

Effect of ocean acidification on the benthic foraminifera *Ammonia* sp.

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Effect of ocean acidification on the benthic foraminifera *Ammonia* sp. is caused by a decrease in carbonate ion concentration

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Abstract

About 30 % of the anthropogenically released CO₂ is taken up by the oceans, which causes surface ocean pH to decrease and is commonly referred to as Ocean Acidification (OA). Foraminifera are one of the most abundant groups of marine calcifiers, estimated to precipitate ca. 50 % of biogenic calcium carbonate in the open oceans. We have compiled the state of the art of OA effects on foraminifera, because the majority of OA research on this group was published within the last 3 yr. Disparate responses of this important group of marine calcifiers to OA were reported, highlighting the importance of a process based understanding of OA effects on foraminifera. The benthic foraminifer *Ammonia* sp. was cultured using two carbonate chemistry manipulation approaches: While pH and carbonate ions were varied in one, pH was kept constant in the other while carbonate ion concentration varied. This allows the identification of the parameter of the carbonate system causing observed effects. This parameter identification is the first step towards a process based understanding. We argue that [CO₃²⁻] is the parameter affecting foraminiferal size normalized weights (SNW) and growth rates and based on the presented data we can confirm the strong potential of foraminiferal SNW as a [CO₃²⁻] proxy.

1 Introduction

During the last 800 000 yr atmospheric CO₂ concentrations ranged from ca. 180 to 300 μatm (Petit et al., 1999; Siegenthaler et al., 2005). Since the start of the industrialization, anthropogenic release of CO₂ has caused atmospheric CO₂ concentrations to steadily increase at a rapidly rising rate (currently ca. 0.5 % yr⁻¹; Fabry et al., 2008). Approximately 30 % of the carbon dioxide emissions are taken up by the oceans (Sabine et al., 2004). As a consequence of this, future surface ocean pH values are predicted to decrease 0.4 units (Caldeira and Wickett, 2005) by the end of this century, which is commonly referred to as Ocean Acidification (OA). Through the associated decrease in

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the calcium carbonate saturation state biogenic calcification of ecologically important organisms such as corals, coccolithophorids and foraminifera, is expected to be hampered. It is generally expected, that coral calcification decreases under lower saturation states (Langdon and Atkinson, 2005). Responses of coccolithophorids with respect to OA are heterogeneous, and inter- and intra-species specific differences have been documented (e.g. Langer et al., 2006, 2009; Langer and Bode, 2011). While the responses of coccolithophorids and corals have been extensively studied in the last 1.5 decades and have been compiled in various studies (e.g. Doney et al., 2009), the majority of OA research on foraminifera was published in the last three years, and no overview of the state of the art exists. Foraminifera are one of the most abundant groups of calcifiers, estimated to precipitate ca. 50 % of biogenic calcium carbonate in the open oceans (Schiebel, 2002). We have compiled the state of the art of OA effects on foraminifera. Disparate responses of this important group of marine calcifiers to OA were reported. In order to extract a coherent picture of OA effects on foraminifera from this wide spectrum of responses it will ultimately be necessary to develop a process understanding of OA effects. The first step is the identification of the parameter of the carbonate system, which causes the effects. Most carbonate chemistry perturbation experiments are characterized by a simultaneous change in several parameters of the carbonate system. This makes it impossible to separate e.g. carbonate ion effects from pH effects and to develop a process-based understanding of OA-effects on foraminifera. We have conducted carbonate chemistry perturbation experiments with the benthic foraminifer *Ammonia* sp., following both the classical approach, i.e. co-varying $[\text{CO}_3^{2-}]$ and pH, as well as keeping pH constant while varying $[\text{CO}_3^{2-}]$ to overcome this problem. The experimental setup used here allows us to distinguish between $[\text{CO}_3^{2-}]$ and pH effects and potentially to identify a single parameter causing observed effects (Langer and Bode, 2011).

2 Material and methods

2.1 Sample collection and culturing

Surface sediments were collected in the Wadden Sea near Dorum, Germany between January and May 2011 and kept at 10 °C as stock-cultures after the removal of macrofauna. Living specimens of *Ammonia* sp. (identified by their brightly colored yellow cytoplasm and pseudopodial activity) were isolated from the stock-cultures (de Nooijer et al., 2007; Raitzsch et al., 2010; Dueñas-Bohórquez et al., 2011) using a 230 µm screen and transferred to well plates at 25 °C. Approximately 10 % of the specimens reproduced asexually after about one week. Juveniles were kept for an additional 2–3 days until they added another ~ 3 chambers before they were transferred to the culture experiments. Our culturing experience has shown that foraminifera have a high mortality when transferred into the experimental conditions earlier than this ontogenetic stage.

2.2 Seawater Preparation

Sterile-filtered (0.2 µm pore-size) North Sea seawater was used to prepare culture media for the experiments as described in Keul et al. (2012). The manipulated seawater was filled headspace-free into borosilicate-flasks; sealed gas tight with Teflon lined caps and kept at 3 °C until used in the experiments. Two different carbonate chemistry perturbations were carried out, with four treatment levels each, leading to a total of 8 treatments (Table 1):

1. TA-manipulation: seawater with a range of pH's and $[\text{CO}_3^{2-}]$, while total inorganic carbon concentration remained constant.
2. pHstable-manipulation: 4 treatments where DIC and TA were manipulated in a way, that pH was kept constant, while the accompanying $p\text{CO}_2$ values matched those of the TA-manipulation.

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2.3 Experimental setup and culturing

Long-term carbonate chemistry perturbation experiments require a special setup, allowing stable carbonate system parameters over a long time-span. We have constructed a special setup (Fig. 1) to allow for stable carbonate system parameters over long incubation periods and to ensure accessibility of the individuals (for feeding, regular water changes, etc). Asexually reproduced juveniles were placed into petridishes containing the manipulated seawater and placed into one of four gas-tight boxes. A gas-mixing system provided a steady gas flow (60 Lh^{-1} , see Hoppe et al., 2012 for a description of the gas flow controller) into the gas tight boxes, at four different $p\text{CO}_2$ concentrations (Table 1). Flow rate was constant and allowed a replacement of air inside the box every 10 min. Culturing took place in a temperature-controlled room at 26°C with a natural day/light cycle (12 h/12 h). To minimize stress for the juveniles temperature and salinity during culturing was kept similar to conditions during reproduction (26°C and $S = 32.8$). Supplied $p\text{CO}_2$ of the gas mixtures was checked regularly. Borosilicate bottles containing the manipulated seawater were stored open in the boxes prior to water exchange to allow for pre-equilibration. Pre-equilibrated seawater was used to exchange the water in the petridishes every 2–3 days. Foraminifera were fed photosynthetically inactive (heat sterilized) algae (*Dunaniella salina*) after water change. To minimize potential effects of bacteria growing on the bottom of the dishes, petridishes were exchanged every two weeks. The culturing period lasted for 59–96 days.

2.4 Sample analysis

2.4.1 Carbonate chemistry

DIC samples were filled headspace free into acid-washed 13 mL-borosilicate flasks and kept at 0°C until measurement (within days). DIC was measured in duplicates photo-metrically (Stoll et al., 2001) with a QuaAAtro autoanalyzer (Seal Analytica, Meqon,

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USA), average precision is 10 $\mu\text{mol/kg-sw}$ based on repeated measurements of an in-house standard. Corrections for inaccuracies in the measurements were carried out by measuring Batch No. 54 of A. Dicksons CRMS (Certified reference Material Seawater, marine Physical Laboratory, Scripps Institution of Oceanography). A two-point NBS-calibrated glass electrode (Schott Instruments, Mainz, Germany) interfaced to a WTW pH-Meter was used to measure pH potentiometrically. Simultaneous measurement of a seawater buffer (Tris/Tris-HCl prepared according to the recipe described in Dickson et al., 2007) allowed conversion of the pH values to the total scale. All pH values reported are on the total scale. Salinity and temperature were measured with a conductivity meter (WTW Multi 340i), interfaced with a TetraCon 325 sensor. pH and DIC (Hoppe et al., 2012) were used to calculate the carbonate system parameters (CO₂SYS program, adapted to Excel by Pierrot et al., 2006). The equilibrium constants for K1 and K2 of Mehrbach et al. (1973) as reformulated by (1987) were used.

2.4.2 Growth rate and SNW

Foraminiferal tests were soaked in conc. NaOCl for ca. 20 min until all organic remains were removed (visual verification under the stereomicroscope), washed three times in deionized water and dried at room temperature over night. Sizes were measured under a stereomicroscope (ZEISS Stemi SV 11) using a Pyser Bar Scale, with a precision of $\pm 7.4 \mu\text{m}$ under the used magnification of 66 \times . Foraminifera were grouped into three size classes according to their length: Size class 1 = 0–250 μm , 2 = 251–300 μm , 3 = > 300 μm . Tests were weighed using a Micro Analytical Mass Balance (Mettler Toledo UMX 2), with a precision of 0.1 μg .

Different terms are used in the literature to describe the rate of growth of foraminifera: growth rate, calcification rate and precipitation rate are among the commonly used terms, which, however, are not formally defined and thusly often confused with each other. We define *growth rate* as the amount of growth (here calculated as the increase in shell weight) of the whole specimen over time whereas *chamber formation rate* is defined as the weight increase in calcium carbonate during chamber formation. While

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these two parameters can be measured (e.g. Glas et al., 2012; Anderson and Faber, 1984), the assessment of the rate of biogenic precipitation of calcium carbonate is complicated, since biogenic calcium carbonate precipitation is mediated by organic membranes, which contribution (e.g. surface area) cannot be determined experimentally (see e.g. Cuif et al., 2011 for an overview). Growth rates were calculated from the incubation period of individual shells and final shell weight and have the unit $\mu\text{gd}^{-1}\text{ind}^{-1}$. (Please note that initial weight could not be measured therefore we assumed a constant initial weight since foraminifera were inserted to the experiment at the same development stage, allowing a comparison of growth rates. From the relationship between weight and size of specimen at the end of the experiment we have calculated that the initial weight was at most ca. 10 % of the final weight on average). Foraminiferal shell weights increase with increasing shell length. The aim of SNW is to remove this effect of shell length on the weight, making it possible to observe non-size related variations in shell-weight, for instance in chamber thickness. Unfortunately the term *size normalized weight* is used and defined incoherently in the literature; consequently a comparison of SNW between different studies might be hampered. We report SNW throughout this paper as the ratio of weight to length calculated for every specimen (unit $\mu\text{g}\mu\text{m}^{-1}$). The factor 100 was added to enhance readability of SNW and growth rates.

2.5 Statistics

All statistical tests were carried out using the statistics software R (www.r-project.org). An ANOVA (analysis of variance) was performed to determine an effect of carbonate chemistry parameters on measured variables (length, weight, growth rate, SNW). Data was log-transformed to ensure normally distributed data (Shapiro test, $p > 0.05$). Both, Levene and Fligner tests confirmed homogenous variances of the dataset. The null hypothesis of the ANOVA (all group means are equal) was rejected if $p < 0.05$. TukeyHSD post hoc tests were performed to determine which means exactly differed from each other. Linear regressions were performed with the built-in linear regression model. The homogeneity of regression slopes was assessed by means of a hoRS

model (homogeneity of regression slopes). The assumption of homogeneity of regression slopes has been rejected if the respective p-value was significant ($p < 0.05$). Average values and 2 SE (standard error) are given throughout the text.

3 Results

3.1 Carbonate chemistry

Four $p\text{CO}_2$ levels were maintained in the airtight boxes in which the petridishes containing foraminifera were placed during the culturing period (180–1400 μatm , *nominal* $p\text{CO}_2$, Table 1). The respective $p\text{CO}_2$ in the culturing media of the two manipulation methods were slightly different due to the complex manipulations of the carbonate system leading to in- or degassing of $p\text{CO}_2$. The variation in $p\text{CO}_2$ in the culturing seawater, however, was in the same range as maintained in the boxes (61–1301 μatm). pH was kept constant in the pH-stable-manipulation (7.99 ± 0.04), while it varied in the TA-manipulation between 7.60 at the highest and 8.32 at the lowest $p\text{CO}_2$ level. Carbonate ion concentration decreased with increasing $p\text{CO}_2$ in the TA-manipulation ($401\text{--}88 \mu\text{mol kg-sw}^{-1}$), whereas it increased with $p\text{CO}_2$ in the pH-stable-manipulation ($21\text{--}563 \mu\text{mol kg-sw}^{-1}$). DIC was kept quasi-constant in the TA-manipulation ($2215 \pm 23 \mu\text{mol kg-sw}^{-1}$), whereas it increased with $p\text{CO}_2$ from 246 to 5729 $\mu\text{mol kg-sw}^{-1}$ in the pH-stable-manipulation. TA increased from low to high $p\text{CO}_2$ by almost a factor of 20 in the pH-stable-manipulation ($342\text{--}6343 \mu\text{mol kg-sw}^{-1}$). The range in the TA-manipulation with $470 \mu\text{mol kg-sw}^{-1}$ was comparably small. Calcite saturation was in all treatments > 1 with a range of ($\Omega = 2.2\text{--}13.8$), despite treatment B1, where the culturing media was undersaturated with respect to calcite ($\Omega = 0.5$).

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3.2 Physiological responses

Detailed growth characteristics such as calcification- versus growth rates, carbonate chemistry factors influencing growth and the variability of all these amongst juvenile foraminifera has not been assessed yet for most foraminiferal species. In general, we observed a high variability in final shell length and weight among specimens. Consequently linear regression of growth characteristic (final length and weight, and factors such as SNW and growth rates derived thereof) versus carbonate chemistry parameters yields low R^2 values (< 1) in general. If the observed high variability in growth characteristic was due to the effects of the carbonate chemistry manipulation, the control group A2 should display lowest variability. Since this was not the case, we can assume that the observed variability has not been induced by our treatments and is a naturally characteristic among the offspring of *Ammonia* sp.

3.2.1 Length and weight

Average final lengths varied between $247(\pm 26)\mu\text{m}$ and $288(\pm 26)\mu\text{m}$. There was no statistical significant effect of any carbonate chemistry parameter on the final length ($p > 0.05$), consequently no linear regressions were performed. Lowest final weight was measured on shells grown in treatment B1 (average: $3.4 \pm 0.5\mu\text{g}$), which was undersaturated with respect to calcite. Based on the results of the ANOVA, all carbonate chemistry parameters despite pH could have had a positive effect on final shell weight ($p < 0.05$). The linear regression model reveals that the carbonate ion concentration can explain the highest amount of variability (29 %) in averaged shell weights and $p\text{CO}_2$ the lowest (6 %).

3.2.2 Growth rates

Growth rates are given as $\mu\text{gd}^{-1}\text{ind}^{-1}$ and are multiplied by a factor of 100. Average growth rates displayed the same variation in the TA-manipulation

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(7.55–11.20 $\mu\text{gd}^{-1}\text{ind}^{-1}$) when compared to the pH-stable manipulation (5.99–12.75 $\mu\text{gd}^{-1}\text{ind}^{-1}$), with a range in variability between ca. 15 and 30 % (2 SE) in both manipulations. Growth rates display a positive correlation with all carbonate system parameters except pH and $p\text{CO}_2$ ($p < 0.05$).

3.2.3 SNW

Average SNW varied between 2.48 (± 0.38) and 1.33 (± 0.14) $\mu\text{g}\mu\text{m}^{-1}$ in the different treatments, whereas measured SNW on single specimens was up to as 4 $\mu\text{g}\mu\text{m}^{-1}$. Linear regression of SNW and carbonate chemistry parameters on all eight treatments together reveals a positive correlation ($p < 0.05$) between SNW and carbonate ion concentration, DIC, TA and $p\text{CO}_2$. However, when separating the two manipulations graphically (Fig. 2) it becomes obvious that the general trend of the two regression slopes (positive/negative) coincide only when plotted against carbonate ion concentration and TA. A tool to assess the difference in regression slopes is hoRS analysis, which checks for homogeneity of regression slopes. The results of this analysis reveals that regression slopes of the two manipulations are homogenous ($p > 0.05$) in the regressions of carbonate ion concentration, DIC and TA, only (represented by a star in Fig. 2).

4 Discussion

4.1 Overview of foraminiferal studies with a focus on carbonate chemistry

Over the recent years, a number of studies (Table 2) have assessed the effects of OA on foraminifera. Approaches were ranging from culturing under different $p\text{CO}_2$ treatments, looking at the geological past either through sediment core tops or whole cores, to assessing whole communities at natural occurring $p\text{CO}_2$ gradients. Studied response parameters were shell weight, SNW, size, growth/calcification rates and shell thickness and changes in communities (diversity, abundance). A multitude of responses

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have been documented which range from no effect of $p\text{CO}_2$, an increase/ decrease (mostly) with increasing $p\text{CO}_2$ to more complex responses, where an initial increase up to a certain intermediate $p\text{CO}_2$ level was followed by a decrease. These differences are most likely not only attributed to the species studied but also to the methods used.

5 Deconvolving method effects from species specific effects can be achieved. Subjecting different species to the same method allows detecting species specific effects, whereas the method effects can be assessed by subjecting the same species to different methods. Deconvolving species specific differences is, for instance, possible in the study of Fujita et al. (2011), where the responses to elevated $p\text{CO}_2$ of three foraminiferal species have been studied. The difference in the response patterns has been speculated by these authors to be attributed to the different calcification pathways of hyaline and porcellanous species (e.g. TerKuile et al., 1989). Calcification was elevated at intermediate levels of $p\text{CO}_2$ in the case of the hyaline species (*Baculogypsina sphaerulata*, *Calcarina gaudichaudii*), whereas a decrease in calcification accompanied increasing $p\text{CO}_2$ values in *Amphisorus hemprichii*, a porcellaneous species. Four studies investigated the effect of elevated $p\text{CO}_2$ on *Marginopora*, a larger benthic foraminifera. A comparison of these studies could help to infer differences in responses attributed to different methods used. Vogel and Uthicke (2012) observed an increase in calcification rates with $p\text{CO}_2$ for *M. vertebralis*, whereas in both the studies of Sinutok et al. (2011) and Kuroyanagi et al. (2009) the opposite effect was detected (the latter study investigate a closely related foraminifera, *M. kudakajimensis*). This difference could be attributed to the employed manipulation methods (Kuroyanagi et al., 2009): TA-manipulation and Vogel and Uthicke (2012): DIC-manipulation) or the chosen culturing setup (static/ flow through). The first option seems unrealistic in the light of a study of Hoppe and co-workers (2011), where the effect of elevated $p\text{CO}_2$ in TA- versus DIC-manipulations was found to be the same for the coccolithophorid *Emiliana huxleyi*. Additionally, opposing responses were also detected by Vogel and Uthicke (2012) and Sinutok et al. (2011), who both used DIC-manipulations. Comparing laboratory to field studies can also shed light on differences in response patterns. Uthicke and

Fabricius (2012) for instance found, that *M. vertebralis* was not present in the field at $p\text{CO}_2$ values of $700 \mu\text{atm}$, as opposed to high abundances at control sites with normal $p\text{CO}_2$. This might indicate that the latter species suffers from increased $p\text{CO}_2$ and that the increased calcification rate with increasing $p\text{CO}_2$ reported by Uthicke and Fabricius (2012) is a laboratory artifact, which does not apply to the field. As a caveat it must be added here that it is also possible that an environmental parameter other than but correlating with $p\text{CO}_2$ caused the absence of *M. vertebralis* at $700 \mu\text{atm } p\text{CO}_2$. A thorough comparison of these studies is beyond the scope of this paper and should be addressed in a proper review paper. However, the variety of responses and response parameters under consideration makes it clear, that there is no uniform response of foraminifera to OA. In order to assess the effect OA might have on foraminifera it is crucial to develop a process understanding of the observed responses. Identification of the carbonate system parameter causing the responses is the first step in the direction of a conceptual model of OA effects. However, in traditional carbonate chemistry perturbations (TA-/DIC-manipulation) parameters are co-varying, rendering it impossible to single out the regulatory parameter. To overcome this problem we have cultured the benthic foraminifera *Ammonia* sp. under two carbonate chemistry manipulations, allowing distinguishing carbonate ion from pH effects.

4.2 Growth rates

The comparison of foraminiferal growth rates is complicated by the fact that, as a rule, juvenile specimens grow faster than adult specimens. Hence comparing the growth rate of a juvenile to the one of an adult will result in a bias, i.e. a relative over-estimation of the juvenile growth rate. However, this bias cannot be detected in our data, because size and growth rates are positively correlated (Fig. 3). This reflects the fact that our specimens were not fully grown when harvested. It will be helpful to clarify the terminology used in the context of foraminiferal growth. In general, rates are often reported in units of [mass of CaCO_3 deposited/time]. The latter unit might be applied to an individual over a period of several weeks, but might also be applied

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to a single chamber-formation event. These two numbers represent distinct parameters and must not be confused, because there are considerable timespans separating two chamber formation events (Hemleben et al., 1987). To illustrate this, we compare our overall average growth rate (which represents the sum of many chamber formation events including the timespans separating them) with the chamber-formation rate determined by Glas et al. (2012). Please note that the latter authors used the term *calcification rate*, again highlighting the need for clarity in matters of foraminiferal rates (growth-, calcification-, chamber-formation-). Our overall average of growth rates is with $0.09 \mu\text{gd}^{-1} \text{ind}^{-1}$ ($= 0.00375 \mu\text{gh}^{-1} \text{ind}^{-1}$) lower than their measured calcification rate ($0.028 \mu\text{gh}^{-1}$, Glas et al., 2012). Hence, the inclusion of non-chamber-formation times reduces the rate by one order of magnitude. We suggest using a terminology as specific as possible, e.g. chamber-formation rate instead of calcification rate, and, most importantly, to exactly report how rates in terms of [mass of CaCO_3 deposited/time] were determined.

4.3 Ecophysiological responses to carbonate chemistry

We used two different methods to manipulate the seawater carbonate chemistry, a TA-manipulation (treatments A1–A4, Table 1) and a pH-stable-manipulation (treatments B1–B4, Table 1). Since the carbonate system parameters co-vary differently in the two experimental approaches, it is possible, by exclusion, to reject certain parameters of the carbonate system as causes for the observed changes in SNW (Table 1). The general idea behind this is, that the responsible parameter should cause the same trends in SNW in both manipulations (e.g. characterized by similar regression slopes).

4.3.1 Shell thickness (as SNW)

When pooling all eight treatments, average SNW is positively correlated with $p\text{CO}_2$ ($R^2 = 0.22$, $p < 0.001$). However, hoRS analysis reveals that regression slopes are heterogeneous (at $p < 0.05$) in the two manipulations- in the pH-stable-manipulation

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average SNW displays a positive correlation with $p\text{CO}_2$ ($R^2 = 0.77$), whereas the correlation of average SNW and $p\text{CO}_2$ is negative ($R^2 = 0.38$) in the TA-manipulation (Fig. 2a). Thus, $p\text{CO}_2$ cannot be the parameter of the carbonate system causing a change in SNW. While average SNW is positively correlated to bicarbonate ion concentration ($R^2 = 0.81$) in the pH-stable-manipulation, the correlation is negative ($R^2 = 0.76$) in the TA-manipulation and hoRS analysis reveals that regression slopes are heterogeneous at $p = 0.05$. Please note that SNW-bicarbonate correlation in the TA-manipulation is based on a much smaller range of bicarbonate concentrations than in the case of the pH-stable manipulation. This renders the correlation less reliable (despite the relatively high R^2). We point out, however, that even assuming that the dashed trend-line in Fig. 2f is vertical, it has to be concluded that bicarbonate cannot be the parameter of the carbonate system causing SNW to vary. The reason is that the range in SNW in the TA-manipulation is, by comparison with the pH-stable manipulation, too large with respect to the scatter in bicarbonate concentration. SNW displays overall a positive correlation with pH (Fig. 2b), however this has to be interpreted as a coincidence, because the slope of the correlation in the pH-stable-manipulation is about a factor of 30 steeper than in the TA-manipulation, if the correlation was causal than the two slopes should be similar. This is also supported by the hoRS model, which indicates that the two slopes are not homogenous ($p \ll 0.05$). The large scatter in SNW in the pH-stable-manipulation cannot be caused by the insignificant differences in pH and must therefore be caused by another carbonate system parameter, excluding pH as the SNW-influencing parameter ($p > 0.05$). A similar reasoning holds true for DIC and TA: If DIC or TA was the controlling factor, SNW values should be more or less identical in the TA-manipulation, given the little variation of DIC and TA in this manipulation (2215 ± 23 and $2490 \pm 202 \mu\text{mol kg-sw}^{-1}$, respectively) when compared to the large range in the pH-stable-manipulation ($246\text{--}5729$ and $342\text{--}6343 \mu\text{mol kg-sw}^{-1}$, respectively). There is no reason why SNW-values should exhibit a large range ($1.89\text{--}2.41 \mu\text{g } \mu\text{m}^{-1}$) in this treatment, which is similar to the range exhibited in the pH-stable-manipulation, where the absolute change in DIC and TA is bigger by one order of magnitude. Consequently

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DIC and TA cannot be the parameters affecting SNW. Hence, based on the exclusion of certain correlations, $[\text{CO}_3^{2-}]$ or Ω are the only two candidates that could be responsible for the observed change in SNW. However foraminifera do not respond to Ω as such, but to the concentrations of Ca^{2+} and CO_3^{2-} and since calcium concentration in the culturing seawater was constant in all treatments ($[\text{Ca}^{2+}] = 9.26 \pm 0.39 \text{ mM}$) we can conclude that carbonate ion concentration is the parameter of the carbonate system affecting SNW (Homogeneous regression slopes at $p = 0.05$) with the following correlation: $100 \cdot \text{SNW} = 1.76(\pm 0.06) + 9.51 \cdot 10^{-4}(\pm 1.0 \cdot 10^{-4}) \cdot [\text{CO}_3^{2-}]$.

4.3.2 Growth rates

Please note that the reasoning of the extensive discussion of SNW applies also to growth rate. We therefore refrain from repeating the chain of arguments and just mention that growth rate and SNW are positively correlated. It is concluded that carbonate ion concentration is the parameter influencing growth rate in *Ammonia* sp. This conclusion tallies with response patterns of other species studied (Manno et al., 2012; Lombard et al., 2010; Russell et al., 2004; Kuroyanagi et al., 2009; Bijma et al., 2002). However, all of the latter studies, with the exception of the one by Bijma et al. (2002), employed either DIC- or TA-manipulation methods and could therefore not identify a single parameter responsible for observed adverse effects.

4.4 Implications for foraminiferal calcification

The conclusion that carbonate ion concentration influences growth rate in *Ammonia* sp. poses the question why this is so. On the basis of our data we cannot answer that question with any confidence but one possibility would be the direct usage of carbonate ions for calcification by *Ammonia* sp. TerKuile et al. (1989) have observed highest DIC uptake between pH 8 and 9 and concluded, that bicarbonate might be the inorganic carbon species that is preferentially taken up by *Amphistegina lobifera*, since this is the prevailing DIC species at that pH range (e.g. Zeebe and Wolf-Gladrow, 2001).

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However, they could not exclude the possibility of CO_2 or CO_3^{2-} as DIC sources. Recent results suggest that foraminifera are capable of manipulating the inorganic carbon speciation by elevating the intracellular pH during calcification (de Nooijer et al., 2009). Model calculations of Wolf-Gladrow et al. (1999) show that the rate of chamber formation determines, what DIC species might be used in the calcification process: While comparably fast (e.g. *Globigerinoides sacculifer*: $15.6 \text{ nmol CaCO}_3 \text{ h}^{-1}$, Wolf-Gladrow et al., 1999) rates can only be explained if both carbonate and bicarbonate ions are used or an internal DIC-pool is assumed, slower growth rates (e.g. *Orbulina universa*, $< 5 \text{ nmol CaCO}_3 \text{ h}^{-1}$, Wolf-Gladrow et al., 1999) can be sustained when only carbonate ions are used in the calcification process. The calculated relative slow chamber formation rate of ca. $0.28 \text{ nmol CaCO}_3 \text{ h}^{-1}$ (Glas et al., 2012) for *Ammonia* sp. would theoretically allow the sole utilization of carbonate ions. This is in accordance with our conclusion based on the correlation between SNW, growth rates and carbonate ion concentration. Up to now it remains unclear whether reduced calcification will affect the survival of foraminifera in future, but evidence has been provided from natural CO_2 rich environments (Fabricius et al., 2011; Dias et al., 2010) that a reduction in foraminiferal diversity and abundance is associated with high $p\text{CO}_2$ /low $[\text{CO}_3^{2-}]$ levels. This could potentially affect marine ecosystems and oceanic uptake of atmospheric CO_2 , since a reduction in planktonic foraminiferal ballast would reduce organic carbon export to deeper waters (Passow, 2004).

4.5 SNW as a carbonate ion proxy

Foraminiferal SNW are proposed to serve as a proxy for seawater carbonate ion concentration and thereby for atmospheric CO_2 concentrations (e.g. Barker and Elderfield, 2002; Moy et al., 2009; Gonzalez-Mora et al., 2008; Naik et al., 2010; de Moel et al., 2009). The sensitivity of the relationship between foraminiferal SNW and $[\text{CO}_3^{2-}]$ from field studies is different between species. The SNW of *Globigerinoides bulloides* decreases by approximately 35% with a decrease in $[\text{CO}_3^{2-}]$ of 250 to $200 \mu\text{mol kg}^{-1}$,

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Table 1. Upper part: calculated and measured carbonate chemistry parameters of the 8 treatments. Other input parameters to calculate the carbonate system are possible and can be found in the supporting online material of Keul et al. (2012). Lower part: mean physiological parameters and 2 SE (standard errors).

	Treatments							
	A1	A2	A3	A4	B1	B2	B3	B4
	Carbonate chemistry							
$p\text{CO}_2$ (μatm) “nominal”	180	380	950	1400	180	380	950	1400
$p\text{CO}_2$ (μatm)	217	479	850	1301	63	396	829	1252
CO_3^{2-} ($\mu\text{mol kg-sw}^{-1}$)	401	224	136	88	21	152	405	563
HCO_3^- ($\mu\text{mol kg-sw}^{-1}$)	1798	1999	2073	2063	223	1499	3536	5131
DIC ($\mu\text{mol kg-sw}^{-1}$)	2205	2236	2232	2187	246	1662	3965	5729
TA ($\mu\text{mol kg-sw}^{-1}$)	2747	2535	2400	2277	342	1884	4436	6343
pH total scale	8.32	8.02	7.79	7.60	7.95	7.98	8.03	8.01
ΩCa	9.8	5.5	3.3	2.2	0.5	3.7	9.9	13.8
	Physiological parameters							
Final weight (μg)	7.3	6.1	5.1	6.3	3.4	5.3	7.3	5.3
2 SE	2.1	1.4	0.9	1.0	0.5	1.6	1.4	1.5
Final length (μm)	288	255	252	280	247	288	280	229
2 SE	27	29	19	18	26	32	31	28
Growth rate (*100) ($\mu\text{g d}^{-1} \text{ind}^{-1}$)	11.20	7.28	7.55	9.71	5.99	9.33	12.75	9.01
2 SE	3.17	2.34	1.17	1.43	0.89	2.72	2.53	2.56
SNW (*100) ($\mu\text{g} \mu\text{m}^{-1}$)	2.41	2.19	1.89	2.14	1.33	1.70	2.48	2.29
2 SE	0.48	0.37	0.23	0.24	0.14	0.33	0.38	0.67

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Table 2. D_U overview of foraminiferal response patterns to changes in carbonate chemistry. Responses are represented by simple trend-plots. PH, pCO_2 and other carbonate system parameters covary in TA- and DIC-manipulation studies. This renders it possible to read off the respective pCO_2 response, were not directly given, to enhance comparability. Analyzed parameters vary by study: shell weight, SNW (size-normalized weight), size, growth/calcification rates and shell thickness. Responses are represented by simple trend-plots. Those studies assessing the affects of OA on foraminiferal communities (diversity, abundance) have not been depicted by these trend-plots (NA – not applicable). The studies were categorized as follows: G = Geological record (G_{CT} = Core tops, G_C = down core), O = open ocean (O_{ST} = sediment trap, O_{PT} = plankton tow), C = culture experiments (C_{rep} = asexually reproduced individuals, $C_{adj/uv}$ = adult/juvenile individuals collected from their natural habitat), O = other type.

Study	Species	Type	Methods	Response to pCO_2	Response parameter
Moy et al. (2009)	<i>G. bulloides</i>	G_{CT} O_{ST} G_C	<ul style="list-style-type: none"> • Comparison of G_{CT} and O_{ST} • Comparison of G_C weights and Vostok pCO_2 		<ul style="list-style-type: none"> • 30–35% decrease in shell weights between O_{ST} and G_{CT} • Link between down core shell weight decrease and high pCO_2 values for last 50 000 yr
Beer et al. (2010)	<i>G. bulloides</i>	O_{PT}	Comparison of O_{PT} SNW and C-system		• Strong interspecies variations: different response of SNW to pCO_2
	<i>G. ruber</i>				• Difference in relative abundances (<i>G. bull.</i> -low carb/high pCO_2 / <i>G. ruber</i> high carb/low pCO_2)
Barker and Edlerfield (2002)	<i>G. bulloides</i>	G_C	Comparison of G_C SNW and C-system		Glacial: highest shell weights → shell weights seem to be C-system influenced

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Table 2. Continued.

Study	Species	Type	Methods	Response to $p\text{CO}_2$	Response parameter	
Gonzalez-Mora et al. (2009)	<i>G. bulloides</i> and <i>G. ruber</i>	G_C	Comparison of G_C weights and Vostok $p\text{CO}_2$ /Mg/Ca-Temp.		Link between down core shell weight decrease and high $p\text{CO}_2$ values	
	<i>N. pachyderma</i>				SNW more Temp-influenced	
Naik et al. (2010)	<i>G. sacculifer</i>	G_C	Comparison of G_C weights and Vostok $p\text{CO}_2$ /Mg/Ca-Temp.		Link between down core shell weight decrease and high $p\text{CO}_2$ values	
deMoel et al. (2009)	<i>G. ruber</i>	G_{CT}	Comparison of weights		<ul style="list-style-type: none"> • Weight: lighter foram. in G_{CT} than in G_C • Age: light shelled specimens are younger 	
		G_C				
Dias et al. (2010)	Various perforate and imperforate species	G_{CT}	Assemblage study @ different natural pH gradients (8.1–6.6)	NA	<ul style="list-style-type: none"> • Reduction in diversity and abundance • Shift from 24 to 4 sp. (all agglutinated) with decreasing pH 	
Haynert et al. (2012)	Dominance:	G_{CT}	Assemblage study @ different natural $p\text{CO}_2$ fluctuation (1200–3300 μatm)	NA	<ul style="list-style-type: none"> • Seasonal community shifts 	
	<i>A. aomoriensis</i>					<ul style="list-style-type: none"> • No dynamic response between pop. Density/diversity and pore water $p\text{CO}_2$
	<i>E. incertum</i> <i>A. cassis</i>					

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Table 2. Continued.

Study	Species	Type	Methods	Response to $p\text{CO}_2$	Response parameter
Manno et al. (2012)	<i>N. pachyderma</i>	C_{ad} C_{juv}	2 pH and 2 Temp. treatments, 6 day incubation, juvenile + adults		Decrease in size, weight and thus calc. rate in low pH treatment (7.8)
Lombard et al. (2010)	<i>G. sacculifer</i> <i>O. universa</i>	C_{juv}	TA manipulation, additional light treatments, 4–7 d incubation		Reduced final shell weight and calcification rate under low carbonate ion concentration in both species
Dissard et al. (2010)	<i>A. tepida</i>	C_{ad}	DIC-manipulation: 230 + 1990 μatm $p\text{CO}_2$		Higher shell-weights in low $p\text{CO}_2$ treatments
Russell et al. (2004)	<i>M. kudakajimensis</i>	C_{juv}	TA-manipulation ($[\text{CO}_3^{2-}] = 110\text{--}470 \mu\text{mol kg-sw}^{-1}$)		Shell weights increase with carbonate ion concentration
Kuroyanagi et al. (2009)	<i>M. kudakajimensis</i>	C_{rep}	TA-manipulation, 10 weeks, 4 pH levels (7.7–8.3)		<ul style="list-style-type: none"> • Weight, shell size, growth rates decrease with decreasing pH • No stat. difference in responses at pH 7.9 + 8.2
Fujita et al. (2011)	<i>B. sphaerulata</i> <i>C. gaudichaudii</i>	C_{rep}	DIC-manipulation		• Weight increases at intermediate $p\text{CO}_2$ levels, then decrease
	<i>A. hemprichii</i>		12 weeks, 5 $p\text{CO}_2$ levels (260–970 μatm)		• Weight decreases with increasing $p\text{CO}_2$
Bijma et al. (1999)	<i>O. universa</i>	C_{juv}	Const. DIC, TA and pH treatments		Increase in shell weight with increase in carbonate ion concentration, below ambient steeper slope than above ambient $p\text{CO}_2$

Table 2. Continued.

Study	Species	Type	Methods	Response to $p\text{CO}_2$	Response parameter
Bijma et al. (2002)	<i>O. universa</i> <i>G. sacculifer</i>	C_{juv}	TA manipulation DIC and pH stable man.		Increase in shell weight with increase in carbonate ion concentration
Haynert et al. (2011)	<i>A. aomoriensis</i>	C_{ad}	DIC manipulation 6 weeks, 5 $p\text{CO}_2$ levels (620–3130 μatm)		<ul style="list-style-type: none"> • Reduced calcification at elevated $p\text{CO}_2$ • Decalcification started at 930 μatm
Allison et al. (2010)	<i>E. williamsoni</i>	C_{ad}	TA manipulation 3 pH (7.7–8.3), 8 weeks		Chambers formed at low pH significantly thinner than at high pH
Cigliano et al. (2010)	11 taxa (<i>E. aculeatum</i> dominance)	O	1 month settlement study @ different natural pH gradients (8.2–7.1)	NA	Fewer individuals and number of taxa in low pH conditions
Uthicke and Fabricius (2012)	<i>M. vertebralis</i>	C_{ad}	DIC manipulation		Reduced calc. at high $p\text{CO}_2$
		O	Natural $p\text{CO}_2$ gradients	NA	Absent in field at $p\text{CO}_2$ of 700 μatm
Vogel and Uthicke (2012)	<i>A. radiata</i> <i>H. depressa</i>	C_{ad}	6 weeks, DIC-manipulation, 4 $p\text{CO}_2$ treatments (470–1925 μatm)		Growth rates not affected by $p\text{CO}_2$
	<i>M. vertebralis</i>				sign. increased calc. rates at high $p\text{CO}_2$
Sinutok et al. (2011)	<i>M. vertebralis</i>	C_{ad}	DIC-manipulation, 4 weeks, (pH 7.4–8.1)		Reduced calcification under elevated $p\text{CO}_2$
Hikami et al. (2011)	<i>C. gaudichaudii</i>	C_{juv}	6 weeks, DIC-manipulation, 4 $p\text{CO}_2$ treatments (250–910 μatm)		Net calcification increased with $p\text{CO}_2$
	<i>A. kudakaji-mensis</i>				Reduced net calcification
	<i>A. hemprichii</i>		const. carbonate ion conc.	NA	constant calcification under constant carbonate ion concentration

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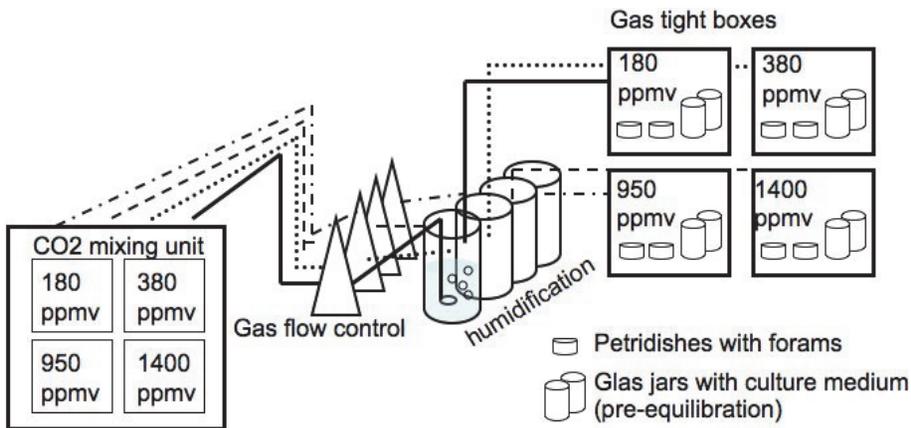


Fig. 1. Culturing setup. An extensive description can be found in the text.

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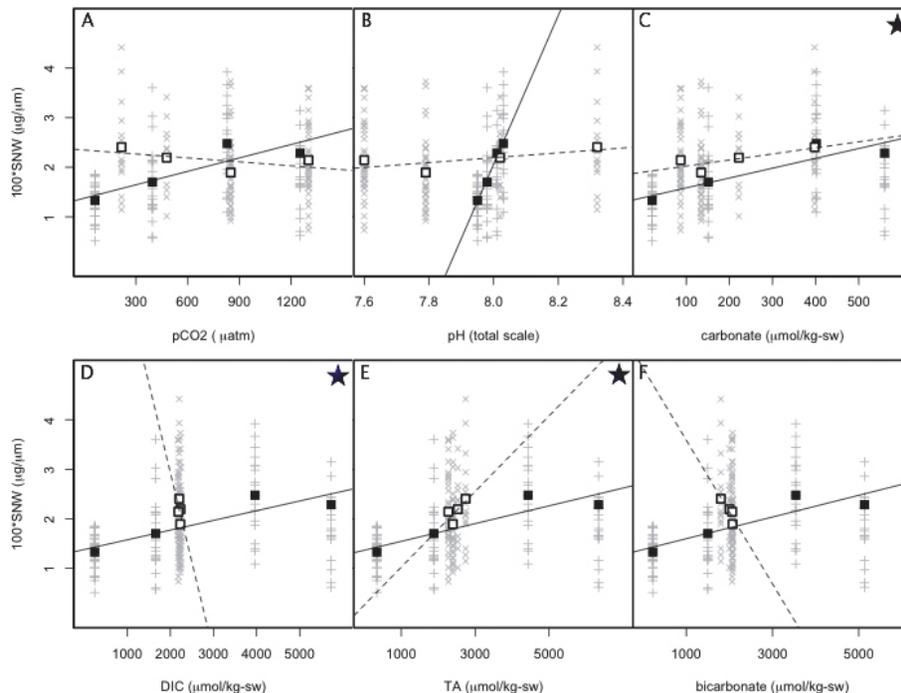


Fig. 2. SNW versus carbonate system parameters. Light grey x and + represent SNW of individual shells in the TA and the pH-stable-manipulation, respectively. Open and closed squares represent average SNW (between 14 and 38 shells per treatment) in the TA- and the pH-stable-manipulation, respectively. Dashed and solid lines represent linear regression lines for SNW versus the respective carbonate system parameter (TA- and pH-stable-manipulation). Stars in the upper right corner represent a statistical significant (hoRS model, at $p < 0.05$) homogeneity of regression slopes. Due to the relatively small ranges in x-axis variations in some correlations (e.g. TA-manipulation in D), the significance of regression slopes and thus the hoRS model is confined. Regression slopes and model outcome are still reported for all carbonate system parameters for the sake of completeness.

