca/(Me/Ca)sw, representing the distribution of the metal (Me), between calcite (ca) and the aqueous phase (sw) from which the minerals form, were calculated for all experimental conditions. The culture experiments were conducted in two paral-

lel series at 10 and 15°C (maximum temperature deviation during the experiment was 0.5°C).

2.2 Measurements with laser Ablation-ICP-MS

2.2.1 Cleaning procedures

Since the foraminifera were cultured without sediment, a rigorous cleaning procedure, required for specimens collected from sediment cores, was not necessary. Instead, a modified cleaning procedure was adopted, in which organic matter is removed by soaking for 30 min in a 3–7% NaOCl solution before analysis (Gaffey and Brönniman, 1993). A stereomicroscope was used during cleaning and specimens were removed from the reagent directly after complete bleaching, in order to avoid dissolution of the final, (often thinner), chambers. The samples were immediately and thoroughly rinsed with deionised water to ensure complete removal of the reagent.

2.2.2 Laser Ablation-ICP-MS

Newly formed chambers were ablated using an Excimer laser (Lambda Physik) with GeoLas 200Q optics inside an ablation chamber flushed with helium (Reichart et al., 2003). Pulse repetition rate was set at 6 Hz, with an energy density at the sample surface of 4 J/cm^2. Ablation craters were 80 μm in diameter (Fig. 2) and ablated material was analyzed with respect to time (and hence depth) using a quadrupole ICP-MS instrument (Micromass Platform ICP-MS). Analyses were calibrated against NIST SRM 610 glass, using concentration data of Pearce et al. (1997) with Ca as an internal standard. Calcium is ideal, because the concentration is constant at 40 wt % in all foraminiferal tests, and because it allows direct comparisons with trace metals to Ca ratios from wet-chemical studies. Concentrations of Mg and Sr were calculated using ^{24}Mg and ^{88}Sr. An in-house matrix matched carbonate standard was used to verify potentially different ablation behaviour for glass and carbonate. Simultaneous monitoring

of Al and Mn allowed us to discard profiles contaminated, or part of the profiles, from further calculations of elemental concentrations.

2.3 Size/weight measurements

Sizes of the foraminiferal tests were measured (maximum diameter) with a stereomi-croscope (ZEISS Stemi SV 11). They were subsequently washed with deionised water, dried in an oven at 50°C for 3 h, and transferred to a desiccator. The following day foraminifera were weighed using a Micro Analytical Lab Balance (Mettler Toledo UMX2) with a precision of 0.1 μg. Test weight versus test size is plotted for each experimental condition (Fig. 3). Tests were weighed after laser ablation. Although some material is removed during ablation, the amount can be neglected since only a small part of the last chamber (from an average of about 20 chambers per individuals) was removed. Moreover, since a similar amount of material was removed from each test, inter experimental differences are not affected. Different experimental conditions (carbonate ion concentration and temperature) may influence the number of new chambers grown during the experiment. To avoid systematic offsets caused by the contrasting experimental conditions only specimens (size range 350–500 μm) that added two or three new chambers during the experiment were used for weight analyses.

2.4 Carbonate system

The semi-enclosed culture system allowed us to bubble the growth medium with air with different preset $p\mathrm{CO_2}$. Differences in $p\mathrm{CO_2}$ result in differences in $[\mathrm{CO_2(aq)}]$, pH and DIC (DIC=$[\mathrm{CO_3^{2-}}]$+$[\mathrm{HCO_3^-}]$+$[\mathrm{CO_2(aq)}]$), while TA (TA$\approx$$[\mathrm{HCO_3^{2}}]$+2$[\mathrm{CO_3^{2-}}]$+$[\mathrm{B(OH)_4^-}]$+$[\mathrm{OH^-}]$+$[\mathrm{H^+}]$) remains constant. Laboratory experiments can be a powerful tool to elucidate natural processes. To reveal the underlying mechanisms, however, it is often necessary to alter the physico-chemical conditions beyond the range typically observed in nature. Therefore, two extreme values for $\mathrm{CO_2}$ (2000 ppm and 120 ppm) were selected. Dissolved inorganic carbon, pH and TA of the

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growth media bubbled with a pCO2 of 2000 ppm are given in Table 1. A pCO$_2$ of 2000 drives the system to lower [CO$_3^{2-}$] (Bjerrum, 1914) and, therefore, decreases the calcite saturation state Ω (Ω=Ion Activity Product (IAP)/ Ksp, where Ksp represents the solubility product of calcite) below saturation (less than 1). On the other hand, bubbling with a low concentration of CO$_2$ (120 ppm) allows us to mimic the impact of extremely low atmospheric pCO$_2$ on the carbonate chemistry of the seawater, with a significant decrease in DIC and an increase in pH (Table 1). This results in a significant increase of the calcite saturation state Ω. As CO$_2$ is more soluble in cold water, pH and Ω are lower at 10°C compared to 15°C. A decrease in salinity from 33 to 24 decreases both [Ca^{2+}] and [CO$_3^{2-}$]. As a result TA decreases by approximately 25% and Ω by 50%. The carbonate system was calculated from TA, DIC, temperature, and salinity using the CO$_2$ Sys program (Lewis and Wallace, 1998) (equilibrium constants of Mehrbach et al. (1973) as refitted by Dickson and Millero (1987) were chosen). Omega values are presented in table 1. In order to cross-check analyses, pH values calculated with the CO$_2$ Sys program (pH calculated), based on DIC and TA measurements, and measured pH values during the experiment (pH measured) are compared in Table 1.

3 Results

3.1 Calcite added and survival rate

In all experiments at least 50% of the specimens added new chambers (Fig. 1), regardless of variation in pCO$_2$ (Table 2). Even at undersaturated conditions (Ω<1) most specimens survived and calcified, no dissolution was observed. At salinity 24, which is closer to their natural environment, the number of new chambers per specimen was higher than at salinity 33. The results of the LA-ICP-MS measurements are shown in Table 2. The limited size (<100 µm) of chambers did not allow multiple analyses of single chambers. To avoid an impact of ontogeny only measurements from specimens between 350 µm to 500 µm were taken into account. None of the newly added

chambers showed abnormalities.

3.2 Weight measurements

Specimens grown at a pCO$_2$ of 2000 ppm, when cultured under the same temperature and salinity conditions, are generally lighter than those grown at a pCO$_2$ of 120 ppm (Fig. 3). Specimens grown at 15°C, when grown under the same pCO$_2$ and salinity conditions, are lighter compared to the specimens grown at 10°C (Fig. 4a and b). Only the newly grown chambers are responsible for the observed differences, since the initial parts of the tests were grown under natural conditions. The observed differences between the different experiments will, therefore, underestimate the impact of the different variables.

3.3 Elemental concentration

The Mg/Ca of *A. tepida* is low (between 0.4 and 0.8 mmol/mol; Table 4) compared to other species (Benthov and Erez, 2006). Overall values of Sr/Ca ratios vary between 1.25 and 1.50 mmol/mol (Table 4). The Mg and Sr partition coefficients are calculated for each experiment and plotted against pCO$_2$ (Fig. 5). At salinity 33, D(Mg) increases strongly with temperature. The increase in D(Mg) with increasing temperature is much less obvious at salinity 24. At 15°C D(Mg) increases with increasing salinity, which is not observed at 10°C. Due to loss of specimens during sample handling, elemental concentrations of the 10°C and salinity 33 experiment, are based on a small number of foraminifera (Table 2), increasing their error. A larger uncertainty could result in an underestimation of the D(Mg) of the experiment at salinity 33, 10°C, explaining the lack in correlation. No appreciable change in D(Mg) with pCO$_2$ was observed in our experiments (Fig. 5a). However, decreases of D(Sr) with increasing pCO$_2$, are clearly visible (Fig. 5b).

4 Discussion

4.1 Temperature and [CO_3^{2-}] impact on shell weight

Shells weight increases with increasing [CO_3^{2-}] (Fig. 3). For the first time we show an experimentally determined [CO_3^{2-}]/"size normalized weight" correlation for a shallow
5 water benthic species. Such a positive correlation between shell weight and carbonate ion concentration is in agreement with previous publications for others calcifying organisms. Indeed, although some coccolithophores show species specific responses (Langer et al., 2006), most studies indicate a decrease in calcification at higher [CO_2] (e.g. Gattuso et al., 1998; Kleypas, 1999; Bijma et al., 1999; Gattuso and Buddemeier,
10 2000; Riebesell et al., 2000; Zondervan et al., 2001). Planktonic foraminiferal culture studies report that ambient water [CO_3^{2-}] primarily controls shell thickness and, by extension, shell weight of two planktonic foraminiferal species *Orbulina Universa* and *Globigerinoides sacculifer* (Russell et al., 2004; Bijma et al., 1999, 2002). On the other hand, it has been suggested that shell thickness is closely related to temperature
15 (Barker and Elderfield, 2002). This link is, however, also through changes in carbonate chemistry as CO_2 solubility in seawater depends on the temperature (see Sect. 2.4). Subsequent dissociation of $CO_{2(aq)}$ into HCO_3^- and CO_3^{2-}, induce a temperature dependence of the open ocean water [CO_3^{2-}]. The co-variation of these two parameters made it difficult to deconvolve their respective impact on shell weight. In sediment cores
20 from the North Atlantic, Barker and Elderfield (2002) observed a decrease in *G. bulloides* shell weight from the last termination towards the Holocene. Considering that [CO_3^{2-}] decreases while temperature increases during the deglaciation, this suggests that [CO_3^{2-}] is the primary control of foraminiferal tests weight. In our experiment, shell weight decreases with increasing temperature (Fig. 4a and b). However, the design
25 of our controlled growth experiments did not allow changing the temperature without affecting [CO_3^{2-}] (Table 1). To still deconvolve the effects of temperature and carbonate ion concentration, test size normalized weight (400 μm) was plotted versus [CO_3^{2-}]

based on alkalinity and DIC measured in the culture media (Fig. 4c) (using the CO2 sys program (Lewis and Wallace, 1998), were the impact of temperature on [CO_3^{2-}] is considered in the calculation). Figure 4c shows a negative correlation between temperature and shell weight. For planktonic foraminifera it has been shown that shell weight increases with increasing temperature (Barker and Elderfield, 2002). This contradicts the observation for *A. tepida*. Many hypotheses could explain these different responses to temperature variations, such as lower optimal growth temperatures. For planktonic symbiont-bearing species (e.g. *G. sacculifer*), variations in symbiotic activity have been shown to impact shell size and therefore shell weight (Be et al., 1982). Additional culture experiments are required to verify whether our observations can be extended to benthic species from the deeper part of the water column.

4.2 [CO_3^{2-}] impact on Mg/Ca

Incorporation of Mg in *A. tepida* tests is independent of changes in the carbonate ion concentration of the culture medium (Fig. 6a) (linear regression p=0.699; 0.902; 0.619; 0.967; for the experimental conditions 24, 10°C; 24‰, 15°C; 33‰, 10°C; 33‰, 15°C, respectively). To our knowledge, only two culture studies previously investigated the effect of [CO_3^{2-}] (or pH) on Mg incorporation into foraminiferal test carbonate. Lea et al. (1999) measured the Mg concentration of the symbiont bearing species O. universa and symbiont barren species *G. bulloides* grown under different pH conditions. They observed for both species a decrease in Mg/Ca ratios of about 6% per 0.1 pH unit increase. Russell et al. (2004) report for the same species a similar Mg/Ca decrease of about 7% (*O. universa*) and 16% (*G. bulloides*) respectively per 0.1 unit increase below ambient pH (8.2). No significant changes in Mg incorporation were observed in the same study above ambient pH. Both Lea et al. (1999) and Russell et al. (2004) modified seawater by adding NaOH and HCl (constant DIC, varying TA), whereas in our experiments carbonate chemistry was modified through bubbling with air with different preset pCO$_2$ (varying DIC, constant TA). This fundamental difference in adjusting pCO$_2$ could potentially affect trace element incorporation differently. When studying

Ammonia tepida

D. Dissard et al.

Full Screen / Esc

the impact of carbonate chemistry on isotopic fractionation, Bijma et al. (1999) tested this by culturing planktonic foraminifera under (1) constant TA, and varying DIC, and (2) constant DIC, and varying TA. For both experimental approaches Orbulina universa shell δ^{18}O and δ^{13}C decreased as [CO_3^{2-}] increased with similar slopes.

5   To our knowledge no others culture studies have been carried out to investigate the Mg incorporation as a function of [CO_3^{2-}] in benthic foraminifera. In the natural environment Martin et al. (2002), Lear et al., (2004), and Elderfield et al. (2006) observed lowered Mg/Ca ratios in the foraminiferal calcite of Cibicidoides species, at temperature below $\sim 3°$C, coinciding with a steep increase in the oceanic [CO_3^{2-}] gradient. Also,

10 Rosenthal et al., (2006) report a decrease of Mg/Ca ratio in the tests of the aragonitic species Hoeglundina elegans below the aragonite saturation level (15 μmol/kg). Therefore, Elderfield at al., 2006 suggested that below a certain Δ[CO_3^{2-}] threshold value, D(Mg) is lowered by a linear carbonate ion effect. In order to compare our values with these studies we calculated the calcite saturation level Δ[CO_3^{2-}], using the equation

15 from Broecker and Peng (1982), where Δ[CO_3^{2-}]=[CO_3^{2-}]$_{in\ situ}$ −[CO_3^{2-}]$_{saturation}$. Calcite [CO_3^{2-}]$_{saturation}$= Ksp/[Ca^{2+}] (Ksp was calculated following Millero (1995), and [Ca^{2+}] is based on measured concentrations in our growth media) (Table 3). The range of Δ[CO_3^{2-}] calculated for our experiments varies from −26 μmol/kg to 213 μmol/kg. These values include the Δ[CO_3^{2-}] range below which D(Mg) should be reduced by a

20 linear carbonate ion effect. However, we do not observe any significant variation in Mg incorporation as a function of Δ[CO_3^{2-}]. Still, in our experimental setup, Δ[CO_3^{2-}] is manipulated by bubbling with preset pCO$_2$ air. In the abyssal ocean, [CO_3^{2-}]$_{saturation}$ increases mainly with water depth as a result of increasing pressure. In that case a potential effect of pressure on the partition coefficient D(Mg), instead of carbonate

25 ion concentration,can not be excluded. Also Rathburn and DeDecker (1997) did not observe any departure from the established Mg/Ca /T°C calibration below 3°C for Cibicidoides sp., whereas Rathmann and Kuhnert (2008), observe only little resemblance between temperature corrected Mg/Ca ratios (*Oridorsalis umbonatus)* and [CO_3^{2-}].

In a recent study Raitzsch et al. (2008) report that variations in DIC affect temperature corrected Mg/Ca values of *C. wuellerstorfi*. In our experiments, Mg partition coefficients in *A. tepida* calcite do not respond to changes in DIC. The variations in D(Mg) observed between experimental conditions (Figs. 5a and 6a), are explained by changes in temperature and salinity alone.

4.3 [CO_3^{2-}] impact on Sr/Ca

The incorporation of Sr increases with increasing [CO_3^{2-}] (increasing pH) (Fig. 6b and c). To test for significance, statistic tests performed with the statistic program R (R Development Core Team (2005); http://www.r-project.org) were applied to the data (Table 5). First, normalities were checked by the means of a shapiro test. Only one experimental condition (S=24, 15°C, 120 ppm) appears to deviate significantly from normality. Subsequently, a F-test was applied to look at the variance to the mean value of the experiments run at same salinity and temperature, but varying pCO$_2$ conditions. None of them appeared to be significantly different. Finally, a F-test (one sided) was made in order to test whether lower [CO_3^{2-}] resulted in lower mean DSr at constant temperature and salinity conditions. When considering alpha=7%, mean DSr measured at enhanced [CO_3^{2-}], are significantly higher than mean DSr measured at lower [CO_3^{2-}], for three of the four experimental conditions (24‰, 10°C; 24‰, 15°C; 33‰, 15°C). For these three conditions, the incorporation of Sr can be considered to increase significantly with increased [CO_3^{2-}]. At salinity 24, Sr/Ca ratios increased from 1.25 to 1.33, and from 1.34 to 1.50, for an increase of 0.8 unit pH, at 10 and 15°C, respectively. At salinity 33, Sr/Ca ratios increased from 1.35 to 1.47 and from 1.38 to 1.48, for the same pH increase of 0.8 unit, at 10°C and 15°C respectively. These results are in good agreement with previous observations made by Lea et al. (1999) (1.1±0.5 % increase per 0.1 pH unit) and Russell et al. (2004) (1.6±0.4% increase per 0.1 pH unit) for O. universa (Fig. 7). However, these two studies also show insensitivity of Sr/Ca to pH in another planktonic foraminiferal species, *G. bulloides.* To explain this species-specific

response, Russell et al. (2004) proposed that changes in ambient pH impact photosynthetic activity of the symbionts and hence calcification rate in *O. Universa*. Strontium in turn is affected by the calcification rate in inorganic calcite precipitation (Nehrke et al., 2007). Since *G. bulloides* has no symbionts, no impact of pH was observed. Ammonia tepida, like *G. bulloides*, is a symbiont barren species; therefore changes in pH (or $[CO_3^{2-}]$) do not (only) affect Sr incorporation via an impact on symbiont activity.

A $[CO_3^{2-}]$ control on benthic Sr/Ca was first suggested by Elderfield et al. (1996). However, the positive correlation of $[CO_3^{2-}]$ with other environmental parameters such as temperature (see Sect. 4.1) or salinity (Zeebe and Wolf Gladrow, 2001) observed in the natural environment makes the interpretation of the Sr incorporation/$[CO_3^{2-}]$ dependence in benthic foraminifera, difficult. Rosenthal et al. (2006) support the observation that higher $[CO_3^{2-}]$ increased the Sr incorporation in the aragonitic benthic foraminifer Hoeglundina elegans in waters undersaturated with respect to aragonite. On the other hand, Rathman and Kuhnert (2007), observed an increase of the Sr incorporation of the endobenthic species O. umbonatus with decreasing $[CO_3^{2-}]$ of the pore-water.

In our experiments, the Sr concentration of *A. tepida* increases with increasing temperature and salinity (Table 4, Figs. 5b and 6b). As explained in Sect. 2.4, CO_2 is more soluble in cold water. Hence an increase in temperature leads to a decrease in $[CO_{2(aq)}]$, and a subsequent increase in $[CO_3^{2-}]$. On the other hand, an increase in salinity by evaporation increases both $[Ca^{2+}]$ and $[CO_3^{2-}]$. As can be seen from Fig. 6b, D(Sr) increases with increasing $[CO_3^{2-}]$. Therewith it appears that $[CO_3^{2-}]$ is the main parameter controlling Sr incorporation. Inorganic precipitation experiments suggest that higher Sr/Ca is associated with higher calcification rates (Lorens, 1981; Tesoriero and Pankow, 1996). In our experiments we observed that, at equal temperature and salinity, increasing $[CO_3^{2-}]$ induced increasing shells weight (see Sect. 4.1). Hence, it seems likely that higher $[CO_3^{2-}]$ induces an increase of the Sr incorporation via increasing calcification rate.

Ammonia tepida

D. Dissard et al.

5   Conclusions

Ammonia tepida shell weight increases with increasing $[CO_3^{2-}]$, and decreases with increasing temperature. Changes in $[CO_3^{2-}]$ or DIC do not affect the Mg partition coefficient of *A. tepida.*, but D(Sr) increases with increasing $[CO_3^{2-}]$ (increasing pH). Furthermore it is shown that A. tepida is able to calcify at undersaturated conditions ($\Omega \sim 0.5$), without showing signs of dissolution.

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D. Dissard et al.

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Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

◄ | ►

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Table 1. Carbonate chemistry of the culture media. Experiments ran for one and a half month. Alkalinity and DIC were analysed every two weeks, salinity and pH every second day. Numbers represent average values of Alkalinity, DIC, salinity and pH measured for each experimental condition. Ω, $[HCO_3^-]$, $[CO_3^{2-}]$, pH cal., and pCO$_2$cal. were calculated with the CO$_2$ Sys program (Lewis and Wallace, 1998) from measured alkalinity, DIC, temperature and salinity.

Experimental Conditions	T ALK (μeq kg^{-1})	DIC (μmol kg^{-1})	Average Salinity	pH meas . (NBS)	pH cal . (NBS)	Ω	$[HCO_3^-]$ (μmol kg^{-1})	$[CO_3^{2-}]$ (μmol kg^{-1})	pCO$_2$cal. (ppm)
Sal 24, 10°C, 120 ppm	1.868(±26)	1.703(±14)	24.70(±0 .40)	8.31(±0 .07)	8.33	3.00	1573	119	232
Sal 24, 10°C, 2000 ppm	1.916(±67)	1.981(±61)	24.77(±0.46)	7.49(±0.04)	7.46	0.49	1868	19	2017
Sal 24, 15°C, 120 ppm	1.891(±33)	1.696(±27)	24.56(±0.35)	8.39(±0.06)	8.33	3.57	1546	141	239
Sal 24, 15°C, 2000 ppm	1.931(±47)	1.971(±83)	24.60(±0.37)	7.53(±0.05)	7.50	0.64	1869	25	1940
Sal 33, 10°C, 120 ppm	2.558(±15)	2.232(±59)	33.20(±0.54)	8.36(±0.09)	8.41	5.68	1987	236	223
Sal 33, 10°C, 2000 ppm	2.507(±44)	2.526(±36)	32.80(±0.52)	7.52(±0.03)	7.59	1.02	2404	42	1803
Sal 33, 15°C, 120 ppm	2.537(±54)	2.175(±81)	32.70(±0.50)	8.39(±0.11)	8.41	3.36	1904	263	229
Sal 33, 15°C, 2000 ppm	2.506(±17)	2.504(±41)	33.14(±0.58)	7.61(±0.03)	7.59	1.23	2383	51	1868

Table 2. Number of individuals at the start of the experiments, number of specimens that added new chambers, total number of added chambers, number of LA-ICP-MS measurements used for elemental concentration calculations.

Experimental Conditions	Number of specimens at the beginning of the experiment	Number of specimens presenting new chambers at the end of the experiment	Number of new chambers added	Number of LA-ICP-MS measurements used for elemental concentrations
Sal 24, 10°C, 120 ppm	50	31	64	10
Sal 24, 10°C, 2000 ppm	50	41	86	19
Sal 24, 15°C, 120 ppm	50	29	82	15
Sal 24, 15°C, 2000 ppm	50	33	83	17
Sal 33, 10°C, 120ppm	50	30	67	5
Sal 33, 10°C, 2000ppm	50	30	63	3
Sal 33, 15°C, 120ppm	50	29	47	11
Sal 33, 15°C, 2000ppm	50	31	65	12

Table 3. Measured [Mg $^{2+}$], [Sr $^{2+}$], [Ca $^{2+}$] (mg/kg), Mg/Ca (mol/mol) and Sr/Ca (mmol/mol) of the growth media. The experiment ran for one and a half month. Growth media were changed every two weeks. The numbers indicated represent average values of [Mg $^{2+}$], [Sr $^{2+}$], [Ca $^{2+}$], Mg/Ca and Sr/Ca for each experimental condition.

Experimental conditions	Average [Mg $^{2+}$] in mg/kg	Average [Sr $^{2+}$] in mg/kg	Average [Ca $^{2+}$] in mg/kg	Average Mg/Ca in mol/mol	Average Sr/Ca in mmol/mol
Sal 24, 10˚C, 120 ppm	775.25±21	4.51±0.09	241.46±5	5.297±51	8.54±0.0259
Sal 24, 10˚C, 2000 ppm	781.78±28	4.56±0.15	244.59±8	5.270±53	8.52±0.0381
Sal 24, 15˚C, 120 ppm	776.78±22	4.53±0.12	242.32±6	5.286±37	8.55±0.0364
Sal 24, 15˚C, 2000 ppm	782.02±28	4.54±0.13	244.28±7	5.279±30	8.50±0.0261
Sal 33, 10˚C, 120 ppm	1083.39±37	6.01±0.21	331.29±8	5.392±81	8.40±0.0844
Sal 33, 10˚C, 2000 ppm	1024.09±27	6.02±0.13	328.62±6	5.390±68	8.37±0.0625
Sal 33, 15˚C, 120 ppm	1084.66±39	6.08±0.20	331.62±9	5.391±69	8.38±0.0635
Sal 33, 15˚C, 2000 ppm	1073.04±25	6.07±0.18	331.17±8	5.344±74	8.38±0.0596

Table 4. Measured Mg/Ca and Sr/Ca ratios in foraminiferal calcite in mmol/mol and calculated partition coefficient $D_{(Mg)}$ and $D_{(Sr)}$ for each experimental condition.

Experimental conditions	Average Mg/Ca in mmol/mol	Average Sr/Ca in mmol/mol	D(Mg)= (Mg/Ca)ca/((Mg/Ca)sw)	D(Sr)= (Sr/Ca)ca/((Sr/Ca)sw)
Sal 24, 10°C, 120 ppm	0.47±0.12	1.33±0.10	$8.84 \times 10^{-5} \pm 3.6 \times 10^{-6}$	$0.156 \pm 4 \times 10^{-3}$
Sal 24, 10°C, 2000 ppm	0.44±0.19	1.25±0.17	$8.35 \times 10^{-5} \pm 2.5 \times 10^{-6}$	$0.147 \pm 2 \times 10^{-3}$
Sal 24, 15°C, 120 ppm	0.52±0.13	1.50±0.09	$9.75 \times 10^{-5} \pm 4 \times 10^{-6}$	$0.176 \pm 5 \times 10^{-3}$
Sal 24, 15°C, 2000 ppm	0.51±0.13	1.34±0.13	$9.64 \times 10^{-5} \pm 4 \times 10^{-6}$	$0.157 \pm 4 \times 10^{-3}$
Sal 33, 10°C, 120 ppm	0.52±0.15	1.47±0.16	$9.63 \times 10^{-5} \pm 3.8 \times 10^{-6}$	$0.175 \pm 5 \times 10^{-3}$
Sal 33, 10°C, 2000 ppm	0.47±0.09	1.35±0.20	$8.69 \times 10^{-5} \pm 4.8 \times 10^{-6}$	$0.161 \pm 7 \times 10^{-3}$
Sal 33, 15°C, 120 ppm	0.79±0.25	1.48±0.13	$1.46 \times 10^{-4} \pm 4 \times 10^{-6}$	$0.176 \pm 3 \times 10^{-3}$
Sal 33, 15°C, 2000 ppm	0.77±0.28	1.38±0.14	$1.45 \times 10^{-4} \pm 4 \times 10^{-6}$	$0.165 \pm 3 \times 10^{-3}$

Table 5. Statistical test (Shapiro-test, F-test, and t-test)applied to DSr values, using statistic program R (R Development Core Team (2005); http://www.r-project.org).

Normality test		
Experimental conditions	p-value Shapiro-test	$[CO_3^{2-}](\mu mol\,kg^{-1})$
Sal 24, 10˚C, 120 ppm	0.12	19
Sal 24, 10˚C, 2000 ppm	0.14	119
Sal 24, 15˚C, 120 ppm	0.73	25
Sal 24, 15˚C, 2000 ppm	**0.005** significant deviation from normality	141
Sal 33, 10˚C, 120 ppm	0.32	42
Sal 33, 10˚C, 2000 ppm	0.3	236
Sal 33, 15˚C, 120 ppm	0.42	51
Sal 33, 15˚C, 2000 ppm	0.1	263
Variance test (F-test)		
Experimental conditions	p-pvalue	variances between the 2 pCO$_2$ traitments
Sal 24, 10˚C	0.07637985	non sign.
Sal 24, 15˚C	0.178337	non sign.
Sal 33, 10˚C	0.63579	non sign.
Sal 33, 15˚C	0.8981978	non sign.

t-test of means one sided, to test whether lower $[CO_3^{2-}]$ show a lower mean $D_{(Sr)}$

Experimental conditions the 2 pCO$_2$ traitments	p-pvalue	t-statistic	
Sal 24, 10˚C	0.05896754	−1.615334	almost sign. Alpha=6 %
Sal 24, 15˚C	0.000305219	−3.851206	significant
Sal 33, 10˚C	0.2187368	−0.871139	excluded
Sal 33, 15˚C	0.06227677	−1.600072	almost sign. Alpha=7 %

Fig. 1.

200μm
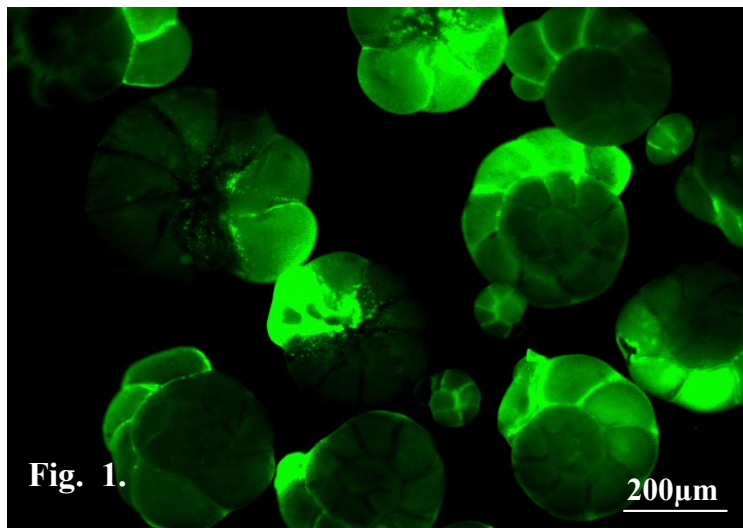
Fig. 1. Newly formed chambers are visible under fluorescent light as a result of the incorporation of calcein.

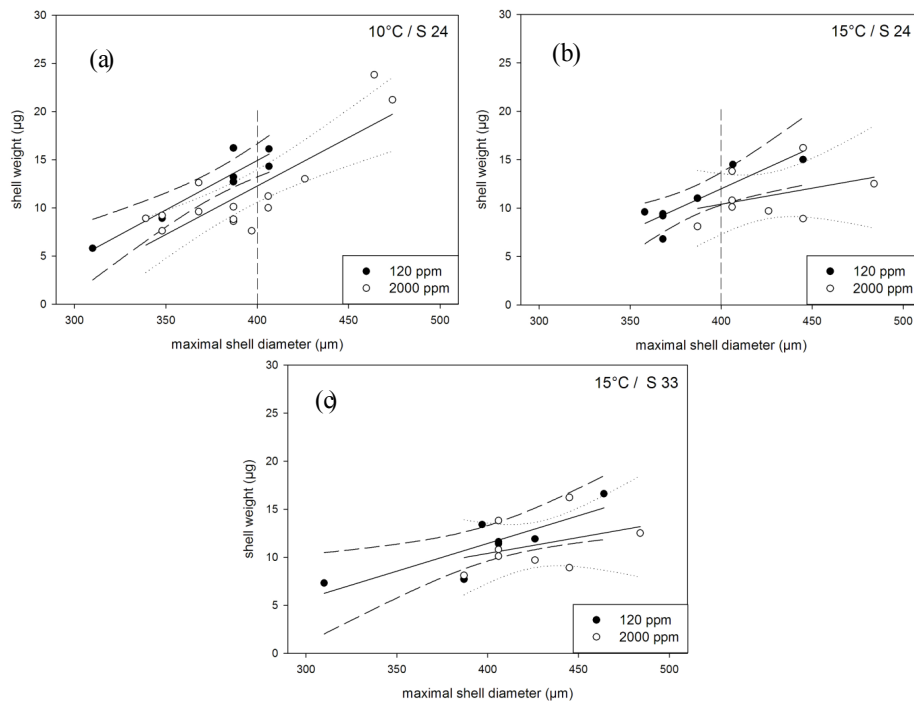**Fig. 2.** Scanning electron microscope image of laser ablation craters in *Ammonia tepida*.

Fig. 3. Weight (μg) versus size (μm) of foraminifera grown under 120 ppm (closed circles) and 2000 ppm (open circles), at 10°C, salinity 24 **(a)**, at 15°C, salinity 24 **(b)**, and at 15°C, salinity 33 **(c)**. Data for 10°C and salinity 33 not available.
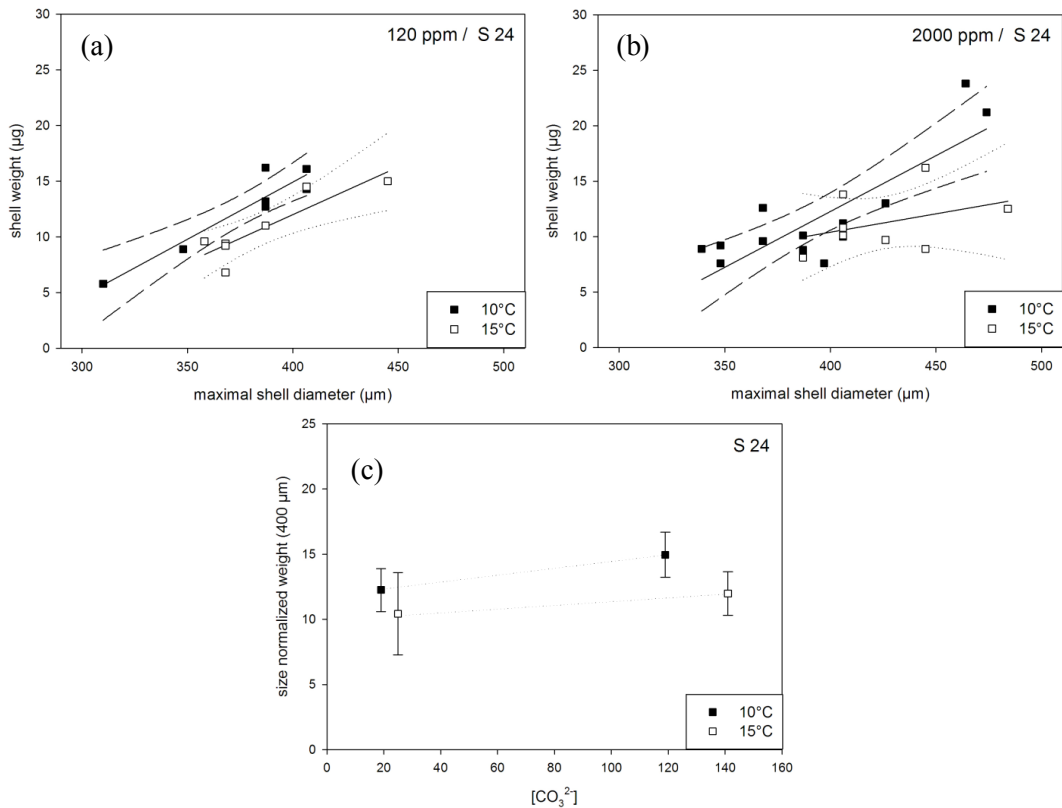
Fig. 4. Weight (μg) versus size (μm) of foraminifera grown at salinity 24, under 120 ppm **(a)** and 2000 ppm **(b)**. Closed squares represent foraminifera grown at 10°C and open squares foraminifera grown at 15°C. **(c)** represents size normalized weight (400 μm), calculated for each experimental condition using the linear regression obtained in Fig. 4a and b, versus [CO_3^{2-}].

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

◄ | ►

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion
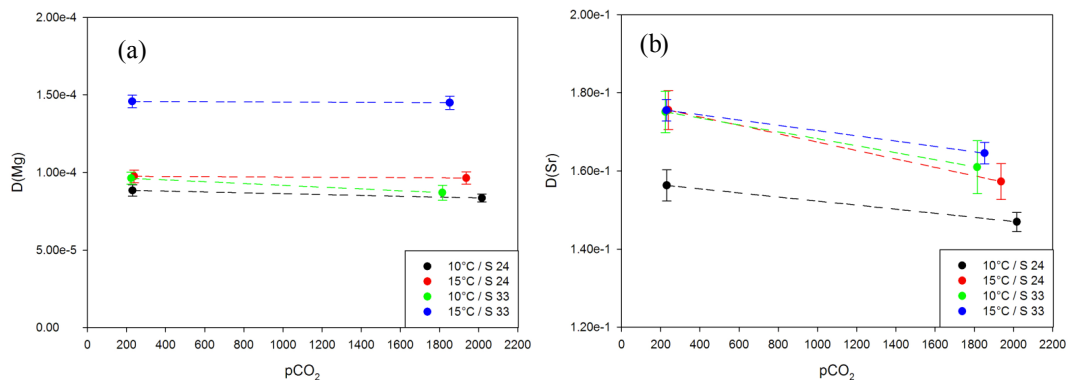
Fig. 5. Mg Partition coefficient (D(Mg)) **(a)** and Sr partition coefficient (D(Sr)) **(b)** at 120 ppm and 2000 ppm, at 10˚C, salinity 24 (black), 15˚C, salinity 24 (red), 10˚C, salinity 33 (green), and 15˚C, salinity 33 (blue). Every point is an average of the partition coefficients calculated per experimental condition.
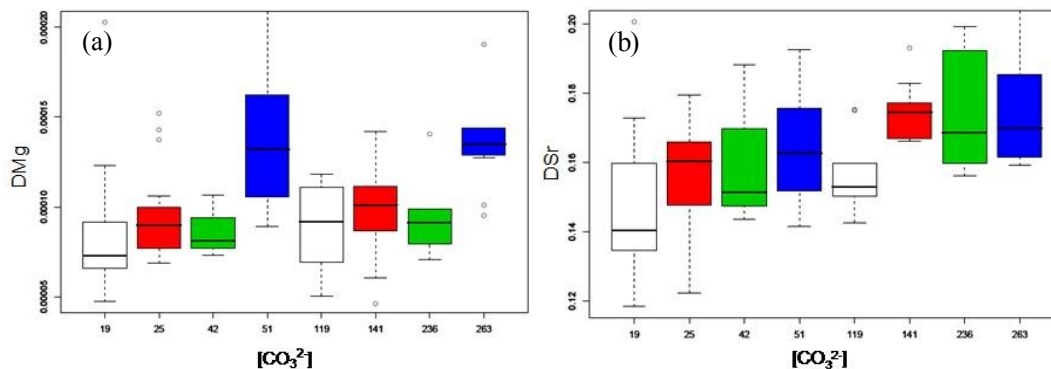
Fig. 6. Mg Partition coefficient (D(Mg)) **(a)** and Sr partition coefficient (D(Sr)) **(b)** versus $[CO_3^{2-}]$ at 10°C, salinity 24 (black), 15°C, salinity 24 (red), 10°C, salinity 33 (green), and 15°C, salinity 33 (blue). The rectangle and the solid lines represent the repartition and the mean of the partition coefficients calculated per experimental condition, respectively.
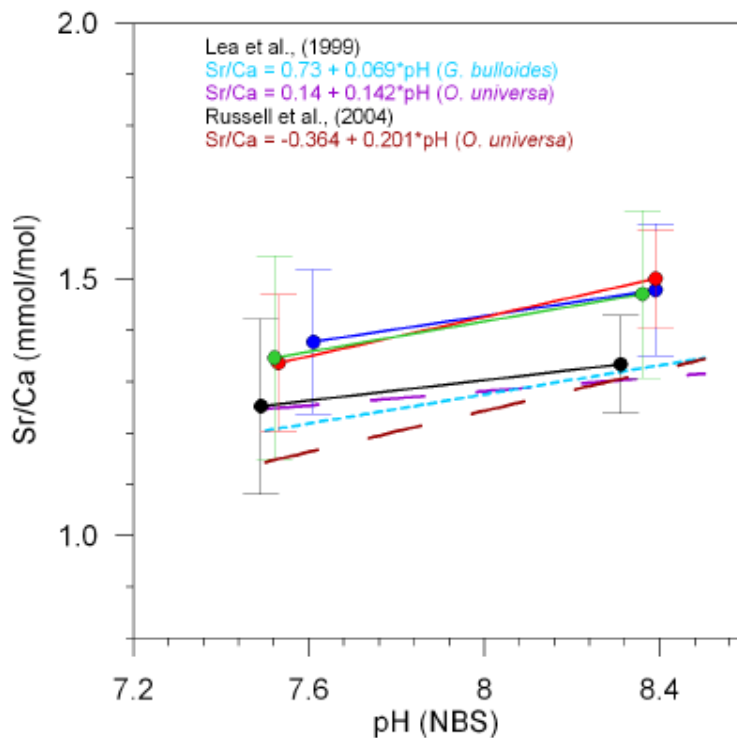
Fig. 7. Sr/Ca ratios in Ammonia tepida (solid lines this study, average of the Sr/Ca ratios calculated per experimental condition, same color code used as in Fig. 6), in Orbulina universa (dashed lines, Lea et al., 1999 and Russell et al., 2004) and in Globigerinoides bulloides (doted lines, Lea et al., 1999), versus pH (NBS).