Influence of test size, water depth, and ecology on Mg/Ca, Sr/Ca, $\delta^{18}O$ and $\delta^{13}C$ in nine modern species of planktic foraminifers

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ABSTRACT
Mg/Ca palaeothermometry in foraminiferal calcite is a widely applied tool in palaeoceanography. However, our understanding of the effects of planktic foraminiferal ecology and early diagenesis on test calcite Mg/Ca is limited. Here we report results of a study designed to shed new light on ecological, size-related and very early (water column) diagenetic controls on Mg/Ca in planktic foraminiferal calcite. We analysed Mg/Ca and stable isotopes of nine modern planktic foraminiferal species across fourteen mostly 50 μm-window sieve fractions in a core-top sample from the North Atlantic Ocean. We also analysed Mg/Ca in four of these nine species from plankton-tow samples collected from 0 to 2500 m water depth in the North Atlantic Ocean and Arabian Sea. Our core-top study confirms that sensitivity of Mg/Ca to change in test size is species-specific but reveals an overall decrease in Mg/Ca with increasing test size in all but one species, Orbulina universa, for which Mg/Ca increases with size. These findings are broadly consistent with known ecological behaviour suggesting that the size-related signal is largely environmentally rather than calcification-rate controlled. Our results underscore the need to undertake Mg/Ca palaeothermometry on narrow size fractions of planktic foraminifers, particularly for shallow-dwelling species such as G. bulloidnes and G. ruber where Mg/Ca is most sensitive to test size across the size range of 200–350 μm. Our plankton-tow data from the Arabian Sea are in agreement with in-situ temperatures. In contrast, our data from the North Atlantic Ocean reveal large variability and marked offsets (to warmer values) from in-situ temperatures that are interpreted to reflect lateral advection from the south, storm-induced vertical mixing of the water column and/or the influence of surface-water salinity on the Mg/Ca signal. None of our plankton-tow Mg/Ca data shows any evidence of test dissolution in the water column. Our study provides important verification that the Mg/Ca signal recorded during calcification does not undergo diagenetic degradation during test transport to the sea floor, thereby satisfying an important precondition of its palaeo-proxy utility.

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1. Introduction
Since the discovery that Mg/Ca in foraminiferal calcite is sensitive to calcification temperature (e.g., Lea et al., 1999; Mashiotta et al., 1999; Nürnberg et al., 1996; Rosenthal et al., 2000), Mg/Ca palaeothermometry has become an increasingly utilised tool in Cenozoic (e.g., Anand et al., 2008; Barker and Elderfield, 2002; Barker et al., 2005; de Vernal et al., 2006; Fehrenbacher et al., 2006; Lear et al., 2000; Mortyn et al., 2011; Nürnberg et al., 2000; Weldeab et al., 2005, 2007a, b; Zuraida et al., 2009) and Cretaceous (e.g., Bice et al., 2005, 2006; Erbacher et al., 2011; Friedrich et al., 2008) palaeoceanographic and -climatic studies. The advantage of Mg/Ca palaeothermometry lies primarily in the potential to record changes in calcification temperature (e.g., McConnell and Thunell, 2005) and to distinguish the temperature component of the $\delta^{18}O$ signal recorded in calcite from salinity and ice-volume effects through paired measurements of Mg/Ca and $\delta^{18}O$ (e.g., Elderfield and Ganssen, 2000; Lear et al., 2000, 2004; Mashiotta et al., 1999; Peck et al., 2006; Visser et al., 2003; Weldeab et al., 2006). We also know, however, of factors other than temperature with the potential to influence test calcite Mg/Ca (e.g., sea water Mg/Ca, salinity, seawater carbonate-ion concentration, and diagenetic alteration) (e.g., Arbuszewski et al., 2010; Dekens et al., 2002; Elderfield et al., 2006; Ferguson et al., 2008; Kisakürek et al., 2008; Rathmann and Kuhner, 2008; Rosenthal et al., 2006; Russel et al., 2004). Thus, to
use the Mg/Ca-palaeothermometer effectively, an extensive calibration effort and an improved knowledge of the imprint on test Mg/Ca of the ecology, ontogeny, and diagenesis of foraminifers are required. Substantial progress has been made to calibrate the Mg/Ca palaeothermometer for different planktic foraminifer species and to compare different calibrations against one another (e.g., Anand and Elderfield, 2005; Dekens et al., 2002; McKenna and Prell, 2004; Meland et al., 2006; Nyland et al., 2006; Regenberg et al., 2009). Striking features of these studies include differences in the resulting calibrations between different species and size fractions (e.g., Anand et al., 2003; Cléroux et al., 2008; Elderfield et al., 2002; Hathorne et al., 2009; McConnell and Thunell, 2005; Pogge von Strandmann, 2008; Sadekov et al., 2008; Skinner and Elderfield, 2005).

Differential stable isotopic fractionation between planktic foraminiferal shell calcite and sea water has long been appreciated. Stable carbon and oxygen isotope uptake in many species is strongly related to ontogeny, depth habitat, presence or absence of symbionts, and other calcification processes, commonly termed vital effects (e.g., Berger et al., 1978; Oppo and Fairbanks, 1989; Rohling and Cooke, 1999; Wetterer and Berger, 1991). Yet the effect of planktic foraminiferal ecology and habitat on the Mg/Ca composition of the test is poorly constrained. While some studies compare Mg/Ca data in two or three different size fractions of a single species (e.g., Anand et al., 2003; Anand and Elderfield, 2005; Ferguson et al., 2008; Pogge von Strandmann, 2008), the most detailed investigation of this problem published to date is that of Elderfield et al. (2002). In that study, increases in Mg/Ca with increasing test size are revealed for most species whereas decreases in Mg/Ca with increasing test size are shown for two deep-dwelling species, Globorotalia truncatulinoides (sin.) and Globorotalia crossiformis. Patterns of Mg uptake during ontogeny are yet to be fully elucidated but the dominant signal (increasing Mg/Ca with increasing test size) has been interpreted to reflect calcification rate-dependent uptake of Mg during shell formation with offsets from temperature-dependent partitioning of Mg into test calcite greatest in smaller size fractions (Elderfield et al., 2002).

The effect of encrustation and dissolution on Mg/Ca during settling through the water column is also still largely unknown. Alteration of tests and Mg/Ca in surface sediments has so far been explained by water-depth-related dissolution (Brown and Elderfield, 1996; Lohmann, 1995; Mekik and Francois, 2006; Rosenthal and Boyle, 1993; Rosenthal et al., 2000). Preferential dissolution of Mg-rich parts of tests settling through the water column would result in decreases in Mg/Ca before arrival at the sea floor, thereby limiting the utility of planktic foraminiferal Mg/Ca data in palaeoceanography (e.g., Brown and Elderfield, 1996; Nouet and Bassinot, 2007; Rosenthal et al., 2000). Moreover, a multitude of published planktic foraminiferal Mg/Ca-paleothermometer calibrations are based on samples obtained from sediment traps and core-top samples (e.g., Anand et al., 2003; Cléroux et al., 2008; Dekens et al., 2002; Elderfield and Ganssen, 2000; McKenna and Prell, 2004), and have presumably, therefore, been exposed to very early diagenetic processes within the water column.

Here we report the results of a two-pronged study designed to improve our understanding of the influence of ecological, size-related, and early diagenetic effects on Mg/Ca in planktic foraminiferal calcite. In a first step, we examine Mg/Ca, δ18O and δ13C in the calcite tests of nine modern species of planktic foraminifers in a core-top sample taken from the North Atlantic Ocean (Supplemental Fig. 1). Our analyses were performed across fourteen narrow (50 µm-window) sieve fractions to capture species-specific differences in ecologic demands and depth habitats. In a second step, we examine surface (above the seasonal thermocline) and subsurface (below the seasonal thermocline) plankton-tow samples from the North Atlantic and Arabian Sea for the influence of water depth on Mg/Ca in four of the same species. This approach allows us to examine the potential influence of planktic foraminifer population dynamics and the effect of dissolution during settling of the tests through the water column in different hydrographic settings (cf. Vincent and Berger, 1981).

2. Material and methods

2.1. Samples

2.1.1. Core-top sample

Mg/Ca ratios of nine planktic foraminiferal taxa Globigerina bulloides, Globigerinoides glutinata, Globorotalia hirsuta, Neogloboquadrina incompta, Globorotalia inflata, Globigerinoides ruber (white), G. truncatulinoides (sin.), G. truncatulinoides (dex.), and Orbulina universa were analysed from the upper 0–1 cm of sediment core MC575/13 from the North Atlantic (47°11′N, 19°34′W) at 4577 m water depth (Kurbjeweit, 2000; Ripperger et al., 2008; Supplemental Fig. 1). Samples were dry sieved and picked from fourteen size fractions: 100–150 µm, 150–200 µm, 200–250 µm, 250–315 µm, 315–400 µm, 400–450 µm, 450–500 µm, 500–550 µm, 550–600 µm, 600–650 µm, 650–700 µm, 700–750 µm, 750–800 µm, and 800–850 µm. Note that not all species are available from all size fractions. Although the number of specimens available in the larger size fractions is small, the obtained dataset is comprehensive. Tests were weighed using a microbalance (Sartorius M55, precision of 1 µg). Individual test weight from smaller size fractions was calculated by weighing batches of 25 tests to improve reproducibility. To check preservation and relative abundance of crust calcite-bearing specimens, ten specimens of each species were analysed under the SEM (Zeiss Sigma at Goethe University Frankfurt) for the size fractions 100–150 µm, 150–200 µm, and 200–250 µm.

2.1.2. Plankton-tow samples

Plankton-tow samples were collected using a multinet (100-µm mesh-size) from Arabian Sea and North Atlantic surface waters down to 2500 m water depth (Table 1). Samples from the upper 100 m of the water column contained mostly cytoplasm-bearing specimens whereas subsurface samples were mainly composed of empty tests. Samples from the Arabian Sea were collected during RV Meteor cruises M31/1, M32/5, and M33/1 in March to September 1995 (Hemleben et al., 1996; Locthe et al., 1996; Schott et al., 1996), and during RV Sonne cruise 119 in May 1997 (Schiebel et al., 2004). Samples from the North Atlantic were collected in April 1992 during RV Meteor cruises M21/1 and M21/2 (Pfannkuche et al., 1993). In-situ temperature and salinity were obtained along with all multinet samples by CTD. Specimens of G. bulloides, G. glutinata, N. incompta, and G. ruber were picked from the 200–250 µm size fraction. Depending on availability, between five and fifteen specimens were used for Mg/Ca determination in plankton-tow samples from both localities. For all sampling stations, SEM analyses were performed to check for preservation and occurrence of crust-bearing specimens through the water column.

2.2. Mg/Ca analysis

Cleaning of the tests followed the protocol of Boyle and Keigwin (1985) to remove clay and organic matter with the reductive step omitted. This latter step was omitted because the reducing reagent causes partial dissolution of carbonate, possibly resulting in lower Mg/Ca values (on average 15% compared to studies without reductive step; see detailed discussions in Barker et al., 2003; Bian and Martin, 2010; Sexton et al., 2006). For plankton-tow samples, the oxidative step using hydrogen peroxide was repeated to entirely remove cytoplasm within the tests. To remove any re-adsorbed contaminants, a final weak acid “polish” was performed. After cleaning, samples were analysed using a Perkin Elmer Optima 4300DV Inductively Coupled Plasma-Optical Emission Spectrometer at the National Oceanography Centre, Southampton, UK. Precision for Mg/Ca is better than 0.21% obtained from dilute solutions containing between 1 and
Fig. 1. Core-top sample MC575/13 (a) Mg/Ca versus sieved size fraction of planktic foraminiferal species, (b) same as (a) but including best-fit regression lines (black lines $r^2 = 0.9$; red lines $r^2 = 0.9$), and (c) relative temperature change estimated based on measured Mg/Ca ratios shown in relation to the 200–250 μm size fraction using a Mg/Ca sensitivity of 10% per 1 °C (e.g., Lea et al., 1999; Anand et al., 2003), (d) Sr/Ca versus sieved size fraction of planktic foraminiferal species.

Table 1
Sampling locations and water depth for plankton tow samples analysed in this study.

<table>
<thead>
<tr>
<th>Cruise</th>
<th>Station number</th>
<th>Sampling date</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Net number</th>
<th>Water depth (m)</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arabian Sea</td>
<td>M 31/3</td>
<td>110.4</td>
<td>14.03.1995</td>
<td>16°12N</td>
<td>60°16E</td>
<td>913–915</td>
<td>0–2500</td>
</tr>
<tr>
<td></td>
<td>M 32/5</td>
<td>414</td>
<td>27.07.1995</td>
<td>14°26N</td>
<td>65°00E</td>
<td>974–976</td>
<td>30–2000</td>
</tr>
<tr>
<td></td>
<td>M 32/5</td>
<td>414</td>
<td>27.07.1995</td>
<td>14°26N</td>
<td>65°00E</td>
<td>974–976</td>
<td>0–2500</td>
</tr>
<tr>
<td></td>
<td>M 33/1</td>
<td>601</td>
<td>30.09.1995</td>
<td>16°09N</td>
<td>60°25E</td>
<td>1007–1009</td>
<td>0–2500</td>
</tr>
<tr>
<td></td>
<td>M 33/1</td>
<td>601</td>
<td>30.09.1995</td>
<td>16°09N</td>
<td>60°25E</td>
<td>1007–1009</td>
<td>0–2500</td>
</tr>
<tr>
<td></td>
<td>SO 119</td>
<td>WEST</td>
<td>24.05.1997</td>
<td>16°12N</td>
<td>60°18E</td>
<td>1284–1286</td>
<td>0–700</td>
</tr>
<tr>
<td>North Atlantic</td>
<td>M 21/1</td>
<td>99</td>
<td>02.04.1992</td>
<td>19°30W</td>
<td>18°34W</td>
<td>640–651</td>
<td>0–2500</td>
</tr>
<tr>
<td></td>
<td>M 21/2</td>
<td>176, 177</td>
<td>29.04.1992</td>
<td>47°03N</td>
<td>18°34W</td>
<td>649–651</td>
<td>0–2500</td>
</tr>
</tbody>
</table>
5 ppm Ca$^{2+}$ (Green et al., 2003) while standards run during our study show a mean reproducibility of ± 0.01 Mg/Ca mmol/mol. G. ruber samples from cruises M31/3, M33/1, and S0119 were cleaned following the same protocol but analysed using a Perkin Elmer Optima 3300 R Inductively Coupled Plasma-Optical Emission Spectrometer at the University of Bremen. Standards and replicate runs of these samples show a mean reproducibility of ± 0.07 Mg/Ca mmol/mol. To monitor the presence of contaminant clay particles or Mn-coatings, Fe/Ca and Mn/Ca ratios were used. Both ratios are low and show no correlation with Mg/Ca ratios (Supplemental Fig. 2).

### 2.3. Temperature calculations

For plankton-tow samples, species-specific calibrations are applied where available (i.e., G. bulloides and G. ruber). For G. bulloides, Mg/Ca-based temperatures are calculated based on the calibration of Elderfield and Ganssen (2000), whereas the species-specific calibration of Anand et al. (2003) is used for G. ruber. For G. glutinata and N. incompta, species-specific calibrations are not available and we therefore apply the multi-species calibration of Anand et al. (2003). Existing calibrations indicate a temperature sensitivity for Mg/Ca of ~10% for a 1 °C change in temperature for almost all planktic foraminiferal species (e.g., Anand et al., 2003; Elderfield and Ganssen, 2000; Lea et al., 1999). For this reason, we estimate relative temperature changes (Fig. 1c) for the species analysed in the core-top sample using the multi-species calibration of Anand et al. (2003).

### 2.4. Stable isotope analysis

Stable oxygen and carbon isotope analyses were performed on the core-top sample for the same planktic foraminiferal species and size fractions as Mg/Ca analyses. Measurements were performed at the Goethe-University Frankfurt (Germany) using a ThermoFinnigan MAT253 mass spectrometer equipped with a Gas Bench II. Results are reported relative to the Vienna Pee Dee Belemnite (VPDB)

### 3. Depth habitats of analysed species of planktic foraminifers

Modern planktic foraminifers show a vertical distribution and pattern of abundance in the water column that is related to their species-specific environmental adaptations and demands (e.g., Bé et al., 1977; Fairbanks and Wiebe, 1980; Hemleben et al., 1989; Schiebel and Hemleben, 2005; Schiebel et al., 2002, 2004). Of the nine different taxa analysed in this study, G. ruber and G. bulloides occupy the shallowest depth habitat. They commonly reach highest abundances in the upper mixed layer (e.g., Fairbanks et al., 1982; Kuroyanagi and Kawahata, 2004; Schmuker and Schiebel, 2002). In the Atlantic Ocean, G. ruber calcifies within the upper 50 m of the water column (e.g., Anand et al., 2003; Farmer et al., 2007), typically reflecting warm (summer) conditions (e.g., Deuser and Ross, 1989; Lončaríć et al., 2006). While also calcifying in the upper mixed layer (highest numbers were found in the upper 20 m of the water column; Schiebel et al., 1997), G. bulloides is most abundant in spring (Schiebel and Hemleben, 2000).

Compared to both mixed-layer species, G. glutinata, N. incompta, and O. universa show their maximal standing stocks slightly deeper in the water column just above and around the thermocline (e.g., Faisbanks et al., 1980, 1982; Kuroyanagi and Kawahata, 2004; Schiebel and Hemleben, 2000). Where calcification depths have been inferred from foraminiferal δ$^{18}$O, estimates of around 50 to 100 m water depth are typically indicated for O. universa (Anand et al., 2003; Farmer et al., 2007). For G. glutinata, in contrast, a wider range of calcification depths has been suggested, reaching from the

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**Fig. 2.** Core-top sample MC575/13 (a) δ$^{18}$O versus sieved size fraction of planktic foraminiferal species, (b) δ$^{13}$C versus sieved size fraction of planktic foraminiferal species.
mixed layer down to the upper limit of the thermocline (Lončarić et al., 2006).

Globorotalids are generally assumed deep-dwelling (e.g., Hemleben et al., 1989). Globigerinoides truncatulinoides is shown to reach maximum abundances below the thermocline (usually >200 m water depth) (e.g., Ganssen and Kroon, 2000; Hemleben et al., 1989; Mulitza et al., 1997; Schiebel et al., 2002). Calcification depths for G. truncatulinoides are reconstructed to cover a wide depth range from below the mixed layer down to several hundreds of metres water depth (e.g., Andan et al., 2003; Lončarić et al., 2006; Regenberg et al., 2009), thereby integrating a wide ontogenetic depth range. The other two globorotalid species analysed here have been reported with their highest standing stocks below the photic zone (G. hirsuta) and from a wide range of water depths (G. inflata) (e.g., Andan et al., 2003; Chiesi et al., 2008; Hemleben et al., 1989; Lončarić et al., 2006; Schiebel and Hemleben, 2000; van Raden et al., 2010). Previous studies imply that G. inflata calcifies in water depths between 20 and 500 m throughout the year (e.g., Chiesi et al., 2008; Elder et al., 2003; Wilke et al., 2006) and living specimens are found in plankton-tows from the Western Mediterranean Sea down to a water depth of 700 m (van Raden et al., 2010). In the South Atlantic, core-top data suggest that G. inflata calcifies constantly within the permanent thermocline at 350 to 400 m water depth (Groeneveld and Chiessi, 2011).

4. Results and discussion

4.1. Our core-top study

Of the nine species analysed, only G. ruber and O. universa are symbiont bearing. Globorotalids are discussed as a species group, according to their generally deeper depth habitat than species of other genera (e.g., Ganssen and Kroon, 2000; Hemleben et al., 1989; Lončarić et al., 2006; Schiebel and Hemleben, 2000). Our Mg/Ca data from the core-top study (Supplemental Table 1) are presented against both test size (sieve size fraction, Fig. 1) and individual weight (Supplemental Fig. 3). Stable isotope data are correlated here with sieved size fractions only (Supplemental Table 2; Fig. 2). In sieve size fractions where all nine species are represented (150–300 μm) our Mg/Ca and δ18O data indicate depth habitat rankings that are broadly consistent with one another and with published ecological findings (Figs. 1 and 2). For a given test size, significant offsets in Mg/Ca are indicated across the species analysed (~2.8, ~1.2 and ~3.8 mmol/mol 100–150 μm, 250–315 μm and 700–750 μm fractions, respectively). Of these nine species, eight show an overall trend towards lower Mg/Ca with increasing test size (Fig. 1a) and weight (Supplemental Fig. 3), the adult stages (spherical chamber) of O. universa being the only exception (Figs. 1a–c). Our data reveal (1) steeper gradients in Mg/Ca for small adult specimens (~250 μm) compared to those seen in larger tests and (2) steeper size-related gradients in deep-dwelling globorotalids than in shallow-dwelling species (Fig. 1). We interpret the smaller size-related Mg/Ca changes recorded in shallow-dwelling species (i.e., G. ruber, G. bulloides, N. incompta) to reflect calcification over a narrower depth range largely within the surface-mixed layer, whereas our results for thermocline and deep dwellers reveal the imprint of calcification with a life cycle involving substantial vertical migration through the water column. This interpretation is supported by our stable isotope dataset that shows a narrower range in δ18O for smallest tests (0.4‰ for 100–150 μm, excluding G. hirsuta) and a divergence of δ18O (1.1‰) for 250–315 μm (Fig. 2) mainly driven by higher values in globorotalids.

4.1.1. Symbiont-bearing species

The highest Mg/Ca values recorded in our dataset are seen in O. universa, a tropical to subtropical species, that has been shown to yield unusually high Mg/Ca ratios in numerous studies (Anand et al., 2003; Elderfield et al., 2002; Lea et al., 1999). O. universa was present at the location of our North Atlantic core-top site (47°N) only during summer when the water column was well stratified at surface-water temperatures >16 °C. Yet, despite being north of its main latitudinal habitat at this location, O. universa has a size-to-weight ratio similar to ‘high light’ laboratory specimens cultivated from waters off Santa Catalina Island, California (Supplemental Fig. 4; Hamilton et al., 2008). Laboratory studies on the two symbiont-bearing species O. universa and G. sacculifer show a positive relationship between test size and ambient light level, possibly attributable to the impact of symbiont photosynthesis on shell calcification processes (Hamilton et al., 2008; Hönisch and Hemming, 2004; Spero and Lea, 1993). The positive trend in our Mg/Ca data with increasing size for O. universa is therefore consistent with the interpretation that

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![Fig. 3](image-url) Comparison between our core-top results and those of Elderfield et al. (2002): (a) Full size range of our study compared to size range of Elderfield et al. (2002) (grey bar), (b) for the size range 200–500 μm (lines represent linear regression). Note that the data of Elderfield et al. (2002) are from 19°N and therefore reflect higher surface-water temperatures and therefore higher Mg/Ca values compared to our data (47°N).
larger test sizes indicate calcification in shallower waters under high-light conditions.

Whereas Mg/Ca values in O. universa show a clear positive trend with increasing test size in accordance to the findings of Elderfield et al. (2002), the second analysed symbiont-bearing species G. ruber lacks this relationship. G. ruber (white) yields a modest decrease of 0.3 mmol/mol in Mg/Ca ratios with increasing test size (Fig. 1a). Small change in Mg/Ca-temperature with size indicates a narrow (and shallow) depth habitat range for G. ruber throughout calcification. This result is consistent with faunal count data from various ocean basins (e.g., Kuroyanagi and Kawahata, 2004) and our δ¹⁸O data (Fig. 2). Unfortunately, the small size range over which data are available from our study (150–315 μm) does not allow us to consider the possible influence of symbiont photosynthesis on G. ruber size-related Mg/Ca values.

4.1.2. Symbiont-barren species: surface dwellers

Highest Mg/Ca values recorded in specimens of the studied symbiont-barren species are recorded in the shallow-dwelling species G. bulloides. Our Mg/Ca and stable isotope data for G. bulloides (Figs. 1 and 2) are consistent with published interpretations of its opportunistic behaviour at surface mixed layer depth habitats and final chamber formation and addition of a gametogenic calcite crust (Supplemental Table 3) at thermocline depths (e.g., Hemleben et al., 1989; Sautter and Thunell, 1991; Schiebel et al., 1997; Ufkes et al., 1998).

Of all nine species analysed in our core-top sample, Mg/Ca is lowest and least variable across sieve-determined test size in N. incompta (Fig. 1a). This species, however, is most abundant in the temperate North Atlantic during summer when dwelling in surface waters (Kuroyanagi and Kawahata, 2004; Schiebel and Hemleben, 2000). Our results appear to lend support to a reported behaviour in which tests of the genera Neogloboquadrina are known to form a massive calcite crust overgrowth in subsurface waters (Kohfeld et al., 1996). Thus our Mg/Ca and SEM data (Fig. 1a; Supplemental Table 3) yield a similar calcification history for N. incompta in the North Atlantic to that indicated by δ¹⁸O and δ¹³C data for N. pachyderma (s) in the Nordic Seas (Simstich et al., 2003). Within our δ¹⁸O dataset, however, N. incompta shows intermediate values (slightly lower than the globorotalids, Fig. 2). This finding indicates that, for this species, the oxygen isotope fractionation factors between sea water and crust and original wall calcite more closely approximate one another than is the case for Mg partitioning into crust and original wall calcite.
4.1.3. Symbiont-barren species: thermoline- and subthermoline dwellers

*G. glutinata* and the group of four *Globorotalia* species analysed exhibit Mg/Ca values that fall between *N. incompta* and the three other mixed-layer dwellers (Fig. 1), and δ18O values higher than surface dwellers (Fig. 2), consistent with the subsurface depth habitat reported in ecological studies (e.g., Hemleben et al., 1989; Schmucker and Schiebel, 2002). Mg/Ca ratios in thermoline-dwelling *G. glutinata* indicate a distinctive signal in depth habitat (Fig. 1a). Small (<150 μm test size) and large (>250 μm) specimens are lowest in test Mg/Ca, indicating reproduction at thermoline depths (Hemleben et al., 1989), and an ascent to shallower water depths (supra-thermoline) surface waters in between (150–250 μm test size). This result is consistent with faunal data from the temperate NE Atlantic and Arabian Sea (Anderson et al., 1979; Schiebel et al., 2001, 2004) but not entirely reproduced by our stable isotope data that lack a decrease towards lower δ18O values in the size fraction >250 μm. Similar population dynamics are seen under other hydrographic conditions, such as upwelling along hydrographic fronts (Lončaric et al., 2006; Storz et al., 2009).

Faunal data and stable isotope analyses of the deep-dwelling *Globorotalia* (e.g., Cléroux et al., 2007; Hemleben et al., 1985, 1989; Mulitza et al., 1997; Norris et al., 1994) suggest an adaptation to a subsurface depth habitat during the neanic ontogenetic stage and an early juvenile development in surface waters. In our dataset, high Mg/Ca-derived temperature estimates of small *Globorotalia* (in particular *G. truncatulinoides* sin.) and δ18O values comparable to surface-dwelling species suggest an early ontogenetic stage in surface mixed waters (see also Weyl, 1978) and subsequent descent into deeper waters, as indicated by decreasing Mg/Ca (Fig. 1), increasing δ18O (Fig. 2), and higher abundance of crust-bearing specimens (Supplementary Table 3) with size.

Left and right coiling morphotypes of *G. truncatulinoides* yield remarkably similar results both for stable isotopes (especially in smaller size fractions) and Mg/Ca (especially between 200 and 450 μm) with overall size-related variations of up to about 0.25% and 0.53 mmol/mol Mg/Ca. Most of the Mg/Ca change is seen in the smaller size fractions (<200 μm; Table 2). In fact, the smallest specimens of these taxa, together with those of *G. inflata* and *G. hirsuta*, yield Mg/Ca values that plot together with the surface-dwelling taxa.

### 4.2. Comparison of our core-top study with published results

For the analysed symbiont-barren species and *G. ruber*, the overall pattern revealed by our dataset is one of a decrease in Mg/Ca with increasing test size (Fig. 1), a signal that is most noticeable in the smallest size fractions and largely consistent with the ecology of the species analysed. In contrast, the most detailed previous size-related pattern revealed by our dataset is one of a decrease in Mg/Ca with increasing test size (Fig. 1a). Small (<150 μm test size) and large (>250 μm) specimens are lowest in test Mg/Ca, indicating reproduction at thermoline depths (Hemleben et al., 1989), and a descent to shallower water depths (supra-thermoline) surface waters in between (150–250 μm test size). This result is consistent with faunal data from the temperate NE Atlantic and Arabian Sea (Anderson et al., 1979; Schiebel et al., 2001, 2004) but not entirely reproduced by our stable isotope data that lack a decrease towards lower δ18O values in the size fraction >250 μm. Similar population dynamics are seen under other hydrographic conditions, such as upwelling along hydrographic fronts (Lončaric et al., 2006; Storz et al., 2009).

A calcification rate control on Mg/Ca data, as suggested by Elderfield et al. (2002), cannot account for our data. It has long been suggested that decreasing calcification rate through ontogeny acts to increase δ13C in planktic foraminiferal tests because of decreased kinetic isotope fractionation and incorporation of metabolic CO2 (e.g., Berger et al., 1978; Ravelo and Fairbanks, 1995; Spero and Lea, 1996). A calcification rate influence on both Mg/Ca and Sr/Ca has also been inferred (Elderfield et al., 2002) based on (1) a linear correlation with test size change in δ13C (increasing test size is associated with increases in δ13C and Mg/Ca but decreases in Sr/Ca) and (2) correspondence of these trace element signals to the results of calcite growth experiments where differential partitioning in Mg and Sr incorporation leads to an opposite response of Mg/Ca and Sr/Ca to calcification rate (Lorens, 1981; Parquette and Reeder, 1995). These trends to higher δ13C (Fig. 2) and lower Sr/Ca (Fig. 1d) seen in larger size fractions are both clearly expressed in our data with a similar gradient of δ13C increase with size over the 125 to 300 μm range indicated for all nine species (Fig. 2). Yet our findings of (1) an overall decrease in Mg/Ca in the tests of especially symbiont-barren planktic foraminifers with increasing test size (Fig. 1) and (2) lack of a consistent relationship between Mg/Ca and δ13C (Fig. 4a) run contrary to the hypothesized calcification rate control. In addition, for six of the nine species we observe changes in Mg/Ca- and δ18O-derived temperatures that follow a 1:1 relationship (Fig. 4c) and/or show a near proportionate temperature difference for both small and large size classes (<200 μm vs. >200 μm; Table 3). For these reasons, we conclude that the size-related Mg/Ca signal at least in the symbiont-barren species is mainly influenced by environmental

### Table 2

<table>
<thead>
<tr>
<th>Size fraction [μm]</th>
<th>Mg/Ca [mmol/mol] G. truncatulinoides (dex.)</th>
<th>Mg/Ca [mmol/mol] G. truncatulinoides (sin.)</th>
<th>Difference Mg/Ca Mg/Ca (dex.)–Mg/Ca (sin.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>150–200</td>
<td>2.816</td>
<td>2.291</td>
<td>0.525</td>
</tr>
<tr>
<td>200–250</td>
<td>2.106</td>
<td>2.209</td>
<td>−0.103</td>
</tr>
<tr>
<td>250–315</td>
<td>1.693</td>
<td>1.693</td>
<td>0.000</td>
</tr>
<tr>
<td>315–400</td>
<td>1.672</td>
<td>1.675</td>
<td>−0.003</td>
</tr>
<tr>
<td>400–450</td>
<td>1.704</td>
<td>1.847</td>
<td>−0.143</td>
</tr>
<tr>
<td>450–500</td>
<td>1.942</td>
<td>1.527</td>
<td>0.415</td>
</tr>
<tr>
<td>500–550</td>
<td>1.646</td>
<td>1.582</td>
<td>0.064</td>
</tr>
<tr>
<td>550–600</td>
<td>1.606</td>
<td>1.630</td>
<td>−0.024</td>
</tr>
</tbody>
</table>

### Table 3

<table>
<thead>
<tr>
<th>Species</th>
<th>&lt;200 μm</th>
<th>&gt;200 μm</th>
<th>Mg/Ca</th>
<th>δ18O-δ13C derived temperature estimates (Δtempr) as a function of test size.</th>
</tr>
</thead>
<tbody>
<tr>
<td>G. ruber</td>
<td>−3.08</td>
<td>−3.97</td>
<td>1</td>
<td>0.271</td>
</tr>
<tr>
<td>G. bulloides</td>
<td>−2.32</td>
<td>−2.12</td>
<td>2</td>
<td>0.462</td>
</tr>
<tr>
<td>O. universa</td>
<td>n/a</td>
<td>5.01</td>
<td>0</td>
<td>2.238</td>
</tr>
<tr>
<td>N. incompta</td>
<td>1.76</td>
<td>1.59</td>
<td>5</td>
<td>2.093</td>
</tr>
<tr>
<td>G. glutinata</td>
<td>−2.74</td>
<td>−2.36</td>
<td>2</td>
<td>1.742</td>
</tr>
<tr>
<td>G. inflata</td>
<td>−4.59</td>
<td>−2.37</td>
<td>2</td>
<td>1.007</td>
</tr>
<tr>
<td>G. truncatulinoides</td>
<td>4.34</td>
<td>0.21</td>
<td>1</td>
<td>0.613</td>
</tr>
<tr>
<td>G. hirsuta</td>
<td>1.67</td>
<td>5.13</td>
<td>1</td>
<td>1.076</td>
</tr>
<tr>
<td>G. crassafornis</td>
<td>−6.20</td>
<td>−3.97</td>
<td>2</td>
<td>1.767</td>
</tr>
</tbody>
</table>

The changes in Mg/Ca reported by Elderfield et al. (2002) broadly follow δ18O calcification temperatures but surface and near-surface dwelling species in that study show larger changes in Mg/Ca than can be accounted for by δ18O-derived changes in temperature, an observation not replicated in our data. A direct comparison of our results with those of Elderfield et al. (2002) indicates that, where data are available from both studies for the same size fractions and species (200–500 μm size range; *G. bulloides*, *G. ruber*, *G. inflata*, *G. truncatulinoides* (sin.), *O. universa*), the two datasets yield results that are remarkably similar in form but offset to lower absolute values at our higher latitude site (0.4 to 1.2 mmol/mol except for *O. universa*; Fig. 3). The reason why we find an overall signal that is opposite in sign to that of Elderfield et al. (2002) arises from the fact that our study spans a significantly greater test size range (100 to 800 μm, in mostly 50-μm bins versus 212 to >500 μm in 50-μm bins for the other study; Fig. 3). In other words, the signal of decreasing Mg/Ca with increasing test size that we report is carried mainly in the smaller and, to a lesser extent, the larger tests. Fig. 3 shows that the signal for the mid-size tests is typically one of rather little change (Fig. 3a), except for *G. truncatulinoides* (sin.) and *O. universa* which show modest decreases and pronounced increases in Mg/Ca, respectively.
factors (e.g., depth habitat or vertical migration) and not by calcification rate.

4.3. Our plankton-tow study

Mg/Ca-ratios for *G. bulloides* and *G. ruber* in our plankton-tow samples from the Arabian Sea are presented in Supplemental Table 4. We compare Mg/Ca-based calcification temperatures with in-situ temperatures measured in the water column by CTD at the time of sampling the foraminifers (Fig. 5) and mean monthly temperatures for the month prior to sampling from the World Ocean Atlas 2005 (Fig. 5, Locarnini et al., 2006). Mg/Ca-based temperature estimates for *G. ruber* are ~1 to 2 °C higher than in-situ sea-surface temperatures in March (NE monsoon, M 33/1; Fig. 5 top left panel) and July (SW monsoon, M 32/5; Fig. 5 bottom left panel) but match mean monthly temperatures well (Fig. 5). For samples obtained in May in the main upwelling region off Oman, and for samples from September (weak SW monsoon), *G. ruber* Mg/Ca-based calcification temperatures are comparable to in-situ temperatures at the sea surface (Fig. 5 top and bottom right panels). Sufficient numbers of *G. bulloides* for analysis were only available for July and September. Mg/Ca-based temperatures for *G. bulloides* are slightly lower than those for *G. ruber* and reflect in-situ temperatures in the Arabian Sea corresponding to ca. 50–100 m water depth in September (M 33/1; Fig. 5 bottom right panel) and are slightly higher than in-situ temperatures in July (M 32/5; Fig. 5 bottom left panel). When compared to mean monthly temperatures, *G. bulloides* Mg/Ca calcification temperatures are comparable to surface-water temperatures (Fig. 5).

A prominent feature of our Arabian Sea dataset is that none of the four sampling sites reveals a significant change in Mg/Ca for *G. ruber* or *G. bulloides* with water depth (variability in Mg/Ca-temperature over the analysed depth range is typically ~1 °C; Supplemental Table 4 and Fig. 5). This finding is consistent with calcification over a narrow range of water depths and no influence of lateral transport/mixing, dissolution, or crust formation (as also revealed by SEM analyses) on the Mg/Ca signal during migration/settling through the water column. The calcification temperatures recorded are generally in good agreement with in-situ measured and mean monthly temperatures (Fig. 5) for the surface mixed layer and therefore consistent with the inferred epipelagic ecology of these two species (e.g., Fairbanks et al., 1982; Kuroyanagi and Kawahata, 2004; Schiebel et al., 2004).

Laboratory experiments (Dueñas-Bohórquez et al., 2009; Kisakürek et al., 2008; Lea et al., 1999; Nürnberg et al., 1996) and core-top studies (e.g., Arbuszewski et al., 2010; Mathien-Blard and Bassinot, 2009) show that salinity influences Mg/Ca ratios in planktic foraminifers. The absolute effect of salinity is, however, still a matter of debate and estimates range from 4 to 7%psu⁻¹ (Kisakürek et al., 2008; Lea et al., 1999; Nürnberg et al., 1996) in laboratory cultures to 27 ± 4%psu⁻¹ for the subtropical Atlantic Ocean (Arbuszewski et al., 2010). Application of a temperature calibration for *G. ruber* that incorporates a salinity effect (Kisakürek et al., 2008) yields temperatures that are 0.5 to 2 °C higher (based on a CTD-derived salinity of 36.3 psu at our sites) than those derived from the species-specific equation of Anand et al. (2003) and consistently higher than in-situ temperatures for all of our Arabian Sea sample set. This discrepancy probably indicates that calibrations using entire tests (Anand et al., 2003) and probably more suited to this sort of application than laboratory studies using typically only the last chamber, which calcified during the course of the experiment (Kisakürek et al., 2008). Furthermore, genetic diversity in *G. ruber* might be responsible for the observed offset between calibrations. Two main morphotypes exist in *G. ruber* (*G. ruber* sensu stricto (s.s.) and *G. ruber* sensu lato (s.l.)) that recently have been shown to represent different genotypes (Aurahs et al., 2011). Comparison of Mg/Ca measurements on both morphotypes shows higher Mg/Ca ratios for *G. ruber* s.s. compared to *G. ruber* s.l., supporting a shallower depth habitat for the *G. ruber* s.s. morphotype (Steinke et al., 2005). In our study, the *G. ruber* s.s. morphotype was analysed, reflecting the shallower habitat, in accordance with our Mg/Ca data representing surface-water conditions. The study of Anand et al. (2003) used specimens from the North Atlantic, whereas the calibration of Kisakürek et al. (2008) is based on specimens from the Red Sea, probably representing a different genotypes or morphotypes.

In contrast to the plankton-tow results from the Arabian Sea, our Mg/Ca-based calcification temperatures from our North Atlantic sites (Supplemental Table 5; Fig. 6) show distinct variability with depth in the water column and poor correspondence to in-situ and World Ocean Atlas-derived temperatures. In the upper 150 m of the water column, Mg/Ca-derived temperatures for *G. bulloides* range between 18 and 21 °C (3.2 to 4.3 mmol/mol), whereas samples from the deeper water column show relatively constant calcification temperatures of around 18 °C (3.2 mmol/mol; Supplemental Table 5, Fig. 6). *G. bulloides* from the North Atlantic and Arabian Sea have been postulated to represent different genotypes (Darling and Wade, 2008) but the general distribution pattern of all *G. bulloides* types, i.e., depths habitat, trophic strategy, and test chemistry, appears to be broadly similar (e.g., Kroon and Ganssen, 1988; Ottens and Nederbragt, 1992; Peeters and Brummer, 2002; Schiebel et al., 1997, 2004). If we assume that genotypic differences of *G. bulloides* do not account for differences in Mg/Ca between our two study sites, we must infer that differences in hydrographic conditions between the North Atlantic Ocean and the Arabian Sea are responsible.

In our plankton-tows from the North Atlantic, *G. glutinata* exhibits slightly higher calcification temperatures than *G. bulloides*. *N. inconsta* shows similar patterns during RV Meteor cruises 21/1 and 21/2 (both April 1992), with higher values in surface waters (Supplemental Table 5, Fig. 6). Mg/Ca-based temperatures for *N. inconsta* and *G. glutinata* are characterized by lowest temperatures between 100 and 700 m depth, and slightly enhanced Mg/Ca-based temperatures at 700–2500 m depth (Fig. 6).

While *N. inconsta* shows relatively high and distinctly variable Mg/Ca through the water column in our North Atlantic plankton-tow study, this species shows comparatively low and rather uniform Mg/Ca in our core-top experiment (compare Figs. 1 and 6). The addition of a secondary calcite crust in subsurface waters (Simstich et al., 2003) can be observed for all specimens below 80 m water depth in our samples but cannot readily explain this discrepancy because the Mg/Ca signal is of the opposite sign in the plankton tow data (Mg/Ca increases below 700 m, Fig. 6). For similar reasons, dissolution cannot explain the signal (e.g., Brown and Eldridge, 1996; Nouet and Bassinot, 2007; Rosenthal et al., 2000). Other possible explanations for the observed signal include population dynamics, i.e., occurrence of assemblages from different water bodies (i.e., lateral advection of tests), and hydrographic changes at the sampling site caused by storms, shift of water-mass fronts, or development of eddies.

Storms occurred at the sampling area in the NE Atlantic prior to both M21/1 and M21/2 sampling intervals (Table 1) during spring 1992 (Schiebel et al., 1995). The two storms caused strong turbulence and vigorous mixing of the surface ocean down to ~200 m water depth, and affected the distribution of planktic foraminifers in the

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**Fig. 5.** Mg/Ca-based temperature estimates against water depths of the planktic foraminiferal species *Globigerina bulloides* (orange) and *Globigerinoides ruber* (red) from the Arabian Sea (RV Meteor cruises M 31/3, top left, M 32/5, bottom left, and M 33/1, bottom right, and RV Sonne cruise SO 119, top right). Samples obtained by plankton tows. Temperature calculations for *G. bulloides* after the calibration of Elderfield and Ganssen (2000), for *G. ruber* after Anand et al. (2003), Broken line and symbols in black indicate in-situ measured temperatures during time of sampling. Broken line and symbols in grey indicate mean monthly temperatures for the month prior to sampling time (after World Ocean Atlas 2005, Locarnini et al., 2006). Please note different depth scales for y-axis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
In the aftermath of both storms, planktic foraminiferal abundance increased, as indicated by the higher numbers of *G. glutinata* in surface waters (see Fig. 7). Those high test concentrations in surface waters around April 4 and 27 can be tracked down the water column, and arrive at depths several days later, according to species and size-specific settling velocity (e.g., Takahashi and Bé, 1984). Thus, at any given time, deeper waters host older test populations than surface waters. The mixing of different populations during storms and during sinking is a potential explanation for the heterogeneous distribution of Mg/Ca ratios in the North Atlantic, and would also explain the similar behaviour of different species, i.e., decreasing Mg/Ca-based temperatures below 200 m, and an increase below 700 m. In summary, species-specific changes in Mg/Ca ratios at different depth of the subsurface water column may be explained by population dynamics and settling behaviour.

Mg/Ca ratios from all analysed species in the North Atlantic plankton-tow samples indicate much higher temperatures than from in-situ measurements and the World Ocean Atlas with an offset of 4 °C to 14 °C (Fig. 6). This is in accordance with recent studies that also show Mg/Ca-derived temperatures for e.g. *G. bulloides* significantly overestimate in-situ temperatures (Martínez-Boti et al., 2011; van Raden et al., 2010). These studies discuss the presence of secondary overgrowth (van Raden et al., 2010) or incompletely calcified tests (Martínez-Boti et al., 2011) as possible reasons for the observed elevated Mg/Ca data. SEM analyses of our specimens, however, did not reveal any obvious crystal overgrowth on shells of *G. bulloides*. Furthermore, specimens from samples below the habitat depth of *G. bulloides* (upper mixed layer, Schiebel et al., 1997) should be completely calcified but still reveal elevated Mg/Ca values.

Mixing events as described above only allow for a small part of this large offset to be explained, suggesting the presence of another mechanism. The reconstructed temperatures varying between 17 °C and 23 °C (Fig. 6) are comparable to surface-water temperatures to the south of the sampling area (30–35°N). Comparison of Mg/Ca between our plankton-tow samples and the studied core-top support this observation. Within the core-top sample, *G. bulloides*, *N. incompta*, and *G. glutinata* show generally lower Mg/Ca values (2.2 to 3.2 mmol/mol, 1.2 to 1.4 mmol/mol, and 1.8 to 2.4 mmol/mol, respectively) than compared to plankton-tow samples (3.1 to 4.3 mmol/mol, 1.9 to 3.7 mmol/mol, and 2.0 to 3.4 mmol/mol, respectively). One possible explanation of this observation could be lateral transport of the analysed tests from warmer water masses into the cooler waters of the sampling area, possibly by the North Atlantic Current or by eddy transport, even if there is no indication of a different water mass in our in-situ CTD data. Within the North Atlantic, eddies can be transported over several hundred kilometres and several weeks (e.g., Kupferman et al., 1986), covering the life span of a planktic foraminifer.
Other controls on the anomalously high Mg/Ca values in our plankton-tow samples could be the influence of environmental factors other than temperature, most likely salinity. A recent compilation of *G. ruber* core-top data from the Atlantic shows a temperature-independent Mg/Ca variability (excess Mg/Ca) that is highly correlated with surface salinity and affects SST estimates at salinities >35 psu (Arbuszewski et al., 2010). In-situ salinity for our sample locations is 35.5 psu (Pfannkuche et al., 1993). Accordingly, the presence of excess Mg/Ca for the analysed species is a possibility that could be an alternative explanation for at least part of the high Mg/Ca values observed in our North Atlantic plankton-tow samples.

5. Conclusions and Implications for palaeoceanographic studies

Our Mg/Ca analyses of a wide range of test sizes of nine species of planktic foraminifera from a core-top sample in the North Atlantic Ocean reveal four main findings.

1. The overall pattern revealed by our dataset is one of decrease in Mg/Ca with increasing test size for symbiont-barren species and the symbiont-bearing species *G. ruber*, a finding that is opposite to earlier investigations. The signal of decreasing Mg/Ca with increasing test size is carried mainly in the smaller and, to a lesser extent, the larger test sizes and therefore in size fractions that are smaller than those typically used in palaeoceanographic studies.

2. For symbiont-barren species, environmental control rather than calcification rate is proposed as a main factor affecting the size-related Mg/Ca signal.

3. Analyses should be carried out on very narrow size fractions, if possible as narrow as 50 µm. Analyses of narrow size classes are even more important for shallow-dwelling species such as *G. bulloides* or *G. ruber* than for deep-dwelling species. Test size related differences in Mg/Ca are small for intermediate sizes of deep-dwelling species (250 to 400 µm), the size range typically used in palaeoceanographic studies.

4. Mg/Ca analyses should ideally be carried out on test size fractions optimised for each species, rather than analysing generalised size fractions for all species. In particular, shallow-dwelling species (e.g., *G. bulloides, G. ruber, G. glutinata*) show a constant gradient of Mg/Ca ratios over the studied size range.

Our water-column data from the Arabian Sea are consistent with calcification over a narrow range of water depths. No influence of lateral transport/mixing, dissolution, or crust formation on the Mg/Ca signal during migration/settling through the water column can be inferred from our data. In contrast to specimens from the Arabian Sea, our data from the North Atlantic reveal large variability and overestimation of in-situ temperatures. This pattern is interpreted to result either from lateral advection of faunal elements from the south, or storm-induced vertical mixing of the upper water column, or the influence of surface-water salinity on the Mg/Ca signal.

Supplementary materials related to this article can be found online at doi:10.1016/j.epsl.2011.12.002.

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References


Hemleben, C., Spindler, M., Breitinger, T., Deuser, W.G., 1985. Field and laboratory studies


