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A reappraisal of the vital effect in benthic foraminifera on Mg/Ca ratios: species specific uncertainty relationships

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Abstract

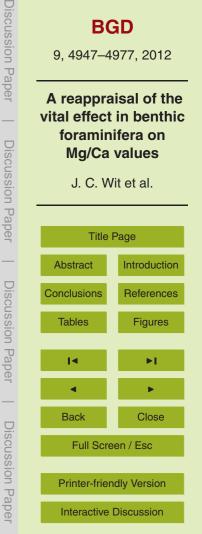
The reconstruction of past temperatures is often achieved through measuring the Mg/Ca value of foraminiferal test carbonate. The diversity in foraminiferal Mg/Catemperature calibrations suggests that there is also a biological control on this proxy. This study presents a new Mg/Ca-temperature calibration for the benthic foraminifer Bulimina marginata, based on cultures under a range of temperatures (4–14°C). Measured Mg/Ca values for B. marginata correlate well with temperature (Mg/Ca=1.10 \pm $0.10e^{0.045\pm0.0097}$, $R^2 = 0.28$, p < 0.01). The inter-individual variability is, however, also significant (standard deviation is 10-35% of the average). Before applying this or any calibration, the effect of the inter-individual variability on the accuracy of the Mg/Ca-10 temperature calibration has to be evaluated. The inter-individual variability is quantified and split in three components, namely (1) an analytical error; (2) an environmental effect and (3) a vital effect. The effect of inter-individual variability on the accuracy of Mg/Ca-temperature calibrations is depending on the sensitivity of the used calibration and the number of individuals measured (Temperature uncertainty 15 = $(0.33 \cdot N^{-0.50})$ /sensitivity). The less sensitive a calibration, the greater is the impact of inter-individual variability. This can partly be circumvented by measuring more individuals. Differences in sensitivity may depend on the stability of the environment in which the foraminifera live and the concurring ecological strategy. This study shows the link between inter-individual variability en sensitivity and their influence on the accuracy of 20

Mg/Ca-temperature calibrations.

1 Introduction

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The ratio of magnesium to calcium in the calcite of benthic foraminifera (i.e. test Mg/Ca) is an important tool to reconstruct past bottom water temperatures. From basic thermodynamic principles it follows that the rate of substitution of Mg-ions for Ca in the CaCO₃ lattice increases with temperature. This explains the temperature dependency





of foraminiferal Mg/Ca. However, most foraminiferal species produce calcite with a Mg content that is approximately an order of magnitude lower than those from inorganic precipitation experiments (Bentov and Erez, 2006; Morse et al., 2007). This implies that there is a strong biological control on Mg incorporation. This difference in element

- (and isotope) composition between biologically and inorganically precipitated calcium carbonate is known as the vital effect. The vital effect varies between species, which is indicated by the large differences in Mg incorporation in foraminiferal test carbonate of different species at the same temperature. The variability in Mg/Ca between individual tests of the same species suggests that the biologically-induced offset might not be
- ¹⁰ constant within one species. A number of field and culture studies have, furthermore, shown that the relation between temperature and test carbonate Mg/Ca differs between species and are therefore best described by species-specific calibrations (Lear et al., 2002; Anand et al., 2003; Rathmann et al., 2004; Elderfield et al., 2006; Rosenthal et al., 2011; Toyofuku et al., 2011; Wit et al., 2012). Most calibrations found so far are described by an exponential function linking Mg/Ca and temperature (Eq. 1)

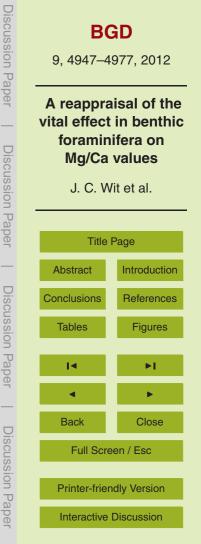
Mg/Ca= $a \cdot e^{(b \cdot T)}$

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where T is the temperature in degrees Celsius and a and b are empirically derived species-specific constants. The pre-exponential constant a, equals the (hypothetical) Mg/Ca at 0 °C and the exponential constant b describes the steepness of the slope with increasing temperature and is often referred to as the sensitivity of the temperature relation.

Here a new Mg/Ca-temperature calibration based on cultured specimens of the benthic foraminifer *Bulimina marginata* is presented. This species lives in shallow to deep infaunal habitats and is capable of living under sub-oxic conditions. Therefore

B. marginata is often found in large abundances at shelf sediments with high organic contents at intermediate water depths (e.g., Jorissen, 1987; Murray, 2006). A Mg/Ca-temperature calibration for *B. marginata* would allow the reconstruction of temperatures under sub-oxic conditions. This calibration could, therefore, enable reconstructions



(1)



helping to unravel the paleo-environment during events with limiting oxygen availability. This requires, however, also insight into the factors potentially offsetting such a calibration (e.g. a vital effect) and the effect on the accuracy of this paleo-thermometer.

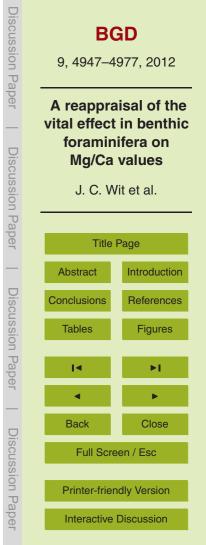
2 Methods

- Living specimens of the benthic, symbiont-barren foraminifer *Bulimina marginata* were collected from two stations in the Bay of Biscay (450 m and 600 m deep). Isolated specimens were placed in culture set-ups between 4 and 14 °C at Utrecht University and the University of Angers. Growth was monitored through incorporation of the fluorescent marker Calcein. This compound is a suitable marker for recognizing newly formed
 calcite (Bernhard et al., 2004), and does not affect the incorporation of Mg and Sr in foraminiferal calcite (Dissard et al., 2009).
- Two different culture setups were used for this Mg/Ca-*T* calibration: (1) an open system using 250 ml water, of which the seawater was replaced weekly to bi-weekly and (2) a closed system with seawater circulation from a large reservoir (251) towards the different experiments (Barras et al., 2010). Seawater from both setups was sampled weekly to monitor temperature, salinity, alkalinity and pH/DIC of the media. Alkalinity, DIC/pH were used to calculate [CO₃²⁻], using the CO2SYS software (Lewis and Wallace, 1998) (Table 1).

Experiments ran for 2–3 months to maximize the chance of sufficient calcite addition. Specimens were harvested by sieving over a 63 µm mesh with de-ionized water. After terminating each experiment, specimens were cleaned for 20 min in 5 % NaClO to dissolve organic matter attached to the surfaces of the foraminiferal shells. Afterwards individual foraminifera were rinsed 3–6 times with MilliQ and 2 times with methanol (Utrecht samples) to prepare the samples for trace metal analysis (Barker et al., 2003;

²⁵ Wit et al., 2010; Rosenthal et al., 2011).

Elements were measured, on newly calcified chambers of adult foraminifera, as a ratio to calcium with laser ablation inductively coupled mass spectrometry (LA-ICP-MS),



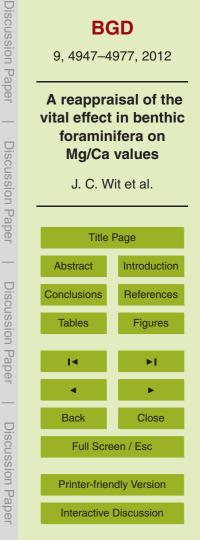


using ²⁴Mg, ²⁶Mg, ²⁷Al, ⁴²Ca, ⁴³Ca, ⁴⁴Ca, ⁵⁵Mn, ⁸⁸Sr and their relative natural abundances (see Reichart et al., 2003; and Wit et al., 2010 for a more detailed description). Element/Ca ratios were calibrated against the NIST 610 and an in-house calcite standard, verifying that differences in ablation energy do not affect measured elemental concentrations (Hathorne et al., 2008; Wit et al., 2010). Of all measured data, about 22 % was discarded because ablation profiles were too short (less than 20–30 pulses at 6 Hz), contamination values for Al were to high (> 20 ppm) or the standard deviation of the measurement was too high (> 70 ppm for Mg). High standard deviations in individual measurements are indicative for a heterogeneous distribution of Mg in the foraminiferal test. Elemental ratios with respect to Ca were based on the average of each ablation profile (Fig. 1). Individual foraminiferal Mg/Ca values were based on the average of uses any ontogenetic effect within the Mg/Ca-temperature calibration, using an ocular with a build in scale bar, which was scaled on a 1 mm slide. Size was determined

¹⁵ by measuring the height of each individual *B. marginata*.

3 Results

All culture experiments were monitored for stability of temperature, salinity, alkalinity and pH/DIC (Table 1). Individuals of *Bulimina marginata* calcified 1–4 new chambers in all experiments (Barras et al., 2010). The Mg/Ca of the newly formed cal-²⁰ cite was measured by laser ablation ICP-MS (Fig. 1). Values for Mg/Ca ranged from 0.75–2.91 mmol mol⁻¹ for individual foraminifera (Table 2). Inter-individual variability is calculated as a standard deviation expressed as a percentage of the average and varied between 5 and 25 %. Figure 2 shows the averaged Mg/Ca values per experiment versus temperature (Table 2). Values for Mg/Ca do not increase with test size ²⁵ ($R^2 = 0.03$, p > 0.10, Fig. 3). The average Mg/Ca increases with temperature (Eq. 2),





the associated R^2 of the correlation is 0.28 (p < 0.01).

 $Mg/Ca=1.10\pm0.10e^{0.045\pm0.0097}$

4 Discussion

4.1 Mg/Ca-temperature calibration for Bulimina marginata

- ⁵ The Mg/Ca values of cultured *Bulimina marginata* correlate significantly (*p* < 0.01) with temperature, although *R*² is rather low due to the relatively large inter-individual variability (Fig. 2). The calibration indicates a relatively low sensitivity of Mg/Ca in the calcite of *B. marginata* to changes in temperature, as expressed by the low exponential constant (0.045±0.009) (Eq. 2). Values for Mg/Ca are relatively low (~ 1–3 mmol mol⁻¹)
 ¹⁰ and similar to values for other calcitic hyaline foraminifera (Lear et al., 2002; Anand et al., 2003; Rathmann et al., 2004; Elderfield et al., 2006; Rosenthal et al., 2011). Analyses by Filipsson et al. (2010) suggested higher Mg/Ca values for *B. marginata*. Their results, however, were based on laser ablation rastering of the test surface. Since the outermost layer of calcite is commonly enriched in Mg (Fig. 1 and Hathorne et al.,
- 15 2009), their results may not be representative for the average chamber wall Mg/Ca. Despite the different analytical procedures and much higher absolute Mg/Ca values, the obtained Mg/Ca-temperature calibration of Filipsson et al. (2010) does have a similar sensitivity as the one presented here.

4.2 Ontogeny

Since the response of Mg/Ca to *T* is relatively low, additional impacts (e.g. size effects), may have a relatively large impact on the Mg/Ca-temperature calibration presented here. A positive and significant correlation between oxygen isotope values and size for *B. marginata*, possibly related to changes in growth rates, has been reported (Barras et al., 2010; Filipsson et al., 2010). An effect of ontogeny on planktonic foraminiferal

Discussion Paper **BGD** 9, 4947-4977, 2012 A reappraisal of the vital effect in benthic foraminifera on Discussion Paper Mg/Ca values J. C. Wit et al. Title Page Introduction Abstract **Discussion** Paper Conclusions References **Tables Figures |**◀ Back Close **Discussion** Paper Full Screen / Esc **Printer-friendly Version** Interactive Discussion



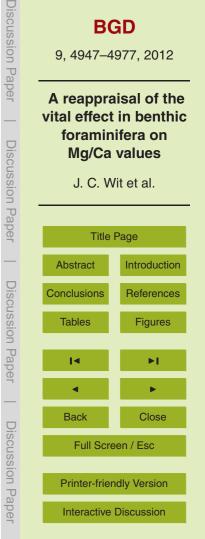
(2)

Mg/Ca has also been stipulated (Nürnberg et al., 1996; Wit et al., 2010; Dueñas-Bohórquez et al., 2011a). Ontogenetic effects for benthic foraminiferal Mg/Ca values are generally less well known, although Hintz et al. (2006) reported elevated Mg/Ca values for the mid-life stage of *Bulimina aculeata* by measuring Mg/Ca on both the whole foraminifer and on micro-dissected chambers. However, the Mg/Ca values re-

- ⁵ whole foraminiter and on micro-dissected chambers. However, the Mg/Ca values reported by Hintz et al. (2006) were exceptionally high (up to 84 mmol mol⁻¹), suggesting that a phase with elevated Mg concentrations biased their results. An ontogenetic trend observed in the results of the micro-dissection method should be directly comparable to laser ablation Mg/Ca measurements of individual chambers. The mid-life stage from
- ¹⁰ Hintz et al. (2006) corresponds to the F-2 chambers from this study. Intra-test variability for the experiment at 14 °C was, therefore, tested by using an analysis of variance (ANOVA), because the experiment contained enough data for this analysis. The ANOVA was designed to test whether Mg/Ca values for F-2 were significantly elevated compared to the F, F-1 and F-3 chamber.
- In our dataset, Mg/Ca for F-2 is not significantly different (F (3, 13) = 0.071, p > 0.10), nor is there a systematic difference in Mg/Ca with size (200–580 µm, $R^2 = 0.03$, p > 0.10), indicating that there is no significant size-related impact on the Mg/Ca of *B. marginata* (Fig. 3). The absence of an ontogenetic effect in Mg/Ca, while a significant effect on oxygen isotopes is recognized (Barras et al., 2010) fits the hypothesis that divalent cations (Ca and Mg) are transported to the site of calcification by a different machanism as the DIC (Free 2002).
- mechanism as the DIC (Erez, 2003; De Nooijer et al., 2009b; Dueñas-Bohórquez et al., 2011b).

4.3 Variability, low sensitivity and temperature reconstructions

Measured inter-individual variability in foraminiferal test carbonate Mg/Ca of cultured foraminifera is larger than for other elements (Dissard et al., 2010a; Dueñas-Bohórquez et al., 2011a, b). The standard deviation in Mg/Ca between individuals is an order of magnitude larger than what can be explained on the basis of the analytical uncertainty (on average 11 % of the mean, Fig. 1). Besides the relatively small analytical errors,



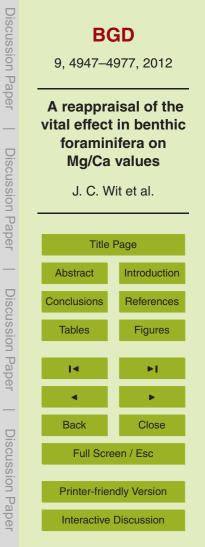


variability in Mg/Ca is caused by a combination of (1) variability in culture conditions (e.g. temperature, salinity, seawater Mg/Ca and carbonate ion concentration) and (2) inherent biological effects (i.e. the vital effect).

- For our results, the first cause of variability in foraminiferal Mg/Ca can be quantified using the measured variability in seawater temperature, carbonate ion concentration, Mg/Ca and salinity (Table 1). For instance, the temperature for the experiment at 6°C varied with a standard deviation of 0.5°C over the course of the experiment (Table 1). Using equation 2, this temperature variability can be translated to a range in foraminiferal Mg/Ca and expressed as a percentage of the Mg/Ca based on the average of the recorded temperature. For the experiment conducted at 6°C, an uncertainty
- of 0.5 °C in temperature thus introduces an uncertainty in the average Mg/Ca value of 2.35 % (Table 3). This uncertainty is the maximum offset caused by variability in temperature for this experiment. A similar procedure can be applied to all other experiments and for the uncertainties in salinity, Mg/Ca_{SW} and carbonate ion concentration
- ¹⁵ using the data from Table 1 and the sensitivities from the concurring Mg/Ca-parameter calibrations (Dueñas-Bohórquez et al., 2009, 2011b; Wit et al., 2012) (Table 3). From this table it can be concluded that in our culture experiment variability in Mg/Ca_{SW} and temperature explain most of the variability in Mg/Ca, whereas variability in the culture medium's salinity and $[CO_3^{2-}]$ play only a minor role.

Variability in environmental parameters other than temperature, affecting Mg/Ca, causes an uncertainty in Mg/Ca-based temperature reconstructions. This uncertainty depends on the sensitivity of the Mg/Ca-T calibration and therefore varies between species. The impact of changes in salinity, Mg/Ca_{SW} and carbonate ion concentration on the uncertainty in reconstructed temperatures was calculated, using differ-

ent Mg/Ca-parameter calibrations (Dueñas-Bohórquez et al., 2009, 2011b; Wit et al., 2012). Using the calibration for *B. marginata* (Eq. 2) with varying sensitivities (exponential constant), the impact on temperature uncertainties of changes in salinity Eq. (1) Mg/Ca_{SW} (0.6 mol mol⁻¹) and carbonate ion concentration (50 μmol kg⁻¹) at any given temperature can be calculated as a function of the sensitivity of the calibration (Fig. 4).



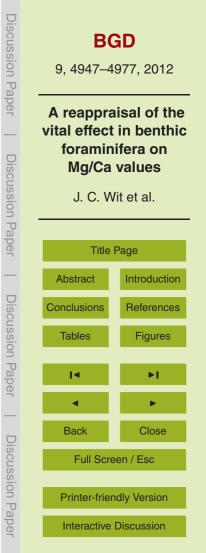


It follows that at a low sensitivity this uncertainty in Mg/Ca translates in to a larger temperature uncertainty, while at higher sensitivities the uncertainty is much smaller (Fig. 4).

- The second source for the large inter-individual variability is the vital effect, caused
 by variability in the efficiency and rate of various cell-physiological processes that constitute the calcification pathway (Erez, 2003; Bentov and Erez, 2006; De Nooijer et al., 2009b). The impact of these processes can be estimated by correcting the observed Mg/Ca values for the maximum analytical error and the environmentally-induced offsets calculated above. If the vital effect would be zero, every measured foraminiferal
 Mg/Ca value would fit the calibrated regression line (Fig. 5). Although impact of the
- vital effect can not be determined directly, we can estimate its magnitude. The two examples in Fig. 5 show how the three types of variability in foraminiferal test Mg/Ca are related to the measured Mg/Ca values. The total range in test carbonate Mg/Ca caused by uncertainties in the four culture parameters over this experiment explains
- ¹⁵ part of the observed inter-individual variability (Fig. 2, Table 4). The remaining component, expressed as the distance of the corrected Mg/Ca to the calibration curve, reflects the offset caused by the vital effect (Fig. 5, Table 4). The estimated vital effect may be larger than plotted, since we assume that analytical and environment-induced offsets are all lower than the measured variability in foraminiferal Mg/Ca: i.e. they all work in the same "direction" (Fig. 5).

The impact of inter-individual variability on the accuracy of paleo-temperature reconstructions can be calculated by assuming the standard deviation in the Mg/Ca values (measure of variability) from this culture study to be applicable to other foraminiferal species as well. The average variability (standard deviation) in the temperature cali-²⁵ bration for *B. marginata* is 16.3% (Table 2). This percentage can be used to calculate a standard error (σ/\sqrt{n}) of the average Mg/Ca value at any given temperature for

a number of foraminiferal Mg/Ca-temperature calibrations. This results in a temperature uncertainty (range of (Mg/Ca + σ/\sqrt{n}) – (Mg/Ca- σ/\sqrt{n})), which is independent of the absolute temperature, but is depending on the number of foraminiferal specimens





analyzed (N). Calculating the temperature uncertainty as a function of the number of specimens analyzed for a different species, the relation between temperature uncertainty and sensitivity can be expressed as:

Temperature uncertainty = $\frac{a}{\text{sensitivity}}$

⁵ The constant *a* varies with the number of individuals analyzed (*N*) for each temperature uncertainty (Eq. 4).

 $a = 0.33 \cdot N^{-0.50}$

Combining Eqs. (3) and (4) results in:

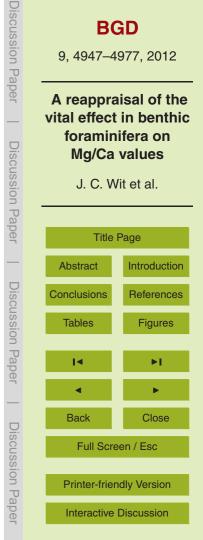
Temperature uncertainty = $\frac{0.33 \cdot N^{-0.50}}{\text{sensitivity}}$

With this equation, the number of specimens that need to be measured for a certain temperature uncertainty as a function of the sensitivity of the used Mg/Ca-temperature calibration (Fig. 6) can be determined. For species with a relatively low temperature sensitivity, relatively many specimens need to be analyzed for the same temperature uncertainty (Table 5). For example, 94 individuals of *B. marginata* need to be analyzed to be analyzed to be analyzed to be analyzed.

5 Controls on sensitivity

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The sensitivity of a calibrated Mg/Ca-temperature relationship is crucial for the accuracy of reconstructed paleo-temperatures. Using a species with a low sensitivity can be compensated by increasing the number of specimens (Eq. 5, Fig. 6). The accuracy will ultimately depend on the combination of analytical errors, the vital effect and absolute calcitic Mg concentration, as an offset in Mg/Ca will have a relatively large impact on



(3)

(4)

(5)



foraminifera with low Mg concentrations. Species that have a similar sensitivity, have calibration curves with a comparable steepness (Fig. 7), but not necessarily the same y-axis intercept. There appear to be three distinct sensitivities in the Mg/Ca response to temperature (Fig. 7). The first group includes only the calibration for the miliolid ben-

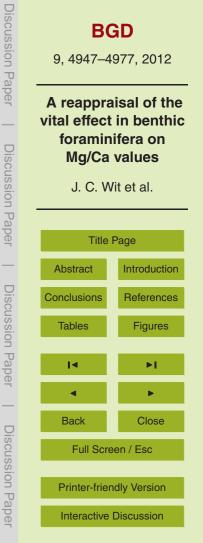
- ⁵ thic foraminifer *Pyrgo* spp. with a sensitivity of 0.16. The sensitivity of the second group varies between 0.09–0.13 and contains the foraminifera *Oridorsalis umbonatus*, *Cibici-doides* spp., *Globigerinoides ruber* (and most other planktonic species) and *Hyalinea balthica*. The third group entails *B. marginata*, *Uvigerina* spp. and *Ammonia beccarii*, which all have Mg/Ca-T sensitivities ranging from 0.04–0.06.
- The miliolid benthic foraminifer *Pyrgo* spp. is the only species studied so far that belongs to the group with high sensitivity in Mg incorporation with respect to increasing temperature. Miliolid foraminifera are calcifying following a different calcification mechanism than hyaline species (low and intermediate group) (Erez, 2003; de Nooijer et al., 2009a). Although the exact influence of this difference in calcification mechanisms on the sensitivity is unknown, it is likely that the difference in sensitivity between hyaline
- and porcelaneous foraminifera is caused by their different calcification pathways.

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The mechanisms responsible for the distinction between low and intermediate groups are unknown, but may be related to their evolutionary history or ecological strategies. Discrimination against Mg during calcification seems taxonomically related at least at a high level, since all known miliolid species produce calcite with high Mg/Ca

- (> 50 mmol mol⁻¹), while only some hyaline species are producing high Mg calcite (Toyofuku et al., 2000). For hyaline species, three different clades were recognized based on 26 SSU sequence analyses (Schweizer et al., 2008). Foraminifers with the lowest temperature sensitivity have representatives from all three clades, indicating that
- ²⁵ the Mg/Ca-*T* sensitivity may not be (fully) related to taxonomic relationships within foraminifera.

Alternatively, differences in ecological strategies might provide an explanation on the species specific Mg sensitivity to temperature. Foraminifera inhabit environments with contrasting food regimes. Both the total amount of organic matter as well as the timing

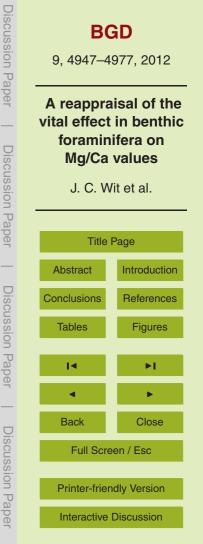




of its availability in benthic habitats is known to determine foraminiferal species composition (e.g., Murray, 2006). The organic load, in turn, affects the chemical conditions of the pore water in which foraminifera calcify. In eutrophic habitats, the enhanced organic matter availability causes high total faunal respiration rates and organic matter ⁵ oxidation, thereby elevating CO₂ levels and lowering the pH and CO₃²⁻ concentration and thus the saturation state of the pore water with respect to calcium carbonate (Ω_{cc}). In eutrophic microenvironments with lower Ω_{cc} , calcification is thought to be impaired by the decreased availability of CO₃²⁻ (Erez, 2003; Bentov and Erez, 2006; Dissard et al., 2010b). Since a higher amount of Mg in foraminiferal test carbonate increases its dissolution potential (Brown and Elderfield, 1996), it may be that active discrimination against Mg during calcification is proportional to the ambient average saturation state of the pore water with respect to calcite and hence be affected by the organic load of the sediment or the related ecological strategy as a response to the availability of food.

The shallow to deep infaunal species *B. marginata* is mainly found at sub-oxic conditions at locations relatively rich in organic matter (Jorissen, 1988, Jorissen et al., 1992). The benthic cosmopolitan *Ammonia beccarii/A. tepida* (Hayward et al., 2004) inhabits shallow marine to brackish environments, often very rich in organic matter (Murray, 1968). The third species with a low Mg-*T* sensitivity, *Uvigerina* spp., is commonly found in mesotrophic environments, often characterized by fine-grained sediments with elevated organic content (Van der Zwaan et al., 1986), and lives in shallow infaunal depth habitats (Van der Zwaan et al., 1986, Fontanier et al., 2002; Schweizer et al., 2005).

The group of species with intermediate sensitivity of Mg incorporation to temperature change contains the benthic species *Cibicidoides* spp., *O. umbonatus* and *H. balthica* and the planktonic species *G. ruber*. Most species within the genus *Cibicidoides* are epifaunal to shallow infaunal living close to or at the sediment-water interface, commonly in mesotrophic to oligotrophic, well oxygenated environments with relatively stable physio-chemical parameters (Jorissen et al., 1998; Gooday et al., 2003). The benthic foraminifer *O. umbonatus* has an epifaunal to shallow infaunal depth habitat and is mainly found in oligotrophic deep-sea environments (Jorissen et al., 1998; Rathmann





et al., 2004). *Hyalinea balthica* is a shallow infaunal living benthic foraminifer, typical for upper bathyal environments with mesotrophic conditions, although in some studies an opportunistic behavior has been described (Hess and Jorissen, 2009; Rosenthal et al., 2011). The planktonic foraminifer *G. ruber* is a shallow dwelling (living in the upper 50 m of the water column), symbiont-bearing species, living preferentially in oligotrophic surface waters (Hemleben et al., 1989). Summarizing, all species of this group are typical for oligotrophic to mesotrophic environments.

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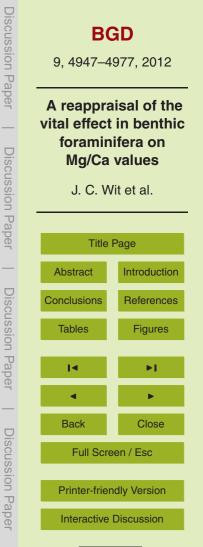
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All species of the low sensitivity group show some characteristics typical of an opportunistic lifestyle. *B. marginata* may reach very high densities in eutrophic settings (e.g., Jorissen, 1987; Jorissen et al., 1992), and is one of the few deep-sea species which reproduce in laboratory conditions (Barras et al., 2010). *Ammonia* spp. contains dominant taxa in a wide range of coastal ecosystems, where they tolerate large salinity and temperature variations. *U. peregrina* and *U. mediterranea* show a reproductive and

growth response to phytoplankton bloom events in the Bay of Biscay (Fontanier et al., 2003, 2006). In the literature, all these taxa are generally considered as opportunists.

It could be expected that species from eutrophic settings have a more opportunistic life strategy than species from mesotrophic or oligotrophic settings. Such an opportunistic life strategy would imply foraminifera to be able to react quickly to a number of environmental settings, of which some are hostile, ensuring a low Mg concentration

- (less soluble and more robust test) to be beneficial to this strategy. The most efficient way to guarantee a calcite test low in Mg is to lower the sensitivity to temperature, since temperature is the main environmental parameter influencing foraminiferal Mg incorporation. Mg/Ca values for the above used species should thus correlate well with the sensitivity of the species specific Mg/Ca-temperature calibration. Foraminiferal test
- Mg/Ca at a given temperature correlates significantly with the sensitivity of the calibration (Fig. 8), indeed indicating that a low sensitivity to temperature is a good strategy to keep Mg concentrations low, although the mechanisms behind this process still stays unknown.





However, also for some species of the intermediate sensitivity group an opportunistic behavior is suspected. This is clearly the case for *Hyalinea balthica*, which has been described with very high densities in eutrophic submarine canyon environments (Hess and Jorissen, 2009). But also *Cibicidoides* species are sometimes occurring in high densities, and dominate the foraminiferal fauna (e.g., Koho et al., 2008). Conversely, both *G. ruber* and *O. umbanatus* are always considered as oligotrophic taxa, without any opportunistic tendency. Summarizing, there is indeed a tendency for the low sensitivity taxa to be more opportunistic than the intermediate sensitive taxa, but the separation between the two groups is not as clear as we would hope. A better knowledge about the ecological strategies of these species is necessary to confirm that the lower temperature sensitivity is indeed the result of a more opportunistic lifestyle.

6 Conclusions

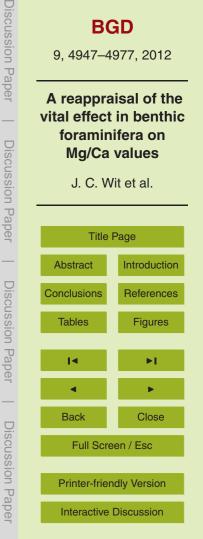
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LA-ICP-MS-measured Mg/Ca in cultured *B. marginata* correlates with temperature, although the sensitivity of Mg incorporation to temperature is low. The calibration is not hindered by any ontogenetic effects. The inter-individual variability within this calibration is too large to be caused by variations in culture parameters over the course of the experiment, but is tied to an intrinsic "vital effect" within the calcification process.

This inter-individual variability influences the practicality of the Mg/Ca thermometer, especially impacting calibrations with a low sensitivity. Foraminifera with this low sensitivity are therefore, not ideal for reconstruction pales to provide the practical for reconstruction pales.

tivity are, therefore, not ideal for reconstructing paleo-temperatures, due to associating large uncertainties or large sample sizes needed for an accurate reconstruction of temperature.

Although the biochemical mechanism responsible for the low sensitivity is yet unknown, it appears that foraminiferal species with this low sensitivity (*B. marginata*, *A. beccarii* and *Uvigerina* spp.) are living in more eutrophic environments. Foraminifera mainly living in oligotrophic to mesotrophic environments should, therefore, be used when reconstructing temperatures with the help of the Mg/Ca temperature proxy.





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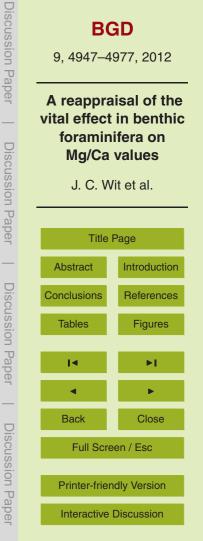
Examples of such taxa are *Cibicidoides* spp., *O. umbonatus*, *G. ruber* but especially *H. balthica* and *Pyrgo* spp.

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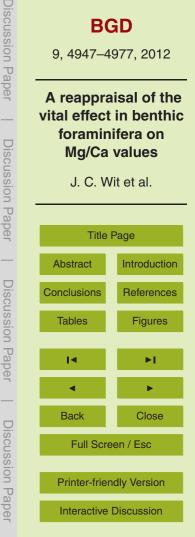
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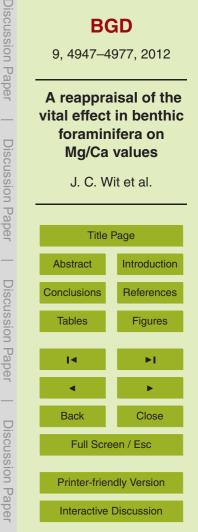
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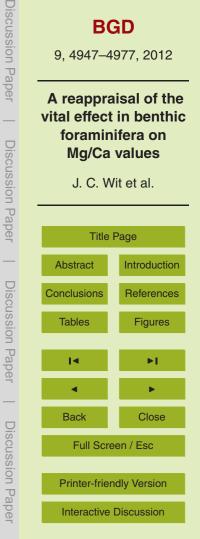
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d deviation c	of the main se	eawater paran	neters for all	temperature	Discussion Paper [9, 4947–4	isal of the in benthic
Salinity (psu)	Alkalinity (µmol1 ⁻¹)	рН	DIC (µmol I ⁻¹)	СО ₃ ^{2–} (µmoII ^{–1})	Discussion Paper	Mg/Ca J. C. W	values /it et al.
35.8 ± 0.1 35.8 ± 0.1	2528 ± 13 2524 ± 12	7.80 ± 0.07 7.80 ± 0.08	2492 ± 23 2480 ± 25	60 ± 8 64 ± 10	on Pa		
35.8 ± 0.1	2452 ± 30	7.93 ± 0.05	2357 ± 24	87±7	per	Title	Page
35.8 ± 0.1	2524 ± 13	7.78 ± 0.09	2473 ± 29	69 ± 12		Abstract	Introduction
35.8 ± 0.1	2454 ± 32	7.94 ± 0.05	2344 ± 41	96 ± 10		Abstract	Introduction
34.7 ± 0.2	2470 ± 73	8.14 ± 0.22	2215 ± 18	187 ± 54)isc	Conclusions	References
35.9 ± 0.1	2473 ± 34	7.98 ± 0.04	2334 ± 32	114 ± 8	SSD	Tables	Figures
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Table 1. Average and standard devia experiments.

Experiments contain samples from cultures a

Temperature

(°C)

 4.1 ± 1.1

 6.0 ± 0.5

 7.9 ± 0.1

 9.3 ± 0.7

 10.2 ± 0.1

 11.3 ± 0.3

 12.7 ± 0.1

 14.0 ± 0.2

9.7

3.2

¹ Utrecht University,

Experiment

1²

2 ²

3 ³

4 ²

5 ²

6 ¹

7 ²

8 ¹

Average

σ

² University of Angers or

³ combined samples.

Table 2. Sample number with single specimen Mg/Ca value for *B. marginata*. Mg/Ca values for individual foraminifers are based on 1–4 laser ablation profiles. The error in the averaged Mg/Ca value per temperature experiment is based on the standard error of the average (σ/\sqrt{n})

Sample	Temperature			Mg/Ca	Average Mg/Ca		
Nr	(°C)	$(mmol mol^{-1})$	(mmolmol ⁻¹)	Nr	(°C)	$(\text{mmol}\text{mol}^{-1})$	$(mmolmol^{-1})$
1	4.1	1.30		37	10.2	1.38	
2	4.1	1.78		38	10.2	1.30	
3	4.1	1.87		39	10.2	1.44	
4	4.1	1.60		40	10.2	2.22	
5	4.1	1.48		41	10.2	1.85	
6	4.1	1.24		42	10.2	2.50	
7	4.1	1.25		43	10.2	1.91	
8	4.1	1.15	1.46 ± 0.09	44	10.2	2.18	
9	6.0	1.80		45	10.2	1.50	
10	6.0	1.64		46	10.2	1.42	
11	6.0	0.91		47	10.2	1.68	
12	6.0	1.30		48	10.2	2.03	1.78 ± 0.11
13	6.0	0.75		49	11.3	2.22	
14	6.0	1.47		50	11.3	1.97	
15	6.0	1.25		51	11.3	1.73	
16	6.0	1.34		52	11.3	1.37	1.82 ± 0.18
17	6.0	1.19	1.30 ± 0.11	53	12.7	1.63	
18	7.9	1.73		54	12.7	1.61	
19	7.9	1.77		55	12.7	1.98	
20	7.9	1.39		56	12.7	2.06	
21	7.9	1.77		57	12.7	1.65	
22	7.9	1.72		58	12.7	1.17	
23	7.9	1.61		59	12.7	1.71	
24	7.9	1.98		60	12.7	1.72	
25	7.9	1.24		61	12.7	1.57	1.68 ± 0.09
26	7.9	1.11		62	14.0	2.31	
27	7.9	1.14		63	14.0	2.33	
28	7.9	1.29		64	14.0	1.91	
29	7.9	1.46		65	14.0	2.11	
30	7.9	1.65		66	14.0	1.87	
31	7.9	1.70		67	14.0	2.72	
32	7.9	1.84		68	14.0	2.26	
33	7.9	2.13		69	14.0	2.32	
34	7.9	2.77	1.67 ± 0.10	70	14.0	2.91	2.31 ± 0.11
35	9.3	1.15					
36	9.3	1.24	1.19 ± 0.04				



Discussion Paper

Discussion Paper

Discussion Paper

Discussion Paper



	σ (%)				
Experiment	Temperature	Salinity ^a	Mg/Ca _{sw} ^b	Carbonate ion ^c	Measured
1	5.4	0.7	2.9	1.4	18.4
2	2.5	0.6	2.9	1.3	25.4
3	0.5	0.6	2.9	1.2	24.3
4	3.4	0.5	2.9	1.5	5.2
5	0.5	0.5	2.9	2.7	21.8
6	1.2	0.9	2.3	3.7	20.0
7	0.5	0.4	2.9	1.3	15.2
8	0.8	0.8	4.3	2.8	14.7

Table 3. Standard deviation (as percentages of the average) based on the measured standard deviation of each parameter during the experiments.

Standard deviations from Table 1 are used and converted to Mg/Ca values using the same Mg/Ca-parameter relations of

^a Dueñas-Bohórquez et al. (2009) $(0.11 \cdot S + 1.00)$

^b Wit et al. (2012) (Mg/Ca= $a \cdot R \cdot e^{(b \cdot T)}$)

^c Dueñas-Bohórquez et al. (2011b) $(0.0012 \cdot [CO_3^{2-}] + 1.50)$.

Not all experiments had Mg/Ca_{sw} data, experiments without Mg/Ca_{sw} measurements were assumed to have variability according to the average variability of the measured experiments.

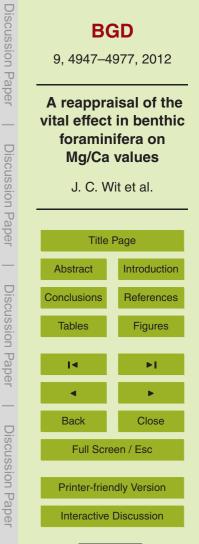




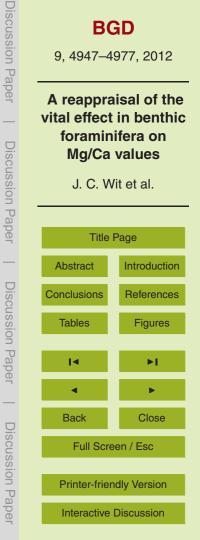
Table 4. Number of individuals needed to obtain a given uncertainty in temperature, based on the sensitivity of a Mg/Ca-temperature calibration and the averaged standard deviation of 16.3%. Uncertainty is expressed as a range (Max–Min) around the average reconstructed temperature.

Species Sensitivity Unce			Uncer	tainty (°C)		
		2.0	1.5	1.0	0.75	0.50	0.25
B. marginata ¹	0.045	13	23	52	93	210	837
A. beccarii ²	0.053	9	17	38	67	151	604
<i>Uvigerina</i> spp. ³	0.053	9	17	38	67	151	604
<i>O. umbonatus</i> ⁴	0.090	3	6	13	23	52	210
G. ruber ⁵	0.100	3	5	11	19	42	170
<i>Cibicidoides</i> spp. ⁶	0.109	2	4	9	16	36	143
H. balthica ⁷	0.123	2	3	7	12	28	112
<i>Pyrgo</i> spp. ⁸	0.160	1	2	4	7	17	66

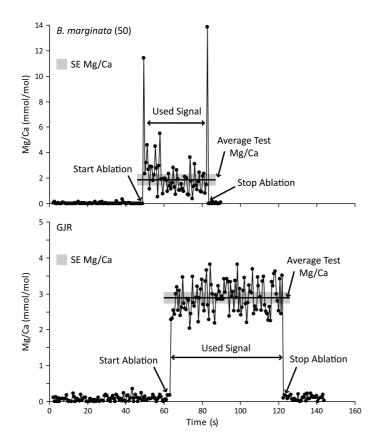
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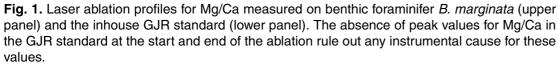
² Toyofuku et al. (2011)

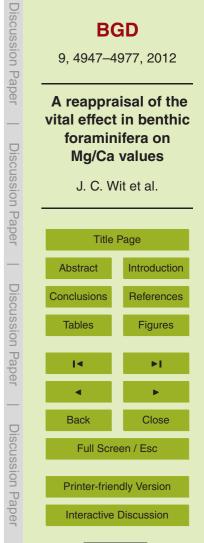
- ³ Elderfield et al. (2006)
- ⁴ Rathmann et al. (2004)
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- ⁶ Lear et al. (2002)
- ⁷ Rosenthal et al. (2011)
- ⁸ Wit et al. (2012)













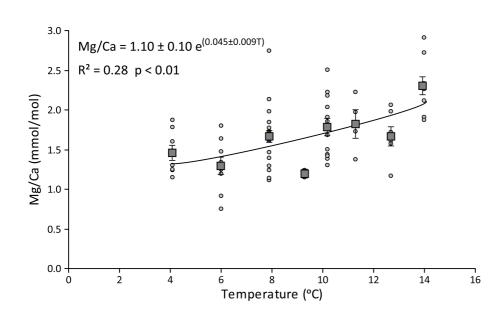
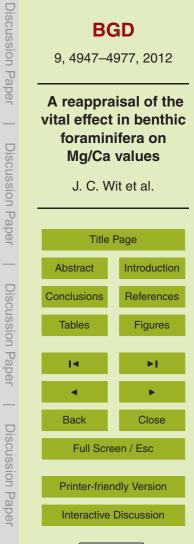
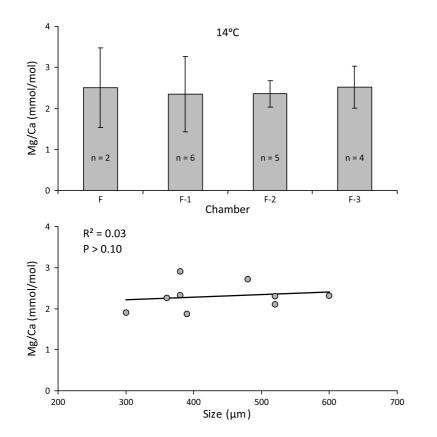
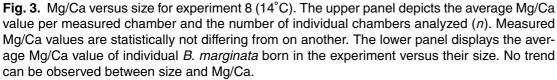
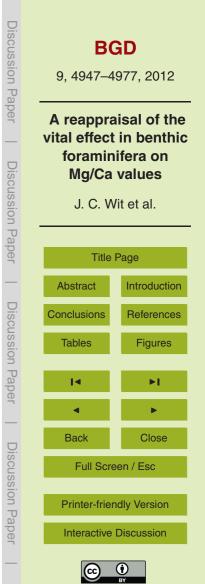


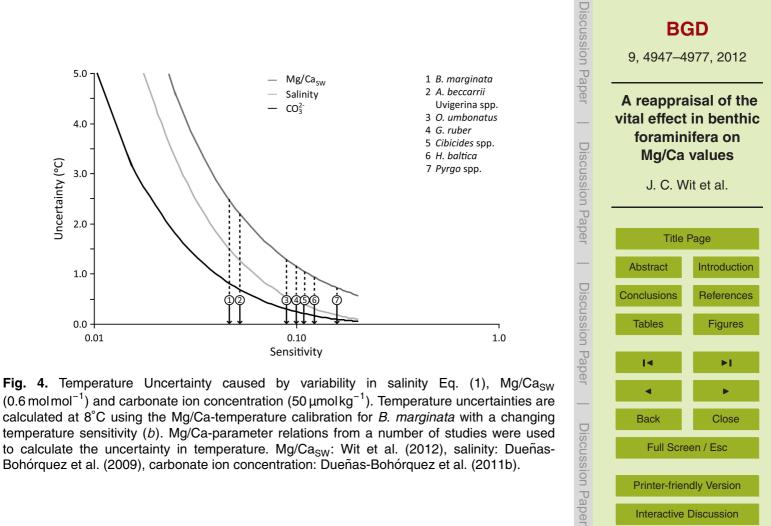
Fig. 2. Mg/Ca versus temperatures for all experiments with *B. marginata*. The error bars are based on the standard error of the mean (σ/\sqrt{n}) .











temperature sensitivity (b). Mg/Ca-parameter relations from a number of studies were used to calculate the uncertainty in temperature. Mg/Ca_{SW}: Wit et al. (2012), salinity: Dueñas-Bohórquez et al. (2009), carbonate ion concentration: Dueñas-Bohórquez et al. (2011b).



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Interactive Discussion

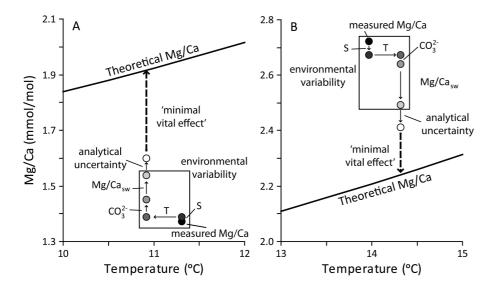


Fig. 5. Maximum correction for variability in culture parameters for measured Mg/Ca values of *B. marginata* 52 (**A**) and 67 (**B**). Corrections are based on the maximum variability of each experiment (Table 3). Variability was expressed as a correction in foraminiferal Mg/Ca using the same relations as for Fig. 4.

