



The influence of salinity on Mg/Ca in planktic foraminifers – Evidence from cultures, core-top sediments and complementary $\delta^{18}\text{O}$

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Abstract

The Mg/Ca ratio in foraminiferal calcite is one of the principal proxies used for paleoceanographic temperature reconstructions, but recent core-top sediment observations suggest that salinity may exert a significant secondary control on planktic foraminifers. This study compiles new and published laboratory culture experiment data from the planktic foraminifers *Orbulina universa*, *Globigerinoides sacculifer* and *Globigerinoides ruber*, in which salinity was varied but temperature, pH and light were held constant. Combining new data with results from previous culture studies yields a Mg/Ca-sensitivity to salinity of $4.4 \pm 2.3\%$, $4.7 \pm 1.2\%$, and $3.3 \pm 1.7\%$ per salinity unit (95% confidence), respectively, for the three foraminifer species studied here. Comparison of these sensitivities with core-top data suggests that the much larger sensitivity ($27 \pm 4\%$ per salinity unit) derived from Atlantic core-top sediments in previous studies is not a direct effect of salinity. Rather, we suggest that the dissolution correction often applied to Mg/Ca data can lead to significant overestimation of temperatures. We are able to reconcile culture calibrations with core-top observations by combining evidence for seasonal occurrence and latitude-specific habitat depth preferences with corresponding variations in physico-chemical environmental parameters. Although both Mg/Ca and $\delta^{18}\text{O}$ yield temperature estimates that fall within the bounds of hydrographic observations, discrepancies between the two proxies highlight unresolved challenges with the use of paired Mg/Ca and $\delta^{18}\text{O}$ analyses to reconstruct paleo-salinity patterns across ocean basins. The first step towards resolving these challenges requires a better spatially and seasonally resolved $\delta^{18}\text{O}_{\text{sw}}$ archive than is currently available. Nonetheless, site-specific reconstructions of salinity change through time may be valid.

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1. INTRODUCTION

The oxygen isotopic composition ($\delta^{18}\text{O}_{\text{foram}}$) and Mg/Ca ratios of planktic foraminifer tests are among the most com-

monly applied proxies for reconstructing past ocean temperature. The theoretical basis for $\delta^{18}\text{O}$ in marine carbonates as a temperature proxy is rooted in the temperature-dependent bonding characteristics of oxygen isotopes (Urey, 1947). Application of the $\delta^{18}\text{O}_{\text{foram}}$ proxy in sediment and laboratory studies requires accounting for variations in the oxygen isotopic composition of seawater ($\delta^{18}\text{O}_{\text{sw}}$), photosynthetic

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activity in symbiont-bearing species, and marine carbonate chemistry (for a summary, see Bemis et al., 1998). In contrast, the mechanism underlying the temperature sensitivity of Mg/Ca is not as well understood. The substitution of Mg^{2+} into marine calcites is thermodynamically favored at higher temperatures (Chave, 1954; Mucci, 1987; Oomori et al., 1987; Koziol and Newton, 1995), but the observed temperature response in foraminiferal calcite is much larger than predicted by theory (i.e. 9% per °C versus 1–3% per °C, Lea et al., 1999; Anand et al., 2003). In addition, planktic foraminifers discriminate heavily against the incorporation of Mg^{2+} into their calcite skeletons, such that their Mg/Ca ratio is 1–2 orders of magnitude lower (e.g., Lea et al., 1999) than inorganically precipitated calcite (Oomori et al., 1987). The discrepancy between theory and observations indicates that the empirical relationship is influenced by additional environmental parameters and/or physiological vital effects.

Laboratory culture experiments that isolate the effects of individual environmental parameters have been used to identify secondary controls on Mg/Ca uptake into planktic foraminifer tests. For instance, Lea et al. (1999) observed a negative relationship between seawater-pH and Mg/Ca uptake, although it was later determined that this effect is greater at lower-than-modern seawater-pH (Russell et al., 2004). Laboratory culture experiments have also established that salinity exerts a small effect on Mg/Ca, which increases by 4–8% per salinity unit (Nürnberg et al., 1996; Lea et al., 1999; Kısakürek et al., 2008; Dueñas-Bohórquez et al., 2011). Recent core-top sediment studies, however, suggest that the Mg/Ca sensitivity to salinity is much greater than that measured in culture experiments, up to 59% per salinity unit (Ferguson et al., 2008; Mathien-Blard and Bassinot, 2009; Arbuszewski et al., 2010). Although data by Ferguson et al. (2008) have been questioned due to the presence of a Mg-rich post-depositional calcite precipitate on Mediterranean foraminifer tests (Hoogakker et al., 2009; Mathien-Blard and Bassinot, 2009), the comprehensive study by Arbuszewski et al. (2010) suggests a large 27% sensitivity to salinity for the tropical planktic foraminifer *Globigerinoides ruber* where ambient salinity exceeds 35. This latter assessment was based on a comparison of Mg/Ca and $\delta^{18}O_{\text{foram}}$ data obtained from the same samples of pooled foraminifera tests, in which $\delta^{18}O_{\text{foram}}$ compositions appeared to agree with mean annual SST (Arbuszewski et al., 2010). Arbuszewski et al. (2010) quantified the salinity effect by calculating ‘Mg-excess’: i.e. that part of the Mg/Ca-signal that deviates from $\delta^{18}O_{\text{foram}}$ -temperature estimates. They also derived an independent Mg/Ca sensitivity to temperature of $4.8 \pm 0.8\%$ per °C, which is $\sim 50\%$ of the temperature sensitivity observed in culture experiments and less than 20% of their inferred salinity control.

In this study we present data from a suite of new culture experiments to verify and extend previous experimental results used to establish the salinity dependence of foraminiferal Mg/Ca. Because our new data corroborate previous laboratory results, we present a detailed analysis of alternative ecophysiological explanations for the core-top sediment results of Arbuszewski et al. (2010) and Mathien-Blard and Bassinot (2009), which is based on known

temperature, salinity and biological effects on these proxies. Instead of a strong salinity effect on Mg/Ca, we find that both Mg/Ca and $\delta^{18}O_{\text{foram}}$ -derived temperatures of *G. ruber* are consistent with its preference for growth during the warm summer season at higher latitudes.

2. METHODS

2.1. Planktic foraminifer culturing

The temperate-subtropical *Orbulina universa* and tropical *Globigerinoides sacculifer* and *G. ruber* (pink) were cultured at the Wrigley Institute for Environmental Studies (WIES) on Santa Catalina Island, California, in July/August 2008, and at the University of Puerto Rico’s Marine Sciences Center on Isla Magueyey (MSCIM) during March and April 2010, respectively. The experiments are the same as described in Allen et al. (2011, 2012). Juvenile foraminifers were hand-collected by SCUBA divers either 3 (WIES) or 13 km (MSCIM) offshore and at 3–5 m water depth. Immediately after collection foraminifers were brought to the laboratory, where each individual was identified and its largest test dimension measured by light microscopy. If the foraminifers did not already hold prey in their spines, they were fed a 1-day old brine shrimp (*Artemia salina*). Specimens were then transferred into individual culture jars that contained the experimental seawater. Jars were sealed with Parafilm® and tight-fitting lids to prevent gas exchange and evaporation.

The seawater used in these experiments was collected at the dive sites, filtered (0.45 μm), and salinity modified by either adding deionized water to reduce salinity or by partial evaporation under a heat lamp to increase salinity. Salinity was measured with an Orion Star Thermo Scientific conductivity meter (salinity resolution = ± 0.1) and ranged between 29.9 and 35.4 in the *O. universa* experiments, and between 33.0 and 40.0 in the *G. sacculifer* and *G. ruber* experiments. In addition to salinity, we also measured alkalinity and pH at the beginning and end of each experiment using a Metrohm 809 open cell autotitrator and pH meter calibrated against NIST buffers and Dickson-certified alkalinity standards. The culture jars were then placed in circulating temperature-controlled water baths, where temperature was kept at 22 ± 0.3 °C in the *O. universa* experiments and at 26 ± 0.3 °C in the *G. sacculifer* and *G. ruber* experiments (Table 1). These conditions are similar to the seawater temperature measured during foraminifer collection at the respective sites. The constancy of the temperature in the baths was monitored by HOBO TidbiT® temperature loggers every 5 min. Because all three species are symbiont-bearing, the baths were illuminated on a 12-h light/dark cycle with cool-white fluorescent lamps, whose output ($>300 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) exceeds the light saturation level (P_{max}) of the symbionts (Jørgensen et al., 1985; Rink et al., 1998). Light levels were monitored with a Biospherical Instruments QSL-2200 scalar PAR irradiance sensor. Foraminifers were observed daily with a hand lens and fed a freshly hatched brine shrimp every other day until each individual underwent gametogenesis. At that

Table 1
Mg/Ca results from these and previously published culture experiments.

	Salinity	Temperature (°C)	Mg/Ca (mmol/ mol)	Analytical uncertainty (mmol/mol)	Mg/Ca _T (mmol/ mol)	Mg/Ca _{CI} (mmol/ mol)	Study
<i>G. sacculifer</i>	26.0	26.5	1.59	0.31	1.42		Nürnberg et al. (1996)
<i>G. sacculifer</i> , Ch. 18	30.0	26.0	4.42	1.30			Dueñas-Bohórquez et al. (2011)
<i>G. sacculifer</i> , Ch. 19	30.0	26.0	3.16	0.24	3.16		Dueñas-Bohórquez et al. (2011)
<i>G. sacculifer</i>	33.0	25.7	3.55	0.07	3.67		This study
<i>G. sacculifer</i>	35.0	26.5	3.81	1.17	3.64		Nürnberg et al. (1996)
<i>G. sacculifer</i>	35.0	26.5	3.91	1.99	3.74		Nürnberg et al. (1996)
<i>G. sacculifer</i>	35.4	25.7	3.76	0.08	3.87		This study
<i>G. sacculifer</i>	35.4	25.7	3.90	0.08	4.00		This study
<i>G. sacculifer</i> , Ch. 18	36.0	26.0	5.16	0.63			Dueñas-Bohórquez et al. (2011)
<i>G. sacculifer</i> , Ch. 19	36.0	26.0	3.80	0.86	3.80		Dueñas-Bohórquez et al. (2011)
<i>G. sacculifer</i> , Ch. 18	39.0	26.0	5.03	1.34			Dueñas-Bohórquez et al. (2011)
<i>G. sacculifer</i> , Ch. 19	39.0	26.0	4.56	0.96	4.56		Dueñas-Bohórquez et al. (2011)
<i>G. sacculifer</i>	40.0	25.3	5.00	0.10	5.24		This study
<i>G. sacculifer</i>	40.0	26.5	7.29	1.06	7.12		Nürnberg et al. (1996)
<i>G. ruber</i> (w)	32.1	24.0	3.60	0.15	4.19		Kısakürek et al. (2008)
<i>G. ruber</i> (p)	33.0	25.7	3.88	0.08	3.99		This study
<i>G. ruber</i> (w)	35.0	24.0	3.80	0.15	4.39		Kısakürek et al. (2008)
<i>G. ruber</i> (p)	35.4	25.7	4.00	0.08	4.09		This study
<i>G. ruber</i> (w)	38.0	24.0	4.70	0.15	5.29		Kısakürek et al. (2008)
<i>G. ruber</i> (p)	40.0	25.3	5.03	0.10	5.25		This study
<i>G. ruber</i> (w)	40.7	24.0	5.50	0.15	6.09		Kısakürek et al. (2008)
<i>G. ruber</i> (w)	44.3	24.0	5.10	0.15	5.69		Kısakürek et al. (2008)
<i>O. universa</i>	27.0	22.0	5.68	3.97	5.68	4.24	Lea et al. (1999)
<i>O. universa</i>	29.9	22.1	7.03	0.20	6.96	6.08	This study
<i>O. universa</i>	29.9	22.1	6.35	0.18	6.29	5.40	This study
<i>O. universa</i>	31.5	22.3	7.49	0.21	7.29	6.47	This study
<i>O. universa</i>	31.5	22.3	8.17	0.23	7.96	7.15	This study
<i>O. universa</i>	33.0	22.0	8.89	1.96	8.89	8.41	Lea et al. (1999)
<i>O. universa</i>	33.3	22.3	10.20	0.29	10.00	9.50	This study
<i>O. universa</i>	33.3	22.3	8.95	0.25	8.74	8.24	This study
<i>O. universa</i>	35.4	22.3	8.82	0.25	8.62	8.29	This study
<i>O. universa</i>	39.0	22.0	10.08	1.57	10.08	10.71	Lea et al. (1999)

Data from this study are based on pooled, culture-grown chambers of 20 *G. sacculifer* specimens, 50 *G. ruber* specimens and 15 *O. universa* specimens. For this study, Dueñas-Bohórquez et al. (2011), Kısakürek et al. (2008), and Lea et al. (1999), the reported analytical uncertainties reflect long-term analytical RSD (2σ), 1 SD of measurements on multiple specimens, 1 SD based on repeat measurements of an in-house standard, and 1 SD of measurements on multiple specimens, respectively. Mg/Ca_T values have been normalized to a single temperature: 26 °C for *G. sacculifer* and *G. ruber* (according to Nürnberg et al. (1996) and Kısakürek et al. (2008), respectively) and 22 °C for *O. universa* (according to Russell et al., 2004). Mg/Ca_{CI} values have been normalized to [CO₃²⁻] = 200 μmol kg⁻¹ according to the equation provided by Russell et al. (2004). For *O. universa* data from Lea et al. (1999), where carbonate ion concentrations were not reported, [CO₃²⁻] was calculated from reported pH and alkalinity estimated from the general salinity-alkalinity relationship at Catalina Island of 68 μmol kg⁻¹ alkalinity per salinity unit.

time the empty test was recovered from the jar, rinsed in deionized water and archived for later analysis.

2.2. Sample preparation and analysis

The archived foraminifer tests contain chambers that were grown in the ocean prior to collection and chambers that were grown under controlled conditions in the laboratory. Because the juvenile trochospiral test of *O. universa* is very thin and often gets absorbed entirely as the final spherical chamber is secreted, it contributes ≤5% to the final test weight (Spero and Deniro, 1987) and is thus considered negligible for the bulk test chemistry. In contrast, the *G. sacculifer* and *G. ruber* trochospiral test that grew prior to

collection may have substantial mass, so the chambers grown in the laboratory need to be isolated from chambers precipitated in the ocean. We accomplished this by amputating all chambers that increased the test size beyond the initial collection measurement with a scalpel. The amputated chambers were then pooled to form individual samples (Spero and Lea, 1993). Each sample thus combines the laboratory-grown chambers of approximately 20 specimens of *G. sacculifer*, 50 *G. ruber* and 15 *O. universa*. *O. universa* tests were crushed between two glass slides prior to cleaning to expose interior surfaces.

The cleaning procedure followed Russell et al. (2004) and comprised rinsing with MilliQ water to remove fine particles, and two oxidation steps for 30 min with hot

(70 °C), buffered H₂O₂ (equal parts 0.1 N NaOH, 30% v/v H₂O₂, Optima grade) to remove organic matter. This strong H₂O₂ treatment is applied to oxidize the much higher concentration of organic matter in cultured foraminifer tests compared to fossil tests (Pak et al., 2004; Russell et al., 2004), which would leave Mg/Ca erroneously elevated if not removed (Barker et al., 2003). Following oxidation, samples were rinsed 5 times with MilliQ and leached 3 times with 0.001 N HNO₃ to remove any re-adsorbed ions.

Elemental analyses of *O. universa* tests were carried out by Inductively Coupled Plasma Mass Spectrometry (ICP-MS, PerkinElmer SCIEX Elan DRC II) in the Godwin Laboratory at Cambridge University (Yu et al., 2005; Allen et al., 2011) and *G. sacculifer* and *G. ruber* samples were analyzed on a Sector-Field Inductively Coupled Plasma Mass Spectrometer (Thermo Scientific Element XR) at Rutgers University (Tali Babila, pers. comm., Allen et al., 2012). Consistency standards were prepared gravimetrically with MilliQ and measured every 3–5 samples (Yu et al., 2005). The long-term relative standard deviation (RSD, 2σ) for Mg/Ca in the Cambridge and Rutgers laboratories is 2.8% and 2.0%, respectively.

3. RESULTS

Table 1 and Fig. 1 present the Mg/Ca ratios of cultured *O. universa*, *G. sacculifer* and *G. ruber* relative to experimental seawater salinity. This compilation combines our new data with previously published culture solution chemistry data by Lea et al. (1999) for *O. universa*, and by Kısakürek et al. (2008) for *G. ruber*, as well as laser ablation calibrations and electron micro probe analyses for *G. sacculifer* by Dueñas-Bohórquez et al. (2011) and Nürnberg et al. (1996), respectively. Despite some differences in culturing, cleaning and analytical techniques, the calibrations display consistent patterns in both absolute Mg/Ca values and sensitivity of Mg/Ca to salinity. The following exponential regressions combine published and new culture data, although we restrict the *G. sacculifer* regression to our new solution chemistry data and the final (19th) chamber laser ablation data by Dueñas-Bohórquez et al. (2011). Linear regressions of these data yield similar sensitivities but we prefer exponential regressions, where the percentage change is fixed over the entire Mg/Ca range and the representation of the sensitivity is thus unambiguous.

$$G. ruber \text{ (pink and white)} : \text{Mg/Ca} = 1.29 \pm 0.83e^{0.033 \pm 0.017 \cdot S}, R^2 = 0.80 \quad (1)$$

$$G. sacculifer : \text{Mg/Ca} = 0.75 \pm 0.34e^{0.047 \pm 0.012 \cdot S}, R^2 = 0.95 \quad (2)$$

$$O. universa : \text{Mg/Ca} = 1.95 \pm 1.53e^{0.044 \pm 0.023 \cdot S}, R^2 = 0.70 \quad (3)$$

These equations indicate a Mg/Ca sensitivity to salinity of $3.3 \pm 1.7\%$ per salinity unit for *G. ruber*, $4.7 \pm 1.2\%$ for *G. sacculifer* and $4.4 \pm 2.3\%$ for *O. universa* ($\pm 95\%$ confidence interval). If the 18th chamber data for *G. sacculifer* (Dueñas-Bohórquez et al., 2011) were included, the Mg/Ca sensitivity to salinity in *G. sacculifer* would be even

smaller. Results of Nürnberg et al. (1996) are based on a single chamber per salinity condition and therefore are not included in the regression. Calibrations using only our new data are similar to those including both new and published data (Suppl. Table S1).

Because some previous culture studies performed salinity experiments at slightly different ambient temperatures, we also tested these regressions after normalizing the Mg/Ca ratio of each foraminifer species to a consistent temperature using published temperature sensitivities established in laboratory culture (Table 1). The temperature differences between experiments are small and regressions using original and temperature-normalized Mg/Ca data agree within 95% confidence bounds (Table S1). Because temperature corrections introduce additional uncertainty, we apply regressions using the original data (not temperature-normalized) throughout the rest of the manuscript.

4. DISCUSSION

4.1. Mg/Ca sensitivity to salinity

The three foraminifer species studied in laboratory experiments incorporate different amounts of Mg into their tests, but the effect of salinity, i.e. 3–5% per salinity unit, is consistent among the three species. This suggests that the process causing the salinity dependence is proportional to the Mg content of the shell. Importantly, the salinity effects observed in the laboratory are at least 5× smaller than the 27% sensitivity to salinity inferred from *G. ruber* tests from Atlantic sediments (Arbuszewski et al., 2010) (Fig. 2). To investigate the cause of this disagreement, we first consider whether culture experiments may have overlooked a larger sensitivity to salinity due to limitations in the experimental design.

Although the experimental seawater modification should concentrate all ions equally with increasing salinity, seawater evaporation at elevated temperature may lead to the degassing of some CO₂, thus lowering the total concentration of dissolved inorganic carbon (DIC) and changing the relative concentrations of alkalinity to DIC. For example, in the *G. ruber* experiments alkalinity increased by 426 μmol kg⁻¹ between low and high salinity treatments, but DIC only by 313 μmol kg⁻¹ (Allen and Hönisch, 2012; Allen et al., 2012). This corresponds to a [CO₃²⁻] increase with salinity in the culture experiments by 81 μmol kg⁻¹, an effect that would not be observed in the natural ocean under conditions of constant temperature, pressure and acidity. Because Russell et al. (2004) observed a negative relationship between Mg/Ca in *O. universa* and the symbiont-barren *Globigerina bulloides* when [CO₃²⁻] falls below 200 μmol kg⁻¹, the experimental variation in [CO₃²⁻] could have caused a bias. No Mg/Ca-[CO₃²⁻] calibrations have been published for *G. sacculifer* and *G. ruber*, and we therefore tested the effect of [CO₃²⁻] by normalizing the *O. universa* Mg/Ca data to [CO₃²⁻] = 200 μmol kg⁻¹, using the equation of Russell et al. (2004). The Mg/Ca sensitivity to salinity in *O. universa* then increases to $6.6 \pm 2.5\%$. Because the uncertainties in our *O. universa*

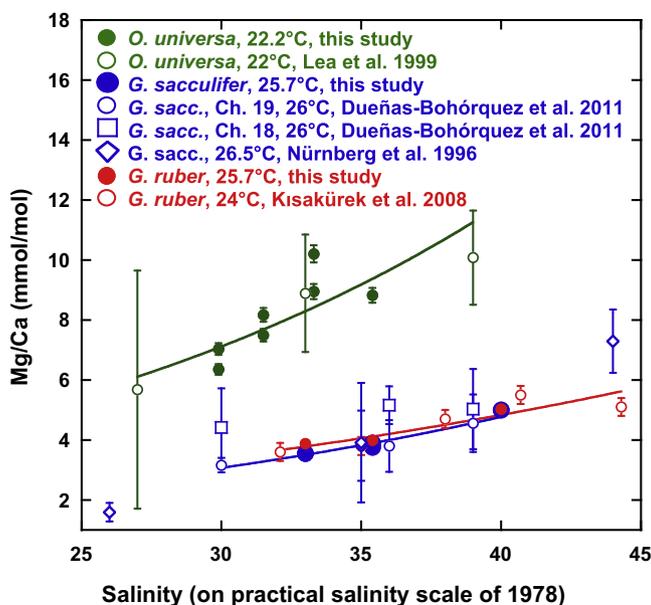


Fig. 1. Results from laboratory culture calibrations of Mg/Ca versus salinity in three species of planktic foraminifers. Closed symbols indicate new data presented herein, where each data point represents a solution chemistry analysis of pooled culture-grown chambers of 15–50 individual foraminifers. Similarly, *G. ruber* data by Kısakürek et al. (2008) were measured by solution chemistry on 2–6 pooled specimens. *Globigerinoides sacculifer* data by Dueñas-Bohórquez et al. (2011) were measured on multiple individual chambers by laser ablation; data by Nürnberg et al. (1996) are based on repeat microprobe measurements of one chamber per sample. Error bars represent the analytical uncertainties reported by original studies, as listed in Table 1. Culture temperatures differ slightly between studies and are indicated in the legend. The larger temperature ranges for *G. ruber* and *G. sacculifer* experiments have little effect on the regressions (Table S1).

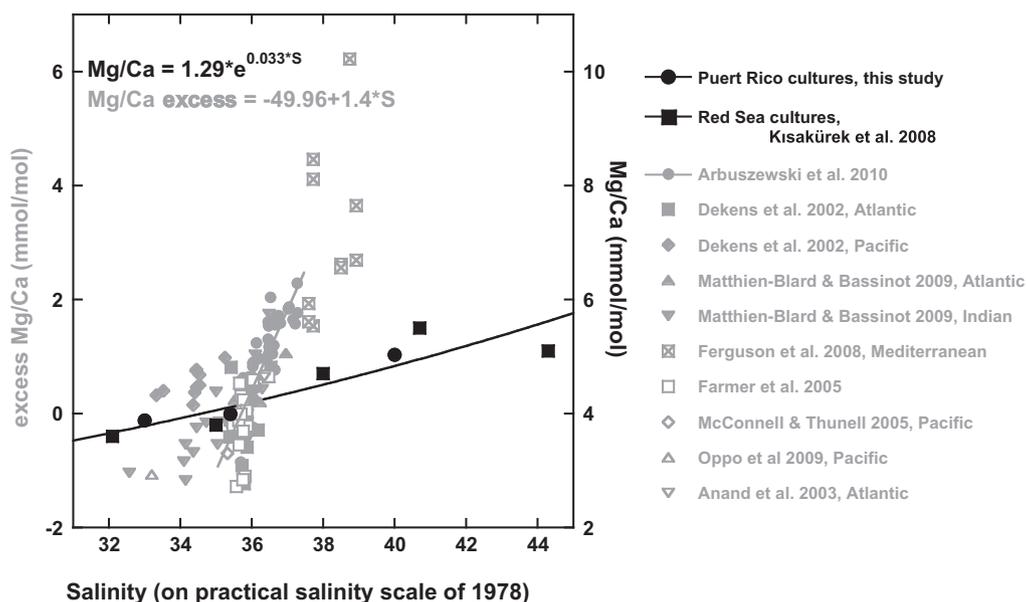


Fig. 2. Excess Mg/Ca in *G. ruber* tests from sediment trap and core-top observations (grey symbols), and Mg/Ca ratios from laboratory cultures (black symbols). Excess Mg/Ca is defined as the part of the Mg/Ca signal that cannot be explained by average annual SST and $\delta^{18}\text{O}_{\text{sw}}$ at the core sites (Arbuszewski et al., 2010). The grey line defines the linear regression through Arbuszewski's core-top data across the salinity range 35–37; the black line is the regression through the combined *G. ruber* culture data of this study and Kısakürek et al. (2008).

culture data (Fig. 1) are relatively large and the carbonate ion effect is not very well resolved below $200 \mu\text{mol kg}^{-1}$ (Russell et al., 2004), we consider this adjusted sensitivity the upper bound of the salinity influence, which is still much

smaller than the 27% sensitivity observed for *G. ruber* from core-top sediments.

Synergistic effects may exist between temperature and the Mg/Ca sensitivity to salinity. It is plausible that the

mechanism responsible for lowering [Mg] in the calcifying fluid is reduced under higher Mg activities in seawater, resulting in even greater Mg incorporation at higher temperatures under elevated salinity. Testing such effects would require an experimental design where both salinity and temperature are varied systematically, but such experiments have not yet been conducted. The existence of a synergistic temperature-salinity effect cannot be ruled out at this time; however, in the absence of a theoretical basis or empirical evidence for such an influence on Mg/Ca we will assume that temperature-salinity amplifications do not play a significant role here.

We therefore conclude that the design of the culture experiments is unlikely to have caused underestimation of the salinity effect on Mg/Ca, and that the culture data cannot be reconciled with the core-top data in this way.

4.2. Comparison with core-top sediments

Recognizing that geochemical data from core-top sediments are subject to multiple uncertainties, Arbuszewski et al. (2010) and Mathien-Blard and Bassinot (2009) established comprehensive core-top data sets of Mg/Ca and $\delta^{18}\text{O}_{\text{foram}}$ in tests of the tropical-subtropical, symbiont-bearing *G. ruber*. To gain insight into the controls on these temperature proxies, both studies compared Mg/Ca and $\delta^{18}\text{O}_{\text{foram}}$ from the same samples and assumed that the oxygen isotopic composition recorded in *G. ruber* tests can be used as a reference for evaluating the Mg/Ca temperature computation (e.g., Mulitza et al., 1998; Peeters et al., 2002; Schmidt and Mulitza, 2002). Here we follow a different approach and do not try to align the proxies with mean annual SST, but rather apply experimentally determined sensitivities to these proxies in order to compare the difference between proxy estimates and oceanographic data, and to assess the ecophysiology of *G. ruber*. From now on we will refer to Mg/Ca temperature estimates as ‘Mg/Ca-Ts’ and to $\delta^{18}\text{O}_{\text{foram}}$ temperature estimates as ‘ $\delta^{18}\text{O}_{\text{foram}}$ -Ts’.

To identify which parameter(s) could be responsible for the observed Mg/Ca difference in salinity sensitivity between cultured and core-top specimens, we review the calibrations and assumptions applied by Arbuszewski et al. (2010) and Mathien-Blard and Bassinot (2009). Both studies assumed that *G. ruber* lives in the surface ocean (0–50 m), but each made different choices regarding foraminifer size, dissolution correction and $\delta^{18}\text{O}_{\text{sw}}$ estimation. For instance, Arbuszewski et al. (2010) analyzed tests in the 250–355 μm size class, cleaned them following the procedures outlined by Boyle and Keigwin (1985/1986) and Barker et al. (2003) including a reductive cleaning step, applied a depth-dependent dissolution correction (Dekens et al., 2002) to their Mg/Ca-Ts, and used a linear regression for Atlantic sea surface salinity (SSS) and $\delta^{18}\text{O}_{\text{sw}}$ data (Schmidt et al., 1999) to estimate the local sea surface $\delta^{18}\text{O}_{\text{sw}}$. In comparison, Mathien-Blard and Bassinot (2009) selected tests in the 250–315 μm size class, cleaned them following the procedure of Barker et al. (2003) (i.e. without a reductive cleaning step), applied a Mg/Ca temperature calibration without dissolution correction (Anand

et al., 2003), and selected local sea surface $\delta^{18}\text{O}_{\text{sw}}$ from the gridded data set of LeGrande and Schmidt (2006). The equations used for translating foraminiferal $\delta^{18}\text{O}_{\text{foram}}$ to temperature yield relatively similar results, where Arbuszewski et al. (2010) used the low light equation established for *O. universa* (Bemis et al., 1998) and Mathien-Blard and Bassinot (2009) the *Uvigerina* equation of (Shackleton, 1974). Following Arbuszewski et al. (2010), Mg/Ca data from Mathien-Blard and Bassinot (2009) were reduced by 10% to account for the lack of a reductive cleaning step. In the following discussion we will first evaluate the effect of the depth correction on Mg/Ca, then infer potential depth habitats from Mg/Ca-Ts, followed by an evaluation of the choice of $\delta^{18}\text{O}_{\text{sw}}$ and the $\delta^{18}\text{O}_{\text{foram}}$ -temperature equation. We conclude our assessment with an analysis of seasonal habitat preferences of *G. ruber*.

4.2.1. Depth correction on Mg/Ca

The depth correction applied by Arbuszewski et al. (2010) is based on the longstanding observation that Mg/Ca in planktic foraminifer tests is prone to partial dissolution in the sediment (Savin and Douglas, 1973; Lorenz et al., 1977; Russell et al., 1994; Brown and Elderfield, 1996; Rosenthal et al., 2000; Rosenthal and Lohmann, 2002; Dyez and Ravelo, 2013). Arbuszewski et al. (2010) used the approach of Dekens et al. (2002), who assessed dissolution using specimens picked from core-top sediments along several depth transects. Dekens et al. (2002) performed a multivariate best-fit analysis and derived a Mg/Ca-temperature calibration for *G. ruber* that has subsequently been verified by the sediment trap calibration of Anand et al. (2003) but the Dekens calibration includes a depth correction for samples obtained deeper than 2.8 km in the Atlantic Ocean. We reevaluate this depth correction applied to *G. ruber* and *G. sacculifer* based on the depth transects studied by Dekens et al. (2002). Fig. 3 shows the original Mg/Ca data, which display relatively constant Mg/Ca values in the Atlantic Ocean, where a significant decrease in Mg/Ca is only observed in the deepest cores of the Ceara Rise (at 4.4 km water depth) and the Sierra Leone Rise (at 5.1 km water depth). Similar observations have been made by Rosenthal and Boyle (1993), who studied Mg/Ca in the same three foraminifer species from the Sierra Leone Rise and observed no change in Mg/Ca above 4.5 km water depth. In contrast, Regenberg et al. (2006) found clear evidence for decreasing Mg/Ca in Caribbean core-tops >3000 m water depth. Because the Caribbean is an enclosed basin, we focus our evaluation on open ocean records here.

The depth-corrected Mg/Ca-Ts for *G. ruber* and *G. sacculifer* from Dekens et al. (2002) are shown in the lower panels of Fig. 3 as a deviation from local SST: i.e. $\Delta T_{\text{depth corrected}} = T_{\text{Mg/Ca depth corrected}} - \text{SST}$. All depth-corrected data in the Atlantic (i.e. water depths >2.8 km but above 4.4 km) produce higher temperature estimates than sediments unaffected by dissolution from <2.8 km water depth. Furthermore, Mg/Ca-Ts from the deepest cores (>4.5 km water depth) are cooler than the shallowest samples from the same transect, indicating the applied correction is too small. This observation is

consistent with estimates of carbonate saturation (ΔCO_3^{2-} , upper panels in Fig. 3), which indicate that bottom water is in fact supersaturated down to ~ 4.4 km and thus suggest favorable conditions for calcite preservation. It appears that the dissolution correction applied to Atlantic cores results in: (1) temperature overestimates for water depths between 2.8 and 4.4 km, and (2) temperature underestimates for the deepest cores (>4.4 km). Based on these observations we suggest that a depth correction may not be appropriate here. Establishing and applying a depth correction at these sites requires independent verification of actual dissolution, for instance by scanning electron microscopic examination of test surface structures and size-normalized shell weights.

The Atlantic latitudinal transect of Arbuszewski et al. (2010) encompasses 64 sediment cores, of which only two cores are from a water depth shallower than 2.8 km, and four cores from water depths >4.4 km. It follows from

above that the dissolution-corrected Mg/Ca-Ts for the majority of cores in this transect likely exceed actual calcification temperatures, whereas the four deepest cores may underestimate calcification temperature. To address this potential artifact, we apply the multispecies temperature equation of Anand et al. (2003):

$$\text{Mg/Ca}(\text{mmol/mol}) = 0.38 \times e^{0.09 \times (\text{SST}(\text{°C}))} \quad (4)$$

and remove the need for making any depth correction for dissolution by excluding the four sediment cores >4.4 km water depth, and a small number of additional cores (VM22-202, VM26-100, VM26-102 and VM27-161) which are from >4.3 km depth and bathed in undersaturated or nearly undersaturated ($\Delta\text{CO}_3^{2-} = -7.5$ to $+3.2 \mu\text{mol kg}^{-1}$) bottom waters (Arbuszewski et al., 2010).

By omitting the depth correction entirely, it is possible that some temperatures are now underestimated. Better verification of the preservation state is clearly warranted

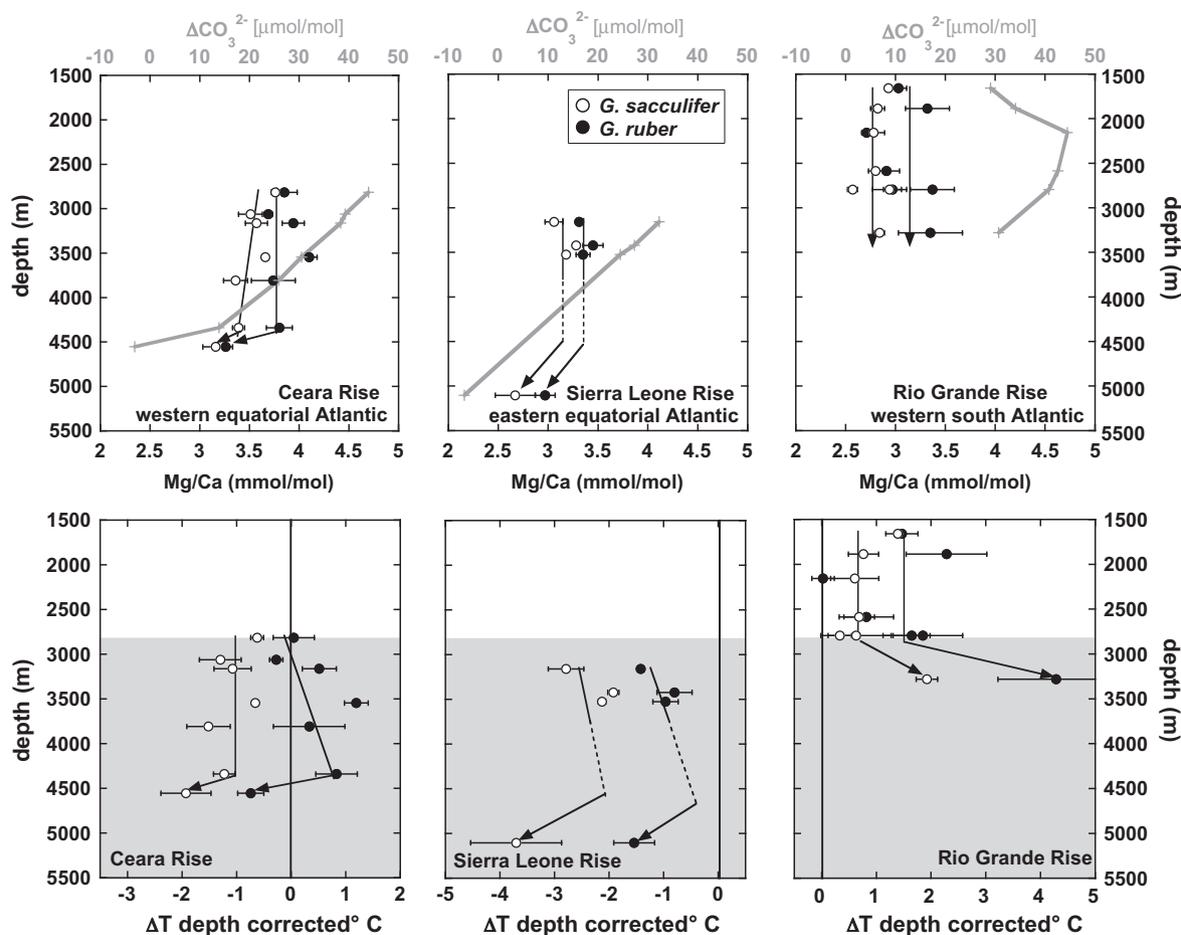


Fig. 3. Reevaluation of the Mg/Ca depth correction from Dekens et al. (2002). Upper panel: Mg/Ca ratios in two foraminifer species *G. sacculifer* and *G. ruber* from three depth transects in the Atlantic Ocean. Arrows indicate the Mg/Ca decrease relative to shallower samples. Grey line and crosses indicate bottom water ΔCO_3^{2-} , i.e. the carbonate saturation, at the respective sample depths. Atlantic Mg/Ca ratios are relatively constant down to ~ 4.4 km water depth, where carbonate is supersaturated. Lower panel: Temperature difference between depth-corrected Mg/Ca-Ts and local mean annual SST. The shaded area indicates depths >2.8 km, which Dekens et al. (2002) recommended for a depth correction. Although in most transects even the shallowest samples do not match mean annual SST (i.e. $\Delta T \neq 0$), an observation similar to Fig. 4, the depth correction creates an additional bias in the Atlantic: compared to shallow core sites, temperatures are overestimated between 2.8 and 4.4 km water depth, whereas the depth correction is insufficient for cores >4.4 km water depth.

but here we focus on the open ocean observations described in Fig. 3, which suggest little or no dissolution in sediment cores <4.4 km water depth. As noted previously by Arbuszewski et al. (2010), the shape of the calcification temperature profile with latitude changes little when the depth correction is omitted; however, each temperature estimate is on average $\sim 2^\circ\text{C}$ cooler than the depth-corrected temperature estimates (Fig. 4a and b).

4.2.2. Foraminiferal depth habitat and salinity normalization

Because Arbuszewski et al. (2010) correct their data for dissolution, some of their Mg/Ca-Ts exceed the highest sea surface temperatures reported in oceanographic data bases (Fig. 4a), leading them to conclude that this offset may be explained by salinity. However, after eliminating the dissolution correction (Fig. 4b) and normalizing Mg/Ca to $S = 35.4$ using Eq. (1) (Fig. 4c and d), we find *G. ruber* Mg/Ca-Ts fall within or below the bounds of maximum summer SST, which means that these temperature estimates are matched seasonally and/or vertically in the water column. Using the seasonally resolved WOA 2009 database in Ocean Data View (ODV, Schlitzer, 2012), we now take the uncorrected Mg/Ca-Ts, normalized to $SSS = 35.4$ using Eq. (1), and find which seasons and water depths are recorded by matching Mg/Ca-Ts and observations at each core site.

Fig. 5a shows Mg/Ca-based growth temperatures occur only during the warmest summer/fall months and in the upper water layers at subtropical to temperate latitudes. In contrast, the low-latitude data indicate that Mg/Ca-based growth temperatures are matched throughout the year at different water depths. We suggest that these observations reflect how the habitat depth and season of maximum flux of *G. ruber* varies with latitude. Averaging these habitat depth estimates and plotting them versus mean annual sea surface salinity yields a negative correlation (Fig. 5b), where *G. ruber* appears to live closer to the sea surface in high-salinity environments (i.e. mid-latitudes) but may live as deep as 60 m in low salinity environments (i.e. near the equator). This result provides an alternative to the hypothesis that Mg/Ca covaries with salinity (Arbuszewski et al., 2010).

The inferred seasonal occurrence is consistent with seasonal plankton net observations by Tolderlund and Bé (1972) at Atlantic Stations Delta (44°N , 41°W), Echo (35°N , 48°W) and Bermuda ($32^\circ06'\text{N}$, $64^\circ39'\text{W}$), where *G. ruber* occurs only in August and September at the northernmost station Delta and from March through December at Echo and Bermuda. Furthermore, the depth habitat preferences are in agreement with plankton net observations that place *G. ruber* in the upper 10 m of the water column at Echo (Tolderlund and Bé, 1972), but with occurrences in deeper tows at Bermuda and the Sargasso Sea (Tolderlund and Bé, 1972; Fairbanks et al., 1980; Deuser, 1987) or throughout the upper 75 m in the central equatorial Pacific (Watkins et al., 1998). To the best of our knowledge no such data are available for the equatorial Atlantic, but because hydrographic conditions near the equator are comparable between the Pacific and Atlantic, for now we assume

that the equatorial Pacific depth habitat (Watkins et al., 1998) is also representative for the Atlantic.

Given this agreement between inferred depth habitat and observations, we used ODV (Schlitzer, 2012) to gather summer and winter salinity at 20 and 50 m water depth from WOA 2009 and derive a new set of calcification temperature estimates (Fig. 4c) by omitting the dissolution correction and applying Eq. (1) (i.e. 3.3% sensitivity to salinity) to normalize all Mg/Ca data to $S = 35.4$, which is typical of tropical Atlantic SSS. We applied summer salinity at 20 m to normalize Mg/Ca data $>15^\circ\text{N/S}$, and averaged annual salinity at 20 and 50 m to normalize Mg/Ca data $<15^\circ\text{N/S}$ (Fig. 4c and d and Suppl. material). These Mg/Ca-Ts are now in good agreement with *G. ruber*'s optimum growth conditions of $23\text{--}26.5^\circ\text{C}$, as observed from plankton studies (Tolderlund and Bé, 1972) and culture experiments (Bijma et al., 1990). This agreement further corroborates that Mg/Ca yields reasonable temperature estimates without requiring a very large (i.e. 27%) sensitivity to salinity. However, because some significant differences remain between Mg/Ca-Ts and $\delta^{18}\text{O}_{\text{foram}}$ -Ts (Fig. 4c), we now turn to evaluating the $\delta^{18}\text{O}_{\text{foram}}$ -Ts.

4.3. Translating foraminiferal $\delta^{18}\text{O}_{\text{foram}}$ to temperature

Arbuszewski et al. (2010) and Mathien-Blard and Bassinot (2009) applied different temperature calibrations for *G. ruber*

$$T(^{\circ}\text{C}) = 16.5 - 4.80 * (\delta^{18}\text{O}_{\text{foram}} - \delta^{18}\text{O}_{\text{sw}} + 0.27), \quad (5)$$

$$T(^{\circ}\text{C}) = 16.9 - 4.00 * (\delta^{18}\text{O}_{\text{foram}} - \delta^{18}\text{O}_{\text{sw}} + 0.20), \quad (6)$$

Eq. (5) (Bemis et al., 1998) has been established for the planktic *O. universa* grown under low light conditions in laboratory culture between 15 and 25°C , and Eq. (6) (Shackleton, 1974) has been established for the benthic genus *Uvigerina*, from core-top sediments for temperatures $<17^\circ\text{C}$. Using Eq. (6) to translate $\delta^{18}\text{O}_{G. ruber}$ data from the Atlantic coretop transects yields on average 0.67°C higher temperatures compared to Eq. (5). It is important to note here that the original Shackleton (1974) equation was a linearization of the O'Neil et al. (1969) quadratic temperature relationship. As such, it is inappropriate for computing tropical temperatures and will always lead to a temperature overestimate at high temperatures. Before we assess the suitability of these calibrations to translate *G. ruber* $\delta^{18}\text{O}_{\text{foram}}$ to temperature, we need to consider the effects of the oxygen isotopic composition of seawater and carbonate chemistry on $\delta^{18}\text{O}_{\text{foram}}$.

4.3.1. The oxygen isotopic composition of seawater

Estimating temperature from $\delta^{18}\text{O}_{\text{foram}}$ requires knowledge of $\delta^{18}\text{O}_{\text{sw}}$ (e.g., Urey, 1948; McCrea, 1950; Urey et al., 1951; Bemis et al., 1998). Arbuszewski et al. (2010) estimated $\delta^{18}\text{O}_{\text{sw}}$ from a linear regression between Atlantic SSS and $\delta^{18}\text{O}_{\text{sw}}$ data from the upper 50 m of the water column ($\delta^{18}\text{O}_{\text{sw}} = 0.238 \times S - 7.69$, $r^2 = 0.66$, $N = 106$, Schmidt et al., 1999), whereas Mathien-Blard and Bassinot (2009) selected local sea surface $\delta^{18}\text{O}_{\text{sw}}$ from the gridded data set by LeGrande and Schmidt (Fig. S1a, 2006). The gridded data set of LeGrande and Schmidt (v. 1.1, 2006)

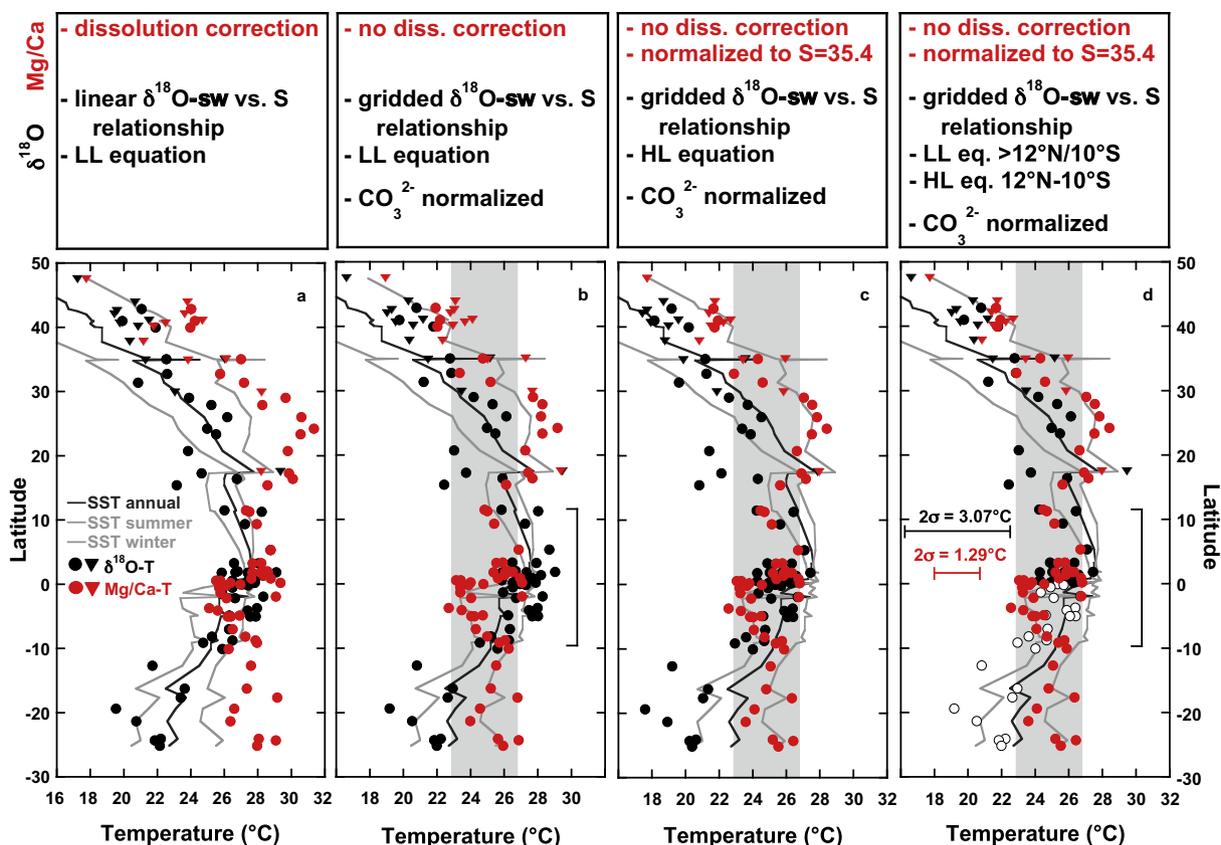


Fig. 4. Temperature estimates from $\delta^{18}\text{O}$ and Mg/Ca in *G. ruber* tests from Atlantic sediments (a–d), with upper boxes indicating normalizations applied to each proxy. The optimal growth temperature for *G. ruber* (23–26.5 °C, Tolderlund and Bé, 1972; Bijma et al., 1990) is indicated in (b–d) by shading. Mg/Ca data are from Arbuszewski et al. (dots, 2010) and Mathien-Blard and Bassinot (triangles, 2009). (a) Mg/Ca-Ts obtained by applying a depth correction to all original values >2.8 km water depth (Dekens et al., 2002), and $\delta^{18}\text{O}_{\text{foram}}$ -Ts using the LL equation (Eq. (5), Bemis et al., 1998) and a linear regression between $\delta^{18}\text{O}_{\text{sw}}$ and salinity (Arbuszewski et al., 2010) to translate foraminiferal $\delta^{18}\text{O}$ to temperature. (b) Same Mg/Ca data but no depth correction was applied. Temperature estimates from $\delta^{18}\text{O}_{\text{foram}}$ are based on the LL-equation as in (a), but are normalized to $[\text{CO}_3^{2-}] = 230 \mu\text{mol kg}^{-1}$, and use $\delta^{18}\text{O}_{\text{sw}}$ based on the gridded data set after LeGrande and Schmidt (2006). The bracket highlights estimates that exceed maximum sea surface temperatures in the 12°N–10°S latitudinal band. (c) Same Mg/Ca-Ts as in (b) but Mg/Ca was normalized to salinity = 35.4 (Eq. (1)). $\delta^{18}\text{O}_{\text{foram}}$ -Ts were translated using the high light equation (Eq. (7), Bemis et al., 1998). In contrast to (b), the $\delta^{18}\text{O}_{\text{foram}}$ -Ts fall within or below the local SST bounds near the equator but the difference to Mg/Ca-Ts is greater in the extratropics. (d) Same Mg/Ca-Ts as in (c), $\delta^{18}\text{O}_{\text{foram}}$ -Ts between 12°N and 10°S are based on the high light equation (bracket, Eq. (7)), $\delta^{18}\text{O}_{\text{foram}}$ -Ts >12°N and >10°S are based on the LL equation (Eq. (5)). Open $\delta^{18}\text{O}$ symbols in (d) highlight South Atlantic data, many of which show a negative deviation from this foraminifer species' optimum growth temperature despite the seasonal presence of optimum temperatures at the core sites. Horizontal bars in (d) show averages for 2σ uncertainties for temperature estimates from $\delta^{18}\text{O}_{\text{foram}}$ (black) and Mg/Ca (red). Sea surface temperatures (SST) have been determined for the summer and winter season and the annual average at each core site (black and grey lines). In contrast to (a), temperature estimates from both proxies in (c, d) are present seasonally in the water column.

is derived from the same global data base as Schmidt et al. (1999); the authors noted, however, that $\delta^{18}\text{O}_{\text{sw}}$ to salinity relationships are only regionally coherent and may vary on seasonal, annual and inter-annual timescales.

A simple cross plot of the $\delta^{18}\text{O}_{\text{sw}}$ estimates derived from the linear regression versus $\delta^{18}\text{O}_{\text{sw}}$ estimates from the gridded data set of LeGrande and Schmidt (2006) (Fig. S1b) shows that both estimates agree within error ($\pm 0.26\text{‰}$ and $\pm 0.15\text{‰}$, respectively) but that the $\delta^{18}\text{O}_{\text{sw}}$ values from the gridded data set are consistently greater than estimates from the linear regression in the 16–36°N/S band by about 0.1‰. Although the uncertainty of $\delta^{18}\text{O}_{\text{sw}}$ estimates is large (Fig. S1b), this latitudinal band is where Arbuszewski et al. (2010) found the highest salinity effect and the greatest devi-

ation between Mg/Ca-Ts and $\delta^{18}\text{O}_{\text{foram}}$ -Ts. In comparison, the study of Mathien-Blard and Bassinot (2009) includes only three samples from this mid-latitude band, and focuses primarily on higher latitudes. This analysis suggests uncertainty in $\delta^{18}\text{O}_{\text{sw}}$ contributes to the discrepancy between $\delta^{18}\text{O}_{\text{foram}}$ -Ts and Mg/Ca-Ts. $\delta^{18}\text{O}_{\text{foram}}$ values may be slightly undercorrected in the 16–36°N/S band and $\delta^{18}\text{O}_{\text{foram}}$ temperatures underestimated by up to 0.5 °C.

Given that LeGrande and Schmidt (2006) provide a more differentiated and better constrained assessment of regional $\delta^{18}\text{O}_{\text{sw}}$, we have applied estimates from their gridded data set to the core-top transect of Arbuszewski et al. (2010) (Fig. 4b and c). Using the data library clone at <http://granger.ldeo.columbia.edu/expert/%28/data/free/>

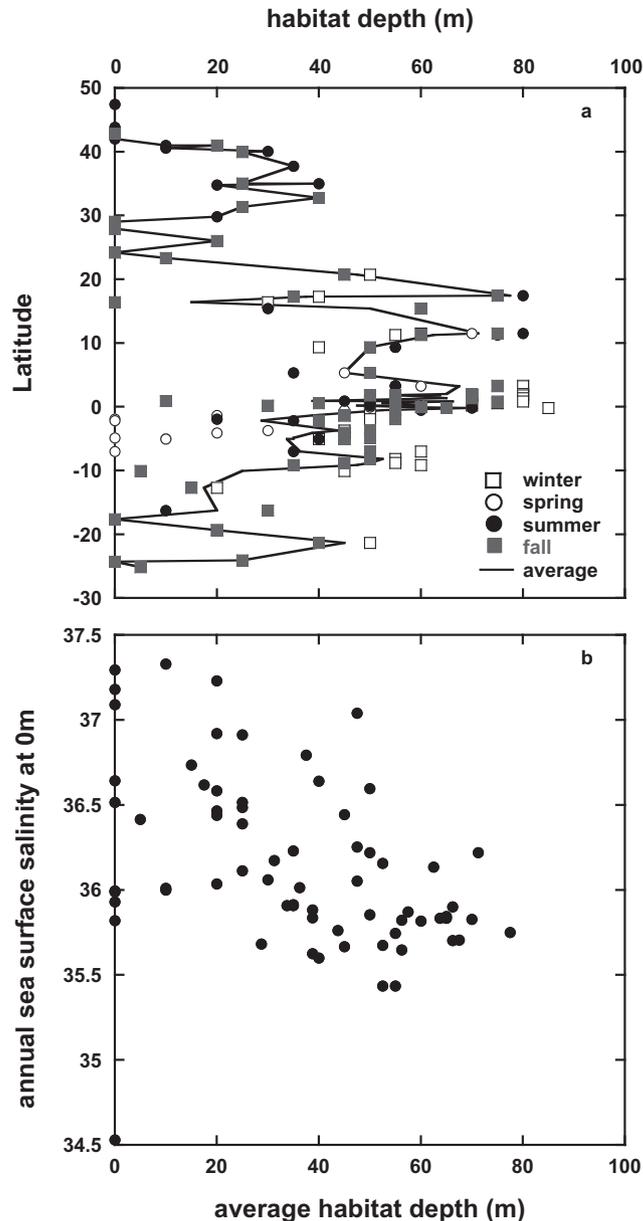


Fig. 5. (a) Seasonal occurrence and depth of salinity-normalized Mg/Ca-Ts from *G. ruber* sampled from Atlantic sediments (data from Fig. 4d and hydrographic data from WOA 2009). Based on Mg/Ca records, *G. ruber* appears to grow only during the warmest summer/fall months in subtropical to temperate latitudes and at shallower depths than in the tropics. (b) Average habitat depth determined in (a) versus annual mean sea surface salinity. The broad negative correlation with SSS hints at a shallower habitat where salinity is high.

alexeyk/LeGrandeSchmidt2006/calculated_d18O.nc%29 readfile/.d18o/, we gathered $\delta^{18}\text{O}_{\text{sw}}$ data for each core site at 0, 20 and 50 m water depth. The local difference in $\delta^{18}\text{O}_{\text{sw}}$ between these depths is generally $<0.02\text{‰}$ and in only two cases as large as 0.04‰ . These differences are smaller than the reproducibility of replicate analyses of *G. ruber* $\delta^{18}\text{O}_{\text{foram}}$ reported by Mathien-Blard and Bassinot (2009), i.e. 0.22‰ (2σ), so we use the values at 20 m for all further calculations.

4.3.2. Marine carbonate chemistry effects on $\delta^{18}\text{O}_{\text{foram}}$

Culture experiments with the planktic foraminifers *O. universa* and *G. bulloides* (Spero et al., 1997; Bijma et al.,

1999) and *G. sacculifer* and *G. ruber* (Bijma et al., 1998) have revealed linearly decreasing $\delta^{18}\text{O}_{\text{foram}}$ and $\delta^{13}\text{C}_{\text{foram}}$ with increasing carbonate ion concentration in all four species. In *G. ruber* the $\delta^{18}\text{O}_{\text{foram}}$ versus $[\text{CO}_3^{2-}]$ relationship has a slope of -0.0022‰ per $\mu\text{mol kg}^{-1}$ (Bijma et al., 1998). We have tested this effect by normalizing all $\delta^{18}\text{O}_{\text{foram}}$ data to $230 \pm 21 \mu\text{mol kg}^{-1}$ (1sd), which is the average $[\text{CO}_3^{2-}]$ determined from the GLODAP data set (Key et al., 2004) for these samples and assumed depth ranges (Suppl. material). Our analysis reveals that this normalization contributes little to resolving the discrepancy between Mg/Ca-Ts and $\delta^{18}\text{O}_{\text{foram}}$ -Ts. The total effect across the Atlantic transect is zero on average, but data in the 16–36°N/S band

are up to 0.5 °C cooler and data >36°N and <16°N/S are up to 0.33 °C warmer than the average (Fig. 4b and Suppl. material). The net effect of this normalization slightly increases the offset between Mg/Ca-Ts and $\delta^{18}\text{O}_{\text{foram}}$ -Ts, except for three samples >36°N, where the offset becomes smaller (Fig. 4b).

4.4. Remaining differences between Mg/Ca and $\delta^{18}\text{O}_{\text{foram}}$ temperature estimates

Using the *O. universa* low light equation (Eq. (5)) and gridded $\delta^{18}\text{O}_{\text{sw}}$ to translate the $[\text{CO}_3^{2-}]$ -normalized $\delta^{18}\text{O}_{\text{foram}}$ data to temperature yields good agreement with the Mg/Ca-T data north of 15°N ($r^2 = 0.82$), but within the 12°N–10°S band the Mg/Ca-Ts fall below annual SST. In contrast, the $\delta^{18}\text{O}_{\text{foram}}$ -Ts tend to exceed annual SST, with several values exceeding the warmest summer temperatures observed in this 12°N–10°S band by up to 1.1 °C (Fig. 4b). South of 10°S the $\delta^{18}\text{O}_{\text{foram}}$ -Ts systematically fall below *G. ruber*'s optimum growth temperature of 23–26.5 °C (Tolderlund and Bé, 1972; Bijma et al., 1990). Given both annual and summer SSTs of 23–26 °C are observed, it is surprising that *G. ruber* should prefer to grow at $T < 22$ °C at these sites. These discrepancies need to be explained, and in the absence of known geochemical effects on Mg/Ca, we will continue to focus on potential uncertainties on the $\delta^{18}\text{O}_{\text{foram}}$ reconstructions, in particular equatorial and South Atlantic $\delta^{18}\text{O}_{\text{sw}}$, possible mixing with glacial-age foraminifers, and the temperature equation used to translate $\delta^{18}\text{O}_{\text{foram}}$.

4.4.1. Insufficient $\delta^{18}\text{O}_{\text{sw}}$ data coverage

The $\delta^{18}\text{O}_{\text{sw}}$ database of Schmidt et al. (1999) has very limited data coverage near core sites in the equatorial and South Atlantic (Fig. S1a). The few available $\delta^{18}\text{O}_{\text{sw}}$ data in those latitudes were collected close to the African and South American coastlines. This is different in the North Atlantic, where a greater number of data are available closer to the core-top transect. In the South Atlantic it is notable that neither the linear regression of Arbuszewski et al. (2010), nor the gridded data set of LeGrande and Schmidt (2006) yields $\delta^{18}\text{O}_{\text{sw}}$ data higher than $1.02 \pm 0.15\text{‰}$ but the database of Schmidt et al. (1999) does list a few $\delta^{18}\text{O}_{\text{sw}}$ data as high as $1.44 \pm 0.05\text{‰}$ on the western side of the South Atlantic Ocean (Fig. S1a). A 0.4‰ underestimate of $\delta^{18}\text{O}_{\text{sw}}$ translates to a ~ 2 °C underestimate of growth temperature, which could bring the South Atlantic Mg/Ca-T and $\delta^{18}\text{O}_{\text{foram}}$ -Ts into agreement, but it is unclear how far those higher values may extend eastward. We have tried without success to gain access to water samples and unpublished $\delta^{18}\text{O}_{\text{sw}}$ data that would improve the data coverage near the core transect. The situation near the equator is similar, with the linear regression and gridded data set yielding $\delta^{18}\text{O}_{\text{sw}}$ data in the range of $0.75\text{–}0.87\text{‰}$, whereas measured $\delta^{18}\text{O}_{\text{sw}}$ data range between 0.48‰ and 0.98‰ . The lowest data ($0.48\text{–}0.69\text{‰}$) are from the eastern equatorial Atlantic, where many of the core sites are located (Fig. S1a). If $\delta^{18}\text{O}_{\text{sw}}$ near south equatorial core sites were overestimated, this would result in $\delta^{18}\text{O}_{\text{foram}}$ -Ts that are too warm. Although this is speculative, it highlights the need for improved characterization of $\delta^{18}\text{O}_{\text{sw}}$.

4.4.2. Potential mixing with glacial-age foraminifers

In addition to uncertainties in $\delta^{18}\text{O}_{\text{sw}}$, Lohmann (1995) has reported the mixing of glacial age foraminifers into Rio Grande Rise core-top sediments, where sedimentation rates are as low as 0.5 cm/ky. Similarly, Billups and Spero (1996) showed that a core-top sample from an even higher sedimentation rate core (1.5 cm/ky) in the central equatorial Atlantic at 5°N, 20.5°W (2930 m depth) contained >20% glacial *G. sacculifer*. Stott and Tang (1996) made similar observations in equatorial and south Atlantic cores, where individual *G. ruber* and *G. sacculifer* from core-top samples had >10% glacial $\delta^{18}\text{O}$ values. Although the data shown in Fig. 4 are from sediment cores retrieved somewhat further east of the Rio Grande Rise, they are near the core site studied by Billups and Spero (1996) and Stott and Tang (1996). Given the relatively deep water depths between 3300 and 3900 m of the cores in this database (Suppl. material), it is likely that comparable low sedimentation rates would be found in cores from the South Atlantic gyre. If mixing with glacial age tests is an issue at these core sites, the added ice volume effect on glacial $\delta^{18}\text{O}_{\text{sw}}$ ($\sim +1.1\text{‰}$) would create a much larger bias on $\delta^{18}\text{O}_{\text{foram}}$ -Ts than on Mg/Ca-Ts. Single test $\delta^{18}\text{O}_{\text{foram}}$ analyses on *G. sacculifer* and *G. ruber* suggest this effect could produce an apparent cooling of 0.5–1 °C (Billups and Spero, 1996; Stott and Tang, 1996). In comparison, 2–3 °C lower glacial temperature translates to 18–27% lower Mg/Ca, which is partly compensated by higher glacial salinity by 1 unit or +3–5% Mg/Ca. This leads to an average glacial Mg/Ca -18% lower than modern, and consequently a diminishing -0.2 °C apparent cooling if bioturbation mixed 10% glacial tests into core-top sediments.

4.4.3. Light effects on $\delta^{18}\text{O}_{\text{foram}}$ in symbiont-bearing species

To date, no culture calibration has been established for $\delta^{18}\text{O}_{\text{foram}}$ in tests of *G. ruber*; Arbuszewski et al. (2010) therefore chose an *O. universa* equation established in laboratory culture under low light conditions (Eq. (5), Bemis et al., 1998), whereas Mathien-Blard and Bassinot (2009) used Shackleton's (1974) core-top calibration for the benthic foraminifer genus *Uvigerina* (Eq. (6)). Both calibrations yield relatively similar results but their adequacy for *G. ruber* has not yet been discussed; we revisit the *O. universa* equation here.

Bemis et al. (1998) cultured the symbiont-bearing *O. universa* under two different light intensities: under light-saturating conditions >380 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (high light, HL) and below the light compensation level at $20\text{–}30$ $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (low light, LL, Eq. (5)) (Rink et al., 1998). The resulting temperature equations differ in their y -axis intercepts, which has been explained by the effect of symbiont photosynthetic activity on elevating the carbonate ion concentration in the foraminiferal microenvironment (Bemis et al., 1998). The HL equation is:

$$T(^{\circ}\text{C}) = 14.9 - 4.80 \times (\delta^{18}\text{O}_{\text{foram}} - \delta^{18}\text{O}_{\text{sw}} + 0.27) \quad (7)$$

Bemis et al. (1998) compared these equations to previous calibrations, including a suite of Atlantic *G. ruber* core-top data from Wang et al. (1995). They noted that where annual SST is warmest, i.e. at the equator, *G. ruber* data are

best described by the HL equation, and where annual SST <25 °C, *G. ruber* data are better described by the LL equation. Similarly, Thunell et al. (1999) found good agreement between the HL equation and *G. ruber* collected from sediment trap material in the Guaymas Basin, Gulf of California. We therefore decided to investigate potential differences in surface-ocean light intensity across the latitudinal transect.

Using the Giovanni online data system of the Goddard Earth Sciences Data and Information Services Center (<http://disc.sci.gsfc.nasa.gov/giovanni/overview/index.html>) to read local photosynthetic active radiation (PAR) and diffuse light attenuation coefficients at 490 nm from SeaWiFS annual data, we determined light intensity at 20 and 60 m water depth at each core site (Fig. S2, Suppl. material). Whereas light intensity at 20 m exceeds 200 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ at all latitudes, light intensity at 60 m water depth falls below 50 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ near the equator. Following photosynthesis measurements by Jørgensen et al. (1985) and Rink et al. (1998), any light level >150 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ exceeds light saturation of the symbiont populations associated with *O. universa* and *G. sacculifer* and would thus suggest using the HL equation, whereas any light level <50 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ falls near or below light saturation and thus would suggest using the LL equation. Based on this light regime, one would predict the HL equation should produce the best temperature estimates everywhere except for the equator, where using the LL equation should yield better estimates. However, applying the HL equation to extratropical samples yields $\delta^{18}\text{O}_{\text{foram}}\text{-T}$ s that fall below the optimum growth temperature of *G. ruber* and even further below Mg/Ca-Ts (Fig. 4c). Assigning the use of the HL and LL equations to samples based on irradiance levels therefore clearly leads to results that are difficult to reconcile (see also Wang et al., 1995; Thunell et al., 1999). Unfortunately, no such light experiments are available for *G. ruber*. However, applying the *O. universa* HL equation to the equatorial *G. ruber* samples decreases $\delta^{18}\text{O}_{\text{foram}}\text{-T}$ s by 1.6 °C and improves the agreement with Mg/Ca (Fig. 5c). Because the latitudinal light regime provides no support for the use of the HL equation near the equator, we looked for alternative clues as to why application of an equation with a lower y-intercept (i.e. the HL equation) may be warranted at low latitudes.

4.4.4. Size effects on $\delta^{18}\text{O}_{\text{foram}}$ in *G. ruber*

Here we focus on the 250–355 μm size fraction chosen by Arbuszewski et al. (2010) for foraminiferal sampling. In a recent test-size study on *G. ruber* in the Gulf of Mexico, Richey et al. (2012) observed a linear decrease in $\delta^{18}\text{O}_{\text{foram}}$ with test size that translates to a +0.7–1.2 °C temperature bias per 100 μm size increase. In contrast, the Mg/Ca ratio of *G. ruber* is constant in small tests and only increased in tests larger than 355 μm diameter, for which the inferred temperature bias is only half as large as in $\delta^{18}\text{O}_{\text{foram}}$. Similar observations have been reported by Elderfield et al. (2002), but they observed a gradual increase in both proxies with test size. It is not clear what causes these composition-size relationships but differences in depth habitat and/or seasonal occurrence are likely candidates (Spero et al.,

2003; Hönisch and Hemming, 2004; Richey et al., 2012). Importantly, Spero and Lea (1993) observed that the symbiont-bearing *G. sacculifer* grows larger tests with increasing light levels, suggesting that the size effect observed by Richey et al. (2012) may also be related to light levels and that the use of the HL temperature equation on $\delta^{18}\text{O}_{\text{foram}}$ in larger *G. ruber* may be more appropriate.

Given the relatively wide size range studied by Arbuszewski et al. (2010) and the higher *G. ruber* growth rates observed under optimal growth conditions (Bijma et al., 1990), we investigated whether the size distribution within the 250–355 μm fraction varies along the Atlantic core transect. We selected four core-top samples from Arbuszewski's Atlantic transect, covering 1–40°N, and measured the average sizes of 30 randomly selected *G. ruber* (*sensu stricto*) tests under a microscope. Although it should be noted that the original size distribution may have been slightly different from ours (the samples are now already depleted in *G. ruber* tests), tests from equatorial regions are on average 80 μm larger compared to higher latitudes (Fig. S3). This size difference hints at a potential bias in test geochemistry. Comparison with the size effect on $\delta^{18}\text{O}_{\text{foram}}$ observed by Richey et al. (2012) suggests that this size difference could explain about half or more of the difference between the HL and LL equation, and that the use of the HL equation is more appropriate in the 12°N–10°S band (see also Thunell et al., 1999). Given these observations we recommend that paleoreconstructions should be based on sieve size ranges that are restricted to 50- μm increments (e.g., 250–300 μm , 300–355 μm), so that any involuntary bias towards selecting the largest tests in a sample is minimized.

4.5. Seasonality of *G. ruber* growth

Our comparison of the Mg/Ca and $\delta^{18}\text{O}$ proxies in the North Atlantic shows that agreement between the two proxies can be improved ($R^2 = 0.70$) if known geochemical proxy sensitivities are applied (Fig. 6). The benefit of this approach lies in the potential to unravel biological controls that cannot be studied in laboratory culture, where water depth is invariant and foraminiferal reproductive success cannot be quantified. The seasonality of *G. ruber* growth has been observed with plankton nets at some locations (Tolderlund and Bé, 1972; Watkins et al., 1998), and it can now be corroborated by comparison of core-top proxy temperature estimates with hydrographic observations of mean annual SST (Fig. 7). The proxy deviation from SST is here expressed as $\Delta T_{\text{Mg/Ca}} = \text{Mg/Ca-T} - \text{SST}$ and $\Delta T_{\delta^{18}\text{O}} = \delta^{18}\text{O}_{\text{foram}}\text{-T} - \text{SST}$ and yields up to +5 °C in mid latitudes and –3 °C near the equator. Although assumptions of habitat depth and season were part of our approach to normalize proxy records to common salinity and $[\text{CO}_3^{2-}]$, the effect of those normalizations is much smaller (<1 °C, Fig. 4) than the deviation of both $\Delta T_{\text{Mg/Ca}}$ and $\Delta T_{\delta^{18}\text{O}}$ from mean annual SST. Despite remaining differences, we suggest that the agreement between the two proxy records is significant and indicates the seasonal preference of *G. ruber* for warmer summer months at higher latitudes. A similar seasonal bias for *G. ruber* Mg/Ca

temperatures was also proposed for Caribbean fossil assemblages during glacial cycles (Schmidt et al., 2006).

Near the equator, however, we cannot determine with certainty whether proxy records indicate greater habitat depth, or whether they may be biased by post-depositional dissolution. Applying a dissolution correction only to equatorial samples would further improve the agreement between the Mg/Ca and $\delta^{18}\text{O}_{\text{foram}}$ estimates (Fig. 4d).

4.6. Deconvolving $\delta^{18}\text{O}_{\text{foram}}$ into temperature and salinity contributions

Paleosalinity estimates have been determined by removing the temperature component from $\delta^{18}\text{O}_{\text{foram}}$ records using Mg/Ca-Ts and the ice volume component using global sealevel estimates. Calculated paleo- $\delta^{18}\text{O}_{\text{sw}}$ are then translated to salinity via a modern $\delta^{18}\text{O}_{\text{sw}}$ -salinity relationship (e.g., Flower et al., 2004; Schmidt et al., 2004; Weldeab et al., 2007). Based on the observations made herein, we revisit this approach.

The line of argument applied in this study uses Mg/Ca to estimate foraminiferal growth temperatures, which were then used to determine *G. ruber*'s depth and season of growth. The correlations shown in Fig. 7a and b suggest a stronger relationship with latitude for Mg/Ca-Ts than for $\delta^{18}\text{O}_{\text{foram}}$ -Ts. Fig. 4d shows the same differences between the two proxy estimates for individual core sites. We have identified uncertainty in $\delta^{18}\text{O}_{\text{sw}}$ and bioturbation as potential sources for uncertainty in the $\delta^{18}\text{O}_{\text{foram}}$ -Ts. However, determining which proxy may be biased depends on the approach. If we had used $\delta^{18}\text{O}_{\text{foram}}$ instead of Mg/Ca to determine *G. ruber*'s growth temperature, which is

the approach originally taken by Arbuszewski et al. (2010) and Mathien-Blard and Bassinot (2009), we would need to search for parameters that could explain deviations of Mg/Ca-Ts from $\delta^{18}\text{O}_{\text{foram}}$ -Ts. With our current state of knowledge we cannot identify whether one proxy is more or less biased than the other, as both proxies yield temperatures that are observed in the water column at the respective core sites. Arbuszewski et al. (2010) aimed to resolve this issue by performing multi-variate regressions that link mean annual temperature and salinity to Mg/Ca, $\delta^{18}\text{O}_{\text{foram}}$ and ΔCO_3^{2-} :

$$\begin{aligned} \text{Mean annual SST } (^{\circ}\text{C}) = & 16.06 + 4.62 * \ln(\text{Mg/Ca}) \\ & - 3.42 * \delta^{18}\text{O}_{\text{foram}} - 0.1 * \Delta\text{CO}_3^{2-}, \end{aligned} \quad (8)$$

$$\begin{aligned} \text{Mean annual SST} = & 34.28 + 1.97 * \ln(\text{Mg/Ca}) \\ & + 0.59 * \delta^{18}\text{O}_{\text{foram}} \end{aligned} \quad (9)$$

Although the results appear promising when compared to modern hydrographic data, the temperature and salinity sensitivities of Mg/Ca and $\delta^{18}\text{O}_{\text{foram}}$ in these regressions do not agree with observations from laboratory cultures (Eqs. (1)–(7), this study, Bemis et al., 1998; Lea et al., 1999; Kısakürek et al., 2008), plankton nets (Anand et al., 2003) or core-top calibrations (Shackleton, 1974; Dekens et al., 2002). Furthermore, because both proxies are used in both regressions, neither proxy may subsequently be used independently to verify the regression's accuracy.

We have tried to reconcile the two proxy estimates, but differences remain (Figs. 4d, 6 and 7) that limit the ability to use paired analyses of Mg/Ca and $\delta^{18}\text{O}_{\text{foram}}$ to reconstruct past salinity (Fig. 8). For instance, a 0.5‰ under- or

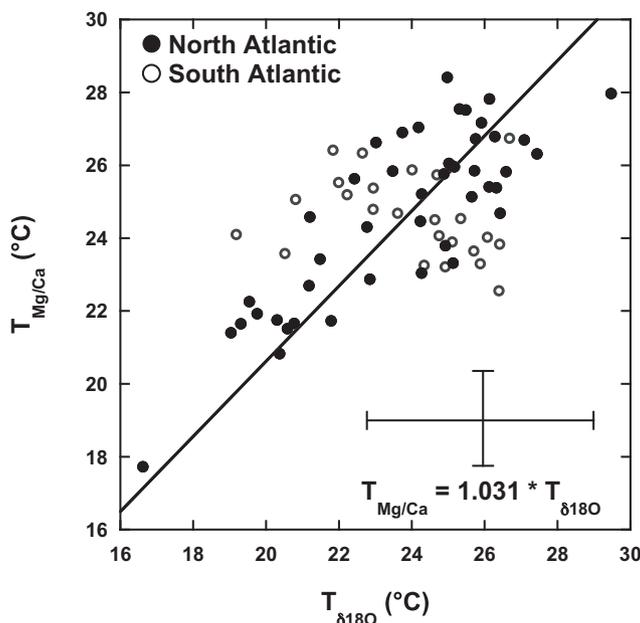


Fig. 6. Comparison of temperature estimates from Mg/Ca and $\delta^{18}\text{O}_{\text{foram}}$ proxies (data from Fig. 4d). The black line describes the linear regression, the cross indicates the relative uncertainty of each data point, which includes the analytical uncertainty of each measurement and of the local $\delta^{18}\text{O}_{\text{seawater}}$ estimate on $T_{\delta^{18}\text{O}}$. While these estimates are reasonably well aligned, Mg/Ca-Ts are generally elevated compared to $\delta^{18}\text{O}_{\text{foram}}$ -Ts. South Atlantic data (small open symbols) show significantly greater scatter than North Atlantic data (large closed symbols). See text and Fig. 7 for comparison of greater uncertainty in South Atlantic $\delta^{18}\text{O}_{\text{foram}}$ -Ts compared to Mg/Ca-Ts.

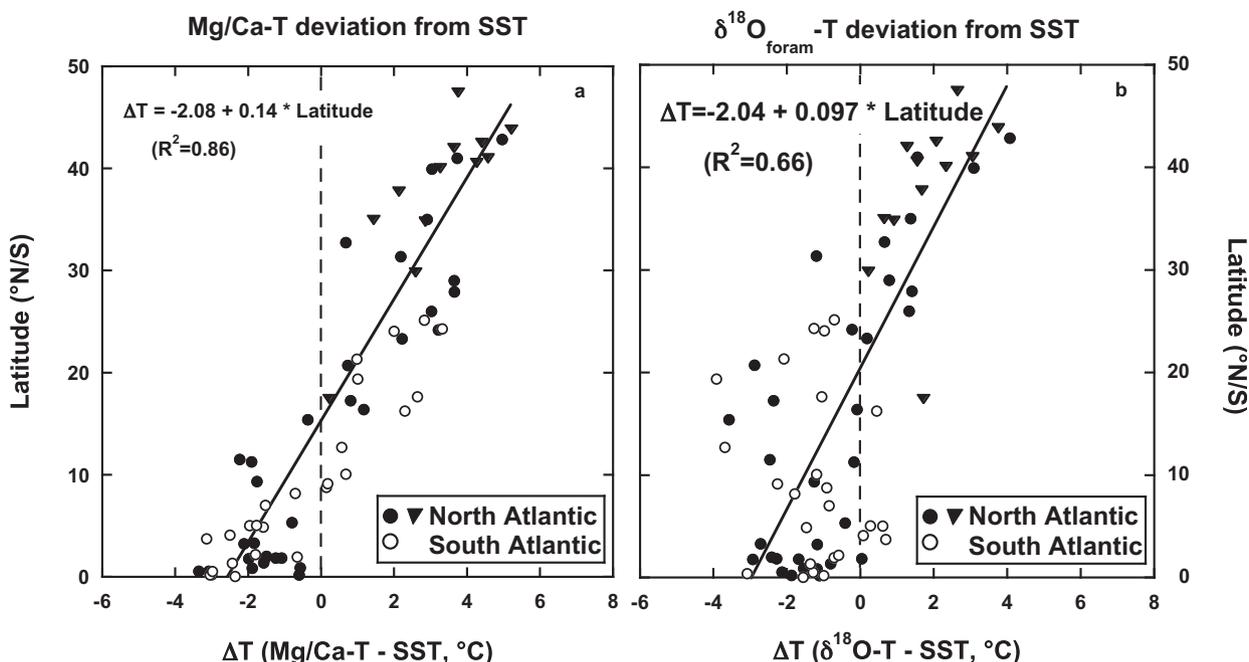


Fig. 7. Deviation of (a) Mg/Ca- and (b) $\delta^{18}\text{O}_{\text{foram}}\text{-T}$ s (as shown in Fig. 4d) from mean annual SST versus degree latitude, where the vertical dashed lines indicate perfect agreement. Closed symbols indicate samples from the North Atlantic; open symbols indicate data from the South Atlantic. Triangles are data from Mathien-Blard and Bassinot (2009), dots from Arbuszewski et al. (2010). The regressions describe data in the North Atlantic only. The overall relationships with latitude are linear and similar in both proxies, suggesting that *G. ruber* growth is restricted to the warmest season at higher latitudes. If salinity exerted a significant effect on either proxy, the greatest deviation should occur around 15–35°N/S latitude, which is not the case. Mg/Ca-Ts in the North and South Atlantic follow the same latitudinal trend (a), whereas South Atlantic $\delta^{18}\text{O}_{\text{foram}}\text{-T}$ s are significantly more scattered than North Atlantic estimates (b). This observation is likely an expression of the spatially poor $\delta^{18}\text{O}_{\text{sw}}$ coverage used to estimate temperature from $\delta^{18}\text{O}_{\text{foram}}$.

overestimate in $\delta^{18}\text{O}_{\text{sw}}$ could erroneously be interpreted as a local salinity difference of ~ 2.1 units (Fig. 8b). Such large uncertainties could inhibit mapping attempts of – for example – last glacial maximum (LGM) salinity changes across entire ocean basins. However, $\delta^{18}\text{O}_{\text{sw}}$ estimates in the equatorial region (i.e. 10°N–10°S) fall closer to observed values than at higher latitudes. This is consistent with DiNezio and Tierney (2013), who recently demonstrated that paired analyses of Mg/Ca and $\delta^{18}\text{O}_{\text{foram}}$ yield LGM salinity patterns in the Indian Ocean that are consistent with model estimates of how glacial exposure of the Sunda Shelf affects salinity. Furthermore, uncertainties should be reduced for down-core reconstructions at a single site. For example, Saraswat et al. (2013) used paired analyses of Mg/Ca and $\delta^{18}\text{O}_{\text{foram}}$ to reconstruct deglacial monsoon changes from a sediment core in the southeastern Arabian Sea. Coherency of their reconstruction with Ba/Ca-based riverine runoff estimates and the Hulu Cave precipitation record affirms the efficacy of the $\delta^{18}\text{O}_{\text{sw}}$ approach on this regional scale. Looking at each temperature proxy individually, the glacial-to-interglacial temperature change for tropical surface ocean reconstructions using Mg/Ca (e.g., Lea et al., 2000; Hönisch and Hemming, 2005; Medina-Elizalde and Lea, 2010), $\delta^{18}\text{O}_{\text{foram}}$ (e.g., Broecker, 1986; Stott and Tang, 1996), foraminiferal assemblages (CLIMAP, 1976) and alkenones (Bard et al., 1997) all yield last glacial temperatures 1–3 °C colder than during the Holocene, demonstrating the fundamental agreement between

different proxy estimates. While this is encouraging, uncertainties of individual temperature proxies often exceed 1 °C, and large spatial and temporal uncertainties remain in local $\delta^{18}\text{O}_{\text{sw}}$ vs. salinity relationships (paragraphs 4.3.1 and 4.4.1). Thus, paleo-salinity estimation should be approached with caution, and possibly only as deviations (Δ) between time periods rather than quantitative patterns (e.g., DiNezio and Tierney, 2013), until the mechanism(s) for these offsets can be resolved.

5. CONCLUSIONS

The salinity effect on Mg incorporation observed in laboratory-cultured planktic foraminifers is 3–5% per salinity unit. Because glacial salinity was $\sim 3\%$ or ~ 1 salinity unit higher compared to the modern ocean, the expected salinity effect on Mg/Ca in glacial foraminifera is an increase of 3–5% or a +0.3–0.5 °C temperature bias. In comparison, a 2–3 °C lower glacial temperature causes glacial Mg/Ca to be $\sim 18\text{--}27\%$ lower (e.g., Lea et al., 1999; Dekens et al., 2002; Anand et al., 2003). Consequently, temperature should exert the dominant control on planktic foraminiferal Mg/Ca on glacial-to-interglacial timescales.

We conclude, based on the culture data, that the apparently larger salinity sensitivity inferred from sub-tropical Atlantic core-tops with elevated Mg/Ca data (Arbuszewski et al., 2010) is not a direct effect of salinity. Our alternative

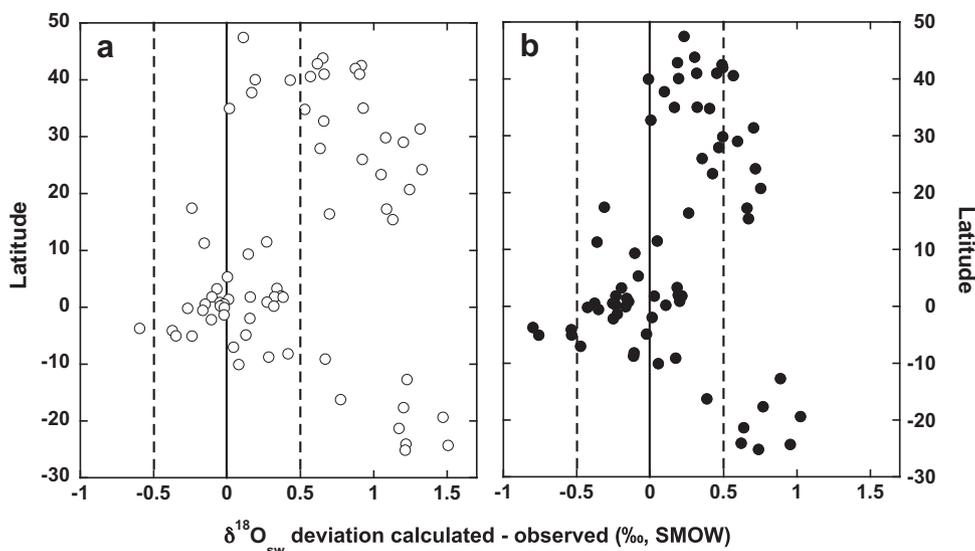


Fig. 8. Deviation of estimated $\delta^{18}\text{O}_{\text{sw}}$ from paired Mg/Ca and $\delta^{18}\text{O}_{\text{foram}}$ compared to observed $\delta^{18}\text{O}_{\text{sw}}$. $\delta^{18}\text{O}_{\text{sw}}$ was estimated using Eqs. (5) and (7), where $\delta^{18}\text{O}_{\text{foram}}$ is measured and temperature is estimated from Mg/Ca. (a) uses the same constraints as in Fig. 4a, (b) applies all normalizations to Mg/Ca and $\delta^{18}\text{O}_{\text{foram}}$ as shown in Fig. 4d. Although the amplitude of the deviation is reduced in (b), a 0.5‰ deviation (dashed lines) translates to a ~ 2.1 unit bias in estimated salinity. Similar to Figs. 4d, 6 and 7b, the largest deviations occur in the South Atlantic, where $\delta^{18}\text{O}_{\text{foram}}$ translates to lower than optimal growth temperatures for *G. ruber*.

hypothesis is that elevated mid-latitude Mg/Ca is caused by the seasonal preference of *G. ruber* for warm summer conditions in the mid-latitudes, as opposed to annual average conditions near the equator. This hypothesis is supported by the observation that, after omitting the dissolution correction above 4.4 km and excluding data from cores deeper than 4.4 km or close to undersaturation, Mg/Ca-Ts from Atlantic core-top sediments fall predominantly in the range 23–27 °C, which is in good agreement with optimum growth conditions for *G. ruber* as determined by plankton observations (Tolderlund and Bé, 1972) and culture studies (Bijma et al., 1990). Our analysis underscores the importance of planktic foraminiferal habitat depth, seasonality and dissolution in controlling observed core-top shell chemistry variability and, by extension, the challenge of interpreting down-core records in terms of changes in mean annual surface conditions.

Although our assessment reveals a much-improved agreement between Mg/Ca- and $\delta^{18}\text{O}_{\text{foram}}$ -Ts compared to earlier studies, some discrepancies remain and their consequences are significant. In particular, reconstructions of surface-ocean salinity using paired $\delta^{18}\text{O}_{\text{foram}}$ and Mg/Ca data are subject to substantial uncertainties and potential biases. The analysis presented here offers a testable template for interpreting global compilations of core-top *G. ruber* Mg/Ca and $\delta^{18}\text{O}$ analyses. To gain greater confidence in such reconstructions, core-top validations like those by Arbuszewski et al. (2010) and Mathien-Blard and Bassinot (2009) would be greatly enhanced by an expanded database of seasonal and vertical plankton abundance through sediment trap arrays and multiple opening and closing nets, direct assessment of the foraminiferal preservation state and the potential impact of bioturbation on pooled geochemical analyses through individual shell analyses. In general, both

Mg/Ca and $\delta^{18}\text{O}_{\text{foram}}$ appear to be reliable indicators of paleotemperatures when seasonality, calcite preservation and uncertainties in modern $\delta^{18}\text{O}_{\text{sw}}$ are taken into account. More comprehensive observations of modern $\delta^{18}\text{O}_{\text{sw}}$ (spatially and seasonally) are a vital next step towards resolving discrepancies between the two proxies.

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APPENDIX A. SUPPLEMENTARY DATA

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.gca.2013.07.028>.

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